VULNERABILITY OF MARINE FISHES TO FISHING: FROM GLOBAL OVERVIEW TO THE NORTHERN SOUTH CHINA SEA

by

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ABSTRACT

Fishing has become a major conservation threat to marine fishes. Effective conservation of threatened species requires timely conservation risk assessment and formulation of socio-economically viable policies. A fuzzy logic expert system is developed to predict the intrinsic vulnerability and depletion risk of marine fishes to fishing. Firstly, the expert system predicts intrinsic vulnerability (i.e., fishes' inherent ability to withstand fishing mortality) from simple parameters of life history and ecology. Secondly, the system predicts the relative depletion risk of marine fishes from their intrinsic vulnerability and exploitation status inferred from catch time-series. These methods reveal the increasing dominance in global catches by fishes with low intrinsic vulnerability, particularly those in coral reefs. The opposite trend is observed in seamounts where species are highly vulnerable to fishing and are increasingly being exploited and serially depleted in recent years. Moreover, risk of population depletion increased greatly from the 1970s to 2000s. Among all extant marine fishes, 10 to 20% are predicted to have high depletion risk. In the northern South China Sea (NSCS), relative abundance of 15 out of the 17 studied taxa declines by over 70% in 15 years. The rate of decline is correlated with the intrinsic vulnerability of the taxa. Using the Ecopath with Ecosim modelling approach, the structures of the NSCS ecosystem in the 1970s and 2000s are reconstructed and compared. The models show that the NSCS ecosystem has changed from being demersal-dominated to pelagic-dominated, with a large decline in overall biomass and decrease in ecosystem maturity. Primary production is largely utilized by the fisheries compared to some 30 years ago when primary production was mainly utilized by marine fauna. The model is able to emulate the changes of observed relative abundance of commercial taxa. Using Ecosim, trade-off between conservation status (indicated by a depletion index) and economic benefits is identified as convexshaped. The 2000s ecosystem appears sub-optimal ecologically and economically, thus improvement in conservation and economic benefits can be achieved simultaneously. However, the resulting social problems due to loss of fishing-related jobs need to be addressed first. Thus, developing viable alternative livelihoods for fishers is a priority to meet conservation and economic objectives.

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1. GENERAL INTRODUCTION¹

In the early 1950s, a large bodied croaker (Sciaenidae) called the Chinese bahaba (*Bahaba taipingensis*), endemic to the region, was common along the coast of the South and East China Sea (Figure 1.1). Its swimbladder was particularly valued as a tonic in traditional Chinese medicine. During spawning in the major estuaries, local fishers targeted bahaba aggregations using artisanal purse seines and gillnets. Catches of over one tonne per haul were common and individuals over 50 kg were often caught. An indirect estimate of annual catch from Hong Kong is over 50 tonnes per year in the 1940s (Sadovy & Cheung 2003). However, in the 2000s, only a few individuals per year were caught along the entire Chinese coast. The species is now listed as 'Critically Endangered' in the IUCN Red List of Endangered Species (Baillie *et al.* 2004). Other stories of fishes being threatened by fisheries exploitation have been documented, such as the Common skate (*Raja batis*) in the North Sea (Brander 1981), the Nassau grouper (*Epinephelus striatus*) in the Caribbean (Sadovy 1993; Sala *et al.* 2003).

Exploitation of the ocean has increased rapidly in recent decades and fishing has been a major form of direct utilization (Pauly *et al.* 2002). Based on fishery statistics compiled by the United Nations Food and Agriculture Organization (FAO), total reported landings from the sea increased from less than 20 to over 82 million tonnes from 1950 to the 2000s. If discards and illegal, unreported and unregulated catches are included, global catches peaked at almost 150 million tonnes in the late 1980s, after which they declined slowly (Pauly *et al.* 2002). In 2003, about one-quarter of the stocks monitored by FAO were said to be underexploited or moderately exploited (3 percent and 21 percent, respectively), 52 percent were fully-exploited (production close to their maximum sustainable limits), while approximately one-quarter were overexploited, depleted or recovering from depletion (16 percent, 7 percent and 1 percent, respectively). These

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represented an increase in the proportion of overexploited and depleted stocks from about 10 percent in the mid-1970s to close to 25 percent in early 2003 (FAO 2004).

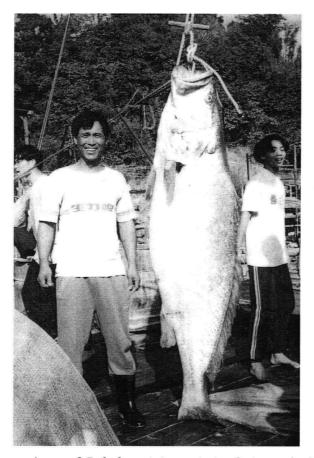


Figure 1.1. A specimen of *Bahaba taipingensis* (> 2m) caught 30 December, 1993, outside Castle Peak Bay, western Hong Kong, as incidental trawler bycatch. Photo originally published in Sadovy and Cheung (2003).

1.1. Fishing as a major conservation threat to marine fishes

Collapses of major fishery stocks and endangerment of a number of marine fishes suggest that marine species are vulnerable to extreme depletions, or even extinction, resulting directly or indirectly from fishing (Roberts and Hawkins 1999; Powles *et al.* 2000; Dulvy *et al.* 2003; Sadovy and Cheung 2003). While the majority of the world's fisheries resources are fully- to over-exploited (Pauly *et al.* 2002; Hilborn *et al.* 2004a), fishing is considered to be a major conservation threat to marine fishes (Reynolds *et al.* 2001; Dulvy *et al.* 2003). Parallel to the increasing scale of fishing, the abundance of

many marine fishes has declined greatly throughout the world over the past five decades. In the north Atlantic, high-trophic-level fishes have declined by two thirds since the 1950s (Christensen *et al.* 2003). Over the past 50 years, breeding populations of 98 populations of marine fishes from around the world declined by a median of 65%, with over 28 populations declining by more than 80% (Hutchings & Reynolds 2004; Reynolds *et al.* 2005a). Commercially-important species can be fished down to a vulnerable level because of their economic value, e.g., Chinese bahaba (*Bahaba taipingensis*, Sciaenidae) (Sadovy & Cheung 2003), Southern bluefin tuna (*Thunnus maccoyii*, Scombridae) (Hayes 1997). However, species with little or no commercial value are not safe from the threats of fishing, since non-targeted species may be threatened through bycatch (e.g., Common skate, *Raja batis*, Rajiidae, Brander 1981; Barndoor skate, *Raja laevis*, Rajiidae, Casey & Myers, 1998). Moreover, fishing activities can create large disturbances and damage to benthic habitats (Jennings *et al.* 2001; Kaiser *et al.* 2002; Kaiser *et al.* 2003). Declines and extinctions can be associated with loss of essential habitats critical to complete the life cycle of the species (McDowall 1992; Watling & Norse 1998).

Fishing may also cause loss of genetic diversity (Law 2000). Some populations of New Zealand snapper (*Pagrus auratus*; Hauser *et al.* 2002) and Atlantic cod (*Gadus morhua*; (Hutchinson *et al.* 2003) exhibit significant declines in genetic diversity over their exploitation history. Also, effective population size, which determines the genetic properties of a population, was about one-fifth of the census population size (estimated total abundance) in some exploited populations of fishes (Hauser *et al.* 2002; Hutchinson *et al.* 2003; Hoarau *et al.* 2004). The low effective population size may result in inbreeding in the population and a loss of genetic diversity (Hauser *et al.* 2002; Hutchinson *et al.* 2003; Hoarau *et al.* 2004). Thus, there is a need to monitor and manage genetic diversity of exploited marine populations (Kenchington *et al.* 2003).

The loss of biodiversity may directly or indirectly affect the functioning of the ecosystem (Loreau *et al.* 2001; Worm & Duffy 2003; Worm *et al.* 2006). Removal of keystone species, which include species that are critical to the ecological function of a community or habitat in their current states (Zacharias & Roff 2001), can result in a state shift in marine ecosystems. For instance, the removal of sea otters in the Aleutian Archipelago resulted in sea urchin population expansion, which virtually excluded fleshy

macroalgae such as kelp and greatly affected their associated communities (Tegner & Dayton 2000; Jackson *et al.* 2001). On the other hand, depletion of algae grazers such as parrotfish led to overgrowth of algae on coral surfaces which largely affected the coral reef ecosystem (Bellwood *et al.* 2004). Some studies suggested that biodiversity is positively correlated with ecosystem function (Tilman *et al.* 1997; Symstad *et al.* 1998; Worm *et al.* 2006), and the stability and resilience of ecosystems (Tilman & Downing 1994; Tilman 1996; Scheffer *et al.* 2001). This is supported by meta-analysis of data showing significant correlations between marine biodiversity and ecosystem functions (Worm *et al.* 2006). Thus, it is generally agreed that a higher species richness is needed to maintain stability of ecosystem processes against environmental variability (Loreau *et al.* 2001).

