

**SIMULATION MODELS FOR ESTIMATING PRODUCTIVITY AND  
TRADE-OFFS IN THE DATA-LIMITED FISHERIES OF  
NEW SOUTH WALES, AUSTRALIA**

by

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## Abstract

Recent shifts towards ecosystem based fisheries management (EBFM) around the world have necessitated consideration of effects of fishing on a larger range of species than previously. Non-selective multispecies fisheries are particularly problematic for EBFM, as they can contribute to erosion of ecosystem structure. The trade-off between catch of productive commercial species and abundance of low-productivity species is unavoidable in most multispecies fisheries. A first step in evaluation of this trade-off is estimation of productivity of different species but this is often hampered by poor data.

This thesis develops techniques for estimating productivity for data-limited species and aims to help clarify EBFM policy objectives for the fisheries of New South Wales (NSW), Australia. It begins with development of an age-structured model parameterised in terms of optimal harvest rate,  $U_{MSY}$ .  $U_{MSY}$  is a measure of productivity, comparable among species and easily communicated to managers. It also represents a valid threshold for prevention of overfishing. The model is used to derive  $U_{MSY}$  for 54 Atlantic fish stocks for which recruitment parameters had previously been estimated. In most cases,  $U_{MSY}$  was strongly limited by the age at which fish were first caught. However, for some species,  $U_{MSY}$  was more strongly constrained by life history attributes. The model was then applied to twelve species of Australian deepwater dogshark (Order Squaliformes), known to have been severely depleted by fishing. Results showed that the range of possible values of  $U_{MSY}$  for these species is very low indeed. These findings enabled a preliminary stock assessment for three dogsharks (*Centrophorus* spp.) currently being considered for threatened species listing. Preliminary results suggest they have been overfished and that overfishing continues. Finally, an Ecopath with Ecosim ecosystem model, representing the 1976 NSW continental slope, is used to illustrate trade-offs in implementation of fishing policies under alternative policy objectives. Results are compared with those of a biogeochemical ecosystem model (Atlantis) of the same system, built by scientists from CSIRO. While there were large differences in model predictions for individual species, they gave similar results when ranking alternative fishing policies, suggesting that ecosystem models may be useful for exploring broad-scale strategic management options.

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## **Dedication**

*For my mother Gillian Forrest  
and my grandmother Daisy Forrest*

# **Chapter 1. General introduction**

## **Context**

The government of the State of New South Wales (NSW), Australia, has undertaken to increase its investment in simulation modelling to aid in development of sustainable fishing strategies. One aspect of this aim is to develop models to aid understanding of “ecosystem-based fisheries management” (EBFM) and its meaning to the State’s fisheries. To this end, in 2002 the NSW Department of Primary Industries (NSW DPI, formerly NSW Fisheries) engaged in a Memorandum of Understanding with the University of British Columbia Fisheries Centre to address this need. Results of this collaboration are presented in this thesis.

This introductory chapter provides a background to the study. It begins with a discussion of sustainability, as it is currently applied to natural resource management in Australia and throughout the world, before reviewing issues important for ecosystem-based management of fisheries. Fisheries operating off the coast of NSW are briefly discussed and, finally, the aims and outline of the thesis are provided.

## **Background**

Australia ratified the Third United Nations Convention on the Law of the Sea (UNCLOS; United Nations 1983) in 1994. In doing so it gained international recognition of its right to custodianship of one of the largest marine areas in the world, covering an estimated 16 million square kilometres (Commonwealth of Australia 1998). This has conferred upon Australia not only rights to the wealth contained within its seas, but also the responsibility to manage its marine environment and living resources in a sustainable manner. A consequence has been the development of Australia’s Oceans Policy, which was established as an “integrated and comprehensive” approach to address Australia’s management and conservation obligations under UNCLOS (Commonwealth of Australia 1998; Wescott 2000; Alder and Ward 2001). These developments followed previous Australian initiatives for sustainable development, the most significant of which was introduction of the Australian National Strategy for Ecologically Sustainable Development (ESD) (Council of Australian Governments 1992; Fletcher *et al.*

2002). ESD has now been accepted as the basis of management of natural resources, including fisheries, throughout Australia and is a management objective of all State and Commonwealth (i.e., Federal<sup>1</sup>) natural resource agencies (Scandol *et al.* 2005). The principles of ESD are codified in the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act), which includes provisions that have consequences for all Commonwealth fisheries and for State fisheries that export their product (Fletcher 2003; Scandol *et al.* 2005; Gibbs 2008).

### **Definitions of sustainability**

Sustainability is one of the most commonly-stated goals of fisheries management. Early definitions of sustainability in fisheries were concerned with single species and were principally aimed at maximising economic returns. The concept of maximum sustainable yield (MSY), which aims to identify the most efficient exploitation rate for maximising long-term yield (Schaefer 1954; Clark 1976; reviewed by Ludwig 2001), was developed in the context of a utilitarian worldview, where natural resources were viewed mainly as commodities (Holling *et al.* 1998). Recognition of limitations of this approach, in a world with increasing environmental problems and a growing human population, led to an internationally-recognised range of definitions of sustainability that extended beyond the view of ecosystems simply for their consumptive value (IUCN/UNEP/WWF 1980; WCED 1987). Sustainable use of natural resources is now commonly understood to include maintenance of biodiversity and functioning ecosystems, accounting for the interconnectedness of human and ecological systems; and consideration of the needs of future generations, as well as meeting current resource needs (WCED 1987). As definitions of sustainability expand to include more human and ecological dimensions, however, there is a danger of them becoming too imprecise to be of management use or too open to interpretation (Suter 1993; Mace 2001). It has also been argued that sustainability of present conditions is an inappropriate goal for fisheries management, where many ecosystems have been significantly altered by fishing (Pitcher and Pauly 1998). These authors propose that restoration of ecosystems is a more appropriate management goal that would result in significant gains, both in existence and consumptive terms (see also Pitcher 2001; 2005; Pitcher and Ainsworth 2008). Broadly-stated sustainable management initiatives

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<sup>1</sup> Australia became a federated country in 1901 when the British colonies of New South Wales, Victoria, Queensland, South Australia, Tasmania and Western Australia joined to become the States of the Commonwealth of Australia. The Australian Capital Territory and Northern Territory and seven offshore territories are also administered by the Commonwealth Government.

have also been criticised for failure to adequately acknowledge the role of uncertainty in preventing scientific consensus and for being vague in identifying links between scientific understanding and achieving sustainability (Ludwig *et al.* 1993). There is now recognition that indicators of sustainable management need to be precisely defined in terms of different sustainability objectives and linked to specific management approaches (Lackey 1998; Robinson 2001). This implies a need to recognise that different sustainability objectives may be in conflict and may vary widely among stakeholders (Suter 1993; Lackey 2001; Mace and Reynolds 2001). For example, maintaining large biomasses of some species may be incompatible with maintenance of economically viable fisheries on other species. Successful management of fisheries will therefore include explicit identification of trade-offs, and incorporate approaches for deciding where to operate along trade-offs, while recognising that different stakeholders have a diverse set of values and objectives (Lackey 2001; Walters and Martell 2004). This will also involve setting qualitative and quantitative measures of the expected benefits, costs, and risks associated with alternative management actions (Murawski 2000; Hall and Mainprize 2004).

### **Ecosystem-based fisheries management**

Following global trends over the past decade, the concept of ecosystem based fisheries management (EBFM) has been introduced into the Australian policy arena at both State and Commonwealth levels (Fletcher 2003; Scandol *et al.* 2005). EBFM is defined as a set of concepts or principles that encapsulate ideas for managing fisheries in ways that recognise their potential to alter whole ecological and human systems (Larkin 1996; Pitcher 2000; FAO 2003; Ward *et al.* 2003; Pikitch *et al.* 2004). For example, one of the stated aims of EBFM in Australia's Oceans Policy is to: "Maintain ecological processes in all ocean areas, including water and nutrient flows, community structures and food webs, and ecosystem links ... [and] ... Maintain marine biological diversity, including the capacity for evolutionary change and viable populations of all native marine species in functioning biological communities" (Commonwealth of Australia 1998). The FAO's Technical Guidelines for Responsible Fisheries (FAO 2003) state that under an ecosystem approach to fisheries, fisheries management should respect the following principles: fisheries should be managed to limit their impact on the ecosystem to the extent possible; ecological relationships between harvested, dependent and associated species should be maintained; the precautionary approach should be applied because the knowledge on ecosystems is incomplete; and governance should ensure both human and ecosystem well-being



and equity. The last point is sometimes expanded to more explicitly describe human considerations. For example, the Worldwide Fund for Nature's EBFM policy document states as one of its principles that "A successful ecosystem-based management system will recognise economic, social and cultural interests as factors that may affect resource management" (Ward *et al.* 2002). A recent evaluation of the performance of 33 countries in meeting the EBFM criteria outlined in Ward *et al.* (2002), found that most countries underperformed in terms of both development of policy and implementation of EBFM (Pitcher *et al.* in press). This reflects the political and institutional challenges associated with adoption of principles of EBFM and the gradual pace of reform at these levels.

Fisheries managers throughout Australia are now faced with the difficult question of what they must do differently to meet the requirements of EBFM. At a recent meeting of the Australian Society for Fish Biology, Fletcher (2003) concluded that existing principles of ESD, for which legislation is already in place, were consistent with principles of ecosystem management. Scandol *et al.* (2005) made a similar finding. However, while guidelines and principles for implementing ESD have components relevant to EBFM, which include attention to impacts on the biological community, water quality and habitat quality (Fletcher *et al.* 2002), they presently lack detail on appropriate ways to measure these components or assess their performance (Scandol *et al.* 2005). Identification of appropriate management strategies for EBFM and ESD in Australia will involve articulation of what is meant by sustainability; identification of species impacted by fisheries; development of some understanding of the nature of interactions between marine organisms and fisheries in marine ecosystems; and evaluation of the contributions of marine ecosystems to society. Many of these needs are beyond the current level of management experience, and there are large data-gaps in most of these areas.

At the Commonwealth level, there have been a number of initiatives to improve information for EBFM (e.g., Fulton *et al.* 2005a,b; 2007; Smith *et al.* 2007). Substantial funding has been provided to survey and map Commonwealth fishing grounds and to conduct research into fields such as trophic ecology, habitat-use and productivity – particularly off the southeast coast (e.g., Bax and Williams 2000). Considerable resources have also been allocated for development of comprehensive management frameworks (Hobday *et al.* 2006; Smith *et al.* 2007) and the modelling tools needed to support EBFM (e.g., Fulton *et al.* 2005a,b; 2007a). At the State level,

fisheries tend to be smaller, lower in value and managed with policies based on cost-recovery (e.g., McColl and Stephens 1997; NSW Fisheries 2001). Because of this, fisheries management agencies have not invested heavily in assessment of commercial fish stocks and the status of the majority of commercial species in Australia is unknown or is unpublished (Phillips *et al.* 2001). Formal stock assessment tends to be the exception rather than the rule, generally being applied only to the most valuable species (such as abalone and rock lobster). As a result, there is currently little ecological information with which to frame EBFM strategies (Hall 2003; Gibbs 2008; Gray 2008). Research into marine ecosystem processes for management of Australia's smaller fisheries is not likely to receive priority in the near future, and this type of information would not be easily integrated into existing management frameworks (Scandol *et al.* 2005). Adoption of EBFM at this level may therefore be a gradual process, initially requiring development of simple assessment tools, based on routinely-collected data, and identification of robust measures for tracking progress.

Setting of qualitative and quantitative measures of the expected benefits, costs, and risks associated with alternative management actions needs to be part of the process of implementing EBFM (Murawski 2000; Hall and Mainprize 2004; Pikitch *et al.* 2004). Recently, a set of international guidelines has been developed by the FAO to support translation of high-level EBFM policy goals to an operational level (FAO 2003). Steps to implementation of operational EBFM listed in the guidelines include:

- 1) identification of operational objectives;
- 2) development of indicators of system-state and setting of corresponding reference points (as targets or limits);
- 3) use of indicators and reference points as management performance measures (i.e. the difference between the value of an indicator and its target or limit reference point);
- 4) application of decision rules based on management performance measures; and
- 5) monitoring and evaluation of management performance.

In this framework, indicators are ecosystem properties that are thought to be modified by the fishery. They should reflect parameters that can be measured or estimated with a degree of certainty and, when compared with agreed target and limit reference points, provide a measure of management performance (FAO 2003). There is now a very large body of literature (e.g., review

by Fulton *et al.* 2005a; Hall and Mainprize 2004; papers in Cury and Christensen 2005) on possible metrics that could be used as indicators of fisheries-induced changes on ecosystems. While indicators and reference points for management of single species have been used in the above framework for some time (Caddy and Mahon 1995; Caddy and McGarvey 1996; Caddy 1999), their adaptation to an ecosystem context is still relatively new.

### **Fisheries in marine ecosystems**

The term ecosystem was first suggested by Tansley (1935) and the concept was later expanded to include feedback loops that could lead to equilibrium, using theory from systems analysis. Odum (1953) defined an ecosystem as a “... natural unit that includes living and non-living parts interacting to produce a stable system in which the exchange of materials between the living and nonliving parts follows circular paths ...”. Concepts of equilibrium, resilience and stability were developed in the 1970s (Holling 1973; May 1973), where predator-prey cycles, competitive interactions and complexity of the system were discussed in terms of the stability they conferred on the system. While the ecosystem concept is probably the most useful framework for discussing the broadscale impacts of human activity on the natural environment, there is debate over whether ecosystems are observable natural entities or whether the ecosystem is a human construct (O'Neill 2001). One of the main arguments against ecosystems being observable natural entities is the issue of boundaries and closure. Suter (1993) suggested that ecosystems do not exist until a policy or problem is specified, at which point ecological boundaries intuitively follow, i.e., if one considers all the processes directly or indirectly acting on organisms, including local and global processes, the boundaries of any ecosystem logically extend to include the whole biosphere. This implies that ecosystems cannot be delimited without a scientific or policy concern (Lackey 1998; 2001).

In the context of marine fisheries, ecosystems are usually thought of conveniently as regions of management jurisdiction, which may have natural geographical or oceanographic boundaries and contain all or most of the life-history phases of managed populations. Often, ecosystems are defined by type of habitat with distinctive compositions of species and physical characteristics, e.g., estuarine, arctic or pelagic ecosystems. Questions about the impacts of fisheries on marine ecosystems usually focus on the ability of fisheries to alter the relative abundances of harvested and non-harvested species and possibly directly or indirectly alter ecological processes such as

competition and predation. Pitcher (2001) identified five major mechanisms by which fisheries alter the structure of marine ecosystems: 1) selective removal of large, long-lived species with low rates of natural mortality; 2) alteration of habitats by trawl gear; 3) reduction of predation by benthic fish leading to an increased biomass of forage species (“fishing down marine foodwebs”; Pauly *et al.* 1998); 4) trophic cascades (reviewed by Pinnegar *et al.* 2000); and 5) increasing instability and unpredictability in the system. Establishing clear explanatory patterns in the relative abundances of interacting species in marine ecosystems is difficult, however, because of: (i) the highly stochastic nature of the natural environment; and (ii) the complexity of interactions among biotic and abiotic processes in marine ecosystems.

### *Trophic interactions*

Link (2002a) presented an extremely complex marine food web, representing the Northeast US Shelf, which had 80 functional groups each having an estimated average of 19 trophic interactions with other groups. Large numbers of trophic interactions such as this lead to highly connected systems in which the effects of fisheries cannot be easily predicted. Even in systems with relatively few species, complex indirect trophic pathways may lead to unexpected effects of fisheries and other human actions (May *et al.* 1979; Yodzis 1994; 2000; 2001). For example, there are often proposals to cull top predators (e.g., seals) in order to increase production of their commercially-fished prey (Yodzis 2001; Lessard *et al.* 2005). However, the presence of intermediary or competing predators that may also benefit from the cull may result in further reductions of the species the cull was intended to benefit (Punt and Butterworth 1995; Yodzis 2000; 2001). Other types of indirect effect occur when trophically-connected species feed on each other at different stages of their life-history, leading to ‘cultivation-dependensation’ effects, which occur when juveniles of a predator are eaten by the adults of one of its prey species (Rudstam *et al.* 1994; Walters and Kitchell 2001). Further examples of complex interactions among fisheries and marine ecosystems can be found in May *et al.* (1979; krill and marine mammals); Sainsbury (1991) and Sainsbury *et al.* (1997; alteration of fish habitat); Livingston and Tjelmeland (2000; boreal systems); and Bogstad and Mehl (1997; Barents Sea).

### *Technological interactions*

Technological interactions occur when multiple species are caught in the same fishing gear. Most fisheries are non-selective to some degree and catch a range of species, including those that

are targeted as well as some that are not. In some fisheries (e.g., shrimp trawls), the non-target component of the catch (bycatch) may exceed the targeted component by a large percentage (Alverson *et al.* 1994). The unwanted portion of the catch is frequently discarded. The issue of bycatch has received much attention in recent years because of its wastefulness (Alverson *et al.* 1994) and because of impacts on charismatic species such as birds, marine mammals, turtles or pelagic sharks (Tasker *et al.* 2000; Bache 2003; Cox *et al.* 2007; Gilman *et al.* 2008). While there has been a lot of progress in development of technological methods to avoid bycatch, these mainly involve exclusion of large animals from trawl nets, exclusion of fish from shrimp nets or devices that deter birds from longlines (e.g., Kennelly and Broadhurst 2002; Cox *et al.* 2007). In many cases, when non-target species are of similar morphology and occupy the same habitat as target species, selectivity cannot be adjusted to exclude all unwanted species. Besides this, many fisheries intentionally target multiple species simultaneously or multiple stocks of the same species.

The complexity of interactions in marine ecosystems can obscure the identification of appropriate policy objectives. Ecosystem-oriented objectives in fisheries management are usually stated in high-level policies. Consequently, they are often broadly defined and difficult to incorporate directly into management plans where consequences of prospective management actions must be related to management objectives (Sainsbury *et al.* 2000). Skeptics of operational ecosystem based management point out that concepts such as ‘ecosystem health’ and function are vaguely defined and mask real issues, such as difficult trade-offs associated with managing human activities in ecosystems (Lackey 1998; 2001). Some authors have cautioned that management will fail if management strategies are forced upon fishers without adequate incentives (Hilborn 2004; 2007c; Grafton *et al.* 2006); or that factors such as inter-agency conflicts, incompatible databases, a lack of research on ecosystem functioning, inconsistent planning cycles and differing agency organizational structures will impair development of a coordinated approach to actively implement EBFM (Szaro *et al.* 1998). To overcome some of these problems, methods of implementing EBFM are currently being widely discussed in the fisheries science and policy arenas (Murawski 2000; FAO 2003; Fletcher 2003; Hall and Mainprize 2004; papers in Browman *et al.* 2004).

## **Trade-offs in fisheries**

Active consideration of trade-offs will be one of the most important components of EBFM (Pitcher and Cochrane 2002; Christensen and Walters 2004a; Hilborn *et al.* 2004; Walters and Martell 2004; papers in Mote Symposium 2004). Walters and Martell (2004) list the main trade-offs affecting fisheries management decisions, which include abundance of fish *vs* fishing effort; profit *vs* employment; present *vs* future harvest; and public expenditure on fisheries *vs* expenditure on other public services. Two trade-offs specific to EBFM are harvest of valued species *vs* abundance of other species that depend on these species for food (predator-prey trade-off); and abundance of unproductive stocks and species *vs* harvest of more productive stocks when non-selective gear catches them all (biodiversity-productivity trade-off).

### *Predator-prey trade-off*

Effects of trophic interactions on calculation of sustainable yields were first shown by May *et al.* (1979) and have since been demonstrated by Yodzis (1994), Christensen and Walters (2004a) and Ainsworth and Pitcher (2008). One of the few attempts to explicitly take trophic interdependencies into account in fishery management is that of the Convention on Conservation of Antarctic Marine Living Resources (CCAMLR), where krill harvests are set with consideration for the needs of species that depend on krill for food (Constable 2000; Constable *et al.* 2001). Such management systems require the setting of clear goals – in this case maintenance of abundance of high trophic level species such as seals and whales. Detection of fishery-induced impacts on trophic interactions may be more straightforward in less diverse ecosystems where trophic interactions are strong (e.g., ecosystems at high latitudes Rudstam *et al.* 1994; Bogstad and Mehl 1997; Constable 2000). In more complex systems, where trophic interactions may be weaker and more diffuse (Link 2002a; Yodzis 2000), direct evaluation of this trade-off will not be possible for most species.

Indicators of overall trophic trends may, therefore, provide useful proxies for measuring the effects of fisheries on trophic dynamics. There is now a growing literature on possible metrics that could be used as indicators of fisheries-induced changes on trophic interactions in ecosystems (e.g., papers in Cury and Christensen 2005; reviewed by Fulton *et al.* 2005a). For example, indicators tracking trends in trophic composition of catches have been used to demonstrate serial depletion in several systems (Pauly *et al.* 1998). Other indicators based on

trophic structure of ecosystems that can be evaluated using ecosystem models have been reviewed by Christensen (2000). One problem with composite trophic indicators based on landings is that similar results can arise from different causal mechanisms and results may not, therefore, reflect the underlying state of the ecosystem but may instead be due to external effects, such as changes in market patterns or spatial structure of fishing fleets (Essington *et al.* 2006). While analysis of suites of indicators to infer impacts of fishing on ecosystems has great potential for focusing discussion with managers and stakeholders, there has been little progress in determining how they might practically be used in making management decisions or negotiation of trade-offs – mainly due to uncertainty about ecosystem processes and lack of credible, local models to predict how systems would respond to proposed management actions (Hall and Mainprize 2004).

#### *Productivity-biodiversity trade-off*

The productivity-biodiversity trade-off (Walters and Martell 2004) arises from technological interactions. The issue of non-selectivity in fisheries means that even well-intentioned management plans can lead to overfishing of some species, as some species or stocks will naturally have greater resilience to fishing than others (Ricker 1958; Paulik *et al.* 1967; Hilborn 1976; Hilborn 1985a). Paulik *et al.* (1967) noted that yields from mixed stock fisheries would always be lower than if the stocks were optimally harvested separately. This effect also is well-known in single species multi-stock fisheries, such as those for Pacific salmon. Hilborn (1985a) showed that the presence of stocks of differing productivity in a mixed stock Pacific salmon fishery would lead to over-optimistic management targets if stocks were assessed as a single unit, and this would therefore lead to overfishing of less productive stocks.

One way to think about implications of the productivity-biodiversity trade-off is to consider its extremes (Mace and Reynolds 2001). At one extreme, managing to maximise fishery productivity inevitably leads to overfishing of some species while sustainable yields are achieved for others. At the other extreme, managing so that no species are overfished ('weak stock' management) can result in significant reductions in total yield (Hilborn *et al.* 2004). This difficult and inevitable trade-off is seldom explicitly acknowledged in fishery management and usually happens 'by default' (Walters and Martell 2004). A common characteristic of fishery development arising from this trade-off is rapid depletion of less productive species as more

productive species continue to attract fishing effort (Pauly 1995; Pitcher and Pauly 1998; Pitcher 2001). Fishery-independent surveys in Australia have shown evidence of such effects in the Gulf of Carpentaria (Harris and Poiner 1991); the North West Shelf (Sainsbury 1991; Sainsbury *et al.* 1997); and the continental slope of NSW (Andrew *et al.* 1997; Graham *et al.* 2001).

Related to this trade-off is one of the most familiar trade-offs in fisheries: that between current and future harvests. This is the trade-off between short-term and long-term yields or profits. Clark (1973; 1976; reviewed by Ludwig 2001) showed that living resources will frequently be treated as non-renewable resources by fishers, especially as discount rates approach or exceed natural population growth rate. This is because reliance on future catches is more risk prone than taking catches now and investing profits elsewhere. In these cases, it may become economically rational to exploit low productivity species to extinction. The effect is magnified if low productivity species are caught as bycatch or are low in value and management priority (Bonfil 2004). Figure 1.1a illustrates the biodiversity-productivity trade-off in terms of long-term yield for five hypothetical species of differing productivity. For any one of the hypothetical species, there is some optimal harvest rate that would maximise yield, indicated by the peak of the curve. Figure 1.1b shows corresponding equilibrium biomasses at the same harvest rates. Figure 1.1 illustrates that, where there are technological interactions among species, optimally harvesting some species may be enough to drive less-productive species to commercial or even biological extinction. The productivity-biodiversity trade-off therefore has significant implications for low-productivity species in multispecies fisheries, where there may be very strong conflict between economic interests and conservation concerns (Reynolds *et al.* 2001; Hilborn *et al.* 2004). Sharks, skates and rays, which typically have lower productivity than most teleosts (Smith *et al.* 1998; Walker 1998; Cortés 2002), may be particularly at risk to these effects (Walker 1998; Musick *et al.* 2000; Dulvy *et al.* 2000; Graham *et al.* 2001; Dulvy and Reynolds 2002).

It is important to recognise that solutions to trade-offs are subjective and science has no power to determine 'right' or 'wrong' solutions (Lackey 2001). Walters (2003) argued that the only way for managers to approach difficult trade-offs such as the differential productivity problem is to honestly appraise the trade-off and have managers, fishers and other stakeholders negotiate where along the trade-off they would like to be. Formal methods exist for evaluating utility of alternative outcomes to different stakeholders (Keeney and Raiffa 1976), although informal



methods involving negotiations among stakeholders (Smith *et al.* 1999) are also effective. The legal system may also be used in conflict resolution relating to fisheries. For example, in 2000 the New South Wales Land and Environment Court found that commercial fishing licences had to meet the requirements of the *Environmental Planning and Assessment Act 1979* (EP&A Act) and, therefore, that environmental impacts of all commercial fisheries had to be assessed (Gibbs 2008). This necessitated a major change in the way that fisheries are assessed and managed in NSW. Similarly, the Commonwealth EPBC Act is a powerful instrument that has the potential to affect many aspects of fishery operations. The 2006 listing of orange roughy (*Hoplostethus atlanticus*) as a Threatened Species under the EPBC Act has resulted in development of a comprehensive conservation programme for the species (which is Australia's first commercially-harvested fish to be listed), which includes spatial fishery closures (AFMA 2006). In all of these approaches, the role of fisheries scientists is to present scientific evidence to inform decisions and to honestly communicate the uncertainty surrounding the information presented (Ludwig *et al.* 1993; Walters and Martell 2004).

### **Productivity of fished populations**

A first step in evaluation of the productivity-biodiversity trade-off and risks to low productivity species is estimation of the relative productivity of harvested species. The ecological basis for sustainable fishing is that most, if not all, fish populations show some degree of improvement in productivity as the adult population is reduced below carrying capacity (Ricker 1954; Beverton and Holt 1957). Productivity is an intrinsic property of fish populations determined by rates of growth, mortality and recruitment. Recruitment productivity is usually understood to be a function of density dependent processes leading to improvement in the rate of juvenile survival as adult stock size is reduced from its unfished state (reviewed by Rose *et al.* 2001; Myers 2002). Density dependent mechanisms of population regulation (i.e., negative feedback mechanisms) appear to be ubiquitous in natural populations (Brook and Bradshaw 2006). In coastal fish species, density dependent effects probably occur mainly in juvenile demersal life stages (Myers 2002). It is usually assumed in fisheries science that density dependent processes occur before fish recruit to the fishery (Myers and Mertz 1998), although this may not always be a valid assumption (Gazey *et al.* in press). Mechanisms for improvements in juvenile survival rate at lower densities include: decreased territorial behaviour; reduced competition for food and space; and decreased vulnerability to predation (Walters and Juanes 1993; Walters and Korman 1999;

Rose *et al.* 2001; Myers 2002). The magnitude of density dependent effects is variable among stocks and species and is understood to be one of the main determinants of the sustainable exploitation rate of a population (Myers 2001). Estimation of recruitment productivity parameters is therefore a core component of fisheries stock assessment (Hilborn and Walters 1992; Punt and Hilborn 1997).

There are a number of alternative parameters can be used to represent productivity in fisheries population models, the simplest being the intrinsic rate of population growth,  $r$ , from the logistic population growth model (e.g., Schaefer 1954). The slope of the stock recruitment function near the origin,  $\alpha$ , i.e., maximum juvenile survival rate (Ricker 1954; Beverton and Holt 1957; see Figure 1.2) is also commonly used. Goodyear (1977) standardized this parameter and expressed it as the recruitment compensation ratio, which is the relative improvement in juvenile survival from the unfished state as spawning stock approaches zero (see also Myers *et al.* 1999; see Figure 1.2). The steepness parameter of Mace and Doonan (1988) is another standardization widely used in Europe and North America.  $F_{MSY}$  is the fishing mortality rate that would produce maximum sustainable yield, MSY.  $F_{MSY}$  and its discrete equivalent, annual exploitation rate,  $U_{MSY}$ , can be shown to be analytically related to recruitment productivity parameters under some assumptions (semelparous species: Hilborn and Walters 1992; Schnute and Kronlund 1996; iteroparous species: Schnute and Richards 1998; Forrest *et al.* 2008, Chapter 2; Martell *et al.* 2008). This implies that a fish population's sustainable exploitation rate is also a productivity parameter, which, under a given selectivity schedule, is as intrinsic to the population as its biological productivity parameters (Schnute and Kronlund 1996).

There are well-known problems with the use of MSY as a management target (Larkin 1977). Notwithstanding ecosystem considerations discussed above, there have been major problems with both estimation and implementation of MSY strategies (Punt and Smith 2001). These problems have been mainly due to incorrect assumptions in estimation of MSY, either in the model or in the data used, and the fact that MSY is a long-term target, while fishers and managers have much shorter time horizons (Holling *et al.* 1998). Despite these problems, MSY and  $F_{MSY}$  are, by definition, indicators of sustainability (at least in a single-species sense) and are based on sound biological theory. In recent years there has been renewed interest in using  $F_{MSY}$  as a limit reference point (rather than a target) in both single species and ecosystem-based

management contexts (Mace 2001; Punt and Smith 2001). Meta-analytical studies have also suggested that  $F_{MSY}$  represents a precautionary limit to fishing mortality for preventing recruitment overfishing (Cook *et al.* 1997; Punt 2000; NAFO 2003; Mace 1994).

As well as being a biologically-valid limit reference point,  $F_{MSY}$  can also be useful in communication of trade-offs to fishery managers and stakeholders.  $F_{MSY}$  is directly comparable among populations and, unlike some recruitment parameters, is easily interpreted by non-scientists (Schnute and Kronlund 1996). It is also of direct management interest, i.e., it is possible to compare species directly in terms of the amount of fishing that can sustainably be applied. While density dependence in recruitment is a determinant of sustainable exploitation rate, it is not the sole determinant, and it does not follow that a stock with strong density dependence can sustain higher harvest rates *per se*. In fact, in a recent meta-analysis of 54 Atlantic fish stocks, Goodwin *et al.* (2006) found that recruitment compensation tended to be stronger in larger, longer-lived, slower-growing stocks – characteristics that tend to be associated with lower resilience to fishing. The idea that fish species have an intrinsic resilience to fishing, which can be presented in terms of a parameter of direct management interest and compared among multiple species (e.g., Fig.1.1), facilitates communication of trade-offs in multispecies or multi-stock fisheries in simple terms, without the implication of setting MSY as a management target. Fishery assessment methods have progressed over the past two decades: equilibrium fitting methods are no longer used for parameter estimation; there is greater awareness of problems with using catch-per-effort data; and advice is now usually given in probabilistic terms (Punt and Smith 2001). In addition, fixed harvest-rate management strategies have been found to be more robust to uncertainty than fixed quota approaches (Walters and Parma 1996; Martell and Walters 2002) and most appropriate to use for low-productivity species (Punt and Smith 1999a). It is in this new context that  $F_{MSY}$  may once again be a useful parameter in the EBFM arena.

### **Models as support tools**

Simulation models are important tools for providing scientific advice for fisheries management. Probably the most common application of models is for estimation of parameters by fitting model predictions to observed data using Bayesian or likelihood methods (Hilborn and Walters 1992; McAllister and Ianelli 1997; Hilborn and Mangel 1997; Punt and Hilborn 1997; Chen *et*

*al.* 2003). Even in data-limited situations, however, simulation models can be useful heuristic tools (e.g., papers in Kruse *et al.* 2005; Cortés 1998; Smith *et al.* 1998; Heppell *et al.* 1999; McAllister *et al.* 2001). The complexity, variability and lack of knowledge about marine systems does not preclude making good policy decisions and scientists and managers do not necessarily need detailed knowledge of all system processes to be able to predict that one policy is preferable to another over a wide range of possible states of nature (Walters and Martell 2004). Policies that consistently outperform others under a range of uncertainty in a simulation framework can be considered relatively robust and worthy of further exploration. Models can also help to identify processes most likely to be important to predicting the effects of policy and help to focus research programmes (Walters 1992; Walters and Holling 1990).

Since the 1950s, different classes of stock assessment models have been used by fisheries scientists to predict the impacts of fishing on fish stocks. These include surplus production models (e.g., Schaefer 1954); dynamic pool models (Beverton and Holt 1957); and fully age-structured biomass dynamic models (Megrey 1989). Most of these types of models have been applied to single species, although some have been extended to a multispecies context (Murawski 1984; Pope 1991; reviews by Bax 1998; Whipple *et al.* 2000). In recent years, whole ecosystem models have been developed to help scientists and managers focus on ecosystem-scale policy questions (Christensen and Walters 2004b; Fulton 2005b; reviews by Bax 1998; Whipple *et al.* 2000; and Plagányi 2007). Probably the most widely used of these is the Ecopath with Ecosim (EwE) family of mass balance ecosystem models (Polovina 1984; Christensen and Pauly 1992; Walters *et al.* 1997). Examples of some applications of ecosystem models built using the EwE can be found in a recent special volume of *Ecological Modelling* (2004; Volume 172 (2-4)). See Christensen and Walters (2004b) and Plagányi (2007) for discussion of the capabilities and limitations of different ecosystem models. See Fulton (2001) and Fulton and Smith (2004) for comparison of the performance of different ecosystem models.

While ecosystem models are unlikely to reach the stage where they can quantitatively and accurately predict all ecosystem dynamics, they may be useful for identifying robust management strategies, exposing trade-offs and clarifying policy objectives. For example, a biogeochemical ecosystem model (Atlantis) has been used for extensive testing of the performance of ecosystem-scale indicators (Fulton *et al.* 2005b) and for evaluation of trade-offs

(Fulton *et al.* 2007a). EwE has also been used extensively for evaluation of trade-offs and has an in-built optimal policy search routine that maximises an objective function weighted according to the value placed on different policy objectives (papers in Pitcher and Cochrane 2002; Christensen and Walters 2004b; Ainsworth and Pitcher 2005; Cheung and Sumaila 2007; Fulton *et al.* 2007b). Use of ecosystem models for this purpose allows trophic effects to be accounted for in predicting performance of alternative management options. EwE has also been used to estimate the effects of trophic interactions on achievable MSY (Walters *et al.* 2005). Results have shown that deterioration in ecosystem structure can occur if harvests of smaller forage species, which form the main prey of larger piscivores, are not constrained. Ecosystem models have also been used for exploration of policy goals for restoration (Pitcher 2001; 2005; Pitcher and Ainsworth 2008). The approach of these authors involves using a variety of scientific, historical and anecdotal sources of information to reconstruct historical ecosystems to demonstrate the potential economic, social and economic gains that could potentially be made with appropriate restoration targets (e.g., Heymans (ed.) 2003; Ainsworth and Pitcher 2005; 2008; Ainsworth *et al.* 2008). Results have suggested that both consumptive and existence values could be greatly improved, compared to present-day ecosystems. Ecosystem models have also been used to address a large number of ecological questions and to explore hypotheses for observed ecosystem-level changes (e.g., decline of Steller sea lions in the north eastern Pacific: Guénette *et al.* 2006; collapse of the northern cod fishery: Bundy 2004; shifts in ecosystem structure in Thailand: Christensen 1998).

This study aims to use single-species and ecosystem-scale models, incorporating some of the ideas above, to aid understanding of issues important for EBFM in the fisheries off the coast of NSW.

## **Fisheries off the coast of New South Wales**

New South Wales is located on the south east coast of Australia and is the country's most populous state (Figure 1.3). Important coastal marine habitats off the coast of New South Wales include estuaries, rocky reefs, mangroves and seagrass beds, as well as diverse continental shelf and slope habitat. Waters tend to be oligotrophic, due to lack of upwelling and tropical water transported south by the East Australia Current and, as a result are less productive than might be

expected. The continental shelf is relatively narrow (generally extending to around 20-40 km offshore), and supports invertebrate and finfish fisheries.

The history of management of the shelf and slope fisheries of NSW is complex and there have been a number of changes in jurisdictional control since fishing began. Jurisdiction of the coastal waters off NSW is now divided between the State and Commonwealth governments. All waters within 3 nautical miles of the coast are under State jurisdiction. Under the 1979 Offshore Constitutional Settlement (see Rothwell 1994; Rothwell and Haward 1996), jurisdiction over waters off NSW beyond 3 nautical miles is shared between the Commonwealth and State governments. South of Barranjoey Point, (at the northern edge of Sydney, 33° 35' S), Australian waters beyond 3 nautical miles offshore are wholly under Commonwealth jurisdiction and are managed by the Australian Fisheries Management Authority (McColl and Stevens 1997). North of Barranjoey Point, all waters are under State jurisdiction to 80 nautical miles offshore, beyond which the Commonwealth has jurisdiction to the edge of the Australian Fishing Zone<sup>2</sup>, 200 nautical miles offshore. Both Commonwealth and State fisheries have undergone significant restructuring over the past three decades (Grieve and Richardson 2001; Tilzey and Rowling 2001). Complex jurisdictional issues pose a number of problems for efficient management of fish stocks in NSW. For example, most trawlers are endorsed to fish in both State and Commonwealth fisheries and there is a period between 1985 and 1997 when there is uncertainty as to whether landings reported to the Commonwealth Government were also reported to the State government. Management problems may also arise as a result of species being distributed cross jurisdictional boundaries, although there has been little documentation of such problems if they occur.

Commercial fishing began on the continental shelf of NSW in 1915, with three steam trawlers owned by the NSW government. The continental slope has supported fisheries since the late 1960s (Graham *et al.* 2001). Until the early 1970s, the fishery operated primarily in continental shelf waters between depths of 50 and 200 metres, targeting mainly tiger flathead (*Neoplatycephalus richardsoni*) then, following declines in this species, jackass morwong

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<sup>2</sup> The Australian Fishing Zone (AFZ) was declared in 1979, some fifteen years earlier than the 1994 declaration of Australia's Exclusive Economic Zone (EEZ). The EEZ did not replace the AFZ – rather there is provision for the two zones to be defined consistently with each other (Rothwell and Haward 1996). The EEZ generally refers to Australia's jurisdiction over the seabed and its resources (such as oil and gas), whereas the AFZ generally refers to jurisdiction over the water column and living marine resources.

(*Nemadactylus macropterus*), redfish (*Centroberyx affinis*) and smaller quantities of other demersal fish species (Klaer 2001). In 1968, two Wollongong trawlers began targeting redfish on the NSW upper slope, leading to an expansion of the trawl fishery into upper slope waters to ~600 m depth (Andrew *et al.* 1997). The expansion onto the slope was further driven by the discovery of large spawning runs of gemfish (*Rexea solandri*) (Klaer 2001). Currently, the Commonwealth Trawl Sector (CTS; formerly the South East Trawl Fishery) is the largest Commonwealth-managed fishery operating off the coast of NSW. Most of the catch now occurs on the continental shelf and slope from approximately 200 to 600 metres in depth (Tilzey and Rowling 2001). In 1992, Individual Transferable Quotas were introduced into the Commonwealth fishery (Grieve and Richardson 2001). There are now currently 20 species or taxonomic groups under quota in the fishery (Tuck and Smith 2006), although more than 80 species are harvested commercially (see Kailola *et al.* 1993; Williams and Bax 2001). Stock assessments are available for a limited number of species caught in Commonwealth fisheries (reviewed by Bruce *et al.* 2002; see Tuck and Smith 2004; 2006 for recent assessments).

During the 1970s, Australia's fisheries were considered 'underexploited' and, with the impending 1979 declaration of the 200 nautical mile Australian Fishing Zone, the Australian government provided considerable funding for exploratory surveys of the waters of the southeast Australian slope (Tilzey and Rowling 2001). This led to a set of surveys of the upper continental slope in the 1970s (Gorman and Graham 1976; 1977). The objective of the early surveys was to locate productive trawl grounds and evaluate the viability of demersal slope fisheries. The initial, exploratory upper slope surveys were done in 1976-1977 and were fully replicated twenty years later in 1996-1997, allowing for some striking comparisons of the abundance of many species (Andrew *et al.* 1997; Graham *et al.* 1997; Graham *et al.* 2001). Analysis of the survey data revealed that there had been significant declines in the abundance of many demersal sharks, skates and several species of bony fish on the continental slope. Notable declines were reported for deepwater dogsharks (*Centrophorus* spp., *Squalus* spp. and *Deania* spp.), as well as sawsharks (Pristiophoridae), angel sharks (Squatinae), school sharks (*Galeorhinus galeus*) and skates (Rajidae). One of the most significant declines in abundance of bony fishes has been that of gemfish (*Rexea solandri*), which was shown to suffer severe recruitment failure in the early 1980s (Rowling 1990; 1997a). The research vessel was decommissioned in 1997 and there have been no fishery-independent surveys on the NSW continental shelf or slope since that time.

Currently, there are seven commercial marine fisheries operated wholly by the State of NSW: Estuary General, Estuary Prawn Trawl, Ocean Trawl, Ocean Haul, Ocean Trap and Line, Rock Lobster and Abalone. All recreational fisheries operating out of NSW ports, regardless of distance offshore, are also State-managed. Except for the valuable abalone and rock lobster fisheries, which are managed by quotas, all fisheries are managed by input (i.e., effort) controls. Management measures include a complex set of gear and mesh size restrictions, seasonal temporal and areal closures and minimum legal lengths of fish (see NSW Fisheries 2001; Gray 2008). Each fishery has a Management Advisory Committee (MAC) that meets regularly and contributes to management decisions. MAC members include commercial fishers and scientists, representatives of environmental groups, indigenous representatives and scientists from other related disciplines.

A Fisheries Management Strategy (FMS) and Environmental Impact Statements (EIS) have recently been developed for all fisheries in accordance with requirements of the EPBC Act, the *Environmental Planning and Assessment Act 1979* and the *Fisheries Management Act 1994* (Gibbs 2008). The objectives of the EISs are to provide detail needed to augment the FMS; to provide assessment of the current activity of each fishery; and to identify links with other parts of the human and ecological environment (Gibbs 2008). While the Environmental Impact Statements make use of information existing about the fisheries of New South Wales and highlight likely interactions among components of the ecosystem, no new ecological research was done to produce them and all so far point out large gaps in understanding of ecosystem processes and the nature of fisheries impacts on these processes, e.g. “The draft FMS has revealed substantial knowledge gaps that affect the management of the Estuary General Fishery. The knowledge gaps cover four main areas – stock assessments of all retained species, bycatch, accuracy and precision of effort data and ecological interactions among retained species. [...] There is little understanding of how fishing pressure affects fish stocks in the Estuary General Fishery. [...] Whilst there is some basic knowledge about the general biology of species in the Estuary General Fishery there is little knowledge about how the species interact” (NSW Fisheries 2001, pp E-250-251).



Recreational fisheries in New South Wales are significant. The recent national survey of recreational fishing estimated that in the financial year 2000-2001, there were approximately 7.7 million recreational fishing 'events' in New South Wales (Henry and Lyle 2003). Catches of several important commercial species were found to exceed commercial catches, a finding consistent with previous surveys of recreational fishing in Australia (Pollock 1980; West and Gordon 1994; Young *et al.* 1999). Prior to the National Survey of Recreational and Indigenous Fishing (Henry and Lyle 2003), recreational fishing surveys were done on a local basis using various methodologies (e.g., State Pollution Control Commission 1981; West 1993; West and Gordon 1994; Steffe and Macbeth 2002a,b). The National Survey of Recreational and Indigenous Fishing represents the first comprehensive survey enabling comparison of recreational activity across the whole country. It has not, however, been repeated and recreational fishing remains a major source of uncertainty in estimates of total catch of many species (Scandol *et al.* 2008).

There are a number of barriers that have prevented reliable stock assessment for the inshore fisheries of NSW. Estuarine and beach fisheries, are small-scale and extremely complex in terms of the number of species landed, targeting practices and gears used. Also, unreliable effort data for a number of gears has meant that catch per unit effort (CPUE) cannot be calculated in many cases (Scandol and Forrest 2001), although considerable progress has recently been made in identifying reliable CPUE series (Scandol *et al.* 2008). Life history data and age- and length-composition of catches are routinely collected for many species and are being incorporated into consistent and easily accessible databases (Scandol 2004). Alternative approaches using these kinds of data will therefore be needed as NSW moves towards more ecosystem-based approaches to managing its fisheries (Scandol *et al.* 2008).

## **Aims of the project**

The aim of this collaborative project between NSW Department of Primary Industries and the University of British Columbia's Fisheries Centre is to provide simulation models to help identify needs for EBFM in NSW. Fisheries in NSW are extremely data-limited and management has not traditionally relied on model outputs for decision-making. The costs associated with collecting data to address the many knowledge-gaps are likely to exceed the

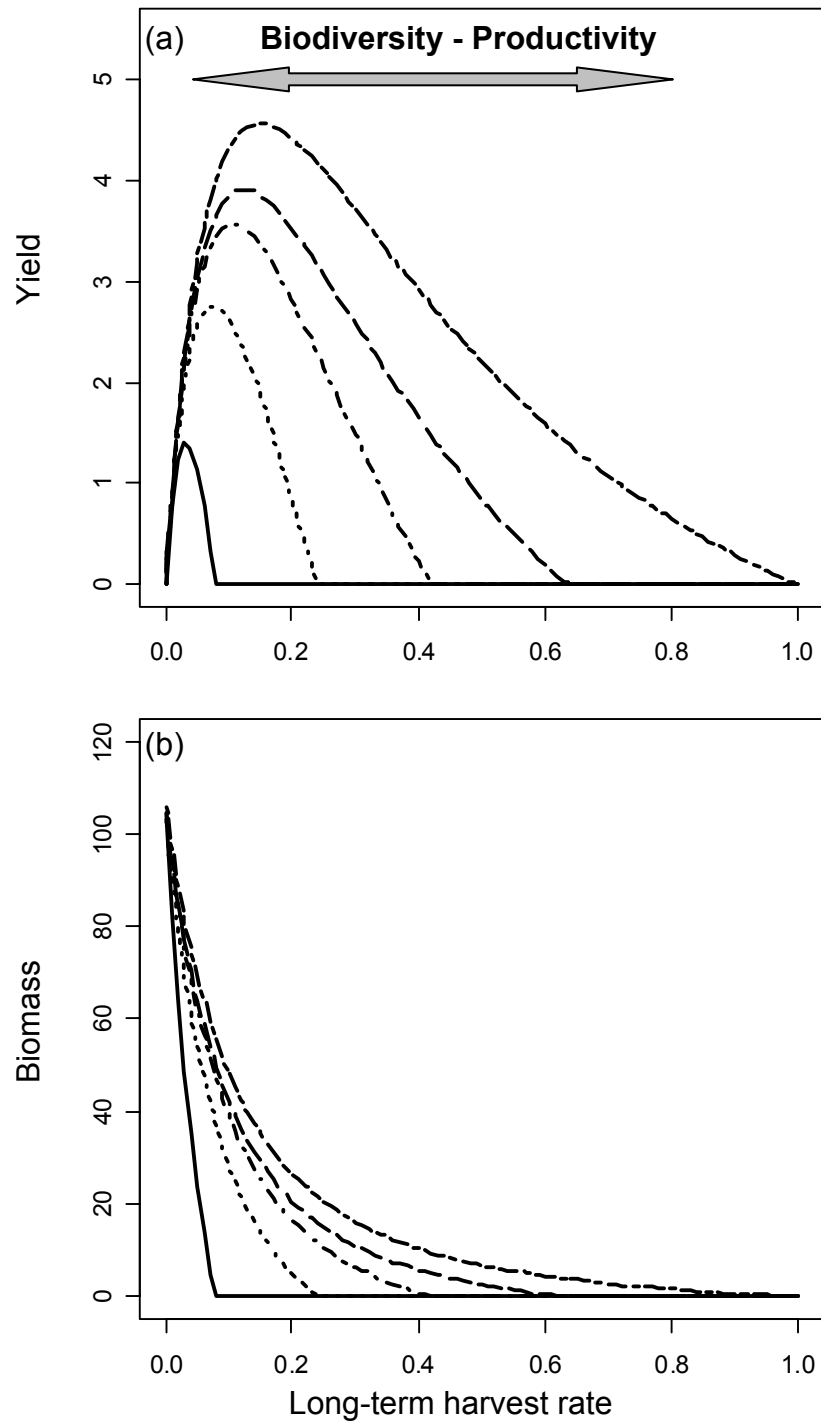
funds available for research in the near future and, therefore, simply doing more research, or collecting more data, is not the way forward. Innovative approaches, such as the development of assessment approaches that rely on more-easily and routinely collected data (such as age, growth and reproductive data) that can be used to estimate suitable reference points should play an important role in determining which species are most at risk from fisheries.

This thesis aims to provide simulation tools that can contribute to understanding of EBFM; to highlight need for consideration of trade-offs; and to help clarify possible EBFM policy objectives. The thesis begins with presentation of a newly-parameterised age-structured model with productivity parameter, optimal harvest rate,  $U_{MSY}$  (Chapter 2). The model has useful equilibrium properties in that it enables examination of the relationship between life history, selectivity, density dependence in recruitment and  $U_{MSY}$ . Chapter 3 explores these relationships for 54 Atlantic stocks for which recruitment parameters have been previously published by other authors (Goodwin *et al.* 2006). Results showed that, for some long-lived, slow-growing species, life history parameters may be the most important determinant of  $U_{MSY}$ . Chapter 4 explores this concept further and applies the model to estimate the maximum possible hypothesis for  $U_{MSY}$  for dogsharks that have been heavily depleted on the continental slope (Graham *et al.* 2001). Results suggest that the optimal harvest rate for these species is extremely low under a broad range of hypotheses about the age at first harvest. Chapter 5 evaluates available data for stock assessment of one species of dogshark that has been listed as Critically Endangered by the IUCN (IUCN 2008). The study reveals severe problems in the quality of available data for sharks in southeastern Australia, typical for sharks around the world. Catch and historical effort data are reconstructed and used in a simple preliminary stock assessment. Finally, in Chapter 6, an ecosystem model of the 1976 NSW continental slope, built using Ecopath with Ecosim, is used to illustrate important trade-offs in implementation of alternative fishing strategies with differing management objectives. To evaluate the effects of model structure on results, results are compared with the predictions an Atlantis model of the same system, built by scientists at CSIRO (Savina *et al.* 2008).

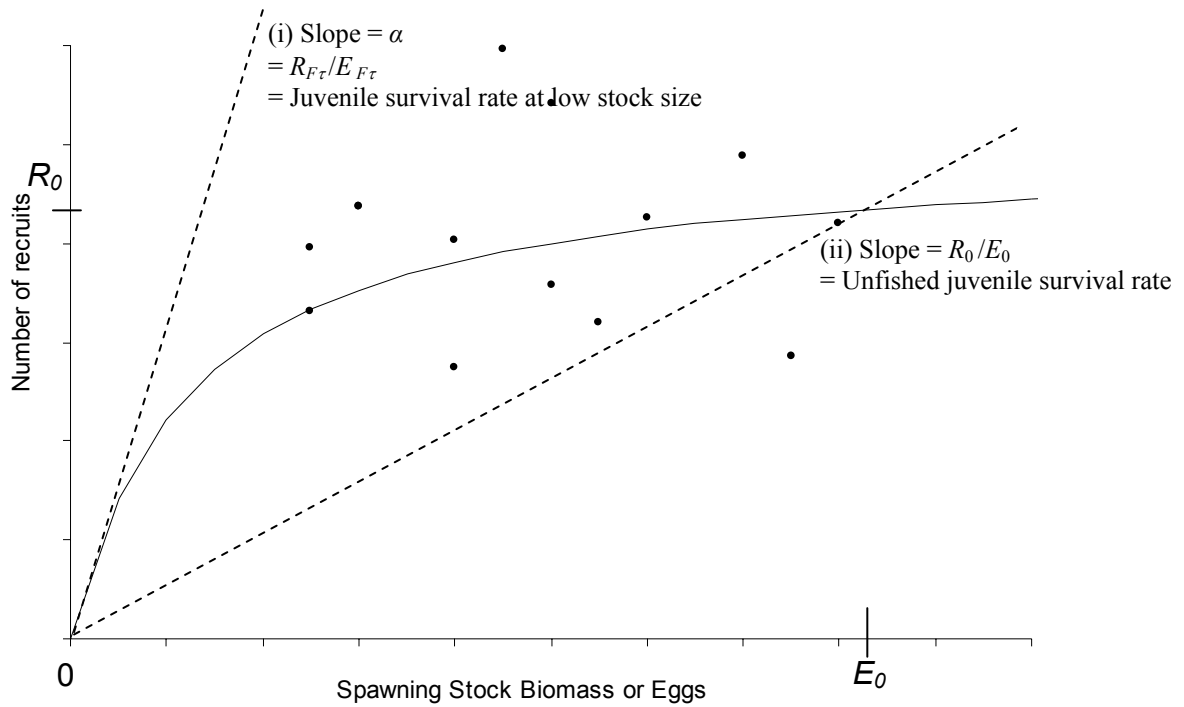
It is hoped that these analyses will provide some tools and insights that can be of use towards implementation of EBFM in NSW, despite severe data-limitations. It is also hoped that important trade-offs have been highlighted and may help managers more clearly think about their

role in identifying and implementing EBFM policies. In addition to the analyses contained in this thesis, the project has facilitated collaboration between State, Commonwealth and international institutions and compiled a large amount of data and literature relevant to the marine ecosystem of NSW. A workshop held in 2003 brought together more than eighty scientists, managers and interested parties who shared their knowledge of the fisheries and ecosystems of the region. Papers from this workshop have been published (Forrest *et al.* (eds) 2008) and will also provide a valuable resource for scientists and managers. Preliminary results presented in this thesis were also discussed at an EBFM workshop at the NSW DPI laboratories in Cronulla in July 2007.

## Figures



**Figure 1.1.** Equilibrium (a) yield and (b) biomass for five hypothetical species in a multispecies fishery, where the  $x$ -axis represents long-term fixed harvest rate and the  $y$ -axis represents relative equilibrium yield or biomass that would be obtained after long-term harvesting at the fixed harvest rate. On each graph, the solid line represents the least productive species and broken lines from left to right represent progressively more productive species.

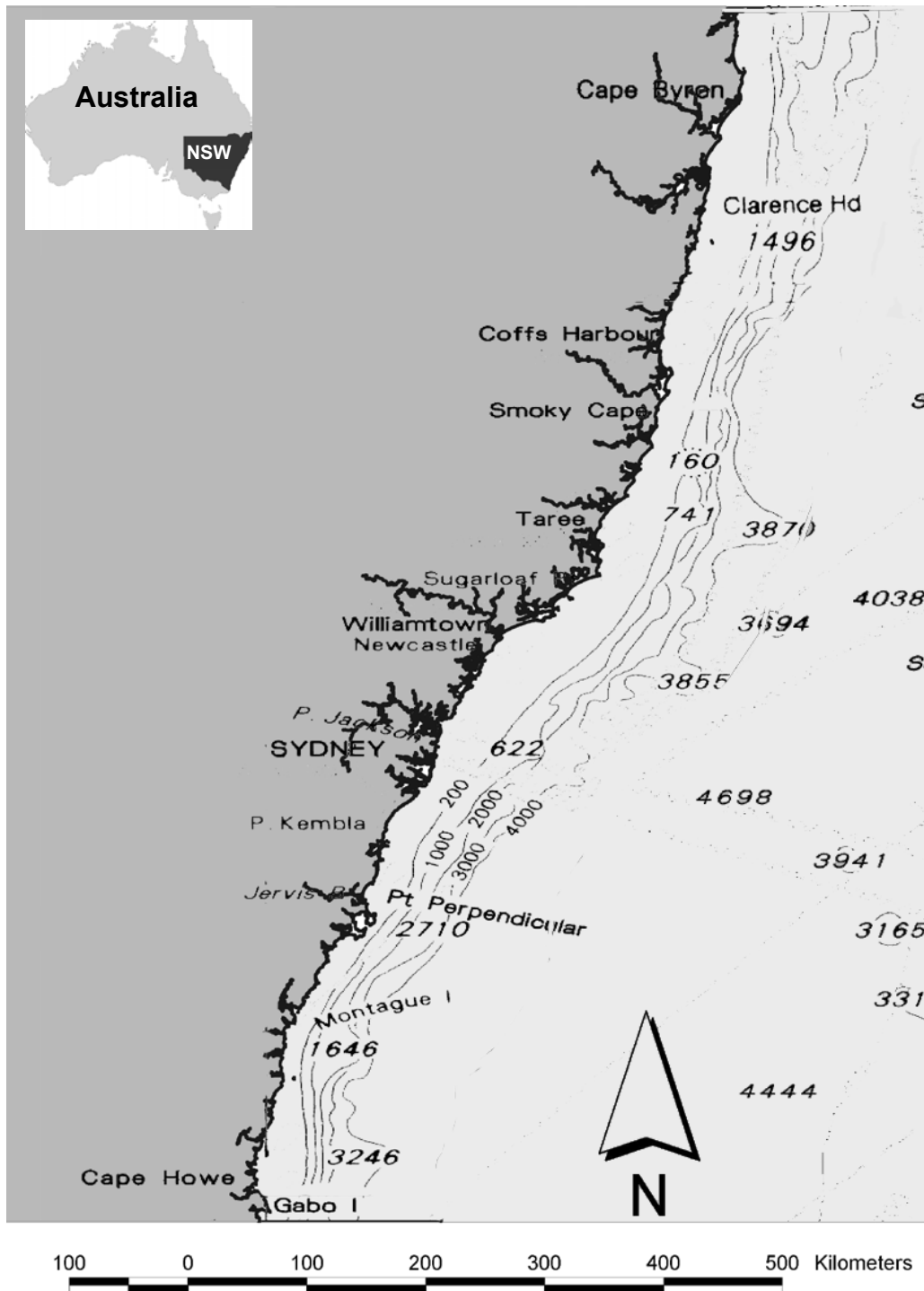


**Figure 1.2.** Stock recruitment relationship for a hypothetical fish population.

Points represent observed number of recruits plotted against spawning stock biomass or number of eggs. The solid line shows a fitted Beverton-Holt (1957) stock recruitment curve. Note that the function can be parameterised in terms of spawning stock biomass or in terms of numbers of eggs,  $E$ . Note also that number of eggs is often assumed directly proportional to spawning stock biomass (see Chapter 4 for cases where this is an inappropriate assumption).

Dashed lines represent juvenile survival rate: (i) close to the origin of the plot; and (ii) at unfished (maximum) production of eggs (i.e.,  $E_0$  where the 0 subscript indicates fishing mortality  $F = 0$ ). The maximum juvenile survival rate, i.e., slope of dashed line (i) is called  $\alpha$  and occurs at the fishing mortality rate  $F_\tau$  (Shepherd 1982), which, if applied consistently, would cause extinction of the stock. The ratio of slopes (i) and (ii) is called the recruitment Compensation Ratio, CR (Goodyear 1977; also called  $\hat{\alpha}$ ; Myers *et al.* 1999) and represents the maximum possible improvement in juvenile survival as stock size is reduced, i.e.,  $CR = \frac{\alpha}{R_0 / E_0}$ .

Note that  $R_0/E_0$  is the inverse of unfished eggs per recruit, and, therefore,  $CR = \alpha E_0/R_0$ . Note that in this thesis,  $E_0/R_0$  is expressed as  $\varphi_{E0}$  (Botsford 1981; see Chapter 2, equation 2.2).



**Figure 1.3.** Map of the study area. Depth contours are measured in fathoms (1 fathom = 1.83 metres). Note that most fishing occurs in waters shallower than 1000 metres (Larcombe *et al.* 2001). *Source:* Jim Craig (NSW DPI).

## Chapter 2. An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity

### Introduction

Maximum sustainable yield (MSY) has formed the basis of many fisheries management strategies since at least the 1950s (e.g., Schaefer 1954). Despite well-documented problems with implementation of MSY policies (Larkin 1977; Punt and Smith 2001), the recent shift towards setting the target fishing mortality rate that achieves MSY ( $F_{\text{MSY}}$  or its dimensionless, discrete equivalent,  $U_{\text{MSY}}$ ) as a limit reference point rather than a target reference point has resulted in renewed interest in MSY as a means of determining precautionary harvest rates in both single species and ecosystem-based management contexts (Mace 2001).

Fisheries stock assessment involves estimating key parameters (leading parameters) by fitting a model to fishery dependent or independent data. The leading parameters of a model are those from which other parameters are derived and are of greatest interest in terms of establishing reference points, even though other ‘nuisance’ parameters (e.g., catchability, growth and selectivity parameters) may be required for a fully-specified model (Walters *et al.* 2006). At the very least, population models require leading parameters that determine the scale and productivity of the population, with the leading parameter describing productivity the main determinant of the behaviour of a fish stock under harvesting and, therefore, its maximum sustainable harvest rate,  $U_{\text{MSY}}$ . There are a number of ways that productivity can be represented in population models, the simplest being the logistic model’s intrinsic rate of growth,  $r$  (e.g., Schaefer 1954). Alternatively, some models use the slope of a stock recruitment function near the origin,  $\alpha$  (e.g., Ricker 1954; Beverton and Holt 1957). Goodyear (1977) expressed productivity in terms of the recruitment compensation ratio (CR), which is the relative improvement in juvenile survival as spawning stock abundance is reduced towards zero (see Figure 1.2 for graphic presentation). In common use is a reparameterised version of the Beverton and Holt recruitment function, which uses the steepness parameter,  $h$ , defined as the proportion of recruits that are produced when egg production (i.e., spawner abundance) is at 20% of

unfished egg production (Mace and Doonan 1988; Hilborn and Walters 1992). Myers *et al.* (1999) expressed  $h$  (called  $z$  in their paper) as a function of lifetime spawners per spawner at low abundance,  $\hat{\alpha}$ . Their meta-analysis, based on stock-recruitment data for more than 700 fish stocks, suggested that the magnitude of compensation in recruitment is a relatively conservative property of fish stocks, with the maximum lifetime production of spawners per spawner rarely exceeding 50. Mathematically,  $\hat{\alpha}$  is the equivalent of CR under certain assumptions about fecundity (see section below). Goodwin *et al.* (2006) reported CR for 54 Atlantic fish stocks, again reporting  $CR < 50$  for the majority of stocks. The finding that CR tends to be confined within certain bounds across multiple species and life histories makes CR a useful productivity parameter for modellers, especially given its analytical relationship to the more familiar  $h$ .

Biological productivity parameters are usually of secondary interest to managers, who tend to be more concerned with measures such as total allowable catch or maximum sustainable harvest rate. Management parameters must therefore be derived from models, either using analytical or numerical relationships. Simple surplus production models (e.g., Schaefer 1954), which do not explicitly incorporate recruitment, provide a direct analytical relationship between  $r$  and  $U_{MSY}$  ( $U_{MSY} = r/2$ ). For semelparous species,  $U_{MSY}$  can be expressed as a function of  $\alpha$ , using Ricker (1954) or Beverton and Holt (1957) recruitment functions (Hilborn and Walters 1992). Schnute and Kronlund (1996) derived analytical relationships between biological and management parameters using a generalised recruitment function for semelparous species. The resulting stock-recruitment function was parameterised in terms of two leading management parameters,  $U_{MSY}$  and  $MSY$ , which could be estimated directly using established stock assessment fitting procedures. Schnute and Richards (1998) extended the approach and developed a generalised age-structured model that could be used for iteroparous species, which incorporated a reparameterised stock recruitment function in terms of  $U_{MSY}$  and  $MSY$ . It assumed knife-edged selectivity and maturity and that natural and fishing mortality occurred separately. Despite these limiting assumptions, their approach enabled direct estimation of  $U_{MSY}$  from data for a much broader range of species than had been previously possible.

The approach of Schnute and Richards (1998) is extended here by presentation of an alternative formulation of the derivation of  $\alpha$  from  $U_{MSY}$ , which incorporates age-specific selectivity and maturity. An age-structured population model is used, which utilises Botsford “incidence”



functions (Botsford 1981; see Walters and Martell 2004) to calculate equilibrium eggs per recruit and vulnerable biomass per recruit, which simultaneously capture the effects of fishing and natural mortality on fish as they age. The method avoids the assumption of knife-edged selectivity and maturity and is flexible to a wide range of selectivity and maturity schedules. These developments broaden the range of fisheries for which  $U_{MSY}$  can be estimated directly.

### **Links between life history and productivity**

There is currently much interest in the link between life history traits and productivity, especially for species that are data-limited (Reynolds *et al.* 2001). While certain life history traits (e.g., late maturity, slow growth, low natural mortality) tend to predispose species towards low values of  $U_{MSY}$ , density dependence in recruitment is also an important determinant. Density dependence principally refers to the improvement in juvenile survival rate as spawning stock size is reduced. Density dependent mortality may occur at a number of life history stages but probably occurs principally in juvenile demersal stages for coastal species (Myers 2002). Mechanisms include increased territorial behaviour and greater competition for food as juvenile density increases, which lead to increased time taken to reach sizes less vulnerable to predation (see Hilborn and Walters 1992; Rose *et al.* 2001; Myers 2002). Foraging arena theory (Walters and Juanes 1993; Walters and Korman 1999; Walters and Martell 2004) has recently been introduced as an overarching explanation for density dependence in juvenile survival rates and predicts that density dependence is an emergent consequence of the trade-off between time spent feeding and risk of predation.

Mechanisms leading to density dependence are complex and subject to considerable interannual variability. On average, however, some species show a stronger response to changes in spawning stock size than others. All other things equal, stronger density dependence implies greater resilience to fishing due to the stock's ability to respond positively to reductions in adult biomass (e.g., Goodyear 1977). Density dependence is difficult to measure in nature due to problems with observing juvenile fish, although the meta-analyses of Myers *et al.* (1999) and Goodwin *et al.* (2006) have improved understanding of the likely range of magnitude of these effects.

Quantifying interactions among life history parameters, density dependence and sustainable harvest rates could aid in understanding the mechanisms that lead to overfishing and could be useful in design of sustainable fishing strategies. The structure of the model, and its analytical

relationship between productivity and  $U_{MSY}$ , allows these linkages to be considered simultaneously.

### **Bayesian estimation**

Bayesian inference is now in mainstream use in fisheries stock assessment (e.g., Punt and Hilborn 1997; Chen *et al.* 2003) and has facilitated a general move towards consideration of population and management parameters as probability distributions, rather than point estimates. Once distributions of a model's leading parameters have been estimated, the past and current state of the fishery, in terms of population size or harvest rates, can also be estimated to determine the probability of exceeding reference points. Combining direct estimation of fishery reference points, such as MSY and  $U_{MSY}$ , with a Bayesian approach can improve communication of scientific results considerably (Schnute and Kronlund 1996; Schnute and Richards 1998). Managers are more familiar with the parameters MSY and  $U_{MSY}$  than their more abstract biological analogues and, in fully developed fisheries, it is likely that MSY and  $U_{MSY}$  lie within management experience. Dialogue between managers and scientists about the range of uncertainty to admit in stock assessments is likely to be more transparent if all parties are discussing parameters with which they are familiar.

This paper proceeds as follows. First an age-structured population model that uses MSY and  $U_{MSY}$  as leading parameters is presented. Some properties of the model are then briefly described, chiefly in terms of its ability to show relationships between life history, density dependence and  $U_{MSY}$ . Finally, a simple Bayesian estimation routine is implemented to illustrate estimation of  $U_{MSY}$  directly.

### **Population model with MSY and $U_{MSY}$ as leading parameters**

The model is an age-structured population model with leading parameters MSY and  $U_{MSY}$  describing scale and productivity of the population respectively. First, the equilibrium structure of the model is described, then time dynamics are incorporated. The key difference between this model and other age-structured models is the analytical linkage between the leading management parameters and recruitment parameters.

Equilibrium recruitment ( $R$ ) under a given constant harvest rate is a function of stock size (expressed in terms of eggs,  $E$ ) and the leading parameters of the model. Here it is described by the Beverton and Holt (1957) recruitment function, i.e.,

$$(2.1) \quad R = \frac{\alpha E}{1 + \beta E}$$

where a recruit is here defined as a fish of age 1. Equilibrium eggs per recruit ( $\varphi_E$ ) can be obtained using an “incidence” function (Botsford 1981; Walters and Martell 2004), which captures the effects of natural mortality and fishing mortality over the lifetime of individuals assuming equilibrium conditions, i.e.,

$$(2.2) \quad \varphi_E = \sum_a^{\infty} l_a f_a$$

where  $f_a$  is relative fecundity at age (assuming fecundity based on weight and a logistic maturity function, Appendix B to Chapter 2).

Survivorship at age,  $l_a$  (the proportion of fish that survive to age  $a$  under a given constant equilibrium harvest rate  $U$ ) is given by

$$(2.3) \quad l_a = \begin{cases} 1 & \text{if } a = 1 \\ \ell_{a-1} s_{a-1} (1 - v_{a-1} U) & \text{if } a > 1 \end{cases}$$

where  $s_a$  is natural survival at age. It is assumed here that  $s_a$  is constant and proportional to the von Bertalanffy growth rate,  $\kappa$ , via the relationship  $s_a = e^{-M}$ , where  $M$  is the instantaneous natural mortality rate, with the simplifying assumption that  $M = 1.5\kappa$  (Beverton and Holt 1959). The term  $s_a(1 - v_a U)$  represents the survival rate under fishing,  $s_{a\_fished}$ . Equation 2.3 represents equilibrium survivorship under a particular constant harvesting regime, and enables calculation

of useful equilibrium per recruit quantities under different harvesting regimes. Note that unfished survivorship is obtained by setting  $U = 0$ .

At equilibrium, total egg production is given by  $E = R\varphi_E$ . Substituting this into equation 2.1 and solving for  $R$  gives

$$(2.4) \quad R = \frac{\varphi_E \alpha - 1}{\beta \varphi_E} \quad (\text{Walters and Martell 2004}).$$

Using this form of the stock recruitment function, Appendix A to Chapter 2 shows how  $\alpha$  can be derived from the leading productivity parameter  $U_{MSY}$ . The scaling parameter ( $\beta$ ) is more easily obtained from leading parameters  $U_{MSY}$  and  $MSY$ . First,  $VB_{MSY} = \frac{MSY}{U_{MSY}}$ , where  $VB_{MSY}$  is equilibrium vulnerable biomass under  $U_{MSY}$ . Recruitment under  $U_{MSY}$  is therefore given by

$$R_{MSY} = \frac{VB_{MSY}}{\varphi_{VB_{MSY}}}, \text{ where } \varphi_{VB_{MSY}} \text{ is vulnerable biomass per recruit at } U_{MSY}, \text{ calculated as}$$

$$(2.5) \quad \varphi_{VB_{MSY}} = \sum_a^{\infty} l_a w_a v_a$$

with  $l_a$  evaluated at  $U = U_{MSY}$  (equation 2.3) and where  $w_a$  is the mean weight-at-age, (derived from the von Bertalanffy (1938) growth function, see Appendix B to Chapter 2) and  $v_a$  is the mean vulnerability-at-age, defined as the proportion of fish of a given age  $a$  vulnerable to the fishing gear. Asymptotic vulnerability can be represented using a simple logistic function (see Appendix B to Chapter 2). Specification of the recruitment function can then be completed by

$$\text{solving equation 2.4 for } \beta \text{ (with } R \text{ and } \varphi_E \text{ evaluated at } U_{MSY}), \text{ i.e., } \beta = \frac{\varphi_{E_{MSY}} \alpha - 1}{R_{MSY} \varphi_{E_{MSY}}}.$$

Once  $\alpha$  and  $\beta$  are known, other important biological properties can be derived. Unfished recruitment,  $R_0$  is obtained using  $\varphi_{E0}$  in equation 2.4. Unfished biomass,  $B_0$ , is then simply a

function of  $R_0$  and unfished biomass per recruit, i.e.,  $B_0 = R_0 \varphi_{B_0}$ , where  $\varphi_{B_0} = \sum_a^{\infty} l_a w_a$ , with  $l_a$  evaluated at  $U = 0$ .

Another productivity parameter of interest is the recruitment compensation ratio, CR (Goodyear 1977). This represents the maximum possible compensatory improvement in juvenile survival as stock size is decreased by fishing (see Figure 1.2). It is easily derived from  $\alpha$ , i.e., unfished juvenile survival rate is  $\frac{R_0}{E_0}$ , but  $\varphi_{E_0} = \frac{E_0}{R_0}$ , so unfished survival is simply  $\varphi_{E_0}^{-1}$ . Since the maximum juvenile survival rate is  $\alpha$ , CR is just the ratio of these two survival rates (Goodyear 1977), i.e.,

$$(2.6) \quad CR = \alpha \varphi_{E_0}.$$

When relative fecundity is described as the product of mean weight-at-age and maturity-at-age (Appendix B to Chapter 2),  $\varphi_{E_0}$  is the same as unfished spawning biomass per recruit (SPR<sub>0</sub>; Gabriel *et al.* 1989). Myers *et al.* (1999) defined maximum lifetime spawners per spawner ( $\hat{\alpha}$ ) as the product of  $\alpha$  and SPR<sub>0</sub> and, therefore, the same as CR. When Beverton and Holt recruitment is assumed, the steepness parameter,  $h$ , of Mace and Doonan (1988) is related to  $\hat{\alpha}$  (i.e., CR) by  $h = \frac{\hat{\alpha}}{4 + \hat{\alpha}}$  (Myers *et al.* 1999; see Michielsens and McAllister (2004) for the Ricker form).

The model is made dynamic by simulating changes in numbers,  $N$ , at age,  $a$ , and years,  $t$ , via the equation

$$(2.7) \quad N_{a+1,t+1} = N_{a,t} s_a (1 - v_{a,t} U_t) \quad (\text{for } a > 1 \text{ and } t > 1)$$

Annual harvest rate,  $U_t$ , is calculated from annual catch,  $C_t$ , i.e.,

$$(2.8) \quad U_t = \frac{C_t}{VB_t}$$

where  $VB_t$  is the biomass of fish vulnerable to the fishing gear,

$$(2.9) \quad VB_t = \sum_a N_{a,t} v_{a,t} w_a$$

Recruits ( $R_t$ , i.e.,  $N_{l,t}$ ) are added to the population using equation 2.1 with number of eggs

calculated as  $E_t = \sum_a f_a N_{a,t}$ . The common simplifying assumption was made that the unfished

stock was at equilibrium and the model was initialised in the first year of fishing with

$$N_{a,1} = R_0 l_a.$$

### **Equilibrium properties: relationships between life history, density dependence and $U_{MSY}$**

The equilibrium model can be used to examine the predicted form of the relationship between density dependence (measured by CR) and  $U_{MSY}$ . The effect of gear selectivity and life history traits (e.g., growth rate, age at maturity, maximum age and natural mortality) on this relationship can also be modelled. Here, a hypothetical fish species with known life history parameters (Table 2.1) is used to show the effect of increasing: (i) age at first harvest; (ii) von Bertalanffy growth rate; (iii) age at maturity; and (iv) maximum age on the relationship between CR and  $U_{MSY}$ . To do this,  $\alpha$  was calculated over a range of hypothesised values of  $U_{MSY}$  (0 to 1, step size 0.0001), using equation 2.A6, and then converted to CR (equation 2.6).

Figure 2.1 shows the form of the relationship between CR and  $U_{MSY}$  (note that  $U_{MSY}$  is the independent variable). The relationship is not dynamic but rather shows the predicted values of CR under a range of hypothesised values of  $U_{MSY}$  (i.e., the degree of improvement in juvenile survival that would be required for each hypothesised value of  $U_{MSY}$  to be true). As the hypothesised value of  $U_{MSY}$  increases, the strength of recruitment compensation that would be

needed for the hypothesis to be true increases rapidly and tends towards a vertical asymptote. Values of  $U_{\text{MSY}}$  to the right of the asymptote are undefined, representing hypotheses of  $U_{\text{MSY}}$  for which  $\alpha$  was predicted to be negative (therefore impossible). The y-axes in Figure 2.1 at  $\text{CR} = 100$  are truncated because, as  $U_{\text{MSY}}$  approached its maximum possible value,  $\text{CR}$  tended rapidly towards very large values of  $\text{CR}$  making comparison of the curves difficult. Since most of the curves become almost vertical by the truncation point, the maximum possible value of  $U_{\text{MSY}}$  can still be seen. As values of  $\text{CR} > 100$  seem to be rare (Myers *et al.* 1999; Goodwin *et al.* 2006), Figure 2.1 shows the region of management interest.

Figure 2.1a shows the relationship between  $\text{CR}$  and  $U_{\text{MSY}}$  at different values of age-at-50%-first-harvest,  $a_h$ . Increasing  $a_h$  causes the curve to shift to the right, increasing the range of values of  $U_{\text{MSY}}$  that can be considered possible. Increasing  $\kappa$  (von Bertalanffy growth rate and proxy for natural mortality) causes the curve to shift to the right, implying a greater range of possible values of  $U_{\text{MSY}}$  for faster-growing species (Figure 2.1b). Increasing age-at-50%-maturity,  $a_{\text{mat}}$  (Figure 2.1c), or maximum age,  $a_{\text{max}}$  (Figure 2.1d), however, causes the curve to shift to the left, implying a smaller range and lower possible values of  $U_{\text{MSY}}$  for later maturing or longer-lived species (although the effect of age at maturity is small). Importantly, Figure 2.1 suggests that, for some species for which Beverton and Holt recruitment can be assumed, there is a maximum possible value of  $U_{\text{MSY}}$  that can be estimated from life history and selectivity data alone.

## Bayesian estimation of MSY and $U_{\text{MSY}}$

### Methods

In this section, the model is used to show how  $\text{MSY}$  and  $U_{\text{MSY}}$  can be estimated using a Bayesian approach. Catch and CPUE data (Figure 2.2) for Namibian Cape Hake (a mixed stock of *Merluccius capensis* and *M. paradoxus*), published in Hilborn and Mangel (1997), were used. This dataset was chosen because: i) it will be familiar to many readers; and ii) CPUE is considered to be a reasonable index of abundance because the degree of schooling in hake is relatively low. The fishery began in the mid-1960s and was largely unregulated, resulting in a large decline in CPUE in the first ten years. Following conservation concerns, catches were

reduced in the 1970s, which resulted in a slight increase in CPUE (Hilborn and Mangel 1997). Life history and selectivity parameters are provided in Table 2.1.

The model with leading management parameters ( $MSY$  and  $U_{MSY}$ ; Model 1) was compared to one with biological leading parameters ( $R_0$  and  $CR$ ; Model 2) to show that very similar results can be obtained using either approach. Model 2 was identical in structure to Model 1, except for the method of calculating the parameters of the recruitment function (i.e., in Model 2  $\alpha$  was obtained from the leading value of  $CR$  and equation 2.6;  $\beta$  was then obtained from the leading value of  $R_0$  and equation 2.4). In both models, in addition to estimating the leading parameters, the instantaneous natural mortality rate,  $M$ , and the standard deviation of the observation error anomalies,  $\sigma$  were also estimated. To obtain the posterior distributions a Metropolis-Hastings algorithm was used, implemented in R, using the function “MCMCmetrop1R” in the MCMC package (Martin and Quinn 2006; R Development Core Team 2006). Markov chain simulation performs a random walk in the parameter space of  $\theta$  (Model 1:  $\theta = (MSY, U_{MSY}, M, \sigma)$  or Model 2:  $\theta = (R_0, CR, M, \sigma)$ ), which converges to a distribution that approximates the joint posterior distribution (Gelman *et al.* 1995). The algorithm was initialized at the maximum likelihood estimates for  $\theta$  and proceeded for 110,000 iterations where the first 10,000 were discarded to allow for convergence. Convergence was assessed by visually examining trace plots and plotting running medians of length 50 to ensure the algorithm was sampling from a stable distribution (see Gelman *et al.* 1995 and Punt and Hilborn 1997 for more details on MCMC methods).

For simplicity estimating process error was not attempted. Lognormal observation error was assumed, i.e.,  $CPUE_t = qVB_t e^{v_t}$ , where  $q$  is the constant of proportionality (catchability) and  $v_t \sim N(0, \sigma)$ . The parameters  $\sigma$  and  $q$  were treated as uncertain but the maximum likelihood estimate (MLE) of  $q$  in the joint posterior distribution was used, taking the approach of Walters and Ludwig (1994), i.e., assuming a linear relationship between  $CPUE_t$  and  $VB_t$ , we estimated  $z_t = \ln(CPUE_t) - \ln(VB_t)$  and

$$(2.10) \quad \bar{z} = \frac{\sum_{t=1}^n z_t}{n}.$$



The MLE of  $q$  was then  $e^{\bar{z}}$  and the observation residuals ( $d_t$ ) used in the log likelihood function were calculated as  $d_t = z_t - \bar{z}$ . The log likelihood of each observation was thus

$$(2.11) \quad L_t = \ln(\sigma) + 0.5 \ln(2\pi) + \frac{d_t^2}{2\sigma_v^2}.$$

Uninformative prior probability distributions were assumed for  $U_{\text{MSY}}$  and MSY in Model 1 and for  $R_0$  in Model 2. A normally distributed prior for  $M$  was assumed, i.e.,  $M \sim N(0.21, 0.1)$ , with the mean based on the assumption  $M = 1.5\kappa$  (Beverton and Holt 1959). A weak, lognormally distributed informative prior for CR to penalise negative (i.e., impossible) values of CR was also assumed.  $R_0$ , CR and MSY were log transformed so the relative scales of parameters in the search routine were similar.  $U_{\text{MSY}}$  was logit transformed to constrain values between 0 and 1.

MSY and  $U_{\text{MSY}}$  had to be estimated numerically in Model 2. For each  $\theta$ , a Newton-Raphson algorithm was used to search over the derivative of the yield function (equation 2A.1) with respect to  $U$  to find the value of  $U$  that maximised yield. Note that the most current parameters for these hake species may not have been used and the selectivity schedule is likely incorrect. The choice of priors for CR and  $M$  will also influence the results, which should therefore be read as illustrative only.

## Results

The weak prior placed on CR had the effect of constraining the posterior values of  $U_{\text{MSY}}$  and MSY to values that were not associated with impossible recruitment parameters (see life history section). The prior placed on  $M$  constrained this parameter within plausible biological bounds (i.e., close to  $1.5\kappa$ ; Beverton and Holt 1959) and therefore also prevented  $U_{\text{MSY}}$  from becoming large. The choice of  $a_h$  relative to  $a_{\text{mat}}$  also affected the results. For fish populations where most individuals vulnerable to the fishing gear have already had the opportunity to spawn,  $U_{\text{MSY}}$  must approach unity. Alternatively, harvesting a population at an age before most individuals have spawned results in lower sustainable harvest rates. This is implicit in Figure 2.1a.

Figure 2.3 shows density plots of the posterior distributions of the leading parameters in each model. The two models give very similar results for the biological parameters and almost identical results for the management parameters. Note that  $R_0$  and CR were obtained analytically in Model 1 and that MSY and  $U_{\text{MSY}}$  were estimated numerically in Model 2. There was no evidence that the parameter estimates did not converge (Figure 2.4). Figure 2.3 shows that estimation of key management parameters was robust to the choice of leading parameters.

## Discussion

Schnute and Kronlund (1996) derived  $\alpha$  from  $U_{\text{MSY}}$  for semelparous species. They demonstrated the advantages of their re-parameterised recruitment function in terms of its amenability to Bayesian fitting procedures and, because a parameter with policy relevance could be directly estimated from data, improved communicability of results. The idea was extended to a generalised age-structured model for iteroparous species by Schnute and Richards (1998), who assumed knife-edge maturity and recruitment. The approach presented here extends these previous works by allowing the inclusion of age-specific maturity and recruitment via the Botsford (1981) “incidence” functions, which incorporate age-schedules of fecundity, mortality and vulnerability. The approach was demonstrated using logistic, age-based selectivity and maturity schedules, but the approach is flexible to any formulation of these. For example, dome-shaped or log-normal selectivity curves may be more appropriate for species where large or old individuals are able to escape fishing due to behavioural, spatial or market-based effects. Certain simplifying assumptions were made, notably that natural mortality,  $M = 1.5\kappa$ . This relationship, suggested by Beverton and Holt (1959) to be an invariant property of fish populations, is widely applied in fisheries models. However, the model is flexible to this assumption, as well as to the assumption that  $M$  is constant with age.

The model was used to illustrate some important relationships between density dependence, life history traits and  $U_{\text{MSY}}$ . It is stressed that the relationship between CR and  $U_{\text{MSY}}$  shown in Figure 2.1 is not dynamic, but rather represents the degree of improvement in juvenile survival that would be required for each hypothesised value of  $U_{\text{MSY}}$  to be true. For a species with a given

growth, survival, maturity and selectivity schedule, there will be a mean curve describing the relationship between  $U_{\text{MSY}}$  and CR representing the set of values of CR and  $U_{\text{MSY}}$  that can be considered possible for the species. This curve can be calculated from life history and selectivity parameters alone, prior to any time series fitting. Figure 1 implies that, for some species, there will be a finite range of possible values of  $U_{\text{MSY}}$ , with its upper bound at the asymptotic value of  $U_{\text{MSY}}$ . This is because  $U_{\text{MSY}}$  maximises yield in terms of weight and is therefore determined by growth, survival and selectivity (Beverton and Holt 1957). The upper bound of  $U_{\text{MSY}}$  represents the harvest rate beyond which long term yield can no longer be maximised for a given growth and selectivity schedule, no matter how strong recruitment compensation is. If there is no other prior information about the productivity of a species and Beverton and Holt type recruitment can be assumed, there is therefore an upper boundary of  $U_{\text{MSY}}$  that can be estimated from life history and selectivity data alone. For species with very steep  $U_{\text{MSY}}$ -CR curves (curves with an upper boundary very far to the left of the  $U_{\text{MSY}}$ -axis), uncertainty in  $U_{\text{MSY}}$  can be reduced considerably, even if the actual value of  $U_{\text{MSY}}$  cannot be estimated due to lack of historical data. If reasonable estimates of CR are available for similar species or from meta-analysis, it may also be possible to construct a reasonable prior for  $U_{\text{MSY}}$  for data-limited species.

The effects of selectivity and life history parameters on the relationship between CR and  $U_{\text{MSY}}$  are not surprising. Increasing (long-term) age at 50% first harvest,  $a_h$ , causes the  $U_{\text{MSY}}$ -CR curve to become less steep and shift to the right (Figure 2.1a). Assuming that the value of CR is a fixed property of a population independent of  $a_h$ , this implies that a greater maximum sustainable harvest rate could be achieved by more selective fishing gear allowing younger fish to escape. This idea is a well-known result of per-recruit type analyses (Beverton and Holt 1957). The relationship between  $\kappa$  and  $U_{\text{MSY}}$  was also very strong. In the equilibrium formulation,  $\kappa$  was used in the model twice: 1) as growth rate affecting the rate at which fish reach maximum weight; and 2) as a proxy for natural mortality,  $M$ , affecting the survivorship schedule (equation 2.3). Although these two effects were confounded, they had the same qualitative effect on the  $U_{\text{MSY}}$ -CR curve, i.e., increasing  $\kappa$  caused the curve to become less steep. For a given value of  $U_{\text{MSY}}$  the amount of recruitment compensation required to support that  $U_{\text{MSY}}$  was less for faster-growing species because: 1) asymptotic maximum weight was reached earlier; and 2) the population had faster turnover. Increasing age at maturity,  $a_{\text{mat}}$ , had a weak influence on the relationship between  $\kappa$  and  $U_{\text{MSY}}$ , although it did cause a slight increase in steepness and a shift

to the left. All other things equal, species with later maturity have a smaller lifetime reproductive capacity and a greater chance of being harvested before they have reproduced. Increasing maximum age,  $a_{max}$ , similarly caused the curve to shift to the left. Higher CR required to support a given  $U_{MSY}$  for longer lived species could be a result of the relatively smaller contribution of older age classes to the total yield due to the decaying survivorship function.

It should be noted that life history parameters tend to covary and can rarely be considered in isolation, i.e., longer-lived species tend to mature later, grow slower, have lower natural mortality. The effects of single parameters on the steepness of the  $U_{MSY}$ -CR curve were singled out, not because these curves necessarily have applicability in themselves, but because they allow the complexity of the interaction among life history traits, selectivity, density dependence and sustainable harvest rate to be seen. Maximum sustainable harvest rate is not a simple function of selectivity, density dependence or individual life history parameters but a complex result of them all. Simplistic assumptions about the effects of one of these factors on  $U_{MSY}$  should not be made without consideration of the other influential factors.

Life history information is easier and cheaper to obtain than recruitment and abundance data, and is routinely collected. Growing conservation concerns and current trends towards more ecosystem-based approaches of managing fisheries (e.g., FAO 2003; Pikitch *et al.* 2004) require consideration of the impacts of fisheries on many more species than previously and there is now a very large body of literature studying the link between life history traits and productivity for data-limited fish. For example, McAllister *et al.* (2001) demonstrated three approaches that could be used to estimate  $r$  for elasmobranchs using only life history information. Beddington and Kirkwood (2005) presented a method for estimating  $F_{MSY}$  based on Beverton and Holt (1959) invariants and parameters describing growth, length at first capture and the steepness parameter,  $h$ . Goodwin *et al.* (2006) showed correlations between a composite life history parameter (unfished spawners per recruit,  $SPR_0$ ),  $\alpha$  and the compensation ratio, CR, for 54 Atlantic teleosts for which stock-recruitment data were available. They found a strong negative correlation between  $SPR_0$  and  $\alpha$ , and a positive correlation between  $SPR_0$  and CR and discussed evolutionary reasons for these observations. Jennings *et al.* (1999) and Denney *et al.* (2002) also searched for correlations between life history and productivity. The general approach of these papers was to analyze stocks for which informative data exists about productivity (e.g.,

population response to fishing pressure) and draw conclusions that could be used in development of management strategies for data-limited species. It is suggested that the model could contribute to such approaches as it provides a link between life history, density-dependence and  $U_{MSY}$  simultaneously.

A simple Bayesian estimation routine was used to illustrate the parameter estimation process. A model with leading management parameters ( $MSY$  and  $U_{MSY}$ ) was compared with a model structurally identical except for its leading parameters ( $R_0$  and  $CR$ ). The same posterior probability densities for management parameters were obtained in both cases. However, it is argued that the first model is advantageous for two reasons: 1) it is more efficient (there is no need to numerically estimate  $MSY$  and  $U_{MSY}$ ); and 2) it enables improved communication of scientific results. Determination of appropriate informative priors is one of the most difficult aspects of stock assessment (see Punt and Hilborn 1997) and the preliminary phases of stock assessment often involve intensive modelling and testing sessions to determine plausible ranges of leading biological parameters. These ranges are often based on the plausibility of the model's predicted  $MSY$  (or  $U_{MSY}$ ). Hoenig *et al.* (1994) have suggested methods for constructing informative priors on  $MSY$  based on historical catch and effort data. Simple analytical relationships have also been suggested for obtaining rough estimates of  $MSY$  and  $U_{MSY}$  (e.g., Gulland 1971; Patterson 1992), which could be used in construction of priors. Models such as the one presented here and that of Schnute and Richards (1998) enable this information to be used in direct estimation of  $U_{MSY}$ , a parameter of primary management interest. It is suggested that dialogue between scientists and managers will be improved if the parameters at the forefront of the analysis are familiar to all parties. It is also suggested this may work in both directions, as managers with a long history of involvement in a fishery will be better able to contribute to the stock assessment process if the focus is on parameters with which they have direct experience.

In summary, this chapter has presented a model with several advantages: 1) it enables direct estimation of parameters of principle management interest; 2) it is flexible to a very wide range of assumptions about growth, survival, maturity and selectivity, including the form of these relationships; and 3) it provides a means of analysing the interaction among important selectivity and life history parameters, density dependence and maximum sustainable harvest rate. It is

amenable to Monte Carlo-type approaches to account for uncertainty in input parameters as well as to Bayesian or likelihood approaches for estimating leading parameters.

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## Tables

**Table 2.1.** Life-history and selectivity parameters used in the model. Parameters are described in the text.

Parameter	Hypothetical fish	Namibian hake
$L_{\infty}$	60 cm	111 cm <sup>a</sup>
$\kappa$	0.12 y <sup>-1</sup>	0.14 y <sup>-1</sup> <sup>a</sup>
$a_0$	-0.5	0
$lwa$	0.0001	0.00001 <sup>b</sup>
$lwb$	3	3 <sup>b</sup>
$a_{max}$	15 y	25 y <sup>b</sup>
$a_{mat}$	2 y	4 y <sup>c</sup>
$ah$	3 y	3 y <sup>d</sup>

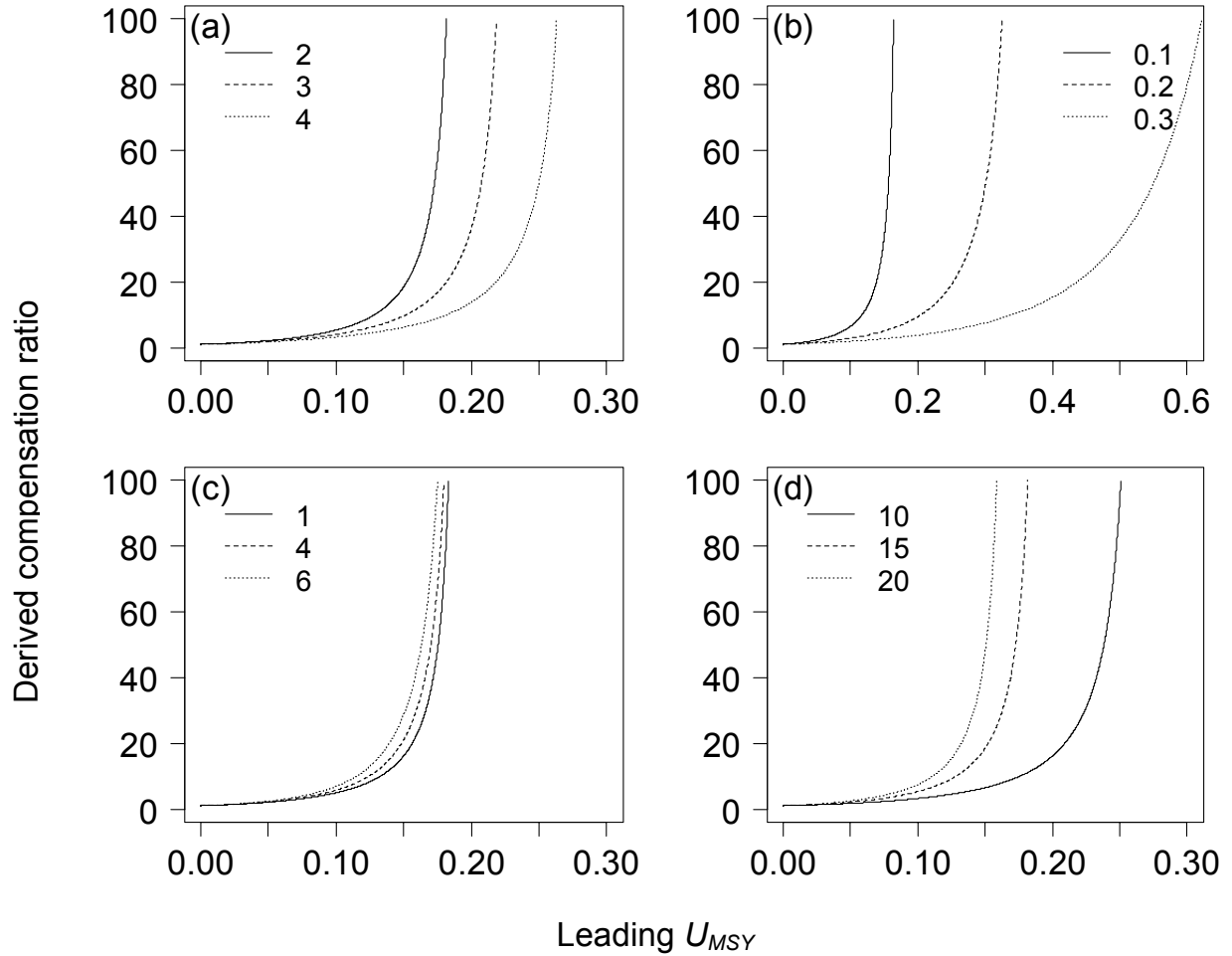
a. Jones 1974 (cited in FishBase, [www.fishbase.org](http://www.fishbase.org)).

b. These parameters produced the approximate mean maximum weight cited in FishBase ([www.fishbase.org](http://www.fishbase.org)).

c. Hilborn and Mangel 1997.

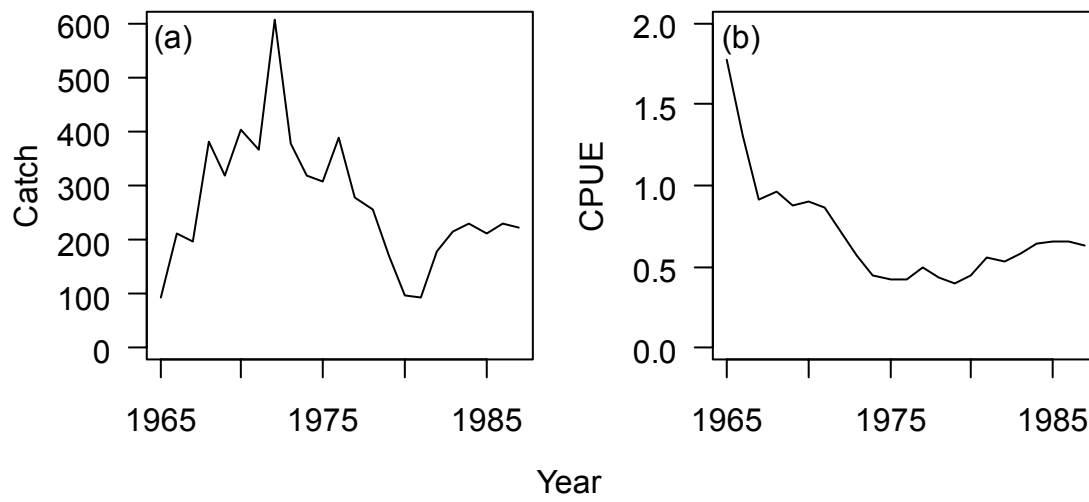
d. Arbitrarily assigned.

## Figures

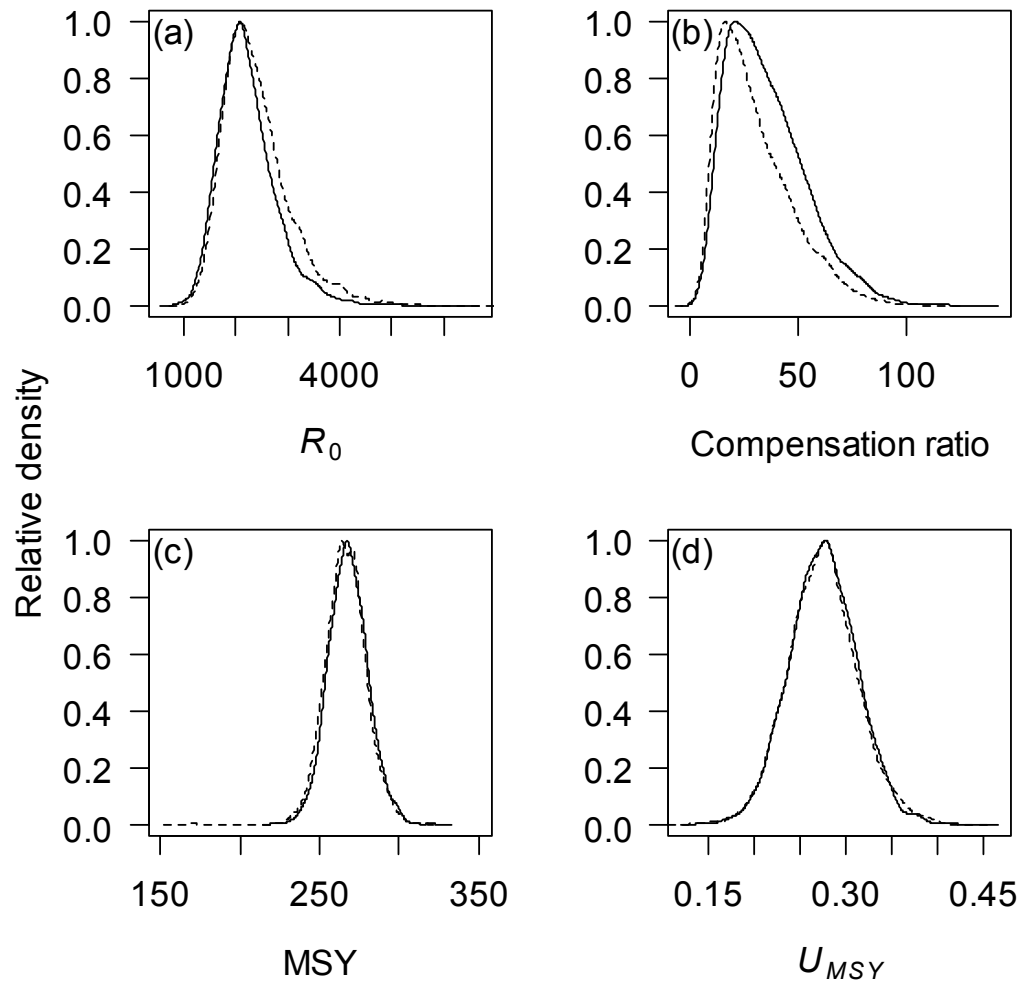


**Figure 2.1.** Effect of different parameters on the relationship between leading productivity parameter  $U_{MSY}$  and the derived compensation ratio, CR for a hypothetical species. Graphs show (a) age-at-50%-first-harvest,  $a_h$  (years); (b) von Bertalanffy growth rate,  $\kappa$  (year<sup>-1</sup>); (c) age-at-50%-maturity,  $a_{mat}$  (years); and (d) maximum age,  $a_{max}$  (years). Parameter values are provided in Table 1. Note truncation of the y-axis at CR = 100 and different scales on the x-axes.

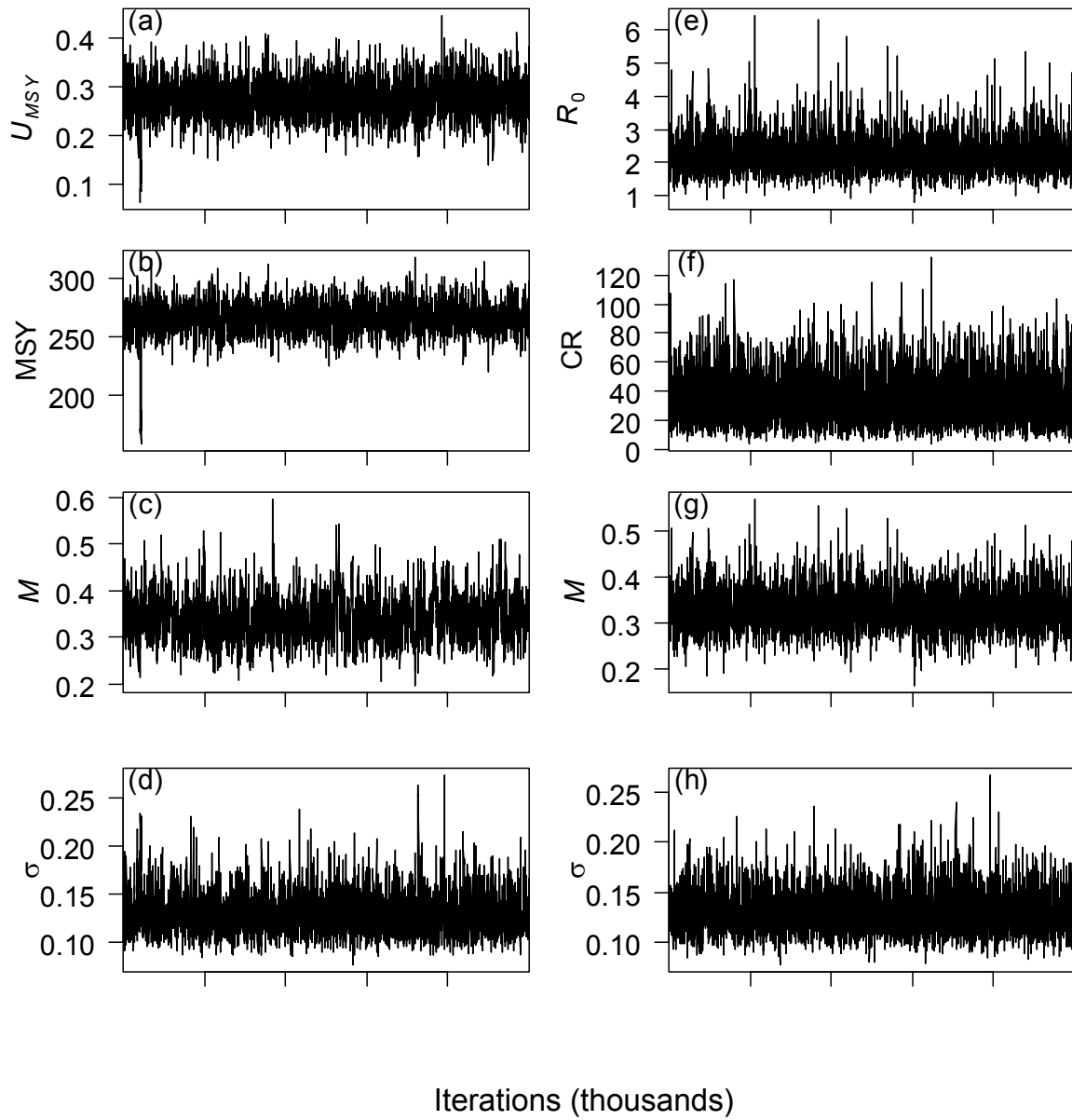




**Figure 2.2.** (a) Catch (thousands of tons) and (b) CPUE (tons per standardised trawler hour) for Namibian hake, used to fit the models. *Data source:* Hilborn and Mangel (1997).



**Figure 2.3.** Density plots showing relative posterior probability density distributions of  $R_0$ , CR, MSY and  $U_{MSY}$  for Model 1 (dashed line) and Model 2 (solid line). Plots obtained from MCMC sample of length 100,000 (burn-in: 10,000 cycles).



**Figure 2.4.** Trace plots of iterations vs sampled values for each estimated parameter indicating convergence of the estimates. Results are shown for Model 1: (a)  $U_{MSY}$ , (b)  $MSY$ , (c)  $M$  and (d)  $\sigma$ ; and Model 2: (e)  $R_0$  (thousands), (f)  $CR$ , g)  $M$  and h)  $\sigma$ .

## Chapter 3. Extension of a meta-analysis of 54 fish stocks for evaluating effects of life history, selectivity and density dependence on optimal harvest rate

$U_{\text{MSY}}$

### Introduction

With the widespread adoption of ecosystem-based fisheries management (EBFM) around the world (FAO 2003; Pikitch *et al.* 2004; Pitcher *et al.* in press), the discussion of sustainable harvesting has shifted to include a much broader range of species than previously. With this has come recognition of the need for new approaches and frameworks for risk assessment of data-limited species (e.g., Smith *et al.* 2007). A basic need for risk assessment for a fish population is an estimate of its productivity. Productivity is a general term that refers to mortality and growth of individuals and recruitment. Recruitment productivity is usually represented by a measure of the degree of density dependence in recruitment, i.e., improvement in juvenile survival rate as adult stock size is reduced (reviewed by Rose *et al.* 2001; Myers 2002). Commonly-used parameters representing density dependence in recruitment include  $\alpha$ , the maximum juvenile survival rate of the Ricker (1954) and Beverton-Holt (1957) stock-recruitment functions; CR, the recruitment compensation ratio (Goodyear 1977; see Figure 1.2 and Chapter 2); and steepness,  $h$  (Mace and Doonan 1988).

A key role of fisheries scientists is identification of thresholds of fishing mortality that should be avoided to prevent overfishing (reviewed by Caddy and Mahon 1995). Stocks are said to be subject to growth-overfishing if they are harvested while individuals are still in the rapid growth phase, implying that greater yields could be achieved if fish were allowed to grow larger before being harvested. Recruitment overfishing is a more serious, but less well-defined, biological issue that occurs when a stock's ability to reproduce itself is compromised by fishing mortality rates that are too high. The fishing mortality rate that would produce maximum sustainable yield,  $F_{\text{MSY}}$ , is, by definition, a valid limit reference point for growth-overfishing. Generally, the recruitment overfishing threshold is understood to be around double the growth overfishing threshold (Goodyear 1993; Mace 1994; 2001; Restrepo *et al.* 1998; but see Cook *et al.* 1997, Punt 2000 and NAFO 2003 for studies showing that fishing mortality thresholds for growth and

recruitment overfishing may be closer together for less productive species). A well-known recommendation is that fish stocks should be managed to avoid growth overfishing, as this will also prevent recruitment overfishing (Gulland 1971). A precautionary means of achieving this is to control selectivity (i.e., the age at which fish become vulnerable to fishing gear) and ensure that fish are given at least one chance to spawn before being harvested (Myers and Mertz 1998; Froese 2004; Froese *et al.* 2008).

There is now a large body of literature studying the link between life history and  $F_{MSY}$  in order to better estimate overfishing thresholds for data-limited fish stocks. Gulland (1971) expressed maximum sustainable yield as a function of the natural mortality rate,  $M$ , and unfished biomass,  $B_0$ , where yield was equal to  $0.5MB_0$ . Kirkwood *et al.* (1994) suggested that, when density dependence in recruitment was accounted for, the proportion of unfished biomass was likely to be of the order of  $0.1-0.3M$ . Beddington and Kirkwood (2005) presented a new method for estimating  $F_{MSY}$  based on Beverton and Holt (1959) invariants and parameters describing growth, length at first capture and an estimate of steepness. Recently, meta-analysis has become popular as an approach for gaining insight about productivity from data-rich stocks, in order to derive general rules for estimation of productivity that can be applied to data-poor stocks. Meta-analysis has been used to estimate recruitment productivity parameters directly (e.g., Myers *et al.* 1999; Dorn 2002; Michielsens and McAllister 2004; Sadovy *et al.* 2007) and also to identify life history traits that correlate well with productivity. For example, there have been a number of recent papers that have correlated life history parameters with empirically observed changes in abundance after fishing (e.g., Jennings *et al.* 1998; 1999; Dulvy *et al.* 2004; 2005; Cheung *et al.* 2005; 2007). Patterson (1992) reviewed stock assessments for 28 pelagic fisheries and concluded that pelagic stocks have tended to collapse when fishing mortality has exceeded 60% of the natural mortality rate,  $M$ . This suggests that the commonly-used rule of thumb of  $F = M$  (Schaefer 1954; Gulland 1971) may be too incautious to avoid recruitment overfishing of pelagic stocks. Others have found correlations between life history and productivity parameters (including maximum population growth rate: Cortés 1998; Smith *et al.* 1998; Denney *et al.* 2002; steepness: Rose *et al.* 2001; and CR, the recruitment compensation ratio: Goodwin *et al.* 2006). Goodwin *et al.* (2006) used standardised unfished spawners per recruit ( $SPR_0$ ; Gabriel *et al.* 1989) as a composite life history parameter to test for relationships between life history and recruitment parameters. They found a strong negative correlation between  $\ln SPR_0$  and  $\ln \alpha$ , and a

weaker positive correlation between  $\ln\text{SPR}_0$  and  $\ln\text{CR}$ . They suggested that stocks with low  $\text{SPR}_0$  (e.g., fast-turnover stocks like herring and anchovy) could be fished down, even at low harvest rates, but were resilient to extirpation because of high reproductive rates at low stock size. Alternatively, longer-lived, slower-growing and later-maturing stocks with high  $\text{SPR}_0$  (e.g., cod, halibut) could likely sustain higher harvest rates without being fished down due to strong recruitment compensation, but would be more vulnerable to extirpation if severely overfished.

Chapter 2 (published as Forrest *et al.* 2008) quantified the relationship between measures of recruitment compensation ( $\alpha$  and CR) and optimal harvest rate  $U_{\text{MSY}}$  in an age-structured model, assuming Beverton-Holt recruitment. It showed that the relationship is strongly affected by certain life-history traits (especially growth rate and maximum age) and, especially, by the age at which species are first captured by the fishing gear (Chapter 2; Figure 2.1). Goodwin *et al.* (2006) suggested that conclusions about responses of fish stocks to different levels of fishing mortality could be made with an understanding of the compensation ratio, as predicted by  $\text{SPR}_0$ . If this were the case, a logical extension of their work would be to show a predictive relationship between  $\text{SPR}_0$  and  $U_{\text{MSY}}$ , which, if it existed, would be very useful for application to data-limited stocks. The analytical relationships between  $\alpha$ , CR and  $U_{\text{MSY}}$  developed in Chapter 2 presents a means of testing whether such a relationship exists, for stocks where life history and recruitment parameters are available.

The parameters provided by Goodwin *et al.* (2006) provide a sufficiently complete dataset for testing this relationship. Therefore, using the model presented in Chapter 2, the work of Goodwin *et al.* (2006) is extended through calculation of  $U_{\text{MSY}}$  for their 54 stocks, under assumptions of both Ricker (1954) and Beverton-Holt (Beverton and Holt 1957) recruitment, given the estimates of CR and life history and selectivity parameters they provided. Correlations between life history parameters and  $U_{\text{MSY}}$  are then explored. The effect of age-at-recruitment to the fishery, which is under management control, is also evaluated. The work presented in Chapter 2 is extended in a number of ways. Firstly, because Ricker recruitment was assumed by Goodwin *et al.* (2006), the relationship between  $\alpha$  and  $U_{\text{MSY}}$  for the Ricker model is derived. Secondly, relationships between life-history and selectivity parameters, density dependence in recruitment (measured by CR) and  $U_{\text{MSY}}$  are examined more thoroughly. Thirdly, a graphic

approach is proposed for identification of stocks for which  $U_{MSY}$  could be significantly increased through changes to the selectivity schedule and stocks for which it could not.

Note that this study makes use of the parameter-estimates of Goodwin *et al.* (2006) in order to explore inter-relationships between life history, selectivity, density dependence and  $U_{MSY}$  and, for tractability, makes a number of simplifying assumptions. The results presented here do not account for the many complexities of management of Atlantic fisheries and should not be considered a stock assessment for these populations.

## Methods

### Deriving $U_{MSY}$ for 54 Atlantic stocks

Chapter 2 showed how the maximum juvenile survival rate,  $\alpha$ , could be expressed as a function of  $U_{MSY}$  when the Beverton-Holt stock-recruitment function was assumed. Goodwin *et al.* (2006) fitted Ricker curves to their stock-recruitment data and reported associated values of  $\alpha$  and CR. Therefore, for comparative purposes, a Ricker version of the relationship between  $\alpha$  and  $U_{MSY}$  was derived. Note that  $\alpha$  and CR are equivalent in both Ricker and Beverton-Holt stock recruitment functions (Myers *et al.* 1999), and the estimates of CR presented by Goodwin *et al.* (2006) can therefore be used to derive  $U_{MSY}$  using both models.

Derivation of the relationship between  $\alpha$  and  $U_{MSY}$  for the Ricker model was done following the steps in Appendix A to Chapter 2, replacing the Beverton and Holt recruitment function with the equilibrium version of the Ricker function, i.e.,

$$(3.1) \quad R = \frac{\ln(\varphi_E \alpha)}{\beta \varphi_E}$$

where R is equilibrium recruitment and  $\varphi_E$  is equilibrium eggs per recruit (Chapter 2, equation 2.2). Note that equation 3.1 was obtained by substituting  $E = R\varphi_E$  into the Ricker equation:

$R = \alpha E e^{-bE}$  (Ricker 1954), where  $E$  is eggs, here assumed directly proportional to spawning stock biomass.

As in Chapter 2, equilibrium yield is assumed to be given by

$$(3.2) \quad Y = UR\varphi_{VB}$$

where  $U$  is long term annual harvest rate and  $\varphi_{VB}$  is equilibrium vulnerable biomass per recruit. Substituting Equation 3.1 into Equation 3.2, taking the derivative and setting it to zero (thereby identifying the local maximum, or MSY), and solving for  $\ln(\alpha)$  gives:

$$(3.3) \quad \ln(\alpha) = \frac{-U_{MSY}\varphi_{VBMSY} \frac{\partial \varphi_{EMSY}}{\partial U_{MSY}}}{\varphi_{EMSY}\varphi_{VBMSY} + \varphi_{EMSY} U_{MSY} \frac{\partial \varphi_{VBMSY}}{\partial U_{MSY}} - \varphi_{VBMSY} U_{MSY} \frac{\partial \varphi_{EMSY}}{\partial U_{MSY}}} - \ln(\varphi_{EMSY})$$

where  $\varphi_E$  and  $\varphi_{VB}$  are evaluated at  $U_{MSY}$ . See Appendix A to Chapter 2 for solutions to  $\frac{\partial \varphi_E}{\partial U_{MSY}}$

and  $\frac{\partial \varphi_{VB}}{\partial U_{MSY}}$ .  $\alpha$  is then obtained by taking the exponent of equation 3.3.  $\alpha$  is a unit-dependent

parameter and, therefore, not directly comparable among stocks, as different units may have been used to measure spawning stock biomass or eggs. Therefore,  $\alpha$  was standardised across stocks by dividing by the unfished juvenile survival rate  $\varphi_E^{-1}$  to give the recruitment compensation ratio CR (Goodyear 1977; Myers *et al.* 1999; see Chapter 2), i.e.,  $CR = \alpha\varphi_{E0}$  (see Figure 1.2).

It is important to realise that the relationship between  $U_{MSY}$  and CR is determined by a population's individual life history and selectivity schedule and, given this relationship, there is a unique value of CR implied by each hypothesised value  $U_{MSY}$  for a population. However, while CR can be calculated analytically, using equation 3.3, given a hypothesis for  $U_{MSY}$ , there is no analytical solution for the reverse relationship (i.e., equation 3.3 cannot be re-arranged and solved for  $U_{MSY}$  because  $\varphi_{EMSY}$  and  $\varphi_{VBMSY}$  are themselves recursive functions of  $U_{MSY}$ ; see



equation 2.2 and 2.3). However, given the values of CR published by Goodwin *et al.* (2006), it was possible to obtain the corresponding estimate of  $U_{MSY}$  for each stock, by calculating CR over a discrete, finely-resolved sequence of hypotheses for  $U_{MSY}$  until the observed value of CR was reached. The  $U_{MSY}$  hypothesis that produced the published value of CR was then the appropriate value of  $U_{MSY}$  for that particular stock. This is illustrated in Figure 3.1. This procedure was done for the 54 stocks considered by Goodwin *et al.* (2006). For comparison, the analysis was repeated using the Beverton-Holt form of equation 3.3 (Chapter 2, equation 2A.6) and the Beverton-Holt stock-recruitment function (equation 2.1). In both cases, a plus group was used to account for unobserved older age classes and the correction to the derivative of survivorship with respect to  $U_{MSY}$ , shown in equation 2A.10, was used. Equations 2A.6 and 3.3 show that the relationship between  $\alpha$  and  $U_{MSY}$  is insensitive to stock size and the model was therefore initialised at a baseline of  $B_0 = 1$ .

Life-history parameters and ages-at-recruitment were published by Goodwin *et al.* (2006). Parameters were missing for some species and were obtained from FishBase (Froese and Pauly 2008; see Table 3.1 for values). For species where  $W_\infty$  was not provided,  $L_\infty$  was first obtained from FishBase then converted to  $W_\infty$  using length-weight parameters obtained from FishBase (Table 3.1). Goodwin *et al.* (2006) used direct estimates of the fecundity schedule. In the absence of this information, fecundity,  $f_a$ , was here assumed to be directly proportional to weight at age,  $w_a$ , through the relationship  $f_a = w_a Mat_a$ , where  $Mat_a$  is maturity-at-age, assumed to be described by a logistic maturity curve (see Chapter 2, Appendix B), with age-at-50%-maturity,  $a_{mat}$ , set to the value published by Goodwin *et al.* (2006) and the steepness parameter,  $\sigma$ , assumed to be  $0.1a_{mat}$ , which assumes almost knife-edged maturity at  $a_{mat}$ . The natural mortality rate,  $M$ , was assumed constant across age classes and the natural survival rate,  $s$ , was assumed to equal  $e^{-M}$  for all age classes (Beverton and Holt 1959). Note that all summations (i.e., the survivorship function, equation 2.3, and all parameters derived from it) were initiated at age-at-recruitment to the fishery,  $a_h$ . This is because Goodwin *et al.* (2006) defined a recruit as a fish entering the fishery rather than the population.

## Uncertainty in parameter values

Because of uncertainty in input parameters, 100 Monte Carlo simulations were used to obtain confidence intervals for the estimates of  $U_{MSY}$ . Life history parameters that were treated as random variables were the von Bertalanffy growth rate,  $\kappa$ ; the natural mortality rate,  $M$ ; maximum weight,  $W_\infty$ ; and  $a_{mat}$ .  $\kappa$  and  $M$  were assumed to be lognormally distributed with mean set to the natural logarithm of the published value and coefficient of variation (CV) of 20% of this mean. This was done to prevent drawing negative values of these parameters, as the mean value was already close to zero.  $W_\infty$  and  $a_{mat}$  were assumed to be normally distributed with mean set to the published value and CV of 20% of this mean. The 20% CV was selected to enable uncertainty to be accounted for without departing too far from parameters characteristic of each stock.

### *Correlations between life history and selectivity parameters and $U_{MSY}$*

The input parameters and calculated values of  $U_{MSY}$  provide a dataset that enabled testing for correlations between life history and selectivity parameters and  $U_{MSY}$ . Goodwin *et al.* (2006) showed that  $\ln SPR_0$  is a reasonable predictor of  $\ln CR$ , suggesting that  $\ln SPR_0$  might be a reasonable indicator of  $U_{MSY}$ . The correlation between  $\ln SPR_0$  and  $U_{MSY}$  was also, therefore, tested. For all parameters, the Pearson's correlation coefficient,  $r$ , between  $U_{MSY}$  and the natural logarithm of the input parameters was calculated and tested for significance. Parameters were log transformed to reduce variance.

## Effect of selectivity on $U_{MSY}$

As in Goodwin *et al.* (2006), selectivity was assumed to be knife-edged (i.e., all individuals of an age-cohort are fully vulnerable to the fishing gear when they reach  $a_h$ ). Age-at-recruitment is an important determinant of  $U_{MSY}$  and has a strong effect on the relationship between CR and  $U_{MSY}$  (Chapter 2). This means that for a given level of recruitment compensation in a stock, increasing the age at which fish are first harvested increases the proportion of the remaining vulnerable stock that can be sustainably harvested. Many of the 54 stocks had reported  $a_h$  of 0 or 1, suggesting that  $U_{MSY}$  for these stocks could be limited by their current selectivity schedule. Therefore the analysis was repeated for a range of values of  $a_h$  (0-6).

## Results

### Derived estimates of $U_{MSY}$

Mean derived estimates of  $U_{MSY}$  (+ standard error) from the 100 Monte Carlo runs for each stock, under both Ricker and Beverton-Holt stock-recruitment assumptions, are shown in Figure 3.2. Overall, the Ricker model predicted higher  $U_{MSY}$  than the Beverton-Holt model and, overall, the range of values of  $U_{MSY}$  predicted by the Beverton-Holt model was much smaller than that predicted by the Ricker model. Mean predicted values of  $U_{MSY}$  from the Ricker model ranged from 0.07 (Atlantic horse mackerel 1) to 0.68 (Atlantic cod 6), while mean  $U_{MSY}$  ranged from 0.06 (Atlantic horse mackerel 1) to 0.46 (Whiting 3) under the Beverton-Holt stock-recruitment relationship. Linear regression of the predicted Ricker  $U_{MSY}$  against the Beverton-Holt  $U_{MSY}$  showed Ricker estimates to be, on average, 1.13 times higher than Beverton-Holt estimates ( $U_{MSY \text{ Ricker}} = 1.13U_{MSY \text{ BH}} + 0.11$ ).

Under Ricker recruitment, the three stocks with extremely high CR (Atlantic cod 6 and 7 and European anchovy; Table 3.1) also had the highest mean  $U_{MSY}$  and the stock with the lowest CR (Atlantic horse mackerel 1) had the lowest mean  $U_{MSY}$ . The correlation between  $\ln CR$  and  $U_{MSY}$  was positive and highly significant (Figure 3.3a;  $r = 0.72$ ,  $P < 0.001$ , 52 *df*). Under Beverton-Holt recruitment, however, while the stocks with the lowest predicted  $U_{MSY}$  also had the lowest CR, the trend did not continue to stocks with the highest CR and the correlation between  $\ln CR$  and  $U_{MSY}$  was not significant (Figure 3.3b;  $r = 0.02$ , n.s., 52 *df*). The strong significant correlation between  $\ln CR$  and  $U_{MSY}$  in the Ricker model was mainly due to the three stocks with extreme estimates of CR (Figure 3.3a). Removal of these stocks resulted in a reduced correlation coefficient, although the relationship was still significant ( $r = 0.46$ ,  $P < 0.01$ , 49 *df*). The relationship between CR and  $U_{MSY}$  under the two different stock-recruitment functions is explored more fully in a later section.

### *Correlations between $U_{MSY}$ and life history parameters*

Correlations between the mean estimate of  $U_{MSY}$  from the 100 Monte Carlo simulations and mean logged values of  $M$ ,  $a_{mat}$ ,  $\kappa$ ,  $W_{\infty}$ ,  $a_{max}$  and  $SPR_0$  are shown in Figures 3.4 and 3.5, with

correlation coefficients shown in Table 3.2. Under Ricker recruitment, none of the relationships were significant except for  $\ln M$ , which was significantly positively correlated with  $U_{\text{MSY}}$  ( $P < 0.05$ ,  $df = 52$ ). Under Beverton-Holt recruitment, the correlation between  $M$  and  $U_{\text{MSY}}$  was highly significant ( $P < 0.001$ ,  $df = 52$ ). Correlations between  $\ln \kappa$  ( $P < 0.001$ ,  $df = 52$ ) and  $\ln a_{\text{max}}$  ( $P < 0.001$ ,  $df = 52$ ) were also highly significant. The correlation between  $\ln \text{SPR}_0$  and  $U_{\text{MSY}}$  was non-significant in both models (Figure 3.4f and 3.5f).

### **Relationship between density dependence, $\text{SPR}_0$ and $U_{\text{MSY}}$**

Because some of the life history parameters used in this study were different from those used by Goodwin *et al.* (2006), the relationship between their published values of  $\text{SPR}_0$  and the ones obtained in the present study was checked (Figure 3.6a). The correlation between the value of  $\text{SPR}_0$  obtained in the present study and the published value of CR was also checked for consistency with the results of Goodwin *et al.* (2006). Estimates of  $\text{SPR}_0$  from the present and previous studies were very strongly correlated ( $r = 0.94$ ,  $P < 0.001$ ,  $df = 52$ ). The slope of the linear regression between the  $\text{SPR}_0$  estimates from the two studies was 1.16, implying that the current study had systematically overestimated  $\text{SPR}_0$  compared to the previous study. This may have been due to the different parameters used for some species or assumptions about the length weight relationship or the relationship between fecundity and weight. It can be noted, however, that a systematic overestimation of  $\text{SPR}_0$  would not affect subsequent correlations between  $\text{SPR}_0$ , CR and  $U_{\text{MSY}}$ . The correlation between the present value of  $\ln \text{SPR}_0$  and published  $\ln \text{CR}$  (Figure 3.6b) was also significant ( $r = 0.44$ ;  $P < 0.01$ ,  $df = 52$ ) and very similar to that reported by the other authors ( $r = 0.48$ ;  $P < 0.001$ ; 52  $df$ ; note they reported the  $r^2$  value). Therefore the non-significant correlation between  $\ln \text{SPR}_0$  and  $U_{\text{MSY}}$  could not simply be attributed to different values of  $\text{SPR}_0$  used in the present study.

The poor correlation between  $\ln \text{SPR}_0$  and  $U_{\text{MSY}}$  can be partly explained by considering the effects of life history parameters on the relationship between CR and  $U_{\text{MSY}}$ . The value of  $\text{SPR}_0$  for a given stock is determined by the combined effect of several different life history parameters (see equations 2.2 and 2.3, where  $\phi_{E0}$  is the equivalent of  $\text{SPR}_0$ ). This is illustrated in Figure 3.7 for a hypothetical stock with parameters given in Table 3.3. In each case,  $\text{SPR}_0$  was calculated with all other parameters held constant while the parameter under consideration was varied.

Figure 3.7 shows that, all other parameters equal,  $W_\infty$  and  $\kappa$  have a positive effect on  $SPR_0$ , while  $a_{mat}$  and  $M$  have a negative effect. Because of these directional effects on the value of  $SPR_0$ , and because there are trade-offs and correlations among certain parameters in nature (Jensen 1996; Winemiller 2005), the same value of  $SPR_0$  can be obtained under a number of different parameter-combinations. For example, a smaller species that matures early could have the same  $SPR_0$  as a larger, later-maturing species. Similarly, a small, fast-growing species could have the same  $SPR_0$  as a larger, slower-growing species, all other parameters equal. The composite parameter  $SPR_0$  has no power to distinguish the values of component parameters.

Now consider the influences of these parameters on the relationship between  $U_{MSY}$  and CR. Chapter 2 showed that the location of the curve describing the relationship between  $U_{MSY}$  and CR (the  $U_{MSY}$ -CR curve) is strongly affected by certain life history and selectivity parameters (Figure 2.1). For example, increasing  $\kappa$  causes the curve to become less steep and shift to the right, whilst changing  $W_\infty$  has no influence. Effectively, this means that increasing  $\kappa$  allows a greater range of values of  $U_{MSY}$  to be considered possible (where actual  $U_{MSY}$  is unknown because CR is unknown). This is illustrated in Figure 3.8a, which shows  $U_{MSY}$ -CR curves for five hypothetical stocks (Table 3.3) with very similar values of  $SPR_0$  ( $SPR_0 \sim 9$ ). Each stock has a different pair of values of  $\kappa$  and  $W_\infty$  with all other parameters held constant (Table 3.3). Stock 1 represents a small, fast-growing species, while Stock 5 represents a larger, slower-growing species.  $W_\infty$  has no effect on the location of the  $U_{MSY}$ -CR curve and, therefore, the differences among location of the curves in Figure 3.8a are due to the effect of decreasing  $\kappa$ . The stock with the highest value of  $\kappa$  (Stock 1) has the rightmost curve and, therefore, the largest range of possible hypotheses for  $U_{MSY}$  over the range of CR shown. Similarly, the stock with the lowest value of  $\kappa$  (Stock 5) has the smallest range of possible hypotheses for  $U_{MSY}$ . Figure 3.8a shows that assuming the same value of CR for these five stocks would result in five different values of  $U_{MSY}$  - despite them all having the same  $SPR_0$ . Similar effects would be seen by varying  $a_{max}$ ,  $M$  and  $a_h$  (Chapter 2; see next section for further discussion of the effect of  $a_h$ ). Given that there are several parameters contributing to the value of  $SPR_0$ , it is easy to see that many different combinations of parameters could result in a similar value of  $SPR_0$ . Therefore, since the contributing parameters have different effects on the relationship between  $U_{MSY}$  and CR, knowledge of  $SPR_0$  alone is insufficient to predict  $U_{MSY}$ .

Figure 3.8b shows the  $U_{MSY}$ -CR curves for the same five hypothetical stocks under Beverton-Holt recruitment (calculated using equation 2A.6). In this case, the same effect of  $\kappa$  on the location of the curves can be seen, but the shape of the curves is markedly different. Differences between the shapes of the Ricker and Beverton-Holt  $U_{MSY}$ -CR curves are due to the different properties of equations 2A.6 (Beverton-Holt) and 3.3 (Ricker). A key difference between them is that the Beverton-Holt formulation, under many life-history and selectivity-parameter combinations, predicts  $U_{MSY}$  to approach a vertical asymptote, beyond which  $\alpha$  is undefined (i.e., predicted to be negative). This asymptote occurs at the value of  $U_{MSY}$  for which the denominator of equation 2A.6 is equal to zero. It is therefore defined as the value of  $U_{MSY}$  for which  $U_{MSY} = -k_2^{-1}$  (where  $k_2 = \frac{\partial \phi_{VBMSY}}{\partial U_{MSY}} \phi_{VBMSY}^{-1}$ ; see Chapter 2, Appendix A). Note that  $U_{MSY} = -k_2^{-1}$  cannot be solved analytically for  $U_{MSY}$  because  $\phi_{VBMSY}$  is a recursive function of  $U_{MSY}$  (see equation 2.3). Truncation of the range of  $U_{MSY}$ , due to this effect, explains the smaller range of  $U_{MSY}$  estimates obtained for the 54 Atlantic stocks with the Beverton-Holt model compared with the Ricker model, which does not share this property (the limits of  $U_{MSY}$  prevent equation 3.3 from becoming undefined).

### Relative effects of selectivity

The above sections have treated age-at-recruitment to the fishery as a fixed parameter, when it is actually under management control, through measures such as mesh and hook size or spatial extent of the fishery. Table 3.4 shows predicted values of  $U_{MSY}$  for the 54 stocks for an ascending sequence of values of  $a_h$ . Four examples are shown in Figure 3.9, all of which show that predicted  $U_{MSY}$  increases with  $a_h$ . This is not a surprising result. It is noteworthy, however, that: i) the magnitude of difference between the highest and lowest predicted values of  $U_{MSY}$  differs among stocks; and ii) while the Ricker recruitment model suggested that there were some values of  $a_h$  for which it would be optimal to fish all of the vulnerable stock ( $U_{MSY} = 1$ ), this was rarely the case under the Beverton-Holt assumption.

The large increase in  $U_{MSY}$  with  $a_h$  shown by many stocks implies that  $U_{MSY}$  is strongly limited by selectivity for these stocks. For some stocks, however, where the increase in  $U_{MSY}$  with  $a_h$

was small,  $U_{MSY}$  was more strongly limited by life history or recruitment parameters than selectivity (i.e., increasing  $a_h$  did not significantly increase  $U_{MSY}$ ). Two of the example stocks in Figure 3.9 (Haddock 5 and Atlantic herring 1) showed a large increase in predicted  $U_{MSY}$  as  $a_h$  increased, under both types of recruitment. The other two stocks (Atlantic horse mackerel 1 and Greenland halibut), however, showed very small increases in predicted  $U_{MSY}$  with increasing  $a_h$ . The effect was more pronounced under Beverton-Holt recruitment (i.e, less increase in  $U_{MSY}$  with increasing  $a_h$ ).

Plotting the relationship between CR and  $U_{MSY}$  can be instructive for understanding these results. Figure 3.10 shows the  $U_{MSY}$ -CR curves for the four stocks shown in Figure 3.9 under the seven values of  $a_h$ . The value of CR reported for each stock in Goodwin *et al.* (2006) is shown on each graph as a horizontal dashed line. Understanding the relationship between selectivity, density dependence and  $U_{MSY}$  is fairly straightforward for the first two stocks. The relationship between CR and  $U_{MSY}$  is strongly affected by  $a_h$ , with increasing  $a_h$  shifting the  $U_{MSY}$ -CR curve to the right. Therefore, as  $a_h$  increases, there is a large increase in the value of  $U_{MSY}$  predicted by the stock's fixed value of CR (compare the values of  $U_{MSY}$  at the intersections of the  $U_{MSY}$ -CR curves and the horizontal CR line in Figure 3.10). For the other two stocks, increasing  $a_h$  did not greatly increase predicted  $U_{MSY}$  (Figure 3.9). However, the reasons differed slightly between the two stocks. Under Ricker recruitment, increasing  $a_h$  for Atlantic horse mackerel 1 had quite a large effect on the location of the  $U_{MSY}$ -CR curve, but the estimated value of CR was so low (CR = 4.7) that the realised effect of  $a_h$  on  $U_{MSY}$  was very small (Figure 3.10). Under Beverton-Holt recruitment for this stock,  $a_h$  had a lesser effect on the location of the  $U_{MSY}$ -CR curve. However, a larger range of values of  $U_{MSY}$  could have still been realised with higher CR (Figure 3.10). Therefore, very low CR was the main factor limiting  $U_{MSY}$  for this stock. For the final stock (Greenland halibut), CR was quite high (37.9) but the curves themselves were highly constrained by life history parameters (Figure 3.10), i.e., increasing  $a_h$  had relatively little effect on the location of the curve and, therefore, the predicted value of  $U_{MSY}$  was similar across  $a_h$ . Therefore, life history traits were the main limiting factor of  $U_{MSY}$  for this stock. Compared to most of the other stocks, Greenland halibut was long-lived and late-maturing ( $a_{max} = 15$ ;  $a_{mat} = 9.2$ ) with a relatively low natural mortality rate ( $M = 0.15$ ).

Curves for all 54 stocks are shown in the Appendix to Chapter 3. Stocks have been categorised into three categories, representing stocks for which mean predicted  $U_{MSY}$  was ‘selectivity-limited’, ‘recruitment-limited’ and ‘life history-limited’. Recruitment-limited stocks were defined as those with  $CR < 10$ . This captures stocks such as Atlantic horse mackerel 1 (Figure 3.11), for which the range of  $U_{MSY}$  was small, due mainly to the low value of  $CR$ . Stocks predicted to be recruitment limited are identified in Table 3.4 (graphs are shown in the Appendix to Chapter 3: Figure 3A.1 and 3A.2). Anomalies in this group were Norway pout and sandeel, which still had relative high  $U_{MSY}$  despite very low  $CR$  ( $CR = 3.1$  and  $4.82$  respectively). These species were both very short-lived ( $a_{max} = 4$ ) and therefore had very shallow, rightward  $U_{MSY}$ - $CR$  curves and therefore intersected with the  $CR$  line at higher values of  $U_{MSY}$  than the other stocks.

Life history-limited stocks (e.g., Greenland halibut; Figure 3.11) were defined as having the *range* of predicted  $U_{MSY}$  (across the tested values of  $a_h$ ) to be less than 0.15 and to have  $CR > 10$ . This captured stocks for which the effect of  $a_h$  on the location of the  $U_{MSY}$ - $CR$  curve was small due to the constraining effect of certain life history parameters. Life history-limited stocks are identified in Table 3.4 and shown in Figure 3A.3. Note that there were no stocks that fell into the life history-limited category under Ricker recruitment. Remaining stocks were classified as selectivity-limited (i.e.,  $CR > 10$  and the range of  $U_{MSY} > 0.15$ ). These stocks are identified in Table 3.4 and are shown in Figures 3A.4 and 3A.5. The boundaries chosen for these categories were arbitrary, based on visual inspection of the graphs in the Appendix to Chapter 3. Obviously, life history, density dependence and selectivity all contribute to all stocks’  $U_{MSY}$  and the range of relative effects of these three factors is continuous in nature. For example,  $U_{MSY}$  for some stocks was both recruitment and life history-limited (e.g., common sole 5 under Beverton-Holt recruitment; Figure 3A.2). The boundaries chosen were intended simply to capture apparent patterns in the current dataset and enable broad-brush observations to be made.

Recruitment-limited stocks included both pelagic and demersal species (e.g., Atlantic horse mackerel 1; Herring 2 and 5, megrim 2 and common sole 5; Table 3.4) that tended towards early maturity and were relatively short-lived, although, they shared these traits with many species that were not classified as recruitment-limited. However, all recruitment-limited stocks had very low  $SPR_0$ . For these stocks, the  $U_{MSY}$ - $CR$  curve was less important for prediction of  $U_{MSY}$  and,



therefore, stocks for which  $U_{MSY}$  is likely to be limited by very low recruitment compensation could be identified as having low  $SPR_0$ . Life history-limited stocks (e.g., European plaice 2-6 and Greenland halibut; Table 3.4) tended to be longer-lived stocks with either slow growth, low natural mortality, or both. There was no obvious trend in  $SPR_0$  for these stocks. However, they could be easily identified by  $U_{MSY}$ -CR curves close to the left of the plot (Figure 3A.3). Given that knowledge of recruitment parameters is not needed to calculate either  $SPR_0$  or the  $U_{MSY}$ -CR curve, these two rules of thumb could be useful in a risk assessment framework for initial rapid identification of species with overfishing thresholds highly constrained by factors not under management control.

## Discussion

Density dependence in recruitment, due to intraspecific competition for resources, is one of the main determinants of the productivity of harvested stocks (Myers 2001; 2002). While a stock may have strong density dependence, however, it does not necessarily follow that it can withstand a high harvest rate, because  $U_{MSY}$  is also governed by other factors, including growth rate, age at maturity, longevity and age at first harvest. The last is important because this factor is under management control, i.e., increasing the age at which fish are first harvested will increase  $U_{MSY}$ .  $U_{MSY}$  is a productivity parameter intrinsic to a fish stock, which reflects the magnitude of density dependence in recruitment, as well as aspects of its life history and the selectivity schedule imposed upon it (Schnute and Kronlund 1996; Chapter 2).  $U_{MSY}$  also represents a valid harvest rate threshold for prevention of both growth and recruitment overfishing of single species (Gulland 1971; Mace 2001; see May *et al.* 1979 and Walters *et al.* 2005 for studies incorporating needs of predators and prey in calculation of MSY).

Results of this study were dependent on a number of simplifying assumptions and the results presented should be considered for their illustrative value and not for management advice. For example, the model assumed knife-edge selectivity, a general logistic maturity curve for all stocks (although age-at-maturity was stock specific), and stationarity in life history parameters and the selectivity schedule. This last assumption is unlikely to be valid, and a number of studies have shown fishery-induced changes on life history parameters (e.g., Hutchings 2005; Olsen *et*

*al.* 2005; Rijnsdorp 2005). Most of these assumptions could be tested with slight modifications to the existing model framework and this would be an avenue for future extension of this work. Despite the limiting assumptions of the present study, the results have been instructive for quantifying and visualising the relative effects of different biological and management parameters on thresholds for overfishing.

Results showed that, for most stocks, changing the selectivity schedule could have a significant impact on  $U_{MSY}$ . This is a well known approach for precautionary management of fisheries (Gulland 1971; Myers and Mertz 1998; Froese 2004). However, there were some stocks for which  $U_{MSY}$  was highly constrained by either life history or recruitment parameters and was little affected by selectivity. Stocks with  $U_{MSY}$  mostly limited by life history parameters could be identified by inspection of the  $U_{MSY}$ -CR curve, calculated over a range of hypothesised ages at recruitment to the fishery. Under Beverton-Holt recruitment, stocks with ‘life history-limited’  $U_{MSY}$  had characteristic curves that were far to the left of the  $x$ -axis, encompassing a small range of  $U_{MSY}$  across all tested values of  $a_h$ . Stocks with these types of curves tended to be longer-lived stocks with slower growth and/or lower natural mortality. Because predicted  $U_{MSY}$  was affected very little by changes to the selectivity schedule, prevention of overfishing of these types of stocks may require more a careful management plan than simply controlling selectivity. The  $U_{MSY}$ -CR curves can be constructed using only life history and selectivity parameters, suggesting they may be a useful tool for rapid assessment of stocks that fall into this category.

For a few stocks,  $U_{MSY}$  was highly constrained by the low density dependence estimated from stock-recruitment data (Goodwin *et al.* 2006). The  $U_{MSY}$ -CR curve was not useful for identifying these ‘recruitment-limited’ stocks. However, these stocks were all characterised by very low  $SPR_0$ , which can be calculated using only life history parameters. While the remaining stocks did not share any defining suite of characteristics, it is still possible to draw conclusions about the likely magnitude of  $U_{MSY}$  for many stocks because there appear to be natural constraints on possible values of CR. Of the 700 teleost stocks analysed by Myers *et al.* (1999), mean estimated CR exceeded 50 for only three species and exceeded 100 for only one species. Apart from the three outlying stocks in the study of Goodwin *et al.* (2006), estimated values of CR fell into a similar range. Most of the Atlantic stocks considered in this study are harvested at a very young

age (0-2 years) and examination of their  $U_{\text{MSY}}$ -CR curves for these ages at recruitment, under all hypotheses of  $\text{CR} < 100$ , indicates strong constraint in the possible value of  $U_{\text{MSY}}$ .

The predictions of the Ricker and Beverton-Holt models differed considerably.  $U_{\text{MSY}}$  predicted by the Ricker model was higher than that obtained using the Beverton-Holt model and the range of values across all stocks was greater in the Ricker case. In particular, the Ricker model predicted  $U_{\text{MSY}} = 1$  for many stocks under high age at recruitment to the fishery. It is important to note that  $U_{\text{MSY}}$  refers to the harvest rate on the vulnerable stock only and, therefore, if there are sufficient spawners and surviving recruits in the unfished population, it may be optimal to harvest all of the vulnerable stock. A value of  $U_{\text{MSY}} = 1$  implies that the stock cannot be growth overfished (see Myers and Mertz 1998), although environmental variability and extreme pitfalls in estimating stock-recruitment parameters precisely (Hilborn and Walters 1992) imply that this would be a very risk-prone management strategy. The Beverton-Holt model rarely predicted  $U_{\text{MSY}} = 1$  or even values of  $U_{\text{MSY}}$  approaching 1. The reasons for the differences between the predictions of the two models can, again, be seen by looking at the shape of the curve describing the relationship between CR and  $U_{\text{MSY}}$ . The Ricker curves tended to ascend less steeply than the Beverton-Holt curves and therefore predicted larger  $U_{\text{MSY}}$  than the Beverton-Holt curve, given the same value of CR. It is probably not useful to try to find biological explanations for these observations as the Ricker and Beverton-Holt stock recruitment relationships are, themselves, statistical approximations of a range of biological processes occurring over a wide range of spatial and temporal scales (Hilborn and Walters 1992). However, the Beverton-Holt recruitment function is consistent with a generalised theory about foraging behaviour in young fish as a mechanism leading to density dependence (Walters and Juanes 1993; Walters and Korman 1999; Walters *et al.* 2000) and is likely to be appropriate for most fish stocks.

Walters and Martell (2004) have discussed differences between the Ricker and Beverton-Holt models and shown how the Ricker model can result in lower estimates of  $\alpha$  than the Beverton-Holt model when extrapolating beyond the observed range of the stock-recruitment data. They state that, because of this, the Ricker model has often been advocated as a more precautionary model because its lower estimates of  $\alpha$  would imply lower  $U_{\text{MSY}}$ . This may appear contrary to the findings of the present analysis but it must be remembered that the present study did not estimate  $\alpha$  from stock-recruitment data (this had already been done by Goodwin *et al.* 2006) and,

therefore, this bias does not apply. The idea that the Ricker model is more precautionary because it produces lower estimates of  $\alpha$  is based on the assumption that the relationship between  $\alpha$  and  $U_{\text{MSY}}$  is similar in both models, which it is not. The present study suggests that the Beverton-Holt model would predict much lower  $U_{\text{MSY}}$  for a given  $\alpha$  (standardised to CR), due to differences in the form of the relationship between  $\alpha$  and  $U_{\text{MSY}}$  between the two models.

Standardised unfished spawners per recruit,  $\text{SPR}_0$ , has been shown to be a useful composite parameter for predicting density dependence (Goodwin *et al.* 2006). Translating this predictive power to  $U_{\text{MSY}}$ , however, requires consideration of whether the parameters that determine  $\text{SPR}_0$  also influence the relationship between  $U_{\text{MSY}}$  and CR. This study showed that  $\text{SPR}_0$  had poor ability to predict  $U_{\text{MSY}}$  (except for the recruitment-limited stocks discussed above), due to confounding of the effects of the different parameters comprising  $\text{SPR}_0$  and their individual effects on the relationship between  $U_{\text{MSY}}$  and CR. Care therefore needs to be taken when interpreting indications of strong density dependence as evidence that a stock can withstand high rates of harvest. Goodwin *et al.* (2006) suggested that stocks with low  $\text{SPR}_0$  (high  $\alpha$ , low CR; e.g., herring, anchovy) could be depleted even at low harvest rates but were resilient to extirpation because of high reproductive rates at low stock size. Alternatively, longer-lived, slower-growing and later-maturing stocks with high  $\text{SPR}_0$  (low  $\alpha$ , high CR; e.g., cod, halibut) could likely sustain higher harvest rates without being fished down due to strong compensation, but would be more vulnerable to extirpation if severely overfished. The results of the present study suggest that stocks with the lowest CR tended to have lower  $U_{\text{MSY}}$  than average, consistent with the arguments of Goodwin *et al.* (2006). However, for stocks with higher recruitment compensation (CR between  $\sim 20$  and 100; excluding the three extreme cases), there was no relationship between  $U_{\text{MSY}}$  and CR under the assumption of Beverton-Holt recruitment. This is because most stocks are currently harvested at very young ages (providing a strong constraint on  $U_{\text{MSY}}$ ) and also because, for some stocks,  $U_{\text{MSY}}$  is strongly constrained by life history parameters such as the growth and natural mortality rates, regardless of the strength of recruitment compensation. It should be noted that the statements of Goodwin *et al.* (2006) refer mainly to the problem of recruitment overfishing and recovery from depletion (see also Denney *et al.* 2002). Note, though, that thresholds for growth and recruitment overfishing may be close together for low productivity species (Punt 2000; NAFO 2003).

It is noteworthy that, under the assumption of Beverton-Holt recruitment,  $U_{MSY}$  was highly positively correlated with the natural mortality and growth rate and negatively correlated with maximum age, consistent with previous findings (e.g., Jennings *et al.* 1998; Dulvy *et al.* 2004) and demonstrated theory (Beverton and Holt 1957; Gulland 1971; Kirkwood *et al.* 1994). This implies that the first priority in data-limited situations should be to obtain: (i) a growth curve, from which one can obtain rough predictions of  $M$  and age-at-maturity (using, for example, Beverton-Holt invariants: Charnov 1993); and (ii) the selectivity schedule that would maximize yield without driving the stock size low enough for density dependence in recruitment to become important (C. Walters, UBC Fisheries Centre, pers. comm.). Therefore, when the size-selection regime can be regulated, a management priority should be to adjust it (Myers and Mertz 1998; Froese *et al.* 2008).

Control of selectivity in fisheries remains one of the biggest challenges in fisheries today (Hall and Mainprize 2005). Mechanisms include regulated changes to mesh or hook size in trawl and line fisheries; and regulation of spatial extent of the fishery so that some age-classes are invulnerable to the fishing gear (to allow growth and/or recruitment to occur). Seasonal temporal closures are often also implemented to allow growth and reproduction before harvesting (e.g., Myers *et al.* 2000). Some of the most successfully-managed fisheries are highly regulated in all these respects (e.g. Pacific halibut: Clark and Hare 2004). Most species, however, especially those that are data-limited, are caught in multispecies fisheries (often as bycatch) where it is very difficult or impossible to control individual ages at recruitment of multiple species.

In recent years, there has been much progress in devising methods to reduce bycatch that have included modifications to gear, such as escape panels in trawl nets, or modifications to the method of fishing, such as deeper setting of longlines to target specific pelagic species. Many of these solutions have been developed by members of the fishing industry or by partnerships between industry, government and scientists. For example, one such partnership has resulted in development of a net that selectively catches haddock, avoiding bycatch of cod and other unwanted groundfish species (Beutel *et al.* 2006). Another recent innovation uses magnets to deter sharks from longline hooks (see Gilman *et al.* 2007). There are, however, disincentives for selective fishing. In the past decade, many developed countries have shifted to individual quota systems (e.g., New Zealand, Iceland, Australia, Canada and the United States) and, while they

have been effective at reducing wasteful fishing effort, they have sometimes resulted in discarding of unwanted fish that exceed quota-limits or hold limits (Arnason 1994; 1996; Annala 1996). Unreported dumping of groundfish by boats fishing under the quota system is believed to have occurred in the years leading up to the collapse of the Newfoundland cod fishery (Angel *et al.* 1994; Blades 1995) and is possibly part of the reason for the collapse (Walters and Maguire 1996; Myers *et al.* 1997). Coggins *et al.* (2007) discuss discarding as a cryptic source of fishing mortality and have demonstrated that discarding may undermine efforts to achieve sustainable harvest rates using length-based regulations, particularly when there are large recreational fisheries.

Changes to the incentive structure in fisheries, e.g., through control of fishing effort and focus on more profitable fisheries, will be an important part of the solution (Grafton *et al.* 2006). Development of adaptive risk assessment approaches and management strategies that are flexible to changes in the fishery and new information are also necessary (Ludwig *et al.* 1993). For example, Smith *et al.* (2007) have described recent developments in ecological risk assessment and harvest strategy frameworks for EBFM in Australian Commonwealth fisheries that vary according to the probable level of risk to each species and the amount of data available for assessment. These types of frameworks will require a suite of tools for assessing species with widely-varying amounts of available data (e.g., Mace and Sissenwine 1993; papers in Kruse *et al.* 2005; Sadovy *et al.* 2007). Presentation of the likely range of  $U_{MSY}$  among stocks in multispecies fisheries can help managers visualise the effects of different levels of fishing effort on multiple stocks simultaneously and can be used to frame discussions of trade-offs inherent in managing non-selective fisheries.

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## Tables

**Table 3.1.** Input parameters used in the model.  $W_{\infty}$  = maximum weight (kg);  $\kappa$  = growth rate ( $y^{-1}$ );  $a_{mat}$  = age at 50% maturity (years);  $a_{max}$  = maximum age (years);  $M$  = natural mortality rate ( $y^{-1}$ );  $SPR_0$  = unfished spawning stock biomass = per recruit; CR = recruitment compensation ratio;  $a_h$  = age at recruitment to the fishery. Parameters in italics were obtained from FishBase. All other parameters were taken from Goodwin *et al.* (2006). CS, Celtic Sea; BB, Bay of Biscay; Channel, English Channel; NS, North Sea.

Species	Stock code	Area	$W_{\infty}$	$\kappa$	$a_{mat}$	$a_{max}$	$M$	$SPR_0$	CR	$a_h$
<i>Gadus morhua</i>	Atlantic cod 1	CS and West Channel	17.61	0.37	2.2	7	0.20	19.96	25.81	1
	Atlantic cod 2	Faroe Plateau	76.13	0.07	3.0	9	0.20	11.58	40.07	2
	Atlantic cod 3	Iceland	33.61	0.12	5.1	14	0.20	18.85	34.83	3
	Atlantic cod 4	Irish Sea	86.17	0.11	2.1	7	0.20	12.69	34.45	1
	Atlantic cod 5	Kattegat	19.89	0.23	2.2	8	0.20	7.86	24.12	1
<i>Clupea harengus</i>	Atlantic cod 6	Northeast Arctic	129.20	0.07	7.0	13	0.30	12.08	2081.28	3
	Atlantic cod 7	NS, Skagerrak, and E. Channel	18.99	0.24	3.7	11	0.22	18.11	297.86	1
	Atlantic cod 8	West Baltic	19.35	0.18	2.8	7	0.22	5.26	77.69	1
	Atlantic cod 9	West Scotland	28.53	0.20	2.0	7	0.20	12.97	58.81	1
	Atlantic herring 1	CS and Southwest Ireland	0.23	0.31	1.0	9	0.50	0.89	20.9	1
	Atlantic herring 2	East Baltic	0.20	0.22	1.8	8	0.25	0.09	5.2	1
	Atlantic herring 3	Iceland	0.41	0.29	3.4	15	0.10	1.89	21.36	2
	Atlantic herring 4	Irish Sea	0.20	0.52	1.6	8	0.50	0.75	32.94	1
	Atlantic herring 5	Norway	0.43	0.23	4.3	16	0.50	0.92	9.52	1
<i>Trachurus trachurus</i>	Atlantic herring 6	NS	0.26	0.45	1.8	9	0.50	0.83	32.8	1
	Atlantic herring 7	West Scotland	0.24	0.45	1.9	9	0.50	0.92	47.24	1
	Atlantic horse mackerel 1	Iberia	0.31	0.22	3.8	12	0.15	0.51	4.66	1
	Atlantic horse mackerel 2	Northeast Atlantic	0.29	0.18	3.6	11	0.15	0.47	54	1
	Atlantic mackerel	West stock	0.65	0.26	1.9	12	0.15	1.68	13.27	1
<i>Scomber scombrus</i>	Blue whiting	Northern ICES	0.33	0.15	2.2	10	0.20	0.36	9.46	1
	Common sole 1	CS	0.80	0.21	3.1	10	0.10	1.91	32.27	1
	Common sole 2	East Channel	0.69	0.15	2.5	11	0.10	1.73	50.29	1
	Common sole 3	Irish Sea	0.60	0.16	2.4	10	0.10	1.64	24.86	2
	Common sole 4	NS	0.71	0.04	2.5	15	0.10	2.30	30.99	1
<i>Merluccius merluccius</i>	Common sole 5	West Channel	0.74	0.18	3.1	12	0.10	2.13	8.06	1
	European anchovy	BB	0.07	0.25	0.5	5	0.12	0.12	330.97	1
	European hake 1	Iberia	5.50	0.15	3.2	8	0.20	1.50	14.17	1
	European hake 2	NS, CS, and Channel	14.21	0.13	3.8	8	0.20	1.78	10.96	1



Table 3.1 continued.

Species	Stock code	Area	$W_{\infty}$	$\kappa$	$a_{mat}$	$a_{max}$	$M$	$SPR_0$	CR	$a_h$
<i>Sardina pilchardus</i>	European pilchard	Iberia	0.08	0.73	1.0	6	0.33	0.11	25.07	1
<i>Pleuronectes platessa</i>	European plaice 1	CS	1.53	0.14	2.9	9	0.12	2.03	43.41	1
	European plaice 2	East Channel	8.77	0.05	2.9	10	0.10	3.03	76.39	1
	European plaice 3	Irish Sea	6.85	0.05	2.9	9	0.12	1.56	22.64	1
	European plaice 4	NS	1.42	0.12	2.5	15	0.10	3.82	30.46	1
	European plaice 5	Skagerrak and Kattegat	1.43	0.11	2.5	11	0.10	2.43	83.39	2
	European plaice 6	West Channel	1.62	0.17	2.9	10	0.12	2.59	30.87	1
<i>Lepidorhombus boscii</i>	Four spotted megrim	Iberia	0.24	0.20	1.0	7	0.20	0.38	17.65	1
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	Northeast Arctic	17.98	0.10	9.2	15	0.15	8.57	37.91	5
<i>Melanogrammus aeglefinus</i>	Haddock 1	Faroe Plateau	5.11	0.18	3.1	8	0.20	5.61	40.45	2
	Haddock 2	Iceland	6.89	0.17	3.8	9	0.20	4.72	32.17	2
	Haddock 3	Northeast Arctic	3.18	0.22	5.9	11	0.25	3.73	42.03	3
	Haddock 4	NS, Skagerrak, and Kattegat	3.24	0.17	2.5	10	1.00	1.83	50.63	1
	Haddock 5	Rockall	0.79	0.22	2.5	7	0.20	1.19	33.4	1
	Haddock 6	West Scotland	1.55	0.23	2.0	8	0.20	1.74	41.91	1
<i>Lepidorhombus whiffiagonis</i>	Megrim 1	CS, West of Ireland, West Channel, and BB	8.87	0.08	2.8	10	0.20	0.73	25.07	1
	Megrim 2	Iberia	5.11	0.08	1.2	0.2	0.20	0.44	4.99	1
<i>Trisopterus esmarki</i>	Norway pout	NS and Skagerrak	0.29	0.59	1.2	4	1.60	0.00	3.11	1
<i>Pollachius virens</i>	Pollock 1	Faroe Plateau	12.14	0.06	5.0	0.2	0.20	10.56	57.56	3
	Pollock 2	Iceland	21.09	0.15	4.9	14	0.20	17.01	20.61	3
	Pollock 3	NS, Skagerrak, Kattegat, West Scotland, and Rockall	49.89	0.07	4.7	10	0.20	5.16	52.03	1
<i>Ammodytoidei</i> spp.	Sandeel	NS	0.03	0.40	1.5	4	0.80	0.01	7.43	1
<i>Merlangius merlangus</i>	Whiting 1	CS and West Channel	8.15	0.05	1.5	7	0.20	1.18	17.81	1
	Whiting 2	Irish Sea	0.61	0.35	1.5	6	0.20	0.64	44.29	1
	Whiting 3	NS and East Channel	0.32	0.71	1.5	8	0.60	0.73	14.07	1
	Whiting 4	West Scotland	2.98	0.08	1.5	7	0.20	1.16	19.13	1

**Table 3.2.** Pearson's correlation coefficient,  $r$ , for relationship between logged life history/selectivity parameters and mean  $U_{\text{MSY}}$  for all stocks under Ricker and Beverton-Holt assumptions for the stock-recruitment relationship.

<i>Ln</i> parameter	$M$	$a_{\text{mat}}$	$\kappa$	$W_{\infty}$	$a_{\text{max}}$	$SPR_0$
<b>Ricker</b>	0.27*	-0.01 <sup>n.s.</sup>	0.25 <sup>n.s.</sup>	0.15 <sup>n.s.</sup>	-0.17 <sup>n.s.</sup>	0.12 <sup>n.s.</sup>
<b>Beverton-Holt</b>	0.85**	-0.22	0.63**	-0.14	-0.46**	-0.24 <sup>n.s.</sup>

\*\* =  $P < 0.01$ ; \* =  $P < 0.05$ ; n.s. = not significant,  $df = 52$ .

**Table 3.3.** Parameters used to make Figures 3.7 (Stock 3) and 3.8.

<b>Stock</b>	$\kappa$	$W_\infty$	$a_{mat}$	$a_{max}$	$M$	$ah$	$SPR_0$
1	0.36	4.2	2.5	10	0.25	2	9.0
2	0.31	4.8	2.5	10	0.25	2	9.0
3	0.25	6	2.5	10	0.25	2	9.1
4	0.23	6.6	2.5	10	0.25	2	9.0
5	0.21	7.4	2.5	10	0.25	2	9.0

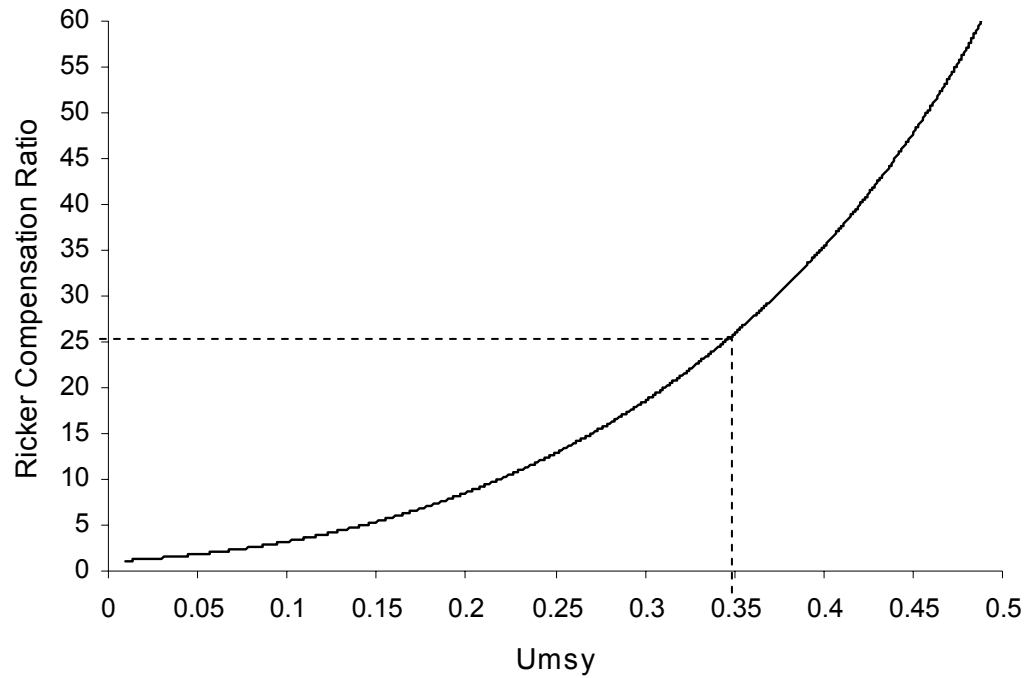
**Table 3.4a.** Mean values of  $U_{MSY}$  obtained for the 54 stocks under a range of values of  $a_h$  assuming Ricker recruitment. (see text for definition of the determinants of  $U_{MSY}$ ). Important: These values are illustrative and not appropriate for management recommendations.

Stock	0	1	2	3	4	5	6	Strongest determinant of $U_{MSY}$
Atlantic cod 1	0.25	0.32	0.45	0.72	0.98	1	1	Selectivity
Atlantic cod 2	0.21	0.24	0.30	0.39	0.54	0.77	1	Selectivity
Atlantic cod 3	0.18	0.21	0.26	0.32	0.40	0.55	0.77	Selectivity
Atlantic cod 4	0.22	0.27	0.35	0.49	0.71	1	1	Selectivity
Atlantic cod 5	0.21	0.26	0.35	0.50	0.70	0.94	1	Selectivity
Atlantic cod 6	0.49	0.56	0.67	0.78	0.92	1	1	Selectivity
Atlantic cod 7	0.44	0.56	0.73	0.93	1	1	1	Selectivity
Atlantic cod 8	0.31	0.40	0.56	0.90	1	1	1	Selectivity
Atlantic cod 9	0.29	0.36	0.51	0.82	1	1	1	Selectivity
Atlantic herring 1	0.21	0.27	0.37	0.53	0.73	0.94	1	Selectivity
Atlantic herring 2	0.11	0.13	0.17	0.21	0.26	0.32	0.38	CR (recruitment)
Atlantic herring 3	0.15	0.17	0.21	0.26	0.33	0.42	0.50	Selectivity
Atlantic herring 4	0.29	0.40	0.65	0.98	1	1	1	Selectivity
Atlantic herring 5	0.13	0.15	0.18	0.22	0.27	0.36	0.43	CR (recruitment)
Atlantic herring 6	0.28	0.38	0.58	0.94	1	1	1	Selectivity
Atlantic herring 7	0.31	0.42	0.67	1	1	1	1	Selectivity
Atlantic horse mackerel 1	0.07	0.08	0.09	0.10	0.12	0.15	0.17	CR (recruitment)
Atlantic horse mackerel 2	0.21	0.25	0.32	0.41	0.59	0.88	1	Selectivity
Atlantic mackerel 1	0.14	0.17	0.20	0.26	0.32	0.40	0.47	CR (recruitment)
Bluewhiting 1	0.13	0.15	0.18	0.22	0.28	0.34	0.40	CR (recruitment)
Common sole 1	0.16	0.19	0.23	0.29	0.37	0.48	0.62	Selectivity
Common sole 2	0.17	0.20	0.24	0.30	0.38	0.50	0.66	Selectivity
Common sole 3	0.14	0.16	0.19	0.23	0.28	0.35	0.44	Selectivity
Common sole 4	0.15	0.17	0.20	0.24	0.31	0.38	0.47	Selectivity
Common sole 5	0.08	0.09	0.10	0.12	0.13	0.16	0.18	CR (recruitment)
European anchovy 1	0.41	0.55	0.96	1	1	1	1	Selectivity
European hake 1	0.16	0.18	0.23	0.29	0.38	0.51	0.65	Selectivity
European hake 2	0.14	0.16	0.19	0.24	0.30	0.41	0.52	Selectivity
European pilchard 1	0.34	0.50	0.92	1	1	1	1	Selectivity
European plaice 1	0.19	0.22	0.27	0.35	0.47	0.64	0.86	Selectivity
European plaice 2	0.18	0.21	0.25	0.30	0.38	0.51	0.69	Selectivity
European plaice 3	0.14	0.16	0.18	0.22	0.27	0.34	0.43	Selectivity
European plaice 4	0.13	0.15	0.17	0.20	0.24	0.29	0.36	Selectivity
European plaice 5	0.20	0.23	0.28	0.35	0.47	0.65	0.92	Selectivity
European plaice 6	0.17	0.19	0.23	0.30	0.38	0.50	0.63	Selectivity
Fourspotted megrim 1	0.19	0.23	0.30	0.40	0.54	0.73	0.95	Selectivity
Greenland halibut 1	0.15	0.16	0.18	0.21	0.24	0.28	0.33	Selectivity
Haddock 1	0.24	0.29	0.37	0.52	0.79	1	1	Selectivity
Haddock 2	0.21	0.25	0.31	0.40	0.58	0.87	1	Selectivity
Haddock 3	0.23	0.28	0.34	0.42	0.56	0.71	0.92	Selectivity
Haddock 4	0.26	0.33	0.44	0.68	0.98	1	1	Selectivity
Haddock 5	0.24	0.29	0.39	0.56	0.87	1	1	Selectivity
Haddock 6	0.26	0.33	0.45	0.69	1	1	1	Selectivity
Megrim 1	0.17	0.19	0.23	0.29	0.37	0.49	0.64	Selectivity
Megrim 2	0.09	0.10	0.13	0.15	0.19	0.24	0.30	CR (recruitment)
Norway pout 1	0.24	0.48	0.95	0.98	0.98	0.98	1	CR (recruitment)
Pollock 1	0.21	0.24	0.29	0.35	0.46	0.66	0.91	Selectivity
Pollock 2	0.16	0.18	0.22	0.26	0.33	0.44	0.58	Selectivity
Pollock 3	0.21	0.25	0.30	0.38	0.51	0.74	0.96	Selectivity
Sandeel 1	0.28	0.43	0.87	1	1	1	1	CR (recruitment)
Whiting 1	0.18	0.21	0.26	0.34	0.46	0.63	0.85	Selectivity
Whiting 2	0.30	0.41	0.62	1	1	1	1	Selectivity
Whiting 3	0.37	0.59	0.98	1	1	1	1	Selectivity
Whiting 4	0.18	0.22	0.28	0.36	0.49	0.67	0.90	Selectivity

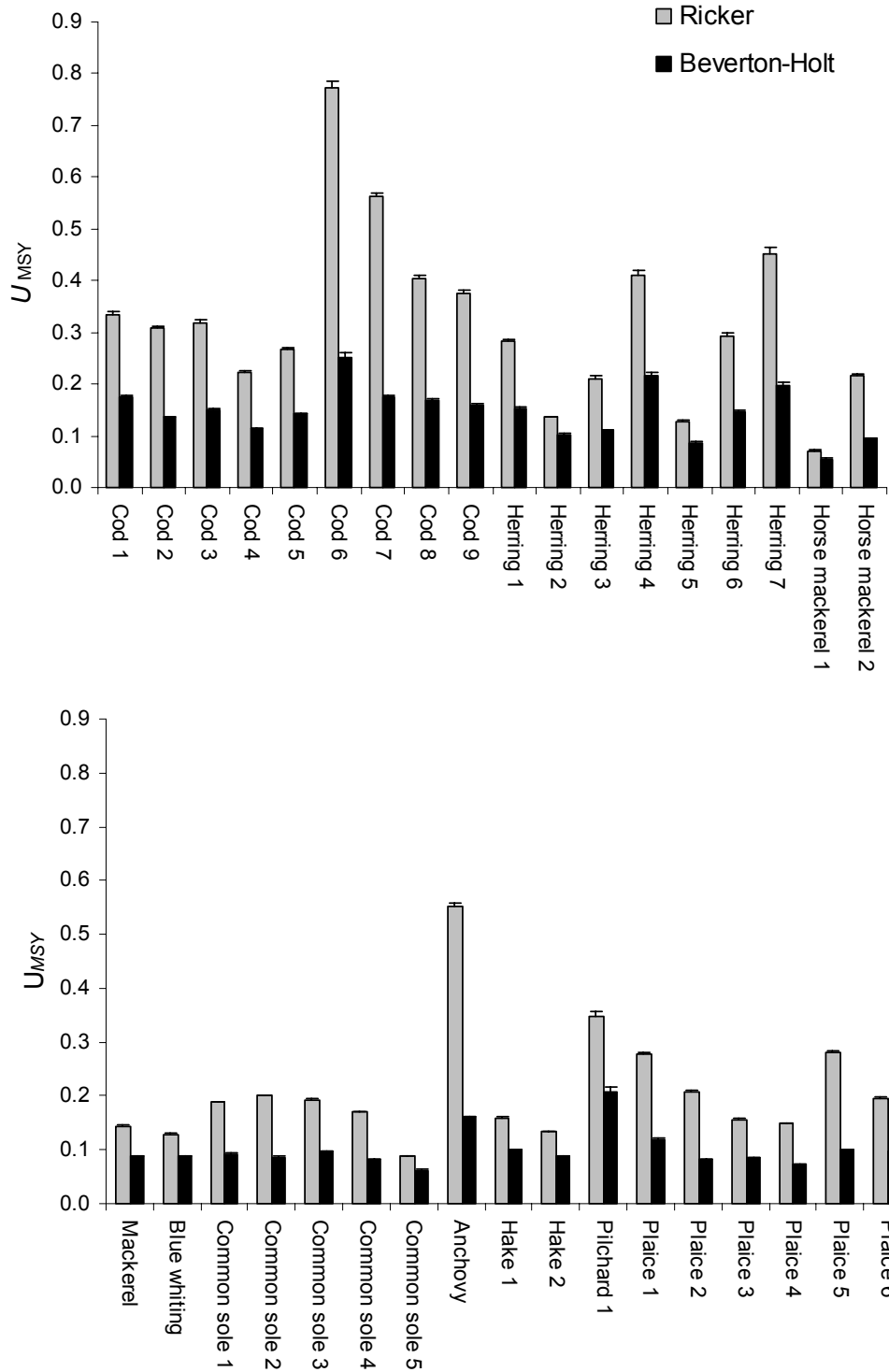
**Table 3.4b.** Mean values of  $U_{MSY}$  obtained for the 54 stocks under a range of values of  $a_h$  assuming Beverton-Holt recruitment (see text for definition of the determinants of  $U_{MSY}$ ).

Stock	0	1	2	3	4	5	6	Strongest determinant of $U_{MSY}$
Atlantic cod 1	0.13	0.17	0.23	0.32	0.44	0.57	0.71	Selectivity
Atlantic cod 2	0.10	0.12	0.14	0.17	0.22	0.28	0.36	Selectivity
Atlantic cod 3	0.09	0.11	0.12	0.15	0.18	0.23	0.29	Selectivity
Atlantic cod 4	0.11	0.14	0.17	0.22	0.29	0.40	0.58	Selectivity
Atlantic cod 5	0.12	0.14	0.18	0.24	0.31	0.40	0.51	Selectivity
Atlantic cod 6	0.12	0.14	0.17	0.22	0.29	0.40	0.56	Selectivity
Atlantic cod 7	0.13	0.16	0.21	0.30	0.43	0.65	0.96	Selectivity
Atlantic cod 8	0.13	0.16	0.21	0.28	0.40	0.57	0.80	Selectivity
Atlantic cod 9	0.13	0.15	0.20	0.27	0.38	0.53	0.74	Selectivity
Atlantic herring 1	0.12	0.15	0.19	0.26	0.34	0.42	0.51	Selectivity
Atlantic herring 2	0.09	0.10	0.13	0.16	0.20	0.24	0.28	CR (recruitment)
Atlantic herring 3	0.08	0.09	0.11	0.13	0.16	0.19	0.23	Life history
Atlantic herring 4	0.15	0.19	0.28	0.43	0.58	0.74	0.85	Selectivity
Atlantic herring 5	0.09	0.10	0.12	0.15	0.18	0.23	0.27	CR (recruitment)
Atlantic herring 6	0.14	0.18	0.26	0.38	0.52	0.67	0.78	Selectivity
Atlantic herring 7	0.15	0.19	0.27	0.40	0.57	0.76	0.91	Selectivity
Atlantic horse mackerel 1	0.05	0.06	0.07	0.08	0.10	0.11	0.13	CR (recruitment)
Atlantic horse mackerel 2	0.09	0.11	0.13	0.16	0.20	0.25	0.32	Selectivity
Atlantic mackerel 1	0.09	0.10	0.12	0.15	0.18	0.22	0.26	CR (recruitment)
Bluewhiting 1	0.09	0.10	0.12	0.15	0.18	0.21	0.25	CR (recruitment)
Common sole 1	0.08	0.09	0.11	0.13	0.16	0.19	0.24	Selectivity
Common sole 2	0.08	0.09	0.10	0.12	0.14	0.17	0.21	Life history
Common sole 3	0.07	0.08	0.10	0.11	0.14	0.16	0.20	Life history
Common sole 4	0.07	0.08	0.09	0.11	0.13	0.15	0.18	Life history
Common sole 5	0.06	0.06	0.07	0.08	0.09	0.10	0.12	CR (recruitment)
European anchovy 1	0.13	0.16	0.22	0.32	0.53	0.53	0.53	Selectivity
European hake 1	0.10	0.11	0.14	0.17	0.22	0.29	0.36	Selectivity
European hake 2	0.09	0.10	0.12	0.15	0.19	0.25	0.31	Selectivity
European pilchard 1	0.19	0.27	0.44	0.68	0.94	1	1	Selectivity
European plaice 1	0.09	0.10	0.12	0.15	0.18	0.23	0.29	Selectivity
European plaice 2	0.07	0.08	0.09	0.11	0.13	0.16	0.20	Life history
European plaice 3	0.08	0.09	0.10	0.11	0.14	0.17	0.21	Life history
European plaice 4	0.07	0.07	0.08	0.09	0.11	0.13	0.14	Life history
European plaice 5	0.08	0.09	0.10	0.12	0.14	0.17	0.21	Life history
European plaice 6	0.08	0.10	0.11	0.14	0.17	0.20	0.25	Life history
Fourspotted megrim 1	0.11	0.13	0.17	0.22	0.29	0.38	0.50	Selectivity
Greenland halibut 1	0.07	0.08	0.09	0.11	0.12	0.14	0.16	Life history
Haddock 1	0.11	0.14	0.17	0.22	0.30	0.40	0.52	Selectivity
Haddock 2	0.11	0.13	0.15	0.19	0.25	0.33	0.43	Selectivity
Haddock 3	0.12	0.14	0.18	0.23	0.29	0.38	0.52	Selectivity
Haddock 4	0.12	0.14	0.18	0.24	0.32	0.43	0.57	Selectivity
Haddock 5	0.12	0.15	0.19	0.25	0.34	0.47	0.64	Selectivity
Haddock 6	0.12	0.15	0.19	0.26	0.35	0.47	0.60	Selectivity
Megrim 1	0.09	0.10	0.12	0.15	0.18	0.22	0.28	Selectivity
Megrim 2	0.07	0.08	0.10	0.12	0.14	0.18	0.22	CR (recruitment)
Norway pout 1	0.34	0.44	0.93	0.96	0.98	0.98	0.97	CR (recruitment)
Pollock 1	0.09	0.10	0.12	0.14	0.17	0.21	0.26	Selectivity
Pollock 2	0.09	0.10	0.12	0.14	0.18	0.22	0.28	Selectivity
Pollock 3	0.10	0.11	0.13	0.16	0.20	0.25	0.32	Selectivity
Sandeel 1	0.21	0.32	0.65	0.93	0.95	0.93	0.94	CR (recruitment)
Whiting 1	0.10	0.12	0.15	0.19	0.25	0.33	0.46	Selectivity
Whiting 2	0.14	0.18	0.26	0.38	0.54	0.75	0.75	Selectivity
Whiting 3	0.24	0.39	0.82	1	1	1	1	Selectivity
Whiting 4	0.11	0.12	0.15	0.20	0.26	0.34	0.48	Selectivity

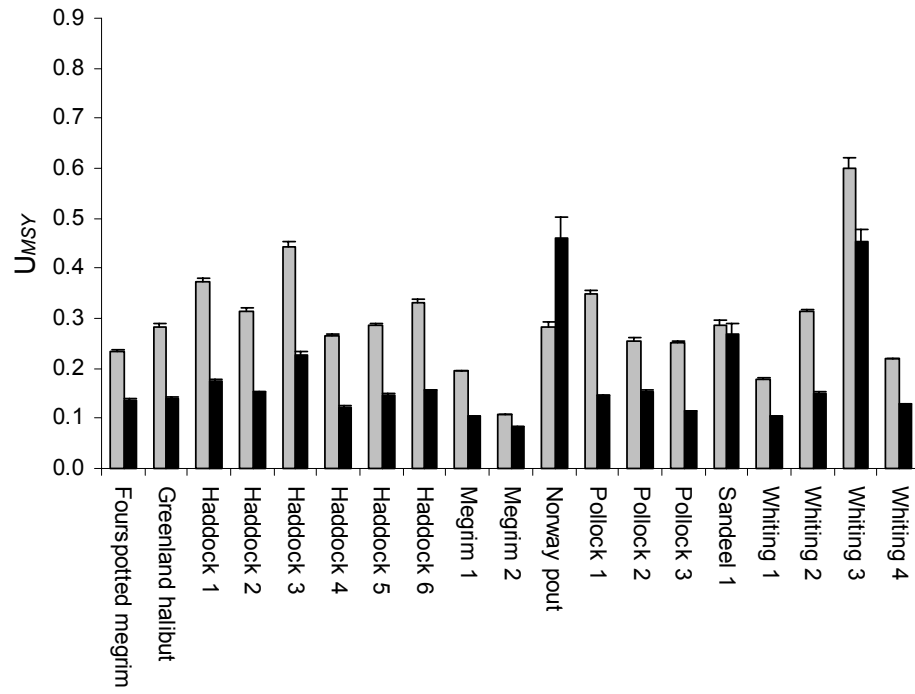
## Figures



**Figure 3.1.** Relationship between  $U_{MSY}$  and CR for a hypothetical stock, with dashed lines showing a unique pair of  $U_{MSY}$  and CR values.

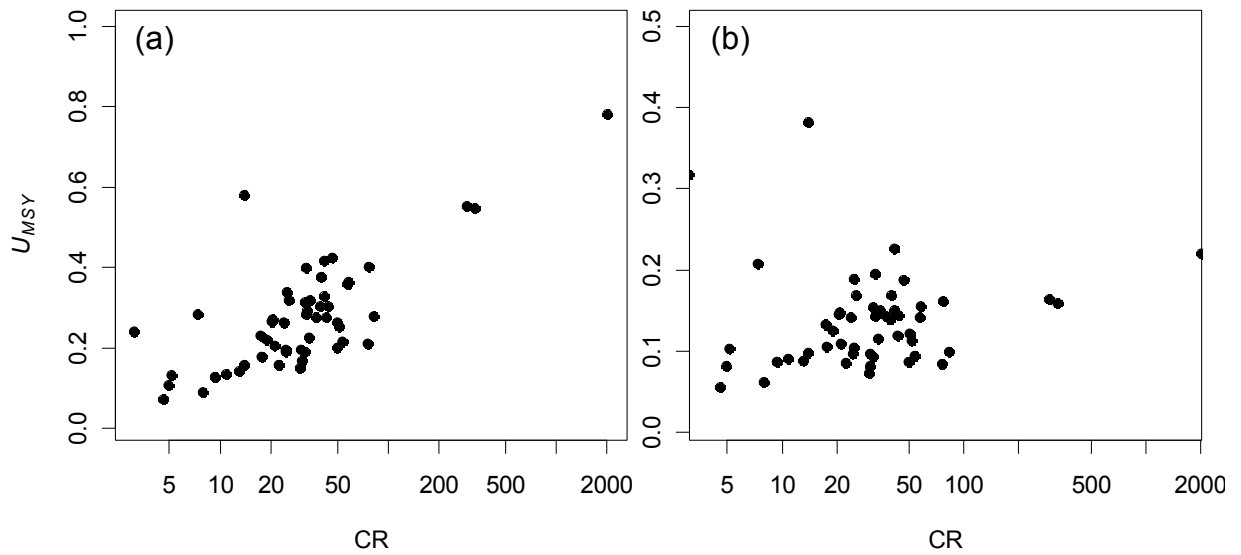


**Figure 3.2.** Mean (+ s.e.) estimates of  $U_{MSY}$  for the 54 stocks of Goodwin *et al.* (2006) under Ricker (grey bars) and Beverton-Holt (black bars) assumptions about the stock-recruitment relationship.  $U_{MSY}$  values are the means of 100 Monte Carlo runs (see text). See Table 3.1 for description of stocks.

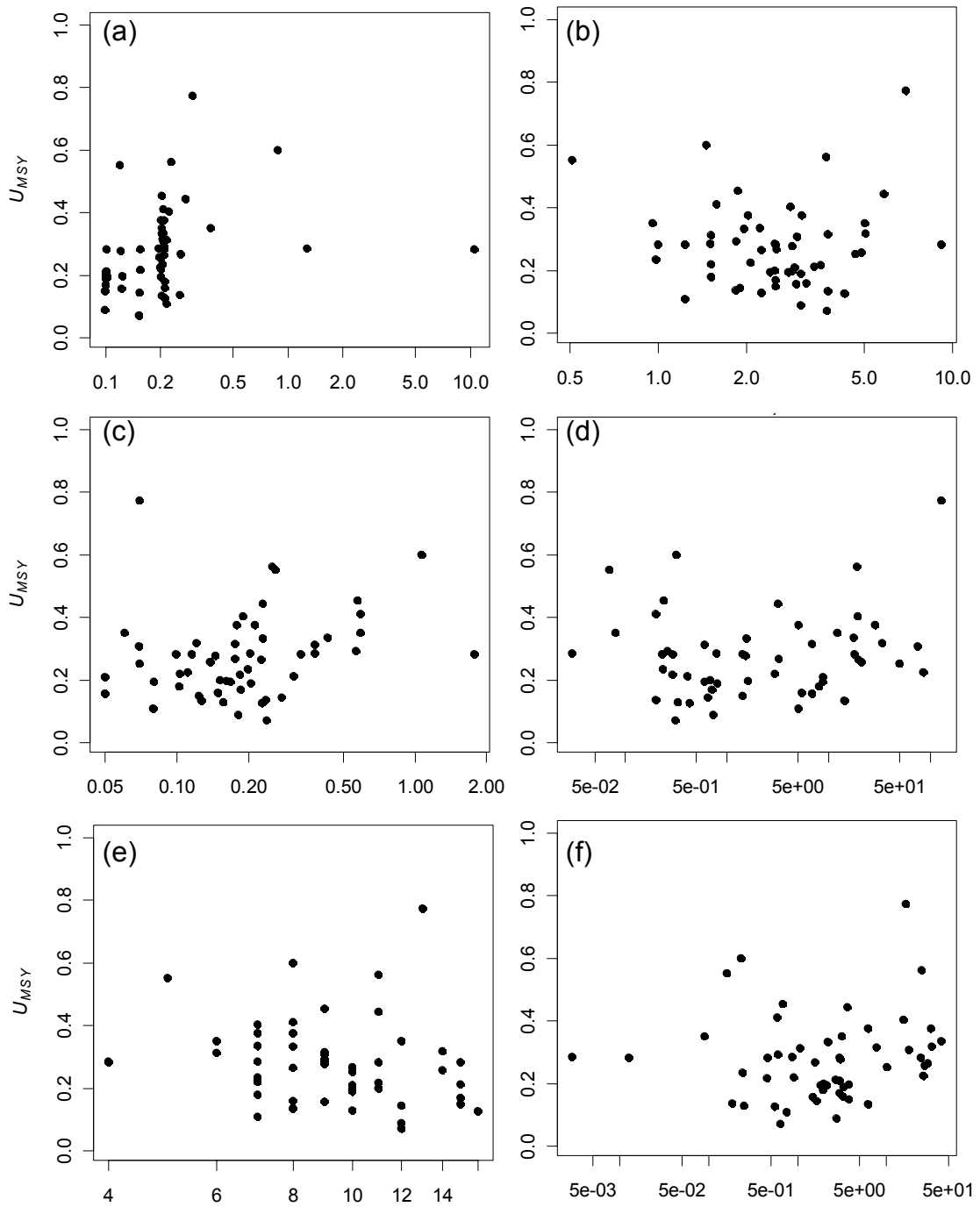


**Figure 3.2 cont.**

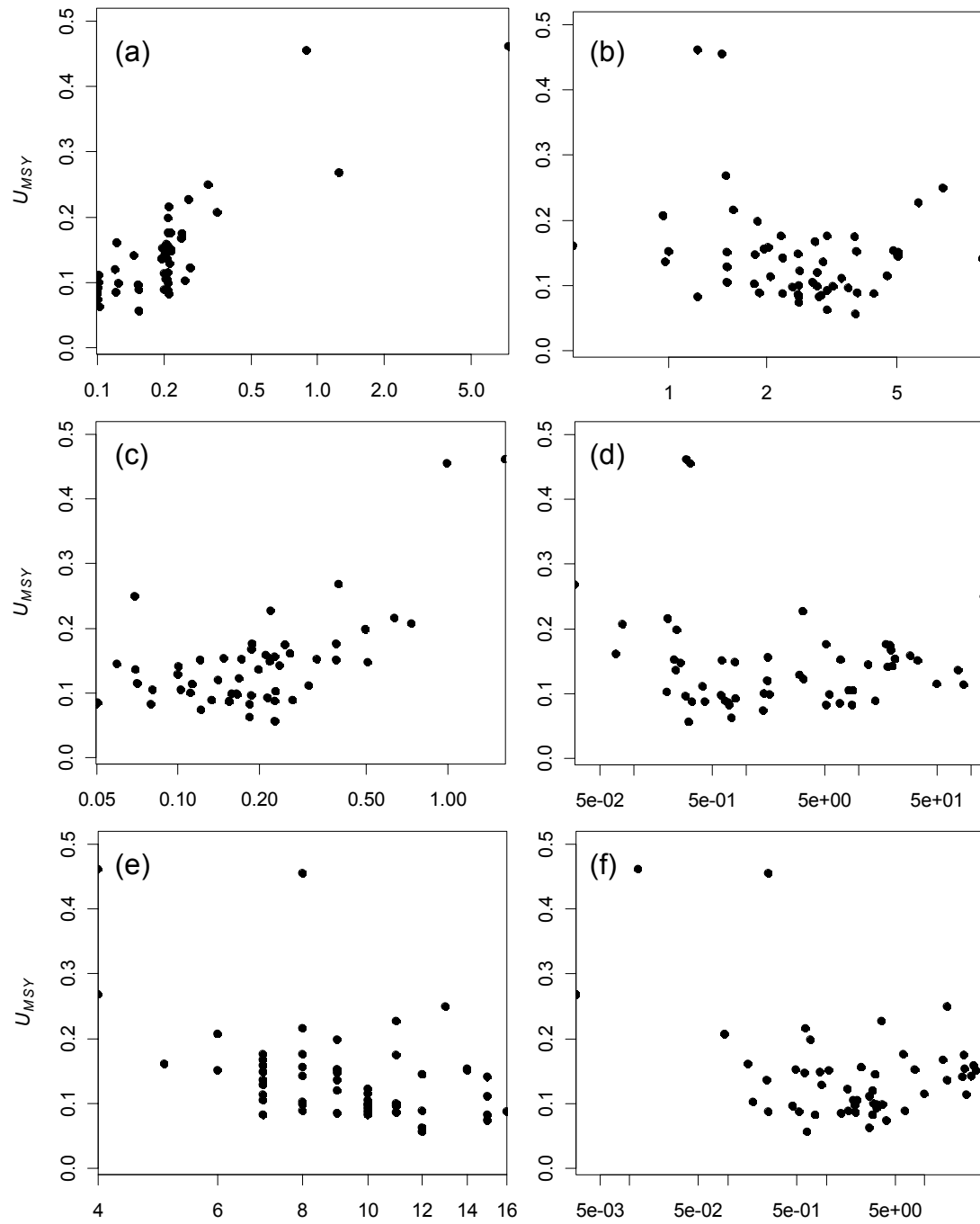




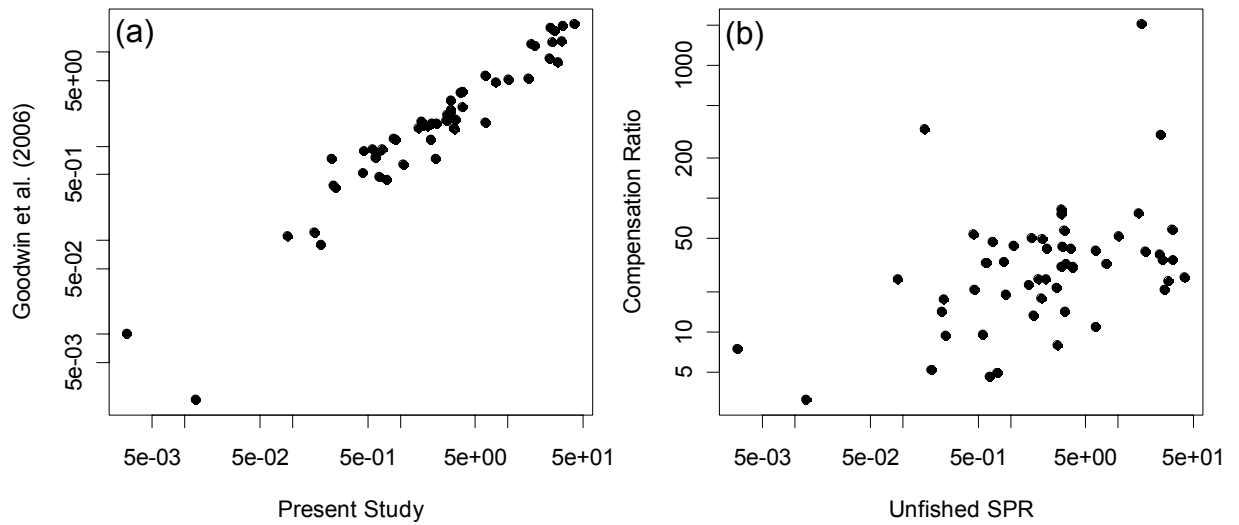
**Figure 3.3.** Relationships between CR and  $U_{MSY}$  under (a) Ricker and (b) Beverton-Holt recruitment. See text for correlation coefficients. Note logarithmic scale and differences in scale of y-axis.



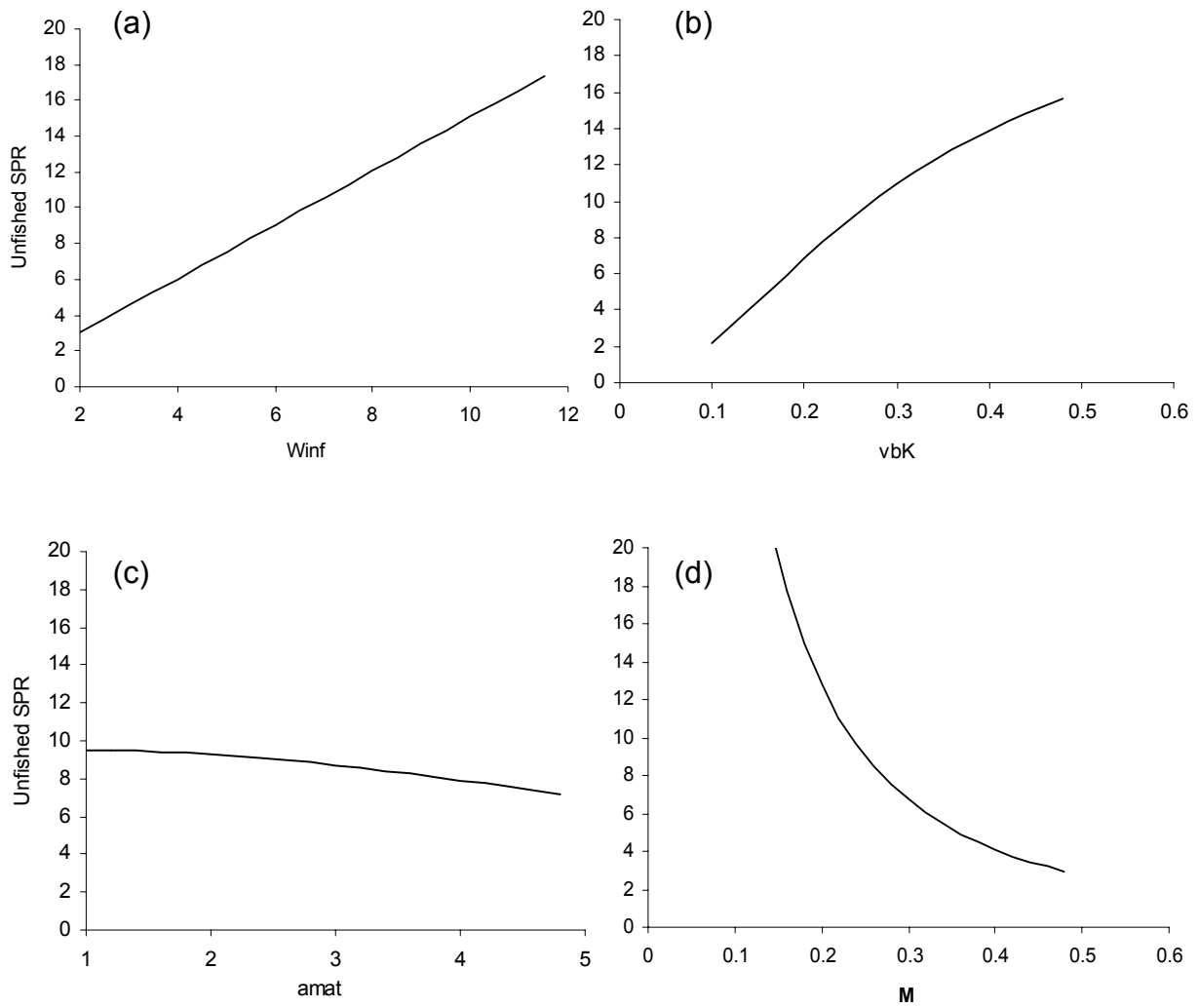
**Figure 3.4.** Correlations between log life history parameters and  $U_{MSY}$  for the Ricker model. Graphs show (a)  $M$ , (b)  $a_{mat}$ , (c)  $\kappa$ , (d)  $W_{\infty}$ , (e)  $a_{max}$  and (f)  $SPR_0$ . Correlation coefficients are given in Table 3.2. Note logarithmic scale.



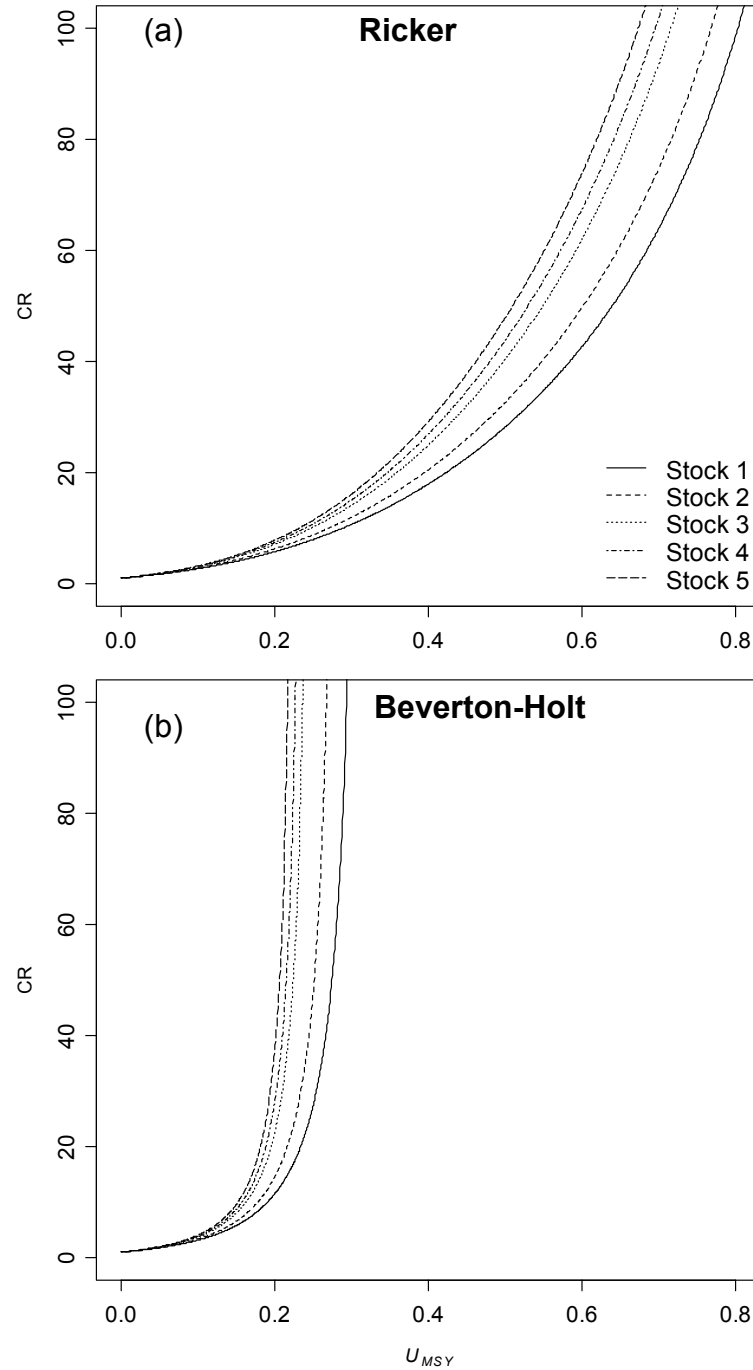
**Figure 3.5.** Correlations between log life history parameters and  $U_{MSY}$  for the Beverton Holt model. Graphs show (a)  $M$ , (b)  $a_{mat}$ , (c)  $\kappa$ , (d)  $W_{\infty}$ , (e)  $a_{max}$  and (f)  $SPR_0$  for the Beverton-Holt model. Correlation coefficients are given in Table 3.2. Note logarithmic scale.



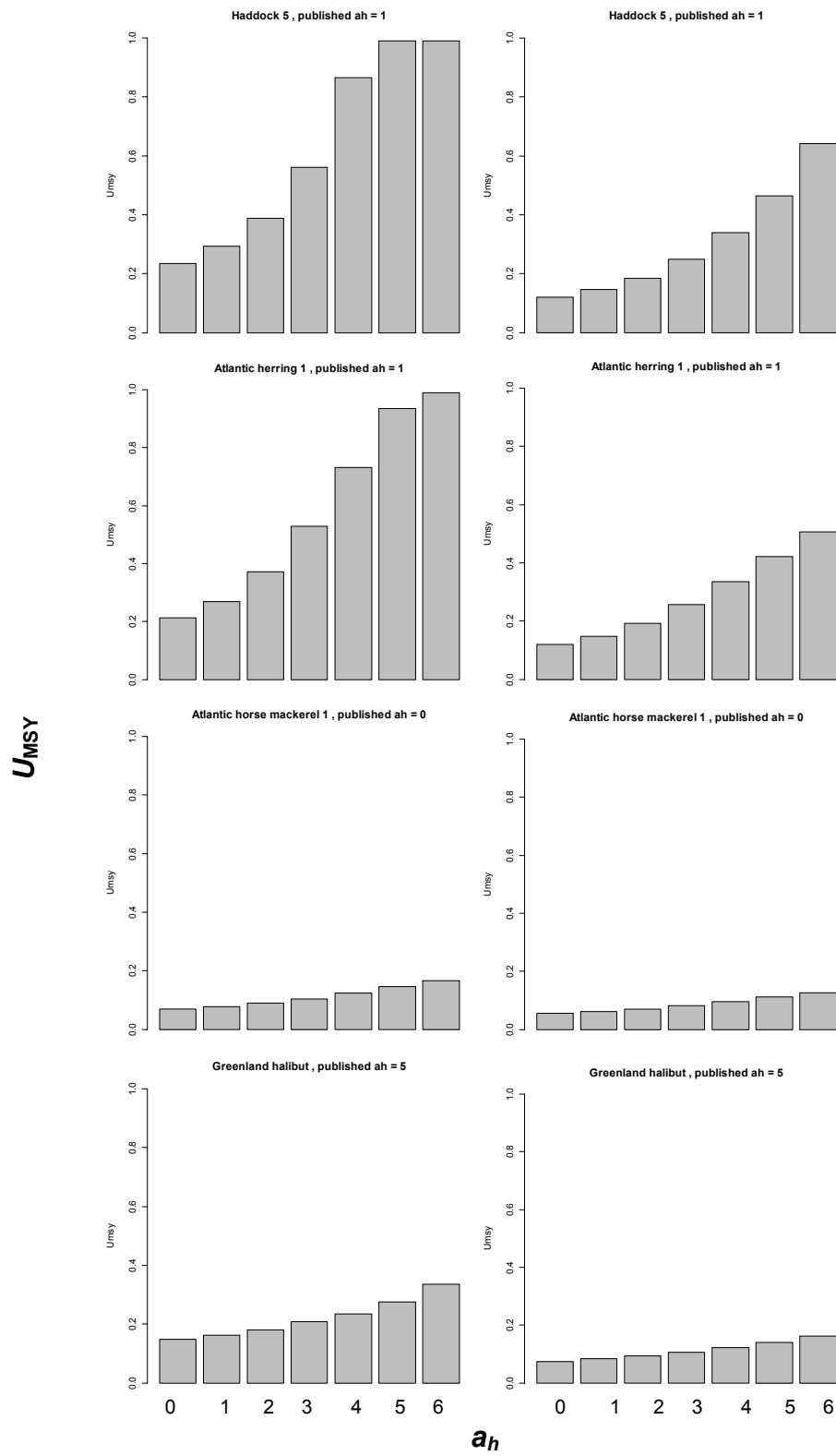
**Figure 3.6.** Correlations between (a)  $SPR_0$  estimated by Goodwin *et al.* (2006) and  $SPR_0$  obtained in the present study; and (b)  $\ln SPR_0$  (present study) and  $\ln CR$  published by Goodwin *et al.* (2006). See text for correlation coefficients.