1.2 Marine fishes may be vulnerable to extinction

There was a general belief in the past that marine fishes would never be extirpated because a single female could produce millions of eggs and have large geographic ranges. Although it has been realized that elasmobranchs (sharks and rays) are vulnerable to extinction because of their life history and ecology (Smith *et al.* 1998; Stevens 1999; Stevens *et al.* 2000), wide-ranging highly fecund fishes were still considered inexhaustible by some. Such perceptions persist since Jean Baptiste de Lamarck stated in the early 19th century that:

'Animals living in the waters, especially the sea waters, are protected from the destruction of their species by man. Their multiplication is so rapid and their means of evading pursuit or traps are so great that there is no likelihood of his being able to destroy the entire species of these animals' (Lamarck 1809, reprinted in 1984).

This means that a small number of adult individuals remaining in the ocean could fill the sea with fishes quickly, assuming that most eggs could develop into adult fish again a few years later. Also, marine fishes generally have wide geographic ranges and produce pelagic eggs that can draft with ocean currents. Thus populations 'somewhere' could always re-colonize a locally depleted area.

The misconception that highly fecund fishes (i.e., the majority of teleosts) are resilient to fishing (the ability of a population to recover) have been seriously scrutinized and largely disproved (Sadovy 2001; Dulvy et al. 2003). High fecundity does not equate with high resilience to fishing (the ability of a population to recover from being depleted by fishing). Resilience depends largely on the survivorships from the egg to the adult stages, instead of the fecundity per se (Sadovy 2001). Fishes that spawn millions of eggs at a time usually have a 'bet-hedging' strategy, in which the production of large number of eggs is evolved to compensate for the low survivorship from egg to spawner (Phillipi & Seger 1989). Life history theory predicts that fishes (and other vertebrates) that are large in size (generally highly fecund in teleosts) and late maturing have low intrinsic rates of population increase (r) (Smith et al. 1998; Musick 1999b; Reynolds et al. 2001). Animals with low r have less ability to recover after reduction of the population, and thus low resilience to fishing. There are examples of highly fecund fishes that are endangered by fishing, e.g., the Chinese bahaba (Sadovy & Cheung 2003), Nassau grouper (Epinephelus striatus) (Sadovy 1993; Sala et al. 2001) and Humphead wrasse (Cheilinus undulates) (Sadovy et al. 2003). The relationship between life history of fishes and their vulnerability to fishing will be explored in detail later.

A large geographic range does not offer much protection to fishes from being threatened by fishing (Dulvy & Reynolds 2002; Dulvy *et al.* 2003; Reynolds *et al.* 2005a). Genetic studies suggested that dispersal of pelagic eggs and larvae might be limited (Swearer *et al.* 1999; Cowen *et al.* 2000). Also, large-scale fishing activities have spread to most parts of the oceans and there are few unexploited refugia left (Pauly *et al.* 2002; Pauly *et al.* 2005). Thus, fishes with high fecundity and large geographic range should not be assumed to be resilient or invulnerable.

Fishing was considered a conservation threat to marine fish only in recent years (Powles *et al.* 2000). In fact, whether the depletion of fish populations by fishing should be a genuine conservation concern was a subject of debate by fisheries scientists and conservation biologists (Carlton *et al.* 1999; Mace & Hudson 1999; Powles *et al.* 2000; Hutchings 2001). For instance, conventional fisheries stock assessment based on simple surplus production models suggests that maximum equilibrium catches from a population could be achieved by reducing stock abundance to a level close to half of the unexploited

stock size – a decline level (under a certain time-frame) that may fall into vulnerable categories under the IUCN Red List criteria. The IUCN Red List, maintained by the World Conservation Union, are widely accepted as the authority for determining extinction risk of animals and plants (Rodrigues *et al.* 2006), although their validity for marine fishes had been questioned (Punt 2000; Reynolds *et al.* 2005a). To resolve this problem, the IUCN included a higher decline thresholds for species in which 'the causes of the reduction in population size are clearly reversible, and understood and have ceased' (IUCN 2001). However, even if the causes of population reduction are reversible, and understood, and management policies are in place, depleted populations may still not be able to recover (Hutchings 2000; Hutchings & Reynolds 2004).

Moreover, no contemporary extinctions of marine fishes have been documented, leading to the uncertainty of whether marine fishes can ever be fished to extinction (Dulvy *et al.* 2003; Reynolds *et al.* 2005a). However, the lack of contemporary extinctions may be due to the difficulty in detecting marine extinctions (Carlton 1993). A study demonstrated a median of 44 years of delayed reporting of possible extinction from the time the last individual of the marine species was sighted since the 1900s, (Dulvy *et al.* 2003). Although reporting ability has improved in recent years (Dulvy *et al.* 2003), given that intensive large scale fishing mainly occurred since the 1950s, extinctions or extirpations caused by fishing may still not be apparent.

A change in our perception of risk of extinction and threat to conservation has led to various studies on the biology of extinction vulnerability of marine fishes in the last decade (Reynolds *et al.* 2005a). Some have suggested treating marine fishes differently from other animals in extinction risk assessments (Musick 1999a). On the other hand, many marine fish stocks have collapsed because of over-exploitation (Hutchings & Reynolds 2004). Although it appears that fish stocks recovered after fishing pressure had been eased (Russ & Alcala 1996; Myers & Worm 2005), the rate of recovery depends on the productivity (intrinsic rate of population increase, r) of the stocks and the level of depletion (Safina *et al.* 2005). Also, many stocks have shown little or no sign of recovery after up to 15 years, while those that have recovered are mainly clupeoid fishes, which are suggested to be intrinsically more resilient (Hutchings 2000; Hutchings & Reynolds 2004). The northern cod is a classic case of the lack of recovery after severe depletion (Shelton & Healey 1999; Hutchings & Reynolds 2004). The lack of recovery of some fish stocks suggested that fishes could be depleted to a level in which their recovery may be impaired. Thus, unless the non-recovery thresholds for fishes are different from those for other organisms, marine fishes should be treated like other animals in extinction risk assessment (Hutchings 2001).

However, because of the lack of documented contemporary extinctions of marine fishes, the definition of their true extinction risk is still unclear (Reynolds *et al.* 2005a). This question may be resolved by improving the understanding of fish population dynamics at low stock sizes, which may help to determine their minimum viable population size. Meta-analysis of stock-recruitment relationships to evaluate stock productivity at low spawner abundance provided useful information to help answer this question (Myers *et al.* 1999; Goodwin *et al.* 2006).

1.3. Life history and vulnerability

Life-history traits, which have evolved to ensure persistence in the face of biotic and abiotic variability (Winemiller & Rose 1992; Wootton 1996; Rochet *et al.* 2000; Winemiller 2005), affect the responses of fish population to exploitation (Adams 1980; Roff 1984; Kirkwood *et al.* 1994). Trade-offs between growth, reproduction and mortality appear to be invariant across a wide range of vertebrates (Charnov 1993; Jensen 1996; Charnov & Downhower 2002). For instance, the ratio of natural mortality to growth rate is very similar across different animal groups. Also, species that are largebodied, long-lived and late-maturing generally have slow growth, low natural mortality, high life-time reproductive outputs but a low intrinsic rate of population increase. The latter directly affect the ability of a species to resist exploitation.

It is possible to put species into a continuum between extreme life history strategies. For instance, based on comparative life-history analysis of 216 North American freshwater and marine fishes, three general life-history patterns were proposed (Winemiller & Rose 1992; Winemiller 2005): "periodic" (large, late-maturing fishes), "opportunistic" (small, early-maturing fishes) and "equilibrium" (intermediate size show

parental care to offspring). Later studies adopted these groupings to relate compensatory responses of fish populations to life history patterns (Rose *et al.* 2001). Fagan *et al.* (1999) proposed parallel categories for a wide range of vertebrates: "persistent" (low population variability relative to their growth rates), "refuge-dependent" (high population variability relative to growth rate, thus population is dependent on the existence of refugia for recolonization), "carrying capacity-dependent" (low population growth rate, low variability, thus would require larger population size). Populations in the same life history groups may respond similarly to disturbances such as fishing and habitat destruction. Thus, qualitative predictions on the responses of populations to disturbances based on these groupings could be made (Rose *et al.* 2001; Winemiller 2005).