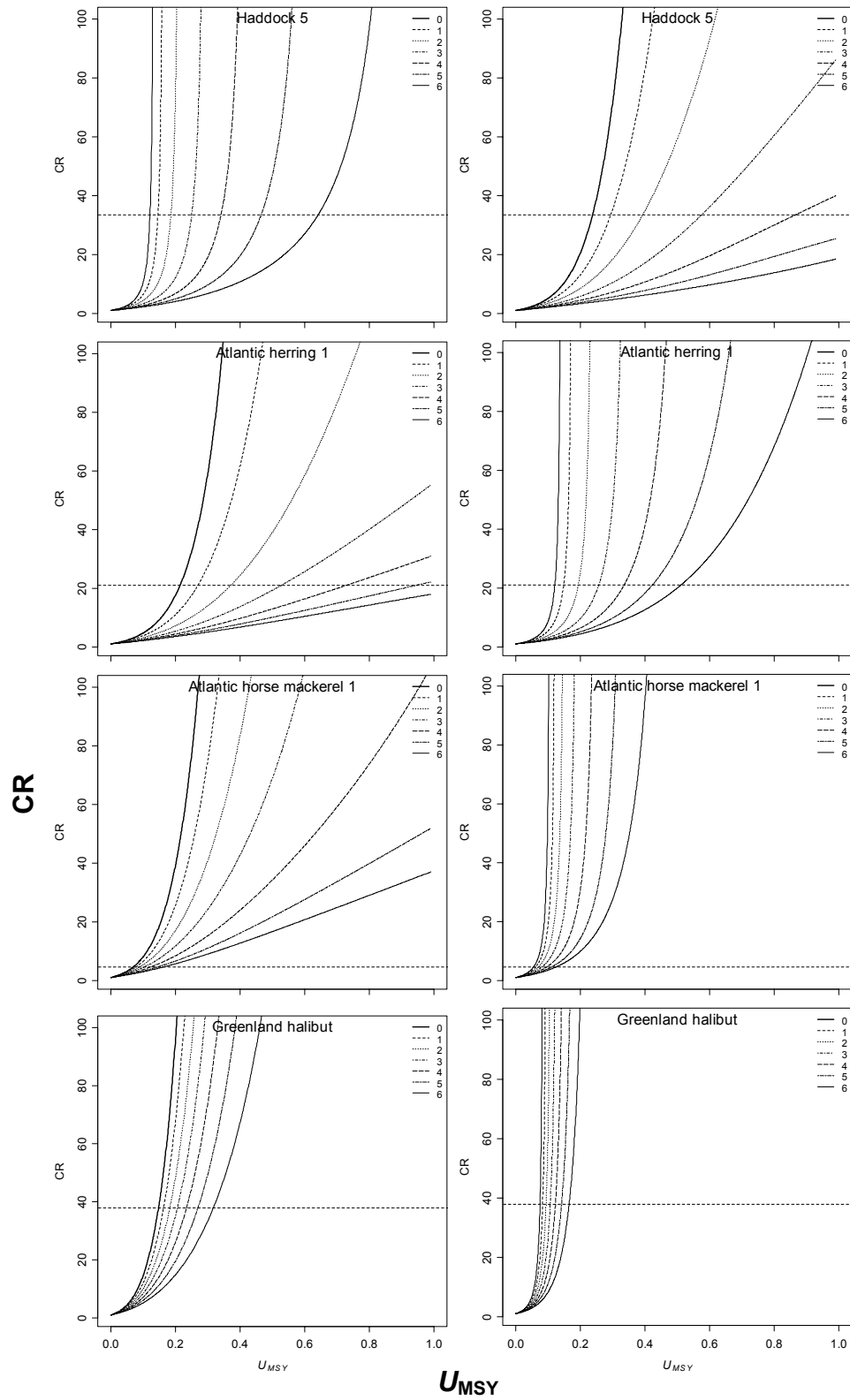
**Figure 3.7.** Relationship of  $SPR_0$  to (a)  $W_{\infty}$ ; (b)  $\kappa$ ; (c)  $a_{mat}$ ; and (d)  $M$ , for a hypothetical fish stock. In each case all other parameters were held constant while the parameter under consideration was varied. See Table 3.3 (Stock 3) for baseline parameters used.



**Figure 3.8.** Relationship between  $U_{MSY}$  and CR for five hypothetical stocks with  $SPR_0 = 9$ , under (a) Ricker and (b) Beverton-Holt stock-recruitment assumptions. Each stock has a different pair of values of  $\kappa$  and  $W_{\infty}$ , but all other parameters are held constant (Table 3.4). Note truncation of the y-axis at CR=100, for readability.



**Figure 3.9.** Predicted  $U_{MSY}$  for four example stocks over a range of ages at first harvest under Ricker (left panel) and Beverton-Holt (right panel) assumptions for the stock-recruitment relationship.



**Figure 3.10.** Predicted  $U_{MSY}$ -CR curves for the four example stocks in Figure 9, over a range of ages at first harvest under Ricker (left panel) and Beverton-Holt (right panel) assumptions for the stock-recruitment relationship. Published estimates of CR for each stock (Goodwin *et al.* 2006) are shown as horizontal dotted lines.



## **Chapter 4. Optimal harvest rate for long-lived, low-fecundity species: deepwater dogsharks of the continental slope of southeastern Australia**

### **Introduction**

Chondrichthyans (sharks, skates, rays and chimaeras) are among the least productive species caught in fisheries, mainly due to life history traits that include low fecundity, late maturity and slow growth (Walker 1998). A number of authors have documented large declines in fished Chondrichthyan populations (e.g., Dulvy *et al.* 2000; Graham *et al.* 2001; Baum *et al.* 2003; Baum and Myers 2004, but see Burgess *et al.* 2005 and Baum *et al.* 2005) and, at the time of writing, 51 Chondrichthyan species were listed as Critically Endangered or Endangered in the IUCN Red List of Threatened Species (IUCN 2008). Sharks are frequently of low value in fisheries and tend to receive little management attention, as priority is usually given to maintaining harvest of more valuable and productive teleosts (Bonfil 2004). The difficult trade-off between abundance of low-productivity species and catch of more productive species is inherent in multispecies fisheries, although it is seldom explicitly acknowledged (Hilborn *et al.* 2004; Walters and Martell 2004). However, with the shift towards more ecosystem-based fisheries management (EBFM) in many countries (FAO 2003; Pikitch *et al.* 2004) there may be a requirement for more explicit recognition and assessment of this trade-off. An important part of the assessment process is obtaining estimates of the relative productivities of species in fisheries. This can be problematic when good quality data are lacking.

Lack of informative time series for sharks has led a number of authors to develop demographic methods for improving estimates of shark productivity using more readily-available life-history information (e.g., Smith *et al.* 1998; Cortés 1998; 2002; Heppell *et al.* 1999; McAllister *et al.* 2001; Dulvy and Reynolds 2002). Demographic approaches have provided valuable estimates of the range of harvesting pressures that can sustainably be applied to shark populations and, in some cases, maximum sustainable harvest rate,  $U_{MSY}$ , has been found to be very low. For example, McAllister *et al.* (2001) used demographic approaches to obtain an informative prior for a surplus production model, applied to large coastal sharks on the US east coast. Their final

median estimate of  $U_{MSY}$  was 0.035 (3.5% of the population could be sustainably fished per year), more than an order of magnitude lower than estimates obtained without incorporating demographic information. Cortés (1998) used a life table approach to estimate  $U_{MSY} = 0.014$  for dusky sharks (*Carcharhinus obscurus*) and  $U_{MSY} = 0.022$  for Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) in the eastern USA.

$U_{MSY}$  is the fixed annual harvest rate that maximises long-term yield of a fish population (see Chapter 2). It is a function of the intrinsic productivity of the population, determined by growth, mortality and density dependence in recruitment, as well as of the selectivity regime of the fishery. In sharks, density dependence in recruitment may occur through decreased rates of predation, competition or cannibalism as population size is reduced, realised through changes to the natural mortality rate in juvenile age groups. Walker (1994) showed evidence for density dependence in the survival rate of juvenile gummy sharks (*Mustelus antarcticus*) in Australia, although Walker (1998) suggested that, for many species, density dependence in survival of juveniles may be less important than density dependence in natural mortality and growth rate across all age classes in determining population size. This author noted that recruitment is commonly assumed to be a linear function of adult stock size in sharks, based on knowledge of shark reproductive strategies (i.e, many sharks have mammal-like reproduction, with each individual producing few large, live young with a relatively high survival rate). This does not imply that stock-recruitment relationships such as the Beverton-Holt (1957) or Ricker (1954) function are inappropriate to use for sharks, as these functions approach linearity for low recruitment compensation (CR values approaching 1).

Chapter 2 (Forrest *et al.* 2008) presented an analytical relationship between  $U_{MSY}$  and CR for iteroparous species (see also Schnute and Richards 1998 and Martell *et al.* 2008). Chapter 2 showed that the relationship between  $U_{MSY}$  and CR is affected by certain life history parameters, particularly growth rate and the age at which fish are first harvested. Chapter 3 further explored these relationships and showed that, for some stocks,  $U_{MSY}$  was more strongly constrained by life history parameters than by either selectivity or the magnitude of recruitment compensation. These stocks tended to be longer-lived with lower natural mortality and slower growth. Graphic presentation of the relationship between CR and  $U_{MSY}$  for these stocks showed that, under Beverton-Holt recruitment,  $U_{MSY}$  had a maximum upper boundary that could not be exceeded, no

matter how strong the recruitment compensation response. The upper boundary could be found using only life history and selectivity information. Based on these findings, it was suggested in Chapters 2 and 3 that the model would be useful for finding the range of possible hypotheses for  $U_{MSY}$  for long-lived, data-limited species. As these characteristics tend to apply to elasmobranchs, it may be possible to place fairly conservative constraints on the management parameter  $U_{MSY}$  for these species, using only life history and selectivity information, despite uncertainty in recruitment parameters.

More than 200 Chondrichthyan species occur in the Australian region (Cavanagh *et al.* (eds) 2003). As in most parts of the world (FAO 2000; Bonfil 2004) data for stock assessment of sharks is extremely limited in Australia. With the exception of a few important commercial species (*M. antarcticus* and *Galeorhinus galeus*: Punt *et al.* 2005) and charismatic threatened species (e.g., *Carcharias taurus*: Otway *et al.* 2003a,b), there have been few attempts to assess sharks in Australia (but see, e.g., Braccini *et al.* 2006a). Deepwater dogsharks (Order Squaliformes) are thought to be particularly vulnerable to overfishing due to life history strategies that place them at the lower end of the shark productivity spectrum (Daley *et al.* 2002). For example, Harrison's dogshark (*Centrophorus harrissoni*), known to be extremely depleted off the continental slope of southeastern Australia (Andrew *et al.* 1997; Graham *et al.* 1997; Graham *et al.* 2001) and listed as Critically Endangered on the IUCN Red List of Threatened Species (IUCN 2008; Cavanagh *et al.* (eds) 2003), does not reach maturity until close to its maximum length and has only 1-2 pups every two years (Daley *et al.* 2002). Like other deepwater dogsharks, it is ovoviviparous, giving birth to large pups that are potentially immediately vulnerable to fishing gear.

Australian deepwater dogsharks are caught mostly as bycatch in multispecies trawl and line fisheries off the continental slope of southeastern Australia, and their flesh and livers have some commercial value (Daley *et al.* 2002). A number of dogshark species were recorded in surveys of the upper continental slope of NSW in 1976 (Gorman and Graham 1976; 1977), around the time that large-scale commercial trawling on the slope began. The surveys were repeated (partially) in 1979 (Gorman and Graham 1979; 1980a,b; 1981) and again in 1996 (Graham *et al.* 1997), resulting in a total of 361 tows in all three sets of surveys. The 1996 surveys found that most species of deepwater dogshark on the upper slope had undergone dramatic declines in the twenty

years since the first surveys, with some sites recording catch rates more than 99% below those in 1976 (Andrew *et al.* 1997; Graham *et al.* 2001). Three species (*C. harrissoni*; *C. zeehaani* and *C. moluccensis*) are currently under consideration for listing as Endangered under the *Environment Protection and Biodiversity Conservation Act 1999*.

In this chapter, limitations on  $U_{MSY}$  for Australian dogsharks are investigated. The model described by Forrest *et al.* (2008; Chapter 2) is systematically applied to show that, for certain growth, selectivity and reproductive schedules that tend to apply to dogsharks, the range of hypotheses for  $U_{MSY}$  that can be considered possible may be very small indeed. The method is first systematically applied to hypothetical ‘species’ over a range of parameter-values representative of dogsharks; and then to 12 deepwater dogshark species from the continental shelf and slope of NSW. In the latter case, Monte Carlo simulations are used to account for uncertainty in life history parameters. Uncertainty in age-at-first-harvest is also considered. To test results for consistency with those from a previously published approach, a demographic model, described by McAllister *et al.* (2001), was used to estimate intrinsic rate of growth,  $r$ , for the 12 dogshark species. The intrinsic rate of growth represents the population production rate and also, therefore, the long-term harvest rate that could lead to extinction of the population,  $U_{Max}$ . Both methods suggest that sustainable harvest rates for deepwater dogsharks are very low indeed. It is proposed that, despite lack of knowledge of recruitment parameters, there is more certainty about  $U_{MSY}$  than might have been expected, given data-limitations. The results of this analysis can be used to inform policy for deepwater dogsharks and may be useful in the development of informative Bayesian priors for stock assessment models.

## Methods

### Calculating the upper limit of $U_{MSY}$

*Equilibrium age-structured model* - The age-structured model with  $U_{MSY}$  as leading productivity parameter was described in detail in Chapter 2 (Forrest *et al.* 2008). The present model differs only in terms of calculation of fecundity at age,  $f_a$ . In many fisheries models, fecundity is represented as a non-saturating function of weight. Sharks, however, tend to produce few large eggs or give birth to large live young and, for energetic and other reasons (e.g., *in-utero*

cannibalism), the number of pups produced is often consistent from year to year, regardless of the shark's size. Population fecundity at age is therefore modelled as a saturating function of litter size and maturity-at-age, given by

$$(4.1) \quad f_a = LS \cdot \frac{1}{1 + e^{\left(\frac{-(a - a_{mat})}{\sigma_m}\right)}}$$

where LS is the maximum annual litter size,  $a_{mat}$  is age-at-50%-maturity (the age at which 50% of individuals are mature) and  $\sigma_m$  determines the steepness of a logistic maturity curve, with smaller values of  $\sigma_m$  resulting in a steeper ogive.

Natural mortality is difficult to measure but may be empirically related to von Bertalanffy growth rate,  $\kappa$  (Beverton and Holt 1959); growth parameters and temperature (Pauly 1980); age at maturity (Jensen 1996); both growth rate and age at maturity (Chen and Watanabe 1989); or maximum age (Hoenig 1983). In a demographic study of two shark species, McAuley *et al.* (2007) compared five different methods to estimate natural mortality rate and obtained similar values for all methods. Here, it is assumed that  $M = 1.5\kappa$  (Beverton and Holt 1959).

#### *Calculating the upper limit of $U_{MSY}$*

Chapter 2 presented the analytical relationship between  $\alpha$  and  $U_{MSY}$  ( $\alpha = f(U_{MSY})$ ; equation 2A.6) and showed that the relationship is influenced by life history and selectivity parameters, notably growth rate, maximum age and the age at first harvest. Chapter 3 showed that, under the assumption of Beverton-Holt recruitment, for a large number of parameter combinations,  $U_{MSY}$  approached an asymptotic maximum value (see the Appendix to Chapter 3). The asymptote (illustrated in Figure 4.1) is defined as the value of  $U_{MSY}$  for which the denominator of  $f(U_{MSY})$  is predicted equal to zero (i.e.,  $f(U_{MSY})$  is undefined at the asymptotic value of  $U_{MSY}$ ). This occurs

when  $U_{MSY} = -k_2^{-1}$  ( $k_2 = \frac{\partial \varphi_{VBMSY}}{\partial U_{MSY}} \varphi_{VBMSY}^{-1}$ ; see Chapter 2, Appendix A).  $U_{MSY} = -k_2^{-1}$  cannot be

solved analytically for  $U_{MSY}$  because  $\varphi_{VBMSY}$  is itself a recursive function of  $U_{MSY}$ , through the effect of  $U_{MSY}$  on survivorship (see equation 2.3). However, it is true that all values of  $U_{MSY}$

lower than the asymptotic limit will satisfy the inequality  $U_{\text{MSY}} + k_2^{-1} < 0$ . Therefore, the maximum possible hypothesis of  $U_{\text{MSY}}$  can be identified by systematically calculating  $U_{\text{MSY}} + k_2^{-1}$  for a finely-scaled, discrete sequence of hypotheses of  $U_{\text{MSY}}$  until the first value predicting  $U_{\text{MSY}} + k_2^{-1} > 0$  is reached. This  $U_{\text{MSY}}$  hypothesis is then discarded and the upper limit of  $U_{\text{MSY}}$  is identified as the largest remaining  $U_{\text{MSY}}$  hypothesis. Note that all  $U_{\text{MSY}}$  hypotheses for which  $U_{\text{MSY}} + k_2^{-1} > 0$  predict impossible, negative predictions of  $\alpha$ . This is illustrated in Figure 4.1.

The above rule can be applied to any fished species where Beverton-Holt recruitment is assumed. For sharks and similar species, however, there is further constraint on possible values of  $\alpha$ , due to the way the stock-recruitment function is parameterised. Because sharks tend to produce large eggs or live young, the degree of certainty in the absolute number of eggs produced per female is usually high. This, and the relative independence of litter size and weight-at-age in sharks, make it appropriate to parameterise their stock-recruitment function in terms of numbers of eggs rather than spawning stock biomass (as is usually the case for teleosts). When the units of the dependent and independent variables of the stock-recruitment function are the same,  $\alpha$  is literally the maximum survival rate from egg or pup to recruit and, therefore, cannot exceed unity. Another way of thinking about this is in terms of the recruitment

compensation ratio CR, which is the ratio of  $\alpha$  and unfished juvenile survival  $\frac{R_0}{E_0}$  (equation 2.6;

see Figure 1.2), or, rearranging,  $\alpha = \text{CR} \frac{R_0}{E_0}$ . If, for example,  $\frac{R_0}{E_0} = 0.2$ , then CR cannot exceed

5, as this would give  $\alpha > 1$ . This implies that, for sharks and similar species that produce few large eggs with high juvenile survival rates (where it is most appropriate to parameterise the  $x$  and  $y$  axis of the stock recruitment function in the same units), the interval over which CR is defined can be calculated from life history data.

To obtain the upper limit of  $U_{\text{MSY}}$  ( $U_{\text{MSY}}^{\text{Lim}}$ ) for each stock, the model was run iteratively over an ascending sequence of hypotheses of  $U_{\text{MSY}}$  (0 to 1, step size 0.001), calculating  $\alpha$  (equation 2.A6) and CR (equation 2.6) at each iteration. The results were then filtered to remove impossible values. At the first round of filtration, all values of  $U_{\text{MSY}}$  that predicted  $U_{\text{MSY}} + k_2^{-1} > 0$  were discarded. If any of the remaining  $U_{\text{MSY}}$  hypotheses resulted in  $\alpha > 1$ , these were also

discarded. The highest remaining value of  $U_{MSY}$  then represented the maximum possible hypothesis for  $U_{MSY}$ , i.e.,  $U_{MSY}^{Lim}$ .

### **Systematic exploration of the effects of life history and selectivity parameters on $U_{MSY}^{Lim}$**

To show the effects of life history parameters on  $U_{MSY}^{Lim}$ , the algorithm was first systematically applied to hypothetical dogshark-like ‘species’, which were defined by combinations of life history parameters that could be reasonably applied to dogsharks (Table 4.1). Because  $U_{MSY}$  is partly determined by selectivity, age-at-50%-first-harvest,  $a_h$ , was also systematically varied. A logistic selectivity function (equation 2B.4) with fixed standard deviation was assumed (Table 4.1). For the present analysis, sensitivity to the form of the selectivity function (e.g., logistic vs dome-shaped) was not tested. The parameter values shown in Table 4.1 were systematically tested in a nested loop structure, thereby calculating  $U_{MSY}^{Lim}$  for all parameter-combinations.

### **Application to deepwater dogsharks**

Table 4.2 shows life history parameters for 12 species of dogshark caught on the continental shelf and slope of NSW. Most species are caught in deep water (> 300 m depth; Daley *et al.* 2002), although *S. megalops* also occurs in shallower water on the continental shelf (Braccini *et al.* 2006a). Parameters were missing for several species and, due to the difficulty of observing deepwater dogsharks, many of the available estimates were based on small-scale studies or opportunistic observations (Daley *et al.* 2002). It was therefore important to account for uncertainty in life history parameters and to test for sensitivity to important, but unavailable, selectivity parameters (i.e., age at recruitment). The algorithm described above was applied to each species in a Monte Carlo simulation framework, treating key parameters  $LS$ ,  $\kappa$ ,  $a_{max}$  and  $a_{mat}$  as random variables. Note that the litter sizes shown in Table 4.2 were halved to account for the fact that most species are believed to give birth only once every two years (or less frequently; Daley *et al.* 2002). For simplicity, other parameters were fixed (see Table 4.2).

### Parameter distributions

Sampled distributions of parameters for each species are shown in the Appendix to Chapter 4. Literature estimates of the growth parameter  $\kappa$  were only available for five species, but were all low and of a similar magnitude (Table 4.2). It was therefore assumed that a common probability distribution of  $\kappa$  was shared by all 12 species. A lognormal probability distribution was assumed, which allowed for a longer right-hand tail while preventing values too close to zero. The mean of the distribution for all species was set to  $\ln(\bar{\kappa})$ , where  $\bar{\kappa}$  is the mean of the literature estimates of  $\kappa$  for the species for which estimates were available. The standard deviation was set to 0.2, an arbitrary value that allowed uncertainty to be considered, while remaining in a range appropriate for these sharks.

All other parameters were drawn from uniform distributions. Estimates of maximum age,  $a_{max}$ , were not available for seven species. In these cases, if possible, the same  $a_{max}$  as congeners was assumed. *D. licha* and *E. granulosus* were assumed to have the same maximum age as *D. calcea*. The upper and lower bounds of the uniform distribution were then set to  $5 + a_{max}$  and  $a_{max} - 5$ , respectively. Although estimates of  $a_{mat}$  were only available for four species, estimates of length-at-maturity  $L_{mat}$  were available for all species (Table 4.2). For species without literature estimates of  $a_{mat}$ , deterministic  $a_{mat}$  was set to the age corresponding to  $L_a = L_{mat}$ , predicted by the von Bertalanffy growth equation (equation 2B.1), using  $\bar{\kappa}$ ,  $L_{\infty}$  and  $a_0$  (where an independent estimate of  $a_0$  was not available, it was set so that the model predicted a newborn pup size that corresponded to the value given in Table 4.2). Note that  $L_{\infty}$  was approximated from  $1.2L_{max}$  (Table 4.2). Parameters to convert length to weight were taken from Daley *et al.* (2002). The upper and lower bounds of the uniform distribution were then set to  $5 + a_{mat}$  and  $a_{mat} - 5$ . Because litter size, LS, was already extremely low for a number of stocks ( $0.5 \text{ y}^{-1}$ ), the lower boundary of the uniform distribution was set to the literature estimate (Table 4.2). The upper limit was set to the literature estimate + 4. Boundaries of all distributions were arbitrarily set to allow the effects of parameter uncertainty to be seen without deviating too far from values characteristic of these sharks.

No selectivity data are available for these stocks. Selectivity-at-age was assumed to follow a steep logistic function, with  $\sigma = 0.1a_h$  (equation 2B.4). Effects of  $a_h$  on  $U_{MSY}^{Lim}$  for each species were evaluated by running the model over a sequence of values of  $a_h$  ranging from  $a_h = 1$  to  $a_h =$



15, with step size 2 years.  $U_{\text{MSY}}^{\text{Lim}}$  was calculated for each species using the algorithm described in the previous section. For each species, for each value of  $a_h$ , 100 Monte Carlo simulations were done, with parameters drawn at random from their respective distributions.

### Demographic analysis

A demographic model (McAllister *et al.* 2001) was used to estimate intrinsic rate of growth,  $r$ , for the 12 dogshark species, given uncertainty in the input parameters described above. The intrinsic rate of growth represents the harvest rate that would lead to extinction of the population,  $U_{\text{Max}}$  (Hilborn and Walters 1992). Therefore estimates of  $U_{\text{MSY}}^{\text{Lim}}$  obtained in the previous section would be expected to be lower than estimates of  $r$ , although it is important to note that the demographic model directly estimates  $r$ , while the approach above estimates the upper limit of  $U_{\text{MSY}}$ . For these reasons, the results from the two approaches are not directly comparable, but are expected to give results of similar magnitude. Note that  $r$  is often used to obtain approximate estimates of  $U_{\text{MSY}} = r/2$  (e.g., McAllister *et al.* 2001) but this rule only holds under the assumptions of the logistic surplus production model (Schaefer 1954).

In the demographic approach, an age-structured model (without explicit representation of density dependent recruitment) was used to obtain  $r$ , which was defined as the ratio of abundance between one time-step and the previous, after stabilisation of the age-structure in the model. The model was initialised by

$$(4.3) \quad N_{a,0} = 1000l_a$$

where  $N$  is female numbers at age  $a$  at time  $t = 0$  and  $l_a$  is unfished survivorship at age (equation 2.3).

For subsequent time-steps, the number of age 0 females was calculated as

$$(4.4) \quad N_{0,t+1} = \sum_{a=0}^{\infty} f_a N_{a,t} .$$

For  $a > 0$ , female numbers at age were calculated by

$$(4.5) \quad N_{a,t+1} = s_{a-1} N_{a-1,t}$$

where  $s_a$  is natural survival rate at age, given by  $e^{-M}$ .

The model was run until the age-structure stabilised. Stabilisation was determined by monitoring the average percent-change in proportions at age between each time step, given by

$$(4.6) \quad \Delta_t = 100 \frac{1}{a_{\max}} \sum_{a=0}^{a_{\max}} \left( \frac{\frac{N_{a,t}}{P_t} - \frac{N_{a,t-1}}{P_{t-1}}}{\frac{N_{a,t-1}}{P_{t-1}}} \right)$$

where

$$(4.7) \quad P_t = \sum_{a=0}^{a_{\max}} N_{a,t}.$$

When  $\Delta_t$  becomes very small ( $\Delta_t < 0.0001\%$ ) the age structure is considered stable and  $r$  can be approximated by

$$(4.8) \quad r = \ln \left( \frac{P_t}{P_{t-1}} \right) \text{ (McAllister *et al.* 2001).}$$

One thousand Monte Carlo simulations were used to sample from probability distributions of the input parameters described above.

## Results

### Systematic calculation of maximum possible $U_{MSY}$

This analysis systematically evaluated the effects of fecundity, longevity, maturity, growth rate and selectivity on the maximum possible hypothesis for  $U_{MSY}$  (i.e.,  $U_{MSY}^{Lim}$ ) for species with life-history attributes characteristic of deepwater dogsharks. Results are presented as contour plots of  $U_{MSY}^{Lim}$ , plotted against  $a_h$  and  $\kappa$ , allowing the effects of growth and selectivity on  $U_{MSY}^{Lim}$  to be seen simultaneously (Figure 4.2). Contour plots are presented in panels to show the effects of  $a_{mat}$  and LS. The contours in Figure 4.2 represent the degree of uncertainty in  $U_{MSY}$  that can be calculated for a given stock prior to any formal stock assessment. It is important to note that contour values represent the *maximum possible* hypothesis for  $U_{MSY}$  and actual values of  $U_{MSY}$  will be in the range  $0-U_{MSY}^{Lim}$ , depending on the species' (unknown) value of  $\alpha$ .

In general, uncertainty in  $U_{MSY}$  was low over the range of parameter-values considered.

Exceptions were more fecund, early-maturing cases with late  $a_h$  (Figure 4.2 c,d). In these cases,  $U_{MSY}^{Lim}$  reached values approaching or equal to 1, implying the existence of possible hypotheses for  $U_{MSY}$  where all vulnerable individuals are harvested. Such a situation could exist if a large enough proportion of the mature stock was invulnerable to the fishery (e.g., due to the existence of spatial refugia) and there was sufficient recruitment compensation to replace the harvested stock. For later ages at maturity and smaller litter sizes,  $U_{MSY}^{Lim}$  tended to be low ( $< 0.1$ ) for all values of  $a_h$  and  $\kappa$ , becoming extremely low ( $< 0.05$ ) for species with very late maturity and/or very small litters (Figure 4.2 e, f, i-l).

Some generalisations can be made about the contribution of individual parameters to the value of  $U_{MSY}^{Lim}$ . Over the parameter-ranges considered here results were almost completely insensitive to the value of  $a_{max}$  and very sensitive to the value of  $a_{mat}$  for some litter sizes (Figure 4.2). In all cases, there was a positive relationship between  $U_{MSY}^{Lim}$  and  $a_h$ , indicated by higher-valued contour lines to the right of every plot. Increasing litter size, LS, also had a positive effect on  $U_{MSY}^{Lim}$ , indicated by the trend towards higher-valued contour plots from left to right in Figure 4.2. The relationship between  $\kappa$  and  $U_{MSY}^{Lim}$  was complex, as its effect was mitigated by the values of other parameters, particularly  $a_{mat}$  and LS. For  $a_{mat} = 5$  (Figure 4.2 b,c,d), increasing  $\kappa$

had a positive effect on  $U_{\text{MSY}}^{\text{Lim}}$  (Figure 4.2 a-d). For  $a_{\text{mat}} = 20$ , however, the relationship was negative (Figure 4.2 i-l). The transition from positive to negative effect of  $\kappa$  on  $U_{\text{MSY}}^{\text{Lim}}$  can be seen in plots g and h of Figure 4.2, where the contours of  $U_{\text{MSY}}^{\text{Lim}}$  curve back on themselves as  $\kappa$  increases. This was caused by the effect of increased natural mortality rate  $M$  that occurred with increasing  $\kappa$  (through the relationship  $M = 1.5\kappa$  assumed here). As  $M$  increased, weight at age, which determines fishery yield, increased, but survivorship-at-age decreased, resulting in few surviving individuals in older age classes. Low survivorship coupled with late maturity (and low fecundity) resulted in few mature individuals and low egg-production (and therefore high unfished juvenile survival relative to  $\alpha$ ). Therefore, as  $\kappa$  was increased, the constraint on  $U_{\text{MSY}}$  imposed by  $\alpha \leq 1$  was reached at successively lower values of  $U_{\text{MSY}}$  (see Figure 4.2 plots e,f, i-l). In general, for the same reasons,  $U_{\text{MSY}}^{\text{Lim}}$  tended to decrease with increasing  $a_{\text{mat}}$ , although the magnitude of the effect varied.

## Dogshark results

The mean and modal values of  $U_{\text{MSY}}^{\text{Lim}}$  obtained from the Monte Carlo simulations were, in general, very low for all 12 species of dogshark, especially when age at first harvest was low (Table 4.3). Box plots of Monte Carlo results show the range of estimates of  $U_{\text{MSY}}^{\text{Lim}}$  for each tested value of  $a_h$ , with the median represented as a black bar inside the box showing the interquartile range, IQR (Figure 4.3). Whiskers represent the range of the results within 1.5IQR, with outliers represented as dots.

Estimates of  $U_{\text{MSY}}^{\text{Lim}}$  were especially low for species in the genus *Centrophorus*, for which mean  $U_{\text{MSY}}^{\text{Lim}} \leq 0.1$  was obtained for all values of  $a_h$  tested (Table 4.3). Similarly low values of  $U_{\text{MSY}}^{\text{Lim}}$  across all  $a_h$  were obtained for *D. quadrispinosa* and *C. crepidater*. For earlier age at first harvest ( $a_h \leq 5$ ), mean  $U_{\text{MSY}}^{\text{Lim}}$  was less than 0.05 for these species and less than 0.07 for all species. Low values of  $U_{\text{MSY}}^{\text{Lim}}$  can be attributed to late maturity and low fecundity coupled with early age at harvest. For all species, increasing  $a_h$  had the effect of increasing both the mean and variance of  $U_{\text{MSY}}^{\text{Lim}}$ , shown by the larger boxes and whiskers (Figure 4.3). Species with the highest mean estimates of  $U_{\text{MSY}}^{\text{Lim}}$  were *D. calcea*, *E. granulosus*, *S. megalops* and *S. mitsukurii* (Figure 4.3.; Table 4.3).

Many population models are parameterised in terms of biological productivity parameters such as CR rather than  $U_{\text{MSY}}$  and limitations on these parameters are therefore also of interest. The unfished juvenile survival rate,  $\frac{R_0}{E_0}$  is the inverse of unfished eggs per recruit,  $\phi_{E0}$ , which can be calculated using only life history parameters. The unfished juvenile survival rate provides a natural constraint on CR when the stock-recruit function is parameterised in terms of numbers of eggs rather than spawning stock biomass, i.e., CR cannot exceed  $\frac{R_0}{E_0}^{-1}$ , otherwise  $\alpha$  would exceed 1. Probability densities of unfished juvenile survival and the implied upper limit of CR ( $\text{CR}^{\text{Lim}}$ ) resulting from the Monte Carlo simulations are shown in Figure 4.4. Mean  $\text{CR}^{\text{Lim}}$  was conservative for most species ( $\sim 20$ ), and very conservative for *Centrophorus* spp. ( $\sim 5$ ), reflecting severe limits on CR implied by very high unfished juvenile survival rates (Figure 4.4).

### Demographic analysis

Mean and modal values of  $r$  ranged from 0.06 - 0.17 (Figure 4.5, Table 4.4). While  $r$  and  $U_{\text{MSY}}^{\text{Lim}}$  are not comparable, estimates of  $r$  from the demographic analysis, representing  $U_{\text{Max}}$ , were, in general, consistent with trends in the estimates of  $U_{\text{MSY}}^{\text{Lim}}$  from the previous section. The least productive species were found to be *Centrophorus* spp. and *D. quadrispinosa*, which had mean estimates of  $r = 0.06 - 0.08$ . The  $U_{\text{MSY}}^{\text{Lim}}$  analysis also found these to be the least productive species for all selectivities tested (Table 4.3). Similarly, the most productive species were found in both studies to be *D. calcea* and *E. granulosus*. In both analyses, modal values were lower than mean values, reflecting slightly skewed probability densities (Figures 4.3 and 4.5). There were highly significant positive correlations between the mean values of  $r$  and  $U_{\text{MSY}}^{\text{Lim}}$  across species, for all tested values of  $a_h$  ( $P < 0.001$ ; 10  $df$ ; see Table 4.5). The slope of the relationship between mean  $r$  and mean  $U_{\text{MSY}}^{\text{Lim}}$  increased as  $a_h$  increased. The value of the slope ranged from 0.23 ( $a_h = 1$ ) to 2.03 ( $a_h = 15$ ), with slope equal to 1 for  $a_h = 11$  (i.e,  $r$  and  $U_{\text{MSY}}^{\text{Lim}}$  approximately equal). See Table 4.5 and Figure 4.6.

## Discussion

Demographic approaches (e.g., Smith *et al.* 1998; Heppell *et al.* 1999; Cortés 1998; 2002; McAllister *et al.* 2001; Dulvy and Reynolds 2002; McAuley *et al.* 2007) have been very useful for estimating productivity of sharks and shark-like species. In one of the first studies applying demographic approaches to estimation of shark productivity, Smith *et al.* (1998) reported spiny dogfish (*Squalus acanthias*) to have the lowest intrinsic productivity of the 26 species they examined. Braccini *et al.* (2006a) reported similarly low values for *S. megalops* in Australia. Cortés (2002) found *S. megalops* and *S. mitsukurii* to have the lowest productivity of 38 species considered. While demographic approaches are instructive, they may be limited because they do not fully account for density dependence in recruitment (Heppell *et al.* 1999) and effects of selectivity on limits to  $U_{MSY}$ . This study has demonstrated that an upper boundary to the range of possible hypotheses of  $U_{MSY}$  is estimable for dogsharks and similar species using information only about life-history and selectivity; and that the upper possible hypothesis for  $U_{MSY}$  may be very small indeed in some cases. Examinations of limitations imposed on  $U_{MSY}$  by limits to the defined range of recruitment parameters proved a useful means of constraining estimates of  $U_{MSY}$ , using prior life history information. Results can be used in construction of informative priors for formal Bayesian stock assessment (e.g., McAllister *et al.* 2001) or directly, for species with very low  $U_{MSY}^{Lim}$ , to inform fisheries policy and harvest control rules (e.g., Braccini *et al.* 2006a).

Systematic exploration of combinations of different parameter on the upper limit of  $U_{MSY}$  implied that there is more certainty in  $U_{MSY}$  as populations tend towards more extreme life history strategies that include later maturity, slower growth and lower fecundity. The systematic analysis highlighted the complexity of the contribution of different parameters to  $U_{MSY}$ , which optimises growth, mortality, survivorship and recruitment over a highly non-linear parameter space. It was beyond the scope of this study to conduct an exhaustive analysis of all the effects of individual parameters on  $U_{MSY}^{Lim}$ , as this would require measurement of the rates of change of multiple variables in at least a five-dimensional parameter space, for a much larger range of values than considered here. However, within the parameter-space considered, some general patterns can be discussed.

Decreasing fecundity (litter size) had a strong negative effect on the maximum possible  $U_{\text{MSY}}$ . All other parameters equal, decreasing litter size decreases the predicted unfished eggs per recruit  $\varphi_{E0}$  and, therefore, must increase unfished juvenile survival, because it is the inverse of  $\varphi_{E0}$ . In other words, sharks with small litters must have high unfished juvenile survival rates. The biological interpretation is that, for a population with very small litters to be able to sustain itself in its unfished state, the survival rate of the few eggs produced must be very high. Modal estimates of the unfished juvenile survival rate in this study ranged from approximately 0.02 to 0.3, much higher than might be expected for most teleosts. The low values of CR found for the dogsharks in this study are consistent with the common assumption of near-linear stock-recruitment relationships for sharks, where recruitment is directly dependent on adult stock size (Bonfil 1994; Walker 1998). Note that Goodwin *et al.* (2006) analysed stock-recruit data for 54 Atlantic teleost stocks and found that CR was higher in stocks that were longer-lived and slower growing, contrary to the findings presented here. The argument of Goodwin *et al.* (2006), however, applies to teleosts, which grow continuously and for which there is a strong relationship between age, body size and fecundity. In evolutionary terms, long-lived teleosts can afford low rates of unfished juvenile survival because they are able to spread their reproductive potential over many lifetime spawnings (Heppell *et al.* 1999). This is not generally the strategy for sharks, which tend to produce few pups with a high chance of survival.

Chapter 2 reported a relatively minor effect of age at maturity on maximum  $U_{\text{MSY}}$  and a larger effect of maximum age,  $a_{\text{max}}$ . Very little to no effect of  $a_{\text{max}}$  was found in the present study, although it is important to note that fecundity in the model used in Chapter 2 was a function of weight and therefore there was no need to constrain  $U_{\text{MSY}}$  hypotheses to those that predicted  $\alpha \leq 1$ . In addition, the hypothetical stock considered Chapter 2 was relatively short-lived (15 y). For the given growth, survivorship and maturity schedule, increasing maximum age made a larger relative difference to potential yield than reducing age at maturity. For the longer-lived species considered here, however, survivorship of older age-classes was very low (extremely low for high  $M$  cases). Increases in potential yield were therefore better achieved when age at maturity was lower than by increasing the number of age classes, because mature older age classes contributed less to the reproductive output of the stock than younger age classes. This effect was increased by the fact that egg-production was very low, further decreasing the contribution of older age classes.

In general, the range of possible values of  $U_{\text{MSY}}$  for the real dogsharks was estimated to be very small. For most species, under the lowest age-at-first-harvest scenarios ( $ah \leq 7$ ), the mean upper limit of  $U_{\text{MSY}}$  was less than 0.1. For *Centrophorus* spp. the mean upper limit to  $U_{\text{MSY}}$  was less than 0.06 for all  $ah \leq 7$  and, even under the highest age-at-first-harvest scenario ( $ah = 15$ ), maximum possible  $U_{\text{MSY}}$  was 0.08 for *C. zeehaani*. Under higher age-at-first-harvest scenarios, for some species (*D. calcea*, *E. granulosus*, *S. megalops* and *S. mitsukurii*) the mean value increased to values greater than 0.2 at  $ah = 15$ . *Etmopterus granulosus* had larger litters than most other species (Table 2.1). The other species had small litters, but, on average, had earlier maturity than other species (Appendix to Chapter 4). The species with the largest litters, *C. plunketi* (19 pups) also had late maturity, hence a more conservative range of  $U_{\text{MSY}}^{\text{Lim}}$  than might be expected from large litters alone. It should be remembered that the values presented here represent the *maximum* hypothesis for  $U_{\text{MSY}}$  that could be admitted in a formal stock assessment, i.e.,  $0 < U_{\text{MSY}} \leq U_{\text{MSY}}^{\text{Lim}}$ .

The results compared favourably with those from the demographic approach, although the quantities estimated are not directly comparable. The demographic model predicted low mean  $r$  ( $< 0.13$ ) for all species. This represents the harvest rate (on the entire stock) that would cause eventual extinction of the stock,  $U_{\text{Max}}$ , i.e., harvest rates greater than  $r$  exceed the rate at which the population is able to replace itself (Hilborn and Walters 1992). There were significant positive correlations between the mean values of  $r$  and  $U_{\text{MSY}}^{\text{Lim}}$  across species, for all tested values of  $a_h$ . The slope of the relationship between mean  $r$  and mean  $U_{\text{MSY}}^{\text{Lim}}$  increased noticeably as  $a_h$  increased. Again, it should be remembered that  $U_{\text{MSY}}^{\text{Lim}}$  represents an upper threshold to  $U_{\text{MSY}}$  implied by life history and selectivity parameters and that the true value of  $U_{\text{MSY}}$  lays in the region  $0 < U_{\text{MSY}} < U_{\text{MSY}}^{\text{Lim}}$ . Therefore, for values of  $a_h$  where the slope was found to be greater than 1 (i.e.,  $U_{\text{MSY}}^{\text{Lim}} > r$ ), it should not be interpreted as an indication that  $U_{\text{MSY}}$  is greater than  $r$ , which is illogical. It should also be noted that demographic approaches such as the one used here are limited by the fact that they do not account for density dependence in recruitment (Heppel *et al.* 1999). It is therefore perhaps not advisable to search for predictive relationships between  $r$  and  $U_{\text{MSY}}^{\text{Lim}}$ , which differ in their interpretations and assumptions. Rather, they should be considered as separate sources of advice. For example, in cases where extinction risk is more of a concern than multispecies considerations, it may be more appropriate



to report  $r$  directly, as this directly represents the fishing mortality that would cause eventual extinction of the stock.

Estimates of  $r$  (i.e.,  $U_{\text{Max}}$ ) are important for management of multispecies fisheries where it is not possible to maintain all stocks at  $U_{\text{MSY}}$  simultaneously. ‘Sustainable overfishing’, where  $U_{\text{MSY}} < U < U_{\text{Max}}$ , may be an acceptable policy that addresses the need for compromise between fishing of important food species and conservation of less productive species (Hilborn 2007a). Punt (2000) reported that the relationship between  $F_{\tau}$  (the instantaneous, age-structured equivalent of  $U_{\text{Max}}$ ) and  $F_{\text{MSY}}$  was a function of the productivity of the stock, and that  $F_{\tau}$  and  $F_{\text{MSY}}$  could be reasonably close in value for low productivity stocks such as sharks. Myers and Mertz (1998) showed that a precautionary approach for moving these reference points further apart (i.e.,  $F_{\text{MSY}} \gg F_{\tau}$ ) is to increase the age at which individuals become vulnerable to fishing gear and to allow at least one spawning before allowing individuals to become vulnerable to capture (see also Froese 2004; Froese *et al.* 2008).

Identification of successful tactics for achieving sustainable fishing limits for dogsharks in southeastern Australia will be challenging. Dogsharks are born relatively large and are potentially immediately vulnerable to hooks and trawl nets and also appear to mature late in life (Daley *et al.* 2002). These authors suggested that spatial closures might be one of the best ways to reduce harvest rates on these species. Recently, three deepwater spatial closures have been announced off NSW, off South Australia and in Bass Strait, aimed at protecting populations of *C. moluccensis*, *C. zeehaani* and *C. harrissoni* respectively (R. Daley, CSIRO, pers. comm.). The NSW area is located over undersea fibre optic cables and was not targeted at any specific dogshark population, although the wider region is known to be inhabited by *C. moluccensis*. The other two locations were selected after observations of aggregations of dogsharks in these areas. All three locations were identified and implemented with collaboration and support from the fishing industry. The success of spatial refugia as a harvest control measure depends upon spatial distribution and movement of the population (Gerber and Heppell 2004; Gerber *et al.* 2005). Very little is known about Australian deepwater dogsharks in these respects, although limited surveys and commercial observations provide some information. There have been no formal tagging studies of deepwater dogsharks in southeastern Australia. Studies in New Zealand have suggested that migration may be extensive in some dogsharks (Clarke and King 1989;

Wetherbee 2000) and this could have important seasonal effects on selectivity. Survey data from NSW and southern Australian waters, and observations from commercial fishing vessels, suggest there is separation of males and females of many species (Andrew *et al.* 1997; Graham *et al.* 1997; Daley *et al.* 2002). This implies that some movement would be necessary for mating and, therefore, that sharks may move outside the closures. The same sources also provide evidence for spatial separation of adults and juveniles of most species, suggesting that strategic avoidance of certain age classes could be possible. There may be natural refugia for some species. Several species (e.g., *C. zeehaani*; *C. harrissoni*) are known to occur in untrawlable canyoned areas (Daley *et al.* 2002), although they are accessible by longliners targeting teleosts pink ling (*Genypterus blacodes*) and blue-eye (*Hyperoglyphe antarctica*).

Walker (1998) discussed effects of size-selectivity in gillnets for sharks but noted that there have been few selectivity studies of sharks in trawl nets. Bycatch reduction devices (BRDs), such as escape panels and grids, have been very effective in reducing bycatch of fish in prawn trawls (Kennelly and Broadhurst 2002; Eayrs 2007) and a number of these devices have been shown to be effective at reducing catches of sharks in particular (Brewer *et al.* 1998). Gilman *et al.* (2008) interviewed fishers and compiled fishery data and literature on 12 pelagic longline fisheries, in eight countries, to assess interactions between sharks and longlining. Fishers employed a range of methods to: (i) increase efficiency in catching target non-shark species; and (ii) decrease shark catches. Both of these methods could be effective at reducing unwanted shark catches, but the latter tended to only be employed when there were disincentives to catch sharks (e.g., legal shark retention limits and large fines). Sharks are often patchily distributed and one of the main methods employed by the fishers to reduce shark catch was to move away from areas with high catch rates. Avoidance of topographic or oceanographic features known to be favoured by sharks, and vessel-to-vessel communication of shark ‘hotspots’ to avoid were also effective. Shark-repellent technologies, involving magnets or chemicals, are being developed to deter sharks from longline hooks but are currently still in testing phases (Gilman *et al.* 2008; see also [www.smartgear.org](http://www.smartgear.org)).

The trade-off between catch of productive commercial species and abundance of low-productivity, low-value species such as sharks is unavoidable in most, if not all, multispecies fisheries. Society’s interests are measured by a broad range of objectives that includes

profitability of primary industries and maintenance of fresh seafood as well as conservation of vulnerable species. Different stakeholders value these objectives differently and good governance, therefore, requires evaluation of costs and benefits of different management strategies, in terms meeting a suite of management objectives, so that acceptable compromises can be negotiated (Fulton *et al.* 2007a; Hilborn 2007a,b). In jurisdictions where protection of vulnerable species is mandated, estimates of the range of harvest rates that can be considered sustainable, even if species are technically overfished, is an important part of the evaluation of trade-offs. The low values of  $U_{MSY}$  and  $U_{Max}$  reported in this study suggest that trade-offs to prevent overfishing of deepwater dogsharks may be severe. There is limited evidence for spatial structuring of dogshark populations in southeastern Australia, suggesting that incentives to encourage avoidance of dogsharks (e.g., Gilman *et al.* 2008) could be important strategies for controlling harvest rates on dogsharks. However, recent expansion of the automatic longline fishery into canyoned areas, and the efficiency with which dogsharks are caught by this gear (R. Daley, CSIRO, pers. comm.), suggests that spatial closures, such as the ones recently implemented, will also be a necessary management tool.

## **Acknowledgements**

This work was greatly advanced by the advice and assistance of Ross Daley and Ken Graham, who generously shared their resources and extensive knowledge of dogsharks. Lengthy discussions with both of them inspired this work. Matias Braccini generously provided life history parameters for dogsharks. James Scandol, Robert Ahrens, Steve Martell, Tony Pitcher and Robbie Klaesi provided helpful comments with early drafts. Funding was provided by the Charles Gilbert Heydon Travelling Fellowship in Biological Sciences, awarded to R.F. by the University of Sydney, Australia; by funds provided to the UBC Fisheries Centre under a Memorandum of Agreement with NSW Department of Primary Industries, Australia; and through an NSERC Discovery Grant to C.W. Preliminary work on this paper was done while R.F. was a visiting scientist at the CSIRO Marine and Atmospheric Research laboratories, Hobart, Australia. Travel to Hobart was funded by the Cecil and Kathleen Morrow Scholarship, awarded to R.F. by the UBC Fisheries Centre.

## Tables

**Table 4.1.** Life history parameters that were systematically varied in the generic dogshark model. Every parameter-combination was tested.  $a_h$  = age at 50% first harvest;  $a_{max}$  = maximum age;  $a_{mat}$  = age at 50% maturity;  $\kappa$  = von Bertalanffy growth rate; LS = litter size;  $L_\infty$  = maximum length;  $a_0$  = theoretical age when fish has zero length;  $lwa$  and  $lwb$  = scalar and exponent of length-weight relationship;  $\sigma_s$  = standard deviation of logistic selectivity curve;  $\sigma_m$  = standard deviation of logistic maturity curve.

		Minimum tested value	Maximum tested value	Step size
<b>Varied parameters</b>	$a_h$	1	10	1
	$a_{max}$	30	60	10
	$a_{mat}$	5	20	5
	$\kappa$	0.04	0.12	0.02
	LS	0.5	10	0.5
<b>Fixed parameters</b>	$L_\infty$	100		
	$a_0$	-5		
	$lwa$	0.001		
	$lwb$	3		
	$\sigma_s$	0.1*ah		
	$\sigma_m$	0.1*amat		

**Table 4.2.** Life history parameters for 12 species of dogshark landed off the coast of southeastern Australia. All size measurements are in centimetres. Where estimates of parameters were available for males and females, the female value was used.

Family	ScientificName	$L_{max}$	$K$	$a_0$	Max. age $a_{mat}$	Age at		Observed length at maturity	Median litter size LS	Pup size at birth	Ref.
						maturity	50% $a_{mat}$				
Centrophoridae	<i>Centrophorus harrissoni</i>	112						98	2	40	1
	<i>Centrophorus moluccensis</i>	93						88	2	32	1
	<i>Centrophorus zeehami</i> *	108			46			96	1	44	1
	<i>Deania calcea</i>	123 <sup>†</sup>	0.05 <sup>††</sup>	-5.1 <sup>††</sup>	35 <sup>†††</sup>		11 <sup>†††</sup>	93 <sup>††††</sup>	4 <sup>†††</sup>	28 <sup>††††</sup>	3 <sup>†</sup> ,4 <sup>††</sup> ,2 <sup>†††</sup> ,1 <sup>††††</sup>
	<i>Deania quadrispinosa</i>	118						108	8	25	1
Dalatidae	<i>Dalatias licha</i>	151						127	9	39	1
Etmopteridae	<i>Etmopterus granulosus</i>	83	0.038	-4.4				60 <sup>†</sup>	10 <sup>††</sup>	21 <sup>††</sup>	3,5 <sup>†</sup> ,1 <sup>††</sup>
	<i>Centroscyllium crepidater</i>	96	0.072	-6.1	54			87 <sup>†</sup>	6 <sup>†</sup>	32 <sup>†</sup>	3
Somniosidae	<i>Centroscyllium owstoni</i>	120						95	8	25	1
	<i>Centroscyllium plunketi</i>	154						137	19 <sup>†</sup>	32	1,3 <sup>†</sup>
	<i>Squalus megalops</i>	83	0.034	-10.8	32		15	50	2		6
	<i>Squalus mitsukurii</i>	107	0.04	-10.1	27		15	69	3.6	28 <sup>†</sup>	7,1 <sup>†</sup>

1. Daley et al. (2002); 2. Clarke et al. (2002b); 3. May and Maxwell; 4. Irvine (2004); (1986); 5. Wetherbee (1996); 6. Braccini et al. (2006); 7. Wilson and Seki (1994).

\*This species was formerly thought to be *Centrophorus uyato* and has recently been reclassified (White *et al.* 2008)

**Table 4.3.** Mean and modal values of 100 Monte Carlo estimates of  $U_{\text{MSY}}^{\text{Lim}}$  for 12 species of dogshark (see Figure 4.3 for boxplots).

Species	Age-at-50%-first-harvest ( $a_h$ )							
	1	3	5	7	9	11	13	15
<b>Mean <math>U_{\text{MSY}}^{\text{Lim}}</math></b>								
<i>C. harrissoni</i>	0.04	0.04	0.05	0.05	0.06	0.07	0.09	0.10
<i>C. moluccensis</i>	0.03	0.03	0.03	0.04	0.04	0.04	0.05	0.06
<i>C. zeehaani</i> *	0.03	0.04	0.04	0.04	0.05	0.06	0.08	0.09
<i>D. calcea</i>	0.06	0.07	0.08	0.09	0.14	0.18	0.24	0.34
<i>D. quadrispinosa</i>	0.03	0.04	0.04	0.04	0.05	0.06	0.06	0.07
<i>D. licha</i>	0.05	0.05	0.06	0.07	0.08	0.09	0.12	0.15
<i>E. granulosus</i>	0.06	0.06	0.08	0.09	0.11	0.16	0.20	0.28
<i>C. crepidater</i>	0.04	0.04	0.05	0.05	0.06	0.07	0.08	0.10
<i>C. owstoni</i>	0.04	0.05	0.06	0.07	0.08	0.09	0.13	0.16
<i>C. plunketi</i>	0.04	0.05	0.06	0.06	0.07	0.08	0.10	0.12
<i>S. megalops</i>	0.05	0.06	0.06	0.07	0.09	0.11	0.14	0.23
<i>S. mitsukurii</i>	0.05	0.06	0.07	0.08	0.09	0.13	0.16	0.24
<b>Modal <math>U_{\text{MSY}}^{\text{Lim}}</math></b>								
<i>C. harrissoni</i>	0.04	0.04	0.05	0.05	0.05	0.06	0.06	0.08
<i>C. moluccensis</i>	0.03	0.03	0.04	0.05	0.05	0.05	0.05	0.05
<i>C. zeehaani</i> *	0.04	0.04	0.05	0.06	0.05	0.06	0.07	0.07
<i>D. calcea</i>	0.06	0.06	0.07	0.07	0.09	0.11	0.15	0.18
<i>D. quadrispinosa</i>	0.04	0.04	0.04	0.04	0.05	0.07	0.05	0.07
<i>D. licha</i>	0.05	0.05	0.06	0.06	0.07	0.09	0.13	0.10
<i>E. granulosus</i>	0.05	0.05	0.07	0.08	0.08	0.12	0.15	0.18
<i>C. crepidater</i>	0.04	0.04	0.05	0.05	0.06	0.06	0.08	0.08
<i>C. owstoni</i>	0.04	0.04	0.06	0.06	0.07	0.08	0.09	0.10
<i>C. plunketi</i>	0.04	0.05	0.06	0.06	0.06	0.09	0.08	0.09
<i>S. megalops</i>	0.05	0.05	0.06	0.06	0.07	0.07	0.11	0.12
<i>S. mitsukurii</i>	0.05	0.05	0.06	0.06	0.06	0.10	0.11	0.14

\*This species was formerly thought to be *Centrophorus uyato* and has recently been reclassified (White *et al.* 2008)

**Table 4.4.** Mean and modal values of 1000 Monte Carlo estimates of the intrinsic rate of growth  $r$  obtained using the demographic approach (see Figure 4.5 for density plots).

Species	$r$	
	Mean	Mode
<i>C. harrissoni</i>	0.08	0.08
<i>C. moluccensis</i>	0.06	0.06
<i>C. zeehaani</i> *	0.07	0.07
<i>D. calcea</i>	0.17	0.14
<i>D. quadrispinosa</i>	0.08	0.09
<i>D. licha</i>	0.12	0.10
<i>E. granulatus</i>	0.18	0.16
<i>C. crepidater</i>	0.09	0.08
<i>C. owstoni</i>	0.13	0.11
<i>C. plunketi</i>	0.12	0.13
<i>S. megalops</i>	0.10	0.09
<i>S. mitsukurii</i>	0.11	0.13

\*This species was formerly thought to be *Centrophorus uyato* and has recently been reclassified (White *et al.* 2008)

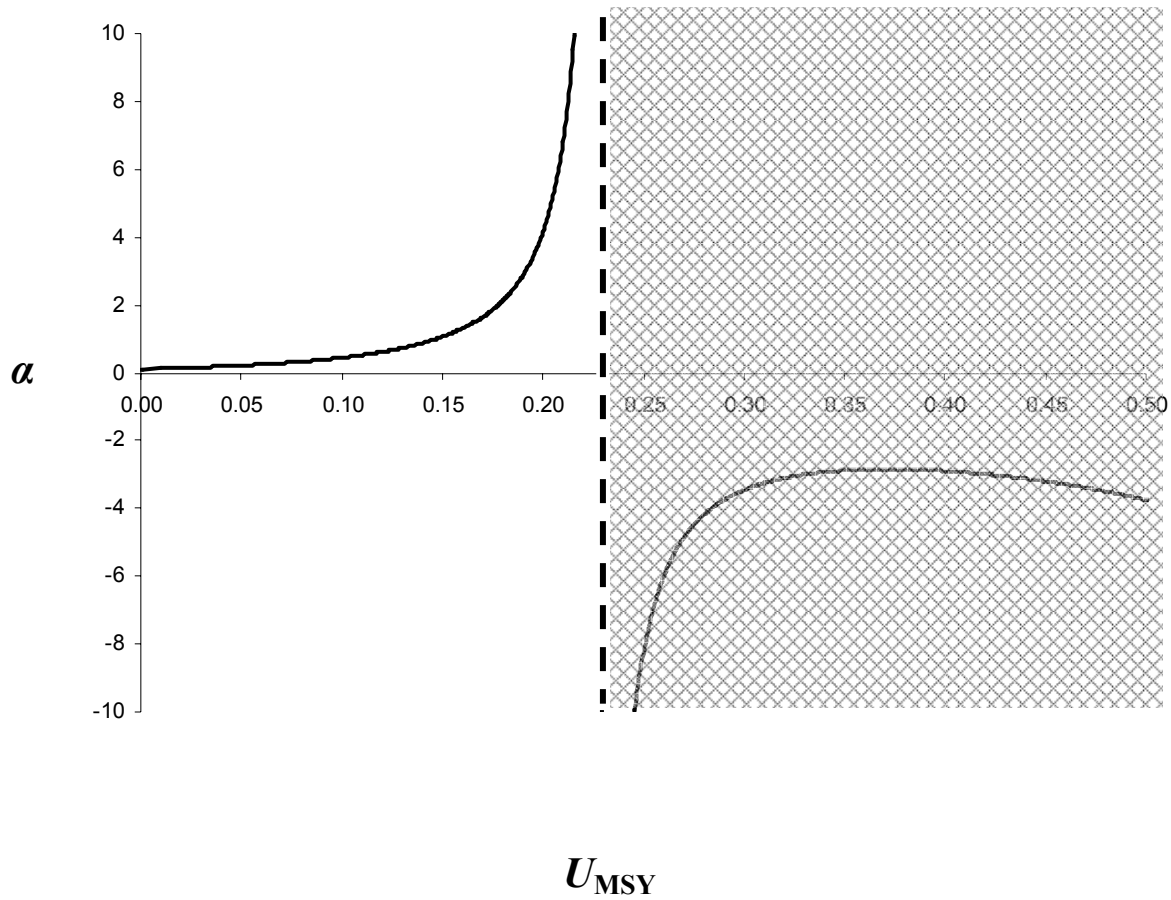


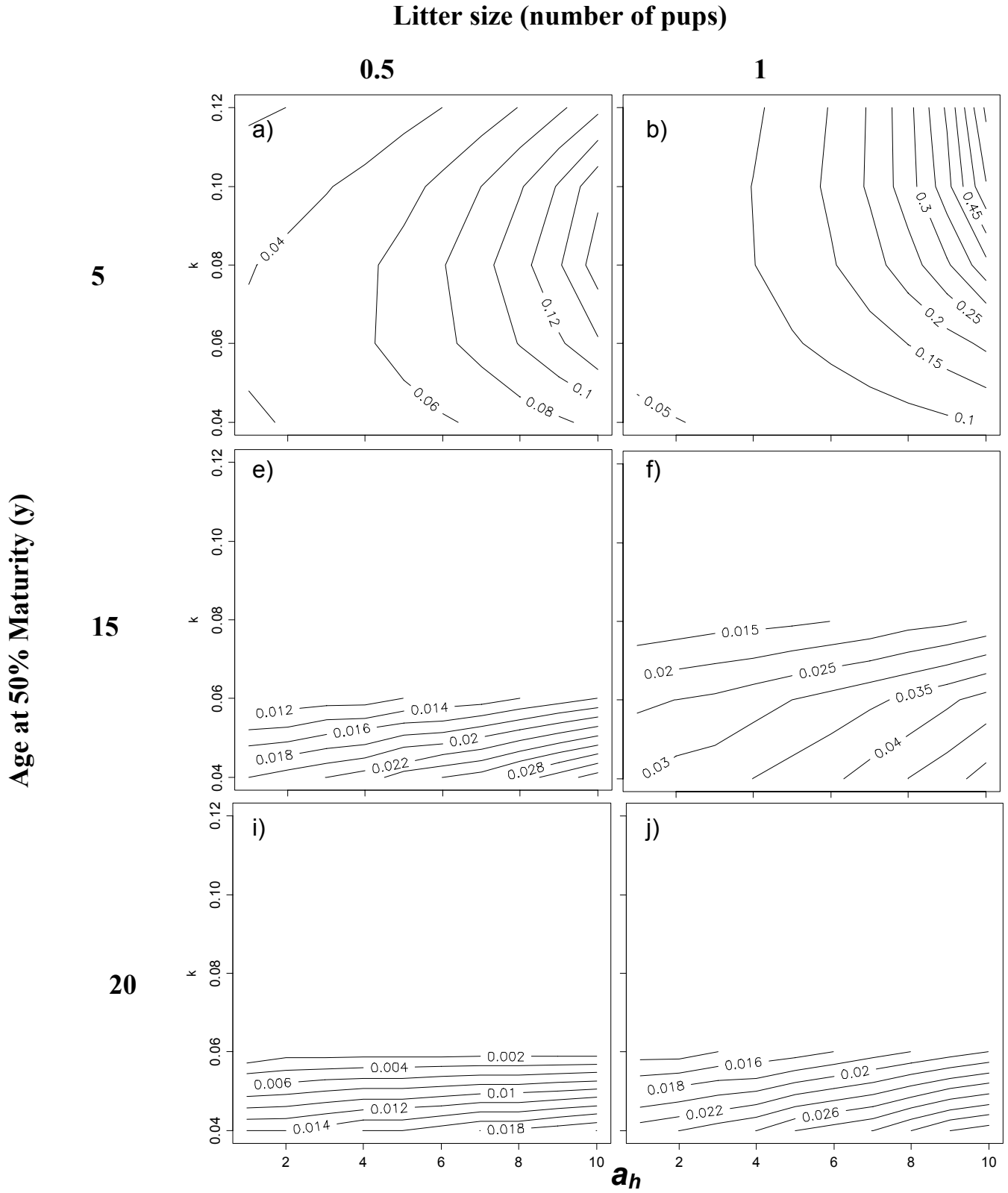
**Table 4.5.** Correlation coefficients, slopes and intercepts of the relationship between the mean values of  $r$  (Table 4.4) and  $U_{\text{MSY}}^{\text{Lim}}$  (Table 4.3) across all 12 species of dogshark, for the eight tested values of  $a_h$  (age-at-50%-first-harvest). See Figure 4.6.

$a_h$	Pearson's correlation coefficient	Slope	Intercept
1	0.924	0.229	0.018
3	0.915	0.271	0.019
5	0.945	0.363	0.016
7	0.942	0.450	0.014
9	0.938	0.685	0.002
11	0.931	1.002	-0.014
13	0.931	1.354	-0.028
15	0.877	2.034	-0.060

## Figures

**Figure 4.1.** Relationship between  $U_{\text{MSY}}$  and  $\alpha$  and under Beverton-Holt recruitment for a hypothetical species. The asymptotic upper limit of  $U_{\text{MSY}}$  is represented as a dashed vertical line (see text). The shaded area represents undefined hypotheses for  $U_{\text{MSY}}$  that give  $\alpha < 0$  (see text).



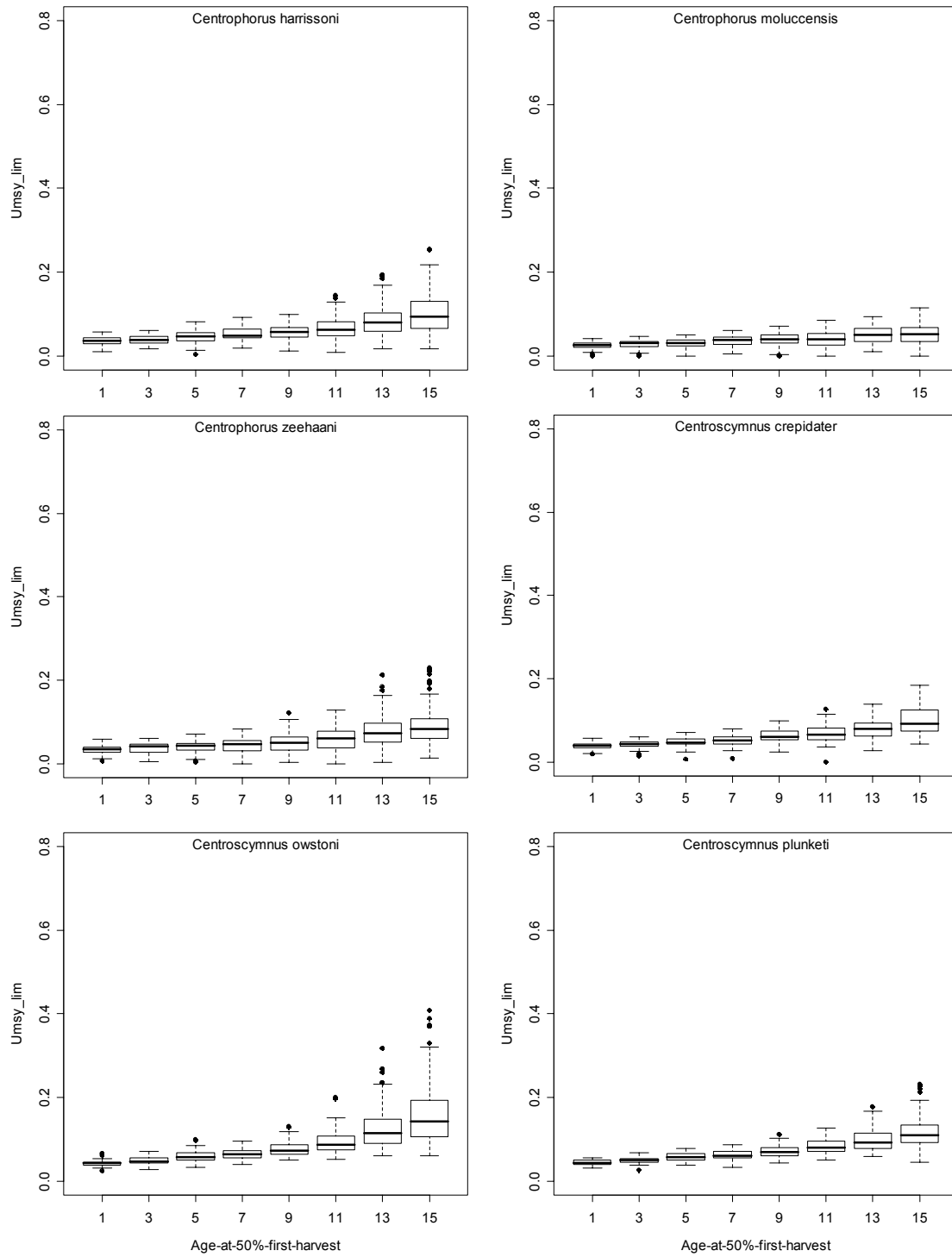


**Figure 4.2.** Contour plots showing maximum possible  $U_{MSY}$  (i.e.,  $U_{MSY}^{Lim}$ ) over a range of tested values of  $a_h$  and  $\kappa$ . Left to right shows the effect of increasing litter size, LS, on  $U_{MSY}^{Lim}$ . Top to bottom shows effect of increasing  $a_{mat}$ .

10



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**Figure 4.3.** Box and whisker plots showing median (black bar), interquartile range (box) and 1.5IQR (whiskers) of estimated  $U_{MSY}^{Lim}$  from 100 Monte Carlo simulations for 12 species of Australian dogshark over a range of age-at-50%-first-harvest,  $a_h$  (continued overleaf).

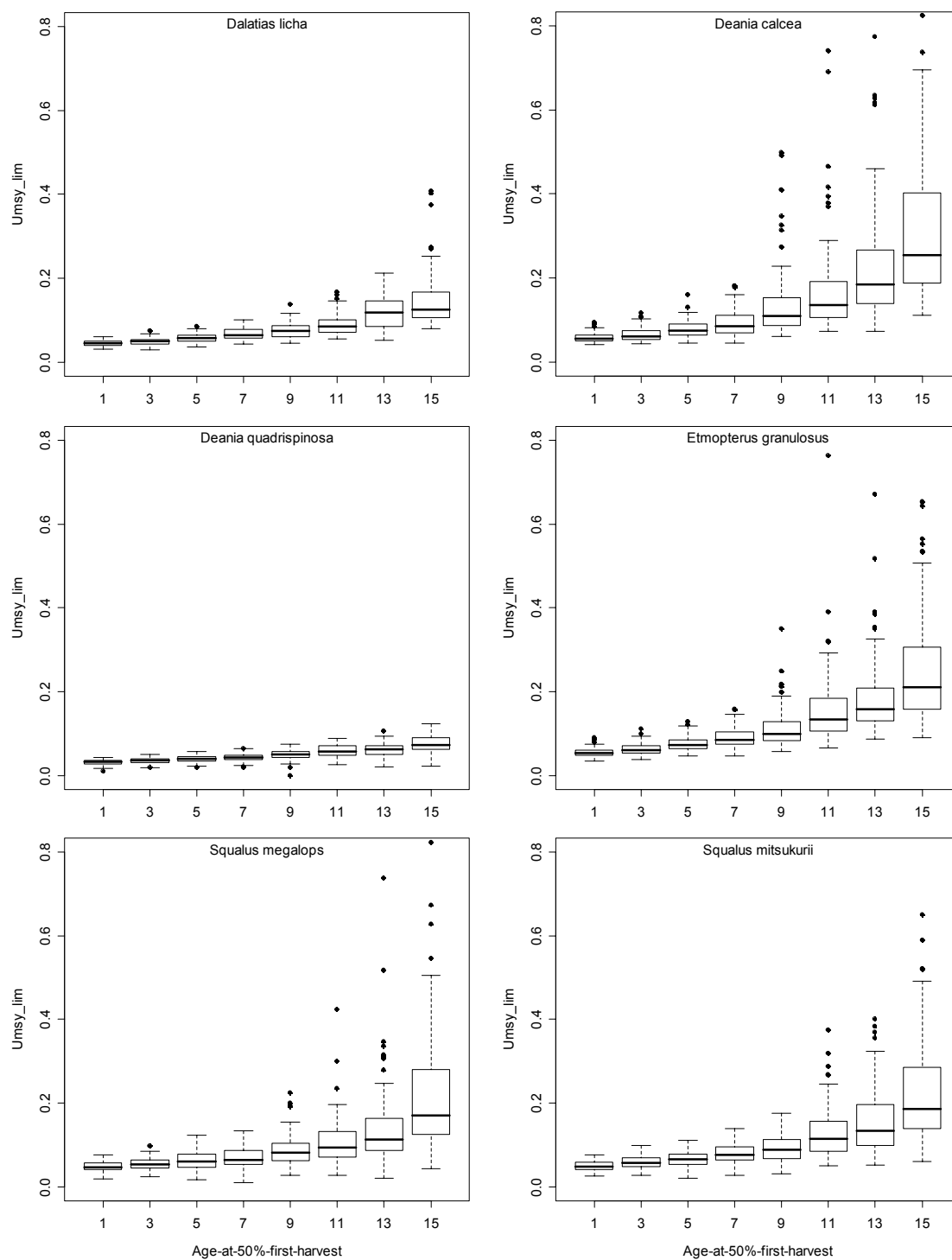
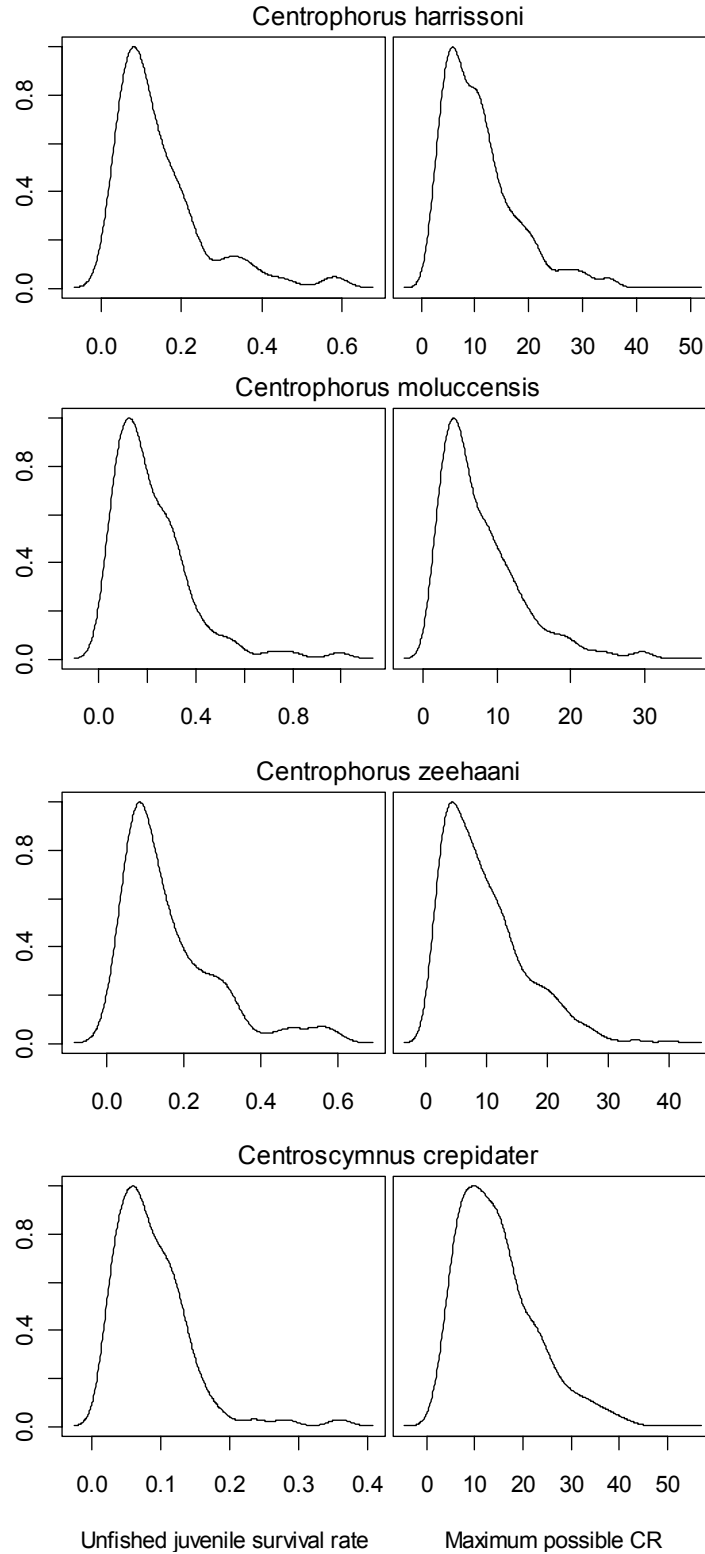
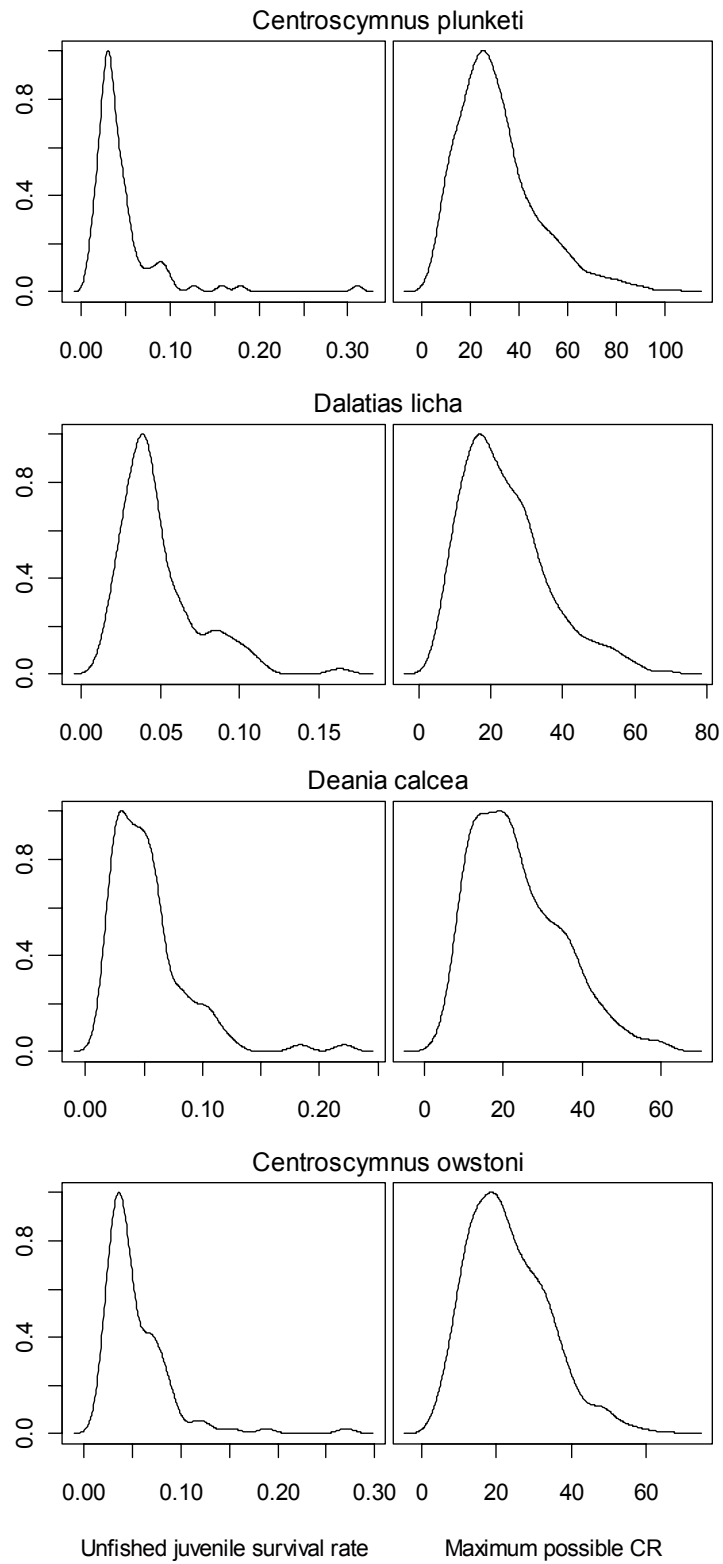


Figure 4.3 cont.

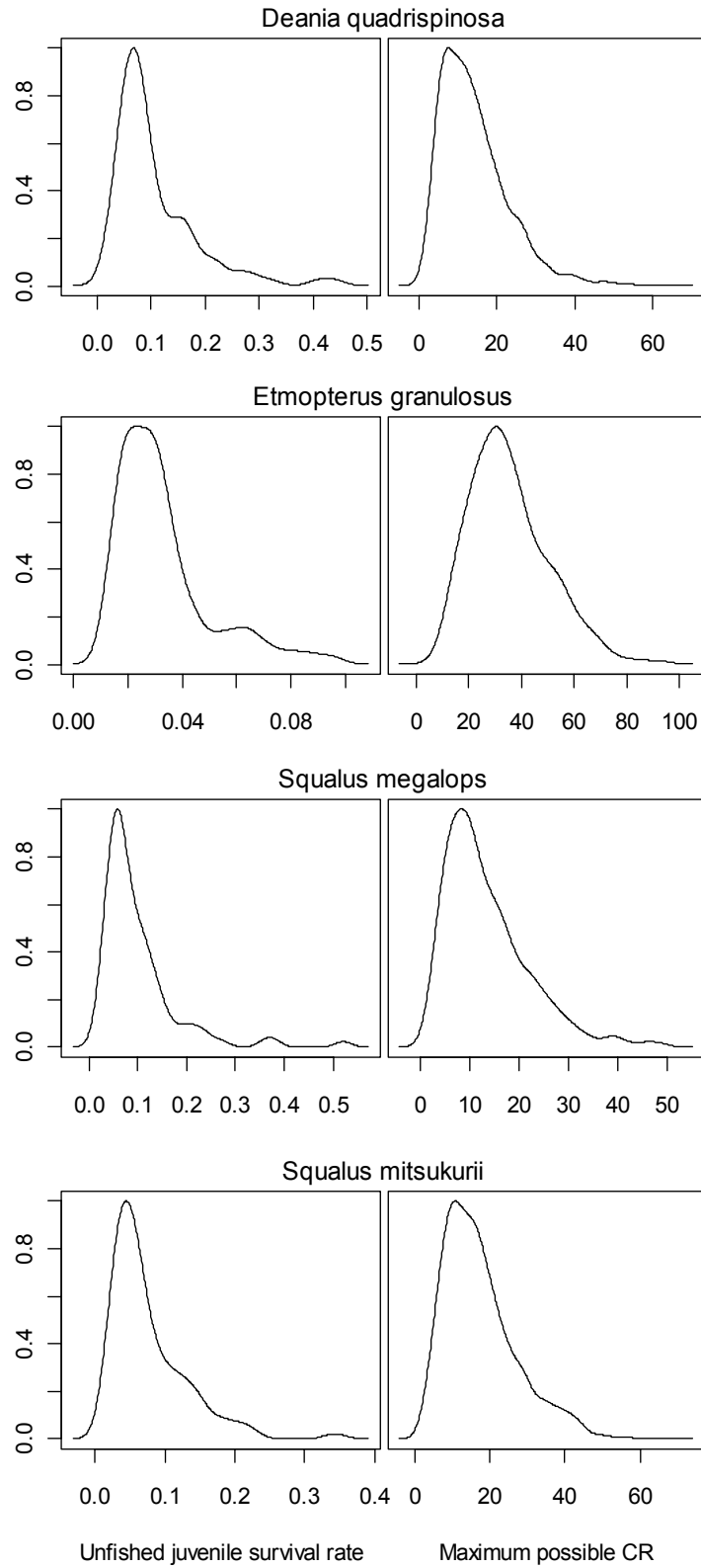


**Figure 4.4.** Relative densities of maximum possible compensation ratio CR (right) for 12 species of dogshark implied by the unfished juvenile survival rate (left); see text and Figure 1.2. Density plots show results from 100 Monte Carlo simulations.

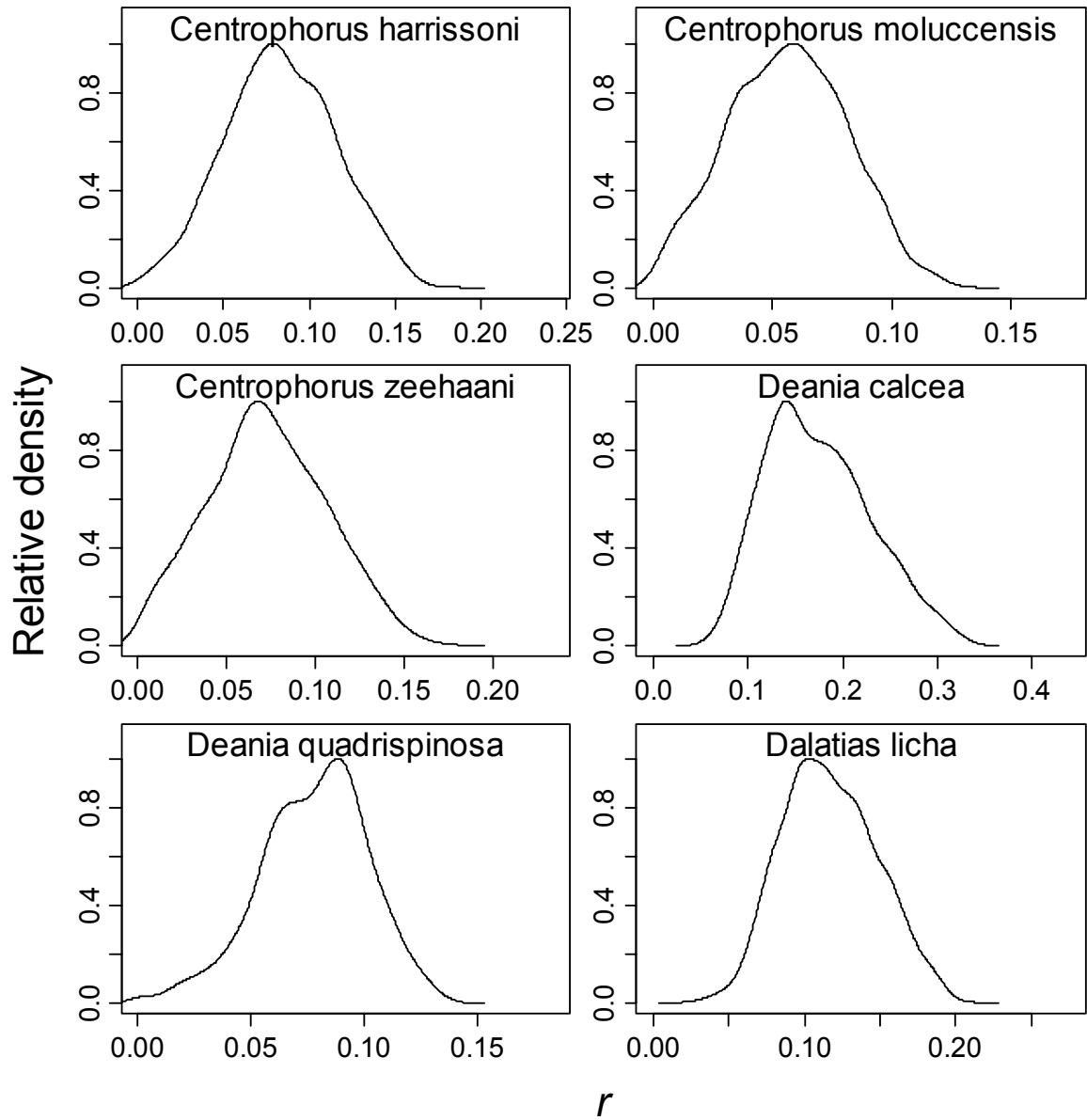


**Figure 4.4 cont.**





**Figure 4.4 cont.**



**Figure 4.5.** Estimates of  $r$  (i.e.,  $U_{\text{Max}}$ ) obtained from the demographic method (results of 1000 Monte Carlo simulations).

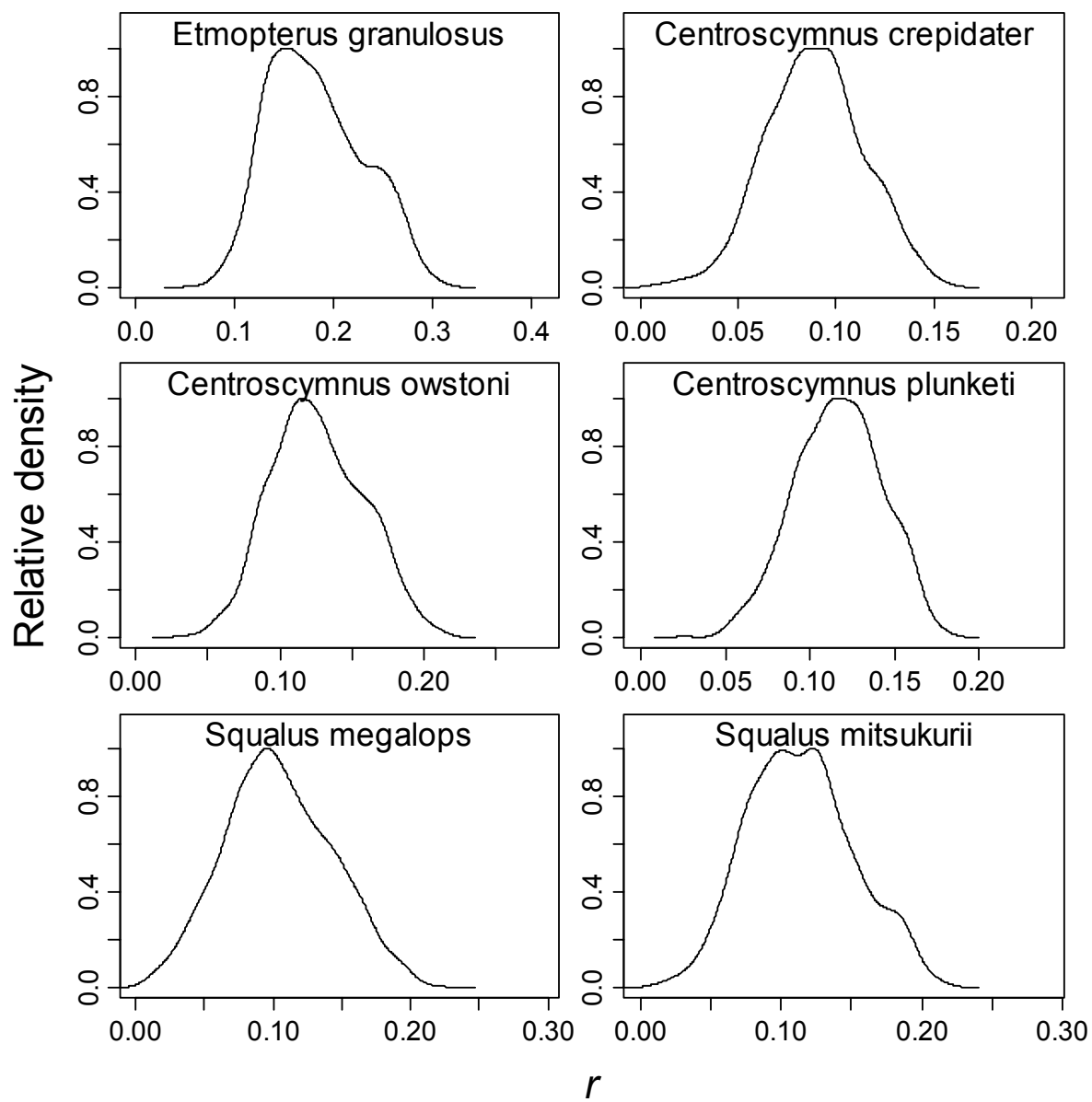
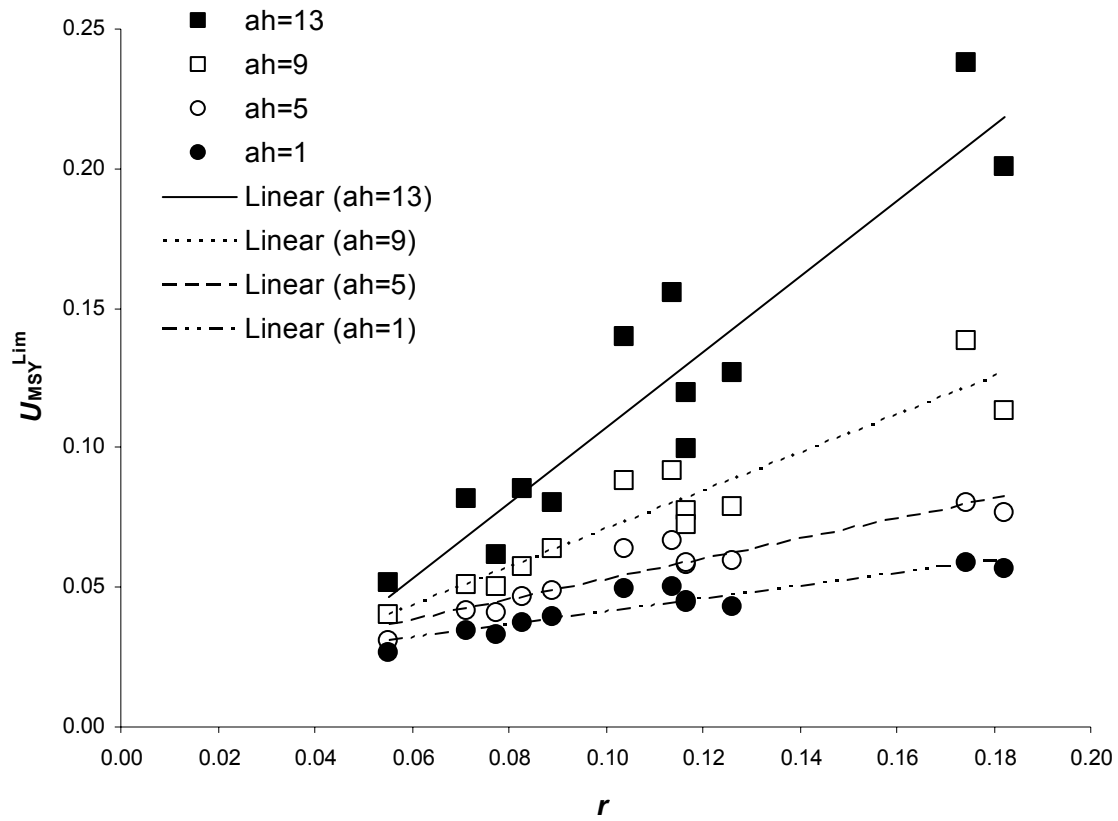


Figure 4.5 cont.



**Figure 4.6.** Relationship between the mean values of  $r$  (Table 4.4) and  $U_{MSY}^{Lim}$  (Table 4.3) across all 12 species of dogshark, for four of the eight tested values of  $a_h$  (age-at-50%-first-harvest). See Table 4.5 for correlation coefficients, and values of slopes and intercepts.

## **Chapter 5. Preliminary reconstruction of catch and harvest rate history of an extremely data-poor genus of dogshark (*Centrophorus*) on the upper continental slope of New South Wales, Australia**

### **Introduction**

Around 12 species of dogshark (Order Squaliformes) are caught on the Australian continental shelf and slope. One species (*Centrophorus harrissoni*) has been listed as Critically Endangered on the IUCN Red List of Threatened Species (IUCN 2008). Its congeners, *C. zeehaani* and *C. moluccensis* are listed as Data Deficient. These three species have recently been given Priority Assessment Listing under the Commonwealth *Environment Protection and Biodiversity Act 1999*, which could see them listed as threatened species (DEWHA 2008). There is therefore a need to assess the current and historical impacts of fisheries on these species. To date, there have been no population assessments of any species of *Centrophorus* in Australia that could contribute to this outcome. Productivity of *Centrophorus* spp. and, therefore, key fisheries reference points  $U_{\text{MSY}}$  (maximum sustainable harvest rate) and  $U_{\text{Max}}$  (the harvest rate that would drive the stock to extinction), have been shown to be very low and to be severely constrained by life history parameters about which there is little uncertainty (Chapter 4). The greatest uncertainty in assessing these populations, therefore, lies with current and historical harvest rates relative to these reference points (i.e., whether these populations are currently or have historically been overfished).

Most historical dogshark landings in southeastern Australia come from slope waters deeper than 200 metres, with the majority of the catch prior to 2000 coming from waters off NSW (Daley *et al.* 2002). Most vessels fishing on the upper continental slope (300-650 m) target valuable teleosts such as blue grenadier (*Macruronus novaezelandiae*), blue-eye (*Hyperoglyphe antarctica*) and pink ling (*Genypterus blacodes*), as well as royal red prawns (*Haliporoides sibogae*). For these vessels, dogsharks are bycatch, although they have some commercial value. Dogshark flesh is sold as ‘flake’, which is a generic term for shark fillets, popular in Australia for their bonelessness. Also, livers of *Centrophorus* spp. (and, to a lesser extent, *Deania* and

*Centroscyrnus* spp.) are valued for their high content of squalene, an oil that is extracted, refined and exported for use in cosmetics (Summers 1987; Deprez *et al.* 1990). At least two vessels are known to have actively targeted dogsharks on the continental slope of NSW during the 1980s and 1990s, motivated by high prices that could be obtained for the livers (R. Daley, CSIRO, unpubl. data). Despite the fact that dogsharks have been caught and marketed in NSW for more than three decades, there are a large problems with their catch and effort data that severely limit their usefulness. These limitations include: i) years of missing catch and effort data; ii) reporting under aggregate species categories (in both landings data and observer data); iii) large-scale unreported discarding, especially in the early years of the fishery; and iv) inconsistencies in reporting methods (among vessels and among reporting agencies). See also Walker and Gason (2007) for description of problems with catch and observer data for dogsharks. These types of problems are common to sharks in fisheries around the world, where there is a general lack of data adequate for stock assessment (FAO 2000; Bonfil 2004).

Commercial trawling on the continental slope of NSW began with two vessels in 1968, and had increased to 12 vessels by 1975. Between 1975 and 1980, the fishery underwent rapid expansion and, by the early 1980s, there were about 60 trawlers operating regularly on the continental slope (Graham *et al.* 2001). With declines in abundance of several targeted teleosts and the introduction of quotas in 1992, this number had dropped to around 40 by the end of the 1990s until, in 2005, there were only around 25 boats still actively fishing on the slope. During the 1970s, Australia's fisheries were considered 'underexploited' and, with the impending 1979 declaration of the 200 nautical mile Australian Fishing Zone (Rothwell and Haward 1996), the Australian government was providing considerable funding for exploratory surveys of the waters of the southeast Australian slope (Tilzey and Rowling 2001). This led to a set of surveys of the upper continental slope by the NSW State-owned Fisheries Research Vessel *Kapala* in the 1970s (Gorman and Graham 1976; 1977). The objective of the early *Kapala* surveys was to locate productive trawl grounds and evaluate the viability of demersal slope fisheries. The initial, exploratory upper slope surveys were done in 1976-1977 and were fully replicated twenty years later in 1996-1997, allowing for some striking comparisons of the abundance of many species (Andrew *et al.* 1997; Graham *et al.* 1997; Graham *et al.* 2001). Analysis of the *Kapala* data revealed that there had been significant declines in the abundance of many demersal sharks, skates and several species of bony fish on the continental slope. Notable declines were reported

for deepwater dogsharks (*Centrophorus* spp., *Squalus* spp. and *Deania* spp.), as well as sawsharks (Pristiophoridae), angel sharks (Squatinae), school sharks (*Galeorhinus galeus*) and skates (Rajidae). Mean catch rates of *Centrophorus* spp. had declined by more than 99% in the period between the two surveys. The surveys were partially replicated in 1979, indicating that large declines in populations of some species may have occurred in the early years of the fishery (Graham *et al.* 2001). These authors and Andrew *et al.* (1997) concluded that fishing was almost undoubtedly the cause of the observed declines. The FRV *Kapala* was decommissioned in 1997 and there have been no fishery-independent surveys on the NSW continental shelf or slope since that time. The paucity of independent survey data and the unreliability of nominal catch and observer data compromises credible stock assessment for dogsharks in NSW.

Chapter 4 showed that productivity parameters for *Centrophorus* spp. were very low and strongly constrained by life history attributes that included low fecundity, slow growth and late maturity. At least two of these species (*C. harrissoni* and *C. zeehaani*) are believed to have narrow distributions, while *C. moluccensis* is believed to be more widely distributed around the Pacific and Indian Oceans (Last and Stevens 1994). *C. harrissoni* has been recorded on the continental slope of eastern Australia from northern NSW to the south east coast of Tasmania (White *et al.* 2008). These authors also note that isolated populations have been observed in depths of 300–680 m on Fraser Seamount, in Queensland and in three isolated locations off the northern coast of New Zealand. They have not been recorded off the Tasmanian west coast or along the south coast of mainland Australia (Last and Stevens 1994). *C. zeehaani* is endemic to Australia, occurring from northern NSW to the southern parts of Western Australia (White *et al.* 2008). Lightly-fished populations have been located in canyons off the coast of South Australia (R.Daley, CSIRO, pers. comm.). It should be noted that *C. zeehaani* was, until 2008, believed to be another, much more widely-distributed species *C. uyato*.

The current chapter collates available information that could be used to reconstruct historical catches of *Centrophorus* spp. and makes a preliminary attempt to place upper and lower boundaries on the magnitude of annual catches between 1990 and 2002, based on information from State and Commonwealth sources. An effort-driven age-structured model is then developed for gaining maximum likelihood estimates of historical harvest rates between 1968 and 2002. Two preliminary case-studies are presented, in which the model is fitted to reconstructed catch

and mean relative survey abundance data for *C. harrissoni* and aggregated *Centrophorus*. Results suggest that, under the assumptions of the model, reasonably precise estimates of annual harvest rate could be obtained for these dogsharks, despite very large uncertainty in historical catches. The approach presented provides a transparent framework for expert review that could eventually contribute to current assessment needs for these species.

## Methods

### Reconstruction of time series of catch and effort

Five data sources were used to reconstruct likely catch scenarios for *Centrophorus* spp. off the coast of NSW. None of these datasets provide a complete catch history for *Centrophorus* spp. However, they may be used together to provide minimum and maximum estimates for different periods during the slope fishery's history. The datasets are:

- 1) *NSW State database: 1986-2002*. Catch records from the State Fisheries of NSW (supplied by James Scandol; NSW Department of Primary Industries);
- 2) *SETF Annual database: 1986-2002*. Annual catch records from the Commonwealth South East Trawl Fishery (SETF) covering the whole coast of NSW and all depths (supplied by John Garvey; Australian Fisheries Management Authority);
- 3) *SETF Slope database: 1986-2002*. Daily catch and effort records by vessel from the Commonwealth SETF on the upper continental slope of NSW only (depth 300-600 m; supplied by Sally Waite; CSIRO);
- 4) *ISMP database: 1992-2002* Observations of catch and discarding from the South East Fishery Integrated Scientific Monitoring Program (ISMP; supplied by Sonia Talman, Marine and Fisheries Research Institute). Details about the ISMP can be found in Garvey (1998) and Knuckey *et al.* (2002);
- 5) *Kapala database: 1976-7, 1979-81, 1996-7*. Catches and catch rates of dogsharks obtained from the FRV *Kapala* surveys (supplied by Ken Graham; NSW DPI). Mean (+ s.e.) catch rates published in Graham *et al.* (2001) are also used.

The names in italics given to each dataset above will be used throughout this chapter.



### *Effort*

Effort records are not available for the first 18 years of the slope fishery (1968-1985), although there are estimates of the number of boats actively fishing. Reconstruction of harvest history necessarily includes consideration of the developmental years of the fishery and, therefore, estimates of effort for the years before official records are available. In this case, we know that dogsharks were caught in the early years of the fishery (Graham *et al.* 2001; Daley *et al.* 2002) and that fishing effort drove fishing mortality. It is therefore appropriate to assume some non-zero fishing effort for this period.

For the years where there are records of both the number of vessels and fishing effort on the slope, there is a strong positive relationship between number of vessels and fishing effort (Figure 5.1a). The mean relationship can be described reasonably well by a linear relationship forced through the origin with equation  $Eff_t = 39.3V_t$ , where  $Eff_t$  is total effort of vessels that reported landing dogsharks (hours) in year  $t$ , and  $V_t$  is total number of vessels that fished on the slope in year  $t$  (Table 5.3). This relationship was used to estimate effort in the years prior to 1986, assuming close to linear increases in the number of vessels between 1968-1974; 1975-1980; and 1981-1985 (Table 5.3). To account for uncertainty in effort, a Monte Carlo approach was used, in which, for the years 1968-1985, each annual effort estimate was assumed to come from a normal distribution with mean set to the deterministic predicted effort (Table 5.3) and the coefficient of variation (CV) set to 0.2. The effort series resulting from 100 Monte Carlo samples of effort in each year are shown in Figure 5.1b. Note that while the slope of the relationship between number of boats and hours fished seems low (39.3 hours per year per vessel), it must be noted that in each year, a large percentage (~25-30%) of vessels that reported catch from the 300-600 m range fished less than 200 hours per year in these depths. Therefore, while there were always some vessels reporting > 1000 hours per year, the relationship was biased downwards by the large number of vessels that fished infrequently on the slope.

### *Catch*

It was not necessary to provide inputs for catch in the earliest years of the fishery because catch was not used to drive the model. However, estimates of catch were needed for at least some years to enable scaling of estimated population size. Nominal landings of dogsharks occur mostly in aggregate categories and cannot be used directly for most years. However, the

possibility of using proportions reported in various databases to disaggregate landings and make minimum and maximum estimates of the catch was investigated.

Catch statistics in NSW date back to 1918 (Klaer 2001). Prior to 1985, however, all landings of Chondrichthyans (sharks, skates, rays and chimaeras) in NSW were reported under a single miscellaneous shark category (Pease and Grinberg 1995). It is not really possible to disaggregate these catches over time, because the catch data include too many species and encompass periods of spatial expansion of the State's pelagic and demersal fisheries and, therefore, movement into fishing grounds containing different assemblages of Chondrichthyans. The ISMP and *Kapala* databases indicate that there may be more than 100 Chondrichthyan species in the waters of NSW. Currently the NSW State database reports Chondrichthyan landings under 22 individual and aggregate categories. The SETF databases contains 35 Chondrichthyan categories.

In 1984, the NSW State database began to record landings of certain sharks by species or genus. Even then, though, reported landings for individual species/genera were very low until after 1991 because sharks were still mostly reported under the miscellaneous shark category. Since 1992, dogsharks have been mostly reported in the NSW State database under four categories: (1) greeneye dogshark, (2) Endeavour dogshark, (3) roughskin shark and (4) unspecified dogshark. Respectively, these categories refer to (1) *Squalus* spp.; (2) *Centrophorus* spp.; (3) *Deania* and *Centroscymnus* spp.; and (4) other dogshark species (e.g., *Etmopterus granulosus* and *Dalatias licha*) plus unspecified dogsharks. Between 1985 and 2000, the SETF databases recorded all dogsharks under the category 'undifferentiated Squalidae'.

Since 2000, dogshark landings have been well-resolved in the SETF databases, with many species reported to species-level (although aggregate categories still occur). However, of the three main species of *Centrophorus* that have been observed on the NSW slope (*C. harrissoni*, *C. moluccensis* and *C. zeehaani*; Graham *et al.* 2001), only *C. moluccensis* is reported to species level. This reflects ambiguity in use of the name Endeavour dogshark, which is used both as a collective name for dogsharks in the genus *Centrophorus* and as the common name for *C. moluccensis* specifically. It is likely that in most cases, when fishers recorded Endeavour dogshark in their logbooks they referred to the general *Centrophorus* category but when landings were encoded into the SETF database they were mistakenly collated as *C. moluccensis* (R.

Daley, CSIRO, pers. comm.). Figure 5.2 shows reported landings of dogsharks caught in the NSW State and SETF fisheries for years when disaggregated data are available. In Figure 5.2a, the period of rapid decline following 1992 is due in part to an overall decrease in effort following restructuring of the fisheries in 1992.

The main State fisheries landing dogsharks were the Ocean Fish Trawl (OFT), the Ocean Prawn Trawl, the Ocean Trap & Line fisheries and a fishery labelled 'Other'. This category contains landings known to have also been reported in the Commonwealth SETF prior to 1997. Figure 5.3 shows reported landings of total Squalidae in the four main fisheries catching dogsharks in NSW. Note that there is some uncertainty about whether catches reported in the OFT were also double-reported to Commonwealth and State agencies, as most licencees were endorsed to fish in both the SETF and the OFT. Reported landings of Squalids by fishery, after removal of 'Other' landings, are shown in Figure 5.3 and summarised in Table 5.4. The possibility that all OFT landings were also reported in the SETF must be considered a possibility in building minimum and maximum scenarios for landings. The decline in landings after 1989 corresponds to the large decline in fishing effort shown in Figure 5.1b.

Logbook, fish market, catch, observer and survey data relating to dogsharks in south-eastern Australian waters have been extensively examined by Daley *et al.* (2002). These authors raised several issues regarding reporting of dogshark landings, including inconsistencies among vessels as to whether reported landings were of whole sharks or trimmed carcasses (head and fins removed). Nominally, reported landings refer to whole weight. However, a survey of fishers revealed that most had reported carcass weight, as it is easier and more accurate to record. Therefore, Daley *et al.* (2002) have provided conversion factors for converting from carcass to whole weight for *Centrophorus* spp., where the whole weight is given as 1.67 times the carcass weight. When dogshark catches were very large, there may have been cases where all of the dogshark was discarded except for the liver, in which case only liver weight would have been recorded in the logbook (R. Daley, CSIRO, pers. comm.).

#### *Proportion of Centrophorus in total Squalid landings*

The proportion of Endeavour dogsharks (i.e., *Centrophorus* spp.) in total State dogshark landings averaged 0.37 (s.e. = 0.044) for the years 1992-2002 (Figure 5.4a, Table 5.5). In the 'Other'

fishery, the average proportion of *Centrophorus* in the total Squalid landings was 0.45 (s.e. = 0.03; Figure 5.4b). It is important to note that these proportions are not indicative of proportions of *Centrophorus* in the total catch (i.e., landings plus discards) of Squalids, as large numbers of *S. megalops* and other species are known to have been discarded (Daley *et al.* 2002). Table 5.5 also shows *Centrophorus* spp. as proportion of retained Squalidae catch in the ISMP database. The proportion of *Centrophorus* spp. in the ISMP database was extremely variable from year to year, ranging from 1% of the total Squalid catch in 1994 to 72% in 1996. From 1998 to 2002, the proportion of *Centrophorus* spp. was consistently below 10% of the total Squalid catch. Inconsistencies in previous years may represent patchiness in selection of fishing vessels in the observer program (only a small proportion of fishing trips carried observers) or fluctuations in the market.

Between 1976 and 1996, there was a large decline in the percentage of *Centrophorus* spp. in the *Kapala* survey data, in relation to the total catch of Squalids. In 1976, *Centrophorus* spp. had made up 63.7% of the total Squalid catch (Table 5.7). In comparison, in 1996, *Centrophorus* spp. made up only 2.7%. Daley *et al.* (2002) visited the Sydney and Melbourne fish markets in 1999 and 2000 and reported that only 2.6% of all dogshark sales were comprised of sharks in the genus *Centrophorus*, with more than 90% of sales made up of *Centroscymnus* and *Deania* spp. The proportion of *Centrophorus* spp. in the *Kapala* data is close to that reported by Daley *et al.* (2002) in their market observations. The State-reported proportions of *Centrophorus* shown in Table 5.5 are, in general, greater than the proportion of sales observed by Daley *et al.* (2002) and also those in the ISMP database (Table 5.5). In earlier years, this may be due to greater proportions of *Centrophorus* in the catch (State and ISMP proportions roughly agree in 1992) or to misreporting of species in State landings. It may also reflect the increased proportion of *Deania* and *Centroscymnus* spp. in SETF catches as markets developed.

#### *Proportion of individual species in total Centrophorus landings*

There were changes in the proportions of the three *Centrophorus* species in the total *Centrophorus* catch in the *Kapala* surveys between 1976 and 1996 (Table 5.7). Excluding 1976 tows where *C. zeehaani* and *C. harrissoni* had been reported under a combined category, *C. harrissoni* made up approximately 20% of the mean *Centrophorus* catch in 1976 and 16% in

1996. *C. zeehaani* made up 69% and 58% of the catch in 1976 and 1996 respectively. The percentage of *C. moluccensis* increased from 11% in 1976 to 27% in 1996.

Annual proportions of *C. harrissoni*, *C. moluccensis*, *C. zeehaani* and “Mixed Endeavour” dogshark in the ISMP database, represented as proportions of total retained *Centrophorus* catch, are shown in Table 5.6 for the years when data were available. Mean (+ s.e.) proportions of each species across years in the ISMP database are shown in Figure 5.5. The black bars in Figure 5.5 suggest that *C. moluccensis*, *C. zeehaani* and Mixed Endeavour dogshark made up roughly equal proportions of the total retained *Centrophorus* catch across all years. However, averaging across all years masked the sharp shift in relative proportions of *C. moluccensis* and Mixed Endeavour dogshark between the first and second half of the dataset (Table 5.6). No *C. moluccensis* were reported before 1998 and the majority (mean 56.5%) of the retained *Centrophorus* catch was reported under the Mixed Endeavour category. From 1998, the proportion of catch reported as Mixed Endeavour dropped sharply and catches of *C. moluccensis* rose correspondingly (Figure 5.5 and Table 5.6). Daley *et al.* (2002) suggested that misrecording of Mixed Endeavour dogshark as *C. moluccensis* in the ISMP database (due to ambiguity in the meaning of ‘Endeavour dogshark’ described above) was known to have occurred in Victoria and other regions of the SETF (Daley *et al.* 2002). Table 5.5 suggests it was also likely to have been a problem in NSW (see also Walker and Gason 2007) and, because of it, the ISMP observer data cannot be considered useful for catch disaggregation.

### *Discarding*

There was limited market acceptance of dogshark carcasses in the early years of the fishery. The high catch rates encountered by the *Kapala* in 1976 imply that initial catch rates in the fishery were also high, therefore suggesting very high levels of discarding in the early years (Graham *et al.* 2001). During the 1980s and 1990s, markets for dogshark flesh and livers (especially *Centrophorus* spp.) developed and would have reduced the amount of discarding. Discarding may have been further reduced after the introduction of quotas for key teleost species in 1992 (Grieve and Richardson 2001), when targeting of certain sharks became more common as fishers sought to supplement their catches (Daley *et al.* 2002). Similarly, relaxation of laws that restricted the sale of dogshark carcasses in the State of Victoria due to mercury content would have further encouraged landing of dogsharks, although Daley *et al.* (2002) suggest that this

would have had a greater effect on *Deania* and *Centroscyrnus* spp. According to the ISMP database, after 1992 and the introduction of quotas, discarding of *Centrophorus* spp was, except for a small spike in 1996, close to or equal to zero (Figure 5.6). The single datapoint in 1992 (the last year before introduction of quotas) suggests that prior to this, discarding of *Centrophorus* could have been high (~60% of reported landings). Discards of other significant slope species *S. megalops* and *D. calcea* are also shown for comparison.

#### *Minimum and maximum estimates of annual Centrophorus catch*

Total SETF Squalid landings (Table 5.4) were used as a starting point for estimating *Centrophorus* catches. Minimum and maximum annual estimates of the proportion of *Centrophorus* in Squalid landings (Table 5.5) were used to make minimum and maximum estimates of total *Centrophorus* landings for the years 1990 – 2002 (Table 5.8). Footnotes describe in detail how each estimate was derived. For the maximum estimate, all *Centrophorus* landings were assumed to have been recorded as carcass weight and were therefore inflated by 1.67 (Daley *et al.* 2002) to represent whole live weight. For the minimum estimate, all landings were assumed to have been correctly reported as whole weights. Minimum and maximum hypotheses for discards were then added to the landings estimates to obtain whole catch estimates for total *Centrophorus* (Table 5.8). The mean proportions of each species in the 1996 *Kapala* data (Table 5.7) were then used to break down estimates of total *Centrophorus* catch (Table 5.8) into species (Table 5.9).

#### **Preliminary effort-driven model to estimate historical harvest rates**

A fishing effort-driven, age-structured model with leading parameters  $B_0$  (unfished biomass), CR (the recruitment compensation ratio) and  $q_c$  (the catchability coefficient) was used to estimate historical annual harvest rates,  $U_t$ , for *C. harrissoni* in NSW. The set of estimated parameters was  $B_0$  and  $q_c$ . Chapter 4 showed that CR, is highly constrained for these species, due to their extremely low fecundity and late maturity. In this analysis, therefore, CR was fixed at its maximum possible value given the deterministic parameter estimates (Chapter 4) and assuming an age at maturity of 18 y (i.e., CR = 3.4). CR was fixed to avoid overparameterisation of an extremely data-poor model, given the relatively low uncertainty in this parameter. Sensitivity to this assumption was tested (see below). Parameter values for these sharks were given in Chapter

4 (Table 4.2) and, for tractability, were assumed known and fixed for this analysis. A Monte Carlo approach was taken, with the maximum likelihood estimates of the parameters and  $U_t$  obtained for each of 50 sampled effort series under the minimum and maximum catch scenarios.

#### *Model description*

The model has the same structure as models in previous chapters (but with different leading parameters). Table 5.10 describes derivation of Beverton and Holt (1957) recruitment parameters  $\alpha$  and  $\beta$  from the leading biological parameters  $B_0$  and CR (Table 5.10: equations T5.10.1 and T5.10.3). The model was initialised at in 1968 ( $t = 1$ ) using the equation

$$(5.1) \quad N_{a,1} = R_0 \cdot l_a$$

where  $N_{a,1}$  is numbers at age  $a$  at time 1,  $R_0$  is number of unfished recruits (equation T5.10.2) and  $l_a$  is unfished survivorship at age (equation T5.10.5; note use of a plus group for the final age class). The number of age 1 recruits in each year,  $R_t$ , was assumed to follow Beverton-Holt recruitment, given by

$$(5.2) \quad R_t = \frac{\alpha E_t}{1 + \beta E_t}$$

where  $E_t$  is number of eggs in year  $t$  obtained from

$$(5.3) \quad E_t = \sum_a^{\infty} f_a N_{a,t}$$

where  $f_a$  is mean fecundity at age given by

$$(5.4) \quad f_a = \text{LS.} \frac{1}{1 + e^{\left(\frac{-(a - a_{mat})}{\sigma}\right)}}$$

where  $LS$  is the median annual litter size,  $a_{mat}$  is age-at-50%-maturity (the age at which 50% of individuals are mature) and  $\sigma$  determines the steepness of the logistic curve (see Chapters 2 and 4). For ages greater than 1, predicted numbers at age  $N_{a,t}$  were obtained using

$$(5.5) \quad N_{a,t} = \begin{cases} N_{a-1,t-1} e^{-(M+v_{a-1}F_{t-1})} & \text{for } a < a_{max} \\ N_{a-1,t-1} e^{-(M+v_{a-1}F_{t-1})} + N_{a,t-1} e^{-(M+v_a F_{t-1})} & \text{for } a = a_{max} \end{cases}$$

where  $(M + v_a F_t)$  represents the instantaneous total mortality rate at age  $a$  in year  $t$ , where  $M$  is instantaneous natural mortality rate assumed equal to  $1.5\kappa$  (Beverton Holt 1959;  $\kappa$  is von Bertalanffy growth rate), and  $v_a$  is vulnerability at age, assumed to be logistic, i.e.,

$$(5.6) \quad v_a = \frac{1}{1 + e^{\left(\frac{-(a-a_h)}{\sigma v}\right)}}$$

and  $a_h$  is age-at-50%-first-harvest and  $\sigma v$  determines steepness of the curve. The fishing mortality rate,  $F_t$ , in year  $t$  was assumed to be related to annual effort through the relationship

$$(5.7) \quad F_t = q_c Eff_t$$

where  $Eff_t$  is annual fishing effort (hours) and  $q_c$  is the scalar relating  $F$  to effort (i.e.,  $q_c$  is the catchability coefficient), assumed for this analysis to be constant. The parameter of interest, annual harvest rate,  $U_t$ , was then obtained from predicted  $F_t$  using  $U_t = 1 - e^{-F_t}$ .

### *Likelihood*

The model was fit to reconstructed catch,  $C_t$  for the years 1990-2002 (Table 5.9) and the index of mean relative abundance,  $I_t$ , obtained from the *Kapala* surveys (Table 5.2). For simplicity, process error (Hilborn and Walters 1992) was not estimated. Lognormal observation error was assumed in both observation models.



Predicted catch at age  $a$  in year  $t$ ,  $\hat{C}_{a,t}$ , was determined using the Baranov equation (Hilborn and Walters 1992), where

$$(5.8) \quad \hat{C}_t = \sum_{a=1} \frac{F_{a,t}}{(M + v_a F_t)} (1 - e^{-(M + v_a F_t)}) N_{a,t} w_a$$

Total annual predicted catches were obtained by summing the catches at age in each year. Equations using instantaneous fishing mortality rates were used rather than annual harvest rates to avoid the assumption of fishing mortality and natural mortality occurring at separate times.

Annual predicted vulnerable biomass,  $VB_t$ , was given by

$$(5.9) \quad VB_t = \sum_a N_{a,t} v_{a,t} w_a$$

and the negative log likelihood  $L$  was given by

$$(5.10) \quad L = -\sum_{t=1} \left( \frac{n_c}{2} \ln(d_{c,t}^2) + \frac{n_l}{2} \ln(d_{l,t}^2) \right)$$

where  $d_{c,t}$  is the difference between log observed and predicted catch at time  $t$  (for  $n_c$  catch observations) and where  $d_{l,t}$  is the maximum likelihood difference between observed and predicted abundance, obtained from the equation

$$(5.11) \quad d_{l,t} = \bar{Z} - \ln\left(\frac{I_t}{VB_t}\right)$$

where  $\bar{Z}$  is the average of logged differences between the observed and predicted indices of

abundance, i.e.,  $\bar{Z} = \frac{\sum \left( \ln\left(\frac{I_t}{VB_t}\right) \right)}{n_l}$  (Walters and Ludwig 1994; see also Chapter 2) for  $n_l$  survey

observations ( $n_I = 3$ ). The term  $\frac{n_c}{2} \ln(d_{c,t}^2) + \frac{n_I}{2} \ln(d_{I,t}^2)$  is the result of using the conditional maximum likelihood estimates of the variance in the normal distributions of the residuals (Walters and Ludwig 1994).

The relationship between  $VB_t$  and  $I_t$ , needed for presentation of results, is given by  $I_t = q_I VB_t$  where  $q_I$  is the scalar, assumed linearly proportional to vulnerable biomass. A random sampling design had been used for the *Kapala* surveys and the same locations were sampled in each sampling period (Andrew *et al.* 1997) so the assumption of linearity is assumed to be valid.  $q_I$  was evaluated at its maximum likelihood value, using the approach of Walters and Ludwig (1994), where

$$(5.12) \quad q_I = e^{\bar{z}}$$

Because the proportions used to break down *Centrophorus* catches into species were so uncertain, an aggregated analysis was also done for all *Centrophorus* combined, using the minimum and maximum catch estimates in Table 5.8. Life history parameters for all three species are similar (Chapter 4; Table 4.2) and parameters for *C. harrissoni* were used.

#### *Monte Carlo simulations*

Simulations were done under the minimum and maximum catch hypotheses given in Table 5.9. For each species, for each catch scenario (minimum and maximum), 50 random effort series were drawn from the distribution described above (Figure 5.1). For each random effort series, the maximum likelihood estimate of  $B_0$  and  $q_c$  were obtained using the non-linear optimisation function 'Optim' implemented in the R modelling environment (R Development Core Team 2006). Parameters  $B_0$  and  $q_c$  were, respectively, log transformed and logit transformed to prevent undefined parameters being tested (i.e., negative values of  $B_0$  and values of  $q_c$  outside the range [0,1].  $B_0$  was initialised at 2000 t and  $q_c$  was initialised at 0.00035. These values were chosen after test simulations as a combination of parameters that would not lead to predicted stock crash. The optimisation routine used was the "L-BFGS-B" method of Byrd *et al.* (1995), with lower and upper boundaries set at -10 and 15. The boundaries were set to prevent the model taking the exponent of a number too large or too small and producing undefined transformed

parameters. The routine found a solution in all simulations (i.e., did not reach the maximum iteration limit). Age-at-50%-first-harvest,  $a_h$ , of these species is unknown and, therefore, the whole process was repeated for a range of values of  $a_h$  (sequence 1:15, step size 2).

### *Sensitivity analysis*

To illustrate the effect of fixing key parameters on model results, a simple sensitivity analysis was done for *C. harrissoni* only. A single effort series was drawn from the distribution described above and  $B_0$ ,  $q_c$  and  $U_t$  were estimated under a range of values of  $\kappa$ ,  $a_{mat}$  and CR, with  $a_h$  fixed at 5. Tested values of  $\kappa$  were (0.045, 0.05, 0.07, 0.09, 0.1); and tested values of  $a_{mat}$  were (15, 20, 25, 30). To show the effect of fixing CR at its maximum possible value, the simulations were repeated for the minimum hypothesis of CR (i.e., CR approaching 1) for three hypotheses of  $a_{mat}$  ( $a_{mat} = 15, 20, 30$ ). All other parameters were held at the fixed deterministic values.

## **Results**

Mean estimates of  $B_0$  and  $q_c$  for all values of  $a_h$  are given in Table 5.11. The quality of fit to the catch estimates and survey indices was variable. The best fits were obtained for  $a_h = 1 - 5$ . Estimates obtained under poor fits to the survey index are indicated with an asterisk. Poor fits are defined as those for which the predicted index of abundance underestimated the mean ( $\pm$  s.e.) 1976 observation for all Monte Carlo trials.

In general, the maximum catch scenarios resulted in very high estimates of peak catches for years before catch records were kept (Figure 5.9). Within analyses, despite very large differences in estimates of historical catch, there was relatively little uncertainty in the estimates of historical harvest rates (Figure 5.10). In all cases, estimates of  $U_t$  were fairly tightly bounded within each  $a_h$  scenario. For both *C. harrissoni* and mixed *Centrophorus*, estimates peaked at around 0.4-0.6 in the late 1980s. The tight bounding of  $U_t$  occurred because relative rate of decline due to fishing is determined only by the harvest rate (i.e., it is insensitive to population size). Therefore, in an effort-driven model, with fixed  $M$  and CR, the rate of decline is determined by the catchability coefficient (equation 5.7). In terms of absolute scale of the model,  $B_0$  and  $q_c$  are highly confounded and, therefore, different combinations of values predict similar harvest rates,

even when there is large uncertainty in absolute catch and biomass. Estimates of  $U_t$  tended to increase as  $a_h$  increased (Figure 5.10). It should be remembered that  $U_t$  is the harvest rate on the vulnerable portion of the population only. Therefore, to produce the same decline in the index of abundance with the same effort series, while leaving successively larger proportions of the population unfished, the model predicted that a greater proportion of the vulnerable population would have to have been harvested.

In all cases (i.e., for all  $a_h$ ), after the first few years of fishery development, maximum likelihood estimates of  $U_t$  exceeded the mean estimate of maximum possible  $U_{MSY}$  reported in Chapter 4 (mean  $U_{MSY}^{Lim} = 0.04-0.1$ : Figure 4.3; Table 4.3) and the mean estimate of  $U_{Max}$  (mean  $U_{Max} = 0.08$ : Figure 4.5; Table 4.4). In the years of peak harvest rate, these reference points were estimated to have been exceeded by more than an order of magnitude.

#### *Sensitivity analysis*

The effect of changing growth rate  $\kappa$  and age-at-50%-maturity  $a_{mat}$  on estimates of historical  $C_t$  and  $U_t$  is shown in Figure 5.11. Not surprisingly, the effect of increasing  $\kappa$  increased estimates of  $C_t$  and decreased estimates of  $U_t$ , as the population was predicted to have become more productive (through the influence of  $\kappa$  on  $M$ ). The difference in estimates of  $U_t$  between the highest and lowest tested value of  $\kappa$  ranged from  $<0.01$  to  $0.15$ , and it should be noted that the stock was always predicted to be overfished even at the highest tested value of  $\kappa$ . The effect of increasing  $a_{mat}$  decreased estimates of  $C_t$  and increased estimates of  $U_t$ , as the population was predicted to have become less productive.

Due to the highly constrained nature of CR for these stocks, the effect of fixing CR at its maximum value (see Chapter 4) was very small (Figure 5.12). This was because the range of possible values of CR was small (i.e., for this stock, with  $a_{mat} = 15$ , the deterministic maximum hypothesis for CR was  $4.55$  and the minimum hypothesis approaching  $1$  (by definition). Setting  $a_{mat} = 20$  changed the range of possible CR to between  $1$  and  $3.3$ , while setting  $a_{mat} = 30$  changed the range of possible CR to between  $1$  and  $1.8$ . Under the lowest tested value of  $a_{mat}$  (i.e., with the biggest difference between minimum and maximum CR), the greatest difference between the estimates of  $U_t$  was  $0.1$ , at the peak of the series.

## Discussion

This chapter represents the first attempt at assessing the current and historical state of sharks in the genus *Centrophorus* on the continental slope of NSW. These species are believed to have been depleted in southeastern Australia (Andrew *et al.* 1997 and Graham *et al.* 2001) and to have extremely low productivity (Daley *et al.* 2002; Chapter 4). In the near future, it is possible that *C. harrissoni* will require development of a management plan if it becomes listed as threatened under the Commonwealth EPBC Act. These species are extremely data-limited, with only the most rudimentary catch and life history data available and, therefore, innovative methods are needed for their assessment. The previous chapter showed how uncertainty in the productivity of these sharks could be quantified and showed uncertainty in CR to be very low. This has enabled a simple stock assessment to be developed, despite severe limitations in the available time series data. However, due to the many assumptions required in reconstruction of historical catch and effort series, the results should be considered preliminary and illustrative of a framework for assessment of these species. Due to logistical constraints, a fully Bayesian analysis was not done, although this should be a priority as an extension of this work, as it would enable a more thorough analysis of the uncertainty in the results. This should involve a testing phase to determine appropriate priors for estimated parameters  $B_0$  and  $q_c$ . The present study should therefore be viewed as a candidate framework for synthesising available data from a disparate set of sources into a stock assessment for these sharks.

Despite large uncertainty in historical catch and biomass, estimates of historical harvest rate were reasonably precise for all scenarios tested. Under all scenarios, for all except the very earliest years in the fishery, harvest rates were estimated to have exceed the maximum possible hypothesis for  $U_{MSY}$  and the mean estimate of  $U_{Max}$  obtained in Chapter 4. In years of peak harvest rate (between 1985 and 1990), the model estimated that  $U_{MSY}$  had been exceeded by more than an order of magnitude and it appears likely that overfishing continues, despite large declines in effort in recent years. Estimates of historical harvest rates depended heavily on the mean estimates of relative abundance reported in Graham *et al.* (2001). Studies reporting large declines in shark populations in other parts of the world (Baum *et al.* 2003; Baum and Myers 2004) have been criticised because the range of the survey was inconsistent among time periods (Burgess *et al.* 2005; but see Baum *et al.* 2005). The 1996 *Kapala* surveys were replicates of the

1976 surveys and trawled the same locations and depth strata with the original fishing gear. The surveys followed a stratified random sampling design, with several replicate tows in each sampling location, resulting in a total of 361 tows during all survey periods. Therefore, while only three data points were used for fitting the models in the present study, they were derived from a large dataset, which had been designed to have power to detect change. It is important to note at this stage that the depletions observed by the *Kapala* surveys may have been local depletions, as all three species are distributed more broadly than NSW (Last and Stevens 1994; White *et al.* 2008). However, for *C. harrissoni* at least, the waters off NSW represent a large portion of the known range of the species (possibly > 50%), with most of the rest of the known population occurring in Australian waters that are currently fished by Commonwealth fisheries (White *et al.* 2008).

To avoid overparameterisation of the model, the compensation ratio, CR, was fixed at its maximum possible value, which was highly constrained by the low fecundity of these species (see Chapter 4). Because of its highly constrained nature, fixing CR had very little influence on estimates of historical harvest rates (i.e., results were very similar to those obtained under the minimum estimate of CR). Therefore, the only parameters estimated directly were the scaling parameters  $B_0$  and  $q_c$ , which fix the carrying capacity of the population and the scale of the relationship between commercial effort and fishing mortality respectively. In terms of setting the size of absolute catches, these parameters are highly correlated (i.e., a large population with small  $q_c$  could produce the same catches as a small population with large  $q_c$  for the same amount of fishing effort). However, of these two parameters, only  $q_c$  determines the harvest rate. Therefore, all other parameters equal, only  $q_c$  determines the rate of change in a population in response to fishing. If only an index of relative abundance is available (and CR is known with some certainty),  $q_c$  can be estimated (but not  $B_0$ ). If an index of relative abundance *and* absolute catches are available, the population can be scaled and  $B_0$  can also be estimated. In the present study, there was very large uncertainty in the catch, for which only rough minimum and maximum estimates for a limited number of years could be made, and this resulted in large uncertainty in estimates of absolute historical catches and  $B_0$  for all species. However, the *Kapala* data provided a highly contrasting index of abundance, which enabled reasonably precise estimation of harvest rate despite the uncertainty in catches and effort. Note that this was only possible because CR was known with some precision and could be fixed.

Before these results are used for decision-making, a more thorough sensitivity analysis, which was beyond the scope and resources of this study, is required to test the effects of the assumptions of the model. The model is amenable to testing for sensitivity to model assumptions and to assumptions about life history and fishery data. Estimates of historical harvest rate were most sensitive to age-at-first harvest and growth rate and less sensitive to age at maturity and the compensation ratio. Detailed analysis of the effect of the weighting factors in the likelihood function would also be required, as the quality of fits among ages at first harvest was variable. Further testing of assumptions about age at maturity and form of the age at maturity function should also be done. The effect of decreasing the assumed age at maturity was to increase the maximum possible value of the compensation ratio, which, in turn, would decrease estimated historical harvest rates. Across the range of ages at maturity tested (15 y to 30 y) predicted historical harvest rates were very similar. This range of ages was obtained by assuming a von Bertalanffy growth function and ‘growing’ the sharks until they reached the published length at maturity. Other growth functions (e.g., Schnute 1981) should be examined to test for the possibility that these sharks reach length at maturity at a younger age.

The present study did not consider spatial or temporal variability in abundance of *Centrophorus* spp., although the *Kapala* and fishery data could be more thoroughly analysed to account for such variability. The model also assumed closed populations and did not admit the possibility of migration of individuals from other areas (e.g., Clark and King 1989; Wetherbee 2000). This study assumed that the natural mortality rate  $M$  was stationary and a constant function of the von Bertalanffy growth rate across all age classes. These may not be valid assumptions for sharks and there has been some debate about the correct form of the relationship between  $M$  and age in sharks (Walker 1998; Cortés 2007). Walker (1994) and Punt and Walker (1998) have suggested that natural mortality in pre-recruited *G. galeus* must be several times higher than in older age classes. Walker (1994) used an asymmetrical  $U$ -shaped function to describe the relationship between  $M$  and age, attributing the decrease in mortality after the first few years of life to improved ability to escape predators and the subsequent increase in older age classes to senescence. The effect of assuming such a relationship in the present analysis (compared to a constant mean relationship) would be to predict lower historical harvest rates on very young and old age classes, but higher historical harvest rates on mid-range age-classes. The overall effect

on predicted harvest rates would depend on the exact form of the function used. Testing for sensitivity to the assumption of constant  $M$  with age is highly recommended for future extensions of this analysis. The catchability coefficient  $q_c$  was assumed fixed in this analysis and assumed to be linearly related to population size. Both of these assumptions are frequently violated in fisheries assessments (Hilborn and Walters 1992). In the present analysis, attempting to estimate additional parameters to describe density dependence in  $q_c$  was avoided to prevent overparameterisation and to keep the analysis simple. Effects of the assumed form and steepness of the selectivity and maturity functions were also not tested.

Missing, highly-aggregated and error-strewn data mean it is almost impossible to perform a completely defensible assessment of *Centrophorus* in southeastern Australia. This problem is by no means limited to NSW and has been raised by numerous authors as a problem in shark fisheries throughout the world, especially when sharks are taken as bycatch (Bonfil 1994; Walker 1998; Musick *et al.* 2000; Dulvy *et al.* 2000; Stevens *et al.* 2000). Roberts (2005) examined shark landings data in the global database of Food and Agriculture Organisation of the United Nations (FAO) and found that 46% of elasmobranch landings in 2003 were listed as ‘unspecified Chondrichthyans’, with a further 17% reported as unspecified ‘sharks’ and 5% as unspecified dogsharks. In NSW, all Chondrichthyans landings were reported as unspecified sharks until the mid-1980s, and many are still recorded in aggregate categories. Since many sharks, skates and rays are caught as unwanted bycatch and have not been subject to any management plan in southeastern Australia, a large proportion of catches is also likely to have gone completely unrecorded. Changes in abundance of dogsharks and other sharks on the continental slope of NSW (Graham *et al.* 2001) would likely not have been noticed if not for the 1976 *Kapala* surveys, which were done more than a decade before detailed shark landings statistics were kept. These surveys led to the CITES listing and to the current interest in status of these populations. It is noteworthy that there are at least twenty species of skates and rays occurring in the estuarine, shelf and slope waters of NSW (May and Maxwell 1980; Cavanagh (ed.) *et al.* 2003). Very little is known about the biology of these species and they are not currently subject to any specific management control. Skates and rays were recorded under only two general categories in the 1976 surveys (*Raja* spp. and undifferentiated Urolophidae) and there is therefore no baseline data upon which to base any strong inferences on the state of these populations, even though, on aggregate, abundance declined between the two survey periods



(Graham *et al.* 2001). Dulvy *et al.* (2000) showed that aggregated catch statistics for skates in the Irish Sea showed stability on aggregate but masked declines in abundance of several species. This followed previously-reported observations of large, less productive skate species being replaced by smaller, more productive species through years of fishing (Dulvy and Reynolds 2002). Significant discarding of other low-productivity deepwater dogsharks, *Etmopterus* spp. and *Squalus* spp., is known to occur in southeastern Australia (Daley *et al.* 2002). However, there is no management plan for these species and, again, little to no data upon which to base stock assessment. In these cases, definitions of EBFM that include terms such as “no species overfished” (e.g., Murawski 2000) are difficult to translate into policy, especially when collection of even the most basic of data is absent.

The lack of response to early signals of the decline of many sharks in the 1979 surveys is indicative of the lack of interest in sharks at a time when economic growth of valuable teleost fisheries in southeastern Australia was a priority. More often than not, the decision to prioritize economic value over conservation of unproductive species such as sharks has happened by default during fishery development, through removal of old large individuals, and through depletion of less productive species, as fisheries for more productive species develop (Pauly 1995; Pitcher 2001). In recent years, public priorities have changed and a precautionary approach to managing fisheries (FAO 1995; 2003) is mandated in many parts of the world, including Australia (e.g., Council of Australian Governments 1992; Commonwealth of Australia 1998; Scandol *et al.* 2005; Gibbs 2008). By the time policy changes to reflect conservation priorities, however, many species may have already become overfished and recovery plans, if mandated, would necessitate severe reductions in fishing effort at a time when profitability of the fishery may have become marginal. This would make trade-offs between economic and conservation objectives even more acute.

From the available information, it appears that sharks in the genus *Centrophorus* have been severely depleted off the coast of NSW and may have been overfished for a number of years. This is supported by reductions in survey and observer data, in reported landings and in fish market sales. However, there is insufficient information to conclude whether effort reductions are having or have had a positive effect on *Centrophorus* spp. Years of incomplete and incorrect recording of catch statistics and observer data have severely compromised scientifically and

legally defensible stock assessments for these species and for Chondrichthyans in general in south eastern Australia. Shark identification guides have now been issued in the Commonwealth fisheries (Daley *et al.* 2002) but many species, including those in the genus *Centrophorus* are still recorded in aggregate categories. Efforts should be made to improve this situation at both the State and Commonwealth level.

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## Tables

**Table 5.1.** Summary of locations and grounds surveyed during the upper slope trawls. Partial surveys were done between 1979-1981 (see text).

Year	Quarter	Location	Coordinates	Ground
1. 1976-77	I-IV	1: Sydney-Newcastle	Between latitudes 33°25' and 33°50'	1: 220 m
2. 1979-81	I-III (incomplete)			2: 275 m
3. 1996-97	I-II			3: 330 m 4: 385 m 5: 440 m 6: 495 m 7: 550 m 8: 605 m
1. 1976-77	I-IV	2: Ulladulla-Bateman's Bay	Between latitudes 35°25' and 35°50'	1: 220 m
2. 1979-81	I-III (incomplete)			2: 275 m
3. 1996-97	I-III (III incomplete)			3: 330 m 4: 385 m 5: 440 m 6: 495 m 7: 550 m 8: 605 m
1. 1976-77	I-III	3: Eden-Gabo Island	Between latitudes 37°05' and 37°50'	1: 220 m
2. 1979-81	I-III (incomplete)			2: 275 m
3. 1996-97	I-III			3: 330 m 4: 385 m 5: 440 m 6: 495 m 7: 550 m 8: 605 m

*Source:* Graham *et al.* (1997)

**Table 5.2.** Mean (and s.e.) catch rates ( $\text{kg h}^{-1}$ ) for *Centrophorus* spp. caught in tows on the upper slope between 300 and 525 m during the 1976-7 (n = 130 tows), 1979-81 (n = 150 tows) and 1996-7 (n = 81 tows) surveys by the FRV Kapala. Means are across all grounds and depths surveyed (300 – 525 m).

Species	1996-7		1979-81		1996-7	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
<i>C. moluccensis</i>	18	3.1	2.3	0.7	<0.1	-
<i>C. harrissoni</i> <sup>†</sup>	37.6	6.9	17.4	4.2	<0.1	-
<i>C. uyato</i> <sup>†</sup>	146.3	36.1	26.7	7.3	<0.1	-
<i>C. harrissoni</i> & <i>C. uyato</i> combined	169.9	30.4	44.1	8.5	<0.1	-

<sup>†</sup> Data from tows where species were recorded separately

Source: Graham *et al.* 2001.

**Table 5.3.** Number of vessels actively fishing on the continental slope of NSW; reported effort (hours) of vessels that caught dogsharks in depths 300-600 m; and effort predicted from the exponential relationship shown. Bold entries represent known data. Numbers of vessels shown in italics are interpolated estimates of number of vessels when data are absent. See also Figure 5.1.

<b>Year</b>	<b>Number of vessels <math>V_t</math></b>	<b>Reported effort (<math>h</math>)</b>	<b>Predicted effort <math>Eff_t = 39.3V_t</math></b>
<b>1968</b>	<b>2</b>		78.6
<i>1969</i>	<i>3</i>		117.9
<i>1970</i>	<i>4</i>		157.2
<i>1971</i>	<i>5</i>		196.5
<i>1972</i>	<i>6</i>		235.8
<i>1973</i>	<i>8</i>		314.4
<i>1974</i>	<i>10</i>		393.0
<b>1975</b>	<b>12</b>		471.6
<i>1976</i>	<i>20</i>		786.0
<i>1977</i>	<i>30</i>		1179.0
<i>1978</i>	<i>40</i>		1572.0
<i>1979</i>	<i>50</i>		1965.0
<b>1980</b>	<b>60</b>		2358.0
<i>1981</i>	<i>63</i>		2475.9
<i>1982</i>	<i>66</i>		2593.8
<i>1983</i>	<i>69</i>		2711.7
<i>1984</i>	<i>72</i>		2829.6
<i>1985</i>	<i>75</i>		2947.5
<b>1986</b>	<b>79</b>	<b>4331.0</b>	3104.7
<b>1987</b>	<b>67</b>	<b>2987.6</b>	2633.1
<b>1988</b>	<b>64</b>	<b>4179.1</b>	2515.2
<b>1989</b>	<b>64</b>	<b>4486.0</b>	2515.2
<b>1990</b>	<b>51</b>	<b>1320.4</b>	2004.3
<b>1991</b>	<b>45</b>	<b>1287.6</b>	1768.5
<b>1992</b>	<b>43</b>	<b>1084.1</b>	1689.9
<b>1993</b>	<b>41</b>	<b>913.5</b>	1611.3
<b>1994</b>	<b>44</b>	<b>1101.3</b>	1729.2
<b>1995</b>	<b>43</b>	<b>889.7</b>	1689.9
<b>1996</b>	<b>45</b>	<b>1564.0</b>	1768.5
<b>1997</b>	<b>48</b>	<b>1523.0</b>	1886.4
<b>1998</b>	<b>40</b>	<b>1023.7</b>	1572.0
<b>1999</b>	<b>41</b>	<b>1116.3</b>	1611.3
<b>2000</b>	<b>46</b>	<b>810.0</b>	1807.8
<b>2001</b>	<b>39</b>	<b>858.0</b>	1532.7
<b>2002</b>	<b>41</b>	<b>1333.8</b>	1611.3

**Table 5.4.** Nominal landings of undifferentiated Squalidae and undifferentiated *Centrophorus* in the State and Commonwealth catch databases.

Undiff. Squalidae		Undiff. Centrophorus			
Database	Total SETF (all depths)	NSW State (excl. OFT)	NSW State (incl. OFT)	NSW State 'Other'	SETF (all depths)
<b>Year</b>					
1986	161.3	-	-	-	-
1987	103.9	-	-	-	-
1988	189.9	-	-	-	-
1989	192.6	-	-	-	-
1990	86.4	13.1	32.0	13.2	-
1991	99.3	12.5	39.0	28.2	-
1992	92.2	7.7	33.9	63.0	-
1993	94.6	6.4	33.3	34.0	-
1994	95.2	5.8	18.0	32.0	-
1995	72.4	7.1	15.4	32.1	-
1996	114.2	10.6	16.9	29.4	-
1997	77.8	7.9	19.6	-	-
1998	51.8	7.2	19.5	-	-
1999	57.2	9.5	20.6	-	-
2000	-	4.6	8.4	-	3.5
2001	-	7.4	14.8	-	3.3
2002	-	4.0	9.4	-	1.9
2003	-	-	-	-	-

**Table 5.5.** *Centrophorus* as proportion of undifferentiated Squalidae in landings in the NSW State and ISMP databases.

<i>Centrophorus</i> proportion of Squalidae landings			
Database	NSW State fisheries	NSW State 'Other'	ISMP
<b>Year</b>	-	-	-
1986	-	-	-
1987	-	-	-
1988	-	-	-
1989	-	-	-
1990	-	-	-
1991	0.34	0.36	-
1992	0.20	0.53	0.45
1993	0.27	0.37	0.11
1994	0.24	0.42	0.01
1995	0.24	0.44	0.02
1996	0.31	0.46	0.72
1997	0.50	-	0.30
1998	0.69	-	0.03
1999	0.47	-	0.04
2000	0.34	-	0.06
2001	0.47	-	0.07
2002	0.38	-	0.09
2003	-	-	0.09

**Table 5.6.** Proportions of the three species of *Centrophorus* in NSW represented as proportion of total *Centrophorus* catch from the ISMP observer database. Mixed Endeavour represents catches recorded under the miscellaneous Endeavour dogsharks category. Note that proportions show proportion of whole catch (i.e., retained + discarded).

Year	Proportion of total <i>Centrophorus</i>			
	<i>C. harrissoni</i>	<i>C. uyato</i>	<i>C. moluccensis</i>	Mixed Endeavour
1992	0.000	0.000	0.000	1.000
1993	0.006	0.429	0.000	0.565
1994	0.042	0.916	0.000	0.042
1995	0.000	0.780	0.000	0.220
1996	0.000	0.000	0.000	1.000
1997	0.000	0.000	0.000	1.000
1998	0.000	0.300	0.700	0.000
1999	0.024	0.116	0.860	0.000
2000	0.000	0.007	0.946	0.047
2001	0.000	0.092	0.898	0.011
2002	0.007	0.301	0.662	0.030
Mean (+s.e.) all years	0.008 (0.004)	0.315 (0.101)	0.348 (0.121)	0.330 (0.125)
Mean (+s.e.) 1992-97	0.010 (0.008)	0.425 (0.191)	0.000 (0)	0.565 (0.196)
Mean (+s.e.) 1998-03	0.007 (0.004)	0.276 (0.122)	0.696 (0.125)	0.021 (0.008)



**Table 5.7.** Mean proportions of the three species of *Centrophorus* in NSW as proportions of total *Centrophorus* catch and total Squalidae catch from the *Kapala* database.

Survey Year	Proportion of <i>Centrophorus</i>		Proportion of Squalidae	
	1976-7	1996-7	1976-7	1996-7
<i>C. harrissoni</i>	0.204	0.158	0.103	0.004
<i>C. uyato</i>	0.690	0.576	0.349	0.015
<i>C. moluccensis</i>	0.106	0.266	0.053	0.007

**Table 5.8.** Minimum and maximum estimates of carcass landings and whole weight catch of *Centrophorus* in NSW to be used for priors in stock assessment model. Footnotes indicate how each estimate was derived.

Year	Estimated total <i>Centrophorus</i> landings		Estimated discards (prop. landings)		Estimated carcass conversion factor		Est. whole weight <i>Centrophorus</i> catch	
	Min	Max	Min	Max	Min <sup>a</sup>	Max <sup>b</sup>	Min	Max
1990	30.85 <sup>1</sup>	45.42 <sup>2</sup>	0	0.25	1	1.67	30.9 <sup>7</sup>	94.8 <sup>8</sup>
1991	35.47 <sup>1</sup>	52.21 <sup>2</sup>	0	0.25	1	1.67	35.5 <sup>7</sup>	109.0 <sup>8</sup>
1992	26.54 <sup>3</sup>	82.35 <sup>4</sup>	0	0.25	1	1.67	26.5 <sup>7</sup>	171.9 <sup>8</sup>
1993	16.66 <sup>3</sup>	68.32 <sup>4</sup>	0	0.1	1	1.67	16.7 <sup>7</sup>	125.5 <sup>8</sup>
1994	6.78 <sup>3</sup>	58.25 <sup>4</sup>	0	0.1	1	1.67	6.8 <sup>7</sup>	107.0 <sup>8</sup>
1995	8.79 <sup>3</sup>	47.63 <sup>4</sup>	0	0.1	1	1.67	8.8 <sup>7</sup>	87.5 <sup>8</sup>
1996	46.10 <sup>3</sup>	99.49 <sup>4</sup>	0	0.1	1	1.67	46.1 <sup>7</sup>	182.8 <sup>8</sup>
1997	31.58 <sup>3</sup>	58.33 <sup>4</sup>	0	0.1	1	1.67	31.6 <sup>7</sup>	107.2 <sup>8</sup>
1998	8.61 <sup>3</sup>	55.37 <sup>4</sup>	0	0.1	1	1.67	8.6 <sup>7</sup>	101.7 <sup>8</sup>
1999	11.77 <sup>3</sup>	47.45 <sup>4</sup>	0	0.1	1	1.67	11.8 <sup>7</sup>	87.2 <sup>8</sup>
2000	8.11 <sup>5</sup>	11.97 <sup>6</sup>	0	0.1	1	1.67	8.1 <sup>7</sup>	22.0 <sup>8</sup>
2001	10.73 <sup>5</sup>	18.15 <sup>6</sup>	0	0.1	1	1.67	10.7 <sup>7</sup>	33.3 <sup>8</sup>
2002	5.92 <sup>5</sup>	11.33 <sup>6</sup>	0	0.1	1	1.67	5.9 <sup>7</sup>	20.8 <sup>8</sup>

**Footnotes**

- a. Assumes all landings reported as whole weight.
- b. Assumes all landings reported as carcass weight.

1. Total SETF Squalid landings (Table 5.4) \* 1991 proportion of *Centrophorus* in NSW State 'Other' fishery (Table 5.5)
2. Total SETF Squalid landings \* 1992 proportion of *Centrophorus* in NSW State 'Other' fishery (Table 5.5)
3. [Total SETF Squalid landings \* minimum of that year's proportions of *Centrophorus* in Table 5.5] + *Centrophorus* landings in NSW State fisheries (excluding OFT landings; Table 5.4).
4. [Total SETF Squalid landings \* maximum of 1992 that year's proportions of *Centrophorus* in Table 5.5] + *Centrophorus* landings in NSW State fisheries (including OFT landings; Table 5.4).
5. Total SETF *Centrophorus* landings (Table 5.4) + *Centrophorus* landings in NSW State fisheries (excluding OFT landings; Table 5.4).
6. Total SETF *Centrophorus* landings (Table 5.4) + *Centrophorus* landings in NSW State fisheries (including OFT landings; Table 5.4).
7. [Minimum estimated *Centrophorus* landings (this Table, col.1) \* Minimum carcass conversion factor] + [Minimum estimated discard proportion \* Minimum estimated *Centrophorus* landings] \* Minimum carcass conversion factor
8. [Maximum estimated *Centrophorus* landings (this Table, col.2) \* Maximum carcass conversion factor] + [Maximum estimated discard proportion \* Maximum estimated *Centrophorus* landings] \* Maximum carcass conversion factor

**Table 5.9.** Minimum and maximum estimates of annual catch (t) for the three species of *Centrophorus* in NSW, based on the mean observation in the 1996 *Kapala* surveys. Estimates were obtained by multiplying the minimum and maximum estimated total catch (Table 5.8) by the mean 1996-7 proportion of each species in the total *Centrophorus* catch (Table 5.7).

Year	<i>C. harrissoni</i>	
	Min	Max
1990	4.9	15.0
1991	5.6	17.2
1992	4.2	27.2
1993	2.6	19.8
1994	1.1	16.9
1995	1.4	13.8
1996	7.3	28.9
1997	5.0	16.9
1998	1.4	16.1
1999	1.9	13.8
2000	1.3	3.5
2001	1.7	5.3
2002	0.9	3.3

**Table 5.10.** Derivation of recruitment parameters for the age-structured model (leading parameters CR and  $B_0$ ).  $M$  = average instantaneous natural mortality rate (assumed constant for all age classes);  $v_a$  = vulnerability at age;  $f_a$  = fecundity at age;  $w_a$  = weight at age. See Table 4.2 (Chapter 4) for parameter values.

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$$(T5.10.1) \quad \alpha = \frac{CR}{\varphi_{E0}}$$

$$(T5.10.2) \quad R_0 = \frac{B_0}{\varphi_{B0}}$$

$$(T5.10.3)^3 \quad \beta = \frac{\alpha \varphi_{E0} - 1}{R_0 \varphi_{E0}}$$

**Natural survival rate at age  $s_a$**

$$(T5.10.4) \quad s_a = e^{-M}$$

**Unfished survivorship at age  $l_a$**

$$(T5.10.5) \quad l_a = \begin{cases} e^{-M(a - ah)} & \text{for } a < a_{max} \\ e^{-M(a - ah)/(1 - s_a)} & \text{for } a = a_{max} \end{cases}$$

**Incidence functions<sup>4</sup>**

$$(T5.10.6) \quad \text{Unfished equilibrium eggs per recruit: } \varphi_{E0} = \sum_{a=1}^{\infty} l_a f_a$$

$$(T5.10.7) \quad \text{Unfished equilibrium vulnerable biomass per recruit: } \varphi_{VB0} = \sum_{a=1}^{\infty} l_a w_a v_a$$

$$(T5.10.8) \quad \text{Unfished equilibrium total biomass per recruit } \varphi_{B0} = \sum_{a=1}^{\infty} l_a w_a$$


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<sup>3</sup> Walters and Martell 2004

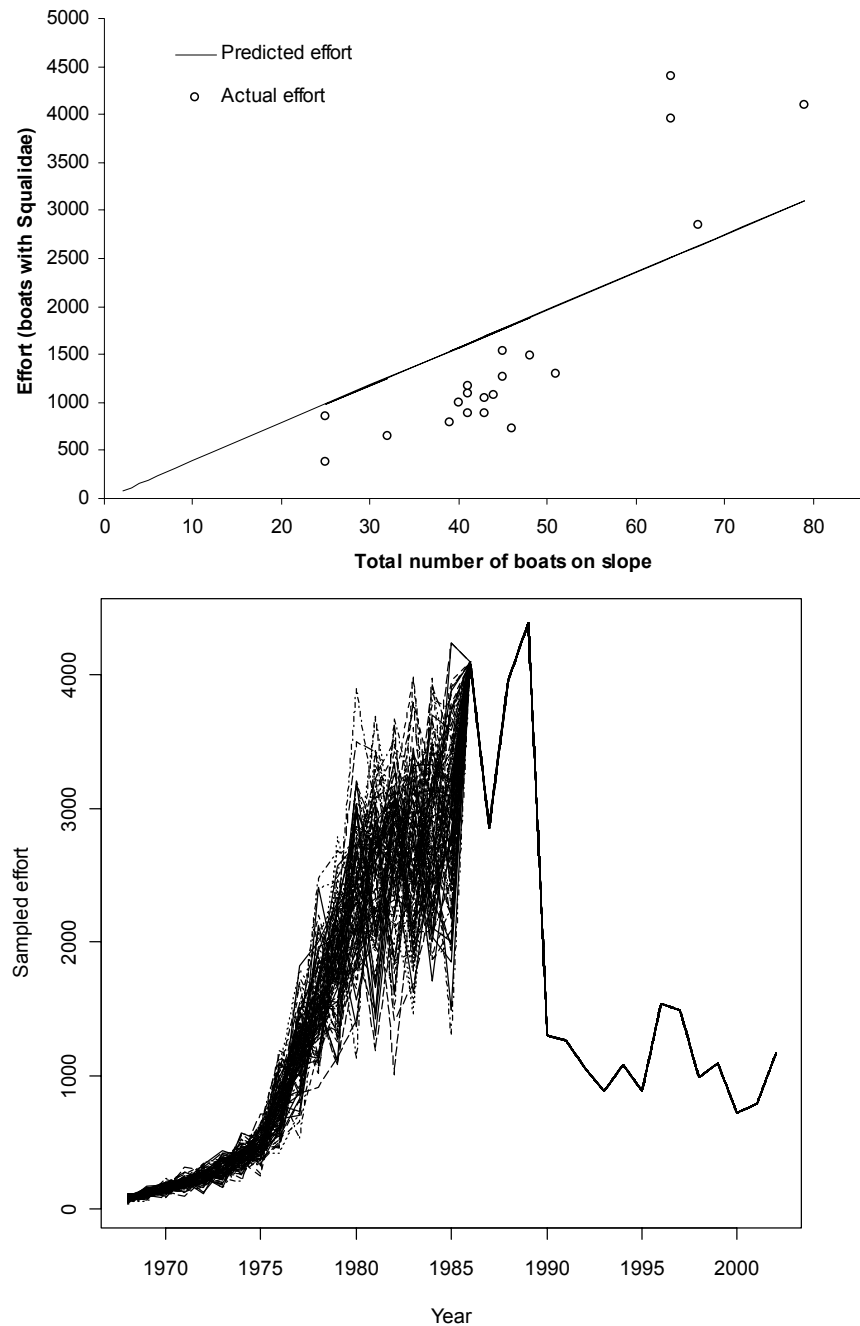
<sup>4</sup> Botsford 1981

**Table 5.11.** (a) Mean estimates of  $B_0$  and  $q_c$  for all values of  $a_h$  for the minimum catch scenarios; and (b) for the maximum catch scenarios (see Table 5.9). Estimates obtained under poor fits to the survey index are indicated with an asterisk. Poor fits are defined as those for which the predicted index of abundance over- or underestimated the 1976 mean ( $\pm$  s.e.) observation for all Monte Carlo trials.

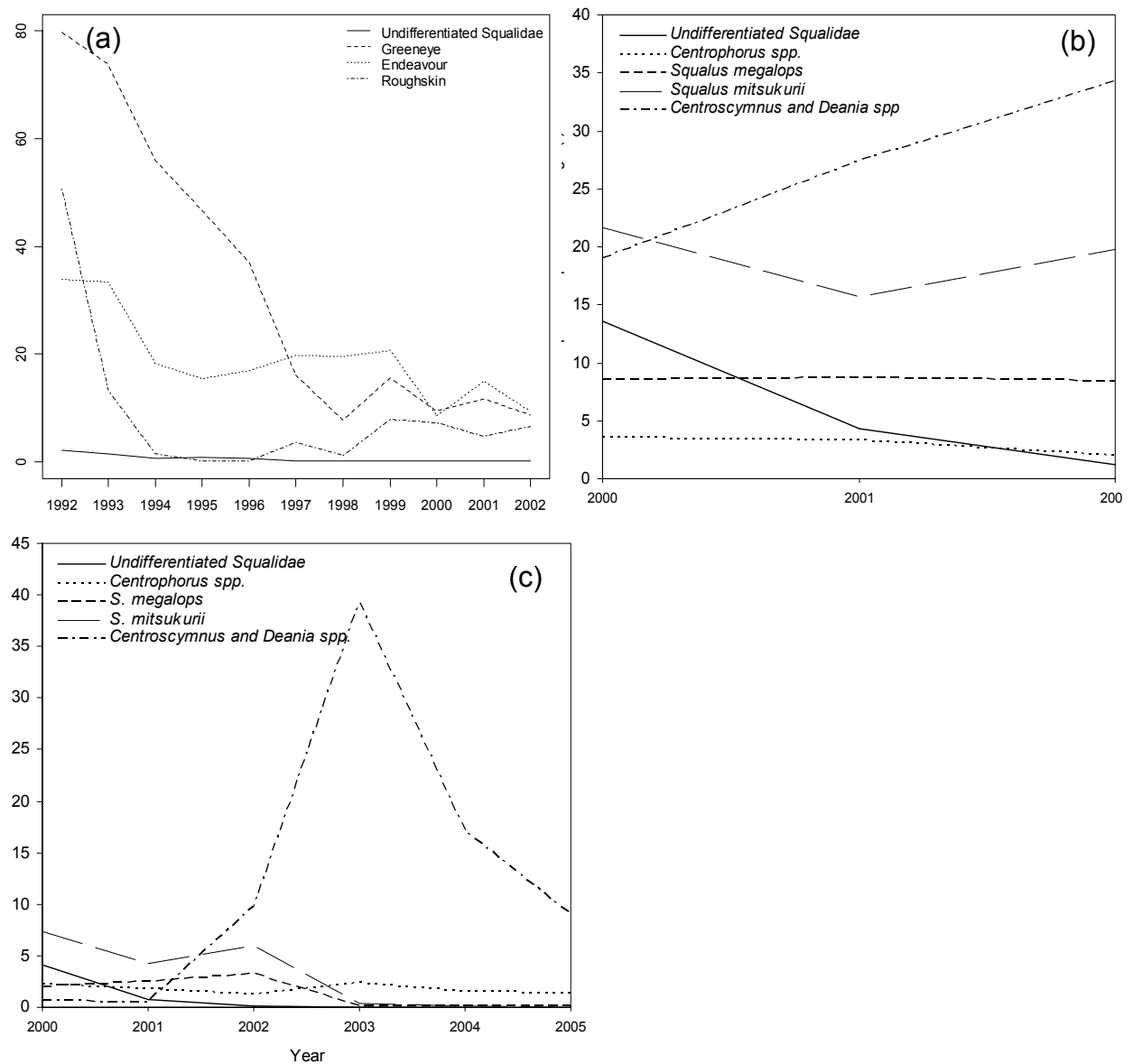
(a)	<i>All Centrophorus</i>		<i>C. harrissoni</i>	
$a_h$	$B_0$	$q_c$	$B_0$	$q_c$
1	50645	0.00015	7508	0.00016
3	50525	0.00016	7424	0.00018
5	51530	0.00019	7572	0.00022
7	23600*	0.00018*	7973*	0.00029*
9	6965*	0.00015*	1868*	0.00022*
11	3502*	0.00016*	3382*	0.00041*
15	2452*	0.00021*	1959*	0.00127*

(b)	<i>All Centrophorus</i>		<i>C. harrissoni</i>	
$ah$	$B_0$	$q_c$	$B_0$	$q_c$
1	270479	0.00014	42058	0.00016
3	268967	0.00016	41296	0.00018
5	272070	0.00019	41777	0.00022
7	167930*	0.00020*	17410*	0.00022*
9	36788*	0.00017*	10631*	0.00024*
11	138602*	0.00028*	3656*	0.00026*
15	16673*	0.00026*	5027*	0.00069*

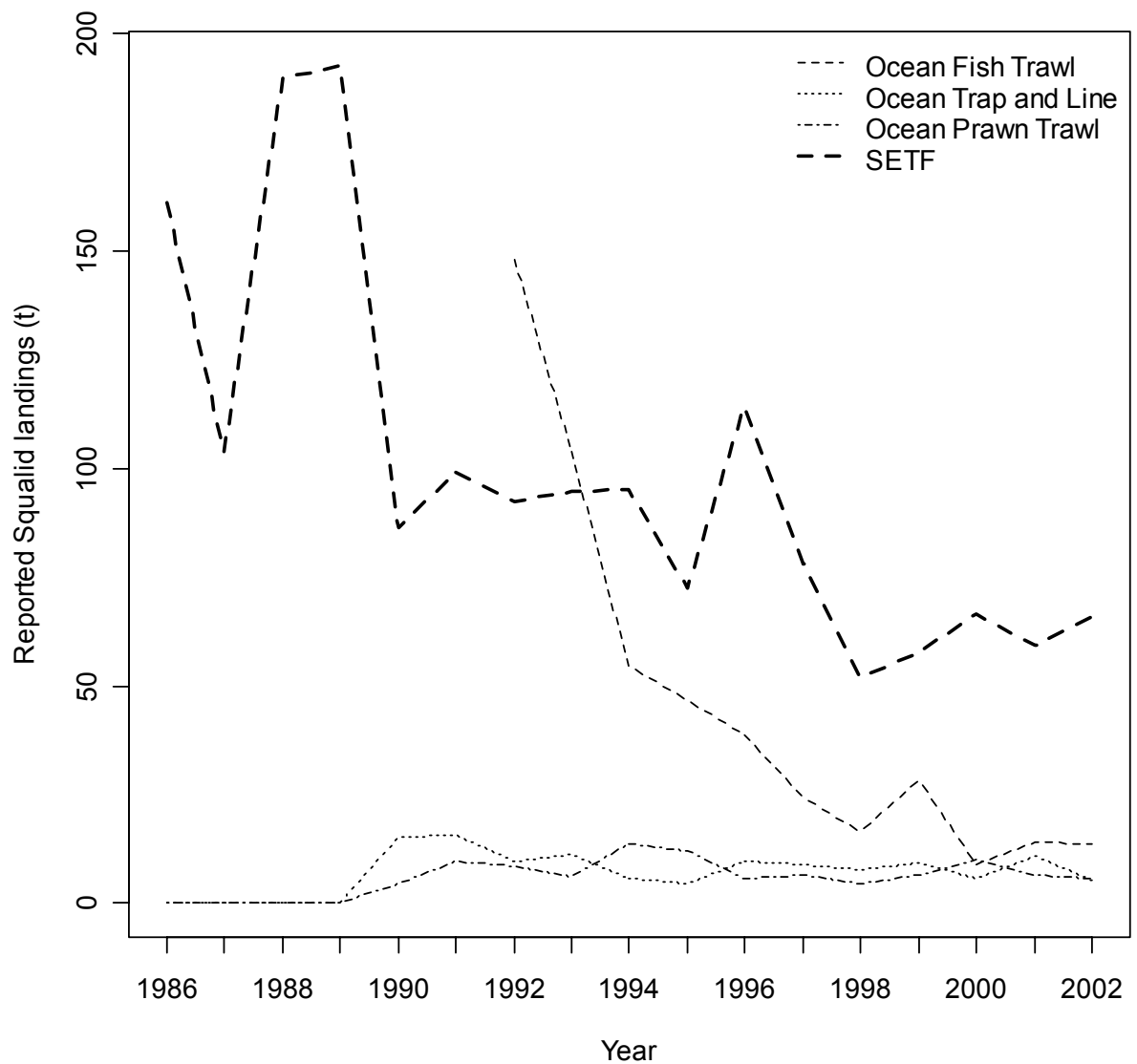
## Figures



**Figure 5.1.** (a) Relationship between number of vessels actively fishing on the continental slope (300-600 m) and nominal effort (hours) for boats reporting dogshark landings for the years 1986-2005; and (b) estimated (1968-1985) and nominal (1986-2005) effort (hours) for boats catching dogsharks on the continental slope. Lines before 1986 represent 100 Monte Carlo samples based on the linear fit shown above (see also Table 5.3).

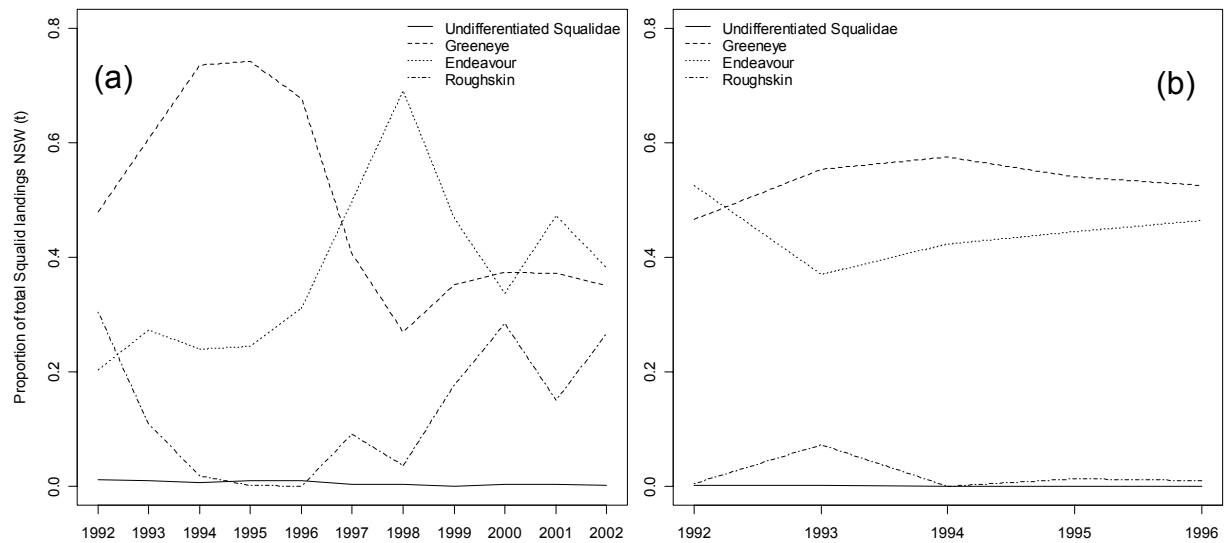


**Figure 5.2.** Reported landings (t) of dogsharks in (a) the NSW State database (excluding landings known to have been reported in the SETF); (b) the SETF Annual database for years after dogshark catches were disaggregated; and (c) the SETF Slope database for years after dogshark catches were disaggregated. The latter is shown to illustrate the rise in landings of *Centroscyrnus* and *Deania* spp. on the continental slope after 2002, although these data were not used in the present analysis.

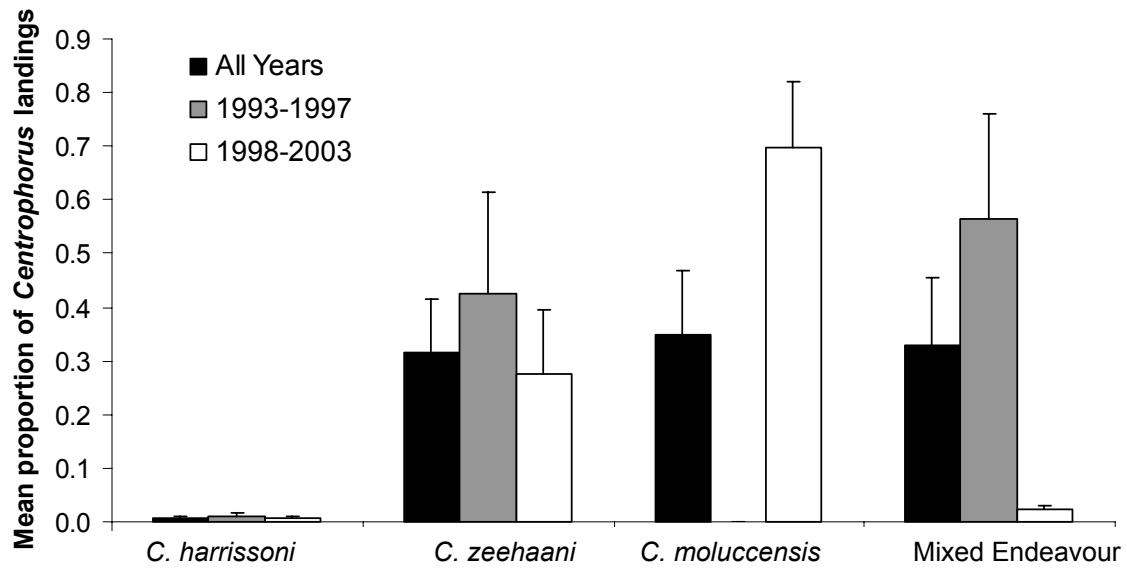


**Figure 5.3.** Reported landings of all dogsharks combined in the NSW State and SETF databases after removal of landings believed or known to have been double-reported to Commonwealth and State agencies (see text). Note that it remains uncertain as to whether landings in the Ocean Fish Trawl were double-reported.

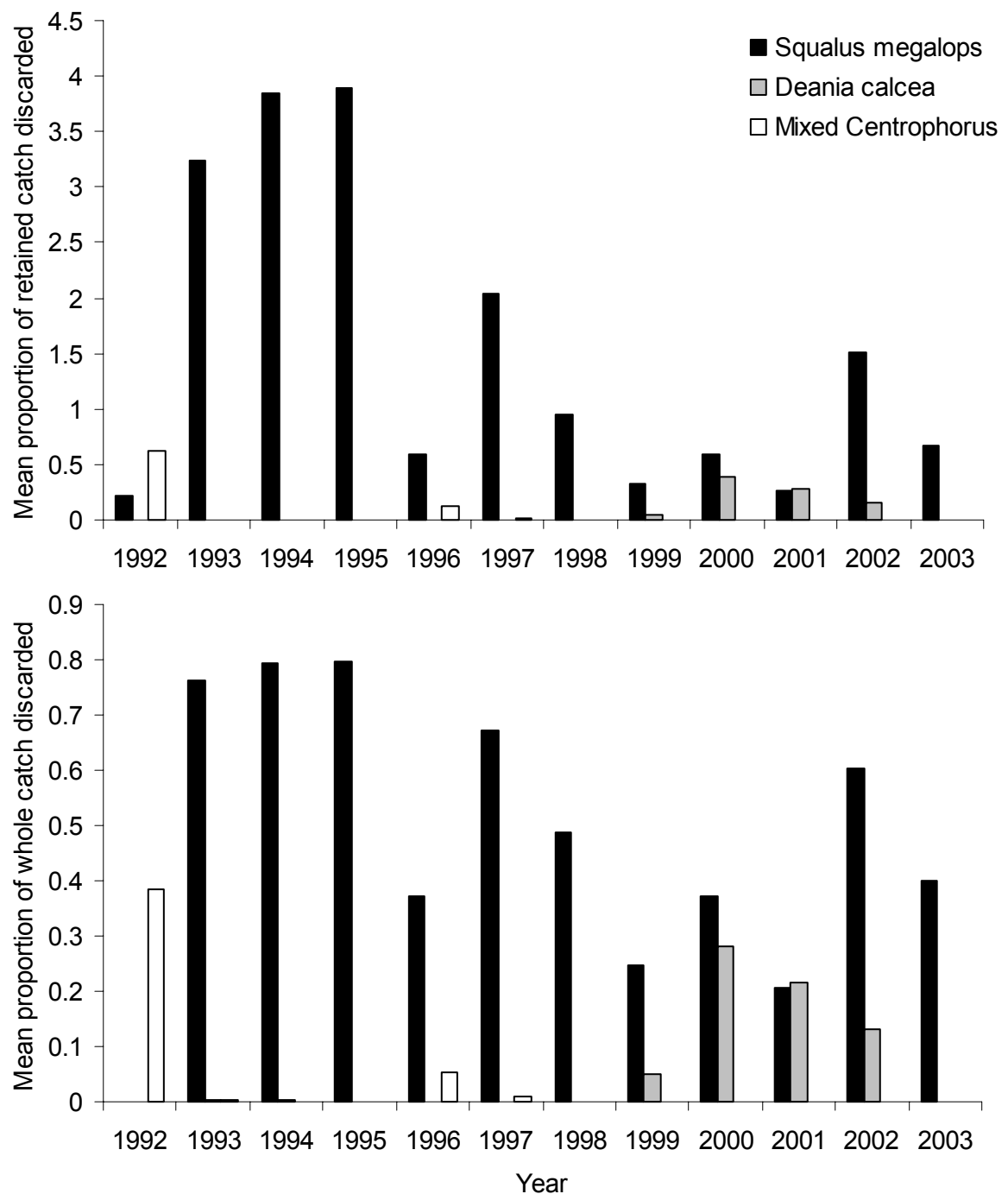




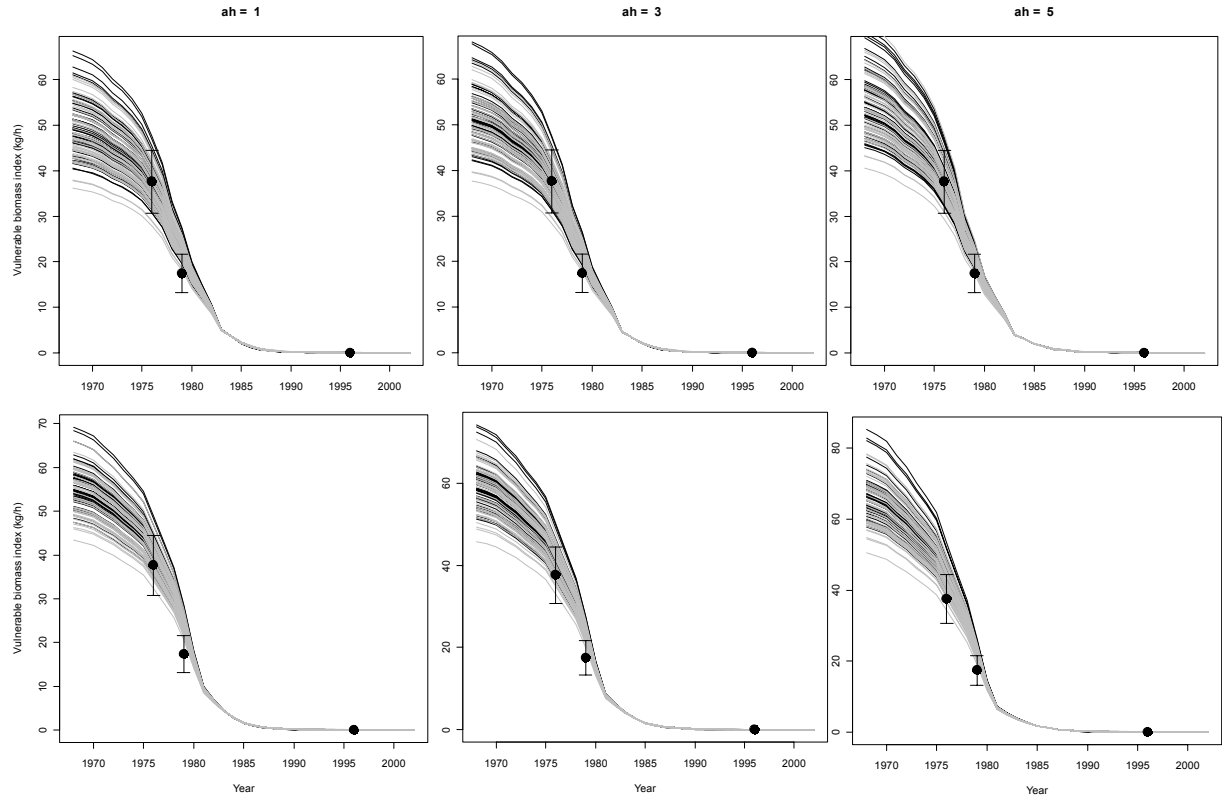
**Figure 5.4.** (a) Proportions of the four reporting categories of dogsharks (as proportion of total dogshark landings) in the NSW State fisheries (excluding the ‘Other’ category); and (b) dogshark proportions in the NSW State database’s “Other” fishery (i.e., SETF) for the years data are available.



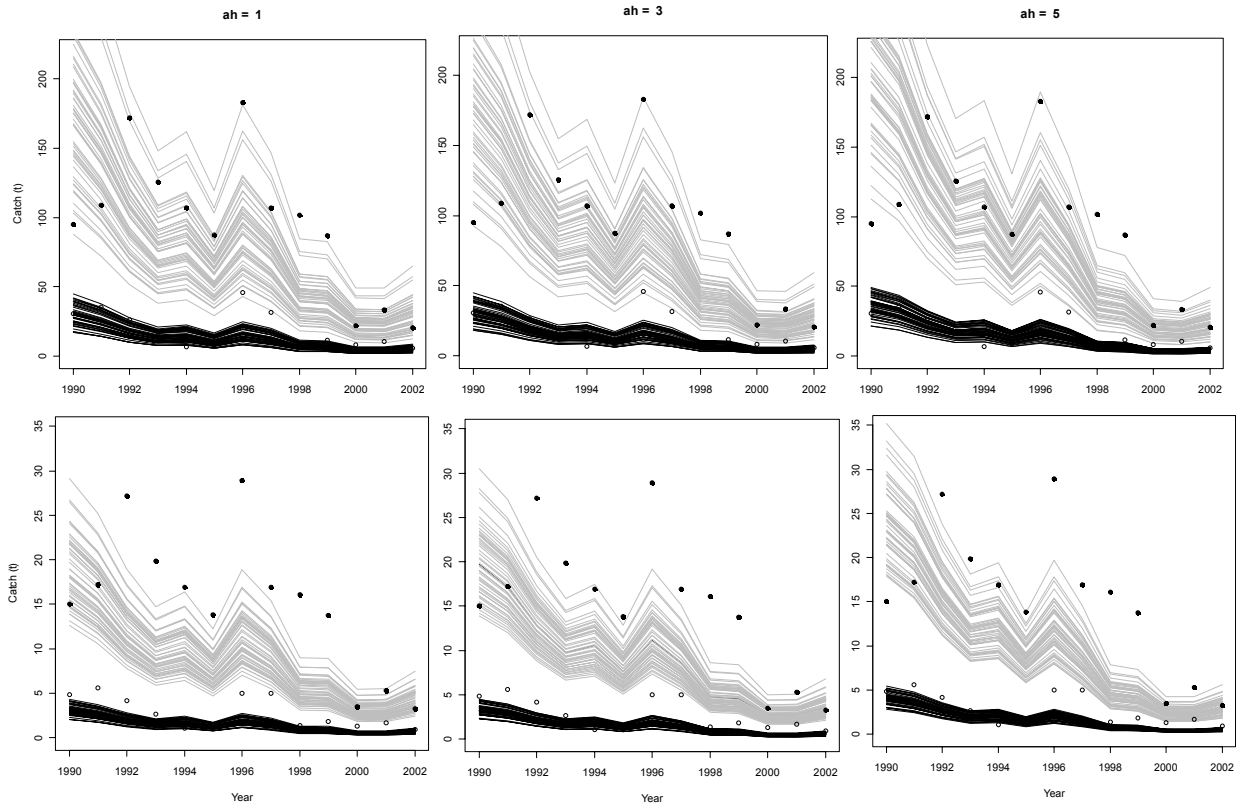
**Figure 5.5.** Mean (+ s.e.) reported proportions of *Centrophorus* spp. across years (1993-2003) in the ISMP observer database, expressed as proportion of whole (i.e., discarded + retained) *Centrophorus* catch (see Table 4 for annual proportions).



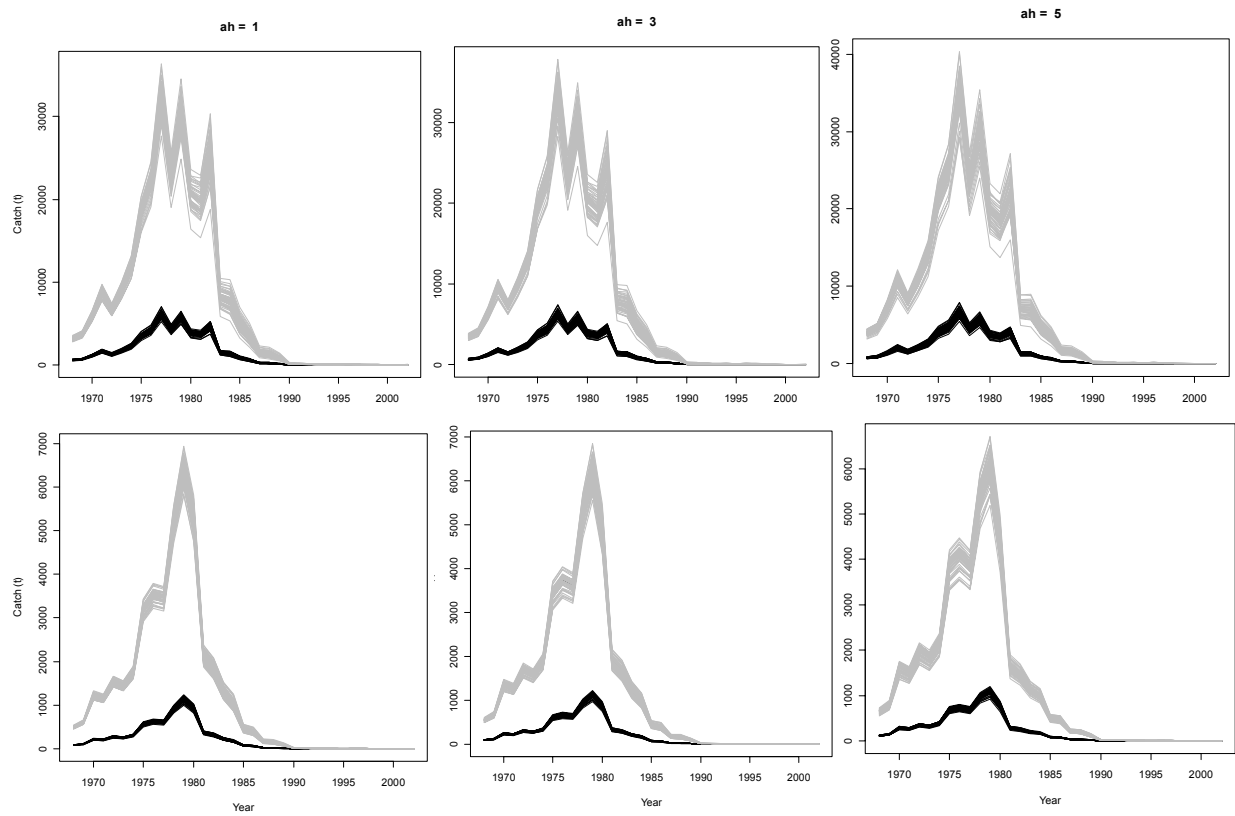
**Figure 5.6.** Proportion of Squalids that were discarded as proportion of (a) retained catch and (b) total catch, as reported by ISMP observers. Only *Centrophorus* spp. and two other significant slope species are shown. Note that discarding of deeper water species (*Dalatias licha* and *Etmopterus* spp.) was also significant.



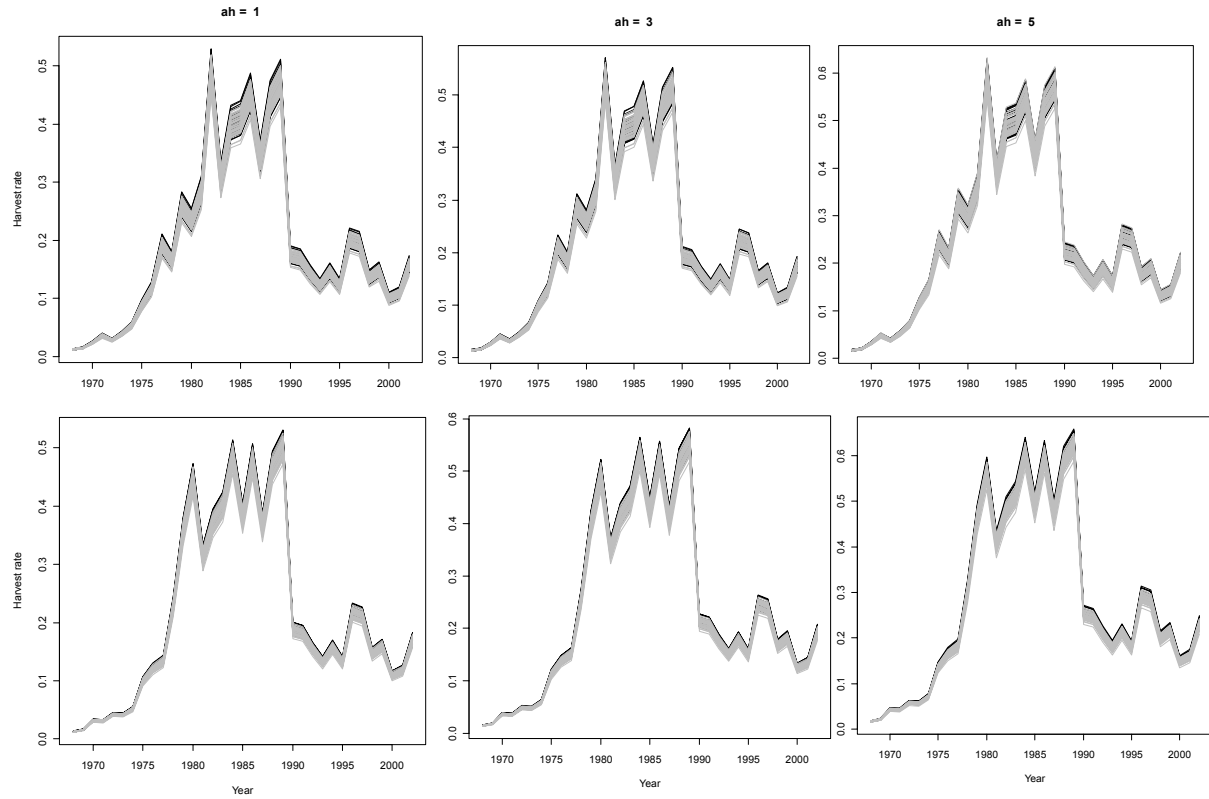
**Figure 5.7.** Fits to survey index for the three best-fitting values of  $ah$  (see text). Top: All *Centrophorus*; Bottom: *C. harrissoni*. Dark lines show fits using minimum catch scenarios, lighter lines show fits using maximum catch scenarios.



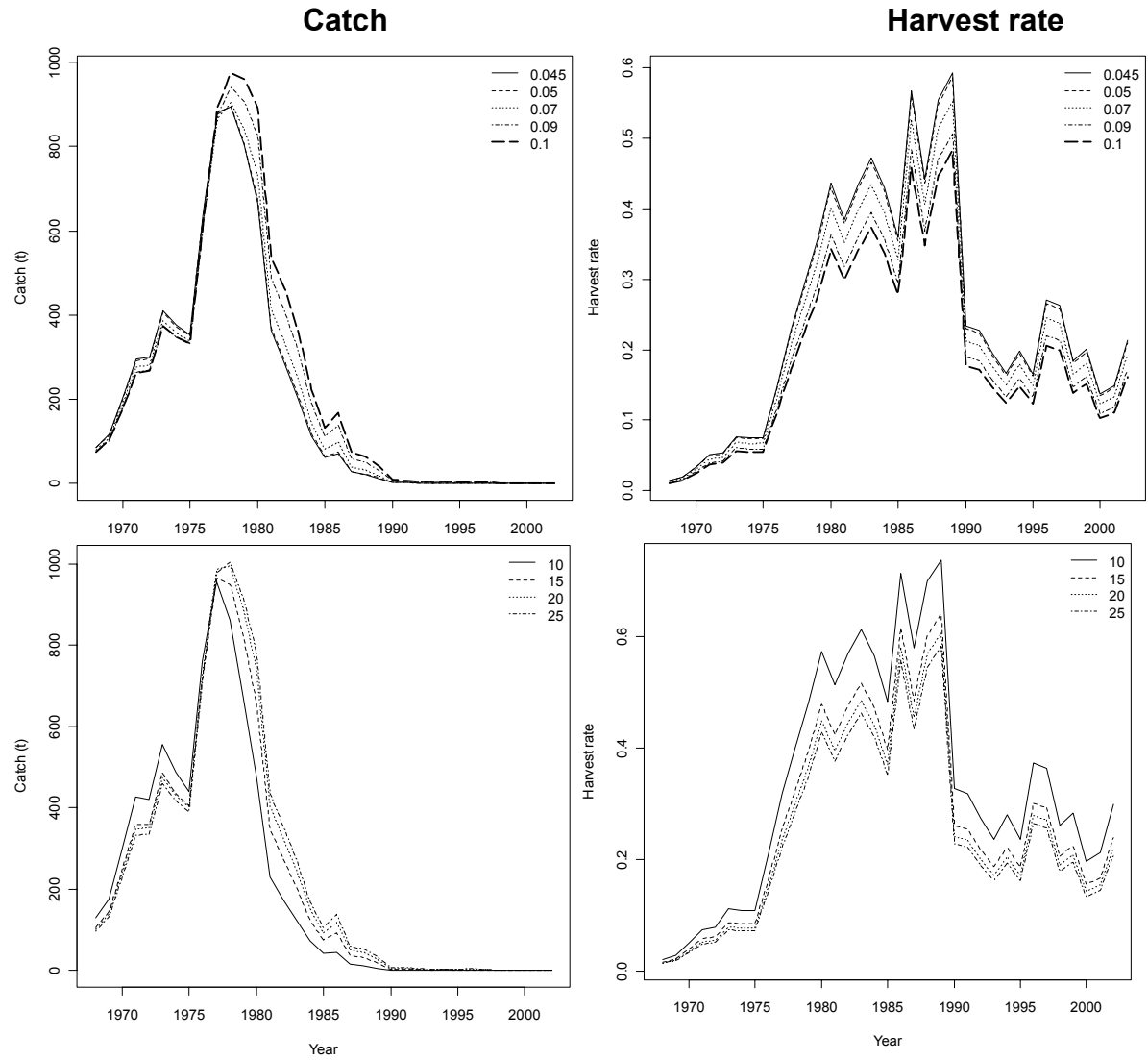
**Figure 5.8.** Fits to estimated catch for the three best-fitting values of  $ah$  (see text). Top: All *Centrophorus*; Bottom: *C. harrissoni*. Dark lines show fits using minimum catch scenarios (open circles), lighter lines show fits using maximum catch scenarios (solid circles).



**Figure 5.9.** Estimated historical catches for the three best-fitting values of  $ah$ . Top: All *Centrophorus*; Bottom: *C. harrissoni*. Dark lines show fits using minimum catch scenarios, lighter lines show fits using maximum catch scenarios.

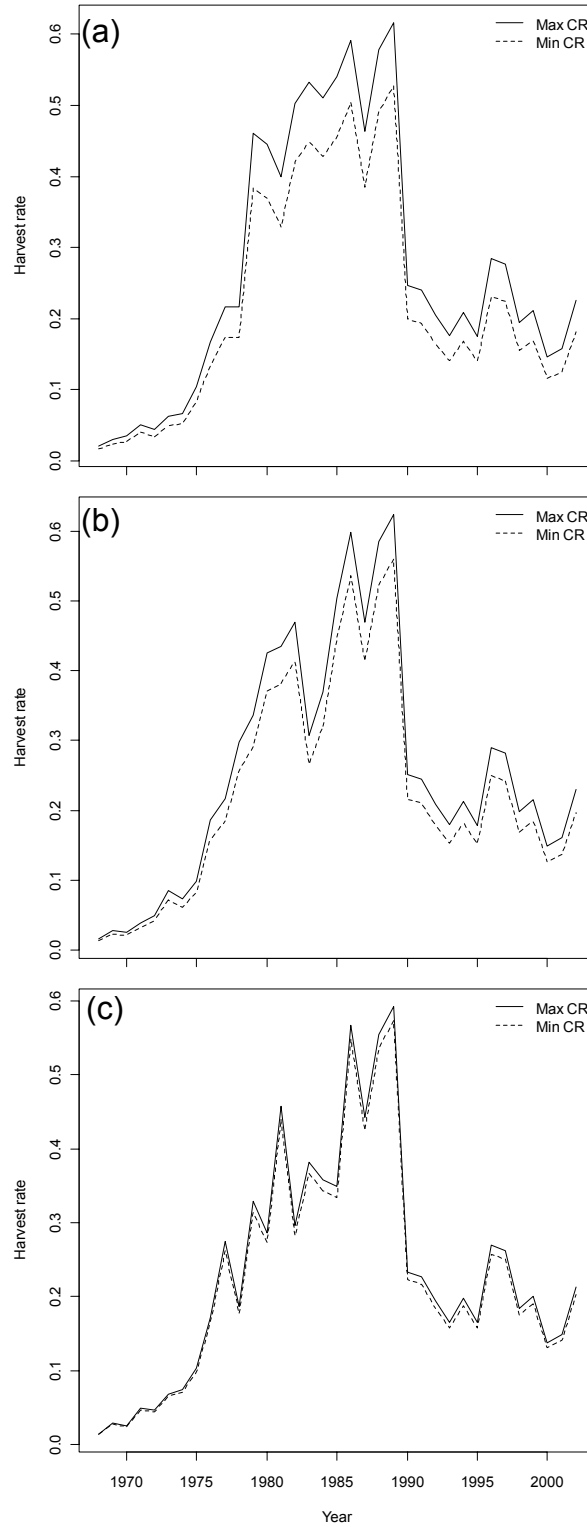


**Figure 5.10.** Estimated historical harvest rate for the three best-fitting values of  $ah$ . Top: All *Centrophorus*; Bottom: *C. harrissoni*. Dark lines show fits using minimum catch scenarios, lighter lines show fits using maximum catch scenarios.



**Figure 5.11.** Sensitivity of estimated historical  $C_t$  and  $U_t$  to value of  $\kappa$  (top) and  $a_{mat}$  (bottom) for  $ah = 5$  for *C. harrissoni*. Simulations were done using the minimum catch scenario.





**Figure 5.12.** Sensitivity of estimated historical  $U_t$  to value of CR for  $a_h = 5$  with (a)  $a_{mat} = 15$ ; (b)  $a_{mat} = 20$ ; and (c)  $a_{mat} = 30$  (see text for meaning of Max and Min CR) for *C. harrissoni*. Simulations were done using the minimum catch scenario

## **Chapter 6. Evaluation of historical fisheries management options for New South Wales trawl fisheries: comparison of two ecosystem models**

### **Introduction**

The discussion of how to manage marine resources has expanded with the shift to ‘ecosystem-based fisheries management’ (EBFM: Pitcher 2000; Ward *et al.* 2002; FAO 2003; Pikitch *et al.* 2004). Governments of many countries, including Australia, have formally adopted EBFM as an integral part of their living aquatic resource use strategies (Commonwealth of Australia 1998). While the policy, legislation and broad public opinion regarding the need for EBFM has made some significant progress over the last ten to fifteen years, there is still much debate over what this form of management will really look like and what tools to use in practice (e.g., Hall and Mainprize 2004; Hilborn 2004; papers in Browman *et al.* 2004). Currently, much fisheries policy is expressed in broad terms such as to maintain functioning or healthy ecosystems or to fish sustainably. Use of vaguely-defined concepts such as ecosystem health (Lackey 2001), or very broad concepts such as sustainability (e.g., WCED 1987; Christensen *et al.* 1996), may obstruct transparent decision-making by not forcing explicit selection from competing policy options (Suter 1993; Lackey 2001), making policy objectives too obscure for informed public debate. Policy statements for fisheries often list a broad range of desired outcomes, including maintenance of economically viable fisheries and fishing communities while aiming to meet various conservation objectives. It may not be possible to achieve all stated objectives simultaneously, however, implying the need to precisely define management goals and consider trade-offs inherent in meeting management objectives (Hilborn *et al.* 2004; Walters and Martell 2004).

Common trade-offs in fisheries include current *vs* future harvests; profit *vs* employment; harvest of prey species *vs* harvest of their predators; and abundance of unproductive species *vs* harvest of more productive species when both are caught in the same gear (see Walters and Martell (2004) for detailed discussion of trade-offs in fisheries). Hilborn *et al.* (2004) suggested four approaches for achieving ecosystem-based sustainable catch limits that included maximisation of total long-

term system yield and “weak stock management” (i.e., no stock is fished above its maximum sustainable yield and weak stocks are those in the fishery with the lowest productivity). These authors simulated management of a US multispecies fishery under these alternative approaches and drew the following conclusions: 1) for ecosystem total yield to be maximised, some species must be overfished; and 2) potential yield would be reduced by 90% (compared with Approach 1) if all species were protected from overfishing. Their results illustrated the difficulty and value-based nature of designing ecosystem-based fishing strategies, given that the two approaches that could be validly described as ‘sustainable’ (and which are commonly stated simultaneously as management goals) were in direct conflict with each other. A key component of EBFM is, therefore, development of approaches to decide where to operate along trade-off contours that account for conflicting stakeholder interests and society’s wider values (Lackey 2001).