Correlations between life history, population regulation and thus vulnerability to fishing are supported by empirical evidence. Meta-analysis using 54 stock-recruitment time-series showed that large-sized, late-maturing fishes had strong density-dependence in low abundance (i.e., have smaller maximum spawner per spawner), but high equilibrium spawner per recruit without exploitation (Goodwin *et al.* 2006). Analysis including data from other vertebrate groups produced similar conclusions, suggesting that the correlations between life history and population dynamics may be applicable to most vertebrates (Fagan *et al.* 1999). Also, empirical studies using historical abundance data of exploited fish populations find significant correlations between the rate of population declines (a proxy of vulnerability to fishing) and life history parameters such as maximum body size and age at maturity (Jennings *et al.* 1998; Jennings *et al.* 1999a, b). Indeed, all current evidence suggests that body size is an important factor in determining vulnerability to fishing (Jennings *et al.* 1998; Jennings *et al.* 1999a, b; Cardillo & Dromham 2001; Reynolds *et al.* 2001; Gaston & Blackburn 2003; Reynolds *et al.* 2005a).

Correlations of life history traits of fishes with other anthropogenic disturbances may be different from those associated with fishing. Freshwater fishes are mainly threatened by habitat destruction and introduction of exotic species (Ricciardi & Rasmussen 1999). This may have led to a weak correlation between body size and vulnerability for some freshwater fishes (Reynolds et al. 2005b). In fact, small freshwater fish may have higher vulnerability (Reynolds *et al.* 2005b) because their distribution range is correlated with body size, and species with a restricted range are generally more vulnerable to habitat destruction. The ability of species to adapt to changing temperature has been suggested as a factor determining the vulnerability of marine fishes to climate change (Roessig *et al.* 2004; Perry *et al.* 2005). Distribution ranges of 36 species of demersal fishes in the North Sea and their relationship with temperature changes over the past three decades suggested that fishes with shorter life cycles and smaller body sizes were able to shift their distribution more easily than other species (Perry *et al.* 2005). This implies that fishes with these characteristics may be better able to adapt to climate change.

Ecological and behavioural characteristics may also affect fishes' vulnerability to fishing. For example, reduction of population below a depensatory abundance threshold can lead to extinction (Liermann & Hilborn 1997). Depensation, termed the Allee effect in the ecology literature (Stephens & Sutherland 1999; Stephens et al. 1999), occurs when fitness (number of offspring per spawner) or *per capita* growth rate decreases at low population size (Stephens et al. 1999; Petersen & Levitan 2001). This is contrary to the compensation effect often assumed to be the norm, in which fitness or per capita growth rate increases at low population size (described by a logistic function) (Liermann & Hilborn 1997). Depensation may result from juvenile predation saturation at high population size (Liermann & Hilborn 1997; Petersen & Levitan 2001), trophic cascade effects in which predation on juveniles increases because of increased predator abundance (Walters & Kitchell 2001), or disruption of spawning aggregations because of reduced spawner abundance or distorted sex-ratio (Sala et al. 2003; Sadovy & Domeier 2005). Meta-analysis of stock-recruitment data showed that depensation might be uncommon in marine fishes (Myers et al. 1995; Liermann & Hilborn 1997). However, reanalysis accounting for the high variance in the original data suggests that it might still be likely that depensation would be more common in marine fishes than previously assumed (Liermann & Hilborn 1997).

Species forming large aggregations can be easily targeted by fishers. Aggregative or shoaling behaviour often results in hyperstability of catch-per-unit-effort (CPUE), which masks the depletion of populations (Hilborns & Walters 1992; Pitcher 1995, 1997; Walters 2003). Moreover, hyperstability of CPUE implies that economic incentives to fishing can be sustained under low resource abundance (Hutchings 1996) and as a result,

bionomic equilibrium may not be reached until populations are depleted to a dangerously low level (Hilborns & Walters 1992; Mackinson *et al.* 1997). In particular, species which form spatially and temporally predictable spawning aggregations are especially vulnerable. Depletion of spawning aggregations may permanently prevent reproduction in these populations (Sala *et al.* 2003; Sadovy & Domeier 2005). At the same time, species with certain reproductive strategies such as hermaproditism or a high level of parental care may also be particularly prone to the effects of fishing (Rowe & Hutchings 2003; Hutchings & Reynolds 2004).

1.4. Approaches to assessing conservation status of fishes

Despite the wide range of impacts from fishing on marine ecosystems and the potential vulnerability of marine fishes to fishing, our understanding of the conservation status of marine fishes - the largest group of vertebrates in the sea - lags behind the increasing rate of their utilization. Relative to other vertebrate groups, the proportion of fish species that have been assessed with the IUCN Red List criteria is very low (Figure 1.2). If we consider marine fishes only, less than 7% of the 15,723 extant species have been assessed using the Red List criteria (Baillie *et al.* 2004). Among this 7%, over 35% of the assessed species were considered 'data deficient', i.e., at the time of the assessment, there were not enough data to determine the status of the species.

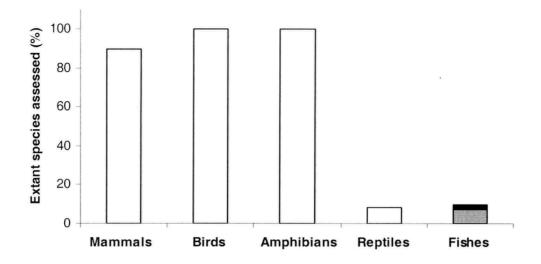


Figure 1.2. Proportion of extant vertebrates that have been assessed under the IUCN Red List of Endangered Species (Baillie *et al.* 2004). The black and grey bars represent marine and freshwater fishes, respectively.

If the current rate of Red List assessment is extrapolated, about 20% of extant marine fish species could be assessed by year 2020 (Figure 1.3). To cover half of the marine fishes under the Red List assessment in this timeframe, the current rate of assessment would have to be tripled. However, the Convention on Biological Diversity has set a "2010 Biodiversity Target" which has a mission statement: "to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on earth." (Decision VI/26, the Convention on Biological Diversity). To achieve such a target, species that are threatened or likely to be threatened should be identified. Given the current rate of Red List assessment for marine fishes, this target seems overly ambitious. The IUCN and its Species Specialist Commission realized the pressing need to increase assessment coverage in fishes and were devising strategies to increase their rate of assessments (Sadovy, Y. J., Chair of the IUCN Specialist Group of Groupers and Wrasses, pers. comm.).

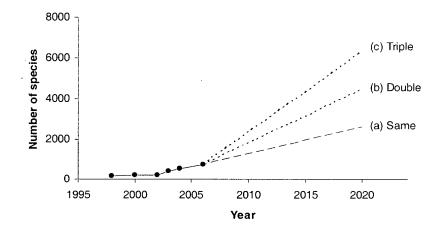


Figure 1.3. The number of marine fishes that have been assessed under the IUCN Red List since 1998 (solid line) and the projected number of assessed marine fishes to 2020 (dotted line) assuming the rate of assessment (number of species per year) (a) remain the same as the average between 2002 and 2005, (b) doubling the average between 2002 and 2005, and (c) tripling the average between 2002 and 2005.

The marine fish species that need to be assessed are numerous, while population data for the majority are lacking. Data limitations restrict the application of conventional assessment approaches to the full spectrum of species, which require understanding of population dynamics (Dulvy *et al.* 2004). Currently, the required population parameters can be estimated only for a small number of marine fishes, mainly commercially-targeted species in developed countries. At the same time, quantitative data on fisheries and population status of exploited species are costly to collect (Silvestre and Pauly 1997; Dulvy *et al.* 2003). Even in cases where time-series of population data are available, such as the North Sea, the power of large-scale monitoring survey to detect population decline in <10 years was low (Maxwell & Jennings 2005). The problem is most apparent in tropical, developing country fisheries where species diversity is high, but resources for monitoring are low (Jennings & Polunin 1996; Johannes 1998). Moreover, the intrinsic rate of increase (*r*), a population parameter that is a key to conventional assessment, is particularly difficult to estimate reliably (Musick 1999a; Reynolds *et al.* 2001).

To rapidly assess the relative conservation status and short-list priority species for detailed assessment, 'rule-of-thumb' approaches were proposed (Fagan *et al.* 2001;

Reynolds *et al.* 2001; Dulvy *et al.* 2003; Dulvy *et al.* 2004). These appraoches use easilyobtainable information to approximately identify vulnerable or "priority" species that are in need of immediate conservation attention. Such approaches are especially useful if their applications are combined with large databases, for instance, FishBase (Froese & Pauly 2004) and the *Sea Around Us* Project database (containing a wide range of fisheries data ranging from spatially disaggregated catch data to prices of fishery catches) (Watson *et al.* 2004; Sumaila *et al.* in press). Results can also help focus longer term research on the priority species so that data could be made available for more accurate extinction risk assessments.

As life history and ecology determine, at least in part, how fish populations respond to exploitation, these attributes could be used to develop 'rule-of-thumb' proxies to evaluate the intrinsic vulnerability of marine fishes to fishing (Reynolds *et al.* 2001; Dulvy *et al.* 2003). In this thesis, vulnerability of fishes is defined as a combination of intrinsic vulnerability and exposure to some external threatening factors. Intrinsic vulnerability to fishing is the inherent capacity to respond to fishing that relates to the fish's maximum rate of population growth and strength of density dependence. The intrinsic factors act synergistically with external threatening factors, such as fisheries exploitations, climate change or coastal development, to the susceptibility of species or populations to depletion, extirpation or extinction. For instance, when species with high intrinsic vulnerability to exploitation are being intensively fished, they are likely to have high risk of population depletion. Proxies of intrinsic vulnerability and the depletion risk resulted from their interactions with the external threatening factors could be determined from easily obtainable information through these 'rules-of-thumb'.

1.5. Integrating biodiversity conservation into fishery management

Developing fishery management policy that conserves marine biodiversity is an important step towards addressing the above problems. Fishing is the largest remaining wild hunting activity in the world (Cury & Cayre 2001) and has been suggested to be a major conservation threat to marine species (Dulvy *et al.* 2003). Although the objectives of most conventional fishery management policies are to maximize the sustainable catch

of target species, they share many similarities with the goals of biodiversity conservation. For instance, the Convention on Biological Diversity (CBD) states that "*the sustainable use of its components and the fair and equitable sharing of the benefits*". Thus, the Convention includes both sustainable use of resouces and the conservation of biological diversity.

Traditional approaches to fishery management may not be adequate to ensure effective conservation of marine species. Although approaches to management of fishery resources have been well developed, they mostly aim to maximize the long term sustainable yield of the resources being targeted (Rosenberg *et al.* 1993; Pitcher 1998). Using a simulation model, Punt (2000) demonstrated that risk of extinction could still be high even when the stock was managed for maximum sustainable yield. On the other hand, it has been suggested that the IUCN Red List criteria are consistent with reference points that provide warning of potential stock collapse in fisheries stock assessment (Dulvy *et al.* 2005). However, conventional approaches to fisheries assessments often focus on a few commercially important species only, while the trophic linkages among ecosystem groups and the effects on non-target species are overlooked. These non-target species may sometimes be more vulnerable and warrant higher conservation concerns than the target species. They can be threatened directly by being caught as bycatch, or indirectly from trophic interactions or habitat modifications (Pauly *et al.* 1998; Dulvy *et al.* 2000; Stobutzki *et al.* 2001).

The insufficiency of traditional approaches has generally been recognized and the ecosystem approach to fishery management is being advocated widely (Pitcher & Pauly 1998; Hall 1999; Pitcher 2001; Pauly et al. 2002; Hall & Mainprize 2004; Pikitch et al. 2004). This is evidenced by the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem, proclaimed in 2001. The Declaration was built on the principles of fisheries management suggested in the United Nations Convention on the Law of the Sea (UNCLOS), the Code of Conduct for Responsible Fisheries and the Convention on Biological Diversity. The Declaration emphasized that "... including ecosystem considerations in fisheries management provides a framework within which States and fisheries management organizations would enhance management performance, ... incorporation of ecosystem considerations implies more effective

conservation of the ecosystem and sustainable use and an increased attention to interactions, such as predator-prey relationships, among different stocks and species of living marine resources; furthermore that it entails an understanding of the impact of human activities on the ecosystem, including the possible structural distortions they can cause in the ecosystem...". Incorporation of this concept practically into fishery management is still in the initial phase (Hall & Mainprize 2004).

Numerous authors have proposed and discussed various tools and approaches (ecological, economic, management, etc.) to put the EBM concept in operation (Sainsbury *et al.* 2000; Sainsbury & Sumaila 2003; Hilborn 2004; Browman & Stergious 2005; Jennings 2005; Zeller & Pauly 2005). Examples of these tools and approaches include the use of indicators in fisheries management framework to evaluate the state of the ecosystem and decide appropriate management actions (Link *et al.* 2002; Jennings 2005; Livingston *et al.* 2005) and developing ecosystem models to explore the effects of fishing and management policies (Pauly *et al.* 2000; Pitcher *et al.* 2005).

Approaches to integrate conservation with fisheries management should generally include a series of steps from assessing vulnerability to exploring policy options (Figure 1.4). Firstly, species that are more vulnerable to extirpation (or extinction), and regions that are associated with higher conservation concerns, should be identified based on approaches that can be applied under data-limited conditions. This is followed by a more detailed assessment on the status of the ecosystem and the associated species in the region. Then, using various analytical tools such as computer simulation models, fisheries management policy options could be explored and the ecological, social and economic consequences resulting from different scenarios evaluated. These should provide useful insights to identify policies to meet conservation and other fisheries management objectives.

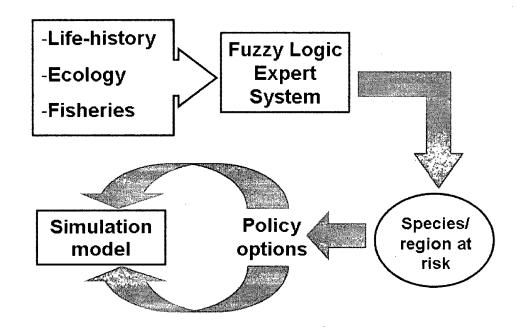


Figure 1.4. Schematic presentations of the proposed framework to identify policy options that integrate conservation into fisheries management.

1.6. Trade-offs between conservation and socio-economic objectives

An important concern in marine conservation is its trade-offs with other resource management objectives (Walters & Martell 2004). A trade-off can be defined as giving up some of one thing to get more of something else. On one hand, catches from fisheries may have to be reduced to lower the risk of stock collapse in the long term (Hilborn *et al.* 2004b). On the other hand, catch should be maximized in the short term to provide economic rent and to maintain the livelihoods of fishing communities. Moreover, in multi-species or multi-stocks fisheries, conservation of species or stocks with lower productivity (or higher vulnerability) may require reduction of catches of the more productive species or stocks.

Instances of trade-offs between conservation and fisheries become more apparent as exploitation threatens increasing number of vulnerable species (Hilborn *et al.* 2004a). For example, in New England in the USA, valuable scallop dredging fisheries were closed in some areas to protect the essential habitat of the depleted groundfish stocks (Worm & Myers 2003; Borodziak *et al.* 2004). Moreover, rebuilding New England groundfish stocks required reduction in fishing effort, and it was expected that some fishing companies might have to be closed because of reduced profitability (Borodziak *et al.* 2004). Also, evidence suggested a top-down trophic relationship between the cod (*Gadus morhua*) and benthic crustaceans such as shrimps and crabs in the north Atlantic (Worm & Myers 2003). Therefore, recovery of the cod populations might reduce the productivity of the valuable invertebrate fisheries. Conservation policies are more likely to be successful if they receive stakeholder support. Thus, reconciling the trade-offs between conservation and other fisheries management objectives in an ecosystem context should be important for effective marine conservation. The first step to such reconciliation is to explicitly display the trade-offs between the benefits and costs of different policies in terms of different objectives, to allow stakeholders to discuss and achieve consensus on management approaches (Walters & Martell 2004).

One problem is the difficulty in understanding and predicting the impact of fisheries and other physical and biological factors on the ecosystem. Single species approaches to fisheries and conservation assessments have been useful in understanding the dynamics of populations and quantify population status, and provide specific reference points with well-quantified uncertainty to management. However, a more holistic view of the ecosystem is needed to compliment the single species approach. Ecosystem simulation modelling is useful to generate alternative hypotheses about responses of ecosystems to fishing, and to reveal trade-offs between different objectives from the ecosystem perspective.