Fisheries management agencies have developed different methods for dealing with trade-offs. Formal methods exist for evaluating utility of different outcomes to stakeholders (Keeney and Raiffa 1976), although informal methods involving negotiations among stakeholders (e.g., Smith *et al.* 1999) are also effective and probably the most common means of conflict resolution. Legislative instruments concerning threatened or endangered species exist in most developed countries (e.g., the USA’s *Endangered Species Act 1973*; Australia’s *Environmental Protection and Biodiversity Act 1999*; Canada’s *Species at Risk Act 2002*), although they have rarely been applied to commercially fished species (but see AFMA (2006) for recent threatened species listing of orange roughy, *Hoplostethus atlanticus*, in Australia). Notwithstanding endangered species, it is important to recognise that solutions to trade-offs are value-based and it is therefore outside the remit of science to determine solutions. Walters (2003) has argued that the only way for managers to approach difficult trade-offs, such as the differential productivity problem, is to honestly appraise the trade-off and have managers, fishers and other stakeholders negotiate a mutually acceptable compromise. In this framework, the role of fisheries management is to develop effective methods for deciding where to operate along trade-offs and the role of fisheries scientists is to present the best scientific evidence to inform this debate and to honestly communicate the uncertainty surrounding the information presented (Ludwig *et al.* 1993; Walters and Martell 2004). This includes providing estimates of qualitative and quantitative measures of the expected benefits, costs, and risks associated with alternative management actions (Murawski 2000; Hall and Mainprize 2004). Examples of costs are reductions in landings

or revenue, reduced biomass of important species, reduced biodiversity and an increase in the number of overfished or perhaps even extinct species. It is important to note that interpretations of costs are subjective, depending on the perspective of the stakeholder. For example, overfishing of low-value vulnerable species may seem like a small cost to some stakeholders but be very important to others. The importance of a cost to a stakeholder also depends on what it is traded off against (Keeney and Raiffa 1976). For example, protection of vulnerable species may be considered more favourably by members of the fishing industry if it does not impact earnings. Furthermore, trade-offs may be asymmetric and stakeholders may be much more strongly averse to some costs than others. For example, stakeholders (and legislation in some cases) may be completely intolerant to costs such as increased risk of extinction or threats to charismatic species. In these types of cases, several authors have recommended an approach consistent with the precautionary principle (FAO 1995), where statistical tests are designed to have strong power to detect trends (such as a decline in abundance), even if it is at the expense of an increase in false positive results (Peterman and M'Gonigle 1992; Maxwell and Jennings 2005; Dulvy *et al.* 2006).

With advances in computing power, simulation modelling has come to the fore as a tool in natural resource management, particularly in relation to modelling multispecies fisheries and marine ecosystems (Plagányi 2007). While it will likely never be possible to duplicate real world systems it is now possible to create models that capture critical components and features. These kinds of models can then be used in a “what-if” sense to give insight into the potential impacts of alternative management options. The most sophisticated form of this kind of model use is Management Strategy Evaluation, MSE (or Operational Management Procedure, OMP), where each step of the adaptive management cycle (resource, industry, monitoring, assessment and management decisions) is represented (Cochrane *et al.* 1998, Butterworth and Punt 1999, Sainsbury *et al.* 2000; Punt *et al.* 2001). Many models and modelling frameworks now exist for use in this way for fisheries (and some multiple use) management questions – see Plagányi (2007) for a review of the current state-of-the-art. Simulation of the full MSE cycle is resource-intensive and a simpler, more commonly-used, approach is ‘open loop simulation’ (Hilborn and Walters 1992), where alternative management policies are set in train and evaluated at the end of the simulation period, with no simulation of feed-back controls during the period. Ecosystem models used in this way may be most useful for providing strategic advice, such as ranking of

management approaches under different policy objectives, rather than providing quantitative tactical advice, such as setting of quotas (Christensen and Walters 2004b; Walters and Martell 2004). In this respect, they may be useful for more clearly defining types of management objectives appropriate for EBFM and highlighting possible trade-offs inherent in alternative objectives (e.g., papers in Pitcher and Cochrane 2002; Christensen *et al.* 2004; Fulton *et al.* 2007a; Morato and Pitcher 2005; Cheung and Sumaila 2007).

### *System metrics*

There is now a growing literature (e.g., papers in ICES 2001; review by Fulton *et al.* 2005a) on possible metrics that could be used as indicators of fisheries-induced changes on ecosystems. Fulton *et al.* (2005a,b) have reviewed a comprehensive set of indicators that have been proposed in the fishery literature as candidates to detect and describe the effects of fishing on marine ecosystem processes and have tested performance of indicators in a full simulation-estimation framework. In their study, a large-scale biogeochemical ecosystem model (the ‘operating’ model) was used to represent the ‘true’ state of nature. This model was used to generate fishery-dependent and independent data, from which a large set of indicators were calculated, using approaches proposed in the literature (e.g., Rice 2000; Link *et al.* 2002; papers in Cury and Christensen 2005). Indicators ranged from single species indices of abundance to complex indicators calculated from ecosystem models constructed using the simulated data. Fulton *et al.* (2005b) recommended that, in order to adequately capture the range of impacts of fisheries and diversity of stakeholder values, a suite of indicators should be chosen that span a wide range of processes, biological groups, and indicator types. Indicators were classified as “early warning”, “strategic” and “integrated system state”. They proposed that the best candidates for detecting signals and characterisation of the ecosystem would be achieved by monitoring species groups from the following categories: groups with fast turnover (i.e., “early warning” indicators); groups targeted by fisheries (groups of significant human interest); and charismatic or vulnerable groups. This last group tends to contain species with slower population dynamics, which may therefore integrate across a number of long-term and system-wide impacts. Simple community-level indicators, such as relative abundance of key functional groups (e.g., forage species and top predators), were among the most robust indicators for detecting ecosystem-level changes. Similarly, changes in ratios of habitat-defined groups (e.g., pelagic:demersal species) or different

trophic groups (e.g., planktivores:piscivores) performed well at indicating broad-scale system change.

### *Uncertainty*

Ecosystem models such as the one used by Fulton *et al.* (2005b) are, by their nature, complex. Good quality data that are informative about system attributes of management interest are seldom available for all components of the system and the large number of parameters required for ecosystem models can lead to a large degree of uncertainty in model results, even when models are calibrated to observed data (Silvert 1981; Duplisea 2000). Furthermore, structural uncertainty (i.e., uncertainties due to model architecture, complexity and the way dynamic processes are represented) can be large. Evaluation of structural uncertainty in models used to give management advice is important (McAllister *et al.* 1999; Punt and Smith 1999b; McAllister and Kirchner 2002). For example, Fulton *et al.* (2003a) showed that model results from a biogeochemical ecosystem model were sensitive to the form of the functional responses used to represent predation and grazing. Yodzis (1994) reviewed a set of predation functions that variously accounted for predator behaviour and interference among predators and concluded that, while it was straightforward to show that the form of the predator-prey model would affect predicted effects of harvesting, there was a lack of empirical evidence in support of any particular model. Plagányi and Butterworth (2004) and Plagányi (2007) reviewed different representations of predator-prey interactions in multispecies and ecosystem models and concluded that, while it is important to include complex trophic interactions in ecosystem models, practitioners must be aware that incorrect assumptions could cause incorrect predictions of both the magnitude and direction of a population's response to fishing or other impacts (see also Bax 1998; Essington 2004). The level of detail included in a model, i.e, its complexity, also affects its predictions (Yodzis 2000; Fulton 2001; Fulton *et al.* 2003b; Plagányi 2007). Marine ecosystems can contain many hundreds of species and some degree of species-aggregation within a modelled representation of any ecosystem is always required. Guidelines resulting from a number of studies (reviewed by Fulton *et al.* 2003b) suggest that serially-linked groups (predators and prey) should not be aggregated into the same functional group and neither should species with rates of mortality differing by more than two or three-fold. There is often a dome-shaped relationship between model-complexity and model-performance, where over-aggregated models can fail to capture important dynamics of the system, while in overly complex models,

errors and uncertainty can become compounded (Bax 1998; Fulton *et al.* 2003b). There are no definitive rules, however, to determine the ‘best’ level of model complexity, which will ultimately be an expert choice depending on the research question. Other structural assumptions that may affect model results include, but are not limited to, representation of density dependent effects on growth and mortality (Walters *et al.* 2000); representation of fishing fleet dynamics, such as form of the selectivity function and density dependent effects on catchability (McAllister and Kirchner 2002); form of the stock-recruitment relationship; and assumptions about effects of habitat structure on trophic interactions (Sainsbury *et al.* 1997).

It is widely recommended that, if ecosystem models are to move into the management arena, comparison of multiple alternative models will be needed (Yodzis 1994; Whipple *et al.* 2000; Fulton and Smith 2004; Plagányi 2007). While large-scale manipulative experiments may be the only means of resolving some of the debates regarding trophic interactions and fisheries (Walters 1986; Walters and Holling 1990), the resource-intensive nature of such experiments means they are rarely done (but see Sainsbury 1988; 1991; Sainsbury *et al.* 1997). Uncertainty about the functioning of marine systems does not necessarily preclude making good policy decisions, however, and detailed knowledge of all system processes may not be needed to be able to predict that one policy is preferable to another over a wide range of possible states of nature (Walters and Martell 2004). Policies that consistently outperform others under a range of structural uncertainty in a simulation framework can be considered relatively robust and worthy of further exploration. Fulton and Smith (2004) have compared predictions of three structurally-distinct ecosystem models and drawn some general conclusions for development of fisheries policy. For example, models agreed that policies focused on management or protection of only higher trophic-level species, or solely on economic objectives, could result in a system far from pristine. They also found that a broad range of indices was needed to capture differences among policy options. In general, while some results were robust to structural uncertainty, many were not, implying that there is still much to learn about the behaviour of ecosystem models under different structural assumptions.

In this paper, two of the modelling frameworks discussed in Plagányi (2007) – Atlantis (Fulton *et al.* 2005b; Fulton *et al.* 2007a,b) and Ecopath with Ecosim (EwE: Polovina 1984; Christensen and Pauly 1992; Walters *et al.* 1997; Christensen and Walters 2004a) – are used to consider the

implications of alternative management policies aimed at achieving a range of ecosystem management goals for the continental shelf and slope of NSW, accounting for both trophic and technological interactions. Here we follow the FAO's (2007) definition of the words 'policy' and 'strategy', where a management strategy is a long-term, broadly-based means of achieving a high-level policy objective (in contrast to a 'tactic', which is aimed at the short-term and is in the form of a specific set of instructions). Throughout the paper, to avoid over-use of multiple terms with similar meaning, the terms policy and strategy are used somewhat interchangeably (i.e., the performance of alternative policies is compared), although it is recognised that each policy would be realised through strategic changes in fishing effort.

While both modelling frameworks include explicit representations of trophic dynamics and fishing, they are structurally very different (see Fulton *et al.* 2007b; Plagányi 2007 for exhaustive comparison). Atlantis has been applied to more than 15 ecosystems to date, can explicitly consider a wide range of impacts (including pollution and habitat alteration) and has flexible representation of physical and biological processes including nutrient mixing, and trophic and recruitment dynamics. Although it is very data-intensive, requiring expert training and support, its ability to represent a wide range of physical, biological and management processes have seen it identified as the best model for management strategy evaluation (Plagányi 2007). EwE is one of the most popular ecosystem modelling softwares and has been applied to huge variety of systems. Examples can be found in Christensen and Pauly (1993), in a special issue of *Ecological Modelling* (2004; vol 172, Issues 2-4) and throughout the peer-reviewed literature. It is relatively easy to use and enables efficient exploration of alternative fishing policies and has a number of useful modules. It is also suited to more data-limited situations (Plagányi 2007) and runs much faster than Atlantis. Given the popularity of EwE throughout the world, and the history of use of Atlantis in southeastern Australia, the need to frame ecosystem-based management questions for NSW presented an opportunity to compare predictions made by the different models and to highlight the potential for multiple models to give some insight into the implications of structural uncertainty.

Models were constructed to represent the period 1976 – 1996, which covers the development of the offshore trawl fishery and the period in which many commercial species and sharks are known to have undergone large declines in abundance (Andrew *et al.* 1997; Rowling 1997a;



Graham *et al.* 2001; Tilzey and Rowling 2001). The offshore trawl fishery also underwent an economic decline and build-up of capacity during this period (Grieve and Richardson 2001). The history of this fishery, which includes depletion of extremely ‘weak stocks’ (*sensu* Hilborn *et al.* 2004) such as dogsharks (Chapters 4 and 5), contrasted with the importance of the fishery to supplies of fresh seafood in southeastern Australia, and its role as an employment sector in coastal communities, provides a platform for exploring how the fishery and ecosystem might have developed if clearly-articulated alternative EBFM policy objectives had been applied in the early years of the fishery. This ‘retrospective forecasting’ approach demonstrates the utility of ecosystem models for presentation of trade-offs and a means of evaluating alternative management objectives for EBFM, accounting for the effects of structural uncertainty.

## **Methods**

### **Modelling frameworks**

#### *Atlantis*

The Atlantis modelling framework (Fulton *et al.* 2005b; Fulton *et al.* 2007) is an explicitly spatial biogeochemical model that was originally developed as an operating model for management-strategy evaluation of tools and approaches for EBFM (e.g., see Fulton *et al.* 2005b; 2007a). It explicitly includes each step of the adaptive management cycle and includes biophysical, social, economic, industry, monitoring, assessment and management modules, although is not necessary to use all of these. The biophysical module is a deterministic box-model that is (coarsely) spatially-resolved in three dimensions. Nutrient-flows (usually nitrogen and silica) are tracked through the main biological groups in the system. The biologically relevant components of Atlantis include various classes of nutrients (nitrogen, silica), detritus (labile, refractory, carrion), primary producers, bacteria, invertebrates and vertebrates (fish, mammals and birds). Multiple functional groups can be defined within each of these components. The selection of groups is largely determined by the need to capture key ecosystem functional characteristics while also addressing management issues. Lower (invertebrate) trophic levels are typically represented as biomass pools, while vertebrates are usually represented using an age-structured formulation. Functional groups are influenced by environmental and habitat conditions in the water column and bottom sediments, and are also linked through trophic

interactions, the functional forms of which are flexible (see Plagányi 2007). The physical environment is represented using a set of polygons matched to the major geographical and bioregional features of the simulated system, with smaller polygons in areas of rapid flux. The industry (or exploitation) module can be adjusted to include the impact of pollution, coastal development, broad-scale environmental change as well as fisheries, although only fisheries impacts were considered here.

#### *Ecopath with Ecosim*

Ecopath with Ecosim has been described extensively elsewhere and readers are referred to Christensen and Pauly (1992), Walters *et al.* (1997), Christensen and Walters (2004b), Plagányi and Butterworth (2004) and Plagányi (2007) for full details and discussion of the strengths and limitations of the approach. Briefly, Ecopath (Christensen and Pauly 1992) is a steady-state approach to ecosystem modelling in which the modelled system must satisfy the thermodynamic constraint of mass balance, set out by the master equation of Polovina (1984; see this thesis Appendix 1). Biological components are a user-defined set of trophically linked functional groups that represent important trophic linkages in the ecosystem and/or are of management interest. Ecosim (Walters *et al.* 1997) is a dynamic extension of Ecopath that uses the ‘foraging arena’ concept (Walters and Juanes 1993; Walters and Korman 1999; Walters *et al.* 1997; Walters and Martell 2004) to model predator-behaviour and its effect on consumption rates. Typically, models are calibrated by adjusting foraging arena parameters until model predictions fit observed trends. A useful feature of Ecosim is the fisheries optimisation routine (Christensen and Walters 2004a), which can be used in a calibrated model to search for long-term levels of fishing effort that would maximise a user-defined objective function. While a spatial module is available (Walters *et al.* 1999), EwE is generally used in its simpler, non-spatial form. In this case, spatial separation of functional groups can be represented implicitly through the diet matrix, where spatially-distinct functional groups do not feed on each other. This approach is used in the present model.

#### **Study area and period**

The baseline models were constructed to represent the ecosystem of the continental shelf and upper slope of NSW in 1976, the year of the first trawl surveys (the Atlantis model required a ten

year ‘burn-in’ period prior to this). The models were designed to cover the same spatial extent: the marine waters of the entire NSW coast (latitude: 29°S – 36°S; Figures 1.3 and 6.1) and from the coastline (including estuaries) to the 800 m isobath (even though Ecopath is non-spatial, the size of the model-areas must be known for calculation of biomass density). Very little fishing occurs beyond this depth range (Larcombe *et al.* 2001). This resulted in a total model area of approximately 48 000 km<sup>2</sup>. In Atlantis, the modelled area was divided into polygons horizontally (boxes) and vertically (layers). There were 43 boxes in total (Figure 6.1) that included: 8 bays and estuaries; a coastal strip, delimited by the 50 m isobath; a shelf strip, delimited by the 200 m isobath; an upper slope strip, roughly delimited by the 800 m isobath; and a set of boundary boxes that correspond to the “outside” of the modelled domain. The three strips were further subdivided latitudinally, to represent pelagic provinces identified by the Integrated Marine and Coastal Regionalisation of Australia bioregionalisation (IMCRA Technical Group 1998), as well as the location of rivers and bays and coastal morphology. Vertically, the model included one sediment layer and five water column layers related to the vertical zonation of physical properties, plankton and other pelagic organisms (Lyne and Hayes 2005). See Bax and Williams (2000) and a special issue of *Marine and Freshwater Research* (Vol. 52 (4), 2001) for detailed descriptions of habitats, species and trophodynamics of this ecosystem and surrounding areas. Dynamic simulations covered the period 1976-1996, the years of the first and last years fishery independent surveys of the study area (Andrew *et al.* 1997).

## **The models**

The major features of the Atlantis and EwE model are described here but readers are referred to Savina *et al.* (2008) and Appendix 1 of this thesis for detailed description of the respective models. The combined catch, survey and observer databases for NSW contain more than 500 teleost species in coastal shelf and slope waters, more than 100 elasmobranchs and approximately 70 edible invertebrate species (Appendix 2). These, in addition to marine mammals, birds, inedible invertebrates and primary producers, were aggregated into functional groups (Table 6.1). The study did not attempt to make both models structurally identical. Instead, to make comparison of the methods as efficient as possible, we chose to design models that best exploited the strengths of each modelling framework. These differences add a further structural difference to two models already differing in underlying function. Both models were more

resolved in the ‘offshore’ components (i.e., more shelf and slope species were individually represented) and less so in the near-coastal components, reflecting the availability of stock assessment and survey data, as well as a research interest in the offshore system.

The Atlantis and EwE models contained 60 and 57 biological functional groups respectively (Table 6.1). In both models, invertebrates were separated into deep and shallow components, commercial and non-commercial, although the groupings differed between models. The Atlantis model had greater resolution of invertebrate groups and included functional groupings based on feeding method (i.e., grazers, filter feeders and deposit feeders). The Atlantis model also had greater resolution of primary producers and zooplankton (Table 6.1). In both models, most teleost species were aggregated into groups based on habitat (demersal, pelagic), depth (inshore, offshore, deep) and diet (herbivorous, omnivorous, piscivorous). See Appendix 1 for definitions. The models also contained separate teleost groups, representing commercially important taxa that have been under quota since 1992. See Table 6.1 for teleost groups explicitly considered and see Bruce *et al.* (2002) for a review of biological and fisheries information on these species. Elasmobranchs were allocated into ten model groups in the EwE model and six groups in the Atlantis model (Table 6.1). Parameters were obtained from the literature (see Savina *et al.* 2008 and this thesis, Appendix 1 for details).

The physical submodel included in Atlantis was driven by water fluxes derived from the 3D oceanic Blue Link OFAM model (Brassington *et al.* 2005; Oke *et al.* 2008). Flows were calculated from the Spinup 4 and 5 runs (which span 1991-2004) of the model (by integrating the daily normal component of currents over each depth band of each box face). These fluxes were corrected to account for hyperdiffusion in the large Atlantis boxes. Water temperature and salinity time series were derived from the same Blue Link simulations. For the eight bays and estuaries explicitly considered, water exchanges with the ocean were estimated from data available on the NSW estuaries website ([www.naturalresources.nsw.gov.au/estuaries](http://www.naturalresources.nsw.gov.au/estuaries)). Flows of fresh water inputs from point sources (rivers) were estimated from the PINEENA Department of Infrastructure, Planning and Natural Resources database, for the 1976 to 1996 period.

Three datasets were needed to calculate commercial landings for the period covered by the study: the NSW historical catch database (1976-1992; Pease and Grinberg 1993); the NSW

State catch database (1985-1996); and the Commonwealth South East Fishery catch database (1985-1996). Discards were estimated using observer data from the database of the South East Fishery Integrated Scientific Monitoring Program (ISMP; Garvey 1998; Knuckey *et al.* 2002). Sydney Fish Market wholesale prices were taken from the NSW DPI catch statistics database. The earliest available prices were from 1984. We made the simplifying assumption that, for each group, the average of prices from 1985-1996 was applicable throughout the simulation period. Therefore, actual changes in profit due to changing prices or rising costs (e.g., cost of fuel) could not be captured. There is a paucity of stock assessment for most species in the ecosystem, as is the case for most of Australia (Phillips *et al.* 2001). Stock assessments are only done for the most commercially-valuable species (Bruce *et al.* 2002). For other stocks, only relative abundances observed in the three fishery-independent surveys (1976, 1979, 1996) were available (see Table 6.2 for list of stock assessments used to calibrate the models). Models were calibrated so that, where possible, model trends matched observed trends when the model was driven by observed catches. Calibration was done in the Ecosim model by adjustment of ‘vulnerability’ parameters representing the rate of consumption by predators (Walters *et al.* 1997; 2000; see Appendix 1). In the Atlantis model, the most uncertain biological and fisheries parameters were adjusted, while keeping all parameters within realistic ranges suggested by the relevant literature and expert knowledge (Savina *et al.* 2008).

### **Optimal policy search**

The same approach for comparison of models was taken as in Fulton and Smith (2004), where the open-loop policy optimisation routine of Ecosim (Christensen and Walters 2004a) was used to estimate relative fishing mortality rate,  $F$ , that would maximise alternative long-term objective functions representing alternative policy objectives. Resulting optimal  $F$ ’s were then used to drive both models for 21 years and predictions at the end of the simulation period were compared. Therefore, after the EwE model was calibrated, the fisheries optimisation routine in Ecosim was used to search for long-term management strategies that would achieve a range of alternative policy objectives. The routine’s algorithm uses an iterative nonlinear optimization procedure (Davidson-Fletcher-Powell method) to find a constant long-term level of fishing effort that would maximise a multi-criterion objective function (Christensen and Walters 2004b). The objective function contains terms representing economic, social, legal (or conservation) and

ecological objectives (see Pitcher and Cochrane 2002; Christensen and Walters 2004b), with weights on each objective determined by the user. Relative fishing effort is used to calculate the relative fishing mortality rate on each species, under the simplifying assumptions of linear relationship between fishing mortality and effort for all species, i.e., reducing effort by some percentage results in the same percentage decrease in fishing mortality on all species. In the present study, the algorithm was used to search for optimal fishing efforts only in the offshore trawl fishery. The resulting optimal fishing efforts were then used to drive both models.

Five policy objectives of potential interest to management in this fishery were identified:

A) Maximise economic benefits; B) Prevent overfishing of the weakest stocks; C) Maximise overall biodiversity; D) Maintain biomass of charismatic species; and E) Maintain the 1976 fishing effort (i.e., *status quo*). Policy A was subdivided into four sub-policies to represent different realisations of economic benefits (see below). The resulting eight policies and objective function weights used in the policy search are given in Table 6.3 and discussed further below.

#### *Economic and social objectives*

One way for economic benefits to flow to fishing communities is through increased employment. In models such as Ecosim, which contain only simplified fishing fleet-dynamics, total catch can be used as a proxy for employment. Initial simulations suggested that catch would be maximised by increasing effort in the offshore trawl fishery more than 20-fold, resulting in extirpation of many commercial predatory species and subsequent increase in their very low-value prey (Table 6.3; Policy Ai). A simple modification of this objective was to aim to maximise total catch from the system but to prevent fishing costs from exceeding earnings (Table 6.3; Policy Aii). This had the effect of placing greater weight on more valuable species and less weight on extinction of predatory species.

Alternatively, economic benefits can be realised through smaller, more profitable fisheries (Hilborn *et al.* 1995; 2007c) and, therefore, an objective function that sought to maximise profit was also tested. This would be expected to produce higher landings of more valuable species. Since actual fishing costs were not known for this period, two scenarios were considered, one with ‘low’ costs (net profit 30% of total income; Table 6.3 Policy Aiii) and one with ‘high’ costs (net profit 10% of total income; Objective Aiv).

### *Ecological objectives*

Policy B sought to manage the fishery so that no species would be overfished. Overfishing was defined as fishing at a rate above that which produces MSY ( $F > F_{\text{MSY}}$ ). Chapter 4 showed that optimal harvest rates for deepwater dogsharks in NSW are extremely low ( $< 5\%$  per year when age at first harvest is low). Ecosim can be used to search for  $F_{\text{MSY}}$  values that account for trophic interactions, using an inbuilt module (Walters *et al.* 2005). This module found the species with the lowest  $F_{\text{MSY}}$  to be greeneye dogshark, with  $F_{\text{MSY}} = 0.023$ . This is consistent with the findings of Chapter 4. Therefore, Policy B sought the relative trawl fishing effort that would result in  $F_{\text{MSY}}$  for this species.

Policy C sought a fishing strategy that would balance harvesting with biodiversity. The search routine was set to search for the relative trawl effort that would maximise the Q-90 biodiversity index of Ainsworth and Pitcher (2006). The Q-90 index is a variant on Kempton's Q index, which measures the slope of the cumulative species abundance curve (Kempton and Taylor 1976) between the 10<sup>th</sup> and 90<sup>th</sup> percentiles.

Policy D sought to maintain or restore abundance of long-lived species. These represent commercial and non-commercial, often charismatic, species (such as sharks, marine mammals and seabirds) that may be directly or indirectly affected through fishing. The objective function aims to maximise the overall Biomass:Production ratio throughout the model. Increasing this ratio increases the summed weighted biomass of long-lived organisms (Christensen *et al.* 2004a) and is consistent with Odum's (1971) description of ecosystem maturity, where mature ecosystems are dominated by large, long-lived organisms (see Christensen 1995). For each objective, searches were repeated with five random starting efforts to ensure results had not been affected by initial conditions.

### **Comparison of Ecosim and Atlantis**

To simulate the effects of the optimal fishing strategies, the resulting optimum trawl fishing efforts for each policy were used to drive the calibrated Ecosim and Atlantis models for 21 years, starting from the 1976 initial conditions and ending in 1996. Resulting annual predictions of

biomass, catch and value for each functional group under each policy were then aggregated into 40 functional groups (Table 6.1) to enable comparison. Predicted biomasses of each functional group, relative to 1976 biomass were compared quantitatively (percentage difference in predicted relative biomass) and qualitatively (whether or not models predicted biomass to have changed in the same direction).

To measure the performance of the eight policies, a suite of 19 indicators of the state of the ecosystem and fishery was developed and these were evaluated at the end of the simulation period. Primary indicators measured the performance of each policy in terms of the stated objective of the policy (e.g., total catch was the primary indicator for policies Ai and Aii). In addition, indicators that have either been identified as key measures of interest by management groups or have been found to be useful measures of the state of the system by previous studies (Fulton *et al.* 2005b) were also evaluated. A full list of the indicators used is given in Table 6.4 (primary indicators are superscripted with P).

Table 6.4a lists indicators that measure the state of biological aspects of the system. In the absence of detailed stock assessment for most species, a rule of thumb was used to define overfishing. A functional group was defined as overfished if its predicted 1996 biomass was less than 40% of its 1976 biomass. This was based on commonly-applied rules now being applied by many management agencies for data-limited species and is consistent with current Australian guidelines where overfished species are defined as those where current biomass is less than 40% of unfished biomass  $B_0$  (Smith *et al.* 2007). In reality, most species in NSW would not have been at  $B_0$  in 1976, having already been fished for a number of years. However, for the purposes of comparison we consider this an adequate proxy and acknowledge that it is a less severe (i.e., lower) overfishing threshold than if groups had been at  $B_0$  in 1976. Groups were defined as extirpated if their predicted 1996 biomass was less than 5% of their 1976 biomass.

Biomasses of a number of aggregated groups were also evaluated. Quota teleosts (Table 6.1) are potentially the most heavily impacted by fisheries and they are also of significant human interest. Elasmobranchs and  $K$ -selected species (MacArthur and Wilson 1967) represent charismatic or vulnerable groups that can indicate long-term impacts (Fulton and Smith 2004; Fulton *et al.* 2005b) and are also of conservation interest. Relative biomasses of dogsharks were also



calculated as these were of particular interest to this study. Relative biomasses of different trophic groups (piscivores and planktivores) can indicate a change in the trophic structure of the system, as can shifts in biomasses of habitat-associated groups such as those occupying pelagic or demersal habitats. The ratios of these groups (i.e., pelagic:demersal and piscivore:planktivore ratios) can also be instructive of shifts to the trophic structure of the system (Fulton *et al.* 2005b). A biodiversity index was also measured, i.e., Ainsworth's (2006) modification of the Kempton Q index (Kempton and Taylor 1976). Indicators of the state of the fishery were also evaluated, i.e., total catch and value of all species; and catch of quota species (Table 6.4b). The biomass, catch and value indicators were evaluated at their absolute 1996 predicted value. The pelagic:demersal and piscivore:planktivore ratios and the biodiversity indicators were evaluated at their predicted state relative to 1976, as managers are often more concerned with the direction of change in these indicators rather than their absolute value.

It has been proposed that one of the most useful applications of ecosystem models is for selection of policies that consistently outperform others over a range of uncertainty (Walters and Martell 2004). Therefore, after the 19 indicators were evaluated, policies were ranked according to the values of each indicator and the rankings compared. Results were also used to illustrate trade-offs between policies. For tractability, a subset of policies representing high, medium and low fishing effort were compared with each other in terms of the predicted differences in a subset of indicators under each policy. For example, trade-offs between Policy Aii and Policy B were measured as differences in predicted catch, value, biodiversity, shark biomass, quota species biomass and differences in the number of overfished and extinct species.

## Results

Relative biomasses predicted by the two models under historical catches are shown in Figure 6.2a for 16 functional groups. The index of relative abundance for each group, where available, is also shown, indicating the level of agreement between observed and predicted relative biomasses. Reasonable fits were obtained for redfish, pink ling and trevallies in both models. Atlantis tended to slightly overestimate biomass for blue grenadier and tiger flathead, while Ecosim tended to slightly underestimate it. Ecosim was able to emulate the trajectory of morwong and gemfish biomass (although tended to underestimate biomass), whereas Atlantis

predicted that they would increase. Both models emulated declines of deepwater dogsharks. Fits obtained for nine shark groups in the EwE model (Figure 6.2b) illustrate that the Ecosim model was able to capture observed declines (Graham *et al.* 2001) for these groups (note that Atlantis aggregated sharks differently and results are therefore not directly comparable).

### **Optimal policy search**

Under the economic policies (Ai-Aiv), optimal fishing effort was greater than the 1976 fishing effort ( $\text{Effort}_{1976} \times 24.7, 13.4, 9.3, 2.4$ , respectively). Under the ecological policies (B-D), optimal fishing effort was less than that in 1976 ( $\text{Effort}_{1976} \times 0.002, 0.51, 0.02$ , respectively). It is notable that the presence of stocks with extremely low productivity, i.e., deepwater dogsharks, meant that maximising ecosystem maturity (Christensen 1995), or prevention of overfishing of the weakest stocks (greeneye dogsharks), required almost complete shutdown of the fishery.

To illustrate how Ecosim arrived at its solutions, coarse-scale results of running the Ecosim model for 50 years under each optimal fishing strategy are shown in Figure 6.3. Prawns and offshore omnivorous fish benefited from the high fishing effort under policy Ai, which depleted piscivorous quota fish, offshore piscivorous fish and sharks. Therefore, catches could be maximised, despite large depletions of several groups, due to lower trophic level groups being released from predation. Offshore omnivorous fish and offshore piscivorous fish were problematic during calibration of the Ecosim model, and produced implausibly high catches (~100 000 tonnes under policy Ai). These two groups were highly aggregated, containing approximately 60 and 40 species, respectively, and were trophically interdependent. Actual catches of these species are also uncertain, due to the recording of landings of many species under a miscellaneous fish category (see Appendix 1) and there was little data with which to constrain the dynamics of these groups. Some of the differences between Atlantis and Ecosim presented below, especially those relating to total catch and value, were the result of differences in predicted behaviour of these groups.

Prawns and omnivorous fish were not adversely affected by an increase in the abundance of their predators under reduced fishing pressure (policies B-D). This is because prawns and omnivorous fish are also commercial target species and also benefit from reductions in fishing, despite

greater abundances of their predators. Note also that, although policies B-D predicted a higher biomass of quota species, these would not necessarily be realised as profits as fishing effort was greatly reduced (optimal effort was almost zero for policies B and D).

Decreasing effort resulted in increased long-term biomass of valuable quota fish and, therefore, the policies that maximised profit (Aiii and Aiv) had lower effort than policies Ai and Aii. It should be noted that catch (proportional to revenue), not profit, is presented in Figure 6.3 and, therefore, while revenue would have been higher under policies Ai and Aii this does not account for the cost of fishing.

### **Comparison of individual groups**

In total, there were 320 comparisons of biomass for individual functional groups (8 scenarios  $\times$  40 aggregated functional groups). Predicted 1996 relative biomasses (to 1976) are shown in Table 6.5 for both models. Predicted direction of change between 1976 and 1996 for the 40 groups is shown in Table 6.6. Qualitative agreement between the two models was achieved for 52 % of comparisons (i.e., the models predicted that biomass would change in the same direction). The best qualitative agreement was achieved for tiger flathead, redfish and gemfish and for deepwater dogsharks, demersal sharks and pelagic sharks, although the magnitude of the difference was sometimes quite large (Table 6.5; Figure 6.4). For other quota species (pink ling, trevallies and jackass morwong), qualitative agreement was obtained under the highest fishing efforts (Policies Ai-Aiii), i.e., both models predicted biomass would decline under higher catch rates, although there were again large quantitative differences (Table 6.5; Figure 6.4). Poor qualitative and quantitative agreement was obtained for blue grenadier, ocean perch, offshore demersal fish and large planktivores (Figure 6.5). Note that the criteria for qualitative agreement was set at its most severe, i.e., a very small difference either side of 'no change' was enough to return a negative qualitative match. Relaxing this criteria so that, say, positive or negative changes within 5% of zero would be regarded as in agreement would have resulted in a greater number of qualitative agreements.

There were a number of groups that were unaffected by changes in effort (i.e., differences among scenarios were negligible). Consistent disagreement between the models for these groups

(zooplankton, gelatinous zooplankton, shallow piscivorous fish, whales, macrophytes and benthos) accounted for more than 20% of the qualitative disagreements between the models (Table 6.6; Figure 6.6). While differences in these groups highlight differences in behaviour of the two models, they did not affect the ranking of different policies as there was no contrast among policies.

In general, Ecosim tended to predict more severe declines of fished species under the economic policies (Ai-Aiv) and tended to make more optimistic predictions for fished species under the ecological policies (B-D). Ecosim also tended to predict stronger indirect trophic effects. This is seen in the graphs for seabirds, pinnipeds, shallow demersal fish and squids, where Ecosim predicted greater contrast among policies (Figure 6.7), although the opposite was true for shallow herbivorous fish and shallow territorial fish. None of these groups are caught in the trawl fishery but interact with trawl species, either as predators or prey. Differences between the two models in this respect are most likely due to differences in the way diets are represented in the models. In Ecosim, diets are explicitly expressed in a matrix of predators and prey. In Atlantis, within the limitations of the functional response representing predation (and rescaled based on habitat dependency and habitat state), a species will eat any encountered species that will fit into its mouth (there is provision to exclude species that are known not to occur in the diet). Seabirds are a special case. In Ecosim, 10% of the diet of seabirds was assumed to come from discards from the fishery and, therefore, Ecosim predicted that they would benefit from increased fishing. Discards were not explicitly represented in this Atlantis model (due to the specific parameterisation used in this case).

Predicted 1996 catches for key commercial teleosts are shown in Figure 6.8. Catches are grouped by species to enable comparison of policies. There were noticeable differences between the two models in terms of which species would respond positively to heavy fishing. For example, Atlantis predicted that catch of redfish and jackass morwong would increase under the heaviest fishing policies shown (Ai and Aiv), while Ecosim predicted much lower catches under these policies (Figure 6.8). Alternatively, Atlantis predicted low catches of tiger flathead and school whiting under heavy fishing pressure, while Ecosim predicted the opposite. These differences most likely reflect different assumptions about productivity of these species in the two models. Atlantis explicitly includes growth, mortality and recruitment parameters. Ecosim explicitly

represents mortality (through the production/biomass ratio), but other components of productivity (growth and recruitment) are dealt with implicitly. In particular, recruitment productivity in Ecosim is influenced by the foraging arena vulnerability parameters (Walters *et al.* 2000), which are the main parameters that are adjusted during model calibration. Both models predicted high catches of prawns under the highest fishing policies and a relatively small reduction in catch under policy B, the lowest fishing policy (Figure 6.8).

### **Performance of optimal policies**

Performance of the eight different policies was measured by the 19 indicators shown in Table 6.4. Managers tend to be concerned about how the system is predicted to change under different policies and, therefore, 1996 predicted values of indicators are shown relative to their 1976 value (Figures 6.9 – 6.11). Exceptions to this were number of overfished and extinct groups, and catch and value, all of which are shown at their absolute predicted 1996 value.

#### *Overfished and extirpated groups*

Both models predicted that the greatest number of overfished groups would occur under the highest fishing effort policies Ai – Aiii (Figure 6.9), although Ecosim predicted that two more groups would be overfished than Atlantis. Both models predicted the same number of overfished species under policy Aiv. Atlantis predicted three overfished groups under the status quo policy, two under policy C (deep demersal fish and skates and rays) and one under policies B and D (deep demersal fish). Ecosim predicted no overfished groups under the status quo policy or policies B-D (Figure 6.9). Ecosim predicted almost twice as many extirpated groups under the three heaviest fishing policies (Figure 6.9). Neither model predicted any extirpations under the status quo or policies B-D.

#### *Relative biomass of composite groups*

Average relative biomasses of quota species, elasmobranchs, dogsharks, pelagic, demersal, planktivorous and piscivorous teleosts, forage species and K-selected species are shown in Figure 6.9. There was good qualitative agreement between the two models for most indicators, despite differences for individual groups discussed above. This likely reflects the better agreement for many quota species and sharks (Figure 6.4), as these groups were well-represented

in the composite indicators (Table 6.4a). Both models predicted lower biomass of sharks, piscivores, K-selected, demersal and quota species under heavier fishing (policies Ai-Aiii), coupled with higher biomass of pelagic, planktivorous and forage species. Both models predicted the opposite trends under the lowest fishing policies (B-D).

#### *Ratios of trophic and habitat-related groups*

The change in pelagic:demersal and piscivore:planktivore ratios is shown in Figure 6.10. Both models predicted a shift towards a more pelagic system under the heaviest fishing policies (values > 1). Ecosim predicted that the pelagic:demersal ratio was more sensitive to changes in fishing effort than Atlantis, with a three-fold change in the indicator under the highest fishing policy. Both models predicted similar changes in the piscivore:planktivore ratio under the different fishing policies, although Atlantis was more sensitive than Ecosim (Figure 6.10). Both models predicted a shift to a less piscivorous system under heavy fishing (values < 1) and to a more piscivorous system under reduced fishing (values > 1).

#### *Biodiversity index*

There was also good agreement between the two models in predicted biodiversity, measured by Kempton's index. Biodiversity was reduced under the highest fishing effort policies and increased under lower fishing policies, although it is noted that Ecosim's predicted increases in biodiversity, achieved by reducing fishing effort under policies B-D, were slight (Figure 6.10).

#### *Catch and value*

Ecosim predicted much higher total catches and value than Atlantis, especially under the highest fishing policies (Figure 6.11). Atlantis predicted similar total catch for the three highest fishing policies (Figure 6.11), suggesting that, as some species were fished down, others took their place (e.g., redfish, prawns and morwong; Figure 6.8). While the much larger catches and value predicted by Ecosim under the higher fishing policies were partly driven by increased catches of prawns, tiger flathead and school whiting (Figure 6.11), they were also driven by persistence of offshore demersal fish groups at very high abundance (Figure 6.5). These groups benefited from a release from predation by sharks and piscivorous quota species (especially gemfish), although absolute catches and biomass were implausibly large (see notes above). Atlantis predicted

depletion of this group under all policies and, overall, catches of more consistent magnitude with observed catches of other species in this fishery.

There was good agreement between the two models in terms of catch of quota species, with similar catches predicted for all the high fishing policies and the status quo. Not surprisingly, both models predicted that catch and value of quota species would be close to zero under the extremely low fishing policies. It is noteworthy, however, that, compared to 1976, predicted value of quota species was not greatly reduced under the optimal policy for biodiversity (policy C), and that the status quo policy produced a more valuable fishery in terms of quota species than any of the policies that increased fishing (Figure 6.11).

### **Ranking of policies**

Policies were ranked in terms of each of the 19 indicators shown in Table 6.4. For all policies, a rank of one represents the lowest value of the indicator and a rank of eight represents the highest. No attempt was made to interpret the ranks as ‘good’, ‘bad’, ‘best’ or ‘worst’, as this would constitute a judgement (i.e., different stakeholders will interpret each indicator differently). Table 6.7 shows the rank of the performance of the eight policies predicted by the two models, in terms of the 1996 predicted values of each indicator.

Despite large structural differences between the two models, there was good agreement in ranking the policies for the majority of indicators. The models were in perfect agreement for biomass of quota species, elasmobranchs, dogsharks and the ratio of pelagic to demersal species. Good agreement (5 or more ranks matched) was obtained for the number of overfished and extinct species, K-selected species, biodiversity, total value and catch of quota species. Poor agreement (less than 4 agreements) was obtained for biomass of pelagic, demersal, planktivorous and forage species and for total catch (Table 6.4). In general, the best agreement was obtained for the least aggregated groups, which had the most available information during model-construction. Conversely, the worst agreement was obtained for highly aggregated data-poor groups (especially forage and pelagic species).

## Trade-offs

Table 6.7 draws attention to some obvious conflicts between management objectives oriented towards maximising catch and profits and those with more conservation-oriented objectives. For example, policies associated with high catch and value (policies Ai-Aiv) tended to also be associated with low biomass of elasmobranchs, K-selected and piscivorous species and had larger numbers of overfished and extinct species. This is represented graphically in Figure 6.12, which shows the values of a subset of indicators on one graph for each policy. To enable graphing on the same plot, Figure 6.12 shows all indicators expressed in relation to 1976. While avoiding subjective terms like ‘best’ and ‘worst’, graphs similar to those in Figure 6.12 can be very useful for helping managers and stakeholders visualise trade-offs associated with different management strategies. For example, policy Ai can be summarised qualitatively as having high catch and value (predicted by Ecosim), low biodiversity, low shark abundance and fewer piscivorous species relative to other policies, whereas policy D has low catches, a low dollar-value, high biodiversity and more sharks and piscivores. Such qualitative statements can be used to characterise different policies in terms of the values that different stakeholders bring to the table. It should be noted that Atlantis and Ecosim did not agree in all respects. Atlantis predicted that policy Ai would result in lower total catch than other policies and that the highest total catches would be realised under Policy Aiv (see also Figure 6.11). Much better agreement was, however, obtained for quota species. Total catch and value could possibly be removed from the graphs because of the large differences in predictions of the models due to the aggregated offshore fish groups discussed above. If this was done, there would be excellent agreement between the two models, in terms of trade-offs among policies.

Results such as these can be used to quantify costs and benefits of alternative policies relative to other policies. For example, both models predicted that a fishing policy aimed at “no species overfished” (Policy B) would result in virtual closure of the fishery and more than a 90% reduction in catch and value of quota species, compared to a policy aimed at maximising landings without running the fishery at a loss (policy Aii; Figure 6.12). Alternatively, implementing policy Aii would result in extirpation of deepwater dogsharks and a 50% reduction in the biodiversity index and biomass of long-lived species. Graphs such as Figure 6.12 can also be used to identify policies with the least severe trade-offs. For example, policy C was predicted



to result in the least overall change in the ecosystem and resulted in only a moderate reduction in catch of quota species. However, policy C did require a 50% reduction in fishing effort in a (1976) fishery that was already quite small. Policy Aiv would allow the fishery to double its 1976 size and would only result in a moderate reduction in biodiversity, although it would still result in several overfished species and near extirpation of deepwater dogsharks. Maintaining the fishery at status quo (i.e., preventing further build-up of capacity) would result in equal or increased catch of quota species and no extirpated or overfished species.

## Discussion

This study compared the predictions of two structurally different models of the ecosystem of the NSW continental shelf and slope during development of its major trawl fishery. Andrew *et al.* (1997) and Graham *et al.* (2001) reported large declines in piscivorous teleosts and sharks between 1976 and 1996, on the fishing grounds targeted by this fishery. They concluded that fishing was the most likely explanation for the widespread declines in abundance. The present study aimed to build ecosystem models that could emulate the observed declines and, in doing so, explore alternative management policies that might have been implemented during development of the fishery if EBFM had been mandated at the time. Since 1996 there have been no fishery independent surveys of any of the fishing grounds in NSW and there have been large changes in the management of the fishery and data collection and storage methods. The study period was therefore restricted to the period spanned by the surveys to avoid results being complicated by recent management developments. The ‘retrospective forecasting’ approach taken enabled exposition of trade-offs inherent in policies with differing management objectives. The findings of Andrew *et al.* (1997) and Graham *et al.* (2001) suggest that trade-offs in this fishery happened, i.e., fishing effort increased considerably during the 20 year period between surveys and there were large reductions in biomass of many species, especially sharks. The results of the present study therefore explore how the fishery might have developed differently if management objectives and trade-offs had been clearly articulated during development of the fishery.

Both models were able to emulate observed changes for key functional groups, although quality of the agreement varied among groups and between models. The best qualitative agreement was

achieved for low-productivity groups (e.g., elasmobranchs) and for several quota species for which there was a reasonable amount of data available for calibration. There was poor agreement for some data-poor quota species (e.g., ocean perch) and for several pelagic and forage groups, about which there is almost no quantitative information in southeastern Australia. In Atlantis, dynamics of these groups were more influenced by bottom-up processes (i.e., by fluctuations in primary production) than in Ecosim, where there were no explicit primary productivity drivers. Atlantis was unable to emulate observed declines for the jackass morwong and gemfish groups. The fit for morwong obtained in the EwE model was also poor and underestimated abundance for most years. The EwE fit was achieved by increasing the foraging arena parameter (Walters *et al.* 1997; 2000) until the population was predicted to decline. Setting lower vulnerability parameters produced similar poor fits to those of Atlantis. The poor fits achieved in both models for this group suggests that some aspect of their dynamics was missing or misrepresented in the models (e.g., recreational fishing impacts). Gemfish has been considered overfished since the late 1980s and is known to have undergone several years of failed recruitment (Rowling 1990; 1997a; Punt and Smith 1999b). A number of hypotheses have been forwarded to explain the stock's failure to recover, even after cessation of targeted fishing. Hypotheses include compensatory recruitment, density dependent changes in selectivity, unreported catches or discards (Punt and Smith 1999b) and an oceanic regime shift (Punt and Smith 1999b; Prince and Griffin 2001; but see Rowling 2001). At face value, gemfish appears to be a relatively productive species (growth rate has been estimated to be  $\sim 0.21 \text{ y}^{-1}$  and  $M$  has been estimated to be between 0.4 and  $0.6 \text{ y}^{-1}$ ; Rowling and Reid 1992; Bruce *et al.* 2002). Other authors have also found it difficult to reproduce its continued low abundance in models (Punt and Smith 1999b). The Ecosim model was able to simulate the decline by increasing the proportion of gemfish biomass available to predators through adjustment of foraging arena parameters (Walters *et al.* 1997; 2000), effectively assuming that trophic and behavioural effects could explain the observed pattern. It should be noted, however, that the fit was poor in that it underestimated abundance for most years, then overestimated abundance at the end of the time series, when reported catches were very low. The trajectory of predicted gemfish biomass in Ecosim was very sensitive to the value of the vulnerability parameter. Setting it to a slightly greater value resulted in predicted extinction of the stock, while setting it lower produced similar results to those predicted by Atlantis. Neither model, therefore, can be said to adequately explain the observed trajectory of

gemfish, which remains an important unanswered question for fisheries management in this region.

To date, calibration of ecosystem models has been something of an *ad hoc* process, where parameters are adjusted until predictions matching observations are achieved (but see Savenkoff *et al.* 2001). The large number of parameters and complexity of modelled processes means that systematic exploration of alternatives common in single species models (e.g., Ludwig and Walters 1985; 1989; McAllister and Kirchner 2002; Punt and Smith 1999b) is rarely done in multispecies or ecosystem models (but see, e.g., Sainsbury 1988; 1991; Sainsbury *et al.* 1997; Bundy 2001; Gu  nette *et al.* 2006). This is partly because of the large number of parameters and the resource- and time-intensive nature of systematic testing, which precludes it from many shorter-term projects. Interactions of large numbers of parameters also make it difficult to separate the effects of single parameters (Silvert 1981; Duplisea 2000). It is important for practitioners to realise that calibrated models may fit the data for the wrong reasons (the large number of parameters means that multiple parameter-combinations could provide similar fits). A calibrated ecosystem model is therefore no more than a hypothesis that is consistent with observations, hence the need to compare models with alternative assumptions.

In the present study, even when good qualitative agreement between models was achieved, the magnitude of the differences in predicted catch and biomass were sometimes very large. Moreover, in some cases, the models predicted that groups would respond in the opposite direction under strong fishing pressure (e.g., redfish, tiger flathead, jackass morwong). The greatest differences were obtained for groups representing miscellaneous offshore demersal teleosts. Ecosim predicted that these groups would benefit greatly from heavy fishing, due to release from predation and competition from sharks and other piscivorous teleosts. Atlantis, however, predicted that these groups would be depleted by heavy fishing. These groups represented more than 100 miscellaneous species in the Ecosim model, about which there is extremely high uncertainty. Catches of most species in these groups were reported under a miscellaneous fish category in early datasets and large assumptions were therefore necessary to include them in the model. These groups were the principal reason for differences between models in indicators of total catch and value. At least part of this difference in the trajectories for deep demersal fish stems from the starting biomass of the group in the two models. In Ecosim

the demersal fish biomass started at roughly 750 000 t for the area. The Atlantis system could not support such a high biomass its starting biomass for this group was a more conservative 245 000 t.

In general, the large differences obtained for many of the modelled groups imply that it would be dangerous to use these models for providing detailed management advice for individual species. It has been noted by numerous authors that ecosystem models are unsuited for providing tactical advice (Fulton *et al.* 2003b; Christensen and Walters 2004b; Plagányi 2007), particularly because of difficulty in interpreting results and addressing uncertainty (Silvert 1981; Duplisea 2000). However, ecosystem models may be very useful for strategic consideration of broader issues such as possible broad impacts of fishing on ecosystems or exploration of ecosystem impacts of different management policies and evaluation of trade-offs. Confidence in results can be improved if they are consistent across a range of structural assumptions (Walters and Martell 2004; Fulton *et al.* 2003b; Fulton and Smith 2004), i.e., if structurally distinct models make the same or qualitatively similar predictions. The present study followed the same approach of Fulton and Smith (2004), where Ecosim was used to search for optimal fishing efforts, which were then used to drive Ecosim and biogeochemical models (the biogeochemical model BM2 used by Fulton and Smith (2004) is the precursor to Atlantis). Unlike the study of Fulton and Smith (2004), however, the models in the present study were constructed by different practitioners in different institutions (although every attempt was made to share information and data). While the aim was to make the models as similar as possible, the resource-intensive nature of building these models and the subjective nature of many of the decisions made by each modeller meant that it was impossible to match every assumption. It is therefore encouraging that the two models that differed in so many respects showed reasonably good agreement in ranking of policies and presentation of trade-offs.

There was good overall agreement in the ranking of the eight alternative policies across a broad range of indicators, despite large differences for individual groups. Note that no attempt was made to distinguish between minor re-orders in rank (e.g., 4 vs 5) and major re-orders (e.g., 1 vs 8). It is possible that minor re-orders in rank could be considered within acceptable bounds of uncertainty, although a more detailed analysis including a clear, less-severe definition of acceptable uncertainty would be required and is a possible avenue for extension of this study.

Notably, excellent agreement was obtained in representation of trade-offs, although it should be noted that models disagreed in terms of total catch and value, due to the problem groups discussed above. Both models predicted that large increases in fishing effort would result in low biodiversity, low abundance of sharks and other long-lived species, more forage and pelagic species and fewer piscivorous and demersal species. Conversely, reducing fishing effort would result in higher biodiversity and greater abundance of sharks, long-lived and piscivorous species, but would also result in a large decrease in catch and revenue, particularly of valuable quota species. Reductions in long-lived, piscivorous and demersal species and corresponding increases in pelagic and forage species under heavy fishing ('fishing down marine foodwebs') has been documented in many other ecosystems around the world (Pauly *et al.* 1998; 2001; Christensen 1998; Stergiou and Koulouris 2000), although some authors have shown that the same effect can be caused by mechanisms other than overfishing, such as eutrophication or development of new markets for lower trophic level species (Caddy *et al.* 1998; Caddy and Garibaldi 2000; Essington 2006). In the present study, the only possible mechanism for predicted increases in forage and pelagic species under heavy fishing was reduction in biomass of sharks and other piscivores. It is not known whether this has really occurred in the ecosystem off NSW, as there is little to no available information about abundance of pelagic species. Prince (2001) notes that many commercial fishers believe the ecosystem to be highly pelagic in nature and that gelatinous zooplankton are one of the primary means of nutrient cycling in the ecosystem. This was not, however, discussed in terms of changes to the system caused by fishing, but rather as an inherent means of nutrient transfer between primary producers and fish for a relatively oligotrophic ecosystem.

Qualitative agreement between the two models with respect to a number of management questions lends credibility to results, although Fulton and Smith (2004) caution about extrapolating too far from the assumptions of the models. Essington (2004) simulated data using a multispecies model with alternative representations of predator-prey interactions and used alternative assessment models to estimate biological and management parameters. This author defined the usefulness of a model as its ability to correctly identify fishing policies that would optimise profits and showed that, under certain approaches to parameter-estimation, the correct answer could be obtained using models that contained incorrect assumptions about predator-prey dynamics. He suggested therefore, that simpler models with incorrect representation of trophic

dynamics could still be useful in a management setting. Ludwig and Walters (1985; 1989) have shown this for single species models using catch per unit effort data, where simple surplus production models produced less biased estimates of underlying parameters than the same age-structured model that had been used to simulate the data, again suggesting that it may not be necessary to correctly represent the underlying system to give sound management advice. While these effects are not directly transferable to the present study, where parameters were not directly estimated and the effects of overparameterisation responsible for their findings do not apply, it is still important to note that useful policy advice is not dependent on accurate representation of all system dynamics (Walters and Martell 2004). For example, good agreement in management advice obtained in the present study despite differences in model predictions for individual functional groups, suggests that the same results were achieved through different mechanisms. However, across a broad range of species with similar characteristics, results were robust. While the present approach of comparing two ecosystem models that are structurally distinct did not allow for systematic exploration of the effects of different assumptions on model results, it may still be an appropriate approach for improving understanding of the use of ecosystem models for management (Fulton and Smith 2004). This study was influenced by the MSE approach, but did not include dynamic assessment or management decisions. This simplification was made due to logistical constraints, but a logical extension of the work presented here would be to test whether dynamic representation of all the assessment components significantly changed the conclusions or allowed for the consideration of more refined management options (as was the case in a full management strategy evaluation for Commonwealth southeast Australian fisheries, Fulton *et al* 2007a).

This study has highlighted a number of potential pitfalls in setting policy objectives. First, using an objective that no species will be overfished may actually imply no fishing at all. Most ecosystems contain very low productivity species such as dogsharks that may be vulnerable to fishing gear. If definitions of ‘ecosystem overfishing’ (Murawski 2000) are required, they need to be clearly articulated – i.e., acceptable levels of overfishing may need to be defined for some species (Hilborn 2007a). Terms such as ecosystem overfishing may not be useful, as it is virtually impossible to prevent overfishing of all species in non-selective fisheries. Even if the meaning of the term is clearly articulated in terms of how overfishing is defined or which species it refers to, it may still be misleading to the public. It is therefore better to focus discussion on trade-offs,

which can be presented in terms of easily-understood indices that have been shown to capture broadscale ecosystem changes. Hilborn *et al.* (2004) simulated management of the multi-sector, multispecies U.S. West Coast Groundfish Fishery under alternative ‘maximise profit’ and ‘no species overfished’ policies and, in agreement with the present study, drew the following conclusions: 1) for ecosystem total yield to be maximised, some species must be overfished; and 2) potential yield would be reduced by 90% (compared with the ‘maximise profit’ policy) if all species were protected from overfishing. Their results, and the present results, illustrate the difficulty and value-based nature of designing ecosystem-based sustainable fishing strategies, given that two approaches that could be validly described as ‘sustainable’ (and which are commonly stated simultaneously as management goals) are often in direct conflict with each other. Walters (2003) has argued that the only solution to such difficult trade-offs is to honestly articulate them and have managers, fishers and other stakeholders negotiate the best compromise. Graphs such as those presented in the present study may facilitate this process, but there must be recognition of the limits of such inputs into debates, which are inherently value-based and can become easily politicised.

It should be remembered that the optimal fishing effort policies presented here are relative to that in 1976, when the fishery was still fairly small. Graham *et al.* (2001) and Tilzey and Rowling (2001) report large increases in capacity during the 1980s (a ten-fold increase in the number of boats fishing the continental slope between 1974 and the early 1980s). While speculation about actual changes in the slope ecosystem has been deliberately avoided in this study, it is noted that the closest hypothetical policy to real events (assuming linear relationship between the number of boats and fishing effort) was policy Aiii. Both models predicted this policy to result in increased catches of quota species; almost 50% reduction in biodiversity, K-selected species and the piscivore:planktivore ratio; and near extirpation of sharks and dogsharks. Trade-offs are expected to become more severe as a system becomes more overfished, i.e., if recovery plans for overfished or threatened species become mandated, very large reductions (or complete cessation) in fishing may be required. It is politically very difficult, however, to reduce fishing capacity once it has been built up and doing so frequently results in severe hardship to individuals and to fishing communities. Overcapacity is a major cause of the world’s present overfishing problems (Ludwig *et al.* 1993; Mace 1997; FAO 1999). It has been estimated that, globally, the cost of fishing outweighs revenue by an estimated US\$60 billion (Christy 1997) with most of the deficit

paid by governments in the form of subsidies (Cochrane 2000). Ludwig *et al.* (1993) describe the effects of subsidization as being ratchet-like, in that it is a very difficult process to reverse once it has begun. In good years or during fishery development (such as when Australia declared the Australian Fishing Zone in 1979 or when Canada claimed its exclusive economic zone in 1977), there is often heavy investment in boats, gear and technology. When catches decline, however, industry often appeals to the government to help avert losses of jobs and investment. Heavy subsidisation has been implicated in the collapse of both the Newfoundland groundfish fishery (Hutchings and Myers 1995; Walters and Maguire 1996) and the Peruvian anchoveta fishery (Muck 1989). In Australia, fisheries have generally not been subsidised to this degree, but there have been several periods of 'buy-back' in the Commonwealth fishery off NSW, resulting from policy directives to implement more cost effective and sustainable fisheries in the face of falling catches and reduced profitability (Grieve and Richardson 2001; AFMA 2005). These have been costly, both to the Government and to southeast coastal fishing communities. Results of the present study suggest that a two-fold increase or decrease in 1976 fishing effort, or maintenance of 1976 levels of effort, would have resulted in a fishery that met a broad range of policy objectives without severe trade-offs. This is in agreement with studies that suggest that economic and ecological benefits can be realised through smaller, more profitable fisheries, where custodianship of the fishery is passed, at least in part, to the fishing industry (Hilborn *et al.* 1995; Parma *et al.* 2003; Castilla *et al.* 2007; Hilborn 2007b,c).

## Conclusions

A few general conclusions can be drawn from this study. Comparison of the two models was important, in that it demonstrated large differences in predictions for individual groups, arising from structural assumptions. Better agreement between models was achieved for species about which there was more information or that had low productivity. However, despite large differences in predictions for individual groups, management advice relating to trade-offs associated with alternative policy objectives was reasonably robust. The results presented here also illustrated the unexpected outcomes that can be associated with different policy objectives. For example, maximising catch was achieved in the Ecosim model by extirpation of many predators, which released other species from predation. Similarly, statements about preventing overfishing of any species must logically include all species caught by the fishery. The presence



of species with extremely low productivity, such as the deepwater dogsharks in this study, implied that a ‘no species overfished’ management strategy would mean virtually no fishing. Care therefore needs to be taken when making such statements.

Good custodianship requires precise definition of management objectives. Simply stating “sustainability” as a management objective is imprecise, as it can justifiably encompass strategies at both ends of a trade-off continuum. Scientists can assist managers and policy-makers by: i) using simulation models to help reduce some of the ambiguity inherent in stated policy-objectives (because simulation requires quantitative definitions); ii) by highlighting possible counter-intuitive or unexpected implications of certain policy objectives; iii) exposing conflicting objectives by presenting results in terms of trade-offs; and iv) accounting for uncertainty (including structural uncertainty) wherever possible (Ludwig *et al.* 1993; Walters and Martell 2004). Comparison of multiple models of the same system can help to identify which results are most sensitive to model specification. While it is resource-intensive to construct multiple ecosystem models, it is much less so than large scale management experiments needed to resolve structural uncertainties in the real world (Walters 1986; Walters and Holling 1992; Sainsbury *et al.* 1997), although this should be done if resources are available.

While there is a need for models to be able to make precise quantitative predictions to aid tactical fisheries management, the large data deficiencies and inherent complexity associated with marine ecosystems make most ecosystem models unsuited to this task at present (Christensen and Walters 2004; Plagányi 2007). As fisheries legislation around the world shifts towards greater emphasis on EBFM, ecosystem models can be very useful for more qualitative analyses, such as determining which fishing strategies are better or worse for meeting competing management objectives; and, in doing so, highlight the value-based nature of defining appropriate goals, especially when the least productive stocks are not charismatic and contribute little to the economic value of the fishery.

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## Tables

**Table 6.1.** Groups for model comparison. See Appendix 1, Table A1.1 for representative species.

<b>Common aggregated group</b>		<b>Contains Ecopath Groups</b>	<b>Atlantis groups</b>
1	Benthos	Small inshore benthic invertebrates, Small slope benthic invertebrates	Shallow filter feeders, Deep benthic filter feeders, Benthic grazers, Benthic deposit feeders, Benthic carnivores, Meiobenthos
2	Macrozoobenthos	Large inshore benthic invertebrates and large slope benthic invertebrates	Macrozoobenthos
3	Lobsters	Rock lobster	Rock lobster, slipper lobsters
4	Squids	Inshore and offshore squid	Cephalopods
5	Detritus	Detritus	Refractory detritus, Labile detritus
6	Blue Grenadier*	Blue Grenadier	Blue Grenadier
7	Tiger flathead*	Tiger flathead	Tiger flathead
8	Ling*	Ling	Ling
9	Offshore demersal fish	Dories, Offshore demersal omnivorous fish, Offshore demersal piscivorous fish, Deep demersal omnivorous fish, Deep demersal piscivorous fish	Deep demersal fish
10	Shallow demersal herbivorous fish	Inshore demersal herbivorous fish	Shallow demersal herbivorous
11	Warehous and Trevalla*	Warehous and Trevalla	Warehous and Trevalla
12	Redfish*	Redfish	Redfish
13	Trevallies*	Trevallies	Trevallies
14	Shallow territorial demersal fish	Small inshore omnivorous fish	Shallow territorial demersal
15	Shallow demersal fish	Inshore demersal omnivorous fish, Inshore demersal piscivorous fish, Snapper	Shallow demersal fish
16	Large planktivores	Large inshore pelagic omnivorous fish	Large planktivores
17	Jackass morwong*	Jackass morwong	Jackass morwong
18	Small planktivores	Small inshore pelagic omnivorous fish	Small planktivores
19	Ocean Perch*	Ocean Perch	Ocean Perch
20	Oceanic planktivores	Offshore pelagic omnivorous fish	Oceanic planktivores
21	School whiting*	School whiting	School whiting
22	Shallow piscivores	Small and large inshore pelagic piscivorous fish	Shallow piscivores

**Table 6.1 cont.**

<b>Common aggregated group</b>		<b>Contains Ecopath Groups</b>	<b>Atlantis groups</b>
23	Oceanic piscivores	Offshore pelagic piscivorous fish	Oceanic piscivores
24	Gemfish*	Gemfish	Gemfish
25	Lg Benthos	Large inshore benthic invertebrates	Commercial filter feeders, Commercial macrozoobenthos
26	Macrophytes		Macroalgae, seagrass
27	Mesopelagics	Mesopelagics	Migratory and Non-migratory mesopelagics
28	Phytoplankton	Phytoplankton	Large and Small phytoplankton
29	Pinnipeds	Seals	Pinnipeds
30	Prawns	Inshore prawns and Royal red prawns	Prawns
31	Seabirds	Seabirds	Seabirds
32	Deepwater dogsharks	Harrison and Southern dogshark, Greeneye dogshark, Endeavour dogshark, Other dogsharks	Deepwater dogsharks
33	Spiky dogshark	Spiky dogshark	Spiky dogshark
34	Demersal sharks	Gummy shark, School shark, Other medium sharks	Demersal sharks
35	Pelagic sharks	Large sharks	Pelagic sharks
36	Skates and rays	Skates and rays	Skates and rays
37	Baleen whales	Baleen whales	Baleen whales
38	Toothed whales	Toothed whales	Dolphins, Toothed whales
39	Gel zooplankton	Gelatinous zooplankton	Gelatinous zooplankton
40	Zooplankton	Zooplankton	Small, meso- and large zooplankton

\* Species under quota since 1992

**Table 6.2.** Indices of relative abundance used to tune the models (only years between 1976 and 1996 were used).

Species	Period	Reference
Jackass morwong	1915-2002 (every 5 years)	Fay 2006
Blue warehou	1986-2003	Punt and Smith 2006
Blue Grenadier	1979-2003	Tuck <i>et al.</i> 2004
Redfish	1965-1995	Rowling 1997b
Gemfish	1970-1999	Supplied by K. Rowling (NSW DPI)
Pink ling	1985 - 2000	Klaer 2006a
Tiger flathead	1915 - 2003	Cui <i>et al.</i> 2006
Silver trevally	1943 - 2004	Supplied by J. Day (CSIRO)

**Table 6.3.** Objective function and resulting optimal trawling effort (relative to the 1976 trawling effort) found by Ecosim's fisheries optimisation routine (see text). Results are the mean of five searches starting with random fishing efforts.

Objective function weight							Results
Policy	Objective	Economic	Social	Mandated rebuilding	Q-90	Ecosystem maturity	Effort relative to 1976
Ai	Maximise yield	0	1	0	0	0	24.7
Aii	Maximise yield (no net loss)	0	1	0	0	0	13.4
Aiii	Maximise profit (low costs)	1	0	0	0	0	9.3
Aiv	Maximise profit (high costs)	1	0	0	0	0	2.4
B	Weakest stocks not overfished	0	0	1	0	0	0.002
C	Maximise biodiversity	0	0	0	1	0	0.513
D	Maximise ecosystem maturity	0	0	0	0	1	0.015

**Table 6.4a.** List of biological indicators to measure performance of alternative policies in the models. Functional groups included in the calculation of each indicator are also shown (see Table 6.1 for description of functional groups). Indicators superscripted by P are primary indicators that directly address the policy objectives set out in Table 6.3.

Indicator	Functional groups included in calculation of indicator
Number of overfished species ( $< 48\% B_{1976}$ ) <sup>P</sup>	All fished groups
Number of extirpated species ( $< 5\% B_{1976}$ )	All fished groups
<b>Average biomass relative to 1976<sup>†</sup></b>	
Quota species	Blue grenadier, jackass morwong, gemfish, ling, ocean perch, tiger flathead, redfish, school whiting, trevallies, warehou and trevalla
Elasmobranchs	Deepwater dogsharks, demersal sharks, pelagic sharks, skates and rays, spiky dogshark
Dogsharks (including spiky dogshark)	Deepwater dogsharks, spiky dogshark
Dogsharks (excluding spiky dogshark)	Deepwater dogsharks
Pelagic teleosts	Large planktivores, small planktivores, oceanic planktivores, shallow piscivores, oceanic piscivores, mesopelagic fish
Demersal teleosts <sup>††</sup>	Blue grenadier, gemfish, jackass morwong, ling, ocean perch, redfish, school whiting, tiger flathead, trevallies, warehou and trevalla, deep demersal fish, shallow demersal herbivorous fish, shallow territorial demersal fish
Piscivorous teleosts	Blue grenadier, gemfish, jackass morwong, ling, ocean perch, redfish, tiger flathead, trevallies, oceanic piscivores, shallow piscivores
Planktivorous teleosts	Large planktivores, small planktivores, oceanic planktivores, mesopelagic fish
Forage species	Cephalopods, large planktivores, small planktivores, mesopelagic fish
K-selected species <sup>P</sup>	Deepwater dogsharks, demersal sharks, pelagic sharks, skates and rays, spiky dogshark, seabirds, baleen whales, toothed whales, pinnipeds
<b>Ratios</b>	
Piscivorous:planktivorous teleosts	See above
Pelagic:demersal teleosts	See above
<b>Biodiversity indices</b>	
Kempton's biodiversity index <sup>P</sup>	All fished groups

† Averaged across all groups included in the indicator

†† Includes species that are primarily demersal but may also feed in the water column

**Table 6.4b.** List of fishery indicators to measure performance of alternative policies in the models. Functional groups included in the calculation of each indicator are also shown (see Table 6.1 for description of functional groups). Indicators superscripted by P are primary indicators that directly address the policy objectives set out in Table 6.3.

Indicator	Functional groups included in calculation of indicator
Total catch <sup>P</sup>	All groups
Total value <sup>P</sup>	
Catch of quota species	Blue grenadier, jackass morwong, gemfish, ling, ocean perch, tiger flathead, redfish, school whiting, trevallies, warehou and trevalla
Value of quota species	



**Table 6.5.** Atlantis and Ecosim predictions of proportional change in biomass between 1976 and 1996. Values of zero imply the group was predicted to have been extirpated. Note that SQ refers to 1976 *Status Quo* policy.

Functional group	Atlantis								Ecosim							
	SQ	Ai	Aii	Aiii	Aiv	B	C	D	SQ	Ai	Aii	Aiii	Aiv	B	C	D
Benthos	0.50	0.51	0.51	0.50	0.50	0.50	0.50	0.50	1.00	0.88	1.03	1.06	1.04	0.96	0.99	0.96
Macrozoobenthos	0.76	0.91	0.90	0.90	0.83	0.60	0.70	0.61	1.00	0.92	1.04	1.08	1.05	0.97	0.99	0.97
Lobsters	0.53	0.53	0.53	0.53	0.53	0.51	0.52	0.51	1.00	1.13	1.04	1.02	1.01	1.02	1.01	1.02
Squids	0.60	0.70	0.69	0.68	0.63	0.56	0.58	0.56	1.01	0.94	1.21	1.22	1.10	0.89	0.96	0.89
Detritus	2.40	2.38	2.38	2.39	2.40	2.41	2.41	2.41	1.00	1.10	0.98	0.95	0.97	1.03	1.01	1.03
Blue Grenadier*	1.10	1.16	1.17	1.18	1.14	1.03	1.07	1.03	1.09	0.00	0.02	0.16	0.90	1.14	1.09	1.14
Tiger flathead*	1.03	0.05	0.07	0.10	0.51	1.96	1.50	1.95	1.08	0.41	0.53	0.65	1.07	1.01	1.03	1.01
Ling*	0.78	0.90	0.96	0.98	0.89	0.52	0.67	0.52	1.02	0.20	0.37	0.49	0.92	1.16	1.06	1.16
Offshore demersal fish	0.34	0.01	0.03	0.05	0.25	0.24	0.33	0.24	0.99	1.24	1.01	0.95	0.93	1.12	1.04	1.12
Shallow dem. herb.	1.14	1.50	1.45	1.42	1.26	0.85	1.02	0.85	0.99	1.00	0.86	0.83	0.89	1.07	1.03	1.07
Warehouse/Trevalla	0.88	0.83	0.83	0.84	0.88	0.87	0.88	0.87	1.00	0.00	0.00	0.00	0.72	1.14	1.07	1.14
Redfish*	0.87	0.50	0.53	0.57	0.76	1.13	0.99	1.13	1.02	0.00	0.00	0.00	0.11	1.60	1.43	1.60
Trevallies*	1.03	0.81	0.91	0.99	1.12	0.70	0.91	0.71	1.00	0.01	0.13	0.32	0.96	1.12	1.04	1.12
Shallow terr. dem. fish	1.13	3.76	3.21	2.87	1.62	0.53	0.83	0.54	1.00	1.05	0.99	0.97	0.99	1.03	1.01	1.03
Shallow dem. fish	0.60	0.42	0.53	0.59	0.67	0.43	0.54	0.43	0.99	1.66	1.32	1.27	1.25	0.99	0.97	0.99
Large planktivores	0.84	0.43	0.62	0.72	0.87	0.76	0.82	0.76	1.09	1.84	1.36	1.23	1.07	0.77	0.99	0.78
Jackass morwong*	2.00	0.54	0.61	0.69	1.38	2.67	2.33	2.67	0.80	0.00	0.00	0.00	0.45	1.02	0.92	1.02
Small planktivores	0.89	1.09	1.03	0.99	0.91	0.92	0.90	0.92	0.99	1.30	0.95	0.89	0.93	1.11	1.03	1.11
Ocean Perch*	1.20	0.11	0.17	0.23	0.77	1.49	1.37	1.49	1.05	0.62	1.33	1.40	1.14	0.84	0.97	0.84
Oceanic planktivores	0.71	0.72	0.72	0.71	0.71	0.71	0.71	0.71	1.02	1.59	1.00	0.89	0.95	0.96	1.01	0.96
School whiting*	1.03	0.13	0.27	0.42	1.04	0.69	0.90	0.70	1.06	0.67	1.62	1.89	1.57	0.61	0.87	0.62
Shallow piscivores	0.87	0.97	0.95	0.94	0.91	0.85	0.88	0.85	0.99	1.44	1.10	1.03	1.02	1.06	1.01	1.06
Oceanic piscivores	0.83	0.50	0.61	0.67	0.81	0.83	0.83	0.83	1.03	1.43	0.91	0.82	0.97	0.93	1.01	0.93
Gemfish*	1.41	0.01	0.02	0.05	0.60	3.29	2.16	3.25	1.01	0.00	0.00	0.00	0.70	1.19	1.09	1.18
Lg Benthos	1.31	1.35	1.35	1.35	1.33	1.28	1.30	1.28	1.00	1.09	1.01	0.99	1.00	1.03	1.01	1.03
Macrophytes	0.33	0.33	0.33	0.33	0.32	0.34	0.33	0.34	1.00	1.17	0.96	0.92	0.95	1.05	1.02	1.05
Mesopelagics	1.19	1.98	1.91	1.85	1.42	1.06	1.11	1.06	0.99	1.35	0.88	0.76	0.86	1.13	1.05	1.13

\*Quota species in the offshore trawl fishery

**Table 6.5 cont.**

Functional group	Atlantis								Ecosim							
	SQ	Ai	Aii	Aiii	Aiv	B	C	D	SQ	Ai	Aii	Aiii	Aiv	B	C	D
Phytoplankton	0.92	0.89	0.90	0.90	0.91	0.95	0.93	0.95	1.00	1.08	0.98	0.96	0.98	1.02	1.01	1.02
Pinnipeds	0.99	0.88	0.90	0.92	0.97	1.00	1.00	1.00	1.28	1.67	1.40	1.35	1.31	1.24	1.26	1.24
Prawns	0.88	0.95	0.94	0.93	0.89	0.89	0.89	0.89	0.99	1.62	1.12	1.00	0.94	1.09	1.02	1.09
Seabirds	0.88	0.90	0.89	0.89	0.88	0.88	0.88	0.88	1.02	3.00	2.06	1.90	1.40	0.82	0.90	0.82
Deepwater dogsharks	0.32	0.04	0.05	0.05	0.13	1.03	0.56	1.01	0.41	0.00	0.00	0.00	0.02	2.05	0.98	2.02
Spiky dogshark	0.59	0.18	0.24	0.30	0.51	0.65	0.62	0.65	1.04	0.00	0.00	0.04	0.96	1.07	1.06	1.07
Demersal sharks	0.61	0.01	0.02	0.03	0.28	1.33	0.92	1.32	1.05	0.00	0.00	0.00	0.14	2.67	1.44	2.61
Pelagic sharks	0.78	0.01	0.02	0.03	0.31	1.98	1.29	1.95	0.98	0.00	0.00	0.00	0.22	4.17	1.86	4.07
Skates and rays	0.11	0.01	0.01	0.01	0.04	0.76	0.25	0.73	1.02	0.00	0.00	0.00	0.14	1.34	1.22	1.33
Baleen whales	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.30	1.00	1.04	1.01	1.00	1.00	1.00	1.00	1.00
Toothed whales	1.00	0.97	0.98	0.99	1.00	0.99	0.99	0.99	1.00	1.02	1.01	1.02	1.01	1.00	1.00	1.00
Gel zooplankton	0.33	0.35	0.33	0.32	0.32	0.35	0.33	0.35	0.99	1.07	0.94	0.92	0.95	1.05	1.02	1.05
Zooplankton	0.85	0.84	0.84	0.84	0.85	0.85	0.85	0.85	1.00	1.10	0.98	0.95	0.97	1.03	1.01	1.03

\*Quota species in the offshore trawl fishery

**Table 6.6.** Qualitative comparison of models. + and - respectively indicates increase and decrease in predicted 1996 biomass under each policy relative to 1976. Y indicates models predicted change in the same direction while N indicates models predicted change in the opposite direction. Note that SO refers to 1976 *Status Quo* policy.

Functional group	Atlantis				Ecosim				Qualitative agreement							
	SQ	AI	AII	AIII	AIV	B	C	D	SQ	AI	AII	AIII	AIV	B	C	D
Benthos	-	-	-	-	-	-	-	-	N	Y	N	N	N	Y	Y	Y
Macrozoobenthos	-	-	-	-	-	-	-	-	N	Y	N	N	N	Y	Y	Y
Lobsters	-	-	-	-	-	-	-	-	N	N	N	N	N	N	N	N
Squids	-	-	-	-	-	-	-	-	N	N	N	N	N	Y	Y	Y
Detritus	+	+	+	+	+	+	+	+	N	Y	N	N	N	Y	Y	Y
Blue Grenadier*	+	+	+	+	+	+	+	+	Y	N	N	N	N	Y	Y	Y
Tiger flathead*	+	-	-	-	-	+	+	+	Y	Y	Y	Y	N	Y	Y	Y
Ling*	-	-	-	-	-	-	-	-	N	Y	Y	Y	Y	Y	N	N
Offshore dem. fish	-	-	-	-	-	-	-	-	Y	N	N	N	N	Y	N	N
Shallow dem. herb.	+	+	+	+	+	-	+	+	N	N	N	N	N	N	Y	N
Warehous/Trevalla	-	-	-	-	-	-	-	-	Y	Y	Y	Y	Y	N	N	N
Redfish*	-	-	-	-	-	+	-	+	N	Y	Y	Y	Y	Y	N	Y
Trevallies*	+	-	-	-	+	-	-	+	Y	Y	Y	Y	N	N	N	N
Shallow terr. dem.	+	+	+	+	+	-	-	+	N	Y	N	N	N	N	N	N
Shallow dem. fish	-	-	-	-	-	-	-	-	Y	N	N	N	N	Y	Y	Y
Large planktivores	-	-	-	-	-	-	-	-	N	N	N	N	N	Y	Y	Y
Jackass morwong*	+	-	-	-	+	+	+	+	N	Y	Y	Y	N	Y	N	N
Small planktivores	-	+	+	-	-	-	-	-	Y	Y	N	N	Y	N	N	N
Ocean Perch*	+	-	-	-	-	+	+	+	Y	Y	N	N	N	N	N	N
Oceanic planktivores	-	-	-	-	-	-	-	-	N	N	Y	Y	Y	Y	N	Y
School whiting*	+	-	-	-	+	-	-	-	Y	Y	N	N	N	Y	Y	Y
Shallow piscivores	-	-	-	-	-	-	-	-	Y	N	N	N	N	N	N	N
Oceanic piscivores	-	-	-	-	-	-	-	-	N	N	Y	Y	Y	Y	N	Y
Gemfish*	+	-	-	-	-	+	+	+	Y	Y	Y	Y	Y	Y	Y	Y
Lg Benthos	+	+	+	+	+	+	+	+	Y	Y	Y	N	N	Y	Y	Y
Macrophytes	-	-	-	-	-	-	-	-	Y	N	Y	Y	Y	N	N	N

\*Quota species in the offshore trawl fishery

**Table 6.6 cont.**

Functional group	Atlantis					Ecosim					Qualitative agreement					
	SQ	Ai	Aii	Aiii	Aiv	B	C	D	SQ	Ai	Aii	Aiii	Aiv	B	C	D
Mesopelagics	+	+	+	+	+	+	+	+	N	Y	N	N	N	Y	Y	Y
Phytoplankton	-	-	-	-	-	-	-	+	Y	N	Y	Y	Y	N	N	N
Pinnipeds	-	-	-	-	-	+	+	+	N	N	N	N	N	Y	Y	Y
Prawns	-	-	-	-	-	-	-	+	Y	N	N	N	Y	N	N	N
Seabirds	-	-	-	-	-	-	-	-	N	N	N	N	N	Y	Y	Y
Deep dogsharks	-	-	-	-	-	+	-	+	Y	Y	Y	Y	Y	Y	Y	Y
Spiky dogshark	-	-	-	-	-	-	-	+	N	Y	Y	Y	Y	N	N	N
Demersal sharks	-	-	-	-	-	+	-	+	N	Y	Y	Y	Y	Y	N	Y
Pelagic sharks	-	-	-	-	-	+	+	+	Y	Y	Y	Y	Y	Y	Y	Y
Skates and rays	-	-	-	-	-	-	-	+	N	Y	Y	Y	Y	N	N	N
Baleen whales	+	+	+	+	+	+	+	-	Y	Y	Y	Y	Y	N	Y	N
Toothed whales	-	-	-	-	+	-	-	+	N	N	N	N	Y	N	N	N
Gel zooplankton	-	-	-	-	-	-	-	+	Y	N	Y	Y	Y	N	N	N
Zooplankton	-	-	-	-	-	-	-	+	Y	N	Y	Y	Y	N	N	N

\*Quota species in the offshore trawl fishery

**Table 6.7.** Predicted rank of the eight different policies, in terms of the value of the indicators listed in Table 6.4. For all indicators the Rank 1 corresponds to the lowest predicted value of the indicator and Rank 8 corresponds to the highest predicted value of the indicator. Indicators for which perfect agreement was obtained are shown in bold font. Note that SO refers to 1976 *Status Quo* policy.

Rank policy											Agreement	
Indicator	SQ	Ai	Aii	Aiii	Aiv	B	C	D	Perfect	Number of agreements		
Number overfished species	Atlantis	4	7	7	6	5	1	3	1	N	5	
	Ecosim	1	7	7	6	5	1	1	1			
Number extirpated species	Atlantis	1	7	7	6	5	1	1	1	Y	7	
	Ecosim	1	8	7	6	5	1	1	1			
Quota species	Atlantis	5	1	2	3	4	8	6	7	Y	8	
	Ecosim	5	1	2	3	4	8	6	7			
Elasmobranchs	Atlantis	5	1	2	3	4	8	6	7	Y	8	
	Ecosim	5	1	2	3	4	8	6	7			
Dogsharks (including spiky)	Atlantis	5	1	2	3	4	8	6	7	Y	8	
	Ecosim	5	1	2	3	4	8	6	7			
Dogsharks (excluding spiky)	Atlantis	5	1	2	3	4	8	6	7	Y	8	
	Ecosim	5	1	2	3	4	8	6	7			
Pelagic teleosts	Atlantis	4	8	7	6	5	1	3	2	N	2	
	Ecosim	4	8	3	1	2	7	5	6			
Demersal teleosts	Atlantis	5	1	2	3	4	8	6	7	N	3	
	Ecosim	4	5	2	1	3	8	6	7			
Piscivorous teleosts	Atlantis	5	1	2	3	4	8	6	7	Y	8	
	Ecosim	5	1	2	3	4	8	6	7			
Planktivorous teleosts	Atlantis	4	8	7	6	5	1	3	2	N	2	
	Ecosim	4	8	3	1	2	7	5	6			
Forage species	Atlantis	4	8	7	6	5	1	3	2	N	2	
	Ecosim	4	8	3	1	2	7	5	6			
K-selected species	Atlantis	5	1	2	3	4	8	6	7	N	5	
	Ecosim	5	3	1	2	4	8	6	7			

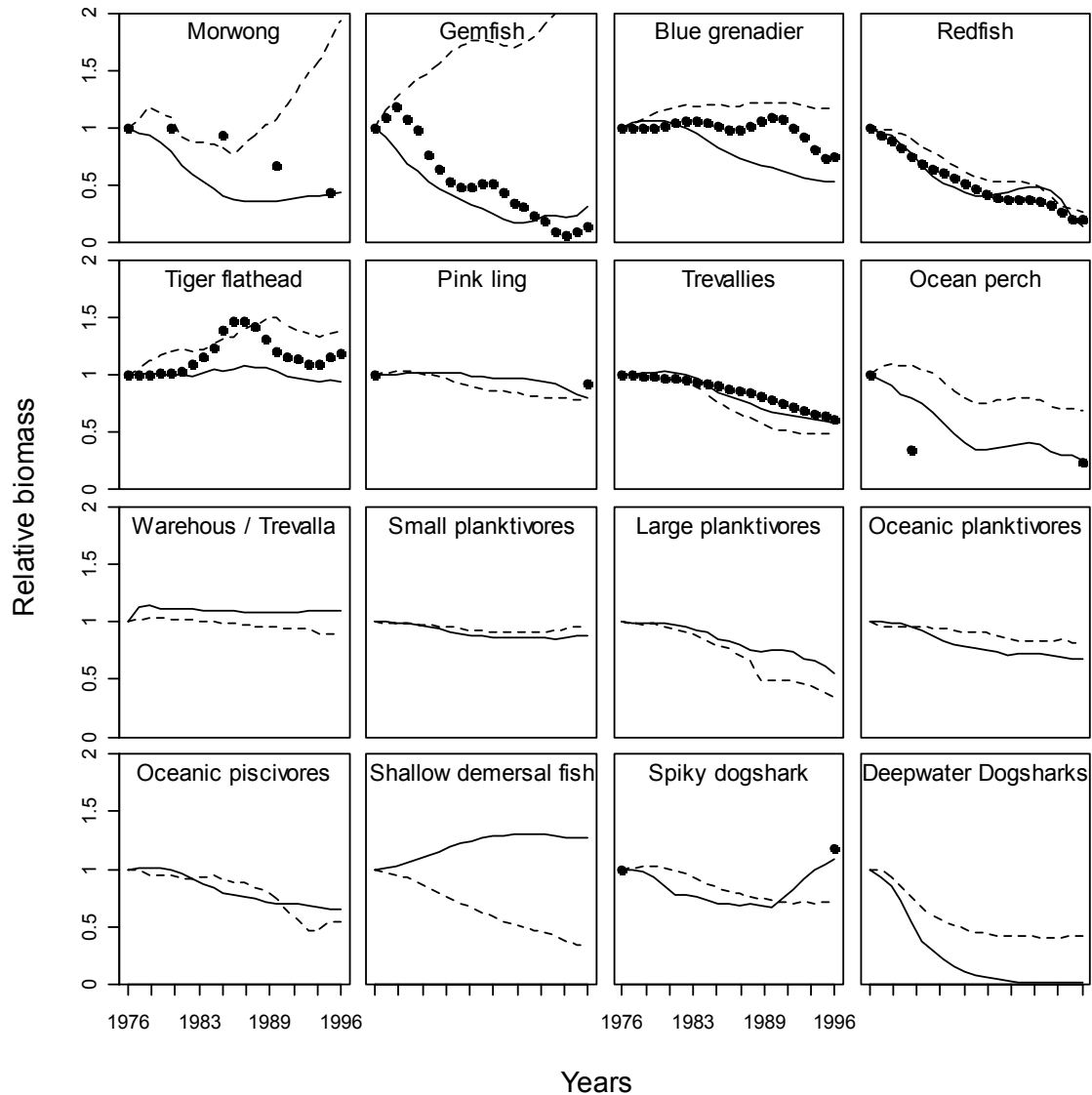
**Table 6.7 cont.**

Indicator	Rank policy								Agreement		Number of agreements
	SQ	Ai	Aii	Aiii	Aiv	B	C	D	Perfect		
Piscivore: planktivore ratio	4	6	8	7	5	1	3	2	N	4	
	4	8	7	6	5	1	3	2			
Pelagic:demersal ratio	5	1	2	3	4	8	6	7	Y	8	
	5	1	2	3	4	8	6	7			
Biodiversity	5	1	2	3	4	7	6	8	N	5	
	5	1	2	3	4	8	6	7			
Total catch	5	4	6	7	8	1	3	2	N	3	
	4	8	7	6	5	1	3	2			
Total value	4	6	5	7	8	1	3	2	N	4	
	4	8	7	6	5	1	3	2			
Quota spp. catch	7	4	5	6	8	1	3	2	N	5	
	4	5	7	6	8	1	3	2			
Quota spp. value	7	4	5	6	8	1	3	2	N	6	
	7	4	6	5	8	1	3	2			

## Figures

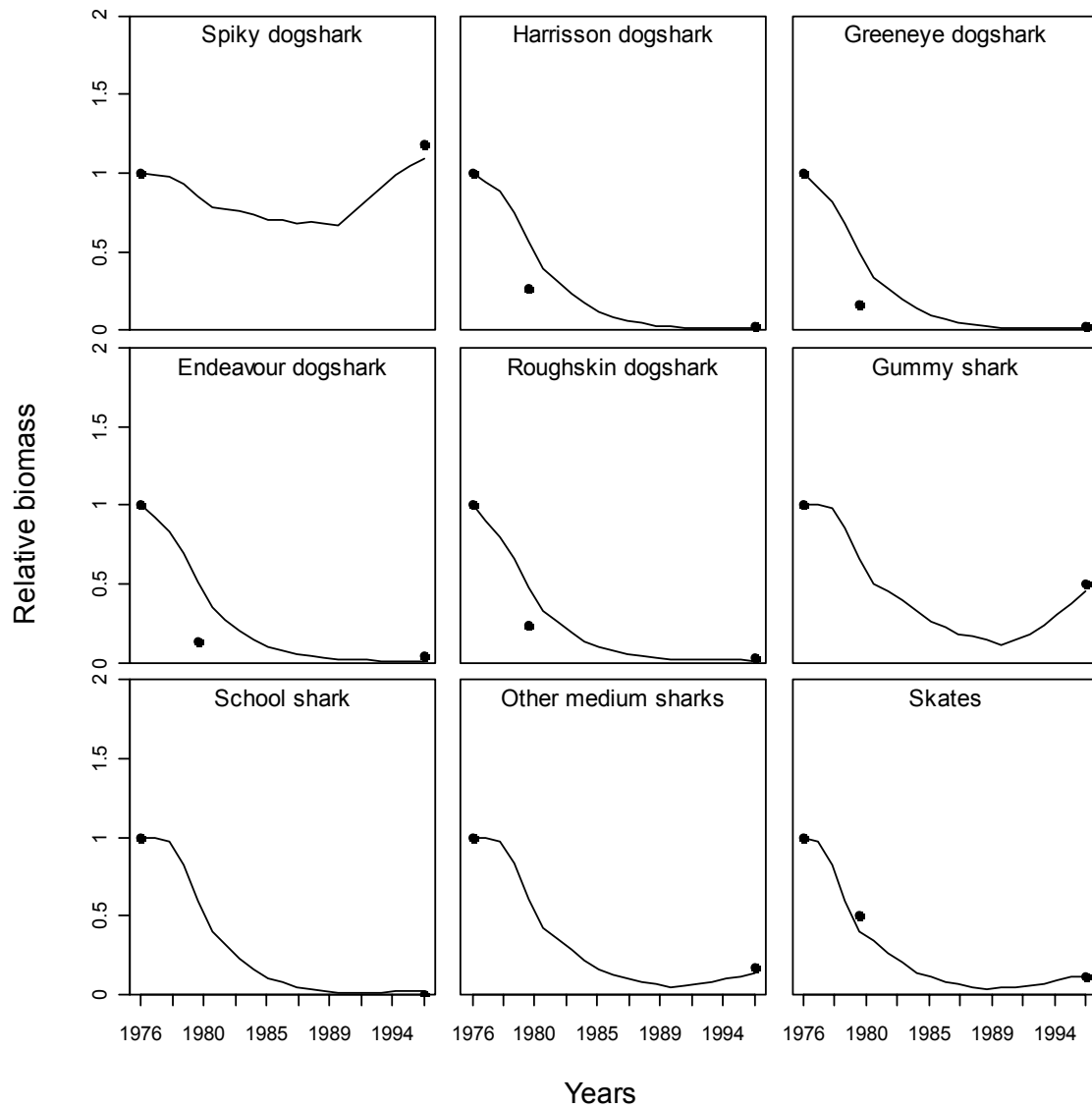


**Figure 6.1.** Map of the study area showing compartments used in the Atlantis model.  
*Source:* Savina et al. (2008).

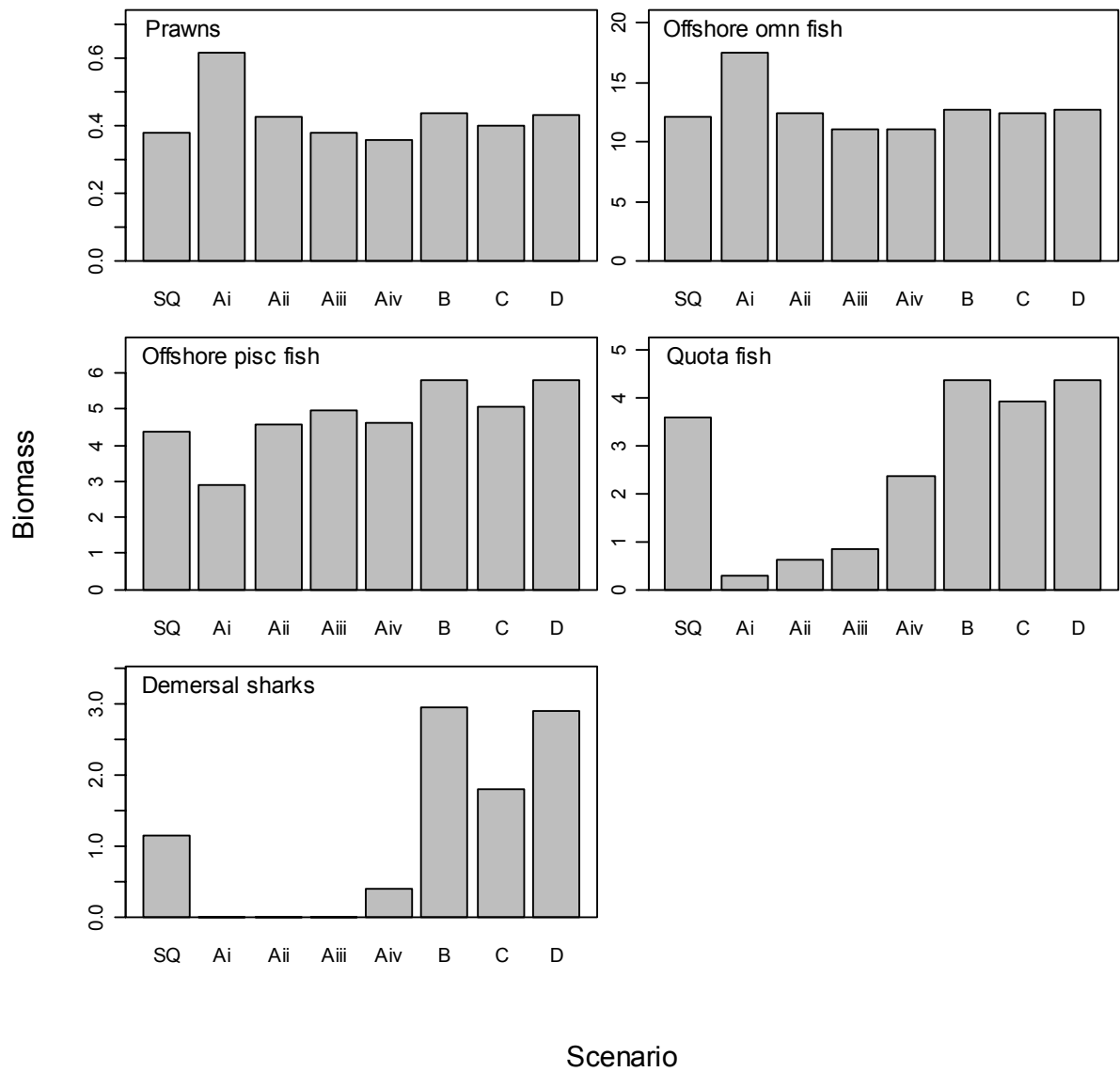


**Figure 6.2a.** Relative biomasses predicted by Ecosim (solid line) and Atlantis (dashed line) for 16 species, with the models driven with historical catches or fishing mortality (see text). Where available, relative indices of abundance are also shown (solid circles). See Table 6.2 for sources of observed data (data points for pink ling, spiky dogshark and ocean perch were mean relative abundances from the *Kapala* data; Graham *et al.* 2001 and Andrew *et al.* 1997).

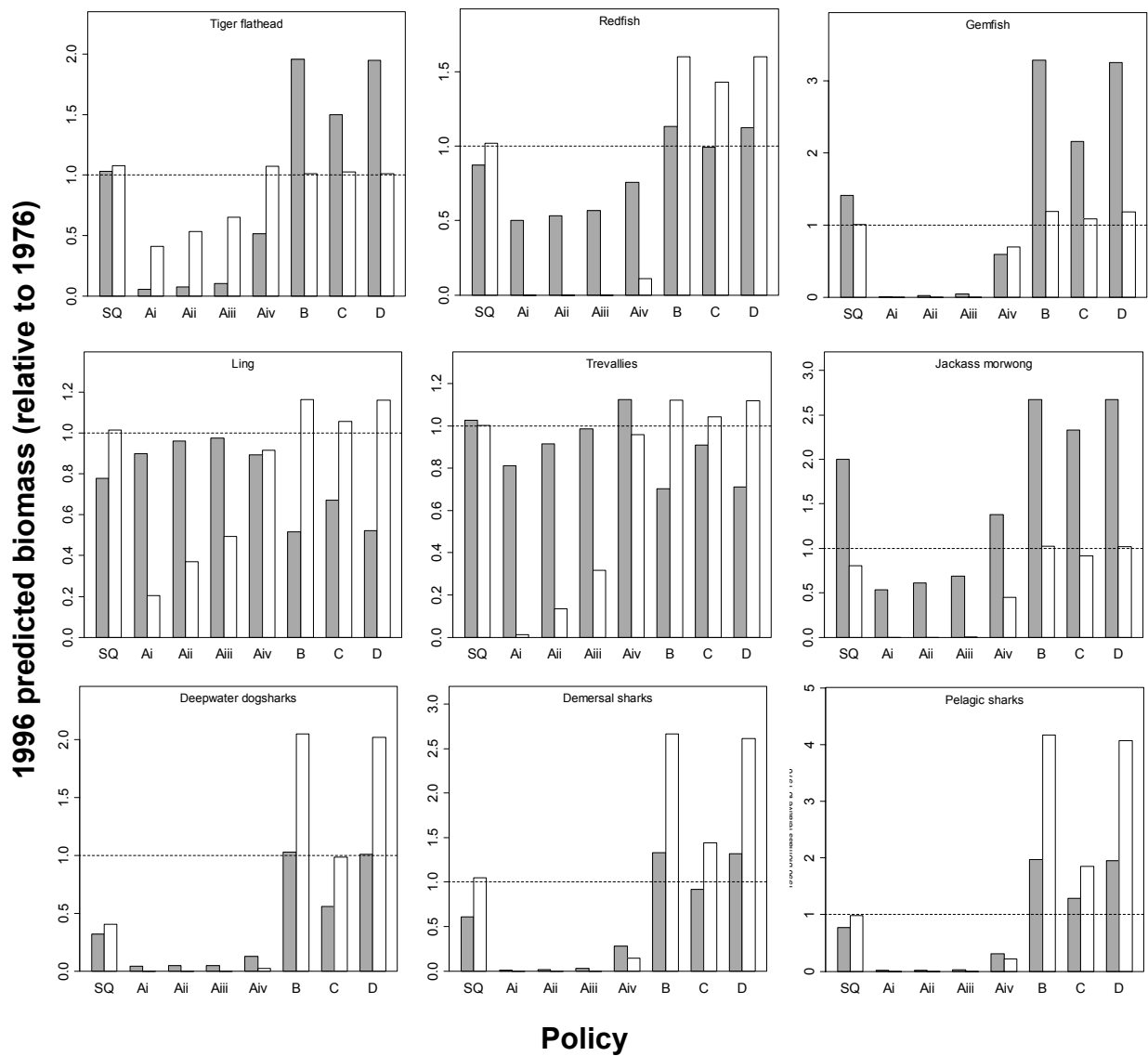




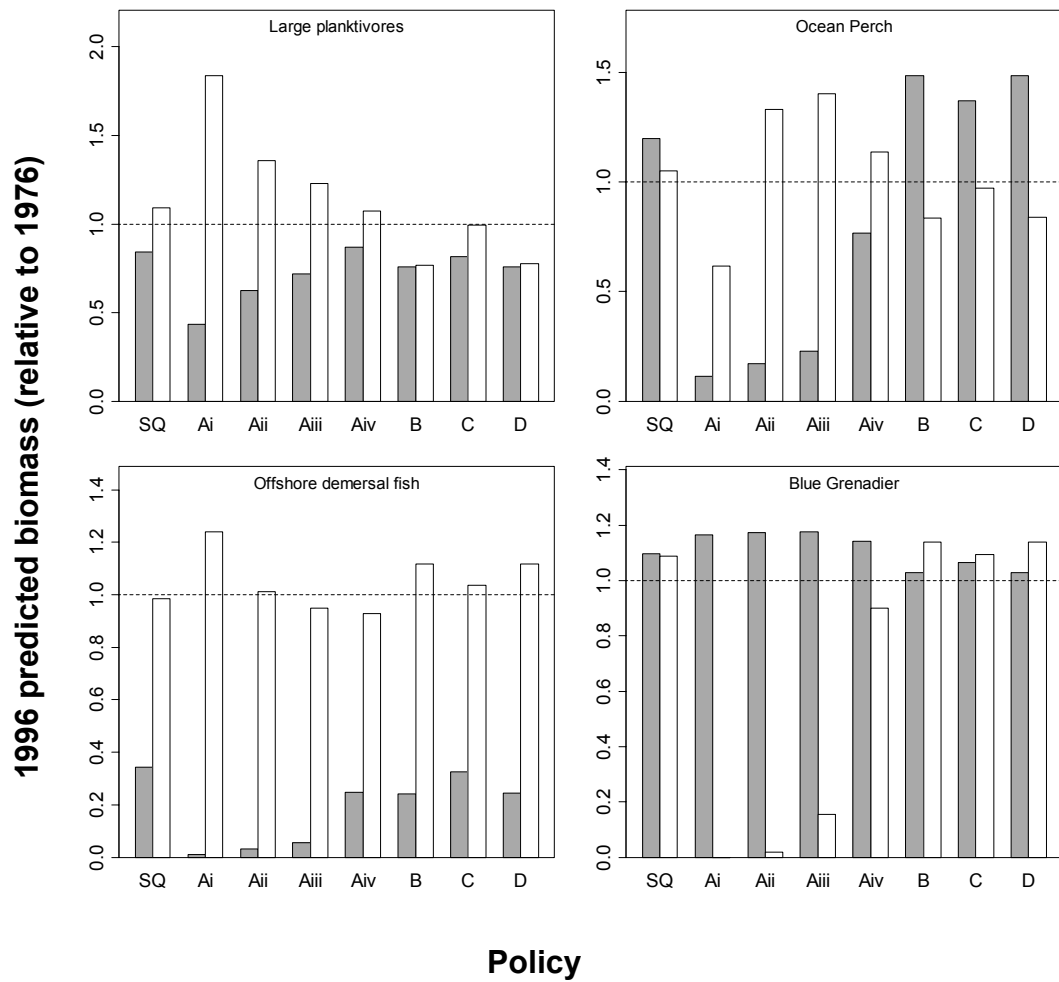
**Figure 6.2b.** Relative biomasses of shark groups predicted by Ecosim (solid line), with the model driven by estimated historical catch rates (Chapter 5, see Appendix 1), compared with relative catch rates (solid circles) observed in the surveys (Graham *et al.* 2001).