1.7. Modelling interactions between ecosystem and fisheries

An array of modelling approaches, with a range of different assumptions and complexity, has been developed to evaluate interactions between organisms and fisheries (Fulton *et al.* 2003). Approaches such as multi-species yield-per-recruit models (Murawski 1984) that incorporate interactions between fishing gears generally assume no biological interactions between species (Hollowed *et al.* 2000). More complicated models that incorporate age-specific dynamics and trophic interactions include multi-species

virtual population analysis (MSVPA) (Sparre 1991). MSVPA extends single species virtual population analysis to a number of trophically-linked populations. In MSVPA, trophic links between the modelled populations are represented explicitly by expressing natural mortality as a function of the abundance and diet composition matrix of the predators (Sparre 1991). However, because MSVPA is data-intensive, requiring long time-series of catch-at-age and diet composition, its applications are limited to a few well-studied fisheries (Christensen 1996).

Ecosystem modelling approaches based on the principle of mass-balance have been more widely used in the last decade (Christensen & Walters 2004a). Mass-balance refers to the principle of conservation of energy in which the energy or biomass entering a system equals the amount produces from it. One of the most widely known approaches in fisheries science is the Ecopath with Ecosim suit of models (Polovina 1984; Christensen & Pauly 1992; Walters *et al.* 1997; Walters *et al.* 1999; Pauly *et al.* 2000). Ecopath was first developed to study coral reefs in Haiwaii (Polovina 1984) and later applied to a wide range of systems. Ecopath is a steady-state, mass-balance model which describe a snapshot of the whole ecosystem at a particular time period. Ecosim, a timedynamic ecosystem simulation framework based on the Ecopath mass-balanced model, was later developed to allow exploration of the effects of fishing on ecosystems (Walters *et al.* 1997).

1.8. Ecopath with Ecosim

Based on the mass-balance principle, Ecopath can be used to develop hypotheses of ecosystem structures that are thermodynamically possible (Polovina 1984; Christensen & Pauly 1992). In most Ecopath models, species, usually those with similar biology and ecology, are aggregated into functional groups to reduce the number of modeled units. The model is governed by the mass-balance principle, which is based on two basic equations. The first one ensures a balance between production, consumption, predation, fishery catch, migrations and other mortalities among and between groups:

$$(P/B)_{i} \cdot B_{i} \cdot (1 - EE_{i}) - B_{j} \cdot (Q/B)_{j} \cdot DC_{ji} - Y_{i} - E_{i} - BA_{i} = 0 \qquad \text{eq. 1.1}$$

The second equation ensures a balance between consumption, production and respiration within a group:

$$Q_i = P_i + R_i + GE_i Q_i \qquad \text{eq. 1.2}$$

where $(P/B)_i$ is the production to biomass ratio of functional group *i*; B_i is the total biomass; EE_i is the ecotrophic efficiency $(1-EE_i \text{ represents mortality other than predation and fishing}); <math>Y_i$ the total catch; E_i is net migration; BA_i is the biomass accumulation; Q/B_j are consumption to biomass ratio for predator groups *j*; DC_{ji} is the proportion of group *i* in the diet of predator groups *j*; *R* is respiration; and *GE* is the proportion of unassimilated food (Christensen & Walters 2004a).

The model maintains mass-balance by solving equations 1.1 and 1.2 for all groups simultaneously. Thus, any of the four basic input parameters (B, P/B, Q/B, EE) in each group has to be estimated to ensure mass-balance. Since EE is difficult to measure empirically, it is usually estimated through the mass-balance process provided that data to estimate other parameters are available. In cases where data for one of B, P/B or Q/B are unavailable, EE is often assumed to be 0.95, or lower in case of top predators (Christensen *et al.* 2004).

Ecosim is a dynamic simulation model which simulates changes of ecosystem that are described under Ecopath. It estimates changes of biomass among functional groups in the ecosystem as functions of abundance among other functional groups, and timevarying harvest rates, taking into account predator-prey interactions and foraging behaviors (Pauly et al. 2000; Walters et al. 2000). Ecosim is governed by the basic equations (Walters et al. 1997):

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i$$
eq. 1.3

and

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + a_{ij} \cdot B_j}$$
eq. 1.4

where equation 1.3 gives the biomass growth rate of group *i*, g_i is growth efficiency, *M* and *F* are natural and fishing mortalities, *I* and *e* are immigration and emigration rates, C_{ji} is the consumption of group *j* organisms by group *i* organism, *v* and *v'* represent rates of behavioural exchange between invulnerable and vulnerable states and a_{ij} represents rate of effective search by predator *j* for prey type *i*. The behaviour of functional groups in dynamic simulations is heavily affected by the 'vulnerability factor' (*v*), which determines the foraging behaviour (i.e., movement between refugia and foraging area) of the functional groups in predator-prey interactions (Walters *et al.* 1997; Walters & Martell 2004).

1.9. Fisheries in the Northern South China Sea (NSCS)

The various issues regarding the challenges in conservation of marine biodiversity are particularly relevant to developing countries fisheries such as those in the northern South China Sea (NSCS). We defined the NSCS as the continental shelf (less than 200 m depth) ranging from 106°53'-119°48' E to 17°10'-25°52' N (Figure 1.5). The continental shelf (less than 200 m depth) falls largely within the Exclusive Economic Zone of the People's Republic of China, but Vietnam also shares part of the Gulf of Tonkin. It is a tropical ecosystem where diverse habitats including coral reefs, estuaries, mangroves, seagrass beds, and others can be found (Morton & Blackmore 2001). Diverse fauna and

flora have been recorded in the area, with over 900 species of fishes (Ni & Kwok 1999), at least five species of sea turtles (Marque 1990), eight species of marine mammals (Jefferson *et al.* 1993) and many invertebrates (Jia *et al.* 2004). Fishery resources are exploited mainly by trawlers (demersal, pelagic and shrimp), gillnets, hook and line, purse seine and other fishing gears such as traps.

Similar to other fisheries in the region (Pauly & Chua 1988), fisheries in the NSCS have undergone dramatic changes over the past five decades. Since the foundation of the People's Republic of China (PRC) in 1949, there was a rapid growth in marine capture fisheries. The growth slowed down towards the 1970s. From the 1950s to 1970s, the fishing fleets were mostly state-owned. However, since the end of 1978, following economic reform, fishing fleets started to be privatized and investment in fisheries increased (Pang & Pauly 2001). This resulted in a large increase in the number of fishing boats and improvement in fishing technology. From 1978 to 2000, the number of mechanized fishing boats from Guangdong, Guangxi and Hainan – the three provinces bordering the coast of the NSCS – increased from 8,109 to 79,249 with their total engine power increasing from 0.55 to 3.6 million KJ (Department of Fishery, Ministry of Agriculture, The People's Republic of China 1991, 1996, 2000). The apparent decline in engine power per boat from the 1970s to the 2000s is due to the large influx of unemployed inland workers and farmers to the fishing sectors in recent years. Many of these fishers fished with small boats with limited technology and mechanization (Pang & Pauly 2001; presentation by Qiu, Y. South China Sea Fisheries Institute, October 2005).

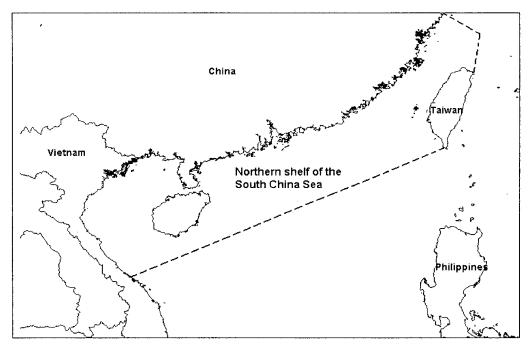


Figure 1.5. Map of the northern shelf of the South China Sea.

The dramatic expansion of fishing fleets, accompanied by mechanization and other technological advancements, resulted in over-exploitation of near-shore, and later, offshore fisheries resources (Shindo 1973; Cheung & Sadovy 2004) – a change that is similar to most other fisheries globally. The trends continued and catch rates of Chinese trawlers in the NSCS dropped by more than 70% from 1986 to 1998 (Lu & Ye 2001). Modelling studies and analysis of landings data suggested a decline in trophic level of catch along the coast of NSCS (Buchary et al. 2003; Cheung & Sadovy 2004). A range of species with high vulnerability to exploitation were extirpated locally or regionally by fishing (Sadovy & Cornish 2000; Sadovy & Cheung 2003; Cheung & Sadovy 2004). For instance, the large yellow croaker (Larimichthys crocea) was one of the most important fisheries in the East and South China Sea. The stocks were greatly depleted starting in the 1970s and supplies of this fish in the market now rely almost solely on aquaculture (Liu & Sadovy unpublished data). Also, two decades ago, fishers supplied the local markets with highly esteemed large reef fishes such as groupers and snappers that were caught from the inshore and, later, offshore reefs in the NSCS (Sadovy 2005). Nowadays, fish traders have to import these fishes from distant locations such as Indonesia, Australia and the South Pacific islands because large-sized fishes, which are more susceptible to overfishing, have been depleted locally (Johannes & Riepen 1995; Sadovy & Vincent 2002; Sadovy 2005). In addition, critical habitats for marine species such as coral reefs and seagrass beds have been damaged or degraded as a result of the use of destructive fishing methods and coastal development (Hutchings & Wu 1987). Therefore, overexploitation in the NSCS raises serious fishery management and biodiversity conservation concerns.