**Figure 6.3.** Ecosim predicted biomass ( $\text{t.km}^{-2}$ ) under the eight optimal fishing policies for five coarse functional groups. Omn = omnivorous, pisc = piscivorous.

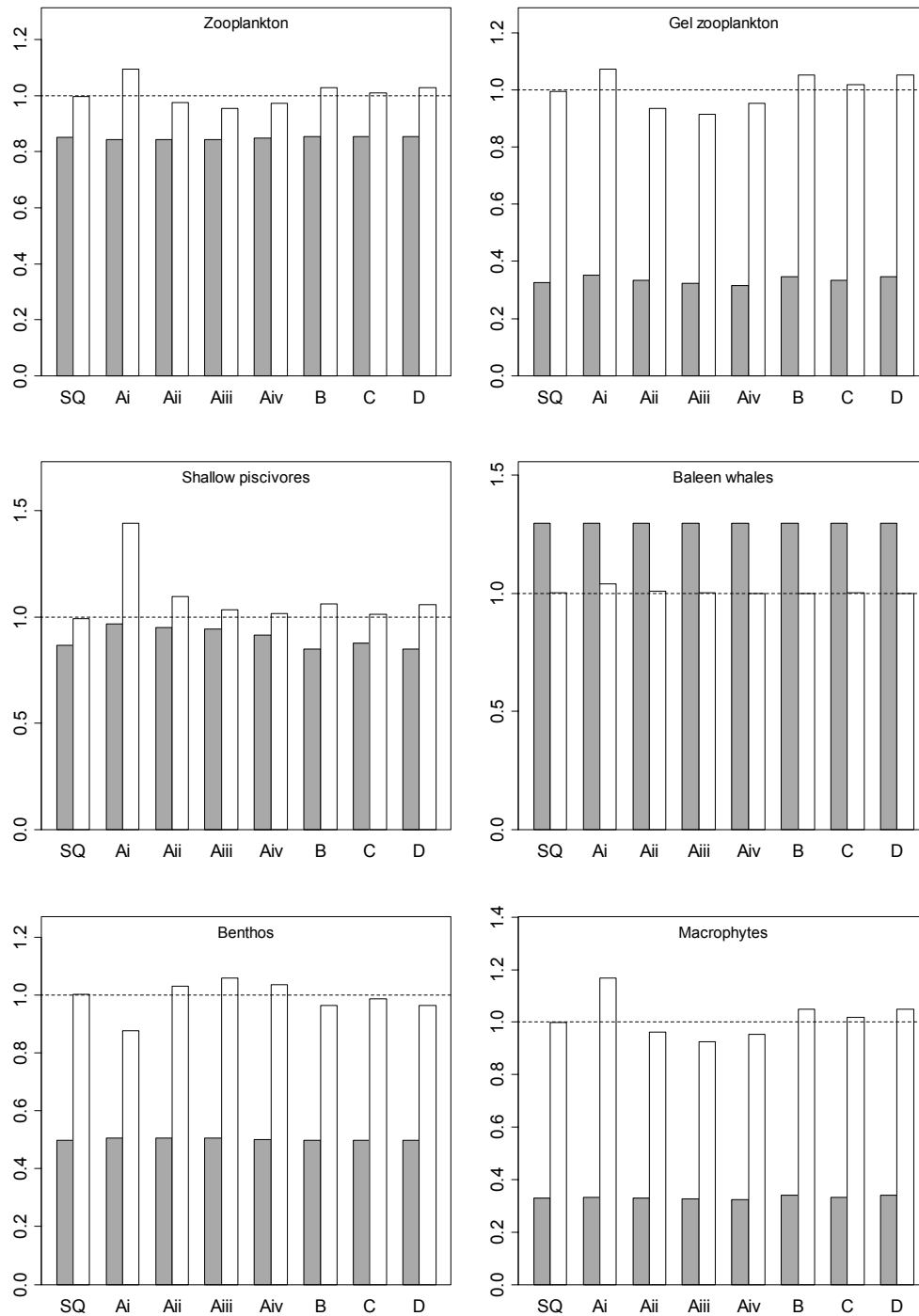


**Figure 6.4.** Relative (to 1976) biomasses of groups, as predicted by Atlantis (grey bars) and Ecosim (white bars), for which qualitative agreement was good under some or all policies (see Table 6.5).



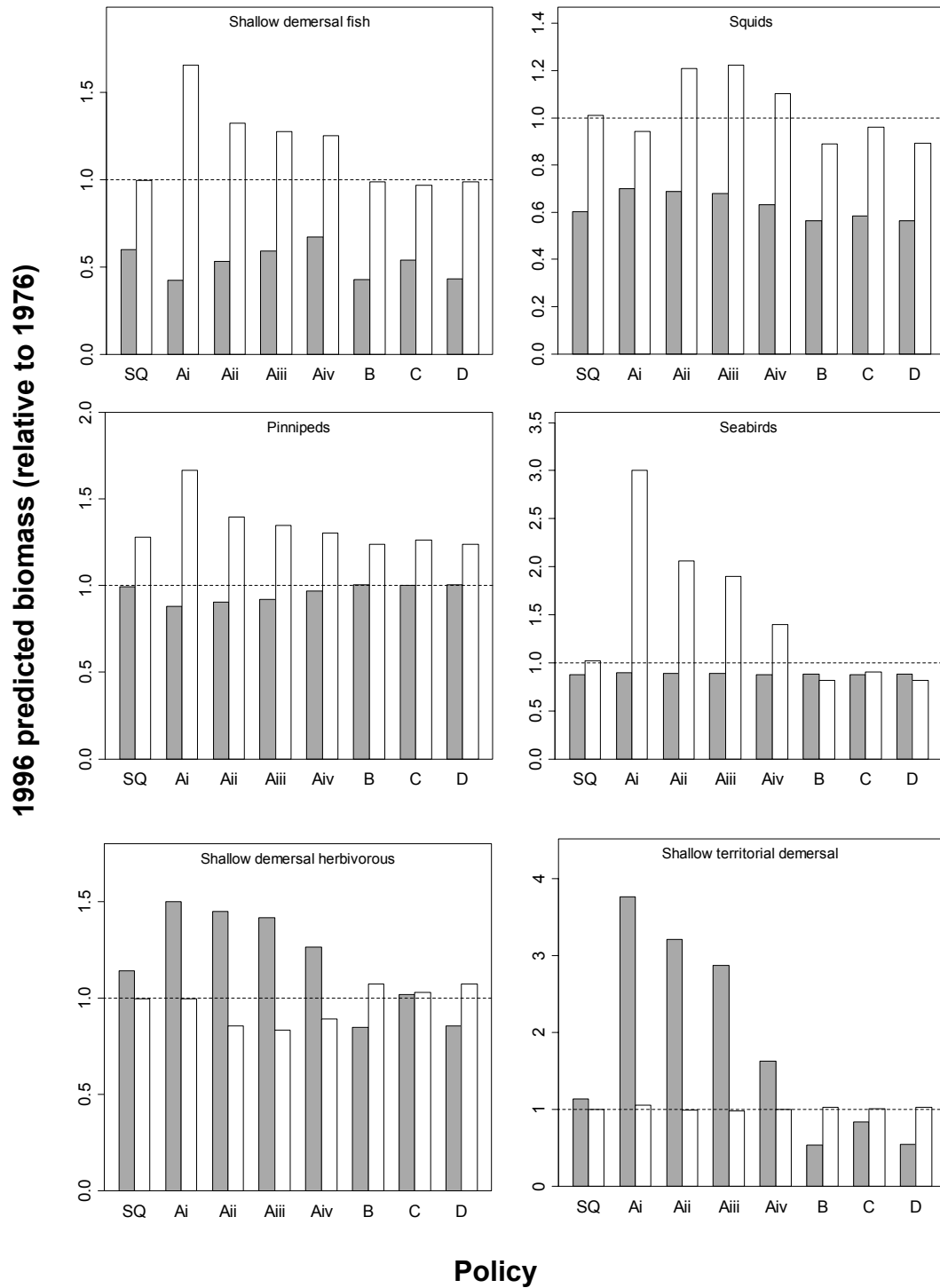
**Figure 6.5.** Relative (to 1976) biomasses of groups, as predicted by Atlantis (grey bars) and Ecosim (white bars), for which qualitative agreement was very poor (see Table 6.5).

1996 predicted biomass (relative to 1976)

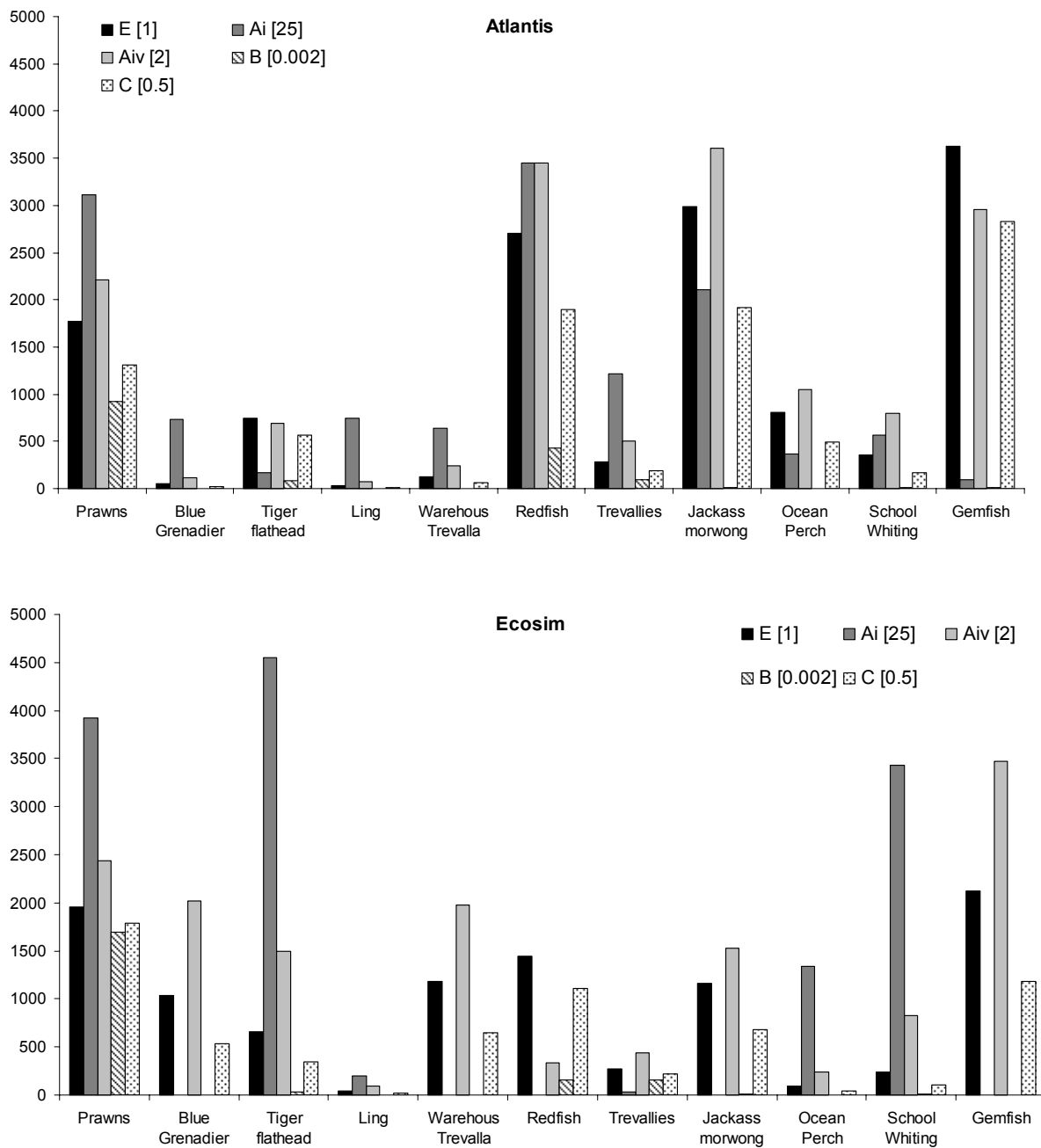


Policy

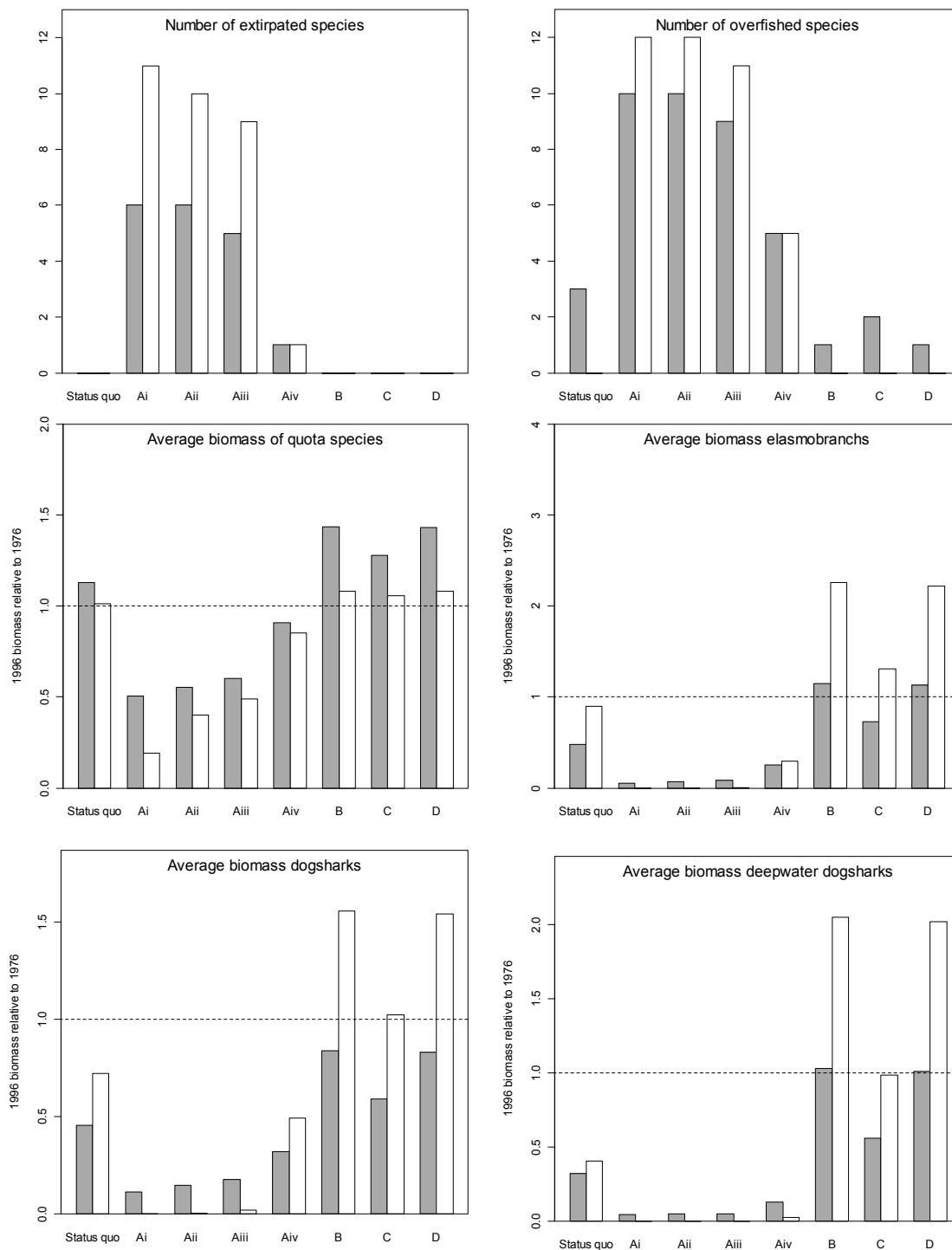
**Figure 6.6.** Relative (to 1976) biomasses of groups, as predicted by Atlantis (grey bars) and Ecosim (white bars), which were insensitive to changes in fishing effort and for which qualitative agreement was poor (see Table 6.5 and text).



**Figure 6.7.** Relative (to 1976) biomasses of groups, as predicted by Atlantis (grey bars) and Ecosim (white bars), which were insensitive to changes in fishing effort and for which qualitative agreement was poor (see Table 6.5 and text).

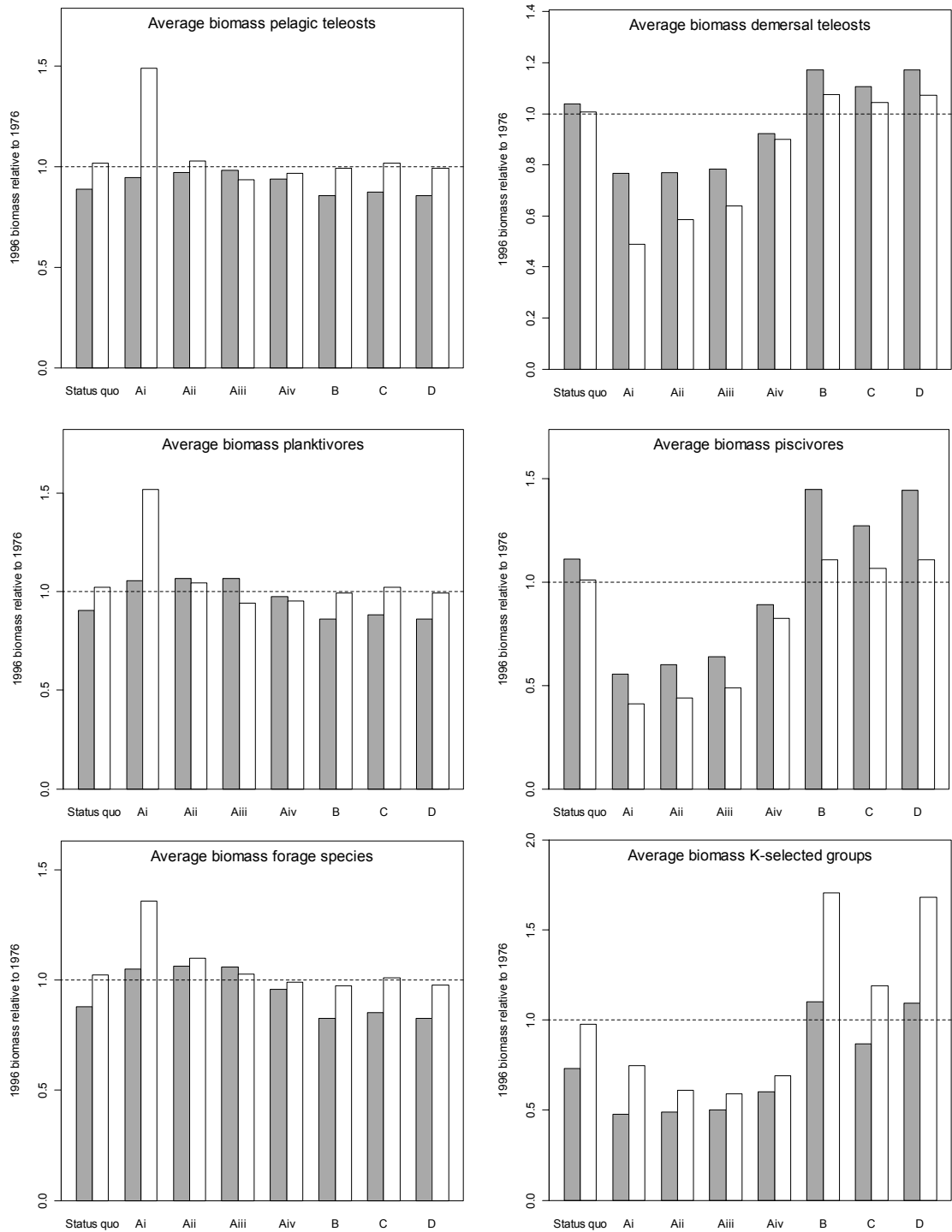


**Figure 6.8.** Predicted catch of key species under five of the eight policies. Policies Aii, Aiii and D are omitted for clarity (results for Policy D were very similar to policy B; results for policies Aii and Aiii were intermediate between results of Ai and Aiv). Note, policy E refers to the *Status quo* policy.

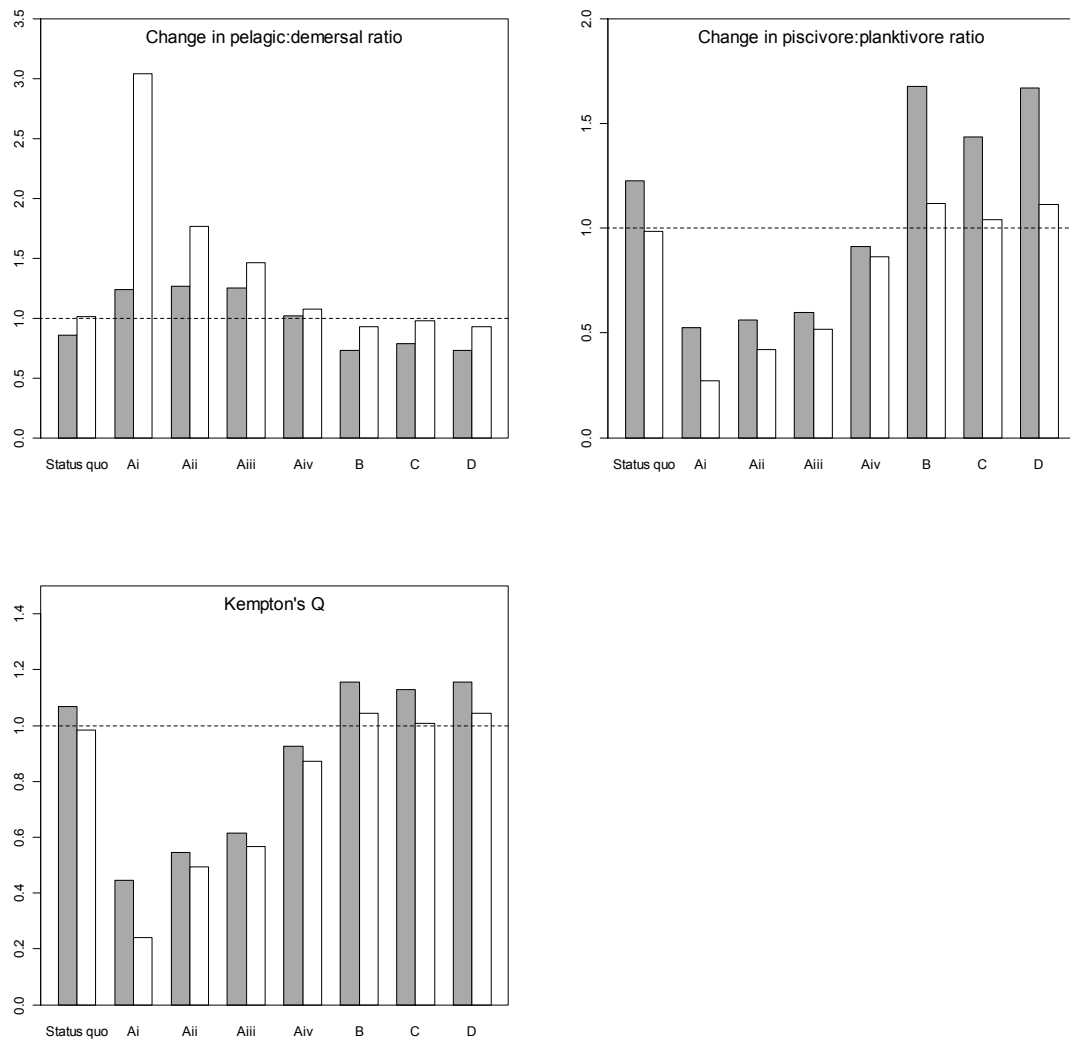


**Figure 6.9.** Indicators based on biomass of key groups of species (see text and Table 6.4a) , as predicted by Atlantis (grey bars) and Ecosim (white bars). Values represent 1996 value of each indicator, relative to its 1976 value.

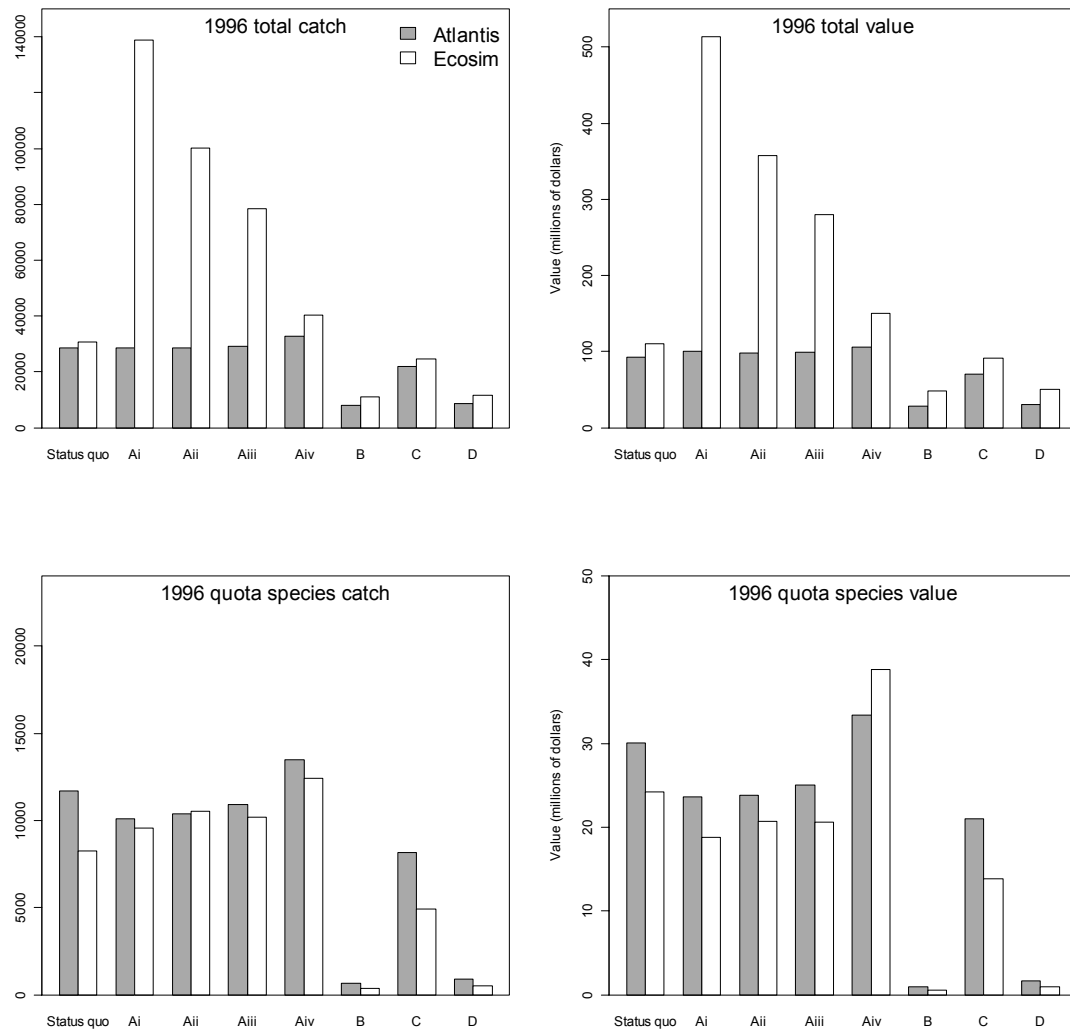




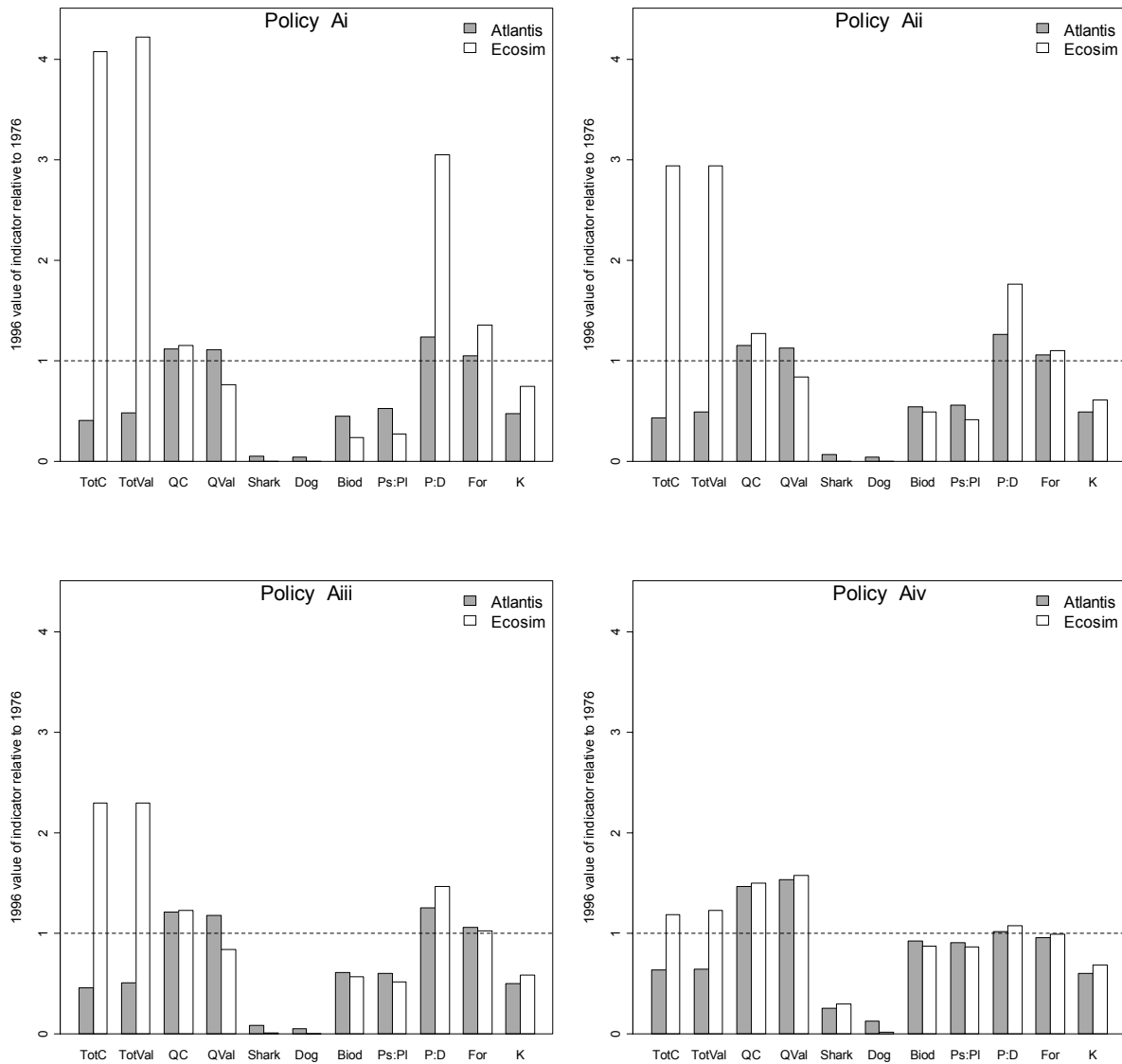
**Figure 6.9 continued.** Indicators based on biomass of key groups of species (see text and Table 6.4a), as predicted by Atlantis (grey bars) and Ecosim (white bars). Values represent 1996 value of each indicator, relative to its 1976 value.



**Figure 6.10.** Indicators measuring biodiversity (Kempton's index; Kempton and Taylor 1976); and the ratios of pelagic to demersal teleosts and piscivorous to planktivorous teleosts, as predicted by Atlantis (grey bars) and Ecosim (white bars).

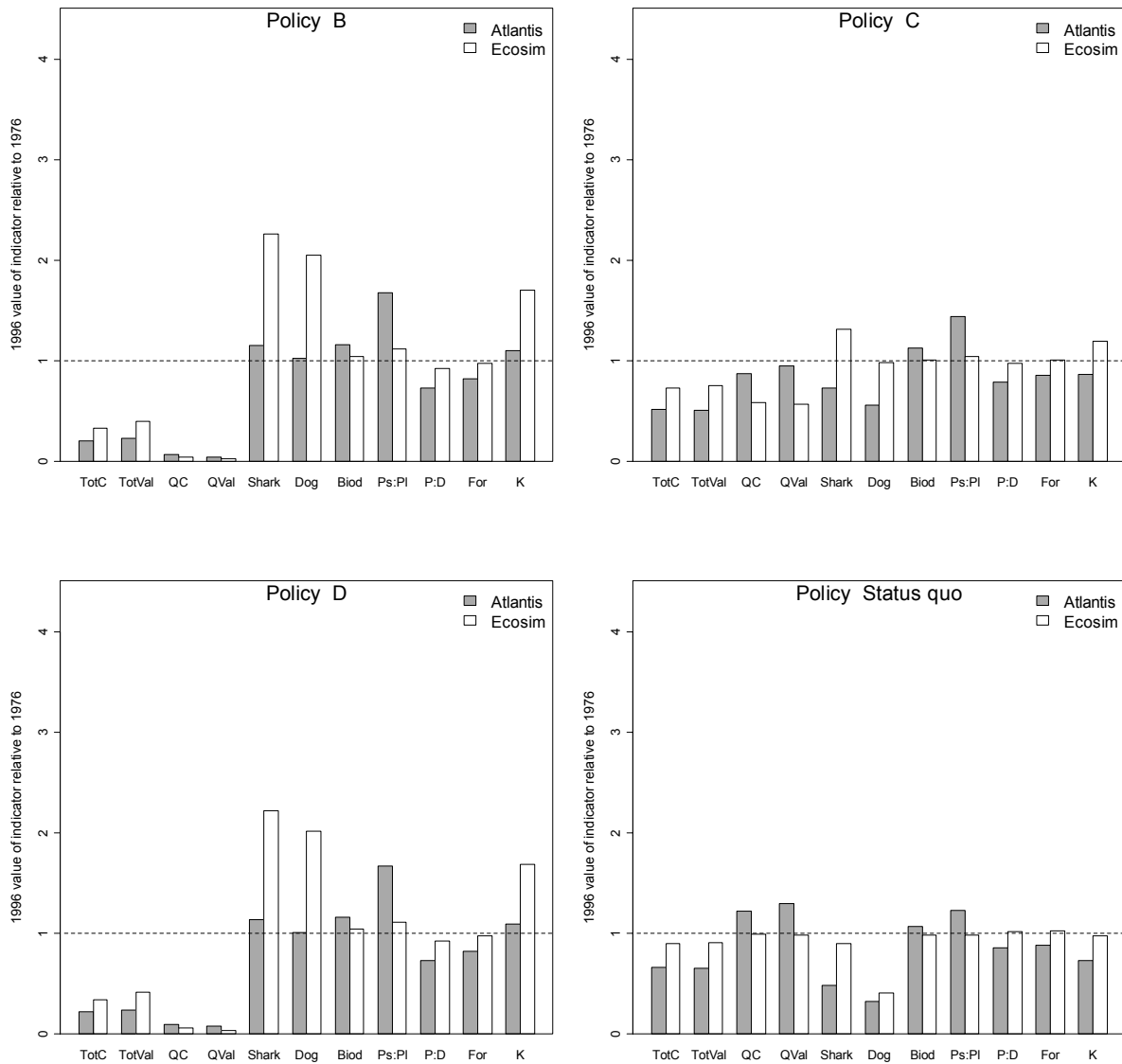


**Figure 6.11.** Indicators based on total catch and value and catch and value of quota species, as predicted by Atlantis (grey bars) and Ecosim (white bars). Absolute predicted 1996 values are shown (see text and Table 6.4b).



**Figure 6.12.** Performance of the eight different policies (see text and Table 6.3) in terms of eleven of the indicators shown in Table 6.4. All indicators are shown as predicted 1996 value relative to 1976 value.

TotC = total catch; TotVal= total value; Shark = average biomass of elasmobranchs; Dog = average biomass of deepwater dogsharks; Biod = Kempton's biodiversity index; Ps:PI = piscivore:planktivore ratio; P:D = pelagic:demersal ratio; For = average biomass of forage species; K = average biomass of K-selected species (see Table 6.4).



**Figure 6.12 continued.**

TotC = total catch; TotVal= total value; Shark = average biomass of elasmobranchs; Dog = average biomass of deepwater dogsharks; Biod = Kempton's biodiversity index; Ps:Pl = piscivore:planktivore ratio; P:D = pelagic:demersal ratio; For = average biomass of forage species; K = average biomass of K-selected species (see Table 6.4).

## **Chapter 7. General discussion: towards ecosystem based fisheries management in New South Wales**

### **Summary**

Since the enactment of the Australian National Strategy for Ecologically Sustainable Development in 1992 and the Commonwealth EPBC Act in 1999, Australian fisheries management agencies have been mandated to ensure that fisheries activities are carried out in a sustainable manner (Fletcher *et al.* 2002; Scandol *et al.* 2005). Traditional definitions of sustainability have tended to focus on single stocks or species, with catch limits determined by estimates of the harvest rate that can be applied sustainably to individual species. However, recent shifts towards EBFM in NSW, Australia and around the world (Garcia and Cochrane 2005) have necessitated consideration of broader definitions of sustainability.

Ecosystem objectives in fisheries management are usually stated in high-level policies and, consequently, are often broadly defined and difficult to incorporate directly into management plans. A recent evaluation of the performance of 33 countries in meeting EBFM criteria found that most countries underperformed, both in terms of policy development and in implementation of EBFM (Pitcher *et al.* in press). This reflects the political and institutional challenges associated with adoption of principles of EBFM as well as uncertainties as to how to proceed with operationalising EBFM (Pitcher *et al.* in press; Hall and Mainprize 2004). Key steps in progress towards implementation of EBFM will be (i) definition of clear management objectives; and (ii) development of qualitative and quantitative metrics that measure the expected benefits, costs, and risks associated with alternative management actions (Murawski 2000; Sainsbury *et al.* 2000). The latter step is proving difficult, as ecosystems contain many data-limited species. There is therefore recognition that EBFM will need to incorporate approaches and frameworks for risk assessment that do not depend on a large amount of data (review by Reynolds *et al.* 2001; Dulvy *et al.* 2004; papers in Kruse *et al.* 2005; this thesis and papers cited therein). The State fisheries of Australia, including those of NSW, are extremely data-limited, with even basic fisheries dependent data missing or unreliable for many species (Hall 2003; Scandol *et al.* 2008; this thesis, Chapter 5). While this situation has improved over the past five years (Scandol *et al.*

2008), there is a current need for tools and approaches that can help managers and scientists think clearly about the steps needed to move towards EBFM.

The concept of “data-limitation” means more than simply not having much data and is probably better thought of as a mismatch between available data and the data requirements of the management strategies being applied (J. Scandol, NSW DPI, pers. comm.). Data-limitation can therefore apply even when there are large datasets but these are not useful for assessing impacts of fishing or policy outcomes. This can be due to data quality issues, lack of information in the data with respect to key variables, or because the data are not relevant to management questions or are not available at appropriate scales for aiding management decisions (Underwood 1998). As policies move towards more reporting requirements for EBFM, fisheries will inevitably become more data-limited. Mace (2001) has warned that there is a limit to the ability of fisheries science institutions to absorb progressively more complex questions. Budget constraints can result in scientists becoming overstretched and, by trying to do too much with too little information, may eventually undermine their own credibility. She poses the question, “is it better to provide weakly supported scientific advice based on inadequate or insufficient data or, at some point, to admit that existing data cannot provide an acceptable foundation for meaningful analyses?” It has therefore been suggested that a solution to the data-limitation problem would be to establish ecosystem-based definitions of overfishing on single species analogues (Murawski 2000; Mace 2001). A problem with this is that broadscale application of single species policies can result in erosion of ecosystem structure (depletion of higher trophic level species) due to overharvest of prey species needed to support the energy needs of higher trophic levels (May *et al.* 1979; Yodzis 1994; Walters *et al.* 2005). Past problems with application of single species approaches should not, however, imply that they cannot play a role in EBFM (Punt and Smith 2001; Daan 2005). Management and conservation concerns will still tend to be driven by concern for individual stocks, and threatened, endangered and protected species will continue to be associated with powerful legislative instruments in many countries. Also, single species assessments that employ tested methods of dealing with uncertainty will still be a core component of fisheries science. Information about individual species is also necessary for construction of multispecies and ecosystem models (Christensen and Walters 2004b). Similarly, status of key species or functional groups (e.g., sharks) may be important for detecting short- and long-term shifts in ecosystem structure (Fulton and Smith 2004; Fulton *et al.* 2005b).

Non-selective multispecies fisheries are problematic for EBFM as they can pose a risk to low productivity species as well as contributing to erosion of ecosystem structure (Pitcher 2000). The trade-off between the catch of productive commercial species and the abundance of low-productivity, low-value species is unavoidable in most, if not all, multispecies fisheries. Society's interests are measured by a broad range of objectives that includes profitability of primary industries and maintenance of fresh seafood as well as conservation of vulnerable species. Different stakeholders value these objectives differently and good governance, therefore, requires evaluation of costs and benefits of different management strategies, in terms meeting a suite of management objectives, so that acceptable compromises can be negotiated (Hilborn 2007a,b). In jurisdictions where protection of vulnerable species is mandated, estimates of the range of harvest rates that can be considered sustainable, even if species are technically overfished, is an important part of the evaluation of trade-offs.

Following the example of previous authors (Schnute and Kronlund 1996; Schnute and Richards 1998) this thesis has presented an analytical relationship between  $\alpha$ , a key recruitment productivity parameter, and  $U_{MSY}$  (Chapter 2). Advantages of the model include: (i) it enables direct estimation of parameters of principle management interest using Bayesian or likelihood methods (McAllister and Ianelli 1997; Punt and Hilborn 1997; Chen *et al.* 2003); (ii) it is flexible to a very wide range of assumptions about growth, survival, maturity and selectivity; and (iii) it provides a means of efficiently quantifying the interaction among selectivity and life history parameters, density dependence in recruitment and maximum sustainable harvest rate for any given stock. Direct estimation of management parameters has a number of advantages, including greater computing efficiency (avoiding the need to numerically search for  $U_{MSY}$ ); improved statistical properties (there is less confounding between the scale and productivity parameters, discussed in detail in Schnute and Kronlund 1996 and Martell *et al.* 2008); and improved communication between managers and scientists in presentation of results and setting of priors (Schnute and Kronlund 1996). In addition, steady-state application of the model may be useful for efficiently learning about factors that contribute to  $U_{MSY}$  for data-limited species.

In Chapter 3, the above model was used to calculate  $U_{MSY}$  for 54 Atlantic fish stocks, for which previous authors had estimated recruitment productivity parameters (Goodwin *et al.* 2006).



Results clearly showed that life history and selectivity parameters influence the relationship between density dependence in recruitment (measured by the compensation ratio, CR) and  $U_{MSY}$ . In biological terms, this means that  $U_{MSY}$  is determined by a suite of attributes (i.e., not just recruitment), and some of these attributes provide a stronger constraint on  $U_{MSY}$  than others. In fact, for some long-lived species,  $U_{MSY}$  was so strongly constrained by growth and mortality that increasing the hypothesised magnitude of density dependence in recruitment had almost no influence on  $U_{MSY}$ . This has important implications, as it is sometimes erroneously assumed that inferences about sustainable harvest rates can be drawn from assumptions about the magnitude of density dependence in recruitment, i.e., species with stronger density dependence can sustain greater harvest rates. This illustrates the problem of communicating the meaning of CR (and other commonly-estimated recruitment parameters such as steepness) to managers and stakeholders. The methodology presented here provides a simple means of graphically separating out the effects of life history, selectivity and CR (or other recruitment parameters) on  $U_{MSY}$ , which could be very useful for facilitating communication between scientists and managers. For data-limited species (i.e., those for which data are insufficient to estimate recruitment parameters), the graphs presented in Chapter 3 also aid identification of stocks where changes to the selectivity schedule could be of benefit for reducing the risk of growth overfishing; those for which it would be less effective; and those for which the magnitude of recruitment compensation has very little effect on  $U_{MSY}$  (implying that investing resources in estimating recruitment parameters may be assigned lower priority).

Chapter 4 developed this idea further for deepwater dogsharks, which are known to have extremely low fecundity (Daley *et al.* 2002), and to have been greatly depleted on the continental slope of NSW (Graham *et al.* 2001). A motivation for studying these species was that the low productivity of these sharks, suggested by the steep decline in abundance and low fecundity, made them candidates as ‘weak stocks’ (*sensu* Hilborn *et al.* 2004) and therefore useful for illustrating differential productivity trade-offs in the offshore trawl fishery. Since work began on this project, however, three species in the genus *Centrophorus* have been given Priority Assessment Listing under the Commonwealth EPBC Act, which could see them listed as threatened species by 2011 (DEWHA 2008). This would necessitate drafting of a comprehensive management plan, as has already been done for orange roughy – currently the only commercially-fished species in Australia that has been listed as threatened (AFMA 2006). There

is therefore a need to assess current and historical impacts of fisheries on these species and evaluate the risks posed by continued fishing mortality. Chapter 4 showed that the maximum possible hypothesis that could be assumed for  $U_{MSY}$  for sharks with life history traits similar to those of *Centrophorus* and other Australian deepwater dogsharks to be very low ( $< 0.1$ ), under a range of reasonable assumptions about age at first harvest and accounting for uncertainty in key life history parameters. An alternative demographic approach (McAllister *et al.* 2001) suggested that the intrinsic rate of population growth for these sharks (which represents  $U_{Max}$ , the long-term harvest rate that would theoretically drive the population to extinction) was also very low ( $< 0.1$  for *Centrophorus* and  $< 0.2$  for all species).

Because of the low uncertainty in productivity of dogsharks, the greatest uncertainty for risk assessment of these populations, therefore, lies with current and historical harvest rates relative to  $U_{MSY}$  and  $U_{Max}$  (i.e., whether these populations are currently or have historically been overfished). Chapter 5 presented a preliminary stock assessment for sharks in the genus *Centrophorus*, incorporating the findings of the previous chapter. Fisheries data available for this task were extremely poor quality, necessitating reconstruction of historical catch and effort data before the assessment could be done. Many of the assumptions included in the reconstruction, and in the model, were subjective and, while they were informed by discussion with Australian experts, a much more thorough review will be required and results should be viewed very cautiously. However, results present a step forward in assessment of *Centrophorus* in Australia and demonstrate a transparent methodology that is amenable to expert review and improvement and possible extension to full Bayesian analysis. Results also demonstrate that assessment of sharks with such extreme life history strategies may be possible, despite lack of stock-recruitment data, due to the strong constraints on productivity implied by life history attributes.

Preliminary results suggested that these sharks have been overfished in southeastern Australia. Estimates of historical harvest rates were robust to very large uncertainty in historical catches and fishing effort, due to the severe reduction in abundance indicated by the survey data. It must be emphasised, however, that highly-aggregated and error-filled fishery-dependent datasets make it almost impossible to perform completely defensible assessments of *Centrophorus* in southeastern Australia. This is currently hindering the assessment process needed to determine whether they should be added to the threatened species list (R. Daley, CSIRO, pers. comm.),

which would in turn afford them a detailed management plan under the EPBC Act. Problems such as this are not limited to NSW and have been raised by numerous authors as a problem in shark fisheries throughout the world, especially when sharks are taken as bycatch (Bonfil 1994; Walker 1998; Musick *et al.* 2000; Stevens *et al.* 2000; Dulvy *et al.* 2000; Barker and Schluessel 2004; Roberts 2005). While this may reflect previous public values and perceptions of sharks, it is no longer acceptable in Australia, where sustainability objectives are stated in fisheries and environmental legislation at every governmental level. While limited resources will continue to preclude fishery-independent surveys for most species (Scandol 2004; Smith *et al.* 2007) systemic problems with identification, reporting and data-entry for shark landings should be addressed as soon as possible to enable public discussion of trade-offs relating to sharks. Unfortunately, many species of shark in southeastern Australia may already have been overfished (Graham *et al.* 2001) and recovery plans, if mandated (e.g., under the EPBC Act), may necessitate severe reductions in fishing effort at a time when the profitability of the fishery is already low (Grieve and Richardson 2001), making trade-offs between economic and conservation objectives even more acute.

Trade-offs arising from differential productivity in the offshore trawl fishery and alternative management objectives were explored in Chapter 6, in which two structurally distinct ecosystem models were presented, representing the continental shelf and slope of NSW during development of the trawl fishery on the slope. Results suggested that even if management plans had been implemented during development of the fishery there would still have been strong trade-offs between economic and ecological objectives, especially those aimed at prevention of overfishing of low productivity dogsharks or biomass of long-lived species. Comparison of the two models highlighted large differences in predictions for individual functional groups arising from structural assumptions. However, despite large differences in predictions for individual groups, management advice relating to trade-offs and performance of alternative policy objectives was generally robust. This supports the findings of previous authors that, while ecosystem models are unsuited for providing tactical advice (Plagányi 2007), they can be very useful for strategic consideration of broader issues such as possible broad impacts of fishing on ecosystems or exploration of ecosystem impacts of different management policies and evaluation of trade-offs.

Results clearly showed that stating “sustainability” as a management objective is imprecise, as it can justifiably encompass strategies at both ends of a trade-off continuum. Scientists can assist managers and policy-makers by: i) using simulation models to help reduce some of the ambiguity inherent in stated policy-objectives; ii) by highlighting possible unexpected or counter-intuitive or unexpected implications of certain policy objectives; iii) exposing conflicting objectives by presenting results in terms of trade-offs; and iv) accounting for uncertainty (including structural uncertainty) wherever possible (Ludwig *et al.* 1993; Walters and Martell 2004). Comparison of multiple models of the same system can help to identify which results are most sensitive to model specification. Most ecosystems contain very low productivity species such as dogsharks that are vulnerable to fishing gear. If definitions of ‘ecosystem overfishing’ (Murawski 2000) are required, they need to be clearly articulated – i.e., acceptable levels of overfishing may need to be defined for some species (Hilborn 2007a). It is suggested here that terms such as ecosystem overfishing may not be useful, as it is virtually impossible to prevent overfishing of all species in non-selective fisheries. Even if the meaning of the term is clearly articulated in terms of how overfishing is defined or which species it includes, it may still be misleading to the public. It is therefore better to focus discussion on trade-offs, which can be presented in terms of easily-understood indices that have been shown to capture broadscale ecosystem changes.

### **Further comments: progressing towards EBFM in NSW**

This thesis has developed and explored a number of modelling tools designed to help fishery managers and scientists think more clearly about issues relating to EBFM, particularly relating to estimation of productivity and trade-offs associated with differential productivity among species caught together in multispecies fisheries. The work presented here represents only a very small component of the range of issues that will need to be considered as fisheries management progresses towards operational EBFM in NSW and Australia. Some other issues worthy of consideration are discussed below.

There were a number of challenges encountered during this project, mostly related to availability and accessibility of reliable fishery dependent data, which prevented specific analysis of the State-managed fisheries in NSW (although it is noted that when the offshore trawl fishery was

developing and expanding it was under State control). It is hoped, however, that the issues raised here and the suggested modelling approaches presented in this thesis will be helpful for implementation of EBFM in both State and Commonwealth managed fisheries in Australia and elsewhere.

The ecosystem models presented here only considered management of fishing effort as a means of controlling fishing mortality. More refined measures for adjusting selectivity in fisheries, through gear modifications, spatial management and behaviour of fishing fleets, can be very effective for limiting fishing mortality. Approaches for adjusting species selectivity were covered in Chapters 3 and 4 and are not discussed again, except to note that many recent solutions to the problem of bycatch have been developed as a result of partnerships between industry, government and scientists (e.g., Beutel *et al.* 2006) or through provision of appropriate disincentives to discard (Hall and Mainprize 2005; Gilman *et al.* 2007). Minimum legal length (MLL) is one of the most common means of preventing growth overfishing in fisheries and is strongly regulated in all Australian fisheries across all gears, commercial and recreational (e.g., NSW Fisheries 2001). An avenue for future research is the estimation of optimum multi-species MLLs, accounting for risks of recruitment and growth overfishing across a range of species. To this end, a universal 10 cm minimum size limit has been implemented in regulation of international trade of seahorses (*Hippocampus* spp.) under the Convention on International Trade in Endangered Species (CITES) of Wild Fauna and Flora (Foster and Vincent 2005). It should be noted, however, that MLLs refer to landings, not catch (i.e., undersize fish must be released). Therefore, MLLs must be accompanied by gear modifications that allow smaller fish to escape if they are to be effective. In some of the shallower inshore fisheries of NSW, e.g., gillnet fisheries, a high percentage of undersized individuals are released alive (Gray 2002). This is uncommon in trawl fisheries or fisheries operating in deep water, however, and MLLs are therefore not effective at controlling fishing mortality. Multispecies versions of the models presented in this thesis (e.g., Chapter 3) could be useful for identification of an optimal multispecies size at first capture that could meet a range of ecological and economic objectives. There is interest in evaluation of costs and benefits of this approach for fish trap fisheries in NSW, where increasing the size of the escape mesh could help reduce growth overfishing of snapper (*Pagrus auratus*) but may also facilitate the escape of legally-sized individuals of other species (J. Stewart, NSW DPI, pers. comm.).

Marine protected areas (MPAs) are considered by many to be one of the main tools limiting fishing mortality in data-limited fisheries (reviewed by Dugan and Davis 1993; Allison *et al.* 1998; Johannes 1998; Ward *et al.* 2001; Browman and Stergiou 2004), mainly because protected areas are thought to be able to act as precautionary buffers against management miscalculations and unforeseen events (Allison *et al.* 1998). Australia is committed to implementing networks of MPAs at both the Commonwealth and State level of government (see [www.environment.gov.au/coasts/mpa/index.html](http://www.environment.gov.au/coasts/mpa/index.html) and [www.mpa.nsw.gov.au/research.html](http://www.mpa.nsw.gov.au/research.html)). Three fishery closures have also recently been implemented specifically for protection of deepwater dogsharks (R. Daley, CSIRO, pers. comm.). It should be noted, however, that the success of MPAs as a harvest control measure depends upon spatial distribution and movement of fish populations at different phases of their life (Gerber and Heppell 2004; Gerber *et al.* 2005). MPAs are less likely to be useful if their creation is not accompanied by an associated decrease in fishing effort outside the MPA (Allison *et al.* 1998; Gu  nette *et al.* 2000; Hilborn *et al.* 2006). If closure to fishing is not complete (e.g., if certain sectors are still allowed to fish inside the MPA, or if poaching occurs), then fishing fleet dynamics will also be an important consideration in determining the efficacy of the MPA.

Fishing fleet dynamics are rarely considered but are very important in the outcome of management strategies (Hilborn 1985b). For example, increases in fish abundance, due to release from commercial fishing pressure, are likely to attract more angling effort when recreational fisheries are also present, thus negating any potential increase in biomass. This effect has been observed following commercial fishing closures in Florida (Walters and Martell 2004) and in stocked rainbow trout lakes in British Columbia (Cox 2000). These arguments also apply to the selectivity-adjustments described above, i.e., benefits in the form of larger fish, arising from control of selectivity in commercial fisheries, may be ‘mopped up’ by recreational anglers before they are realised by commercial fishers, who may have foregone profits in the process. Like many jurisdictions around the world, recreational fisheries in NSW form a very large (Henry and Lyle 2003) open access fishery, which operates alongside highly regulated commercial fisheries. In situations like this, it will be difficult to gain support from the fishing industry for proposed changes to management, even if the changes are intended to provide long-term economic and ecological benefits (Hilborn 2000). Implementing management approaches that account for

behaviour and incentives of fishers will therefore be an important component of EBFM, both in terms of gaining support from the fishing industry and enforcement of regulations (Hilborn 2004; 2007b,c; Grafton *et al.* 2006). This may involve a shift to smaller, more profitable fisheries with guarantee of access rights and long-term benefit from imposed catch restrictions (Hilborn 2007a,b,c). This rights-based approach has been applied successfully in some molluscan fisheries in Chile (Castilla 1994; 1997) and Argentina (Parma *et al.* 2003), but may not be so easily applied in the diverse multi-species inshore fisheries in NSW, especially with the presence of large recreational fisheries, where recreational catches of some species may exceed commercial catches (West and Gordon 1994; Henry and Lyle 2003).

Opportunities should also be taken to learn more about processes operating within the ecosystem. The primary way in which scientists gather information about processes in natural systems has traditionally been through either measurement or manipulative experimentation (e.g., Underwood 1990; 1997). Unfortunately, however, there is often a mismatch between the type or scale of information provided by ecological research and that needed for effective management. Most important ecological policy issues involve coarse scales, while most scientific information is finely-scaled and narrowly focused and therefore only indirectly relevant to many ecological policy questions (Peters 1991; Underwood 1998; Lackey 2001). Walters and Holling (1990) partition scientific approaches to advising management into two types: i) the ‘science of parts’ (reductionist experimental science where the focus is narrow enough to develop precise, falsifiable hypotheses with predefined acceptable levels of uncertainty); and ii) the ‘science of the integration of parts’, where the results of the first type are used, but gaps are identified, alternatives are invented and the consequences of action are evaluated against planned and unplanned disturbances of the system (i.e., ‘adaptive management’; Walters 1986; Walters and Holling 1990). In adaptive management, large-scale system perturbations are deliberately caused by different managerial actions and treated as manipulative experiments with uncertain outcomes. Each decision is thought of as having a “dual effect”: i) it immediately affects the system; and ii) it impacts in the longer term on the amount of information about the system that future decision-makers will have (Walters 1986).

Adaptive management can be ‘active’, where historical data are used to devise a number of hypotheses about system process and the system is deliberately managed and monitored in such

a way as to be able to distinguish among the competing hypotheses (e.g., Sainsbury 1991; Sainsbury *et al.* 1997). While it may be politically difficult to implement active adaptive management, opportunities for adaptive learning present themselves in the form of large-scale decisions that are made for other reasons (i.e., “passive” adaptive management). The challenge is then for scientists and managers to devise monitoring programmes that will enable managers to determine whether the working hypothesis is likely. Unfortunately, outcomes of managerial decisions are often not monitored or evaluated (Buckley 1991; Underwood 1998). The reasons for this are varied but are usually linked to the costs of monitoring and, more importantly, to failure to articulate clear hypotheses about how the system is expected to respond. While it is relatively easy to design hypotheses about system dynamics, it is not so easy to generate testable hypotheses that are relevant to potentially large or sudden changes in the structure of managed ecosystems. By focusing on the causes of large changes, however, single species and ecosystem models may be useful for evaluation of existing process knowledge in order to screen the credible hypotheses and identify where to concentrate limited resources (Walters and Holling 1990). Subjects that may be worthy of investigation in NSW include: effects of fishing small pelagic species on the abundance or catch of piscivores; effects of restoration of highly piscivorous fish on other components of the ecosystem; effects of MPAs; and potential costs and benefits of directly monitoring recreational and commercial fishing mortality rates.

Progress towards EBFM in Australia, NSW and around the world will be gradual process as management institutions and fishing industries absorb an ever-growing list of demands from law and policy-makers. At present, many fishery managers feel overwhelmed by demands of EBFM superimposed on their daily management duties and are uncertain as to how EBFM should be implemented. Pragmatic solutions will be found by breaking the problem into tractable components that can be measured and tracked as progress is made. One of the most important issues for EBFM is acknowledgement that many of the policy objectives commonly stated for EBFM are in conflict and cannot be met simultaneously. Identification of resulting trade-offs will enable the metrics needed to evaluate them to be clearly articulated. This in turn will facilitate negotiation of trade-offs, either through formal analytical methods, the consultative process or legal means. Continued development of risk assessment approaches and management strategies that are flexible to new information will also be important (Ludwig *et al.* 1993; Hilborn *et al.* 2004; Smith *et al.* 2007).



There have been a large number of positive developments in NSW since this project began. These include significant improvements in storage and accessibility of fishery dependent data (Scandol 2004) and identification of reliable short CPUE series for most species (Scandol *et al.* 2008). Most significant is probably the development of a consistent risk assessment framework for all harvested species and identification of species for which data collection or further analysis of existing data should be a priority (Astles *et al.* 2006; Scandol *et al.* 2008). The number of species that have 'Uncertain' or 'Undefined' status has steadily fallen over the past five years (although more than 50% of species, including most elasmobranchs, still have this status). At the Commonwealth level, a hierarchical framework for ecological risk assessment has recently been developed that takes level of risk and data availability into account in determining the appropriate method of assessment and management (Hobday *et al.* 2006; Smith *et al.* 2007). The approach extends to a much broader range of species than has previously been assessed, including non-target species, and represents a transparent methodology for identifying species for which more data or management attention is required, appropriate to the risk of unsustainable harvesting from current management strategies. Recent collaborative projects between NSW DPI and CSIRO (Chapter 6; Savina *et al.* 2008; Hayes *et al.* 2007) suggest the possible extension of some of these approaches to the State fisheries in the future.

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## Appendix A to Chapter 2. Derivation of $\alpha$ from $U_{MSY}$

For a given selectivity schedule, equilibrium yield,  $Y$ , for any long-term fixed exploitation rate,  $U$ , is predicted to be:

$$(2A.1) \quad Y = UR\varphi_{VB},$$

where recruits,  $R$ , are defined as fish of age 1 and  $\varphi_{VB}$  is equilibrium vulnerable biomass per recruit (equation 2.5). Substituting the Beverton and Holt recruitment function (equation 2.4) into equation 2A.1 and rearranging gives

$$(2A.2) \quad Y = \frac{\alpha U \varphi_{VB}}{\beta} - \frac{U \varphi_{VB}}{\beta \varphi_E}.$$

There are actually three functions of  $U$  contained in equation 2A.2 because  $l_a$  (a component of the functions  $\varphi_{VB}$  and  $\varphi_E$ ) is also a function of  $U$ .  $Y$  is a convex function of  $U$ , with  $Y=0$  at either  $U=0$  or  $U_{\text{extinction}}$ , with maximum  $Y$  occurring between these at  $U_{MSY}$ . Solving  $\frac{\partial Y}{\partial U} = 0$  for  $U$  therefore gives the value of  $U$  that maximises the function (i.e.,  $U_{MSY}$ ).

Differentiating  $Y$  with respect to  $U$  in equation 2A.2, gives

$$(2A.3) \quad \frac{\partial Y}{\partial U} = \frac{\alpha \varphi_{VB}}{\beta} + \frac{\alpha U}{\beta} \left( \frac{\partial \varphi_{VB}}{\partial U} \right) - \frac{\varphi_{VB} \varphi_E + U \varphi_E \left( \frac{\partial \varphi_{VB}}{\partial U} \right) - U \varphi_{VB} \left( \frac{\partial \varphi_E}{\partial U} \right)}{\beta \varphi_E^2}.$$

Setting  $\frac{\partial Y}{\partial U} = 0$ , and solving for  $U_{MSY}$ , gives

$$(2A.4) \quad U_{MSY} = \frac{1 - \alpha \varphi_E}{\frac{\alpha \varphi_E - 1}{\varphi_{VB}} \left( \frac{\partial \varphi_{VB}}{\partial U_{MSY}} \right) + \frac{1}{\varphi_E} \left( \frac{\partial \varphi_E}{\partial U_{MSY}} \right)}$$

with  $\varphi_E$  and  $\varphi_{VB}$  evaluated at  $U_{MSY}$ . Note that the stock-recruitment scalar,  $\beta$ , is absent from equation 2A.4, as  $U_{MSY}$  is independent of the units used to count the population.

By setting:  $k_1 = \left( \frac{\partial \varphi_E}{\partial U_{MSY}} \right) \varphi_E^{-1}$  and  $k_2 = \left( \frac{\partial \varphi_{VB}}{\partial U_{MSY}} \right) \varphi_{VB}^{-1}$ , equation 2A.4 can be expressed

$$(2A.5) \quad U_{MSY} = \frac{1 - \alpha \varphi_E}{k_1 + k_2 (\alpha \varphi_E - 1)}$$

and

$$(2A.6) \quad \alpha = \frac{1 - k_1 U_{MSY} + k_2 U_{MSY}}{\varphi_E (1 + k_2 U_{MSY})}$$

$\frac{\partial \varphi_E}{\partial U_{MSY}}$  and  $\frac{\partial \varphi_{VB}}{\partial U_{MSY}}$  can be solved analytically as recursive functions of  $\varphi_E$  and  $\varphi_{VB}$  in the

following manner. Equation 2.5 expressed  $\varphi_{VB}$  as the sum of the product of survivorship to age ( $l_a$ ), vulnerability at age ( $v_a$ ) and weight-at-age ( $w_a$ ). Expanding equation 2.5 gives

$$(2A.7) \quad \frac{\partial \varphi_{VB}}{\partial U_{MSY}} = \frac{\partial \ell_1 v_1 w_1}{\partial U_{MSY}} + \frac{\partial \ell_2 v_2 w_2}{\partial U_{MSY}} + \frac{\partial \ell_3 v_3 w_3}{\partial U_{MSY}} + \dots + \frac{\partial \ell_\infty v_\infty w_\infty}{\partial U_{MSY}}$$

Assuming that mean weight-at-age is independent of harvest rate, then the  $v$  and  $w$  terms factor out of the derivatives. Because  $l_1$  (survivorship at age 1) is, by definition, 1, its derivative with respect to  $U_{MSY}$  is zero so the first term disappears. Therefore,

$$(2A.8) \quad \frac{\partial \varphi_{VB}}{\partial U_{MSY}} = \sum_a^\infty v_a w_a \frac{\partial \ell_a}{\partial U_{msy}}$$

$\frac{\partial \ell_a}{\partial U_{MSY}}$  is then easily obtained, i.e.,  $\ell_a = \ell_{a-1} s_{a-1\_fished}$ , where  $s_{a-1\_fished}$  is given by

$s_{a-1}(1 - v_{a-1}U)$  with  $U$  set to  $U_{MSY}$ . The derivative of  $s_{a-1\_fished}$  with respect to  $U_{MSY}$  is simply  $(-s_{a-1}v_{a-1})$  and, therefore,

$$(2A.9) \quad \frac{\partial \ell_a}{\partial U_{MSY}} = s_{a-1}(1 - v_{a-1}U_{MSY}) \left( \frac{\partial \ell_{a-1}}{\partial U_{MSY}} \right) - \ell_{a-1} s_{a-1} v_{a-1}$$

Since  $\frac{\partial \ell_1}{\partial U_{MSY}}$  is by definition zero, equation 2A.9 can be solved recursively and substituted into

equation 2A.8.  $\frac{\partial \varphi_E}{\partial U_{MSY}}$  is solved in exactly the same way, except that  $f_a$  is used instead of  $v_a w_a$ .

The parameters  $k_1$  and  $k_2$  can now be solved and substituted into equation 2A.6 to give a function expressing  $\alpha$  in terms of a leading productivity parameter,  $U_{MSY}$ . The resulting formula can be easily implemented in a spreadsheet or any appropriate programming language. The derivation can be checked numerically by running the model under a range of constant harvest rates and checking that the harvest rate that produces maximum long term yield is the same as the leading  $U_{MSY}$ .

Note that, if desired, equations 2.3 and 2A.9 can easily be modified to include a plus group (i.e., individuals of age  $a_{max}$  and older). For  $a = a_{max}$ , survivorship would be given by

$\ell_a = \frac{\ell_{a-1} s_{a-1\_fished}}{1 - s_{a\_fished}}$ . For  $a = a_{max}$ ,  $\frac{\partial \ell_a}{\partial U_{MSY}}$  would then be given by

$$(2A.10) \quad \frac{\partial \ell_a}{\partial U_{MSY}} = \frac{(1 - s_{a\_fished}) \left( s_{a-1}(1 - v_{a-1}U_{MSY}) \left( \frac{\partial \ell_{a-1}}{\partial U_{MSY}} \right) - \ell_{a-1} s_{a-1} v_{a-1} \right) - s_a v_a s_{a-1\_fished} \ell_{a-1}}{(1 - s_{a\_fished})^2}.$$



## Appendix B to Chapter 2. Growth, maturity and gear selectivity functions

### Growth schedule

Von Bertalanffy (1938) growth was assumed:

$$(2.B1) \quad L_a = L_\infty \cdot \left(1 - e^{-\kappa(a - a_0)}\right)$$

where  $L_a$  is the length at age  $a$ ,  $L_\infty$  is the theoretical maximum length of the fish,  $\kappa$  is the instantaneous growth rate and  $a_0$  is the theoretical age at which the fish has zero length. Length is converted to weight using the conversion factors  $lwa$  and  $lwb$ , i.e.,  $w_a = lwa L_a^{lwb}$

### Maturity and selectivity schedules

Logistic gear selectivity and maturity schedules were assumed, as these were believed to be common in fisheries, although other appropriate formulations could be substituted for these.

Relative fecundity-at-age,  $f_a$ , was assumed proportional to body weight, and was modelled as

$$(2B.2) \quad f_a = w_a Mat_a.$$

Maturity-at-age,  $Mat_a$  was given by the logistic function:

$$(2B.3) \quad Mat_a = \frac{1}{1 + e^{\left(\frac{-(a - a_{mat})}{\sigma}\right)}}$$

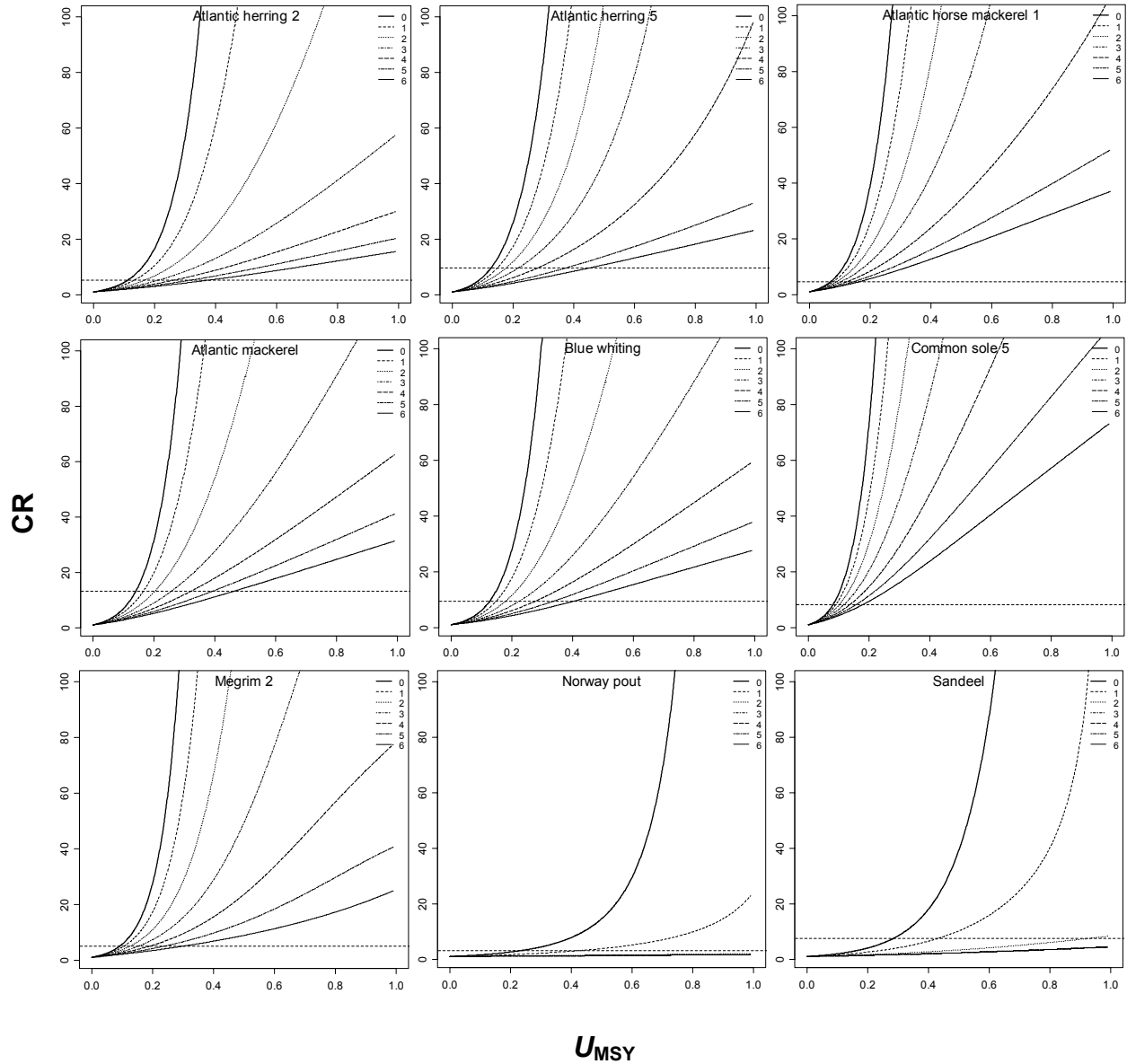
where  $\sigma$  determines the steepness of the curve, with smaller values of  $\sigma$  resulting in a steeper curve. It was assumed that  $\sigma = 0.2a_{mat}$ , implying a relatively steep curve (i.e., most individuals mature around the same age).

Similarly, vulnerability to fishing gear at age ( $v_a$ ) was given by

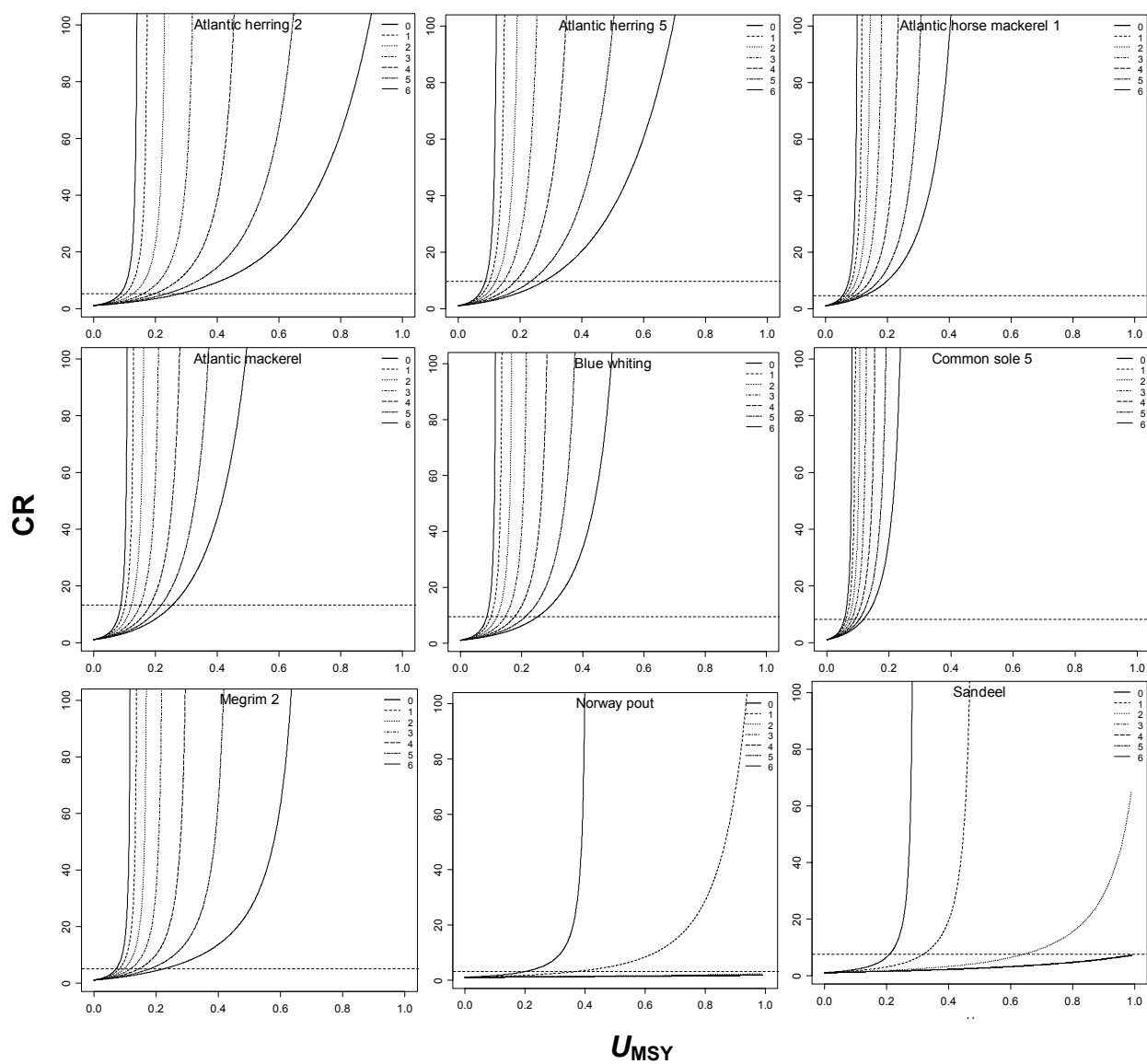
$$(2B.4) \quad v_a = \frac{1}{1 + e^{\left(\frac{-(a-ah)}{\sigma}\right)}}$$

with  $\sigma = 0.1a_h$ . This implies a relatively steep selectivity schedule. In the absence of other information, it is fairly common to assume steep or knife-edged maturity and selectivity schedules.

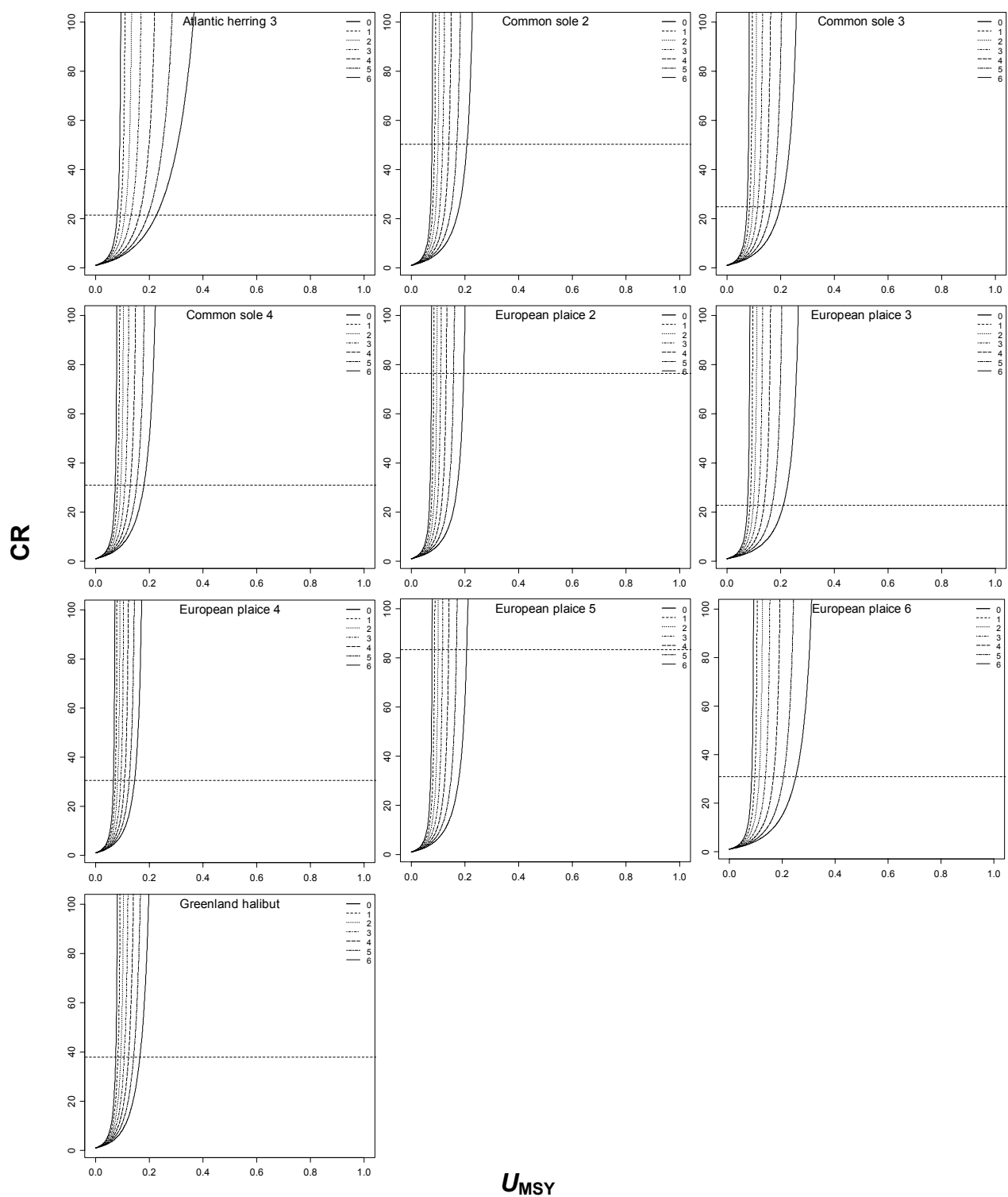
## Appendix to Chapter 3. $U_{MSY}$ -CR curves for 54 Atlantic fish stocks



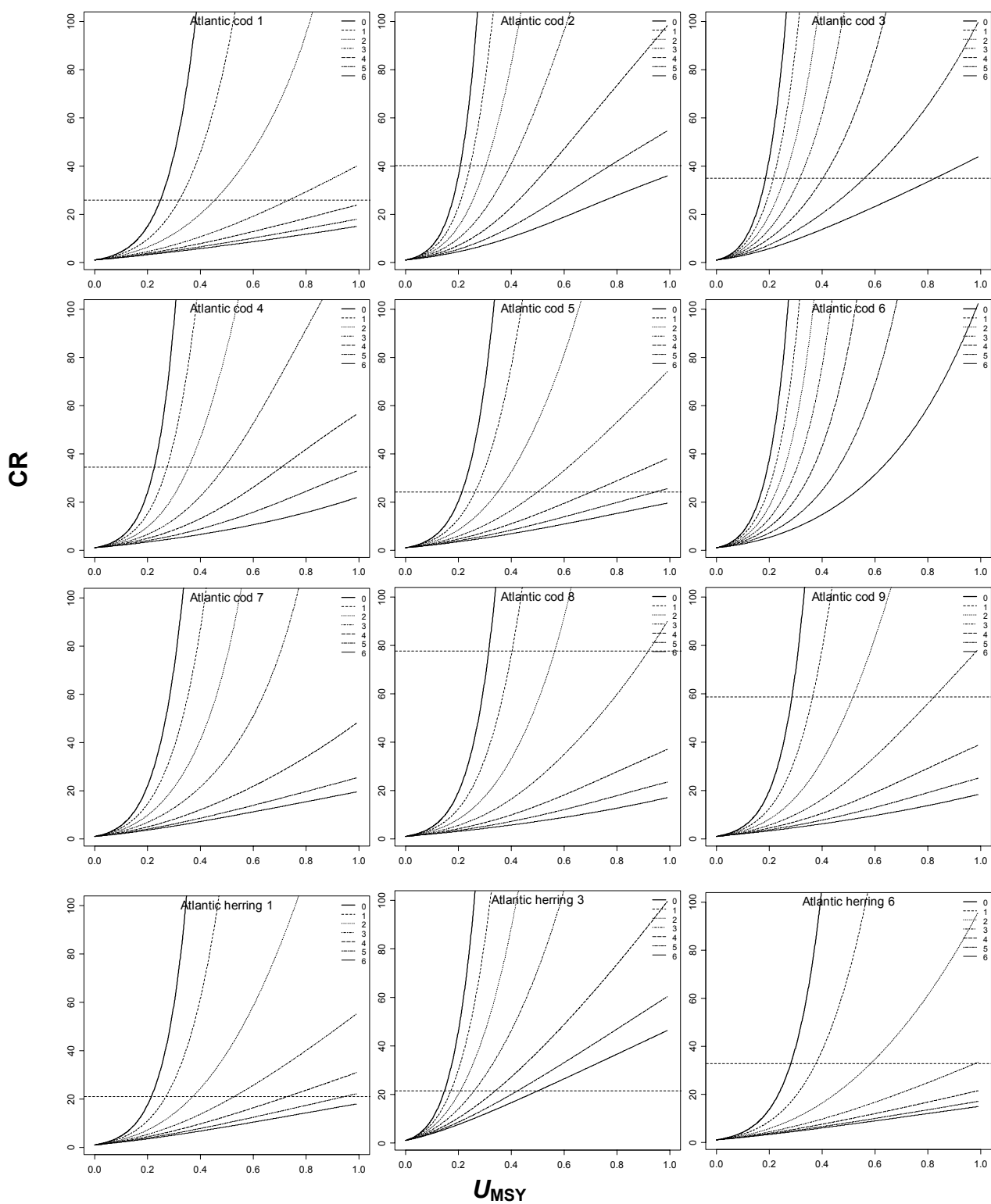
**Figure 3A.1.**  $U_{MSY}$ -CR curves for stocks for which recruitment compensation was the most limiting factor determining  $U_{MSY}$ , assuming Ricker recruitment. Curves are shown for seven values of age at recruitment to the fishery, 0-6.



**Figure 3A.2.**  $U_{MSY}$ -CR curves for stocks for which recruitment compensation was the most limiting factor determining  $U_{MSY}$ , assuming Beverton-Holt recruitment. Curves are shown for seven values of age at recruitment to the fishery, 0-6.



**Figure 3A.3.**  $U_{MSY}$ -CR curves for stocks for which life history parameters were the most limiting factor determining  $U_{MSY}$ , assuming Beverton-Holt recruitment. Curves are shown for seven values of age at recruitment to the fishery, 0-6.



**Figure 3A.4.**  $U_{MSY}$ -CR curves for stocks for which selectivity was the most limiting factor determining  $U_{MSY}$ , assuming Ricker recruitment. Curves are shown for seven values of age at recruitment to the fishery, 0-6.

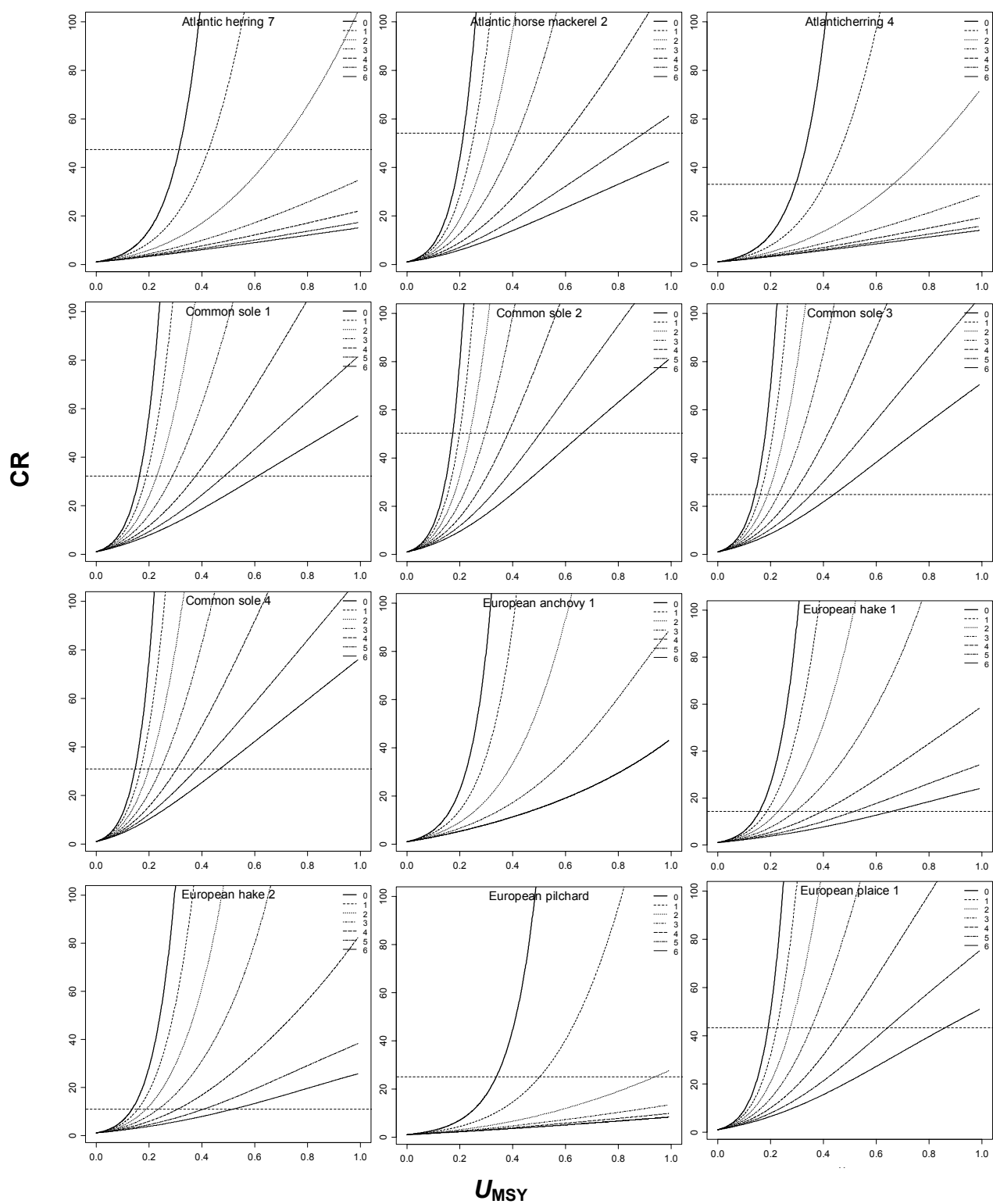


Figure 3A.4 cont.

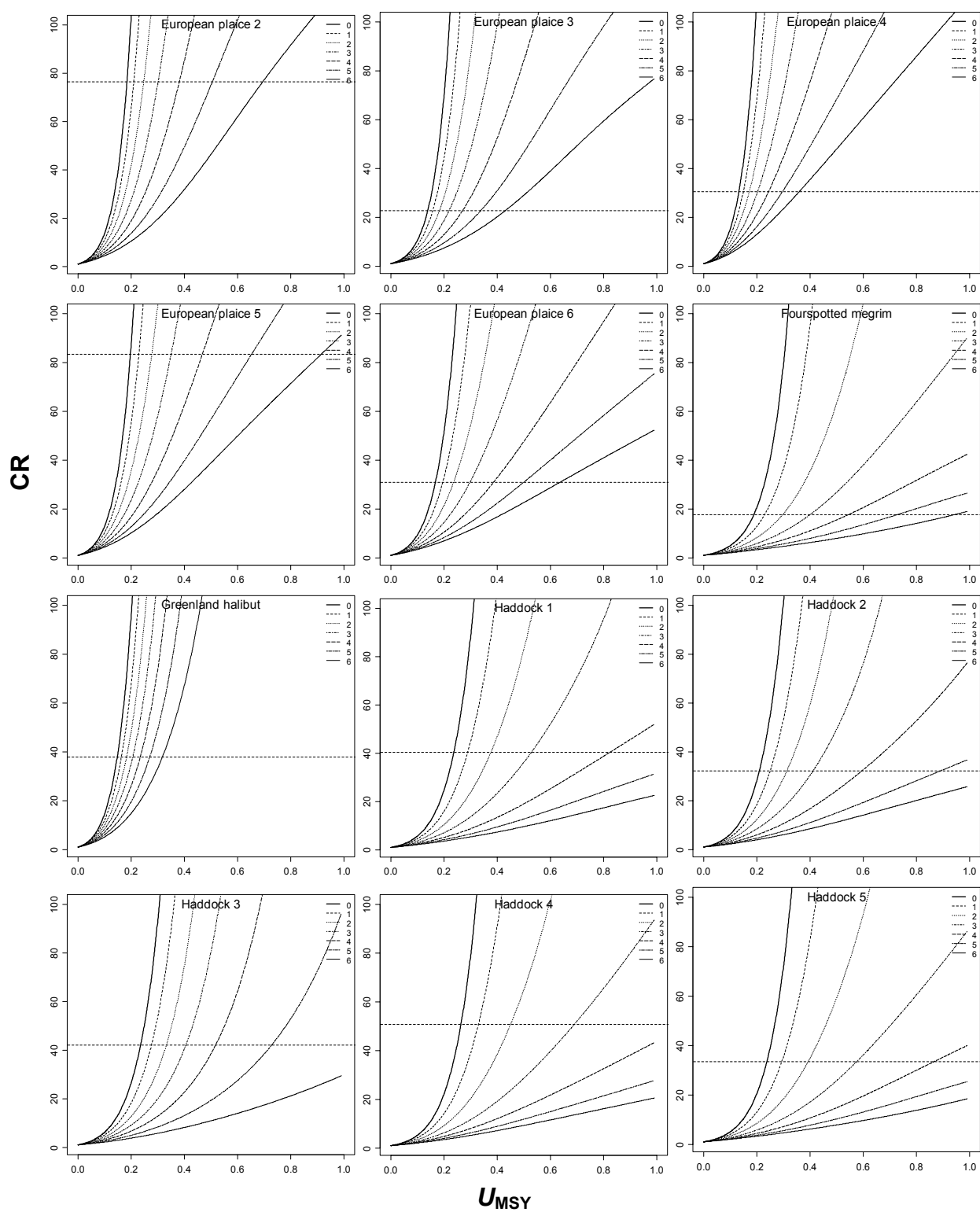


Figure 3A.4 cont.



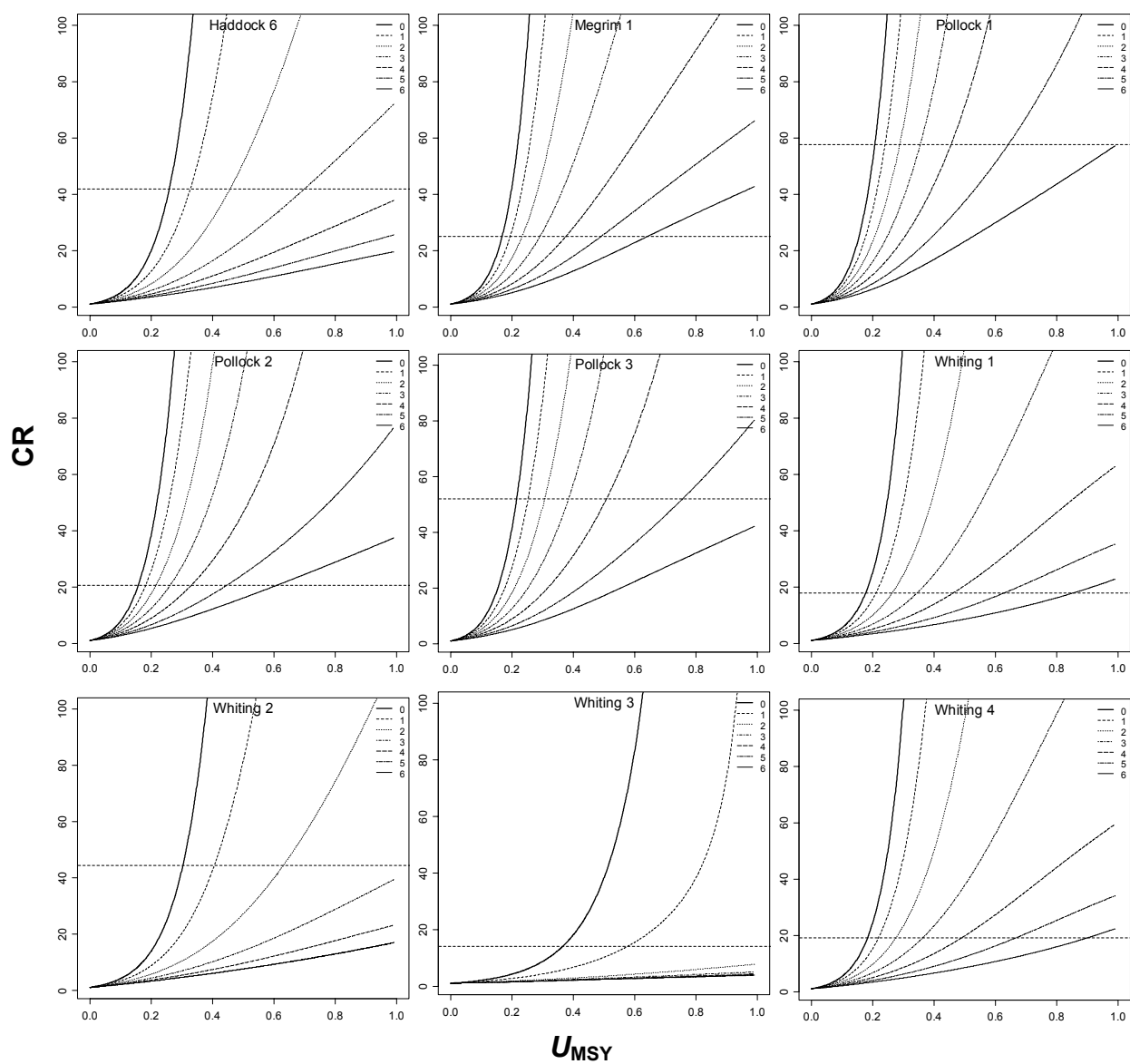
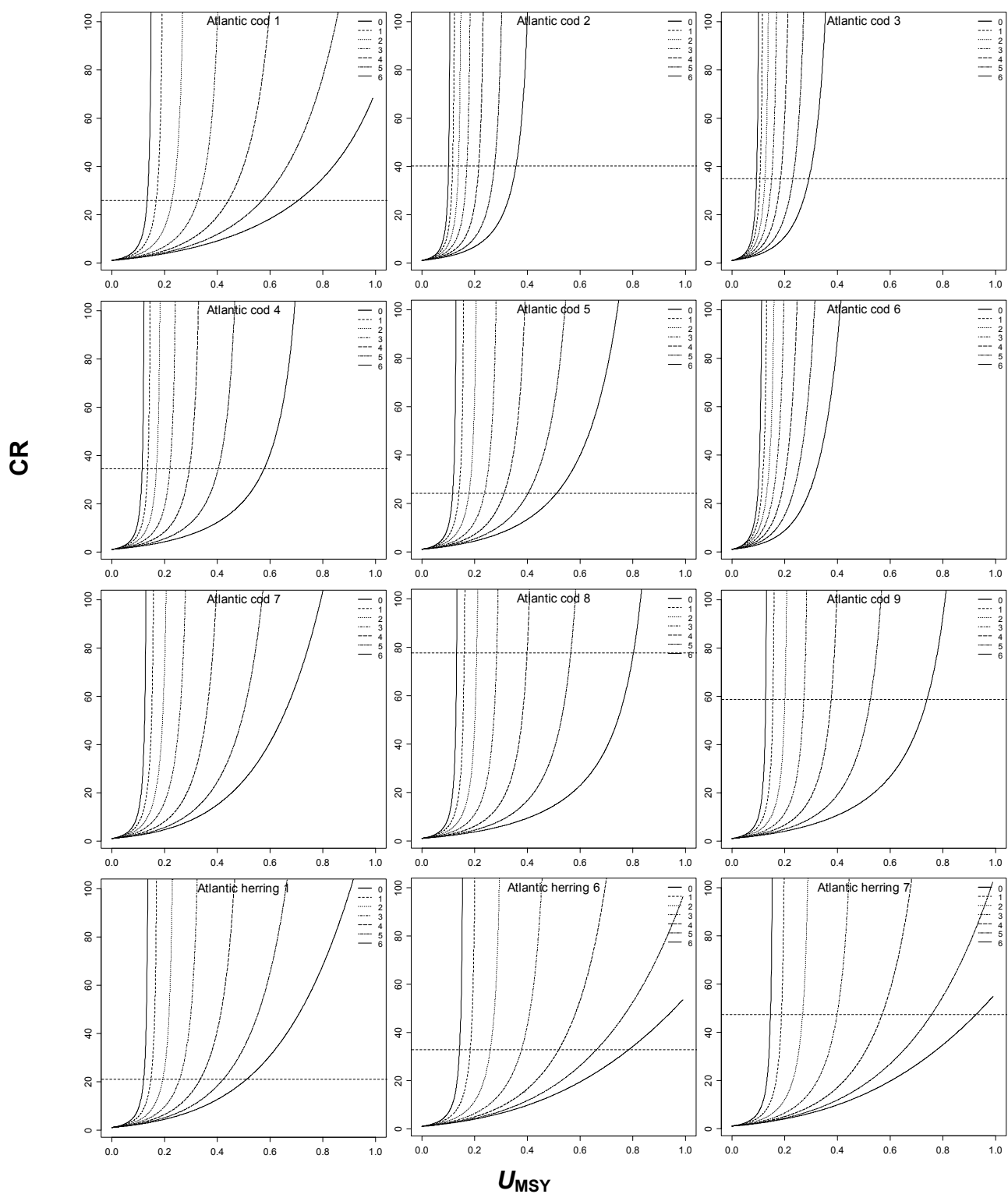


Figure 3A.4 cont.



**Figure 3A.5.**  $U_{MSY}$ -CR curves for stocks for which selectivity was the most limiting factor determining  $U_{MSY}$ , assuming Beverton Holt recruitment. Curves are shown for seven values of age at recruitment to the fishery, 0-6.

CR

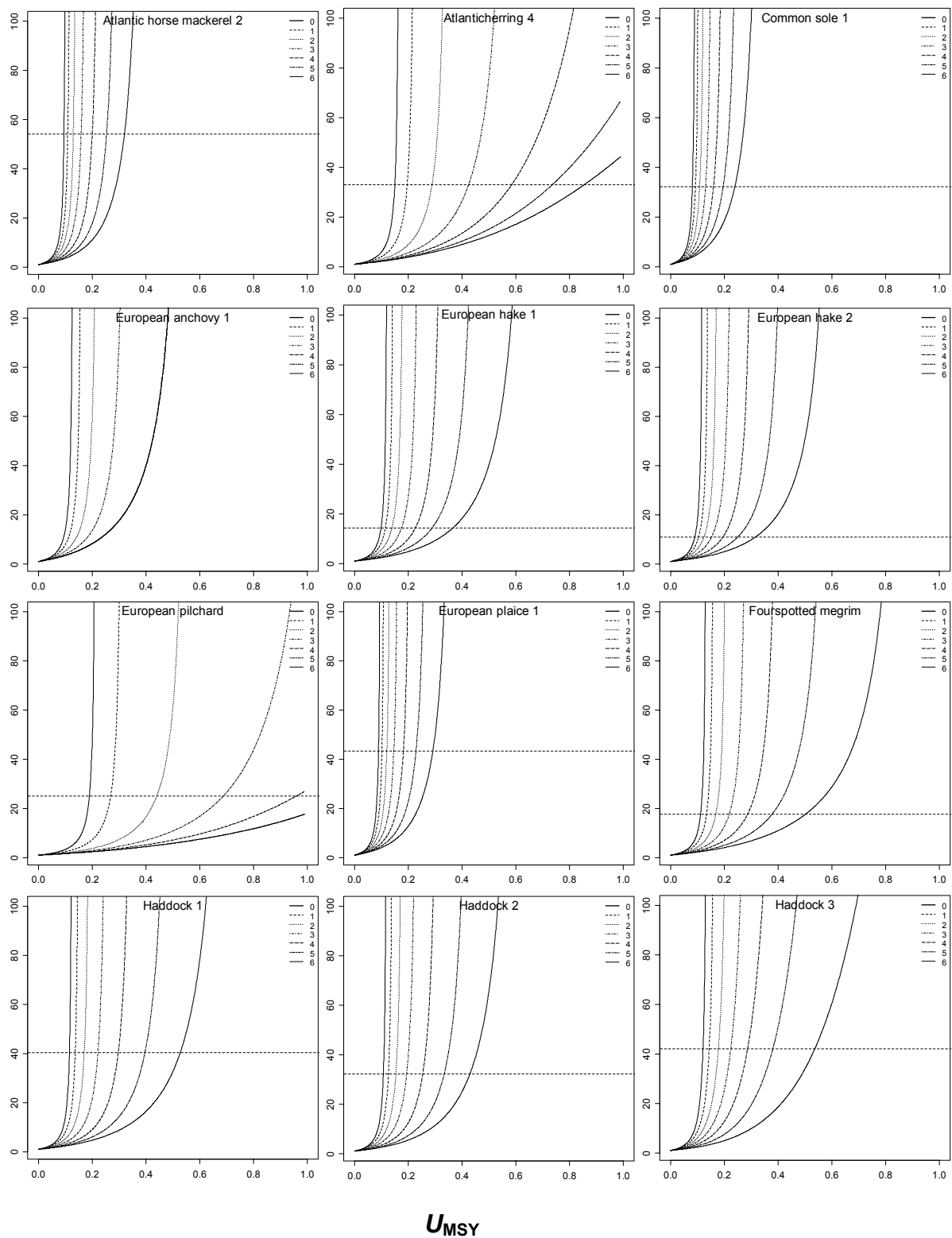


Figure 3A.5 cont.

CR

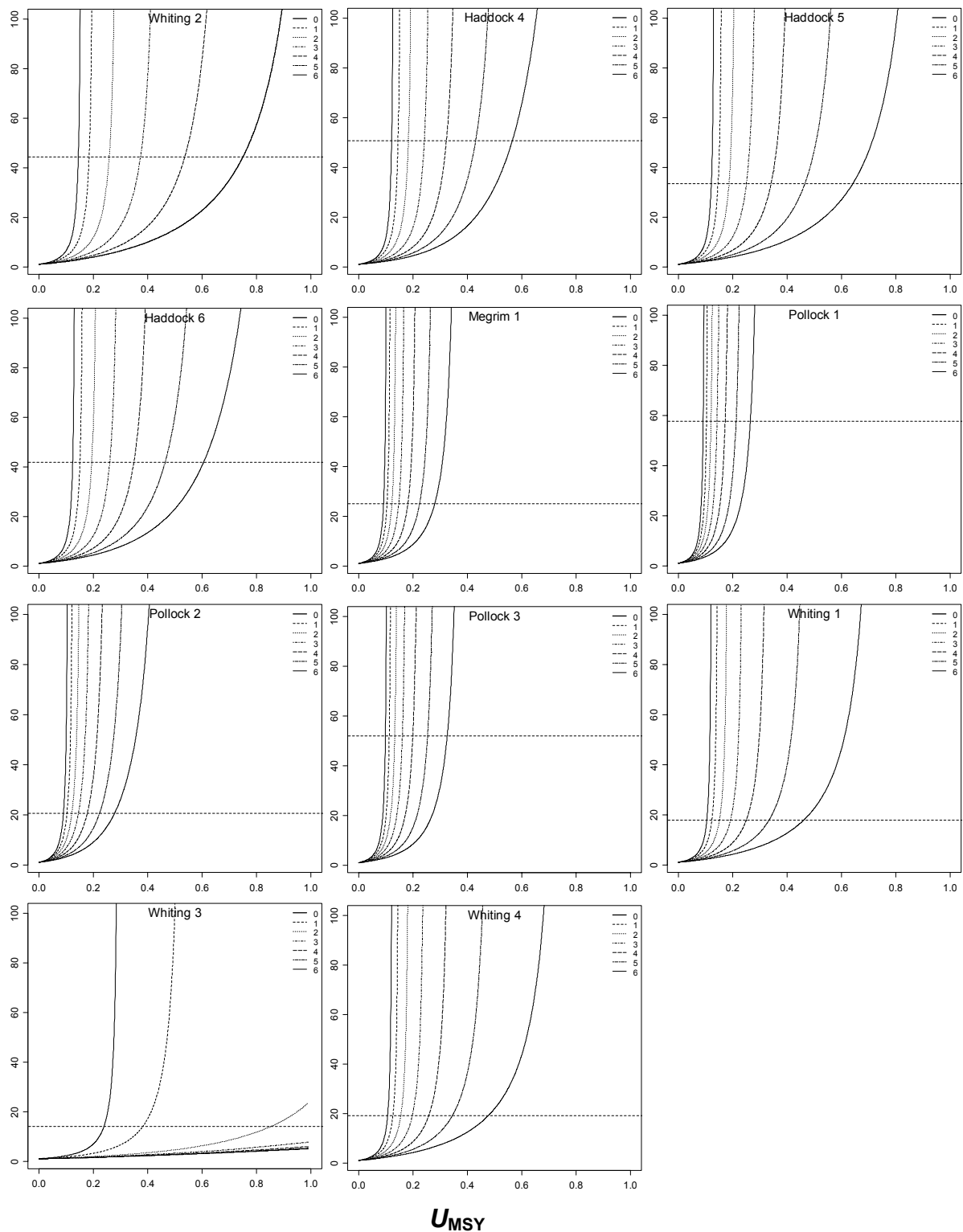
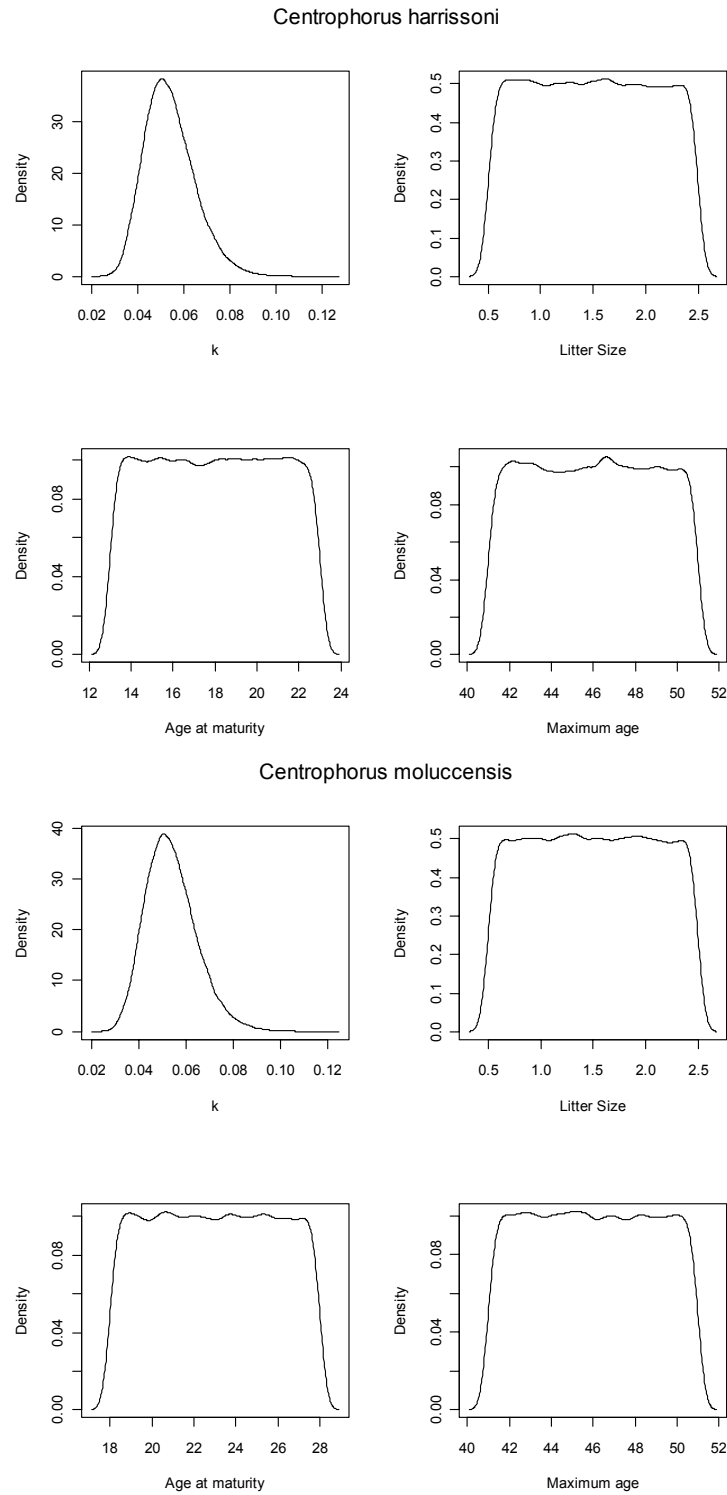
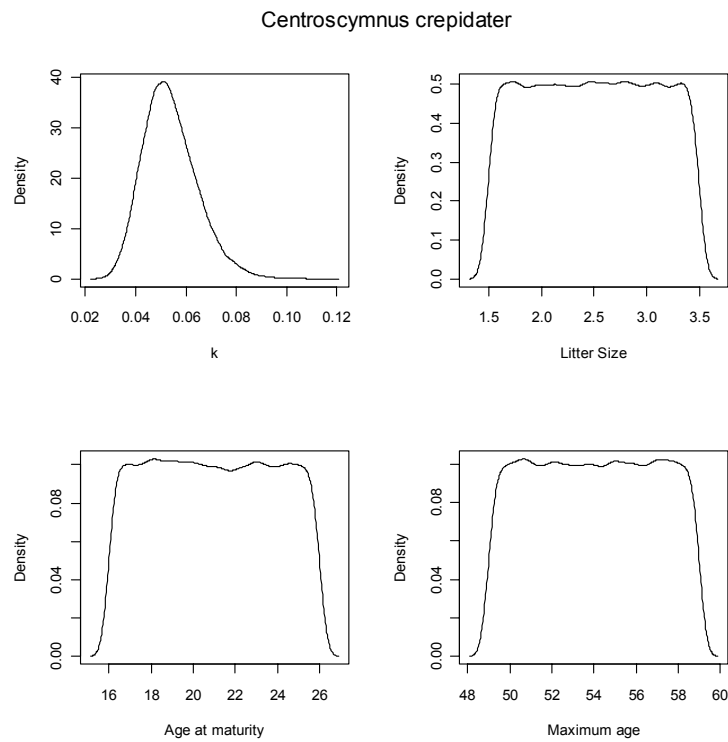
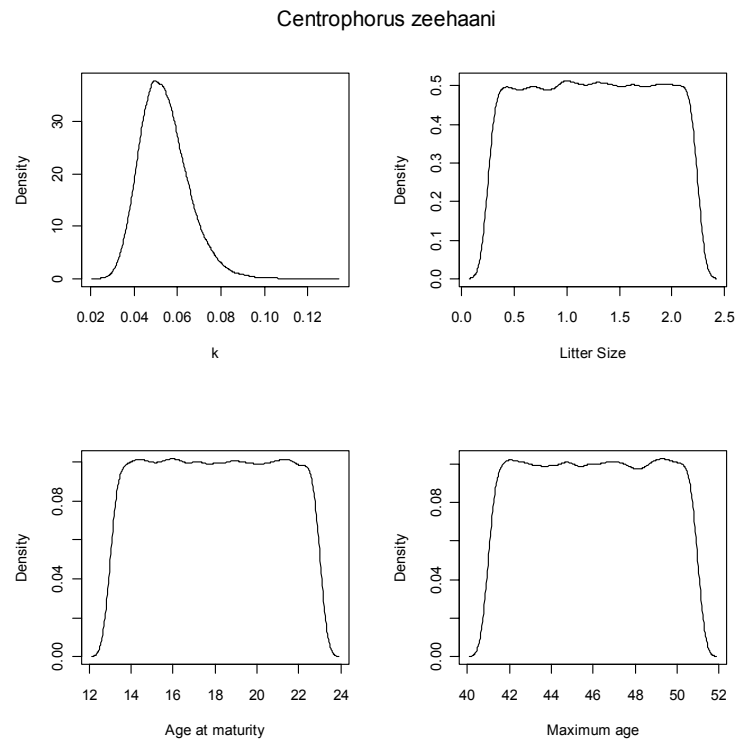


Figure 3A.5 cont.

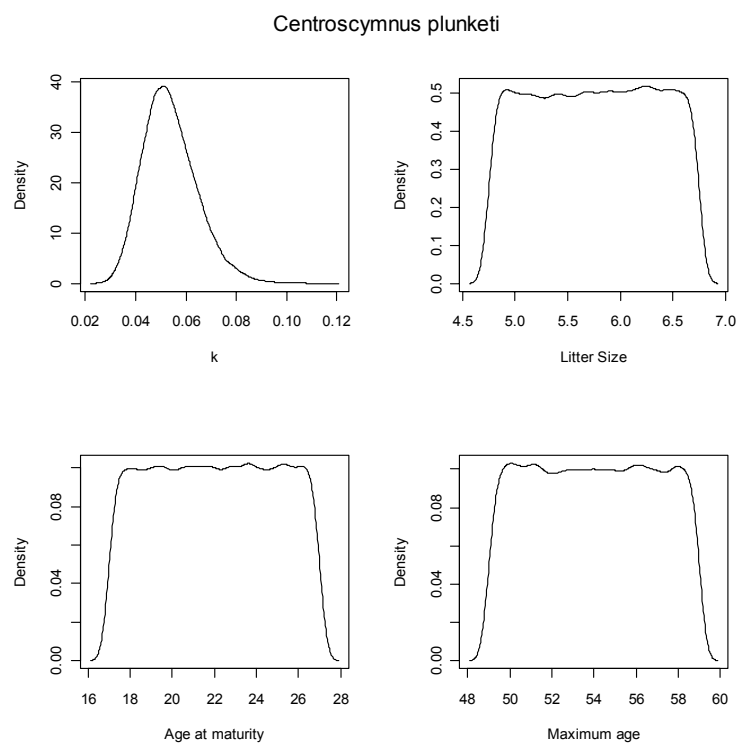
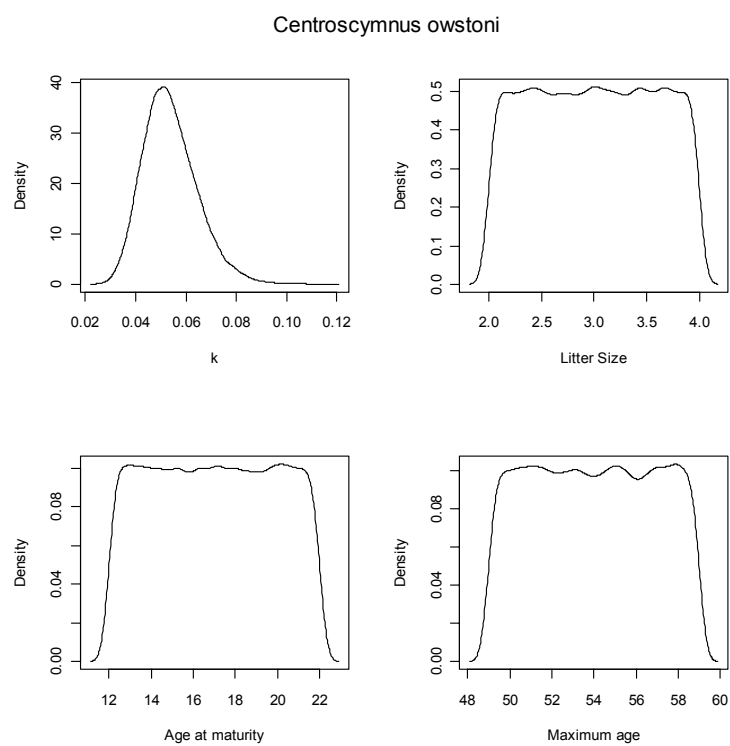
## Appendix to Chapter 4. Distributions of input parameters in dogshark model



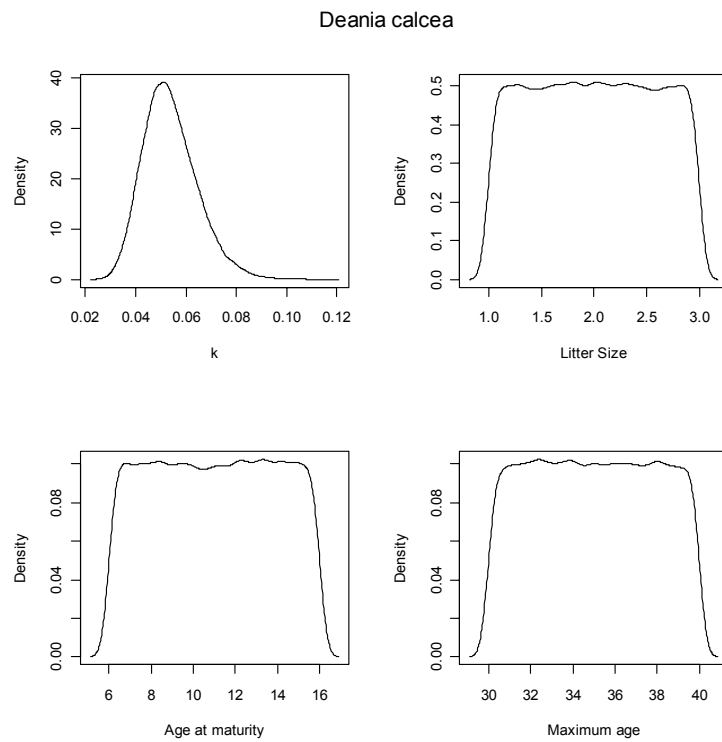
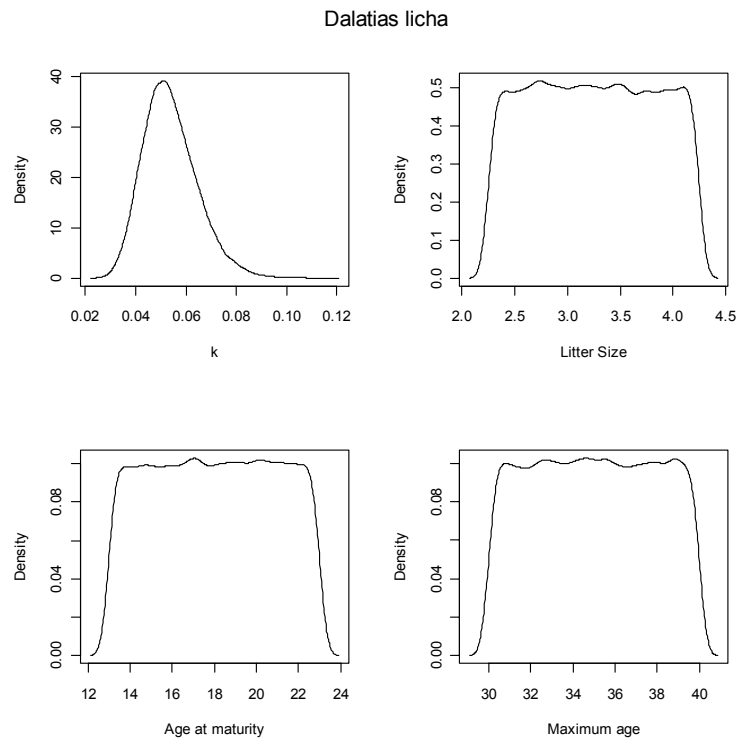
**Figure 4A.1.** Probability distributions of the four parameters ( $\kappa$ , LS,  $a_{mat}$  and  $a_{max}$ ) treated as uncertain in the analysis for 12 species of Australian dogshark.



**Figure 4A.1. cont.**

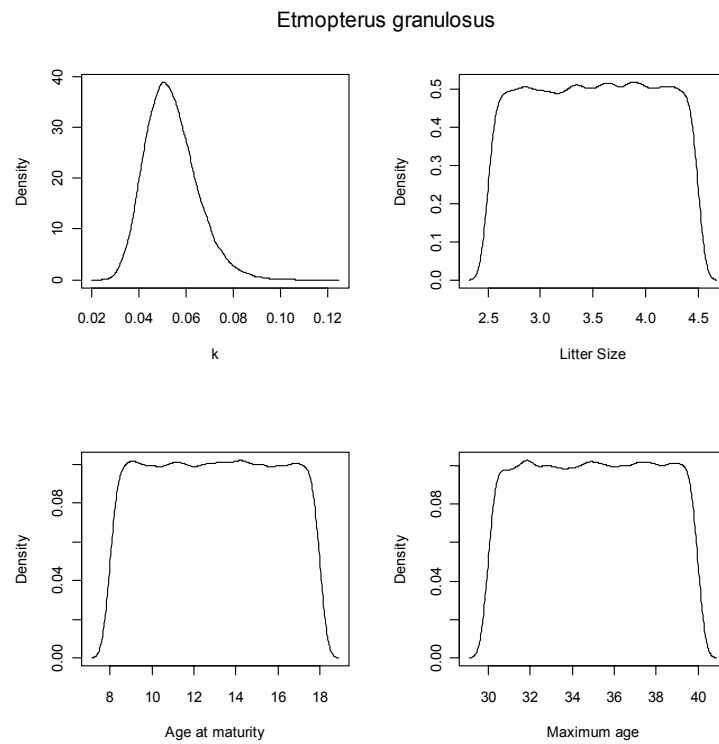
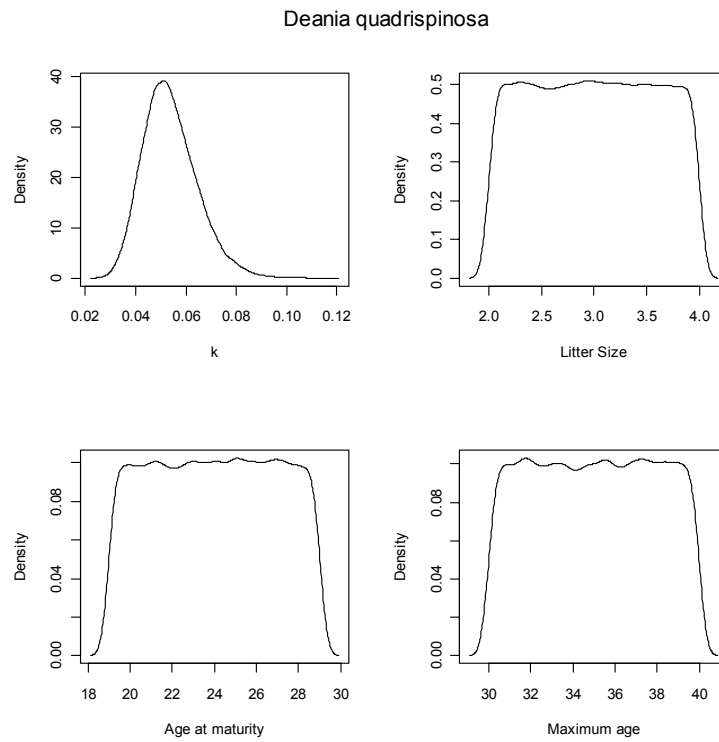


**Figure 4A.1. cont.**

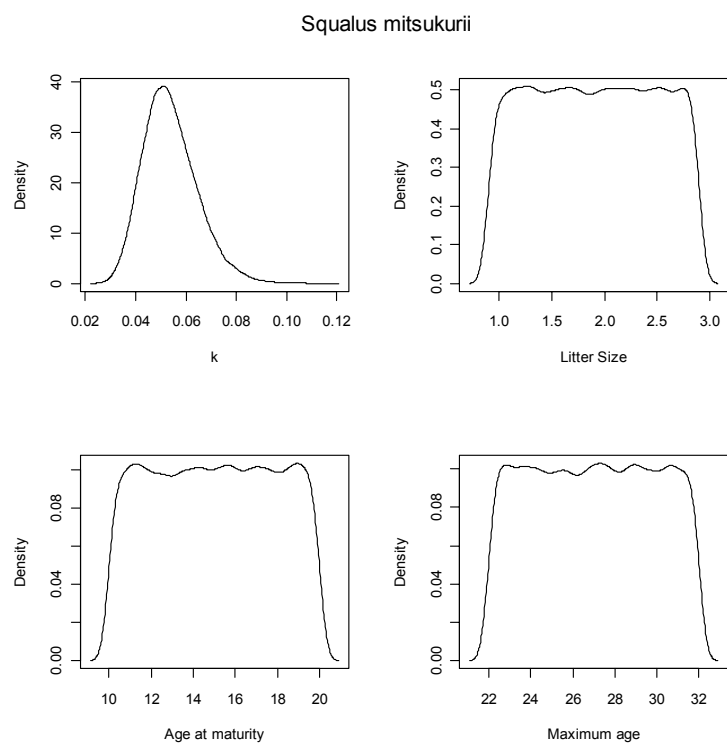
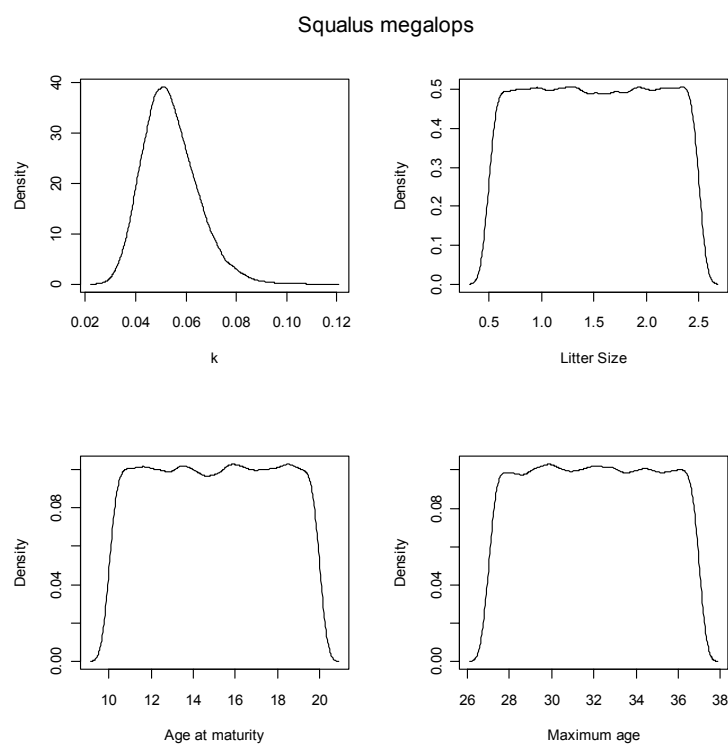


**Figure 4A.1. cont.**





**Figure 4A.1. cont.**



**Figure 4A.1. cont.**

## **Appendix 1. Ecopath with Ecosim model of the continental shelf and slope of New South Wales**

### **Introduction**

Three sets of surveys of the upper continental slope of NSW (the *Kapala* surveys) showed large changes in species composition between 1976 and 1996 (Andrew *et al.* 1997; Graham *et al.* 2001). In particular there were significant declines in the abundance of many demersal sharks, particularly deepwater dogsharks, skates and some teleosts. There have been very few stock assessments of the marine species occurring in NSW (see Bruce *et al.* 2002 for review) and there is limited understanding of the effects of fishing on the shelf and slope marine ecosystem.

Ecosystem models have been used to model southeastern Australian marine ecosystems for different historical periods (Bulman *et al.* 2006; Klaer 2006b; Fulton *et al.* 2007a). Klaer (2006) simulated changes in the structure of the demersal fish community on the NSW continental shelf between 1915 and 1961, using an Ecopath with Ecosim (EwE) model (Christensen and Walters 2004) with a highly simplified food web. Bulman *et al.* (2006) presented a much more complex EwE model of the southeastern Australian shelf (including waters off NSW), covering the period 1994 to 2003. Until recently, however, there has been no attempt to incorporate the data from the 1976 and 1996 surveys into an ecosystem model.

In 2002 the NSW Department of Primary Industries (NSW DPI) engaged in a Memorandum of Understanding with the University of British Columbia Fisheries Centre (UBC FC) for the purpose of producing simulation models of the NSW marine ecosystem. Also, a collaborative project between NSW DPI and the Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) was launched in 2004, with similar purpose. Both collaborations were aimed at providing models that could contribute to understanding of the impacts of fisheries on the marine ecosystem of NSW and, therefore, aid progress towards ecosystem-based fishery management (EBFM) in NSW. One aspect of the collaboration between NSW DPI and CSIRO was a comparison of the predictions of two structurally different ecosystem models of the NSW continental shelf and slope for the period 1976 to 1996 (see this thesis, Chapter 6). These models

were prepared by scientists at CSIRO and, through the collaboration between NSW DPI and UBC FC, by the present author. The CSIRO model was built using the Atlantis ecosystem modelling framework (Fulton *et al.* 2005b; 2007a,b; see Pláganyi 2007) and was described in detail by Savina *et al.* (2008). The UBC FC model was built using Ecopath with Ecosim (EwE) and is described here. The main goal for these models was to explore trade-offs implicit in hypothetical alternative policies and to compare the predictions of two structurally distinct ecosystem models (see Chapter 6). The extreme paucity of ecological data in this system necessitated using parameters from similar species in different ecosystems and the use of some large assumptions about diets and relative biomasses. Results should therefore be considered illustrative, as was their intended purpose.

### Ecopath with Ecosim

Ecopath with Ecosim is a an approach to ecosystem modelling that has been applied to a large number of ecosystems throughout the world. In Ecopath (Christensen and Pauly 1992), users define a set of functional groups, which share trophic and life history characteristics and/or are of management interest. The modelled system must satisfy the thermodynamic constraint of mass balance, set out by the master equation of Polovina (1984), so that for every species or functional group ( $i$ ) in the modelled ecosystem, with predators ( $j$ ):

$$(A.1) \quad B_i(P/B)_i EE_i = Y_i + \sum_j (B_j(Q/B)_j DC_{ij}) + E_i + B_{Acci}$$

where  $B_i$  is biomass;  $(P/B)_i$  is production to biomass ratio (equivalent to total mortality,  $Z$  under most conditions; Allen 1971);  $EE_i$  is ecotrophic efficiency (the fraction of production consumed within the system);  $Y_i$  is fisheries catch;  $(Q/B)_j$  is consumption per unit of biomass of predators;  $DC_{ij}$  is the fraction of  $i$  in the diet of each of its predators,  $j$ ;  $E_i$  is the net migration rate and  $B_{Acci}$  represents accumulated biomass of species  $i$ . The model is ‘balanced’ by solving the resulting set of linear equations using a matrix inversion method. While  $DC_{ij}$  and  $E_i$  must be entered for each species, only four of the other five biological parameters ( $B_i$ ,  $(P/B)_i$ ,  $EE_i$ ,  $(Q/B)_i$ , and  $B_{Acci}$ ) need to be entered, with the last estimated by Ecopath during balancing. It is possible to use energy-related or nutrient-related units in the model. Nutrient-related units ( $\text{t.km}^{-2}.\text{y}^{-1}$ ) are the most commonly-used and have been used in the present model.

Ecosim (Walters *et al.* 1997) is a dynamic extension of Ecopath represented by a series of coupled differential equations of the form

$$(A.2) \quad \frac{\partial B_i}{\partial t} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) B_i$$

representing the change in biomass of group  $i$ ,  $B_i$ , during the time interval  $\delta t$ , where  $g_i$  is the net growth efficiency (production/consumption ratio);  $I_i$  is the immigration rate;  $M_i$  is the natural mortality rate due to factors other than predation;  $F_i$  is the instantaneous fishing mortality rate; and  $e_i$  is the emigration rate (Walters *et al.* 1997). Consumption rates,  $Q_{ji}$ , are calculated using the ‘foraging arena’ concept (Walters and Juanes 1993; Walters *et al.* 1997; 2000; Walters and Martell 2004), where  $B_i$  is divided into two biomass pools that are, respectively, vulnerable and invulnerable to predators. The transfer rate ( $v_{ij}$ ) between these two pools determines the availability of prey  $i$  to predator  $j$  and, therefore, the rate of per capita consumption of prey  $i$  by its predator  $j$ . In Ecosim, users can adjust the parameter representing the maximum consumption rate  $Q_{ij}^{max}$  of each prey by each of its predators, relative to the Ecopath base rate. From this,  $v_{ij}$  is estimated from  $Q_{ij}^{max} = v_{ij} B_i$  (see Walters *et al.* (2000) for details). Adjustment of the parameter  $Q_{ij}^{max}$  is one of the principal means by which users can ‘tune’ a model to improve agreement with observed indices of abundance (see Walters *et al.* (2000); Bundy (2001); Christensen and Walters (2004); and Plagányi and Butterworth (2004) for discussion of sensitivity of model predictions to this parameter). Typically, lower values of this parameter result in lower sensitivity to fishing pressure.

## Study area and period

The present model was constructed to represent the ecosystem of the continental shelf and upper slope of NSW in 1976, the year of the first trawl surveys. After balancing the base Ecopath model, dynamic simulations in Ecosim were run until 1996, the final survey year. The model was not spatially explicit. However, model boundaries were needed to determine species composition and density of biomass, and to define the extent of the data to use. Longitudinal boundaries of the model were the northern and southern borders of NSW (29°S and 36°S). Latitudinally, the model extended from the coastline (including estuaries) to approximately the

800 m isobath. Very little fishing occurs beyond this depth range (Larcombe *et al.* 2001). These boundaries resulted in a total model area of approximately 48 000 km<sup>2</sup> (see Figure 6.1). Naturally, some species were distributed over a wider range, and it was assumed that densities of wider-ranging species within the model area were consistent with their densities outside the model area. Although this assumption may not always be correct, it is a common assumption in ecosystem models, and is necessary to prevent models from becoming intractably large or complex. To partially overcome this for highly migratory species, it was assumed that a proportion of the diet came from outside the model area and was unaffected by dynamics within the model (assuming constant conditions outside the model area). This is a recommended approach for representing highly migratory species within these models (Walters and Martell 2004).

### **Key data sources**

A number of data sources were used to identify species in the modelled area and to calculate catches and discards. These included the NSW State catch database, 1984-1996 (supplied by NSW DPI); the NSW historical catch database 1940-1992 (Pease and Grinberg 1995; supplied by NSW DPI); the Commonwealth South East Fishery catch and effort database, 1985-1996 (supplied by the Australian Fisheries Management Authority); the ISMP database 1992-1996, containing observations of catch and discarding from the Commonwealth South East Fishery Integrated Scientific Monitoring Program (Garvey 1998 and Knuckey *et al.* 2001; supplied by the Victoria Marine and Fisheries Research Institute); catch rate data from the FRV *Kapala* surveys (supplied by NSW DPI); and various literature sources (notably May and Maxwell 1980; West 1993; Kailola *et al.* 1993; Bannister *et al.* 1996; Yearsley *et al.* 1999; Bulman *et al.* 2001; Kennelly and McVea 2003; Kaschner 2004; and Ganassin and Gibbs 2005).

The study was mainly concerned with the effects of trawling on deepwater dogsharks and other shelf and slope species (see Chapter 6). Therefore the model was more resolved in the ‘offshore’ components (i.e., more shelf and slope species were individually represented). Note that the history of management of the shelf and slope fisheries of NSW is complex and there have been a number of changes in jurisdictional control, fishery names and management methods over the past four decades (Grieve and Richardson 2001; Tilzey and Rowling 2001; see Chapter 1).

Prior to 1992, all fisheries landings off NSW were reported to the State. Landings between 1940 and 1992 are reported in Pease and Grinberg (1995) and this was the primary source of catch data for the Ecopath model. In this database, there is only one offshore trawl fishery. Since 1984, offshore trawl landings have been reported in three trawl fisheries: the Commonwealth South East Fishery (SEF), the State Ocean Fish Trawl (OFT) and State Ocean Prawn Trawl (OPT), with the latter operating on more northerly fishing grounds than the other two. For simplicity, and to avoid having to disaggregate trawl landings prior to 1984, only one offshore trawl fishery is included in the model. Note, however, that much of the information used for parameterisation of shelf and slope species came from research relating to the SEF and, therefore, it is occasionally referred to throughout this Appendix.

## Species list

The above sources resulted in a list containing almost 900 separate taxonomic groups (excluding birds), with approximately 150 of these as aggregated species complexes, and the rest individual species. The final list, which includes invertebrates, fish and marine mammals, is given in Appendix 2. Note that there also are approximately 122 species of seabird occurring commonly in NSW and approximately 80 more that occur occasionally or rarely (Ganassin and Gibbs 2005). These are not included in Appendix 2, but are listed in Ganassin and Gibbs (2005). Note also that the list of invertebrates is incomplete and represents only species that have been caught in commercial fisheries or in surveys. Compilation of the species list in Appendix 2 represented a challenge, as several of the sources above, including some of the *Kapala* data and the NSW State Catch database, reported species by common name only. Many species have multiple common names (e.g., *Girella tricuspidata* = luderick or blackfish) and, in other cases, different databases expressed the same name in different ways. For example, the three-spotted crab (*Portunus (Portunus) sanguinolentus*) was expressed as 3-spot crab; crab, 3-spot; crab, three-spotted etc.). To enable efficient and consistent querying of the databases, it was necessary to match each species/taxonomic grouping with a unique common name and assign a code to each one. There is a comprehensive list of standardised codes for Australian aquatic species (Codes for Australian Aquatic Biota (CAAB); [www.marine.csiro.au/caab/](http://www.marine.csiro.au/caab/)). These codes were used during all database queries on catch, discards, diet etc. Several databases used old versions of the CAAB codes and considerable effort was also spent ensuring that correct CAAB codes were assigned to records with older codes. Appendix 2 therefore represents a standardised list of

species/taxonomic groupings occurring in NSW, correctly matched to unique taxonomic codes and common names, which, it is hoped, will provide a useful resource beyond the present study.

The species listed in Appendix 2, as well as birds and primary producers, were allocated into 56 functional groups, representing trophically similar groups or species of particular interest to management or this project. May and Maxwell (1986), Kailola *et al.* (1993), West (1993), Bulman *et al.* (2001), NSW Fisheries (2001), Yearsley *et al.* (2001) and *FishBase* (Froese and Pauly 2008) were used to guide allocation into groups. Most teleost species were aggregated into groups based on habitat (demersal, pelagic), depth (inshore, offshore, deep) and diet (herbivorous, omnivorous, piscivorous). Omnivores were defined as having a diet dominated by invertebrate prey. Species with a diet consisting mostly of fish (> 50%) were assigned into piscivorous groups. Pelagic fish were also divided into small (< 60 cm maximum length) and large (> 60 cm maximum length) categories. Many species live in a large range of depths throughout their life history. Inshore groupings, therefore contained species mostly associated with coastal waters (< 60 m depth). Offshore groupings contained species mostly occurring on the continental shelf (60 – 200 m); and deep groupings contained species in water deeper than 200 m (continental slope). The functional groups of the model, and representative species, are given in Table A1.1. See Appendix 2 for full list of species in each group.

## Diets

For most offshore species, diets (Table A1.2) were based on data published in Bulman *et al.* (2001) and in Bulman *et al.* (2006). There have been few comprehensive diet studies for inshore species. There is, however, a dataset of diets of fishes in Botany Bay, collected between 1977 and 1979 (SPCC 1981), which was used. This dataset (supplied by NSW DPI) was of limited use because most fish prey were recorded as ‘unknown fish’, but it could be used to identify herbivorous, omnivorous and piscivorous species. Kailola *et al.* (1993) gave information about predators and prey for a large number of commercially-fished species and much extra qualitative information was extracted from this source. *FishBase* (Froese and Pauly 2008) was also used extensively. Additional sources used to estimate diet of individual groups, where appropriate, are given in the Parameters section below. It should be noted that many of the numerical estimates in the diet were based on subjective adjustments, as many studies mentioned reported abundances in the diet in terms of frequency of occurrence, rather than percentage of mass. Also, as the diet



matrix is usually the most uncertain part of a model, it was adjusted considerably during balancing of the model, as suggested by Christensen *et al.* (2005). The diet matrix for the model is shown in Table A1.2. Resulting trophic levels (Lindeman 1942) of the 56 living model groups are shown in Figure A1.1a and Table A1.3.

## Parameters

Parameters used in the Ecopath model are shown in Table A1.3. For groups where estimates of starting biomass were unobtainable (macrophytes, zooplankton, gelatinous zooplankton, squid, most invertebrate groups and aggregated fish groups), biomass was estimated by Ecopath during balancing. In these cases EE was set to 0.95 for all groups, which reflects the assumption that most of the production is consumed within the modelled system. Exceptions were the mixed benthic invertebrate groups, where EE was set to 0.75 and macrophytes and zooplankton, where EE was set to 0.5. These groups are highly productive and the lower EEs reflect the assumption that a smaller proportion of the production of these groups is consumed by higher trophic levels, i.e., carcasses either sink to the sea floor or are otherwise exported from the food web (Christensen *et al.* 2005).

Estimates of total mortality ( $P/B$ ) were entered for all model groups. Rather than estimate Consumption/Biomass,  $Q/B$ , independently (e.g., using the equation of Palomares and Pauly 1998), a constant production/consumption ratio ( $P/Q$ ) of 0.2 was assumed for most groups (Parsons *et al.* 1984; Christensen 1995) and  $Q/B$  was estimated from  $\frac{P/B}{P/Q}$ . Exceptions were marine mammals and seabirds, where estimates of  $Q/B$  from the published literature were used.

Important note: It is important to realise that the model presented here was intended to explore hypothetical historical management scenarios and produce results that could be compared with a structurally-different ecosystem model (see Chapter 6). Many of the parameters used were rough estimates at best and it is not the intention for this model to be used in any way to provide real stock assessment advice.

### **Seabirds**

Seabird parameters were taken from Bulman *et al.* (2006), where biomass of mixed seabirds was  $0.004 \text{ t.km}^{-2}$  and biomass of penguins was  $0.001 \text{ t.km}^{-2}$ .  $P/B$  and  $Q/B$  were set to  $1 \text{ y}^{-1}$  and  $80 \text{ y}^{-1}$  respectively for both groups (Bulman *et al.* 2006).

### **Marine mammals**

There were three groups of marine mammals in the model: seals, toothed whales and baleen whales. In this region, there are approximately 25 species of toothed whale and approximately seven species of baleen whale (Bannister *et al.* 1996; Kaschner 2004). The distribution and abundance of these species in Australian waters is uncertain, with most estimates based on sightings (Ganassin and Gibbs 2005). In addition, several species of baleen whale (e.g. humpback whales, *Megaptera novaeangliae*, and southern right whales, *Eubalaena australis*) are highly migratory and their residence time and feeding behaviour in the southeast shelf system are not well understood (Bannister *et al.* 1996). Despite these difficulties, the marine mammal database of Kaschner (2004) was used to approximate biomass of baleen and toothed whales, which were estimated to be  $0.03$  and  $0.011 \text{ t.km}^{-2}$  respectively. For both species,  $P/B$  was set to  $0.02 \text{ y}^{-1}$  and  $Q/B$  was set to  $13 \text{ y}^{-1}$  (after Blanchard *et al.* 2002). This source was also used to set  $P/B$  and  $Q/B$  for seals, which were set to  $0.06 \text{ y}^{-1}$  and  $15.9 \text{ y}^{-1}$  respectively. Biomass of seals in the Bass Strait areas has been estimated at around  $0.051 \text{ t.km}^{-2}$ . The population of seals in NSW is considered to be much smaller than that in more southern waters (Ganassin and Gibbs 2005) and, in the absence of other information, seal biomass was set to  $0.0051 \text{ t.km}^{-2}$  (an order of magnitude smaller than in more southern waters). Goldsworthy *et al.* (2003) provided information on the diet of seals. Pauly *et al.* (1998) and Kailola *et al.* (1993) were used for diet composition of whales.

## **Shark groups**

### *Dogsharks*

Dogsharks (Order: Squaliformes) were separated into five groups separated out to a similar level of resolution as in the *Kapala* dataset (Graham *et al.* 2001). Starting biomass of these groups was set to match that used by Savina *et al.* (2008) in their Atlantis model. The Atlantis model of these authors only considered two dogshark groups: spiky dogshark (*Squalus megalops*) and deepwater dogsharks (i.e., all other dogshark species, groups 43-46 in Table A1.1). Biomass of spiky dogsharks in both models was taken from the working of Fulton *et al.* (2007a) who estimated it to be 17 000 t ( $0.354 \text{ t.km}^{-2}$ ). Biomass of all other dogsharks was taken from the same source and estimated to be 30 000 t. Mean relative proportions of dogsharks in the *Kapala* surveys were used to split this figure into the four remaining dogshark groups in the Ecopath model (see Table A1.3). Natural mortality of these sharks is likely to be very low ( $<0.1 \text{ y}^{-1}$ , see Chapter 4). However, fishing mortality for these groups in 1976 is likely to have been on the order of  $0.1 - 0.2 \text{ y}^{-1}$  (see Chapter 5). Therefore, P/B was set to 0.2 for all groups initially. These values were adjusted slightly during calibration to improve the fit to the observed changes in abundance. Because these groups were not at steady state in 1976, a negative biomass accumulation (*BA*) was added for all groups except spiky dogshark. This parameter corrects for groups not being at steady state in the initial year and greatly assisted during calibration of the model. *BA* values were -0.05, -0.09, -0.08 and  $-0.1 \text{ y}^{-1}$ , for groups 43-46 respectively. Negative biomass accumulation was not added for spiky dogshark, as this species was not observed to decline between 1976 and 1996 (Graham *et al.* 2001). Chapter 5 discussed the extreme data limitations for these species and the parameters used here were based on educated guesswork. The approach to setting productivity parameters was *ad hoc* but produced a calibrated model that could emulate declines of dogsharks under fishing, to enable comparison of alternative hypothetical management scenarios (Chapter 6). There is no doubt that these species have low productivity (Daley *et al.* 2002; this thesis, Chapter 4) and the estimates used are within plausible boundaries. Diets of dogsharks were based on observations reported by Graham (2005; 2008).

### *Gummy shark, school shark and mixed demersal sharks*

The commercially important gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) were allocated into separate groups. The remaining shark species were

allocated into three groups, medium sharks, large sharks and skates/rays (see Appendix 2). Savina *et al.* (2008) used the working of Fulton *et al.* (2007a) to obtain an estimate of 10 000 t of medium sized sharks in the model area in 1976. As for dogsharks, mean relative abundance estimates from the 1976 *Kapala* database were used to disaggregate this biomass into the gummy shark, school shark and mixed medium shark groups in the present model.  $P/B$  for gummy shark and school shark were set at 0.38 and 0.32  $y^{-1}$ , based on mortality estimates given in Bruce *et al.* (2002).  $P/B$  for the mixed medium shark group was assumed to be 0.22  $y^{-1}$ , similar to dogsharks.

#### *Large sharks*

Large pelagic sharks (group 50) were not recorded in the trawl surveys and there are no estimates of their abundance. Therefore the biomass parameter was left free during balancing (with  $EE$  set to 0.9). This resulted in an estimate of 0.031  $t.km^{-2}$  for this group.  $P/B$  was set to 0.3  $y^{-1}$ , midway between the values for large pelagic sharks used by Bulman *et al.* (2006) and Cox *et al.* (2002). Diet of the large sharks group was based on estimates in Stevens (1984).

#### *Skates and rays*

Biomass of skates and rays was set to the same value used by Savina *et al.* (2008), which was based on the working of Fulton *et al.* (2007a), i.e., 0.42  $t.km^{-2}$ . Bulman *et al.* (2006) used *FishBase* to obtain a mean estimate of  $P/B = 0.35 y^{-1}$  for rays, based on six species, and this value was used in the present model.

#### **Inshore teleosts – mixed groups**

There were eight inshore mixed teleost groups, representing coastal and estuarine species (Table A1.1, groups 10-17). There was no data with which to estimate biomass for these groups and biomass was left free during balancing, with  $EE$  set to 0.95. Resulting biomasses estimated by Ecopath are shown in Table A1.3. Estimates of total mortality were available for some representative species. Scandol and Forrest (2001) and West (1993) were used to guide setting of  $P/B$  for inshore herbivorous, omnivorous and piscivorous demersal fish (groups 11-13; Table A1.3). Estimates were not available for representative species of other groups and the values used by Goldsworthy *et al.* (2003) were used to guide setting of  $P/B$  for small inshore omnivorous fish, and the inshore pelagic groups (Table A1.3).

### **Offshore and deep demersal teleosts – mixed groups**

There were four mixed offshore demersal teleost groups (offshore demersal omnivorous, offshore demersal piscivorous, deep demersal omnivorous and deep demersal piscivorous fishes), each containing a very large number of species (Appendix 2). Biomasses of offshore demersal omnivorous, offshore demersal piscivorous and deep demersal omnivorous fishes (groups 36-38, Table A1.3) were left free to be estimated by Ecopath during balancing. Biomass of deep demersal piscivorous fish (group 39) was fixed at  $0.5 \text{ y}^{-1}$ , to constrain its dynamics during Ecosim simulations as its biomass tended to become extremely large under fishing (see brief discussion in Fishery section). Such diverse groups contain species with a diverse range of life history attributes and mortalities.  $P/B$  was subjectively set to  $0.8 \text{ y}^{-1}$  for the omnivorous demersal groups (groups 36 and 38) and a slightly lower value ( $0.5 \text{ y}^{-1}$ ) for the offshore demersal piscivorous group, to represent the mixture of mortalities present (see Bulman *et al.* 2006).  $P/B$  for deep demersal piscivorous fish was set to  $0.22 \text{ y}^{-1}$ , consistent with estimates of total mortality reviewed by Bulman *et al.* (2006) for several deepwater species (e.g., *Helicolenus barathri*, *Genypterus blacodes*, *Hyperoglyphe antarctica*).

### **Offshore pelagic teleosts – mixed groups**

There is no data for biomass of pelagic omnivorous fish (group 40), such as jack mackerel (*Trachurus declivis*) and redbait (*Emmelichthys nitidus nitidus*), in this ecosystem. However, they have been shown to be important prey for many species of fish (Bulman *et al.* 2001) and marine mammals (Goldsworthy *et al.* 2003) on the shelf and slope. Therefore, biomass was set to a high value ( $1.5 \text{ t.km}^{-2}$ ) to allow the model to balance. Savina *et al.* (2008) based initial estimates of biomass of pelagic piscivorous fish on the working of Fulton *et al.* (2007a), who estimated historical total biomass of pelagic piscivores (group 41) to be approximately 20 300 t for the whole south and southeast Australian coast. Many of these species are highly migratory and several (e.g. many tunas and mackerels) are found in warmer waters. It was therefore assumed that a large percentage (80%) of this biomass occurred in the waters of NSW. To account for the highly migratory nature of many pelagic piscivorous species, 30% of the diet was set as ‘imported’ (i.e., occurring outside the modelled food web).  $P/B$  for omnivorous and piscivorous pelagic fish were set to 2 and  $0.7 \text{ y}^{-1}$  respectively, after Cox *et al.* (2002). Diets for large pelagic fish (group 41) was based upon published diets for southern bluefin tuna (*Thunnus*

*maccoyii*), skipjack, yellowfin and other tunas and large pelagic fishes (Young *et al.* 1997; Moteki *et al.* 2001; Tanabi 2001).

### **Mixed mesopelagic teleosts**

These species (which include members of the Myctophidae, Stomiidae and Malacosteidae families) may be extremely abundant, although they are not harvested. Mesopelagic teleosts are important prey items for a number of commercial species (Bulman 2001; Bulman *et al.* 2001) and several species of dogshark (Daley *et al.* 2002; Graham 2005; 2008). Bulman *et al.* (2006) cites localised Tasmanian studies reporting densities of more than 400 t.km<sup>-2</sup> (May and Blaber 1989). In the present model, biomass was left free and estimated by Ecopath (with EE set to 0.95). This resulted in an estimate of 10.7 t.km<sup>-2</sup>. *P/B* was set to 2 y<sup>-1</sup>, similar to values used by other authors for mesopelagic fishes (Gribble 2001; Goldsworthy *et al.* 2003; Heymans *et al.* 2004).

### **Individual teleost groups**

The model contained twelve additional teleost groups, representing commercially important taxa. Seven groups represented species currently under quota in the Commonwealth trawl fishery (Bruce *et al.* 2006): redfish (*Centroberyx affinis*), pink ling (*Genypterus blacodes*), gemfish (*Rexea solandri*), blue grenadier (*Macruronus novazelandiae*), silver trevally (*Pseudocaranx dentex*), tiger flathead (*Neoplatycephalus richardsoni*) and school whiting (*Sillago flindersi*). A further four groups each contained one or more related species currently under quota in the trawl fishery: (Warehou and Trevalla: *Seriolleva brama*, *S. punctata* and *Hyperoglyphphe antarctica*); Morwongs (*Nemadactylus macropterus* and *N. douglasii*); Dories (*Zeus faber*, *Zenopsis nebulosus*, *Cyttus australis*); and Ocean perch (*Helicolenus percoides* and *H. barathri*). See Bruce *et al.* (2002) and references therein for full review of biological and fisheries information on these species. Snapper (*Pagrus auratus*) were also included as a separate model group, even though they are not under any quota, as they are an important food and recreational species in NSW.

#### *Redfish*

Redfish (*C. affinis*) is an important species in the offshore trawl fishery and was one of the main species that led to expansion of the shelf trawl fishery into continental slope waters (Graham *et*

*al.* 2001). K. Rowling (NSW DPI, pers. comm) provided an estimate of 26 766 t ( $0.552 \text{ t.km}^{-2}$ ) of biomass of redfish for 1976 (based on the 1998 cohort analysis), and this estimate was used in the present model. Several studies have estimated total mortality  $Z$  for redfish. Using catch-curve analysis, Morison and Rowling (2001) estimated  $Z$  to be in the range  $0.12 \text{ y}^{-1} - 0.271 \text{ y}^{-1}$ , depending on sex, location and assumed age at recruitment, with an average of  $0.18 \text{ y}^{-1}$  for both sexes in all regions (age at recruitment = 4 y). Bruce *et al.* (2002) cite several studies that have estimated natural mortality  $M$  for redfish (although they provide no estimates of  $F$  or  $Z$ ). Three studies estimated  $M$  to be between  $0.1$  and  $0.15 \text{ y}^{-1}$ , with one study estimating  $M$  at  $0.01 \text{ y}^{-1}$ , which seems extremely low. Given the above biomass estimate, exploitation rate  $U$  (Catch/Biomass) appears to have been around  $0.18$  in 1976, when landings and discards were accounted for, implying that all of the mortality of redfish would have been due to fishing if  $Z = 0.18 \text{ y}^{-1}$  is correct. The estimate of  $P/B$  was therefore adjusted upward to  $0.22 \text{ y}^{-1}$  to allow for some natural mortality in the model. This is within the range of the estimates published in Morison and Rowling (2001).

### *Pink ling*

Populations of pink ling (*G. blacodes*) are distributed around the southern half of Australia. Unlike many other species in the *Kapala* surveys, pink ling was not observed to have undergone a large decrease in abundance between 1976 and 1996 (Andrew *et al.* 1997). Pooled across locations, catch rates of ling in 1996 were actually significantly larger than catch rates in 1976 in one of the four depth zones and were not significantly different in two other depth zones (Andrew *et al.* 1997). Analysis by Klaer (2006a) for the whole ling stock disagrees with this observation, suggesting that the stock decreased by between one-third and one-quarter between 1977 and 1985. The pink ling stock is thought to have been close to pristine in 1977 (Klaer 2006). This author reports virgin ling spawning stock biomass from NSW to Bass Strait to be between 27 000 and 36 000 tonnes. In the present study, it was assumed that one-quarter of the stock was in NSW and that the whole stock was 1.5 times the spawning stock. Using the mid-point of the estimates of Klaer (2006), this gives a rough estimate of 11 800 t ( $0.25 \text{ t.km}^{-2}$ ).  $P/B$  for pink ling was set to  $0.22 \text{ y}^{-1}$  (Bulman *et al.* 2006).

### *Gemfish*

Gemfish (*R. solandri*) have been targeted on the upper continental slope of NSW since the 1970s, although young gemfish have been caught on the shelf since 1915 (Kailola *et al.* 1993). Since the 1970s, most of the trawl catch has been taken during the winter spawning migration (Rowling 2001). The eastern stock of gemfish (which occurs off NSW) underwent a recruitment collapse in the late 1980s and has failed to show any significant recovery, despite severe catch restrictions (Rowling 1990; 1997; 1999; 2001). Stock assessments suggest that the stock had fallen to 35-40% of its virgin biomass by the mid 1980s (Rowling 2001). This author identifies three major phases of the gemfish fishery. The first phase, between the early 1970s and 1988 was characterised by large ( $> 3000$  t) catches and little to no regulation. Following a period of declining catch rates and reduction in the average size of fish, a 'global' Total Allowable Catch (TAC) was introduced in 1988. The TAC was converted to Individual Vessel Quotas (IVQs) in 1989. Following four years of poor recruitment, accompanied by declining catches, the targeted fishery was closed completely until 2000 (with a single re-opening in 1997). During this period, a limited amount of gemfish bycatch was allowed. Rowling (1999) discussed the uncertainty surrounding biomass of gemfish during the history of its assessment and reported estimates of 1979 mature biomass ranging from 5000 t to 28 000 t (Allen 1989), although he reported that the maximum estimate of spawning fish was downgraded to around 11 000 t in later analyses. In the present study, a total biomass (including males and immature fish) of 22 000 t ( $0.46 \text{ t.km}^{-2}$ ) was assumed for 1976. This may be too high. however, it was extremely difficult to obtain a plausible fit for this group (given the catch) with lower biomasses.  $P/B$  was assumed to be  $0.75 \text{ y}^{-1}$ . This is towards the lower end of the range of estimates of  $Z$  ( $0.59\text{-}1.22 \text{ y}^{-1}$ ) reported by Bruce *et al.* (2002).

### *Blue grenadier*

Blue grenadier (*M. novazelandiae*) are a deep water species ( $\sim 200 - 1000$  m) occurring in southern Australian waters from NSW to southern Western Australia (Kailola *et al.* 1993). Raw estimates of abundance of blue grenadier since 1979 were supplied to Savina *et al.* (2008) by the authors of Tuck *et al.* (2006), who converted these to total biomass, using growth parameters and assumed proportion of the stock in NSW. Their calculations resulted in a rough total biomass estimate of  $0.8 \text{ t.km}^{-2}$ , which was used in the present model.  $P/B$  was set to  $0.55 \text{ y}^{-1}$ , based on estimates of  $M$  ranging from  $0.2\text{-}0.31 \text{ y}^{-1}$  in Bruce *et al.* (2002) and the assumption that



sustainable  $F$  is similar to  $M$  ( $F$  was estimated to be around  $0.35 \text{ y}^{-1}$  in 1994 and does not seem to have had a major impact on the stock; Bruce *et al.* 2002). It is acknowledged that the estimate used here is higher than that used by Bulman *et al.* (2006), who used a value of  $P/B = 0.27 \text{ y}^{-1}$ .

#### *Warehou and trevalla*

This group contained several species of the family Centrolophidae (Appendix 2). However, the most abundant (and commercially important) species are blue warehou (*Seriolella brama*), spotted warehou (*Seriolella punctata*) and blue-eye trevalla (*Hyperoglyphe antarctica*). All three species feed primarily on pelagic tunicates (Kailola *et al.* 1993; Bulman *et al.* 2001). There have been no quantitative assessments for blue-eye (Bruce *et al.* 2002), limited assessments for spotted warehou and regular assessments for blue warehou since 1998 (Bruce *et al.* 2002). Age-structured abundance estimates of blue warehou since 1986 were made available by CSIRO to Savina *et al.* (2008). Based on this and rough proportions of the three species in the working of Fulton *et al.* (2007a), a very rough guesstimate of  $0.137 \text{ t km}^{-2}$  was made for 1976 biomass of the group. Natural mortality estimates range from  $0.2\text{--}0.33 \text{ y}^{-1}$  for these species (Bruce *et al.* 2002), although these authors do not give estimates of  $F$ . Smith and Wayte (2001) provided an estimate of  $Z = 1.2 \text{ y}^{-1}$  for spotted warehou and Bulman *et al.* (2006) used an estimate of  $0.2 \text{ y}^{-1}$  for blue-eye, based on estimates in Smith and Wayte (2004). Therefore an intermediate estimate of  $0.5 \text{ y}^{-1}$  was used in the present model.

#### *Trevallies*

This group mainly represents the quota species silver trevally (*Pseudocaranx dentex*), although it also contains other carangids of lesser commercial importance (Appendix 2). Silver trevally is an important commercial, recreational and export species in NSW, although its biology and population dynamics are poorly understood (Rowling and Raines 2000). Biomass in NSW in 1976 was assumed to be approximately  $0.22 \text{ t.km}^{-2}$ , approximately one-quarter of the estimate of total Australian biomass of the stock supplied to Savina *et al.* (2008) by J. Day (CSIRO).  $P/B$  was set to 0.25 after the estimate of  $Z$  given by Rowling and Raines (2000) for 1985-1990.

#### *Tiger flathead*

Tiger flathead (*N. richardsoni*) was one of the first commercially-fished species on the continental shelf of NSW and has been targeted since at least 1915 (Kailola *et al.* 1993; Klaer

2001). There has been some stock assessment of tiger flathead (Cui *et al.* 2001; Punt 2005), although the earlier assessment was hampered by issues of data quality (Bruce *et al.* 2002). Estimates of total southeast Australian biomass of tiger flathead in 1976 were supplied to Savina *et al.* (2008) by P. Cui (CSIRO; see Cui *et al.* 2006). Assuming that one-third of the total Australian stock occurred in NSW, a total biomass estimate of approximately 0.1 t.km<sup>-2</sup> was obtained. Total mortality of tiger flathead has been estimated to be between 0.46 and 1.1 y<sup>-1</sup> (Bruce *et al.* 2002). In the present study an intermediate  $P/B$  of 0.7 y<sup>-1</sup> was used.

### *School whiting*

School whiting are endemic to the southern Australian continental shelf, ranging from southern Queensland to southern Western Australia, with a large proportion of the catch landed in NSW waters (Kailola *et al.* 1993). There have been recent stock assessments for school whiting (see Punt *et al.* 2001), although these do not include estimates of abundance in the 1970s. Klaer (2006) used an estimate of 0.25 t.km<sup>-2</sup> for school whiting in 1961 and, in the absence of other information it was assumed here that the 1976 biomass was 0.13 t.km<sup>-2</sup> (approximately half of the 1961 biomass). Bruce *et al.* (2002) give a range of estimates of 1.1-1.5 y<sup>-1</sup> for  $Z$  for this species. Goldsworthy *et al.* (2003) estimated  $P/B$  to be 1.76 y<sup>-1</sup> and this estimate was used in the present model.

### *Snapper*

Snapper are distributed around Australia in subtropical and temperate shelf waters and are fished commercially and recreationally throughout Australia. Approximately half of the commercial catch historically came from NSW waters, although a large proportion of the catch now also comes from Western Australia (Kailola *et al.* 1993). There have been no formal stock assessments of snapper in NSW and biomass is unknown (but see Ferrell and Sumpton 1997). Therefore, biomass of this group was left to be estimated by Ecopath during balancing (see Table A1.3).  $P/B$  was set to 0.5 y<sup>-1</sup>, based on estimates of  $F$  and  $M$  supplied by J. Stewart (NSW DPI).

### *Morwongs*

The two main species in this group were jackass morwong (*Nemadactylus macropterus*) and grey morwong (*N. douglasii*). Jackass morwong are distributed all around southern Australia, while the range of grey morwong is restricted to the southeast (Kailola *et al.* 1993). Jackass

morwong have recently been assessed, with total spawning biomass since 1920 estimated at 5-yearly intervals (Fay 2006). The 1975 estimate from this study was inflated to account for non-spawning stock and grey morwong (assuming that the relative ratio of grey morwong to jackass morwong in the catch was representative of relative abundance of these two species). The resulting adjusted estimate of biomass used in the Ecopath model was  $0.55 \text{ t.km}^{-2}$ .  $P/B$  for this group was set to  $0.23 \text{ y}^{-1}$ , after Bulman *et al.* (2006) and Klaer and Thomson (2004).

### *Dories*

This group contains three main species: John dory (*Zeus faber*), mirror dory (*Zenopsis nebulosus*) and silver dory (*Cyttus australis*). These are highly predatory, commercially important species (Kailola *et al.* 1993; Bulman *et al.* 2001), with wide distribution on the Australian shelf. There have been few stock assessments of dories and there are no estimates of abundance for the 1970s. Biomass was therefore arbitrarily set at  $0.12 \text{ t.km}^{-2}$  ( $\sim 5000 \text{ t}$ ).  $P/B$  for this group was set to  $0.3 \text{ y}^{-1}$ , after Bulman *et al.* (2006)

### *Ocean perch*

This group contains two species, ‘shelf’ ocean perch (*Helicolenus percoides*) and ‘slope’ ocean perch (*H. barathri*), with the latter species occurring in deeper water. There have been no quantitative assessments of either species (Bruce *et al.* 2002). Bulman *et al.* (2006) used a biomass estimate of  $0.18 \text{ t.km}^{-2}$  for the slope species and  $0.27 \text{ t.km}^{-2}$  for the shelf species. An intermediate estimate of  $0.22 \text{ t.km}^{-2}$  was used here. Bulman *et al.* (2006) used an estimate of  $0.26 \text{ y}^{-1}$  for  $P/B$  of both species, while Goldsworthy *et al.* (2003) used  $0.59 \text{ y}^{-1}$ . Again, an intermediate value was used in the present model, with  $P/B$  set to  $0.4 \text{ y}^{-1}$ .

## **Invertebrates**

The model contained twelve invertebrate groups (listed in Table A1.1). There were two pelagic groups (zooplankton, gelatinous zooplankton), four groups of mixed benthic invertebrates (small, large, inshore, offshore) and five taxon-specific groups, representing commercially important invertebrates (inshore squid, inshore prawns, rock lobsters, offshore squid, royal red prawns). The final group, the non-commercial antlered and paddle crabs (*Dagnaudus petterdi* and *Ovalipes mollerii*), was included because they were observed to have increased significantly in the survey catch between 1976 and 1996 (Andrew *et al.* 1997). Except for lobsters and royal

red prawns, no attempt was made to enter biomass for invertebrates, which was estimated by Ecopath during balancing.

Estimates of  $P/B$  for zooplankton and gelatinous zooplankton (Table A1.1) were set to  $20\text{ y}^{-1}$  and  $10\text{ y}^{-1}$  respectively (Bradford-Grieve *et al.* 2003). The same source was used to set  $P/B$  for inshore and offshore squid (Table A1.1) to  $8\text{ y}^{-1}$  for both groups and for small benthic invertebrates (e.g., worms and small ( $< 2\text{ cm}$ ) crustaceans and gastropods) to  $10\text{ y}^{-1}$ .  $P/B$  for large inshore invertebrates (e.g., crabs, octopus, large gastropods) was set to  $2.5\text{ y}^{-1}$  Bulman *et al.* (2001).  $P/B$  for large offshore invertebrates was set slightly lower at  $1.8\text{ y}^{-1}$ .

### *Lobsters*

This group mainly represented the commercially important eastern rock lobster (*Jasus edwardsii*). Biomass of rock lobsters in 1990 has been estimated as  $0.04\text{ t.km}^{-2}$  and total mortality has been estimated at around  $0.25\text{ y}^{-1}$  (G. Liggins, NSW DPI, pers. comm.). In the absence of other information, the 1976 biomass estimate was assumed to be double the 1990s value ( $0.08\text{ t.km}^{-2}$ ).

### *Prawns*

There were two prawn groups in the model, one containing estuarine, coastal and shelf species (mainly *Metapenaeus macleayi* and *Melicertus plebejus*) and the other containing royal red prawns (*Haliporoides sibogae*), which inhabit deeper slope waters. Royal red prawns have been fished in NSW since 1975 and are mainly caught south of Sydney in depths from 400-600 m (Baelde 1991). They are a food source for deepwater dogsharks (Graham 2005). Royal red prawns are the main target for offshore prawn trawlers and the stock is under quota in the Commonwealth fishery. There have been no formal stock assessments and there are no estimates of spawning stock biomass (Bruce *et al.* 2002). Natural mortality ( $M$ ) for these prawns has been estimated to be between  $0.4$  and  $0.8\text{ y}^{-1}$  in the early 1990s, with total mortality ( $Z$ ) between  $1.2$  and  $1.6\text{ y}^{-1}$  (Bruce *et al.* 2002). Absent better information, it was therefore assumed that  $Z=1.6\text{ y}^{-1}$ , although it is acknowledged that it may have been lower in the early years. 1976 biomass was set to  $0.02\text{ t.km}^{-2}$  (Bruce *et al.* 2002) during the simulations.

Inshore prawns have a long history of exploitation in the estuarine and coastal fisheries of NSW (Ruello 1973; Glaister *et al.* 1990). Glaister *et al.* (1987) estimated natural mortality for king prawns to be of the order of  $0.06 \text{ week}^{-1}$  for king prawns (*M. plebejus*), although it is difficult to determine how to scale this up to an annual average estimate, as prawn productivity is highly influenced by local stochastic events such as rainfall, especially for school prawns (Ruello 1973; Glaister 1978). For simplicity, as inshore prawns were not of principal interest in this study,  $P/B$  was set to  $2.5 \text{ y}^{-1}$ , as for other large invertebrates.

#### *Antlered and paddle crabs*

During the 1976-7 surveys by FRV *Kapala*, catches of ‘trash’ species antlered and red paddle crabs were negligible and not recorded. They were, however, caught in large quantities during the 1996-7 surveys (averaging up to  $170 \text{ kg.h}^{-1}$ ) and outweighed fish in some tows (Andrew *et al.* 1997). Despite a complete lack of data on these species, they are included because they may have benefited in some way from the introduction of trawling on the continental shelf and slope.  $P/B$  was set to  $1.8 \text{ y}^{-1}$ , the same as for large slope benthic invertebrates.

### **Primary producers**

There were two groups representing primary producers: phytoplankton and macrophytes. There is a lack of data on marine primary production for the period covered by the model and the Ecosim model was not driven by any primary production series. Biomass of phytoplankton was set to  $9.5 \text{ t.km}^{-2}$ , to match the estimate obtained by Savina *et al.* (2008) in the Atlantis model of the same system.  $P/B$  was set to  $200 \text{ y}^{-1}$ , within the range of estimates used in more productive southern Australian waters ( $368 \text{ y}^{-1}$ , Bulman *et al.* 2006), the west Florida shelf ( $182 \text{ y}^{-1}$ ; Okey *et al.* 2004) and the Central Pacific Ocean ( $194 \text{ y}^{-1}$ , Cox *et al.* 2002). Absent any information about the biomass of macrophytes it was left free to be estimated by Ecopath.  $P/B$  was set to  $80 \text{ y}^{-1}$ , after Okey *et al.* (2004).

### **Fisheries**

The model explicitly considered five commercial fisheries: estuarine; lobster, inshore ocean; trap and line; and offshore trawl. Fisheries were resolved at this level to reflect the resolution of reporting in the historical catch database (Pease and Grinberg 1995), the only source of landings data prior to 1984. Since 1984, catch statistics have been resolved at much finer detail, reflecting

the more than 50 fishing gears currently in use in NSW. Construction of catch time series for model fitting therefore involved allocation of post-1984 catches from the various fishing gears into the categories above. For the period when the historical and current catch databases overlapped (1984-1992) there was excellent agreement between the two databases using this approach (Figure A1.2).

A fifth, recreational, fishery was included because it represents a significant proportion of fishing mortality for a number of species in NSW (Henry and Lyle 2003). There is no information about recreational catches in the 1970s, but it is assumed that they were probably large. Therefore, a hypothesised estimated of recreational catch (25% of inshore and estuarine commercial catch) was assumed for inshore species. Note that recent estimates of recreational catch for some inshore species in NSW have exceeded commercial catch (West and Gordon 1994; Henry and Lyle 2003) and, therefore, while the 25% assumed may seem large, it may not be an overestimate. There is no way to verify the magnitude of the recreational catch, but including a rough estimate of unreported catches is preferable to assuming no recreational catch at all (Pitcher *et al* 2002).

#### *Catch of offshore mixed teleost groups*

Some assumptions were necessary to determine catch for groups 36-39 (Appendix 2), as the historical catch database only included landings data for commercially important species. Most species would have been recorded as ‘trash’ or ‘miscellaneous’ fish or not recorded at all. Their prevalence in more recent databases implies that they must have been present in 1970s catches, although their relative abundance remains unknown. Even the *Kapala* database recorded only a few of these species in 1976, making comparison with 1996 difficult.

In order to drive the model with realistic catches, it was necessary to adjust historical catches to account for unreported landings (species landed under a miscellaneous category) and for unreported discards (caught but not landed). The general approach was to use the ISMP observer database to obtain the 1992 ratio of unreported species to reported species and apply that ratio to the reported 1976 landings for the group. For example, the offshore demersal omnivorous fish group (group 36) was represented by only one species in the 1976 reported landings (*Chelidonichthys kumu*), while there were 43 species from this group reported in the ISMP data.

There is no way to verify the appropriateness of applying a ratio from the 1990s to the 1970s, and it is certain to be incorrect. There are, however, no other data with which to estimate unreported catch of non-commercial species in the 1970s.

### *Discards*

Except for a few species (e.g., redfish: Rowling 1997), there are no data on discarding in the trawl fishery prior to 1992. After 1992, the Integrated Scientific Monitoring Program (ISMP) provided observer data from a subset of the trawl fleet. In the absence of pre-1992 discard data, the general approach was to apply the 1992 ratio of discarded catch to retained catch to years prior to 1992. For inshore fisheries, while there have been a number of studies on discarding in recent years (e.g., Liggins 1996; Liggins and Kennelly 1996; Liggins *et al.* 1996) the inshore model groups and fisheries were too aggregated for these estimates to be useful. Rather, an estimate of 5% of reported landings for each group was assumed.

### *Prices*

Sydney Fish Market wholesale prices were taken from the NSW DPI catch statistics database. The earliest available prices were from 1984. We made the simplifying assumption that, for each group, the average of prices from 1985-1996 was applicable throughout the simulation period.

## **Time series data and calibration**

There is a paucity of stock assessment for most species in the ecosystem and stock assessments are only done for the most commercially-valuable species (Bruce *et al.* 2002; Tuck and Smith 2004; Tuck and Smith 2006). For other stocks, only relative abundances observed in the three fishery-independent surveys (1976, 1979, 1996) were available (Andrew *et al.* 1997; Graham *et al.* 2001). See Chapter 6, Table 6.2 for list of time series used to calibrate the models.

Calibration was done in the Ecosim model by driving the model with fishing mortality rate or catches and adjusting foraging arena ‘vulnerability’ parameters until predicted relative abundance trends matched observed relative abundance trends as closely as possible. Note that in the absence of time series of historical fishing mortality, historical catches can be used to ‘drive’ an Ecosim model, where historical catches are subtracted from Ecosim’s simulated stock size at each time step. This is sometimes called ‘conditioning on catch’. A possible disadvantage of this

approach is that catch is a result of the interaction between fishing effort and abundance, and ignoring this interaction assumes that catches have purely compensatory impacts on stock size - i.e., when simulated stock size declines, the fixed catches can cause progressively larger calculated fishing mortality rates (Christensen *et al.* 2005). However, in the absence of any other information about fishing mortality, conditioning on catches is the only available option. It was possible to obtain an approximate time series of fishing mortality for the stocks which had a continuous series of biomass estimates for the whole simulation period (gemfish, redfish, trevallies, tiger flathead). Also, a time series of fishing mortality was available for blue grenadier (supplied by G. Tuck, CSIRO). In addition, the time series of  $F$  obtained for the dogshark *Centrophorus harrissoni* (this thesis, Chapter 5, age at first harvest = 3) was used to drive abundance of all dogsharks except spiky dogshark. This species did not decline between 1976 and 1996 (Graham *et al.* 2001) and it was therefore assumed that its fishing mortality rate had been half of that of the other dogshark species. For other shark groups, fishing mortality was assumed to be 1.5 times that of dogsharks. This was an arbitrary assumption and helped to improve the fit of the model.

### **Final note**

It is important to note that after vulnerability parameters were adjusted, the time series used to drive the model were removed and not used in either the policy search or the subsequent analyses of the effects of the alternative optimal fishing efforts on the ecosystem (Chapter 6). That is, the time series of catch, biomass and fishing mortality rate needed for calibration of the model were not of further interest in this study, which was focused on the hypothetical historical management scenarios presented in Chapter 6. This represents a departure from the usual approach with ecosystem models, of calibrating a model then projecting it into the future under alternative scenarios to give current management advice. The present model, however, was constructed for the purpose of performing the analyses presented in Chapter 6, which were intended to: (i) illustrate trade-offs among alternative historical fishing policies in the same ecosystem; and (ii) allow comparison of alternative ecosystem models. The striking changes in abundance on the continental slope between 1976 and 1996 (Andrew *et al.* 1997); Graham *et al.* 2001) and the possibility of using dogsharks to illustrate the differential productivity trade-off (Walters and Martell 2004) made this an interesting study area and period for this purpose. However, the large subjective assumptions, at every level, in this model make it suitable only for



illustrative purposes. It is not, therefore, appropriate to use this model to discuss real changes in the ecosystem under the historical management regime. All further results from this model are presented in Chapter 6.

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## Tables

**Table A1.1.** Functional groups of the Ecopath model. See Appendix 2 for more complete lists of representative species / taxonomic groups.

Group	Group name	Example species / taxonomic groups
1	Phytoplankton	Phytoplankton
2	Macrophytes	Macroalgae, seagrass
3	Zooplankton	Copepods, Euphausiids
4	Gelatinous zooplankton	Chaetognaths, salps, ctenophores, jellyfish
5	Inshore squid	<i>Loligo chinensis</i> , <i>Sepioteuthis australis</i>
6	Small inshore benthic invertebrates	Small crustaceans, gastropods, polychaetes, sipunculids
7	Large inshore benthic invertebrates	Octopus, cuttlefish, large gastropods, crabs
8	Inshore prawns	<i>Metapenaeus macleayi</i> , <i>Melicertus plebejus</i>
9	Lobsters	<i>Jasus edwardsii</i>
10	Small inshore omnivorous fish	Tetraodontidae, Gobiidae, Syngnathidae, Apogonidae
11	Inshore demersal herbivorous fish	<i>Mugil cephalus</i> , <i>Girella tricuspidata</i>
12	Inshore demersal omnivorous fish	<i>Acanthopagrus australis</i> , <i>Sillago ciliata</i> , Monacanthidae
13	Inshore demersal piscivorous fish	<i>Platycephalus fuscus</i> , <i>Epinephelus</i> spp. Anguillidae,
14	Small inshore pelagic piscivorous fish	<i>Arripis trutta</i> , <i>Pomatomus saltatrix</i>
15	Small inshore pelagic omnivorous fish	<i>Engraulis australis</i> , <i>Sardinops neopilchardus</i>
16	Large inshore pelagic piscivorous fish	<i>Argyrosomus hololepidotus</i> , <i>Seriola lalandi</i> , <i>Sarda australis</i>
17	Large inshore pelagic omnivorous fish	<i>Scomber australasicus</i> , <i>Trachurus novaezelandiae</i>
18	Small slope benthic invertebrates	Small crustaceans, gastropods, polychaetes
19	Large slope benthic invertebrates	Octopus, cuttlefish, large gastropods, crabs
20	Royal red prawns	<i>Haliporoides sibogae</i>
21	Antlered and paddle crabs	<i>Ovalipes mollerii</i> , <i>Dagnaudus petterdi</i>
22	Offshore squid	<i>Nototodarus gouldi</i>
23	Redfish	<i>Centroberyx affinis</i>
24	Pink Ling	<i>Genypterus blacodes</i>
25	Gemfish	<i>Rexia solandri</i>
26	Blue Grenadier	<i>Macruronus novaezelandiae</i>
27	Warehou and Trevalla	<i>Seriola brama</i> , <i>S. punctata</i> , <i>Hyperoglyphe antarctica</i>
28	Trevallies	<i>Pseudocaranx dentex</i> , <i>Caranx</i> spp.
29	Tiger flathead	<i>Neoplatycephalus richardsoni</i>
30	School whiting	<i>Sillago flindersi</i>
31	Snapper	<i>Pagrus auratus</i>
32	Morwongs	<i>Nemadactylus macropterus</i> , <i>Nemadactylus douglasi</i>
33	Dories	<i>Zeus faber</i> , <i>Zenopsis nebulosus</i>

**Table A1.1 cont.**

<b>Group</b>	<b>Group name</b>	<b>Example species / taxonomic groups</b>
34	Ocean perch	<i>Helicolenus percoides</i> , <i>Helicolenus barathri</i>
35	Mesopelagic fish	Myctophidae, Melanostomiidae, Malacosteidae
36	Offshore demersal omnivorous fish	<i>Nelusetta ayraudi</i> , <i>Lutjanus</i> spp., <i>Lethrinus</i> spp., <i>Lepidotrigla</i> spp.
37	Offshore demersal piscivorous fish	<i>Trichiurus lepturus</i> , <i>Conger wilsoni</i> , <i>Polyprion americanus</i> , <i>Platycephalus bassensis</i>
38	Deep demersal omnivorous fish	<i>Beryx splendens</i> , <i>Caelorinchus</i> spp., Triglidae, Peristediidae,
39	Deep demersal piscivorous fish	<i>Ruvettus pretiosus</i> , <i>Rexea antefurcata</i> , <i>Cyttus traversi</i>
40	Offshore pelagic omnivorous fish	<i>Trachurus declivis</i> , <i>Emmelichthys nitidus nitidus</i>
41	Offshore pelagic piscivorous fish	<i>Katsuwonus pelamis</i> , <i>Xiphias gladius</i> , <i>Thunnus albacares</i> , <i>Acanthocybium solandri</i>
42	Spiky dogshark	<i>Squalus megalops</i>
43	Harrison and southern dogshark	<i>Centrophorus harrissoni</i> , <i>Centrophorus zeehaani</i>
44	Greeneye dogshark	<i>Squalus mitsukurii</i>
45	Endeavour dogshark	<i>Centrophorus moluccensis</i>
46	Other dogsharks	<i>Centroscymnus plunketi</i> , <i>Centroscymnus crepidater</i> , <i>Etmopterus</i> spp., <i>Dalatias licha</i>
47	Gummy shark	<i>Mustelus antarcticus</i>
48	School shark	<i>Galeorhinus galeus</i>
49	Other medium sharks	<i>Squatina</i> spp., Pristiophoridae, Scyliorhinidae, Heterodontidae, Triakidae, <i>Chimaera</i> spp.
50	Large sharks	<i>Galeocerdo cuvier</i> , <i>Carcharhinus</i> spp., <i>Sphyrna</i> spp., Lamnidae,
51	Skates/rays	Rajidae, Torpedinidae, Narcinidae, Urolophidae, Dasyatidae
52	Toothed whales	<i>Delphinus delphis</i> , <i>Tursiops truncatus</i> , <i>Stenella</i> spp., <i>Mesoplodon</i> spp.
53	Baleen whales	<i>Eubalaena australis</i> , <i>Megaptera novaeangliae</i> , <i>Balaenoptera</i> spp.
54	Australian fur seal	<i>Arctocephalus pusillus doriferus</i>
55	Penguins	<i>Eudyptula minor</i>
56	Seabirds	<i>Phalacrocorax</i> spp., <i>Pelecanus conspicillatus</i> , <i>Larus</i> spp. <i>Sterna</i> spp. (see Ganassin and Gibbs 2005)
57	Detritus	Dead matter, carcasses, discarded fish

**Table A1.2.** Diet matrix used in the model. Based on SPCC (1981); Bulman *et al.* (2001; 2006); Kailola *et al.* (1993) and other sources referred to in the text.

Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15
Phytoplankton	0.85	0.33		0.20				0.05	0.12				0.002
Macrophytes				0.10	0.20			0.04	0.19	0.04	0.01		0.22
Zooplankton	0.005	0.31	0.65	0.15				0.05	0.09	0.09	0.05	0.19	0.54
Gel zooplankton		0.03	0.28					0.05		0.01		0.00	0.05
Inshore squid			0.06									0.10	
S insh ben invert					0.45	0.30	0.40	0.75	0.22	0.63	0.32	0.12	0.05
L insh ben invert							0.10	0.05		0.04	0.20	0.02	
Inshore prawns									0.05	0.10	0.15	0.05	0.01
Rock Lobsters					0.0001								
Small insh omn fish			0.01						0.002	0.06	0.10		
Insh dem herb fish											0.10	0.20	
Insh dem omn fish										0.001	0.05	0.002	
Insh dem pisc fish												0.07	
S insh pel pisc fish												0.02	
S insh pel omn fish			0.01								0.01	0.16	0.06
L insh pel pisc fish													
L insh pel omn fish											0.01	0.05	
S slope benthic inverts													
L slope benthic inverts													
Royal red prawns													
Antlered and paddle crabs													
Offshore squid													
Redfish													
Pink Ling													
Gemfish													
Blue Grenadier													
Warehou and Trevalla													
Trevallies													
Tiger flathead													
School whiting													
Snapper												0.02	
Morwongs													
Dories													
Ocean perch													
Mesopelagics													
Offshore dem omn fish													
Offshore dem pisc fish													
Deep dem omn fish													
Deep dem pisc fish													
Offshore pel omn fish													
Offshore pel pisc fish													
Spiky dogshark													
Harrison dogshark													
Greeneye dogshark													
Endeavour dogshark													
Other dogsharks													
Gummy shark													
School shark													
Other medium sharks													
Large sharks													
Skates/rays													
Toothed whales													
Baleen whales													
Aus fur seal													
Penguins													
Seabirds													
Detritus													
(carcasses/discards)	0.15	0.33		0.55	0.35	0.70	0.50	0.01	0.25	0.03			0.01
Import									0.08	0.003	0.01		0.07

**Table A1.2 cont.**

Prey \ Predator	16	17	18	19	20	21	22	23	24	25	26	27	28
Phytoplankton			0.44										
Macrophytes			0.13										0.001
Zooplankton	0.12	0.38	0.09	0.11			0.53	0.47			0.00	0.30	0.03
Gel zooplankton	0.01						0.19	0.01			0.00	0.60	0.01
Inshore squid	0.11	0.04											
S insh ben invert	0.02	0.53			0.20			0.02					0.61
L insh ben invert	0.01												
Inshore prawns	0.13	0.01						0.05		0.05			0.00
Rock Lobsters									0.01				
Small insh omn fish		0.01											
Insh dem herb fish	0.22												
Insh dem omn fish	0.05												
Insh dem pisc fish	0.07												
S insh pel pisc fish													0.01
S insh pel omn fish	0.17	0.001					0.01	0.07					0.05
L insh pel pi sc fish													
L insh pel omn fish	0.05												0.01
S slope benthic inverts			0.04	0.33	0.50	0.20		0.04					0.14
L slope benthic inverts				0.001					0.15			0.04	
Royal red prawns										0.01		0.00	
Antlered and paddle crabs													
Offshore squid							0.07		0.07	0.14	0.05	0.05	
Redfish													
Pink Ling								0.00	0.05		0.01		
Gemfish											0.02		
Blue Grenadier									0.37		0.02		
Warehou and Trevalla	0.00								0.01				
Trevallies													
Tiger flathead									0.05				
School whiting	0.00												
Snapper	0.01												
Morwongs	0.02								0.04				
Dories	0.01								0.03				
Ocean perch											0.02		
Mesopelagics		0.02					0.21	0.19	0.00		0.75	0.01	
Offshore dem omn fish								0.001	0.15	0.10			
Offshore dem pisc fish									0.08	0.68	0.03		
Deep dem omn fish											0.09		
Deep dem pisc fish										0.01	0.004		
Offshore pel omn fish								0.15					0.06
Offshore pel pisc fish													
Spiky dogshark													
Harrison dogshark													
Greeneye dogshark													
Endeavour dogshark													
Other dogsharks													
Gummy shark													
School shark													
Other medium sharks													
Large sharks													
Skates/rays													
Toothed whales													
Baleen whales													
Aus fur seal													
Penguins													
Seabirds													
Detritus													
(carcasses/discards)		0.02	0.29	0.56	0.30	0.80							0.08
Import													

**Table A1.2 cont.**

Prey \ Predator	29	30	31	32	33	34	35	36	37	38	39	40	41
Phytoplankton												0.10	
Macrophytes													
Zooplankton		0.01	0.57	0.11				0.12	0.03	0.10		0.54	0.001
Gel zooplankton						0.18	0.09	0.06	0.05	0.12		0.20	0.04
Inshore squid			0.16			0.10							
S insh ben invert		0.05	0.07	0.30									0.00
L insh ben invert				0.16									0.00
Inshore prawns		0.15	0.05	0.05	0.02	0.05							
Rock Lobsters													
Small insh omn fish		0.04			0.02	0.02							
Insh dem herb fish													
Insh dem omn fish													
Insh dem pisc fish													
S insh pel pisc fish													
S insh pel omn fish	0.04			0.08									0.08
L insh pel pisc fish													0.004
L insh pel omn fish					0.05								0.01
S slope benthic inverts	0.01	0.57	0.01	0.20		0.03	0.89	0.34	0.03	0.25			
L slope benthic inverts	0.05			0.10		0.11		0.25	0.08	0.07	0.17		
Royal red prawns					0.01								
Antlered and paddle crabs													
Offshore squid					0.08			0.12		0.11	0.17		0.05
Redfish	0.01				0.04								
Pink Ling	0.05												
Gemfish	0.03				0.05	0.05							
Blue Grenadier	0.04								0.01		0.02		
Warehou and Trevalla													
Trevallies													0.00
Tiger flathead	0.01				0.06								
School whiting	0.06				0.06	0.06							
Snapper													0.03
Morwongs	0.01								0.00				
Dories	0.02												
Ocean perch					0.01	0.01					0.01		
Mesopelagics	0.07				0.09		0.02	0.04	0.19	0.20	0.03		0.04
Offshore dem omn fish	0.34				0.20	0.30			0.52	0.09		0.17	
Offshore dem pisc fish	0.07				0.23	0.05			0.05				
Deep dem omn fish	0.09					0.04					0.39		
Deep dem pisc fish													
Offshore pel omn fish	0.00	0.05	0.14		0.09				0.05		0.21		0.41
Offshore pel pisc fish													0.02
Spiky dogshark													
Harrison dogshark													
Greeneye dogshark													
Endeavour dogshark													
Other dogsharks													
Gummy shark													
School shark													
Other medium sharks													
Large sharks													
Skates/rays													
Toothed whales													
Baleen whales													
Aus fur seal													
Penguins													
Seabirds													
Detritus													
(carcasses/discards)	0.09	0.13				0.01		0.06		0.05			
Import													0.32

**Table A1.2 cont.**

Prey \ Predator	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Phytoplankton															
Macrophytes															
Zooplankton										0.02		0.20			
Gel zooplankton															
Inshore squid														0.29	0.14
S insh ben invert										0.13					0.05
L insh ben invert						0.15		0.02		0.13					
Inshore prawns	0.06									0.09			0.05		0.01
Rock Lobsters						0.04		0.00	0.01						
Small insh omn fish										0.12					
Insh dem herb fish								0.02	0.05		0.19				0.05
Insh dem omn fish								0.02	0.01	0.04	0.05		0.01		
Insh dem pisc fish										0.01	0.01		0.01		
S insh pel pisc fish								0.01	0.05	0.01	0.05		0.07		
S insh pel omn fish											0.10	0.10	0.05		0.25
L insh pel pisc fish								0.01	0.05		0.05		0.01		
L insh pel omn fish	0.02							0.01	0.05		0.05		0.03		0.05
S slope benthic inverts					0.10	0.12				0.10					
L slope benthic inverts	0.11	0.16	0.28	0.13	0.32	0.34	0.01	0.19		0.32	0.04				
Royal red prawns	0.01		0.03	0.01	0.01										
Antlered crabs	0.01	0.01	0.01	0.01	0.00		0.00	0.01		0.01					
Offshore squid	0.29	0.07	0.17	0.10	0.16	0.10		0.08	0.05		0.09	0.10	0.15	0.14	0.10
Redfish	0.02	0.02	0.01				0.01	0.05	0.02				0.02		
Pink Ling	0.00							0.01	0.04	0.00					
Gemfish	0.02	0.001							0.05						
Blue Grenadier	0.08		0.06					0.06							
Warehou and Trevalla								0.01	0.01		0.05		0.01		
Trevallies	0.01							0.01	0.10	0.00	0.04		0.01		0.001
Tiger flathead									0.01		0.01		0.00		
School whiting	0.10							0.11	0.01	0.01	0.05		0.05	0.01	0.01
Snapper						0.06		0.01	0.05		0.05		0.02		0.01
Morwongs	0.00								0.05				0.02		
Dories								0.01	0.01				0.01		
Ocean perch								0.00		0.00					
Mesopelagics		0.70	0.05	0.69	0.15	0.09	0.12								
Offshore dem omn fish	0.22		0.19				0.11	0.01	0.01	0.01					
Offshore dem pisc fish								0.05	0.01						
Deep dem omn fish		0.05	0.19	0.05	0.22		0.06	0.07							
Deep dem pisc fish					0.01			0.03	0.01						
Offshore pel omn fish						0.02	0.48	0.14	0.09		0.05	0.10	0.50	0.56	0.24
Offshore pel pisc fish						0.04	0.14		0.09		0.05				
Spiky dogshark	0.01								0.03		0.001		0.001		
Harrison dogshark		0.00						0.00							
Greeneye dogshark			0.01					0.00							
Endeavour dogshark				0.01				0.00							
Other dogsharks					0.01										
Gummy shark									0.01						
School shark									0.002						
Other medium sharks									0.04						
Large sharks								0.005	0.03						
Skates/rays								0.02	0.03						
Toothed whales									0.001		0.001				
Baleen whales											0.001				
Aus fur seal									0.001		0.001				
Penguins															
Seabirds									0.04		0.001				
Detritus (carcasses/discards)	0.05					0.10									0.10
Import											0.09	0.50			



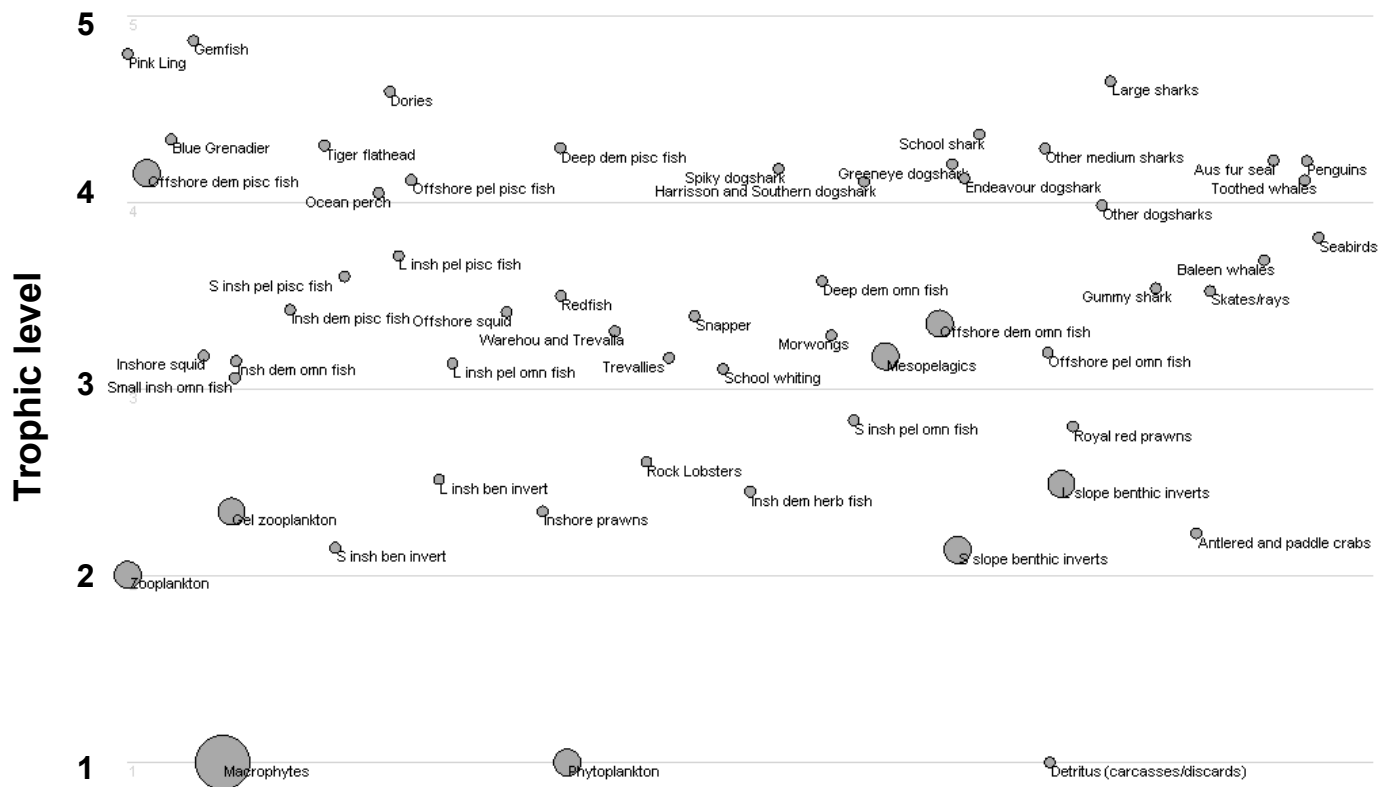
**Table A1.3.** Parameters of the model after balancing. Parameters shown in bold were estimated by Ecopath.