Revisions of the current management policy and tactics are needed to conserve fishery resources and biodiversity in the NSCS. The Chinese fishery management authorities recognized the current status of fishery resources (Lu & Ye 2001) and has initiated a range of fishery management policies. These include limiting new entry to fisheries and prohibiting the use of some destructive fishing methods (He 2001). However, the degree to which regulations have been enforced has been questioned (Li *et al.* 1999). Since 1998, the Chinese authorities have implemented a seasonal moratorium (June and July) in the NSCS. So far, published empirical studies that evaluate the effect of the moratorium on the exploited populations or ecosystem dynamics in the NSCS are lacking. Studies using ecosystem simulation models suggested that the effects of the moratorium should be small given the sustained high fishing effort in the region (Pitcher *et al.* 2002; Cheung & Pitcher 2006). Evaluating alternative policy options and management scenarios should provide useful information on their relative pros and cons for the authorities to make policy decisions.

1.10. Research objectives

The main objectives of this thesis are to predict the extinction vulnerabilities of marine fishes to fishing, and evaluate the trade-offs between conservation and the socioeconomic objectives of fisheries management in an ecosystem context. This includes an understanding of the intrinsic vulnerability to fishing (inherent capacity to respond to fishing in relation to their susceptibility to depletions and extirpations) which represents the first step to idenfity priority species for conservation and research efforts. Also, extinction or extirpation vulnerabilities of exploited species can be evaluated by combining intrinsic vulnerabilities with estimated levels of fishing exploitation. In the first half of this thesis, new methods to evaluate vulnerabilities to fishing are developed and then used to perform global analyses on the vulnerability of fishes. Using the new methods, the second half of the thesis focuses on a case study of the Northern South China Sea ecosystem. The thesis is structured into nine chapters, with Chapters 1 and 9 being the general introduction and conclusion of the thesis, respectively. The structure of the thesis is summarized in a flow diagram (Figure 1.6).

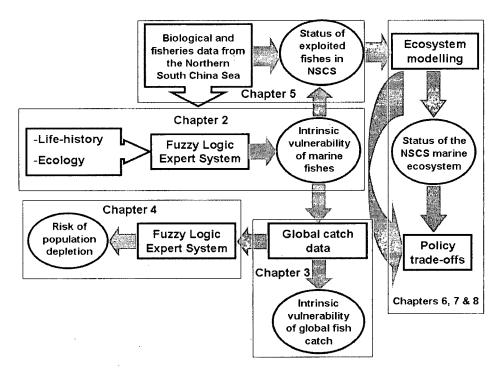


Figure 1.6. A flow diagram showing the structure of this thesis.

As understanding intrinsic vulnerabilities to fishing can be considered the first step to assessing the status of exploited marine fishes, Chapter 2 aims to develop a method that integrates easily-obtainable life history and ecological characteristics of marine fishes to provide quantitative indicator of intrinsic vulnerability. Specifically, a fuzzy logic expert system is developed to calculate intrinsic vulnerabilities to fishing. Fuzzy set theory, originally developed by Zadeh (1965), can classify a subject to different categories with a gradation of membership (instead of classifying membership as either 'true' or 'false' as in the classical logic system) and is suggested to be particularly suitable to fisheries analyses (Mackinson *et al.* 1999; Mackinson 2000a). In fact, fuzzy algorithms have been widely applied in fisheries science (Saila 1996), including stock-recruitment models (Mackinson *et al.* 1999; Chen 2001), predicting fish shoaling

behaviour (Mackinson 2000b), identifying sub-stocks of fish (Zhang 1994), and assessing species for the IUCN Red List (Akcakaya *et al.* 2000). Tinch (2000) proposed the use of fuzzy logic to assess extinction risks for different Pacific salmon stocks. An expert system is an artificial intelligence system which is designed to mimic how expert(s) solve problems. It is usually a computer program that uses heuristic rules to describe the available expert knowledge. In this Chapter, rules (expressed in IF-THEN clauses) (Kasabov 1996) are extracted from published literature describing known relationships, between biological characteristics and vulnerability. Input and output variables are defined by fuzzy sets. Conclusions from different lines of evidence are combined to provide qualitative and quantitative predictions on the intrinsic vulnerability of marine fishes to fishing. Predictions from the expert system are validated using comparisons with empirical data and with other published estimates of the intrinsic vulnerability of fishes.

Chapter 3 identifies marine fishes most vulnerable to exploitation in different environments by comparing life history traits, represented by an index of intrinsic vulnerability predicted from the methodology developed in Chapter 2. I evaluate the difference in intrinsic vulnerabilities of fishes, and the global changes in the mean intrinsic vulnerability of fishes in catches comprising different communities, including those on coral reefs, at seamounts and in estuaries. This reveals the changes in the species composition of catch in relation to the intrinsic vulnerability of the species. In addition, the relationship between the spatial distributions of fishes listed under the IUCN Red List of Threatened Species and the rates of decline of average vulnerability of the taxa in the catches is evaluated. The findings help understand the mechanism leading to changes in fish community structures from fishing, and identify species assemblages that potentially suffer high conservation risks from fishing.

Chapter 4 predicts the risk of population depletion of exploited fishes from fishing. Exploitation status of fishes is inferred from temporal features of their catch time-series. Combining the intrinsic vulnerability from the methods developed in Chapter 2 with inferred exploitation status, this chapter aims to predict the relative depletion risk of 460 exploited marine fishes from fishing. This analytical approach is validated by comparison with the IUCN Red List categories using simulated data from a population model. Extrapolating the depletion risk of the 460 species to marine fishes globally, the proportion of marine fishes facing high depletion risk from fishing is estimated. The results allow comparison of depletion risk from large-scale human activities between marine fishes and other vertebrates.

Chapter 5 evaluates the status of 17 species of demersal taxa in the northern South China Sea (NSCS) using spatially explicit CPUE data of demersal trawlers from 1973 to 1988. The data are standardized with a generalized linear model to obtain the time-series changes in relative catch rate during this period. Intrinsic vulnerabilities of the 17 taxa are estimated and their relationship with the changes in CPUE is examined. The relationship between the intrinsic vulnerability predicted from the expert system developed in Chapter 2 and the catch rate decline is evaluated, with a hypothesis that the two are positively related (i.e., species with higher intrinsic vulnerability would have a stronger rate of decline). The estimated vulnerability is then applied to extrapolate the population status of other taxa in the region.

Chapter 6 describes the past (the early 1970s) and present (the 2000s) status of the NSCS ecosystem using the Ecopath with Ecosim modelling approach. Mass-balanced ecosystem models of the early 1970s and the 2000s are constructed based on published literature, unpublished reports from government surveys, and global databases. By comparing the structure and dynamics of the past and present systems, ecosystem changes over the past three decades are evaluated. Parameter uncertainty is addressed by the estimation 'pedigrees', and by sensitivity and perturbation analyses.

Chapter 7 aims to improve the NSCS ecosystem model by fitting the 1970s NSCS model with time-series CPUE data obtained from Chapter 5 in Ecosim dynamic simulation modelling. Parameters that control the types of trophic control between predators and preys are estimated by the time-series fitting. The estimated parameters are then transferred to the 2000s NSCS model. Moreover, a 'Depletion index' is developed to infer the risk of depletion of stocks or species that have been aggregated into functional groups. This index becomes an objective function for the conservation of vulnerable fishes in the multi-criteria policy optimization analysis in Chapter 8.

Chapter 8 identifies the trade-offs between conservation and socio-economic objectives of fisheries management in the NSCS. The analyses are based on dynamic

simulation models using Ecopath with Ecosim. Using a numerical optimization routine, fishing efforts that would maximize the benefits to specified conservation, economic and social objectives are estimated. The Depletion index developed in Chapter 7 becomes an objective function for the conservation of vulnerable fish. The possible trade-offs between conservation and other objectives are then mapped quantitatively. At the end, the costs and benefits of the various trade-offs are evaluated and discussed.

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2. A FUZZY LOGIC EXPERT SYSTEM TO ESTIMATE INTRINSIC VULNERABILITIES OF MARINE FISHES TO FISHING²

2.1. Introduction

Growing evidence indicates that marine species may be under the threat of local, and ultimately global, extinction, due to the direct or indirect effects of fishing (Pitcher 1998; Roberts & Hawkins 1999; Wolff 2000; Reynolds et al. 2001; Dulvy et al. 2003). Commercially important species can be fished down to a vulnerable level because of their economic value (Clark 1973; Sumaila 2004), e.g., Chinese bahaba (Bahaba taipingensis, Sciaenidae) (Sadovy & Cheung 2003), and Southern bluefin tuna (Thunnus maccoyii, Scombridae) (Hayes 1997). However, species with little or no commercial value are also not safe from the threats of fishing. Non-targeted species may be threatened through bycatch (e.g., Common skate, *Raja batis*, Rajiidae, Brander 1981; Barndoor skate, *Raja* laevis, Rajiidae, Casey & Myers 1998), or by fishing activities that create large disturbance and damages to benthic habitats (Jennings et al. 2001; Kaiser et al. 2002, 2003). Declines and extinctions can be associated with the loss of essential habitat critical to complete the life cycle of the species (McDowall 1992; Watling & Norse 1998). Given the overexploited status of most fishery resources in the world (Jackson et al. 2001; Pitcher 2001a; Pauly et al. 2002; Hilborn et al. 2004), timely identification of species or populations that are vulnerable to local extinction (= 'extirpation') is urgently needed so that appropriate counter-measures can be formulated and implemented (Jennings et al. 1999a; Dulvy et al. 2004).

Conventional assessments of extinction vulnerability involve an in-depth understanding of population dynamics (e.g., Matsuda *et al.* 2000), and so lack of data limits rapid assessment for marine fish species. Currently, the required population parameters are available only for a small number of marine fishes, mainly commercially targeted species in developed countries. Collecting the necessary quantitative data on the

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population status is costly (Reynolds *et al.* 2001; Dulvy *et al.* 2003). The problem is most apparent in tropical, developing country fisheries where species diversity is high but resources for monitoring are limited (Jennings & Lock 1996; Johannes 1998). Moreover, the intrinsic rate of increase r, a key population parameter for conventional assessment, is particularly difficult to estimate reliably (Musick 1999; Reynolds *et al.* 2001; Dulvy *et al.* 2003).

2.1.1. Life history and ecological characteristics as proxies for intrinsic vulnerability

Life-history and ecological traits, which have evolved to ensure persistence in the face of biotic and abiotic variability, have been suggested as 'rule-of-thumb' proxies to evaluate the intrinsic vulnerability of marine fishes to fishing (see Chapter 1; Jennings *et al.* 1998 1999 *a, b*; Reynolds *et al.* 2001). Here, extinction risk is a combination of intrinsic vulnerability and exposure to some threatening factors. Intrinsic vulnerability to fishing is the inherent capacity to respond to fishing that relates to the fish's maximum rate of population growth and strength of density dependence. Responses of fish populations to exploitation are, at least in part, determined by life history and ecological characteristics (Adams 1980; Roff 1984; Kirkwood *et al.* 1994; Dulvy *et al.* 2003; Sadovy & Domeier 2005). Selected life history parameters and ecological characteristics are correlated with intrinsic vulnerabilities (Jennings *et al.* 1999*a, b*; Denney, *et al.* 2002; Rowe & Hutchings 2003; Sadovy & Domeier 2005), some of which are suggested to be used as 'rules-of-thumb' for the triage of vulnerable species (Dulvy *et al.* 2004). However, while these 'rules-of-thumb' are available, little effort is given to how they may be combined and applied to assess a large number of species.

Since life history and ecological traits contribute concurrently to increasing fishing vulnerability, an indicator conflating them should be useful in comparing vulnerability across species. Moreover, information for the majority of species is incomplete. Therefore, it is difficult to establish an index of extinction vulnerability from a wide range of life history and ecological characteristics using conventional techniques.

Rule-based systems that classify fishes into ordinal extinction vulnerability levels are available (Dulvy *et al.* 2004). These systems are based on population parameters and biological characteristics and generally employ classical logic, which classifies fish exclusively to categories of each biological characteristic. An example is the scheme of Musick (1999), adopted by the American Fisheries Society (AFS) that aims to identify the 'productivity' (assumed the inverse of vulnerability) of fishes (hereafter called 'AFS's scheme'). AFS's scheme determines fish productivity level (high, medium, low, very low) from pre-defined categories of life history and population characters such as intrinsic rate of increase, longevity, age at first maturity, fecundity and the von Bertalanffy growth parameter, *K*. The productivity estimates are then used to assess threshold population levels for extinction (Musick 1999; Musick, *et al.* 2000).

2.1.2. Fuzzy logic expert system

Fuzzy set theory can be useful in deriving an index of intrinsic vulnerability. Our knowledge of fish biological and ecological characteristics is associated with vagueness. Vagueness or uncertainty also occurs when we infer vulnerability to fishing from a variety of intrinsic characteristics. For example, we know that large fishes tend to be associated with higher extinction risk. However, it is difficult to provide a clear cut definition of what 'large fish' is, i.e., to separate large and small body size, and thus high and low extinction vulnerability. Moreover, other biological characteristics may confer low risk on a species despite large size. Such vagueness and uncertainty can be addressed by fuzzy set theory (or 'fuzzy logic').

In fuzzy set theory, originally developed by Zadeh (1965), a subject can belong to one or more fuzzy set(s) with a gradation of membership, instead of classifying membership as either 'true' or 'false' as in the classical logic system. The degree of membership is defined by fuzzy membership functions (e.g., Figure. 2.1). For instance, based on the fuzzy membership functions presented in Figure 2.1a, fish with a maximum length of 68 cm can be classified as medium and large size, with degree of membership (from 0 to 1) of 0.7 and 0.3, respectively. Fuzzy logic also allows conclusion(s) to be reached from premise(s) with a gradation of truth. Membership can be viewed as a representation of the 'possibility' of association with the particular set (instead of the 'probability' used in frequentist or Bayesian statistics) (Zadeh 1995; Cox 1999). Kandel *et al.* (1995), Laviolette *et al.* (1995) and Zadeh (1995) provide discussion on the applications of fuzzy logic and probability theory. An expert system is an artificial intelligence system which is designed to mimic how expert(s) solve problems. It is usually a computer program that uses heuristic rules to describe the available expert knowledge. Rules are expressed in the form:

IF A THEN B

where A is the premise while B is the conclusion (Kasabov 1996). The actions defined by the rules are 'fired' (= operated) when the degree of membership of the premises exceeds certain threshold values. The threshold values define the minimum required membership of the premises that an expert would expect for that particular rule to be fired and are generally defined by subjective criteria. Conflicting rules are allowed to fire jointly.

In this paper, a fuzzy expert system is used to develop an index of the intrinsic vulnerability of marine fishes based on published relationships between life history and ecological characteristics and intrinsic vulnerability of marine fishes. Individual species are treated as the unit of assessment here, but the methodology can be applied to individual populations or sub-stocks. The new index is validated by correlations with empirical data. The empirical data include the observed rate of population decline of fishes in the North Sea (Jennings *et al.* 1999a) and Fiji (Jennings *et al.* 1999b), and species listed in the IUCN list of threatened species (Baillie *et al.* 2004). We evaluate the robustness of the system and its assumptions using various sensitivity analyses. We compare the pros and cons of the fuzzy expert system with other approaches in terms of its practical application. The technical details of fuzzy set theory and the fuzzy expert system are presented in Appendix 2.1 and 2.2.

2.2. Methods

2.2.1. Structure and functioning of the fuzzy expert system

We developed a fuzzy expert system (hereafter called fuzzy system, developed using Microsoft Excel and Visual Basic for Applications) which aimed to evaluate the extinction vulnerability of marine fishes based on easily-obtainable life history and ecological characteristics i.e., features available through FishBase (Froese & Pauly 2004, www.fishbase.org). The input variables include maximum length, age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality rate, fecundity (minimum number of eggs or pups per female per year), strength of spatial behaviour, and geographic range (Figure 2.1). The outputs are expressed as four verbal categories referring to the levels of intrinsic vulnerability to extinction: (1) very high, (2) high, (3) moderate and (4) low (Figure 2.2). Intrinsic vulnerability is also expressed on an arbitrary scale from 1 to 100, with 100 being the most vulnerable. Membership (maximum of 1) to each of the input and output verbal category is defined by a fuzzy membership function (Figures 2.1, 2.2).