Group name	Trophic level	Biomass (t.km <sup>-1</sup> )	Production/ Biomass (y <sup>-1</sup> )	Consumption./ Biomass (y <sup>-1</sup> )	Ecotrophic efficiency	Prod./ Cons.
Phytoplankton	<b>1</b>	9.5	200	-	<b>0.99</b>	-
Macrophytes	<b>1</b>	<b>46.00</b>	8.00	-	0.50	-
Zooplankton	<b>2.01</b>	<b>25.20</b>	20.00	57.00	0.50	<b>0.35</b>
Gelatinous zooplankton	<b>2.34</b>	<b>6.65</b>	10.00	30.00	0.50	<b>0.33</b>
Inshore squid	<b>3.18</b>	<b>0.05</b>	8.00	<b>40.00</b>	0.95	0.20
Small insh. benthic invertebrates	<b>2.15</b>	<b>0.68</b>	10.00	<b>50.00</b>	0.75	0.20
Large insh. benthic invertebrates	<b>2.52</b>	<b>0.19</b>	2.50	<b>12.50</b>	0.75	0.20
Inshore prawns	<b>2.35</b>	<b>0.31</b>	2.50	<b>12.50</b>	0.95	0.20
Lobsters	<b>2.61</b>	0.08	0.25	<b>1.25</b>	0.54	0.20
Small inshore omnivorous fish	<b>3.06</b>	<b>0.12</b>	2.00	<b>10.00</b>	0.95	0.20
Inshore demersal herbivorous fish	<b>2.45</b>	<b>0.41</b>	0.60	<b>3.00</b>	0.95	0.20
Inshore demersal omnivorous fish	<b>3.15</b>	<b>0.15</b>	0.60	<b>3.00</b>	0.95	0.20
Inshore demersal piscivorous fish	<b>3.43</b>	<b>0.10</b>	0.50	<b>2.50</b>	0.95	0.20
Small inshore pelagic pisc. fish	<b>3.6</b>	<b>0.06</b>	0.75	<b>3.75</b>	0.95	0.20
Small insh. pel. omnivorous fish	<b>2.83</b>	<b>0.55</b>	2.30	<b>11.50</b>	0.95	0.20
Large inshore pelagic pisc. fish	<b>3.71</b>	<b>0.06</b>	0.60	<b>3.00</b>	0.95	0.20
Large inshore pelagic omn. fish	<b>3.14</b>	<b>0.15</b>	0.76	<b>3.80</b>	0.95	0.20
Small slope benthic invertebrates	<b>2.14</b>	<b>26.84</b>	10.00	<b>50.00</b>	0.75	0.20
Large slope benthic invertebrates	<b>2.49</b>	<b>9.84</b>	1.80	<b>9.00</b>	0.75	0.20
Royal red prawns	<b>2.8</b>	0.02	1.60	<b>8.00</b>	<b>0.80</b>	0.20
Antlered and paddle crabs	<b>2.23</b>	<b>0.01</b>	1.80	<b>9.00</b>	0.95	0.20
Offshore squid	<b>3.42</b>	<b>1.36</b>	8.00	<b>40.00</b>	0.95	0.20
Redfish	<b>3.5</b>	0.55	0.22	<b>1.10</b>	<b>0.90</b>	0.20
Pink Ling	<b>4.8</b>	0.25	0.22	<b>1.10</b>	<b>0.91</b>	0.20
Gemfish	<b>4.87</b>	0.46	0.75	<b>3.75</b>	<b>0.42</b>	0.20
Blue Grenadier	<b>4.34</b>	0.80	0.55	<b>2.75</b>	<b>0.70</b>	0.20
Warehou and Trevalla	<b>3.31</b>	0.14	0.50	<b>2.50</b>	<b>0.55</b>	0.20
Trevallies	<b>3.17</b>	0.22	0.25	<b>1.25</b>	<b>0.60</b>	0.20
Tiger flathead	<b>4.31</b>	0.10	0.70	<b>3.50</b>	<b>0.64</b>	0.20
School whiting	<b>3.11</b>	0.13	1.73	<b>8.65</b>	<b>0.62</b>	0.20
Snapper	<b>3.39</b>	<b>0.24</b>	0.50	<b>2.50</b>	0.95	0.20
Morwongs	<b>3.29</b>	0.55	0.23	<b>1.15</b>	<b>0.30</b>	0.20
Dories	<b>4.59</b>	0.12	0.30	<b>1.50</b>	<b>0.79</b>	0.20
Ocean perch	<b>4.05</b>	0.22	0.40	<b>2.00</b>	<b>0.72</b>	0.20
Mesopelagic fish	<b>3.18</b>	<b>10.67</b>	2.00	<b>10.00</b>	0.95	0.20
Offshore demersal omn.s fish	<b>3.35</b>	<b>11.43</b>	0.80	<b>4.00</b>	0.95	0.20
Offshore demersal pisc. fish	<b>4.16</b>	<b>4.05</b>	0.50	<b>2.50</b>	0.95	0.20
Deep demersal omnivorous fish	<b>3.58</b>	<b>0.58</b>	1.00	<b>5.00</b>	0.95	0.20
Deep demersal piscivorous fish	<b>4.29</b>	0.50	0.22	<b>1.10</b>	<b>0.85</b>	0.20
Offshore pelagic omnivorous fish	<b>3.2</b>	1.50	2.00	<b>10.00</b>	<b>0.73</b>	0.20
Offshore pelagic piscivorous fish	<b>4.12</b>	0.35	1.50	<b>7.50</b>	<b>0.13</b>	0.20

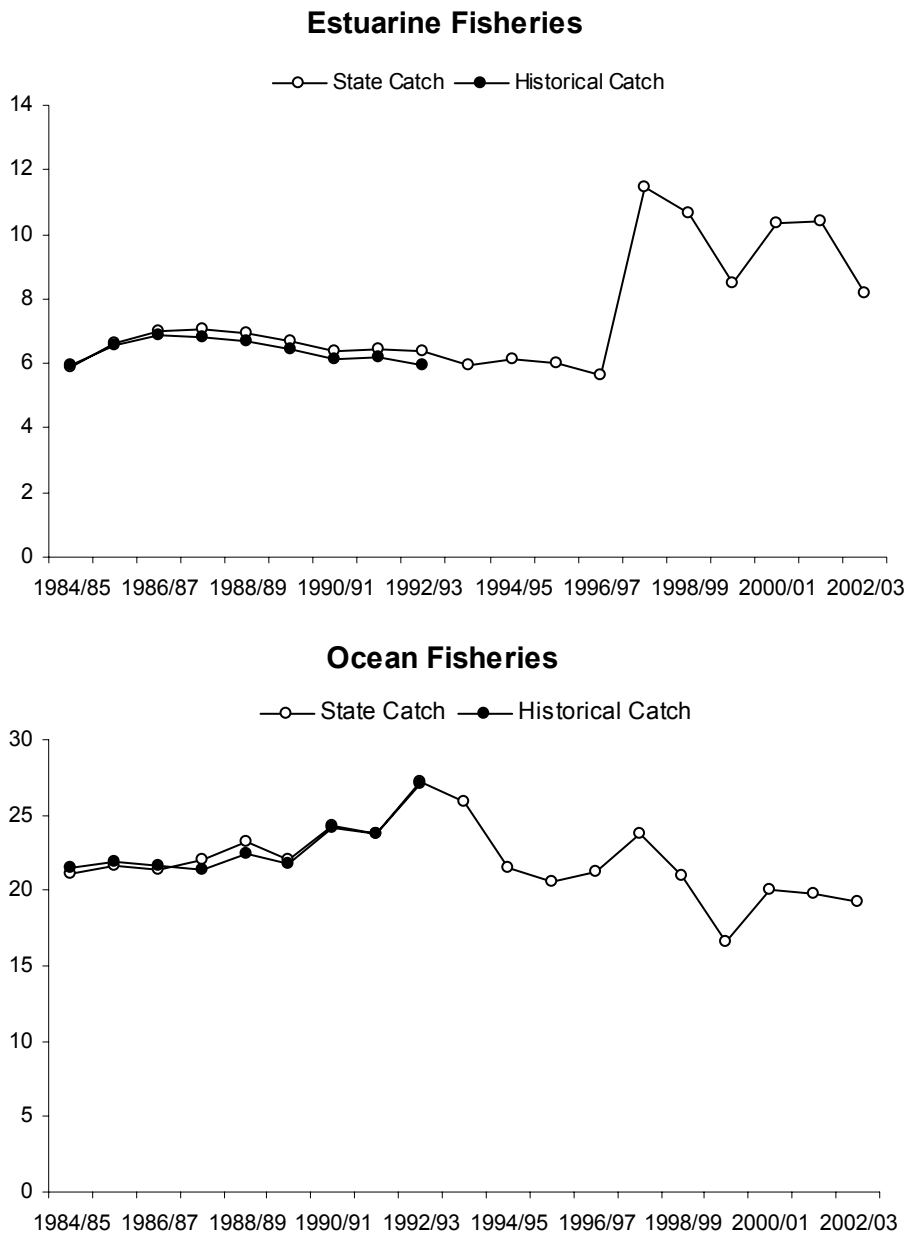
**Table A1.3 cont.**

<b>Group name</b>	<b>Trophic level</b>	<b>Biomass (t.km<sup>-1</sup>)</b>	<b>Production/Biomass (y<sup>-1</sup>)</b>	<b>Consumption./Biomass (y<sup>-1</sup>)</b>	<b>Ecotrophic efficiency</b>	<b>Prod./Cons.</b>
Spiky dogshark	<b>4.18</b>	0.35	0.21	<b>1.05</b>	<b>0.32</b>	0.20
Harrison and southern dogshark	<b>4.11</b>	0.40	0.21	<b>1.05</b>	<b>0.34</b>	0.20
Greeneye dogshark	<b>4.21</b>	0.14	0.20	<b>1.00</b>	<b>0.21</b>	0.20
Endeavour dogshark	<b>4.13</b>	0.04	0.21	<b>1.05</b>	<b>0.27</b>	0.20
Other dogsharks	<b>3.99</b>	0.05	0.25	<b>1.25</b>	<b>0.13</b>	0.20
Gummy shark	<b>3.54</b>	0.02	0.38	<b>1.89</b>	<b>0.52</b>	0.20
School shark	<b>4.37</b>	0.01	0.32	<b>1.60</b>	<b>0.58</b>	0.20
Other medium sharks	<b>4.29</b>	0.17	0.22	<b>1.10</b>	<b>0.87</b>	0.20
Large sharks	<b>4.65</b>	<b>0.03</b>	0.30	<b>1.50</b>	0.90	0.20
Skates/rays	<b>3.53</b>	0.42	0.35	<b>1.75</b>	0.61	0.20
Toothed whales	<b>4.12</b>	0.01	0.02	13.00	<b>0.77</b>	<b>0.002</b>
Baleen whales	<b>3.69</b>	0.03	0.02	13.00	<b>0.23</b>	<b>0.002</b>
Australian fur seal	<b>4.23</b>	0.01	0.06	16.00	<b>0.94</b>	<b>0.004</b>
Penguins	<b>4.22</b>	0.00	1.00	80.00	<b>0.00</b>	<b>0.01</b>
Seabirds	<b>3.81</b>	0.00	1.00	80.00	<b>0.47</b>	<b>0.01</b>
Detritus (carcasses/discards)	<b>1</b>	1.00	-	-	<b>0.48</b>	-

## Figures



**Figure A1.1a.** Trophic level of the model's 56 living functional groups. See Table A1.1 for description of groups and A1.2 for diet composition. Size of the circle indicates relative biomass.



**Figure A1.2.** Comparison of total catch (thousands of tonnes) reported from estuarine and ocean fisheries in the NSW historical catch database (Pease and Grinberg 1995) and the current NSW State catch database.

## Appendix 2. List of species and taxonomic groups in the marine ecosystem of NSW.

See Appendix 1 text for sources. See Appendix 1, Table A1.1 for description of Ecopath groups.

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
3	28 702000	Euphausiidae	<i>Euphausiidae</i> - undiff.	Krill
4	35 000000	-	<i>Asciadiacea</i> - undiff.	Ascidians (group code)
4	11 120000	-	<i>Scyphozoa</i> - all spp	Jellyfish
5	23 617000	Loliginidae	<i>Loliginidae</i> - undiff.	Squid, loliginids
5	23 617010	Loliginidae	<i>Loliolus noctiluca</i>	Squid, Bottle
5	23 617901	Loliginidae	<i>Photololigo chinensis complex</i>	Broad squid
5	23 617901a	Loliginidae	<i>Photololigo etheridgei broad</i>	Squid, Broad
5	23 617901b	Loliginidae	<i>Photololigo sp4 slender</i>	Squid, Slender
6	23 226001	-	<i>Anadara (Anadara) trapezia</i>	Sydney cockle
6	11 173000	-	<i>Order Alcyonacea</i> - undiff.	Octocorals (group code)
6	23 359001	Donacidae	<i>Donax (Plebidonax) deltoides</i>	Pipi
6	23 220000	Mytilidae	<i>Mytilidae</i> - undiff.	Mussel, Unspecified
6	23 220001	Mytilidae	<i>Mytilus edulis</i>	Mussel, Blue
6	22 056000	Nereididae	<i>Nereididae</i> - undiff.	Beachworms
6	28 756901	Palaemonidae	<i>Macrobrachium</i> spp	Shrimp, Weed
6	28 030000	Stomatopoda	<i>Order Stomatopoda</i> - undiff.	Shrimp, Mantis
6	28 803004	Thalassinidae	<i>Thalassinidae</i> - undiff.	Nipper
7	28 910001	-	<i>Chaceon bicolor</i>	Crystal crab
7	25 102000	-	<i>Class Asteroidea</i> - undiff.	Starfish (group code)
7	25 200000	-	<i>Class Echinoidea</i> - undiff.	Sea urchins (family code)
7	24 000000	-	<i>Class Gastropoda</i>	Shellfish, Unspecified
7	25 246000	-	<i>Echinidae</i> - undiff.	Urchins
7	25 000000	-	<i>Echinodermata</i> - undiff.	Echinoderms (group code)
7	28 820003	-	<i>Linuparus sordidus</i>	White champagne lobster
7	28 840003	-	<i>Munida haswelli</i>	Long-armed craylet
7	23 659000	-	<i>Octopodidae</i> - undiff.	Octopuses (family code)
7	23 650000	-	<i>Order Octopoda</i> - undiff.	Octopods (group code)
7	23 270000	-	<i>Pectinidae</i> - undiff.	Scallops (family code)
7	23 607000	-	<i>Sepiidae</i> - undiff.	Cuttlefish (family code)
7	27 000000	-	<i>Subphylum Crustacea</i> - undiff.	Crustaceans (group code)
7	28 821008	-	<i>Thenus orientalis</i>	Sandbug
7	28 850000	Brachyura	<i>Brachyura</i> - undiff.	Crab, Unspecified
7	25 211001	Diadematidae	<i>Centrostephanus rodgersii</i>	Urchins, purple
7	24 038006	Haliotidae	<i>Haliotis rubra</i>	Abalone, Blacklip
7	23 659901	Octopodidae	<i>Octopus</i> spp	Octopus
7	23 257001	Ostreidae	<i>Crassostrea gigas</i>	Oyster, Pacific
7	23 257002	Ostreidae	<i>Ostrea (Eostrea) angasi</i>	Oyster, Drift
7	23 257000	Ostreidae	<i>Ostreidae</i> - undiff.	Oyster, Unspecified
7	23 257006	Ostreidae	<i>Saccostrea glomerata</i>	Oyster, Sydney rock
7	28 835000	Paguridae	<i>Paguridae</i> - undiff.	Crab, Hermit
7	23 270001	Pectinidae	<i>Amusium balloti</i>	Scallop, Queensland
7	23 270901	Pectinidae	<i>Amusium</i> spp	Scallop, Saucer

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
7	23 270007	Pectinidae	<i>Pecten fumatus</i>	Scallop, Tasmanian
7	28 911001	Portunidae	<i>Charybdis (Charybdis) feriata</i>	Crab, Coral
7	28 911019	Portunidae	<i>Charybdis (Charybdis) miles</i>	A swimmer crab
7	28 911018	Portunidae	<i>Charybdis (Gonioneptunus) bimaculata</i>	A swimmer crab
7	28 911003	Portunidae	<i>Ovalipes australiensis</i>	Crab, two spot
7	28 911000	Portunidae	<i>Portunidae</i> - undiff.	Crab, Blue Swimmer & Sand
7	28 911005	Portunidae	<i>Portunus (Portunus) pelagicus</i>	Crab, Blue Swimmer
7	28 911006	Portunidae	<i>Portunus (Portunus) sanguinolentus</i>	Crab, Three-spotted
7	28 911008	Portunidae	<i>Scylla serrata</i>	Crab, Mud
7	28 821010	Scyllaridae	<i>Ibacus brucei</i>	Bug, Bruce's
7	28 821019	Scyllaridae	<i>Ibacus chacei</i>	Bug, smooth
7	28 821004	Scyllaridae	<i>Ibacus peronii</i>	Bug, Balmain
7	28 821901	Scyllaridae	<i>Ibacus</i> spp	Bug, Balmain western
7	28 821000	Scyllaridae	<i>Scyllaridae</i> - undiff.	Lobster, Unspecified
7	28 821902	Scyllaridae	<i>Scyllarides</i> spp	Lobster, Shovelnose
7	28 821006	Scyllaridae	<i>Scyllarides squamosus</i>	Lobster, Slipper
7	23 607001	Sepiidae	<i>Sepia apama</i>	Cuttlefish, Giant
7	23 607901	Sepiidae	<i>Sepia</i> spp	Cuttlefish
7	25 247001	Toxopneustidae	<i>Helicoidaris erythrogramma</i>	Urchins, green
7	25 247002	Toxopneustidae	<i>Helicoidaris tuberculata</i>	Urchins, red
7	24 045003	Turbinidae	<i>Turbo (Ninella) torquatus</i>	Turban Snail, Sydney
7	24 045901	Turbinidae	<i>Turbo</i> spp	Snails, Turban
7	24 207000	Volutidae Cymbiolinae	<i>Volutidae</i> - undiff.	Bailer Shell
8	28 711047	-	<i>Melicertus latisulcatus</i>	Western king prawn
8	28 711055	-	<i>Trachypenaeus (Trachysalambria) curvirostris</i>	Southern rough prawn
8	28 711050	Penaeidae	<i>Fenneropenaeus merguensis</i>	Prawn, banana
8	28 711046	Penaeidae	<i>Marsupenaeus japonicus</i>	Prawn, Blue-tailed tiger
8	28 711048	Penaeidae	<i>Melicertus longistylus</i>	Prawn, red spot
8	28 711052	Penaeidae	<i>Melicertus plebejus</i>	Prawn, Eastern King
8	28 711022	Penaeidae	<i>Metapenaeus bennettiae</i>	Prawn, Greasyback
8	28 711026	Penaeidae	<i>Metapenaeus endeavouri</i>	Prawn, Endeavour
8	28 711029	Penaeidae	<i>Metapenaeus macleayi</i>	Prawn, School
8	28 711000	Penaeidae	<i>Penaeidae</i> - undiff.	Prawn, Unspecified Ocean
8	28 711044	Penaeidae	<i>Penaeus esculentus</i>	Prawn, Tiger
8	28 711051	Penaeidae	<i>Penaeus monodon</i>	Prawn, Leader
9	28 784000	-	<i>Astacidea and Palinura</i> - undiff.	Lobsters (group code)
9	28 820001	Panuliridae	<i>Jasus (Jasus) edwardsii</i>	Lobster, Southern Rock
9	28 820002	Panuliridae	<i>Jasus (Sagmariasus) verreauxi</i>	Lobster, Eastern Rock
9	28 820004	Panuliridae	<i>Linuparus trigonus</i>	Lobster, barking
9	28 820013	Panuliridae	<i>Panulirus versicolor</i>	Crayfish, Painted
10	37 990004	-	<i>aquarium fish</i> - undiff.	Aquarium fish
10	37 437020	Acanthuridae	<i>Acanthurus xanthopterus</i>	Surgeonfish, Ring-tailed
10	37 437035	Acanthuridae	<i>Prionurus microlepidotus</i>	Surgeonfish, Sawtail
10	37 437000	Acanthuridae, Zanclidae	<i>Acanthuridae, Zanclidae</i> - undiff.	Surgeonfish
10	37 310012	Ambassidae	<i>Ambassis jacksoniensis</i>	Perchlet, Port Jackson

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
10	37 310018	Ambassidae	<i>Ambassis marianus</i>	Perchlet, Yellow
10	37 327008	Apogonidae	<i>Apogon fasciatus</i>	Soldierfish, Four-banded
10	37 327009	Apogonidae	<i>Apogon nigripinnis</i>	Soldierfish, Black-finned
10	37 327032	Apogonidae	<i>Siphamia cephalotes</i>	Siphonfish, Woods
10	37 327017	Apogonidae	<i>Siphamia roseigaster</i>	Siphonfish, Pink-breasted
10	37 246000	Atherinidae	<i>Atherinidae</i> - undiff.	Hardyhead
10	37 465900	Balistidae	<i>Balistidae</i> - undiff.	triggerfishes (group code)
10	37 408058	Blenniidae	<i>Omobranchus anolius</i>	Blenny, Oyster
10	37 408073	Blenniidae	<i>Petroscirtes lupus</i>	Blenny, Wolf
10	37 408076	Blenniidae	<i>Plagiotremus tapeinosoma</i>	Blenny
10	37 460049	Bothidae	<i>Chascanopsetta lugubris</i>	A lefteye flounder
10	37 346000	Caesionidae, Lutjanidae	<i>Caesionidae, Lutjanidae</i> - undiff.	Fusilier
10	37 279001	Centriscidae	<i>Centriscops humerosus</i>	A bellowsfish
10	37 365037	Chaetodontidae	<i>Chaetodon ephippium</i>	Coralfish, Saddled
10	37 365039	Chaetodontidae	<i>Chaetodon guentheri</i>	Butterfly Fish
10	37 365040	Chaetodontidae	<i>Chaetodon kleinii</i>	Butterfly Fish
10	37 365011	Chaetodontidae	<i>Heniochus acuminatus</i>	Bullfish, Feather-finned
10	37 374001	Cirrhitidae	<i>Cirrhitichthys aprinus</i>	Hawkfish, Common
10	37 416007	Clinidae	<i>Cristiceps australis</i>	Weedfish, Crested
10	37 416024	Clinidae	<i>Heteroclinus whiteleggii</i>	Weedfish
10	37 469013	Diodontidae	<i>Dicotylichthys punctulatus</i>	Porcupine Fish, Three-barred
10	37 469000	Diodontidae	<i>Diodontidae</i> - undiff.	Porcupine fishes (family code)
10	37 429020	Eleotridae	<i>Gobiomorphus australis</i>	Gudgeon, striped
10	37 429002	Eleotridae	<i>Philypnodon grandiceps</i>	Gudgeon, Flat-headed
10	37 366001	Enoplosidae	<i>Enoplosus armatus</i>	Old Wife
10	37 327010	Epigonidae	<i>Epigonus denticulatus</i>	A cardinalfish
10	37 327018	Epigonidae	<i>Epigonus robustus</i>	A cardinalfish
10	37 327035	Epigonidae	<i>Epigonus telescopus</i>	Cardinal fish
10	37 278001	Fistulariidae	<i>Fistularia commersonii</i>	Flutemouth
10	37 278002	Fistulariidae	<i>Fistularia petimba</i>	Flutemouth, Smooth
10	37 278000	Fistulariidae	<i>Fistulariidae</i> - undiff.	Flutemouths (family code)
10	37 320000	Glaucosomatidae	<i>Glaucosomatidae</i> - undiff.	Perch, Unspecified
10	37 428030	Gobiidae	<i>Acanthogobius flavimanus</i>	Goby, Oriental
10	37 428008	Gobiidae	<i>Arenigobius bifrenatus</i>	Goby, Bridled
10	37 428002	Gobiidae	<i>Arenigobius frenatus</i>	Goby, Half-bridled
10	37 428069	Gobiidae	<i>Bathygobius krefftii</i>	Goby,
10	37 428093	Gobiidae	<i>Cryptocentroides cristatus</i>	Goby,
10	37 428141	Gobiidae	<i>Favonigobius exquisitus</i>	Goby, Exquisite sand
10	37 428005	Gobiidae	<i>Favonigobius lateralis</i>	Goby,
10	37 428184	Gobiidae	<i>Lubricogobius ornatus</i>	Goby,
10	37 428192	Gobiidae	<i>Mugilogobius stigmaticus</i>	Goby,
10	37 428199	Gobiidae	<i>Nesogobius</i> sp	Goby,
10	37 428009	Gobiidae	<i>Pseudogobius olorum</i>	Goby,
10	37 428246	Gobiidae	<i>Redigobius macrostoma</i>	Goby,
10	37 361008	Kyphosidae	<i>Girella zebra</i>	Zebra fish
10	37 361005	Kyphosidae	<i>Microcanthus strigatus</i>	Stripy

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
10	37 361004	Kyphosidae	<i>Scorpis aequipinnis</i>	A sweep
10	37 361009	Kyphosidae	<i>Scorpis lineolata</i>	Sweep
10	37 384025	Labridae	<i>Austrolabrus maculatus</i>	Wrasse, Black-spotted
10	37 384095	Labridae	<i>Coris picta</i>	Combfish
10	37 384028	Labridae	<i>Labroides dimidiatus</i>	Wrasse, Blue Streak
10	37 384041	Labridae	<i>Notolabrus gymnogenis</i>	Wrasse, Crimson Banded
10	37 384150	Labridae	<i>Pseudolabrus guentheri</i>	Gunther's Rainbowfish
10	37 384151	Labridae	<i>Pseudolabrus luculentus</i>	Wrasse, Lord Howe Island
10	37 341012	Leiognathidae	<i>Leiognathus moretoniensis</i>	Pony Fish
10	37 398002	Leptoscopidae	<i>Crapatalus munroi</i>	Sandfish
10	37 348001	Lobotidae	<i>Lobotes surinamensis</i>	Tripletail
10	37 465065	Monacanthidae	<i>Paramonacanthus otisensis</i>	Leatherjacket, dusky
10	37 347000	Nemipteridae	<i>Nemipteridae</i> - undiff.	Bream, threadfin
10	37 466000	Ostraciidae	<i>Ostraciidae</i> - undiff.	Box Fish
10	37 466004	Ostraciontidae	<i>Lactoria cornuta</i>	Cowfish
10	37 356002	Pentacerotidae	<i>Monodactylus argenteus</i>	Diamond Fish
10	37 311033	Percichthyidae	<i>Macquaria colonorum</i>	Perch, Estuary
10	37 311034	Percichthyidae	<i>Macquaria novemaculeata</i>	Australian bass
10	37 390001	Pinguipedidae	<i>Parapercis allporti</i>	A sandperch
10	37 316018	Plesiopidae	<i>Trachinops taeniatus</i>	Hula
10	37 372002	Pomacentridae	<i>Chromis hypsilepis</i>	Puller, Brown
10	37 372049	Pomacentridae	<i>Chromis nitida</i>	Puller, Shining
10	37 372083	Pomacentridae	<i>Mecaenichthys immaculatus</i>	Damselfish, Mauve
10	37 372096	Pomacentridae	<i>Parma polylepis</i>	Parma
10	37 372097	Pomacentridae	<i>Parma unifasciata</i>	Parma, One-barred
10	37 372000	Pomacentridae	<i>Pomacentridae</i> - undiff.	Damselfishes
10	37 372111	Pomacentridae	<i>Pomacentrus coelestis</i>	Damselfish, Blue
10	37 245020	Pseudomugilidae	<i>Pseudomugil signifer</i>	Pacific blue-eye
10	37 103001	Retropinnidae	<i>Prototroctes maraena</i>	A southern grayling
10	37 386000	Scaridae	<i>Scaridae</i> - undiff.	Parrotfish
10	37 287048	Scorpaenidae	<i>Centropogon australis</i>	Fortesque
10	37 311007	Serranidae	<i>Epinephelus coioides</i>	Cod, Estuary
10		Soleidae	<i>Aseraggodes macleayanus</i>	Sole, many-banded
10	37 282010	Syngnathidae	<i>Hippocampus abdominalis</i>	Seahorse, Big-bellied
10	37 282027	Syngnathidae	<i>Hippocampus whitei</i>	Seahorse, Whites
10	37 282029	Syngnathidae	<i>Solegnathus spinosissimus</i>	A pipefish/seahorse
10	37 282017	Syngnathidae	<i>Stigmatopora argus</i>	Pipefish, Spotted
10	37 282018	Syngnathidae	<i>Stigmatopora nigra</i>	Pipefish, Wide-bodied
10	37 282000	Syngnathidae	<i>Syngnathidae</i> - undiff.	pipefishes and seahorses
10	37 282008	Syngnathidae	<i>Urocampus carinirostris</i>	Pipefish, Hairy
10	37 321008	Terapontidae	<i>Bidyanus bidyanus</i>	Perch, silver
10	37 467014	Tetraodontidae	<i>Arothron stellatus</i>	Puffer Fish
10	37 467038	Tetraodontidae	<i>Canthigaster callisterna</i>	Toby
10	37 467043	Tetraodontidae	<i>Canthigaster valentini</i>	Toby, Black-saddled
10	37 467001	Tetraodontidae	<i>Contusus richiei</i>	A toadfish
10	37 467008	Tetraodontidae	<i>Lagocephalus inermis</i>	Toado
10	37 467045	Tetraodontidae	<i>Liosaccus aerobaticus</i>	Toado
10	37 467050	Tetraodontidae	<i>Reicheltia halsteadi</i>	A toadfish
10	37 467000	Tetraodontidae	<i>Tetraodontidae</i> - undiff.	Toadfish



Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
10	37 467056	Tetraodontidae	<i>Torquigener altipinnis</i>	A toadfish
10	37 467030	Tetraodontidae	<i>Torquigener pleurogramma</i>	Toado, Weeping
10	37 467061	Tetraodontidae	<i>Torquigener squamicauda</i>	Toado, Brush-tailed
11	37 361006	Kyphosidae	<i>Girella elevata</i>	Drummer, Black
11	37 361007	Kyphosidae	<i>Girella tricuspidata</i>	Luderick
11	37 361001	Kyphosidae	<i>Kyphosus sydneyanus</i>	Drummer, Southern Silver
11	37 381001	Mugilidae	<i>Aldrichetta forsteri</i>	Mullet, yellow-eye
11	37 381004	Mugilidae	<i>Liza argentea</i>	Mullet, Fantail
11	37 381002	Mugilidae	<i>Mugil cephalus</i>	Mullet, Sea
11	37 381000	Mugilidae	<i>Mugilidae</i> - undiff.	Mullet, Unspecified
11	37 381003	Mugilidae	<i>Myxus elongatus</i>	Mullet, Sand
11	37 381011	Mugilidae	<i>Myxus petardi</i>	Mullet, Pink-eye
11	37 381009	Mugilidae	<i>Valamugil georgii</i>	Mullet, Silver
11	37 355001	Mullidae	<i>Upeneichthys lineatus</i>	Mullet, Red
12	37 188005	Ariidae	<i>Arius graeffei</i>	Catfish, Forktailed
12	37 188010	Ariidae	<i>Arius midgleyi</i>	Silver cobbler
12	37 465000	Balistidae, Monacanthidae	<i>Balistidae, Monacanthidae</i> - undiff.	Leatherjacket, Unspecified
12	37 460012	Bothidae	<i>Engyprosopon grandisquamum</i>	Flounder, Spiny-headed
12	37 460001	Bothidae	<i>Lophonectes gallus</i>	Flounder, Crested
12	37 461000	Bothidae & Pleuronectidae	<i>Pleuronectidae</i> - undiff.	Flounder, Unspecified
12	37 142001	Chanidae	<i>Chanos chanos</i>	Milkfish
12	37 375001	Chironomidae	<i>Chironemus marmoratus</i>	Kelp Fish
12	37 463000	Cynoglossidae	<i>Cynoglossidae</i> - undiff.	tongue soles (family code) incl lemon sole
12	37 463001	Cynoglossidae	<i>Paraplagusia bilineata</i>	Sole, Lemon-tongue
12	37 990015	Cynoglossidae, Soleidae	<i>Cynoglossidae &amp; Soleidae</i>	Sole, mixed
12	37 349007	Gerreidae	<i>Gerres erythrouros</i>	A silver biddy
12	37 349005	Gerreidae	<i>Gerres subfasciatus</i>	Silver biddy
12	37 350000	Haemulidae	<i>Haemulidae</i> - undiff.	Sweetlip, Unspecified
12	37 350012	Haemulidae	<i>Plectorhinchus gibbosus</i>	Sweetlips, Brown
12	37 350023	Haemulidae	<i>Plectorhinchus picus</i>	Sweetlips, Golden spotted
12	37 361000	Kyphosidae, Scorpididae	<i>Kyphosidae, Scorpididae</i> - undiff.	
12	37 384002	Labridae	<i>Achoerodus gouldii</i>	Western blue groper
12	37 384043	Labridae	<i>Achoerodus viridis</i>	Groper, Blue
12	37 384055	Labridae	<i>Bodianus bimaculatus</i>	A wrasse
12	37 384042	Labridae	<i>Choerodon venustus</i>	Tuskfish, Venus
12	37 384105	Labridae	<i>Eupetrichthys angustipes</i>	Wrasse, Slender
12	37 384000	Labridae	<i>Labridae</i> - undiff.	Wrasse, mixed
12	37 384020	Labridae	<i>Pictilabrus laticlavius</i>	Wrasse, Senator
12	37 384167	Labridae	<i>Thalassoma lunare</i>	Wrasse, Moon
12	37 465043	Monacanthidae	<i>Acanthaluteres spilomelanurus</i>	Leatherjacket, Bridled
12	37 465002	Monacanthidae	<i>Acanthaluteres vittiger</i>	Leatherjacket, Toothbrush
12	37 465025	Monacanthidae	<i>Brachaluteres jacksonianus</i>	Leatherjacket, Pigmy
12	37 465039	Monacanthidae	<i>Eubalichthys bucephalus</i>	Leatherjacket, Black Reef
12	37 465003	Monacanthidae	<i>Eubalichthys mosaicus</i>	Leatherjacket, Deep-bodied
12	37 465008	Monacanthidae	<i>Meuschenia australis</i>	A leatherjacket

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12	37 465059	Monacanthidae	<i>Meuschenia trachylepis</i>	Leatherjacket, Yellowfin
12	37 465009	Monacanthidae	<i>Monacanthus chinensis</i>	Leatherjacket, Fan-bellied
12	37 465063	Monacanthidae	<i>Paraluteres prionurus</i>	Leatherjacket, Black-saddled
12	37 465017	Monacanthidae	<i>Paramonacanthus oblongus</i>	Leatherjacket, Hair-finned
12	37 465007	Monacanthidae	<i>Scobinichthys granulatus</i>	Leatherjacket, Rough skinned
12	37 465037	Monacanthidae	<i>Thamnaconus degeni</i>	Leatherjacket, Degen's
12	37 465038	Monacanthidae	<i>Thamnaconus modestoides</i>	A leatherjacket
12	37 355000	Mullidae	<i>Mullidae</i> - undiff.	Goatfish
12	37 355028	Mullidae	<i>Parupeneus rubescens</i>	Goatfish, Black spot
12	37 355014	Mullidae	<i>Upeneus tragula</i>	Goatfish, Bar-tailed
12	37 076002	Nemichthyidae	<i>Avocettina acuticeps</i>	A snipe eel
12	37 385005	Odacidae	<i>Neodax balteatus</i>	Whiting, Rock
12	37 068019	Ophichthidae	<i>Malvoliophis pinguis</i>	Eel, Snake
12	37 068001	Ophichthidae	<i>Ophisurus serpens</i>	Eel, Serpent
12	37 460009	Paralichthyidae	<i>Pseudorhombus arsius</i>	Flounder, Large-toothed
12	37 460004	Paralichthyidae	<i>Pseudorhombus duplciocellatus</i>	Flounder, northern
12	37 460002	Paralichthyidae	<i>Pseudorhombus jenynsii</i>	A sand flounder
12	37 460032	Paralichthyidae	<i>Pseudorhombus</i> sp	Flounder, Pseudorhombus
12	37 460031	Paralichthyidae	<i>Pseudorhombus tenuirastrum</i>	Flounder, Smooth
12	37 461001	Pleuronectidae	<i>Ammotretis rostratus</i>	Flounder, Long-snouted
12	37 461003	Pleuronectidae	<i>Rhombosolea tapirina</i>	Flounder, Greenback
12	37 192001	Plotosidae	<i>Cnidoglanis macrocephalus</i>	Catfish, Estuary
12	37 192004	Plotosidae	<i>Euristhmus lepturus</i>	Catfish, Longtailed
12	37 192002	Plotosidae	<i>Plotosus lineatus</i>	Catfish, Striped
12	37 990017	Plotosidae, Ariidae	<i>Catfishes</i> , unspecified	Catfish, Unspecified
12	37 363001	Scatophagidae	<i>Scatophagus multifasciatus</i>	Butterfish
12	37 354022	Scieanidae	<i>Johnius australis</i>	Jewfish
12	37 287018	Scorpaenidae	<i>Gymnapistes marmoratus</i>	Cobbler
12	37 287040	Scorpaenidae	<i>Pterois volitans</i>	Firefish, Red
12	37 311907	Serranidae	<i>Serranidae</i> subfam	Anthiinae
12	37 385009	Sillaginidae	<i>Haletta semifasciata</i>	Whiting, Grass
12	37 330000	Sillaginidae	<i>Sillaginidae</i> - undiff.	Whiting, Unspecified
12	37 330001	Sillaginidae	<i>Sillaginodes punctata</i>	Whiting, King George
12	37 330003	Sillaginidae	<i>Sillago analis</i>	A whiting
12	37 330010	Sillaginidae	<i>Sillago ciliata</i>	Whiting, Sand
12	37 330015	Sillaginidae	<i>Sillago maculata</i>	Whiting, Trumpeter
12	37 330005	Sillaginidae	<i>Sillago robusta</i>	Whiting, Stout
12	37 462017	Soleidae	<i>Brachirus nigra</i>	Sole, Black
12	37 462029	Soleidae	<i>Pardachirus hedleyi</i>	Sole, peacock
12	37 353004	Sparidae	<i>Acanthopagrus australis</i>	Bream, Yellowfin
12	37 353003	Sparidae	<i>Acanthopagrus butcheri</i>	Bream, Black
12	37 353015	Sparidae	<i>Allotaius spariformis</i>	Sea Bream, Cape Morton
12	37 342001	Sparidae	<i>Brama brama</i>	Bream, Ray's
12	37 353002	Sparidae	<i>Dentex tumifrons</i>	Bream, Cape Morton
12	37 353013	Sparidae	<i>Rhabdosargus sarba</i>	Tarwhine
12	37 353000	Sparidae	<i>Sparidae</i> - undiff.	Breams (family code)

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12	37 464000	Triacanthidae, Triacanthodidae	<i>Triacanthidae, Triacanthodidae</i> - undiff.	Tripodfish
13	37 056001	Anguillidae	<i>Anguilla australis</i>	Eel, Shortfin River
13	37 056002	Anguillidae	<i>Anguilla reinhardtii</i>	Eel, Longfin River
13	37 056000	Anguillidae	<i>Anguillidae</i> - undiff.	Eel, Unspecified
13	37 235000	Belonidae	<i>Belonidae</i> - undiff.	Longtom
13	37 224011	Moridae	<i>Pseudophycis breviuscula</i>	Cod, Bearded
13	37 063003	Muraenesocidae	<i>Muraenesox bagio</i>	Eel, Pike
13	37 060006	Muraenidae	<i>Gymnothorax prasinus</i>	Eel, Moray
13	37 311087	Percichthyidae	<i>Maccullochella macquariensis</i>	Cod, Trout
13	37 296021	Platycephalidae	<i>Platycephalus arenarius</i>	Flathead, Northern Sand
13	37 296007	Platycephalidae	<i>Platycephalus caeruleopunctatus</i>	Flathead, eastern blue spot
13	37 296004	Platycephalidae	<i>Platycephalus fuscus</i>	Flathead, Dusky
13	37 296006	Platycephalidae	<i>Platycephalus laevigatus</i>	rock flathead
13	37 296036	Platycephalidae	<i>Platycephalus longispinis</i>	Flathead, Spiny
13	37 296038	Platycephalidae	<i>Platycephalus marmoratus</i>	Flathead, Marbled
13	37 287008	Scorpaenidae	<i>Scorpaena papillosa</i>	Cod, Red Rock
13	37 311090	Serranidae	<i>Acanthistius ocellatus</i>	Wirrah
13	37 311035	Serranidae	<i>Acanthistius serratus</i>	Cod, Wirrah
13	37 311083	Serranidae	<i>Cephalopholis miniata</i>	Cod, Coral
13	37 311140	Serranidae	<i>Cephalopholis sexmaculata</i>	Cod, Saddled rock
13	37 311044	Serranidae	<i>Cromileptes altivelis</i>	Cod, Barramundi
13	37 311077	Serranidae	<i>Epinephelus daemeli</i>	Cod, Black
13	37 311147	Serranidae	<i>Epinephelus ergastularius</i>	A rockcod
13	37 311040	Serranidae	<i>Epinephelus quoyanus</i>	Cod, honeycomb
13	37 311060	Serranidae	<i>Epinephelus septemfasciatus</i>	Cod, Bar
13	37 311086	Serranidae	<i>Epinephelus undulatostratus</i>	Cod, Maori
13	37 070001	Synbranchidae	<i>Diastobranchus capensis</i>	A basketwork eel
14	37 344002	Arripidae	<i>Arripis trutta</i>	Australian salmon
14	37 344004	Arripidae	<i>Arripis truttaceus</i>	Western Australian salmon
14	37 334000	Pomatomidae	<i>Pomatomidae</i> - undiff.	Tailor (family code)
14	37 334002	Pomatomidae	<i>Pomatomus saltatrix</i>	Tailor
15	37 097001	Argentinidae	<i>Argentina australis</i>	A herring smelt
15	37 085000	Clupeidae	<i>Clupeidae</i> - undiff.	Pilchard, mixed
15	37 085023	Clupeidae	<i>Herklotsichthys castelnaui</i>	Herring, Southern
15	37 085026	Clupeidae	<i>Hyperlophus translucidus</i>	Sprat, Translucent
15	37 085005	Clupeidae	<i>Hyperlophus vittatus</i>	Sprat, Sandy (whitebait)
15	37 085002	Clupeidae	<i>Sardinops neopilchardus</i>	Pilchard
15	37 086001	Engraulidae	<i>Engraulis australis</i>	Anchovy, Australian
15	37 102006	Galaxiidae	<i>Galaxias maculatus</i>	Whitebait (Glass fish)
15	37 234006	Hemiramphidae	<i>Arrhamphus sclerolepis</i>	Garfish, River
15	37 234000	Hemiramphidae	<i>Hemiramphidae</i> - undiff.	Garfish, Unspecified
15	37 234007	Hemiramphidae	<i>Hemiramphus far</i>	Garfish, shortbill
15	37 234014	Hemiramphidae	<i>Hyporhamphus australis</i>	Garfish, eastern sea
15	37 234001	Hemiramphidae	<i>Hyporhamphus melanochir</i>	Garfish, Southern sea
15	37 354003	Sciaenidae	<i>Protonibea diacanthus</i>	black jewfish
15	37 311052	Serranidae	<i>Lepidoperca occidentalis</i>	A rockcod
16	37 337046	Carangidae	<i>Scomberoides lysan</i>	Queenfish
16	37 337025	Carangidae	<i>Seriola dumerili</i>	Amberjack

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16	37 337007	Carangidae	<i>Seriola hippos</i>	Samson Fish
16	37 337006	Carangidae	<i>Seriola lalandi</i>	Kingfish, Yellowtail
16	37 354001	Sciaenidae	<i>Argyrosomus hololepidotus</i>	mullet
16	37 354903	Sciaenidae	<i>Argyrosomus japonicus</i> and <i>Protonibea diacanthus</i>	Mullet
16	37 441020	Scombridae	<i>Sarda australis</i>	Bonito
17	37 337003	Carangidae	<i>Trachurus novaezelandiae</i>	Yellowtail
17	37 337907	Carangidae	<i>Trachurus</i> spp	Horse mackerels
17	37 441001	Scombridae	<i>Scomber australasicus</i>	Mackerel, Blue
18	11 229000	-	Order Actinaria - undiff.	Burrowing sea anemone
18	10 000000	-	Porifera - undiff.	Sponge
19	25 400000	-	Class Holothuroidea - undiff.	Holothurians (group code)
19	25 416003	-	<i>Holothuria (Halodeima) atra</i>	Lolly Fish
19	25 416025	-	<i>Holothuria (Mertensiothuria) fuscus</i>	White Teat Fish
19	25 416004	-	<i>Holothuria (Metriatyla) scabra</i>	Sand Fish
19	25 416006	-	<i>Holothuria (Microthela) nobilis</i>	Black Teat Fish
19	28 850901	-	infraorder Brachyura	Giant crabs
19	28 880024	-	<i>Leptomithrax waitei</i>	A spider crab
19	23 207001	-	<i>Livonia mammilla</i>	False bailer shell
19	28 735000	-	Oplophoridae - undiff.	Carid prawns (family code)
19	none	-	Order gorgonacea	Hard coral
19	28 775000	-	Physetocarididae - undiff.	Carid prawns (family code)
19	28 880000	Majidae	Majidae - undiff.	Spider crabs (family code)
19	23 653000	Opisthoteuthidae	Opisthoteuthidae - undiff.	Octopods (family code)
19	28 865001	Raninidae	<i>Ranina ranina</i>	Crab, spanner
19	28 821001	Scyllaridae	<i>Ibacus alticrenatus</i>	Bug, Deepwater
19	28 925001	Xanthidae	<i>Pseudocarcinus gigas</i>	Crab, Giant Tasmanian
20	28 712001	-	<i>Aristaeomorpha foliacea</i>	Red prawn
20	28 770014	Pandalidae	<i>Plesionika martia</i>	Prawn, carid
20	28 712008	Penaeidae	<i>Aristaeopsis edwardsiana</i>	Prawn, Scarlet
20	28 711035	Penaeidae	<i>Parapenaeus australiensis</i>	Prawn, Racek
20	28 714005	Solenoceridae	<i>Haliporoides sibogae</i>	Prawn, Royal Red
20	28 714000	Solenoceridae	Solenoceridae - undiff.	Prawns, Solenocera
21	28 860001	-	<i>Dagnaudus petterdi</i>	Crab, antlered
21	28 911020	-	<i>Ovalipes molleri</i>	Crab, red paddle
22	23 632000	-	Bathyteuthidae - undiff.	Deepsea squids
22	23 636001	-	<i>Eucleoteuthis luminosa</i>	Arrow squid
22	23 630000	-	Histioteuthidae - undiff.	Sail, jewel squid or umbrella squids
22	23 610000	-	Idiosepiidae - undiff.	Squids (family code)
22	23 636007	-	<i>Ommastrephes bartramii</i>	Red ocean squid
22	23 615000	-	order Teuthoidea - undiff.	Squid (group code)
22	23 617005	-	<i>Sepioteuthis australis</i>	Southern calamary
22	23 636011	-	<i>Todarodes filippovae</i>	Southern Ocean arrow squid
22	23 636004	Ommastrephidae	<i>Nototodarus gouldi</i>	Squid, Arrow
23	37 258003	Berycidae	<i>Centroberyx affinis</i>	Redfish
24	37 228002	Ophidiidae	<i>Genypterus blacodes</i>	Ling

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25	37 439002	Gempylidae	<i>Rexea solandri</i>	Gemfish
26	37 227001	Merlucciidae	<i>Macruronus novaezelandiae</i>	Grenadier, Blue
27	37 445000	Centrolophidae	<i>Centrolophidae</i> - undiff.	trevallas (family code)
27	37 445004	Centrolophidae	<i>Centrolophus niger</i>	Rudderfish
27	37 445001	Centrolophidae	<i>Hyperoglyphe antarctica</i>	Trevalla, Blue-eye
27	37 445003	Centrolophidae	<i>Schedophilus huttoni</i>	A trevalla
27	37 445014	Centrolophidae	<i>Schedophilus labyrinthica</i>	Ocean blue-eye
27	37 445005	Centrolophidae	<i>Seriolella brama</i>	Warehou, Blue
27	37 445901	Centrolophidae	<i>Seriolella brama and Seriolella punctata</i>	Warehou, Blue and Silver
27	37 445011	Centrolophidae	<i>Seriolella caerulea</i>	White warehou
27	37 445006	Centrolophidae	<i>Seriolella punctata</i>	Warehou, Silver
27	37 445002	Centrolophidae	<i>Tubbia tasmanica</i>	A trevalla
28	37 337018	Carangidae	<i>Alectis ciliaris</i>	Pennant fish
28	37 337000	Carangidae	<i>Carangidae</i> - undiff.	Trevallies and Jacks
28	37 337011	Carangidae	<i>Carangoides chrysophrys</i>	Trevally, Long nose
28	37 337039	Carangidae	<i>Caranx sexfasciatus</i>	Trevally, Bigeye
28	37 337060	Carangidae	<i>Decapterus tabl</i>	A trevally/jack
28	37 337029	Carangidae	<i>Elagatis bipinnulata</i>	Rainbow Runner
28	37 337012	Carangidae	<i>Gnathanodon speciosus</i>	Trevally, Golden
28	37 337062	Carangidae	<i>Pseudocaranx dentex</i>	Trevally, Silver
28	37 337063	Carangidae	<i>Pseudocaranx wrighti</i>	Skipjack trevally
28	37 337014	Carangidae	<i>Seriolina nigrofasciata</i>	Kingfish, banded
28	37 337904	Carangidae	<i>Trachinotus spp</i>	Dart
28	37 337053	Siganidae	<i>Caranx lugubris</i>	Trevally, Black
29	37 296001	Platycephalidae	<i>Neoplatycephalus richardsoni</i>	Flathead, Tiger
30	37 330002	Sillaginidae	<i>Sillago bassensis</i>	Whiting, Western school
30	37 330014	Sillaginidae	<i>Sillago flindersi</i>	Whiting, Eastern School
31	37 353001	Sparidae	<i>Pagrus auratus</i>	Snapper
32	37 377000	Cheilodactylidae	<i>Cheilodactylidae</i> - undiff.	Morwong, Unspecified
32	37 377009	Cheilodactylidae	<i>Cheilodactylus fuscus</i>	Morwong, Red
32	37 377001	Cheilodactylidae	<i>Cheilodactylus nigripes</i>	Morwong, Magpie
32	37 377002	Cheilodactylidae	<i>Nemadactylus douglasii</i>	Morwong, Grey
32	37 377003	Cheilodactylidae	<i>Nemadactylus macropterus</i>	Morwong, Jackass
33	37 264000	Zeidae	<i>Zeidae</i> - undiff.	Dory, Unspecified
33	37 264003	Zeidae	<i>Zenopsis nebulosus</i>	Dory, Mirror
33	37 264004	Zeidae	<i>Zeus faber</i>	Dory, John
34	37 287093	Sebastidae	<i>Helicolenus barathri</i>	Perch, ocean (offshore)
34	37 287001	Sebastidae	<i>Helicolenus percoides</i>	Reef ocean perch
35	37 110000	Malacosteidae	<i>Malacosteidae</i> - undiff.	Loosejaws (family code)
35	37 109000	Melanostomiidae	<i>Melanostomiidae</i> - undiff.	Scaleless dragonfishes
35	37 122000	Myctophidae	<i>Myctophidae</i> - undiff.	Myctophidae
35	37 122011	Myctophidae	<i>Myctophum punctatum</i>	A lanternfish
35	37 121001	Neoscopelidae	<i>Neoscopelus macrolepidotus</i>	A new lanternfish
35	37 112001	Stomiidae	<i>Stomias affinis</i>	A scaly dragonfish
35	37 112000	Stomiidae	<i>Stomiidae</i> - undiff.	Scaly dragonfishes
36	37 327000	Apogonidae, Dinolestidae	<i>Apogonidae, Dinolestidae</i> - undiff.	Cardinalfishes
36	37 466002	Aracanidae	<i>Anoplocapros inermis</i>	A boxfish

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36	37 466003	Aracanidae	<i>Aracana aurita</i>	A boxfish
36	37 466001	Aracanidae	<i>Aracana ornata</i>	A boxfish
36	37 460000	Bothidae, Achiropsettidae, Paralichthyidae	<i>Bothidae, Achiropsettidae, Paralichthyidae</i> - undiff.	lefteye flounders (family code)
36	37 990014	Bothidae, Pleuronectidae	<i>Bothidae &amp; Pleuronectidae</i>	Flounder
36	37 331005	Branchiostegidae	<i>Branchiostegus serratus</i>	Tilefish, serrate
36	37 331006	Branchiostegidae	<i>Branchiostegus wardi</i>	Tilefish, pink
36	37 279002	Centriscidae	<i>Macroramphosus scolopax</i>	Snipefish, Longspine
36	37 279003	Centriscidae	<i>Notopogon lilliei</i>	A bellowsfish
36	37 279005	Centriscidae	<i>Notopogon xenosoma</i>	A bellowsfish
36	37 377004	Cheilodactylidae	<i>Nemadactylus valenciennesi</i>	Blue morwong
36	37 120004	Chlorophthalmidae	<i>Chlorophthalmus cf nigromarginatus</i>	A greeneye
36	37 120000	Chlorophthalmidae, Paraulopidae	<i>Chlorophthalmidae &amp; Paraulopidae</i> - undiff.	Cucumberfishes and Greeneyes (family code)
36	37 458001	Citharidae	<i>Brachypleura novaezeelandiae</i>	Flounder, yellow dabbled
36	37 469002	Diodontidae	<i>Allomycterus pilatus</i>	Burrfish, Deepwater
36	37 469005	Diodontidae	<i>Diodon holocanthus</i>	A porcupine fish
36	37 469001	Diodontidae	<i>Diodon nictemerus</i>	Porcupine Fish, slender-spined
36	37 345901	Emmelichthyidae	<i>Emmelichthys</i> spp	Bonnetmouths
36	37 345002	Emmelichthyidae	<i>Plagiogeneion macrolepis</i>	A bonnetmouth
36	37 345900	Emmelichthyidae	<i>Plagiogeneion</i> spp	Bonnetmouths
36	37 362004	Ephippidae	<i>Platax teira</i>	Batfish, Silver
36	37 327001	Epigonidae	<i>Epigonus lenimen</i>	A cardinalfish
36	37 349001	Gerreidae	<i>Parequula melbournensis</i>	Silverbelly
36	37 320003	Glaucosomatidae	<i>Glaucosoma scapulare</i>	Perch, Pearl
36	37 141001	Gonorhynchidae	<i>Gonorynchus greyi</i>	Beaked salmon
36	37 261005	Holocentridae	<i>Ostichthys kaianus</i>	A squirrelfish/soldierfish
36	37 361010	Kyphosidae	<i>Atypichthys strigatus</i>	Australian mado
36	37 361003	Kyphosidae	<i>Tilodon sexfasciatum</i>	Tilodon sexfasciatum
36	37 384003	Labridae	<i>Notolabrus tetricus</i>	Wrasse, blue-throated
36	37 384023	Labridae	<i>Pseudolabrus psittaculus</i>	Wrasse, rosy
36	37 351009	Lethrinidae	<i>Lethrinus miniatus</i>	Sweetlip, Emperor
36	37 351008	Lethrinidae	<i>Lethrinus nebulosus</i>	Emperor, Spangled
36	37 351902	Lethrinidae	<i>Lethrinus</i> spp	Emperors
36	37 346033	Lutjanidae	<i>Lutjanus adetii</i>	Hussar
36	37 346015	Lutjanidae	<i>Lutjanus argentimaculatus</i>	Jack, Mangrove
36	37 346004	Lutjanidae	<i>Lutjanus sebae</i>	Snapper, queen
36	37 346012	Lutjanidae	<i>Lutjanus</i> sp.	Perch, Moses
36	37 346032	Lutjanidae	<i>Pristipomoides filamentosus</i>	Jobfish
36	37 331001	Malacanthidae	<i>Branchiostegus sawakinensis</i>	A tilefish
36	37 331000	Malacanthidae	<i>Malacanthidae</i> - undiff.	Moonfish
36	37 465036	Monacanthidae	<i>Meuschenia freycineti</i>	Leatherjacket, Six-spined
36	37 465040	Monacanthidae	<i>Meuschenia galii</i>	A leatherjacket
36	37 465005	Monacanthidae	<i>Meuschenia scaber</i>	Leatherjacket, Velvet
36	37 465903	Monacanthidae	<i>Monacanthidae</i> - undiff.	Leatherjackets
36	37 465006	Monacanthidae	<i>Nelusetta ayraudi</i>	Leatherjacket, Chinaman
36	37 465024	Monacanthidae	<i>Paramonacanthus filicauda</i>	Leatherjacket, Threadfin

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36	37 259001	Monocentridae	<i>Cleidopus gloriamaris</i>	A pineapplefish
36	37 356001	Monodactylidae	<i>Schuettea scalaripinnis</i>	Batfish, Southern
36	37 355029	Mullidae	<i>Upeneichthys vlamingii</i>	A goatfish
36	37 347027	Nemipteridae	<i>Pentapodus emeryii</i>	Bream, purple
36	37 287045	Neosebastidae	<i>Maxillicosta whitleyi</i>	A scorpionfish
36	37 287009	Neosebastidae	<i>Neosebastes entaxis</i>	A scorpionfish
36	37 287019	Neosebastidae	<i>Neosebastes incisipinnis</i>	A scorpionfish
36	37 287002	Neosebastidae	<i>Neosebastes nigropunctatus</i>	A scorpionfish
36	37 287005	Neosebastidae	<i>Neosebastes scorpaenoides</i>	Perch, Ruddy gurnard
36	37 287006	Neosebastidae	<i>Neosebastes thetidis</i>	A scorpionfish
36	37 228020	Ophidiidae	<i>Dermatopsis macrodon</i>	Blindfish
36	37 369002	Oplegnathidae	<i>Oplegnathus woodwardi</i>	Conway
36	37 466008	Ostraciontidae	<i>Lactoria reipublicae</i>	A boxfish
36	37 120001	Paraulopidae	<i>Paraulopus nigripinnis</i>	Cucumberfish
36	37 357002	Pempheridae	<i>Parapriacanthus elongatus</i>	A bullseye
36	37 357004	Pempheridae	<i>Parapriacanthus ransonneti</i>	A bullseye
36	37 357006	Pempheridae	<i>Pempheris analis</i>	Bullseye
36	37 357008	Pempheridae	<i>Pempheris compressa</i>	Bullseye, Compressed
36	37 357001	Pempheridae	<i>Pempheris multiradiata</i>	Bullseye, Common
36	37 357000	Pempherididae, Leptobramidae	<i>Pempherididae, Leptobramidae</i>	Bullseyes (family code)
36	37 367001	Pentacerotidae	<i>Paristiopterus gallipavo</i>	Brown-spotted boarfish
36	37 367002	Pentacerotidae	<i>Paristiopterus labiosus</i>	Boarfish, giant
36	37 367003	Pentacerotidae	<i>Pentaceros recurvirostris</i>	Boarfish
36	37 367004	Pentacerotidae	<i>Pentaceros decacanthus</i>	Bigspine boarfish
36	37 367000	Pentacerotidae	<i>Pentacerotidae</i> - undiff.	Boarfish
36	37 367009	Pentacerotidae	<i>Pseudopentaceros richardsoni</i>	A boarfish
36	37 367005	Pentacerotidae	<i>Zanclistius elevatus</i>	Blackspot boarfish
36	37 461004	Pleuronectidae	<i>Ammotretis lituratus</i>	Spotted flounder
36	37 461002	Pleuronectidae	<i>Azygopus pinnifasciatus</i>	Flounder, Banded-fin
36	37 372005	Pomacentridae	<i>Parma microlepis</i>	Scalyfin, White-ear
36	37 326000	Priacanthidae	<i>Priacanthidae</i> - undiff.	Bigeyes (family code)
36	37 326002	Priacanthiidae	<i>Cookeolus japonicus</i>	A bigeye
36	37 326001	Priacanthiidae	<i>Priacanthus macracanthus</i>	Bigeye, Red
36	37 326901	Priacanthiidae	<i>Priacanthus</i> spp	Bullseye
36	37 287058	Scorpaenidae	<i>Notesthes robusta</i>	Bullrout
36	37 287066	Scorpaenidae	<i>Scorpaena cardinalis</i>	Red rock cod
36	37 287046	Sebastidae	<i>Trachyscorpia capensis</i>	Cape scorpionfish
36	37 311002	Serranidae	<i>Caesioperca lepidoptera</i>	Perch, Butterfly
36	37 311095	Serranidae	<i>Caprodon longimanus</i>	Perch, longfinned
36	37 311102	Serranidae	<i>Lepidoperca brochata</i>	A rockcod
36	37 462000	Soleidae	<i>Soleidae</i> - undiff.	Soles (family code)
36	37 467005	Tetraodontidae	<i>Arothron firmamentum</i>	Starry toado
36	37 467002	Tetraodontidae	<i>Omegophora armilla</i>	A toadfish
36	37 467004	Tetraodontidae	<i>Sphoeroides pachygaster</i>	A toadfish
36	37 467003	Tetraodontidae	<i>Tetractenos glaber</i>	A toadfish
36	37 467009	Tetraodontidae	<i>Torquigener pallimaculatus</i>	A toadfish
36	37 464002	Triacanthidae	<i>Triacanthus biaculeatus</i>	A tripodfish
36	37 288001	Triglidae	<i>Chelidonichthys kumu</i>	Gurnard, Red

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36	37 288007	Triglidae	<i>Lepidotrigla modesta</i>	Gurnard, Minor
36	37 288008	Triglidae	<i>Lepidotrigla mulhalli</i>	Gurnard, Rough-snouted
36	37 288002	Triglidae	<i>Lepidotrigla papilio</i>	A gurnard
36	37 288010	Triglidae	<i>Lepidotrigla</i> sp	
36	37 288014	Triglidae	<i>Pterygotrigla leptacanthus</i>	A gurnard
36	37 288030	Triglidae	<i>Satyrichthys lingi</i>	A gurnard
36	37 255017	Trychichthidae	<i>Optivus elongatus</i>	Roughy, Violet
36	37 255015	Trychichthidae	<i>Trachichthys australis</i>	Roughy
36	37 269001	Veliferidae	<i>Metavelifer multiradiatus</i>	A veifin
36	37 462004	Zebrias	<i>Zebrias quagga</i>	A sole
36	37 264005	Zeidae	<i>Cyttus novaezealandiae</i>	Dory, New Zealand
37	37 990005	-	<i>Mixed eels</i>	Unid. eel sp
37	37 311053	Acropomatidae	<i>Apogonops anomalus</i>	Cardinalfish, Three-spined
37	37 117003	Aulopidae	<i>Aulopus curtirostris</i>	A threadsail
37	37 117001	Aulopodidae	<i>Aulopus purpurissatus</i>	Sergeant Baker
37	37 229003	Carapidae	<i>Echiodon rendahli</i>	A pearlfish
37	37 067012	Congridae	<i>Bassanago bulbiceps</i>	A conger eel
37	37 067013	Congridae	<i>Bassanago hirsutus</i>	Deep-sea conger eel
37	37 067007	Congridae	<i>Conger verreauxi</i>	Eel, Conger
37	37 067001	Congridae	<i>Conger wilsoni</i>	Eel, Short-finned Conger
37	37 067000	Congridae	<i>Congridae</i> - undiff.	Conger eels (family code)
37	37 226000	Gadidae, Phycidae	<i>Gadidae, Phycidae</i> - undiff.	-
37	37 297000	Hoplichthyidae	<i>Hoplichthyidae</i> - undiff.	Ghost flatheads
37	37 384035	Labridae	<i>Bodianus flavipinnis</i>	A wrasse
37	37 384001	Labridae	<i>Bodianus vulpinus</i>	Pigfish
37	37 384040	Labridae	<i>Ophthalmolepis lineolatus</i>	Wrasse, Maori
37	37 378002	Latrididae	<i>Latridopsis forsteri</i>	Trumpeter, Bastard
37	37 378001	Latrididae	<i>Latris lineata</i>	Trumpeter, Tasmanian
37	37 264010	Parazenidae	<i>Cyttopsis roseus</i>	A dory
37	37 311000	Percichthyidae, Serranidae	<i>Percichthyidae, Serranidae</i> - undiff.	Cod, Unspecified
37	37 296035	Platycephalidae	<i>Neoplatycephalus aurimaculatus</i>	Toothy flathead
37	37 296000	Platycephalidae	<i>Platycephalidae</i> - undiff.	Flathead, Unspecified
37	37 296003	Platycephalidae	<i>Platycephalus bassensis</i>	Flathead, Sand
37	37 296901	Platycephalidae	<i>Platycephalus bassensis and Platycephalus caeruleopunctatus</i>	Flathead, sand mixed
37	37 296037	Platycephalidae	<i>Platycephalus speculator</i>	Southern flathead
37	37 296011	Platycephalidae	<i>Ratabulus diversidens</i>	Flathead, spiky
37	37 311170	Polyprionidae	<i>Polyprion americanus</i>	Bass groper
37	37 311902	Polyprionidae	<i>Polyprion americanus and Polyprion oxygeneios</i>	Hapuku/Bass Groper mixed
37	37 990024	Polyprionidae	<i>Polyprion americanus, Polyprion oxygeneios, Hyperoglyphe antarctica, Schedophilus labyrinthica</i>	Bass groper
37	37 311006	Polyprionidae	<i>Polyprion oxygeneios</i>	Hapuku
37	37 354020	Sciaenidae	<i>Atractoscion aequidens</i>	Teraglin
37	37 287026	Scorpaenidae	<i>Dendrochirus zebra</i>	Lionfish, pygmy
37	37 287000	Scorpaenidae	<i>Scorpaenidae</i> - undiff.	Coral scorpionfishes
37	37 311901	Serranidae	<i>Aethaloperca, Anyperodon and Epinephelus</i> spp.	Rockcods (group code)



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37	37 311003	Serranidae	<i>Caesioperca rasor</i>	Perch, Barber
37	37 311001	Serranidae	<i>Lepidoperca pulchella</i>	Perch, Orange
37	37 321001	Terapontidae	<i>Pelates quadrilineatus</i>	Trumpeter
37	37 321005	Terapontidae	<i>Pelates sexlineatus</i>	Trumpeter, Six-lined
37	37 321000	Terapontidae	<i>Terapontidae</i> - undiff.	Trumpeter, Unspecified
37	37 440006	Trichiuridae	<i>Tentoriceps cristatus</i>	A hairtail
37	37 440004	Trichiuridae	<i>Trichiurus lepturus</i>	Hairtail
37	37 288032	Triglidae	<i>Lepidotrigla argus</i>	A gurnard
37	37 288003	Triglidae	<i>Lepidotrigla vanessa</i>	Gurnard, Butterfly
37	37 400006	Uranoscopidae	<i>Ichthyoscopus spinosus</i>	A stargazer
37	37 400003	Uranoscopidae	<i>Kathetostoma laeve</i>	Stargazer, Common
37	37 400005	Uranoscopidae	<i>Pleuroscopus pseudodorsalis</i>	A stargazer
37	37 400007	Uranoscopidae	<i>Uranoscopus bicinctus</i>	A stargazer
37	37 400008	Uranoscopidae	<i>Uranoscopus cognatus</i>	A stargazer
37	37 264002	Zeidae	<i>Cyttus australis</i>	Dory, Silver
37	37 263000	Zeniontidae	<i>Zeniontidae</i> - undiff.	Dories (family code)
38	37 114000	Alepocephalidae	<i>Alepocephalidae</i> - undiff.	Slickheads (family code)
38	37 117000	Aulopidae	<i>Aulopidae</i> - undiff.	Threadsails (family code)
38	37 258002	Berycidae	<i>Beryx splendens</i>	Alfonsino
38	37 258004	Berycidae	<i>Centroberyx gerrardi</i>	Bight redfish
38	37 258005	Berycidae	<i>Centroberyx lineatus</i>	Swallowtail
38	37 267001	Caproidae	<i>Antigonia rhomboidea</i>	A boarfish
38	37 308004	Dactylopteridae	<i>Dactyloptena orientalis</i>	Gurnard, flying
38	37 254001	Diretmidae	<i>Diretmichthys parini</i>	A spinyfin
38	37 232010	Macrouridae	<i>Caelorinchus acutirostris</i>	A whiptail
38	37 232001	Macrouridae	<i>Caelorinchus australis</i>	Javelin
38	37 232002	Macrouridae	<i>Caelorinchus fasciatus</i>	Banded whiptail
38	37 232014	Macrouridae	<i>Caelorinchus innotabilis</i>	A whiptail
38	37 232031	Macrouridae	<i>Caelorinchus kaiyomaru</i>	A whiptail
38	37 232017	Macrouridae	<i>Caelorinchus matamuus</i>	A whiptail
38	37 232045	Macrouridae	<i>Caelorinchus maurofasciatus</i>	A whiptail
38	37 232003	Macrouridae	<i>Caelorinchus mirus</i>	Gargoyle fish
38	37 232047	Macrouridae	<i>Caelorinchus parvifasciatus</i>	Rattail, small banded
38	37 232020	Macrouridae	<i>Caelorinchus</i> sp. W5	
38	37 232039	Macrouridae	<i>Coryphaenoides dossenus</i>	A whiptail
38	37 232015	Macrouridae	<i>Coryphaenoides serrulatus</i>	A whiptail
38	37 232004	Macrouridae	<i>Lepidorhynchus denticulatus</i>	A whiptail
38	37 232005	Macrouridae	<i>Lucigadus nigromaculatus</i>	A whiptail
38	37 232000	Macrouridae	<i>Macrouridae</i> - undiff.	Macrourids
38	37 232007	Macrouridae	<i>Malacocephalus laevis</i>	A whiptail
38	37 232035	Macrouridae	<i>Mesobius antipodum</i>	A whiptail
38	37 232028	Macrouridae	<i>Trachyrincus longirostris</i>	A rattail/whiptail/grenadier
38	37 266005	Oreosomatidae	<i>Allocyttus niger</i>	Oreo Dory
38	37 266004	Oreosomatidae	<i>Allocyttus verrucosus</i>	Oreo Dory, Warty
38	37 266001	Oreosomatidae	<i>Neocyttus rhomboidalis</i>	Oreo Dory, Spiky
38	37 266002	Oreosomatidae	<i>Oreosoma atlanticum</i>	An oreodory
38	37 266000	Oreosomatidae	<i>Oreosomatidae</i> - undiff.	Oreodories (family code)
38	37 266003	Oreosomatidae	<i>Pseudocyttus maculatus</i>	Oreo dory, smooth
38	37 253000	Polymixiidae	<i>Polymixiidae</i> - undiff.	Beardfishes (family code)

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38	37 305001	Psychrolutidae	<i>Psychrolutes marcidus</i>	A blobfish
38	37 108012	Stomiidae	<i>Heterophotus ophistoma</i>	A stareater
38	37 464010	Triacanthodidae	<i>Bathyphylax bombifrons</i>	A deepwater tripodfish
38	37 464004	Triacanthodidae	<i>Macrorhamphosodes platycheilus</i>	A deepwater tripodfish
38	37 464014	Triacanthodidae	<i>Macrorhamphosodes uradoi</i>	A deepwater tripodfish
38	37 288901	Triglidae	<i>Lepidotrigla</i> spp	
38	37 288004	Triglidae	<i>Peristedion picturatum</i>	A gurnard
38	37 288005	Triglidae	<i>Pterygotrigla andertoni</i>	Gurnard, Spotted
38	37 288000	Triglidae, Peristediidae	<i>Triglidae &amp; Peristediidae</i> - undiff.	Gurnard, mixed
38	37 231001	Zoarcidae	<i>Melanostigma gelatinosum</i>	An eelpout
39	37 311054	Acropomatidae	<i>Synagrops japonicus</i>	A temperate ocean-bass
39	37 210009	Antennariidae	<i>Antennarius striatus</i>	Anglerfish
39	37 210014	Antennariidae	<i>Kuiterichthys furcipilis</i>	A frogfish
39	37 210000	Antennariidae, Tetrabrachiidae, Lophichthyidae	<i>Antennariidae, Tetrabrachiidae, Lophichthyidae</i> - undiff.	
39	37 228000	Aphyonidae, Bythitidae, Ophidiidae	<i>Aphyonidae, Bythitidae, Ophidiidae</i> - undiff.	
39	37 258001	Berycidae	<i>Beryx decadactylus</i>	Imperador
39	37 311004	Callanthiidae	<i>Callanthias allporti</i>	Perch, Rosy
39	37 311055	Callanthiidae	<i>Callanthias australis</i>	A rockcod
39	37 427000	Callionymidae	<i>Callionymidae</i> - undiff.	Stinkfishes (family code)
39	37 427014	Callionymidae	<i>Eocallionymus papilio</i>	A stinkfish
39	37 427001	Callionymidae	<i>Foetorepus calauropomus</i>	Stinkfish, Common
39	37 427015	Callionymidae	<i>Repomucenus calcaratus</i>	Stinkfish, Spotted
39	37 132000	Cetomimidae	<i>Cetomimidae</i> - undiff.	whalefishes (family code)
39	37 401000	Champsodontidae	<i>Champsodontidae</i> - undiff.	Gaper fish
39	37 211000	Chaunacidae	<i>Chaunacidae</i> - undiff.	Anglerfish
39	37 211003	Chaunacidae	<i>Chaunax endeavouri</i>	A coffinfish
39	37 211004	Chaunacidae	<i>Chaunax penicillatus</i>	A coffinfish
39	37 073000	Derichthyidae	<i>Derichthyidae</i> - undiff.	duck-billed and neck eels
39	37 224001	Euclichthyidae	<i>Euclichthys polynemus</i>	A morid cod
39	37 226790	Gadidae	<i>Gadus morhua</i>	Cod, Atlantic
39	37 439008	Gempylidae	<i>Lepidocybium flavobrunneum</i>	Oilfish, Black
39	37 439009	Gempylidae	<i>Rexea antefurcata</i>	A gemfish
39	37 439003	Gempylidae	<i>Ruvettus pretiosus</i>	Oilfish
39	37 106000	Gonostomatidae, Phosichthyidae	<i>Gonostomatidae, Phosichthyidae</i>	Lightfishes and lighthousefishes
39	37 265000	Grammicolepididae	<i>Grammicolepididae</i> - undiff.	Scaly dories (family code)
39	37 265003	Grammicolepididae	<i>Xenolepidichthys dalgleishi</i>	A scaly dory
39	37 081002	Halosauridae	<i>Halosaurus pectoralis</i>	A halosaur
39	37 297002	Hoplychthyidae	<i>Hoplichthys citrinus</i>	A ghost flathead
39	37 297001	Hoplychthyidae	<i>Hoplichthys haswelli</i>	Flathead, Ghost
39	37 208000	Lophiidae	<i>Lophiidae</i> - undiff.	goosefishes (family code)
39	37 208003	Lophiidae	<i>Lophiodes mutilus</i>	A goosefish
39	37 224000	Melanonidae, Moridae	<i>Melanonidae, Moridae</i> - undiff.	
39	37 224009	Moridae	<i>Halargyreus johnsonii</i>	A morid cod

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39	37 224010	Moridae	<i>Lepidion microcephalus</i>	A morid cod
39	37 224005	Moridae	<i>Lotella rhacina</i>	A morid cod
39	37 224002	Moridae	<i>Mora moro</i>	A morid cod
39	37 224006	Moridae	<i>Pseudophycis bachus</i>	A morid cod
39	37 224003	Moridae	<i>Pseudophycis barbata</i>	A morid cod
39	37 224004	Moridae	<i>Tripteryphycis gilchristi</i>	A morid cod
39	37 004002	Myxinidae	<i>Eptatretus cirrhatus</i>	New Zealand hagfish
39	37 004001	Myxinidae	<i>Eptatretus longipinnis</i>	Hagfish
39	37 083000	Notacanthidae	<i>Notacanthidae</i> - undiff.	Spiny eels (family code)
39	37 083001	Notacanthidae	<i>Notacanthus sexspinis</i>	A spiny eel
39	37 212001	Ogcocephalidae	<i>Halieutaea brevicauda</i>	A deepwater batfish
39	37 228013	Ophidiidae	<i>Brotulotaenia crassa</i>	A cusk eel
39	37 228001	Ophidiidae	<i>Dannevigia tusca</i>	Tusk
39	37 228007	Ophidiidae	<i>Hoplobrotula armata</i>	A cusk eel
39	37 228036	Ophidiidae	<i>Pycnocraspedum squamipinne</i>	A cusk eel
39	37 106002	Phosichthyidae	<i>Phosichthys argenteus</i>	A lighthousefish
39	37 106001	Phosichthyidae	<i>Polymetme corythaeola</i>	A lighthousefish
39	37 296002	Platycephalidae	<i>Neoplatycephalus conatus</i>	deepwater flathead
39	37 272002	Regalecidae	<i>Regalecus glesne</i>	An oarfish
39	37 439000	Scombrolabracidae, Gempylidae	<i>Scombrolabracidae, Gempylidae</i> - undiff.	
39	37 287103	Sebastidae	<i>Trachyscorpia</i> sp.	Scorpion fish
39	37 311005	Serranidae	<i>Othos dentex</i>	A rockcod
39	37 118001	Synodontidae	<i>Saurida undosquamis</i>	A deepsea lizardfish
39	37 118002	Synodontidae	<i>Trachinocephalus myops</i>	Lizardfish/grinner
39	37 255004	Trachichthyidae	<i>Gephyroberyx darwinii</i>	Darwin's roughy
39	37 255009	Trachichthyidae	<i>Hoplostethus atlanticus</i>	Orange Roughy
39	37 255001	Trachichthyidae	<i>Hoplostethus intermedius</i>	A sawbelliy
39	37 255003	Trachichthyidae	<i>Paratrachichthys</i> sp. 1	
39	37 255010	Trachichthyidae	<i>Sorosichthys ananassa</i>	A roughy
39	37 255000	Trachichthyidae	<i>Trachichthyidae</i> - undiff.	Roughies and sawbellies
39	37 271001	Trachipteridae	<i>Trachipterus jacksonensis</i>	A ribbonfish
39	37 440001	Trichiuridae	<i>Benthodesmus elongatus</i>	Frostfish, slender
39	37 440002	Trichiuridae	<i>Lepidopus caudatus</i>	Frostfish, southern
39	37 288006	Triglidae	<i>Pterygotrigla polyommata</i>	Gurnard, sharp-beaked
39	37 400002	Uranoscopidae	<i>Ichthyoscopus barbatus</i>	A stargazer
39	37 400018	Uranoscopidae	<i>Kathetostoma canaster</i>	Stargazer, Speckled
39	37 400000	Uranoscopidae	<i>Uranoscopidae</i> - undiff.	Stargazer
39	37 400001	Uranoscopidae	<i>Xenocephalus armatus</i>	A stargazer
39	37 264001	Zeidae	<i>Cyttus traversi</i>	Dory, King
40	37 337002	Carangidae	<i>Trachurus declivis</i>	Mackerel, Jack
40	37 337077	Carangidae	<i>Trachurus murphyi</i>	Peruvian jack mackerel
40	37 345001	Emmelichthyidae	<i>Emmelichthys nitidus nitidus</i>	Redbait
40	37 233000	Exocoetidae	<i>Exocoetidae</i> - undiff.	Flyingfishes (family code)
40	37 268001	Lampridae	<i>Lampris guttatus</i>	Opah
40	37 446000	Nomeidae	<i>Nomeidae</i> - undiff.	Driftfishes (family code)
40	37 441005	Scombridae	<i>Thunnus alalunga</i>	Albacore
41	37 338001	Coryphaenidae	<i>Coryphaena hippurus</i>	Dolphinfish
41	37 327002	Dinolestidae	<i>Dinolestes lewini</i>	Seapike, Long-finned

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
41	37 439001	Gempylidae	<i>Thyrsites atun</i>	Barracouta
41	37 444005	Istiophoridae	<i>Istiophorus platypterus</i>	Sailfish
41	37 444006	Istiophoridae	<i>Makaira indica</i>	Marlin, Black
41	37 444003	Istiophoridae	<i>Makaira mazara</i>	Marlin, Blue
41	37 444007	Istiophoridae	<i>Tetrapturus angustirostris</i>	Spearfish, Shortbill
41	37 444002	Istiophoridae	<i>Tetrapturus audax</i>	Marlin, Striped
41	37 470002	Molidae	<i>Mola mola</i>	An ocean sunfish
41	37 126000	Paralepididae	<i>Paralepididae</i> - undiff.	Barracudinas (family code)
41	37 335001	Rachycentridae	<i>Rachycentron canadum</i>	Cobia
41	37 094001	Salmonidae	<i>Salmo salar</i>	Atlantic salmon
41	37 441024	Scombridae	<i>Acanthocybium solandri</i>	Wahoo
41	37 441009	Scombridae	<i>Auxis thazard</i>	Leadenall
41	37 441008	Scombridae	<i>Cybiosarda elegans</i>	Bonito, Leaping
41	37 441010	Scombridae	<i>Euthynnus affinis</i>	Tuna, Mackerel
41	37 441025	Scombridae	<i>Grammatorcynus bicarinatus</i>	Mackerel, Scaly
41	37 441003	Scombridae	<i>Katsuwonus pelamis</i>	Tuna, Skipjack
41	37 441007	Scombridae	<i>Scomberomorus commerson</i>	Mackerel, Spanish
41	37 441015	Scombridae	<i>Scomberomorus munroi</i>	Mackerel, Spotted
41	37 441000	Scombridae	Scombridae - undiff.	Tuna, Unspecified
41	37 441002	Scombridae	<i>Thunnus albacares</i>	Tuna, Yellowfin
41	37 441004	Scombridae	<i>Thunnus maccoyii</i>	Tuna, Southern Bluefin
41	37 441011	Scombridae	<i>Thunnus obesus</i>	Tuna, Bigeye
41	37 441013	Scombridae	<i>Thunnus tonggol</i>	Tuna, Northern Bluefin
41	37 382003	Sphyraenidae	<i>Sphyraena acutipinnis</i>	A pike
41	37 382002	Sphyraenidae	<i>Sphyraena novaehollandiae</i>	Barracuda/Snook
41	37 382001	Sphyraenidae	<i>Sphyraena obtusata</i>	A pike
41	37 382000	Sphyraenidae	<i>Sphyraenidae</i> - undiff.	Pikes (family code)
41	37 442001	Xiphiidae	<i>Xiphias gladius</i>	Swordfish, Broadbill
42	37 020901	Squalidae	<i>Squalus</i> (all spp)	Dogfish, mixed
42	37 020006	Squalidae	<i>Squalus megalops</i>	Dogfish, Spiky
43	37 020010	Centrophoridae	<i>Centrophorus harrissoni</i>	Dogfish, Harrison's
43	37 020902	Centrophoridae	<i>Centrophorus harrissoni</i> , <i>Centrophorus moluccensis</i> and <i>Centrophorus zeehaani</i>	Shark, <i>Centrophorus</i> mixed
43	37 020011	Centrophoridae	<i>Centrophorus zeehaani</i>	Dogfish, southern
44	37 020007	Squalidae	<i>Squalus mitsukurii</i>	Shark, Dogfish Greeneye
44	37 020041	Squalidae	<i>Squalus</i> sp. F	Dogfish, Greeneye
45	37 020001	Centrophoridae	<i>Centrophorus moluccensis</i>	Dogfish, Endeavour
46	37 020009	Centrophoridae	<i>Centrophorus squamosus</i>	Leafscale gulper dogshark
46	37 020904	Dalatiidae	<i>Centroscymnus</i> and <i>Deania</i> spp	Dogfish, <i>Squalus</i> spp
46	37 020012	Dalatiidae	<i>Centroscymnus crepidater</i>	golden dogfish
46	37 020019	Dalatiidae	<i>Centroscymnus owstoni</i>	Owston's dogfish
46	37 020013	Dalatiidae	<i>Centroscymnus plunketi</i>	Plunket's dogfish
46	37 020906	Dalatiidae	<i>Centroscymnus</i> spp	A dogfish
46	37 020002	Dalatiidae	<i>Dalatias licha</i>	Black shark
46	37 020003	Dalatiidae	<i>Deania calcea</i>	Brier shark
46	37 020905	Dalatiidae	<i>Deania calcea</i> and <i>Deania quadrispinosa</i>	Platypus shark
46	37 020004	Dalatiidae	<i>Deania quadrispinosa</i>	Dogfish, longsnout

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
46	37 020021	Dalatiidae	<i>Etmopterus granulosus</i>	Southern lantern shark
46	37 020005	Dalatiidae	<i>Etmopterus lucifer</i>	A dogfish
46	37 020015	Dalatiidae	<i>Etmopterus pusillus</i>	Slender lantern shark
46	37 020027	Dalatiidae	<i>Etmopterus</i> sp. A	
46	37 020907	Dalatiidae	<i>Etmopterus</i> spp	Southern lantern shark
46	37 020014	Dalatiidae	<i>Isistius brasiliensis</i>	Cookie-cutter shark
46	37 021001	Dalatiidae	<i>Oxynotus bruniensis</i>	Shark, Roughskin
46	37 020000	Squalidae	<i>Squalidae</i> - undiff.	Dogfish, Unspecified
46	37 020008	Squalidae	<i>Squalus acanthias</i>	White-spotted spurdog
46	37 020038	Squalidae	<i>Squalus</i> sp. B	Eastern highfin spurdog
47	37 017001	Triakidae	<i>Mustelus antarcticus</i>	Shark, Gummy
48	37 017008	Triakidae	<i>Galeorhinus galeus</i>	Shark, School
49	37 013000	Brachaeluridae	<i>Brachaeluridae</i>	
49	37 013007	Brachaeluridae	<i>Brachaelurus waddi</i>	Blind shark
49	37 015000	Brachaeluridae	<i>Scyliorhinidae</i> - undiff.	Catsharks (family code)
49	37 043001	Callorhynchidae	<i>Callorhynchus milii</i>	Elephant fish
49	37 018029	Carcharhinidae	<i>Negaprion acutidens</i>	Lemon shark
49	37 042005	Chimaeridae	<i>Chimaera</i> sp. A	
49	37 042006	Chimaeridae	<i>Chimaera</i> sp. B	
49	37 042000	Chimaeridae	<i>Chimaeridae</i> - undiff.	Shark, Ghost
49	37 042003	Chimaeridae	<i>Hydrolagus lemures</i>	Blackfin ghostshark
49	37 042001	Chimaeridae	<i>Hydrolagus ogilbyi</i>	Ogilby's ghostshark
49	37 042011	Chimaeridae	<i>Hydrolagus</i> sp. B	
49	37 006001	Chlamydoselachidae	<i>Chlamydoselachus anguineus</i>	Frilled shark
49	37 990003	Elasmobranchii	<i>Sharks</i> – undiff.	Shark, Unspecified
49	37 007000	Heterodontidae	<i>Heterodontidae</i> - undiff.	Horn and Port Jackson Sharks
49	37 007003	Heterodontidae	<i>Heterodontus galeatus</i>	Crested horn shark
49	37 007001	Heterodontidae	<i>Heterodontus portusjacksoni</i>	Shark, Port Jackson
49	37 013900	Orectolobidae	<i>Orectolobidae</i>	Shark, Carpet
49	37 013003	Orectolobidae	<i>Orectolobus maculatus</i>	spotted wobbegong
49	37 013001	Orectolobidae	<i>Orectolobus ornatus</i>	Shark, Wobbegong (ornate)
49	37 013002	Parascylliidae	<i>Parascyllium collare</i>	Collared carpet shark
49	37 013005	Parascylliidae	<i>Parascyllium ferrugineum</i>	Rusty carpet shark
49	37 023002	Pristiophoridae	<i>Pristiophorus cirratus</i>	Common sawshark
49	37 023001	Pristiophoridae	<i>Pristiophorus nudipinnis</i>	Southern sawshark
49	37 023003	Pristiophoridae	<i>Pristiophorus</i> sp. A	Eastern sawshark
49	37 044001	Rhinochimaeridae	<i>Harriotta raleighana</i>	Bigspine spookfish
49	37 044002	Rhinochimaeridae	<i>Rhinochimaera pacifica</i>	Pacific spookfish
49	37 015014	Scyliorhinidae	<i>Apristurus</i> sp. A	Deepsea catshark
49	37 015015	Scyliorhinidae	<i>Apristurus</i> sp. B	Long-snouted catfish
49	37 015017	Scyliorhinidae	<i>Apristurus</i> sp. D	Beachport deepwater catshark
49	37 015018	Scyliorhinidae	<i>Apristurus</i> sp. E	Bulldog catshark
49	37 015027	Scyliorhinidae	<i>Asymbolus analis</i>	Grey spotted catshark
49	37 015022	Scyliorhinidae	<i>Asymbolus parvus</i>	Dwarf catshark
49	37 015024	Scyliorhinidae	<i>Asymbolus rubiginosus</i>	Catshark, orange spotted
49	37 015007	Scyliorhinidae	<i>Cephaloscyllium fasciatum</i>	Reticulate swell shark
49	37 015001	Scyliorhinidae	<i>Cephaloscyllium laticeps</i>	Shark, Draughtboard

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
49	37 015013	Scyliorhinidae	<i>Cephaloscyllium</i> sp. A	Swell Shark A
49	37 015009	Scyliorhinidae	<i>Galeus boardmani</i>	Sawtail shark
49	37 024900	Squatinae	<i>Squatina</i> (all spp	
49	37 024001	Squatinae	<i>Squatina australis</i>	Shark, angel (inshore)
49	37 024004	Squatinae	<i>Squatina</i> sp. A	Shark, angel (offshore)
49	37 017003	Triakidae	<i>Furgaleus macki</i>	Shark, Whiskery
49	37 017004	Triakidae	<i>Mustelus</i> sp. B	
49	37 017000	Triakidae	<i>Triakidae</i> - undiff.	Hound sharks (family code)
50	37 012001	Alopiidae	<i>Alopias vulpinus</i>	Thresher shark
50	37 018030	Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	Shark, Grey Reef
50	37 018001	Carcharhinidae	<i>Carcharhinus brachyurus</i>	Shark, bronze whaler
50	37 018023	Carcharhinidae	<i>Carcharhinus brevipinna</i>	Shark, spinner
50	37 018021	Carcharhinidae	<i>Carcharhinus leucas</i>	Shark, Bull
50	37 018039	Carcharhinidae	<i>Carcharhinus limbatus</i>	Shark, Black Tip
50	37 018003	Carcharhinidae	<i>Carcharhinus obscurus</i>	Shark, dusky whaler
50	37 018901	Carcharhinidae	<i>Carcharhinus, Loxodon and Rhizoprionodon</i> spp	Blacktip shark (group code)
50	37 018022	Carcharhinidae	<i>Galeocerdo cuvier</i>	Shark, tiger
50	37 018004	Carcharhinidae	<i>Prionace glauca</i>	Shark, Blue whaler
50	37 018000	Carcharhinidae, Hemigaleidae	<i>Carcharhinidae, Hemigaleidae</i> - undiff.	Shark, whaler
50	37 011001	Cetorhinidae	<i>Cetorhinus maximus</i>	Basking shark
50	37 005001	Hexanchidae	<i>Heptanchias perlo</i>	Sharpnose sevengill shark
50	37 005002	Hexanchidae	<i>Notorynchus cepedianus</i>	Broadnose sevengill shark
50	37 010003	Lamnidae	<i>Carcharodon carcharias</i>	Shark, White pointer
50	37 010001	Lamnidae	<i>Isurus oxyrinchus</i>	Shortfin mako shark
50	37 010000	Lamnidae	<i>Lamnidae</i> - undiff.	Shark, Mako
50	37 008001	Odontaspidae	<i>Carcharias taurus</i>	Grey Nurse Shark
50	37 008003	Odontaspidae	<i>Odontaspis ferox</i>	Sand tiger shark
50	37 019001	Sphyrnidae	<i>Sphyrna lewini</i>	Scalloped hammerhead shark
50	37 019004	Sphyrnidae	<i>Sphyrna zygaena</i>	Smooth hammerhead shark
50	37 019000	Sphyrnidae	<i>Sphyrnidae</i> - undiff.	Shark, Hammerhead
51	37 035000	Dasyatidae	<i>Dasyatidae</i> - undiff.	Stingray
51	37 035001	Dasyatidae	<i>Dasyatis brevicaudata</i>	Smooth stingray
51	37 035008	Dasyatidae	<i>Dasyatis fluviorum</i>	Stingray, Estuary
51	37 035004	Dasyatidae	<i>Dasyatis kuhlii</i>	Blue spotted stingray
51	37 035002	Dasyatidae	<i>Dasyatis thetidis</i>	Stingray, Black
51	37 035010	Dasyatidae	<i>Dasyatis violacea</i>	Pelagic stingray
51	37 990001	Dasyatidae, Myliobatidae, Gymnuridae, Urolophidae	<i>Dasyatidae, Gymnuridae, Myliobatidae and Urolophidae</i>	Stingray/Stingaree
51	37 039001	Myliobatidae	<i>Myliobatis australis</i>	Ray, Eagle
51	37 028002	Narcinidae	<i>Narcine tasmaniensis</i>	Tasmanian numbfish
51	37 023000	Pristiophoridae	<i>Pristiophoridae</i> - undiff.	Shark, Saw
51	37 031001	Rajidae	<i>Irolita waitii</i>	Southern round skate
51	37 031018	Rajidae	<i>Notoraja</i> sp. A	-
51	37 031009	Rajidae	<i>Pavoraja nitida</i>	Peacock skate
51	37 031002	Rajidae	<i>Raja australis</i>	Sydney skate

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
51	37 031010	Rajidae	<i>Raja gudgeri</i>	Bight skate
51	37 031007	Rajidae	<i>Raja lemprieri</i>	Thornback skate
51	37 031005	Rajidae	<i>Raja</i> sp. A	Skate, Longnose
51	37 031028	Rajidae	<i>Raja</i> sp. B	-
51	37 031011	Rajidae	<i>Raja</i> sp. F	-
51	37 031900	Rajidae	<i>Raja</i> spp	-
51	37 031006	Rajidae	<i>Raja whitleyi</i>	Melbourne skate
51	37 031000	Rajidae	<i>Rajidae</i> - undiff.	Skates (family code)
51	37 990018	Rajiformes	<i>Skates and rays, unspecified</i>	Skates and/or rays
51	37 027009	Rhinobatidae	<i>Aptychotrema rostrata</i>	Ray, Shovelnose
51	37 027001	Rhinobatidae	<i>Aptychotrema vincentiana</i>	Western shovelnose ray
51	37 026002	Rhinobatidae	<i>Rhina ancylostoma</i>	Shark ray
51	37 027000	Rhinobatidae	<i>Rhinobatidae</i> - undiff.	Shovelnose rays
51	37 026001	Rhinobatidae	<i>Rhynchobatus djiddensis</i>	White-spotted guitarfish
51	37 027002	Rhinobatidae	<i>Trygonorrhina fasciata</i>	Ray, Fiddler
51	37 027006	Rhinobatidae	<i>Trygonorrhina</i> sp. A	Shark, Banjo
51	37 027010	Rhynchobatidae	<i>Rhinobatos typus</i>	Ray, white-spotted Shovelnose
51	37 028001	Torpedinidae	<i>Hypnos monopterygium</i>	Coffin ray
51	37 028900	Torpedinidae	<i>Torpedinidae</i> - undiff.	Torpedo rays (group code)
51	37 028003	Torpedinidae	<i>Torpedo macneilli</i>	Short-tail torpedo ray
51	37 028000	Torpedinidae, Narcinidae, Hypnidae	<i>Torpedinidae, Narcinidae, Hypnidae</i> - undiff.	Numbfish
51	37 038014	Urolophidae	<i>Trygonoptera</i> sp. B	Eastern shovelnose stingaree
51	37 038006	Urolophidae	<i>Trygonoptera testacea</i>	Common stingaree
51	37 038000	Urolophidae	<i>Urolophidae</i> - undiff.	Stingaree
51	37 038001	Urolophidae	<i>Urolophus bucculentus</i>	Sandyback stingaree
51	37 038002	Urolophidae	<i>Urolophus cruciatus</i>	Stingaree, Crossback
51	37 038008	Urolophidae	<i>Urolophus expansus</i>	Wide stingaree
51	37 038004	Urolophidae	<i>Urolophus paucimaculatus</i>	Stingaree, Sparsely-spotted
51	37 038018	Urolophidae	<i>Urolophus</i> sp. A	Kapala stingaree
51	37 038005	Urolophidae	<i>Urolophus sufflavus</i>	Yellowback stingaree
51	37 038007	Urolophidae	<i>Urolophus viridis</i>	Greenback stingaree
51	37 038009	Urolophidae	<i>Urolophus westraliensis</i>	Brown stingaree
52	41 116001	Delphinidae	<i>Delphinus delphis</i>	Short beaked common dolphin
52	41 116002	Delphinidae	<i>Feresa attenuata</i>	Pygmy killer whale
52	41 116003	Delphinidae	<i>Globicephala macrorhynchus</i>	Short-finned pilot whale
52	41 116004	Delphinidae	<i>Globicephala melas</i>	Long-finned pilot whale
52	41 116005	Delphinidae	<i>Grampus griseus</i>	Risso's dolphin
52	41 116006	Delphinidae	<i>Lagenodelphis hosei</i>	Fraser's dolphin
52	41 116011	Delphinidae	<i>Orcinus orca</i>	Killer whale
52	41 116012	Delphinidae	<i>Peponocephala electra</i>	Melon-headed whale
52	41 116013	Delphinidae	<i>Pseudorca crassidens</i>	False killer whale
52	41 116015	Delphinidae	<i>Stenella attenuata</i>	Pantropical spotted dolphin
52	41 116016	Delphinidae	<i>Stenella coeruleoalba</i>	Striped dolphin
52	41 116017	Delphinidae	<i>Stenella longirostris</i>	Spinner dolphin
52	41 116018	Delphinidae	<i>Steno bredanensis</i>	Rough-toothed dolphin

Ecopath Group	CAAB Code	Family	Scientific Name	Common Name
52	41 116019	Delphinidae	<i>Tursiops truncatus</i>	Bottlenose dolphin
52	41 119001	Kogiidae	<i>Kogia breviceps</i>	Pygmy sperm whale
52	41 119002	Kogiidae	<i>Kogia simus</i>	Dwarf sperm whale
52	41 119003	Physeteridae	<i>Physeter catodon</i>	Sperm whale
52	41 120001	Ziphiidae	<i>Berardius arnuxii</i>	Arnoux's beaked whale
52	41 120002	Ziphiidae	<i>Hyperoodon planifrons</i>	Southern bottlenose whale
52	41 120005	Ziphiidae	<i>Mesoplodon densirostris</i>	Blainville's beaked whale
52	41 120006	Ziphiidae	<i>Mesoplodon ginkgodens</i>	Ginkgo-toothed beaked whale
52	41 120007	Ziphiidae	<i>Mesoplodon grayi</i>	Gray's beaked whale
52	41 120008	Ziphiidae	<i>Mesoplodon hectori</i>	Hector's beaked whale
52	41 120009	Ziphiidae	<i>Mesoplodon layardii</i>	Strap-toothed whale
52	41 120012	Ziphiidae	<i>Ziphius cavirostris</i>	Cuvier's beaked whale
53	41 110001	Balaenidae	<i>Eubalaena australis</i>	Southern Right whale
53	41 112001	Balaenopteridae	<i>Balaenoptera acutorostrata</i>	Dwarf minke whale
53	41 112002	Balaenopteridae	<i>Balaenoptera borealis</i>	Sei whale
53	41 112003	Balaenopteridae	<i>Balaenoptera edeni</i>	Eden/Bryde's whale
53	41 112004	Balaenopteridae	<i>Balaenoptera musculus</i>	Blue whale
53	41 112005	Balaenopteridae	<i>Balaenoptera physalus</i>	Fin whale
53	41 112006	Balaenopteridae	<i>Megaptera novaeangliae</i>	Humpback whale
54	41 131003	Otariidae	<i>Arctocephalus pusillus doriferus</i>	Australian fur seal



## Co-authorship statement

Chapter 2, “An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity”, was written in collaboration with Steven Martell, Michael Melnychuk and Carl Walters, of the UBC Fisheries Centre. The work arose from an original idea by Carl Walters, who invited students to derive  $\alpha$  from  $U_{MSY}$  using his suggested approach. Following our successful completion of the task, he invited myself and Michael Melnychuk to develop the idea into a paper. The Bayesian estimation component of the analysis was done, at the suggestion of an anonymous reviewer, in collaboration with Steven Martell, with whom the analysis was shared. I take responsibility for programming of the analysis of the equilibrium properties of the model, approximately 90% of the text, derivation of  $\frac{\partial \ell_a}{\partial U_{MSY}}$  for the plus group, all manuscript preparation, and any mistakes. Copyright permission to publish this paper as a thesis chapter was granted by the *Canadian Journal of Fisheries and Aquatic Sciences*. Further acknowledgements can be found at the end of Chapter 2.

Chapter 4, “Optimal harvest rate for long-lived, low-fecundity species: deepwater dogsharks of the continental slope of southeastern Australia” was co-authored with Carl Walters. The idea of using the model presented in Chapter 2 to identify limitations of  $U_{MSY}$  for sharks was my own. Carl Walters directed my ideas at critical phases of the analysis, which went through many redevelopments, and was therefore integral to the final product. I was responsible for identification of methods and analytical approach, analysis, presentation of results and text (with suggested edits from Dr Walters) and take full responsibility for any errors or omissions. Further acknowledgements can be found at the end of Chapter 4.

Chapter 6, “Evaluation of historical fisheries management options for New South Wales trawl fisheries: comparison of two ecosystem models” was co-authored with Elizabeth Fulton and Marie Savina (Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia) and Tony Pitcher (UBC Fisheries Centre). The collaborative project was initiated by Tony Pitcher and by members of CSIRO and NSW Department of Primary Industries. The Atlantis ecosystem model was built entirely by Marie Savina and Elizabeth Fulton (and their colleagues) and all simulations using Atlantis were done by these authors. They also wrote the

description of the Atlantis model in the Methods section; identified the core list of indicators that would be used to measure performance of the alternative policies; decided aggregation of model functional groups for comparison; and performed the first comparison with preliminary results. The idea to build models representing the NSW continental slope in 1976, with focus on dogsharks as ‘weak stocks’, was mine. I was responsible for building, calibrating and running the Ecopath with Ecosim model; identification of the eight alternative policies; the optimal policy search; preparation of the fishing mortality input file for Atlantis; and all programming required for analysing the final comparisons. Decisions about the presentation and layout of results were mine and I wrote approximately 90% of the text. Further acknowledgements can be found at the end of Chapter 6.

All other chapters and appendices, including ideas, analysis and presentation, are my own work, except for generous contributions acknowledged on the Acknowledgements page (p. xi) and at the end of each chapter. All errors and omissions are my own.