The fuzzy system includes sets of heuristic rules that allow the inferences of the intrinsic vulnerability based on the inputs. Essentially, fishes are classified into different verbal categories of life history and ecology with associated degrees of membership based on the input fuzzy sets (Figure 2.1). The inputs trigger the pre-specified rules that relate the different input verbal categories to intrinsic vulnerability. The heuristic rules were developed based on relationships described in the published literature (Table 2.1), excluding publications overwhelmingly disproved by empirical data. Each rule is weighted and we made an initial assumption of equal weighting with 0.5 for all rules. We assumed the minimum membership required to trigger the rules (threshold value) to be 0.2. This means that the system considers the premises to be false unless they have membership of 0.2 or more. Thus the system screens out premises that have very low degree of membership.

At the end, the system estimates the degree of membership to the four categories of intrinsic vulnerability for a fish taxon (Figure 2.2), and provides a quantitative index of vulnerability. The system also provides lower and upper bounds of the vulnerability index (see Appendix 2.1 and 2.2 for details on the development of the fuzzy sets and heuristic rules, and functioning of the fuzzy expert system).

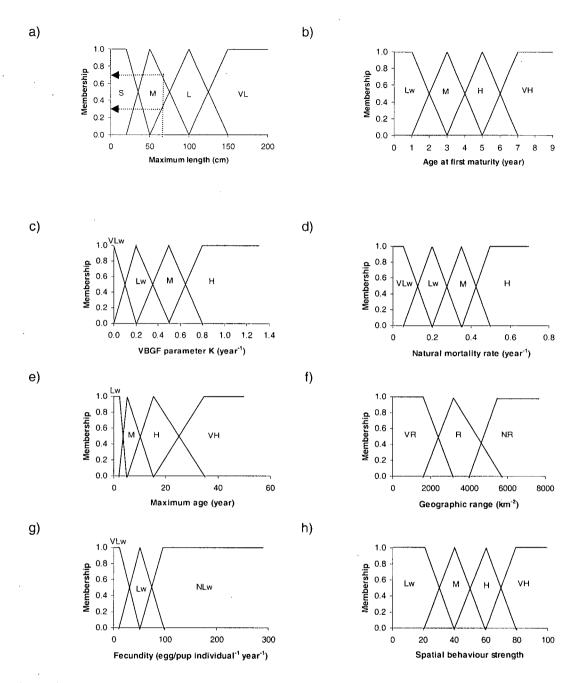


Figure 2.1. Fuzzy sets defining the input life history and ecological characteristics: (a) maximum body length, (b) age at first maturity (T_m), (c) von Bertalanffy growth parameter *K*, (d) natural mortality rate (M), (e) maximum age (T_{max}), (f) geographic range (km^2), (g) annual fecundity (egg or pup female-1 year-1), (h) strength of aggregation behaviour (see Appendix 2.3). VLw – very low, Lw – low, NLw – not low, M –medium/moderate, H – high, VH – very high, L – large, VL – very large, R – restricted, VR – very restricted, NRV – not restricted, S - small. A fish species with maximum body length of 68 cm corresponds to 'medium body size' and 'large body size' with membership of 0.7 and 0.3 respectively (threshold value = 0.2)

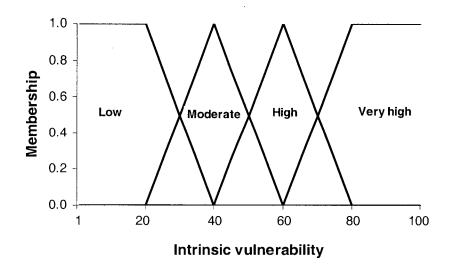


Figure 2.2. Output fuzzy sets for the intrinsic vulnerability of marine fishes. The 'Low' and 'Very high' vulnerabilities are defined by trapezoid membership functions while the 'Moderate' and 'High' vulnerabilities are defined by triangle membership functions. Intrinsic vulnerability was scaled arbitrary from 1 to 100.

Attribute	Rule		Conditions	··· · ·	Consequences	Supporting evidence ¹	Opposing evidence ²
1	1	IF	Maximum length ³ is very <i>large</i>	THEN	Vulnerability is very high	8, 11, 13, 14, 15, 16, 17,	
1	2	IF	Maximum length ³ is <i>large</i>	THEN	Vulnerability is high	21, 24, 27, 28, 29	
1	3	IF	Maximum length ³ is <i>medium</i>	THEN	Vulnerability is moderate	_	
1	4	IF	Maximum length ³ is <i>small</i>	THEN	Vulnerability is low	-	
2	5	IF	Age at first maturity (t_m) is very high	THEN	Vulnerability is very high	1, 2, 3, 4, 5, 11, 14, 15,	28
2	6	IF	Age at first maturity (t_m) is high	THEN	Vulnerability is high	19, 20, 24, 33	
2	7	IF	Age at first maturity (t_m) is medium	THEN	Vulnerability is moderate	_	
2	8	IF	Age at first maturity (t_m) is low	THEN	Vulnerability is <i>low</i>	_	
3	9	IF	Maximum age (t_{max}) is very high	THEN	Vulnerability is very high	13, 19, 33	14
3	10	IF	Maximum age (t_{max}) is high	THEN	Vulnerability is high	_	
3	11	IF	Maximum age (t_{max}) is medium	THEN	Vulnerability is moderate	_	
3	12	IF	Maximum age (t_{max}) is low	THEN	Vulnerability is <i>low</i>		

 Table 2.1. Heuristic rules defined in the fuzzy system to assign relative vulnerabilities to fishes.

Table 2.1.Con't

Rule		Conditions		Consequences	Supporting evidence1	Opposing evidence2
13	IF	VBGF (k) is very low	OR	· · · · · · · · · · · · · · · · · · ·	5, 6, 13, 19, 28, 33	11
		Natural mortality (<i>M</i>) is very low	THEN	Vulnerability is very high ⁴		
14	IF	VBGF K is low	OR		-	
		Natural mortality (M) is low	THEN	Vulnerability is high ⁴	-	
15	IF	VBGF K is medium	OR		-	
		Natural mortality (<i>M</i>) is <i>medium</i>	THEN	Vulnerability is <i>medium</i> ⁴	-	
16	IF	VBGF K is high	OR		······	
		Natural mortality (M) is high	THEN	Vulnerability is <i>low</i> ⁴	-	
17	IF	Geographic range is <i>restricted</i> ⁵	THEN	Vulnerability is high	8, 19, 22	
18	IF	Geographic range is very restricted	THEN	Vulnerability is very high	-	
19	IF	Fecundity is <i>low</i> ⁶	THEN	Vulnerability is high	1, 2, 3, 4, 5, 19, 20	11, 14, 18, 23, 26
20	IF	Fecundity is very low	THEN	Vulnerability is very high	-	28, 31
20	IF	Spatial behaviour strength is low ⁷	THEN	Vulnerability is low	7, 9, 10, 12, 25, 32	
21	IF	Spatial behaviour strength is moderate	THEN	Vulnerability is moderate	-	
22	IF	Spatial behaviour strength is high	THEN	Vulnerability is <i>high</i>	-	
23	IF	Spatial behaviour strength is very high	THEN	Vulnerability is very high	-	
	13 14 15 16 17 18 19 20 21 22	13 IF 14 IF 15 IF 16 IF 17 IF 18 IF 19 IF 20 IF 21 IF 22 IF	13IFVBGF (k) is very low Natural mortality (M) is very low14IFVBGF K is low Natural mortality (M) is low15IFVBGF K is medium Natural mortality (M) is medium16IFVBGF K is high Natural mortality (M) is high17IFGeographic range is restricted18IFGeographic range is very restricted19IFFecundity is low20IFFecundity is very low20IFSpatial behaviour strength is low 721IFSpatial behaviour strength is moderate22IFSpatial behaviour strength is high	13IFVBGF (k) is very lowORNatural mortality (M) is very lowTHEN14IFVBGF K is lowORNatural mortality (M) is lowTHEN15IFVBGF K is mediumORNatural mortality (M) is mediumORORNatural mortality (M) is mediumTHEN16IFVBGF K is highORNatural mortality (M) is highTHEN17IFGeographic range is restricted ⁵ THEN18IFGeographic range is very restrictedTHEN20IFFecundity is low ⁵ THEN20IFSpatial behaviour strength is low 7THEN21IFSpatial behaviour strength is moderateTHEN22IFSpatial behaviour strength is highTHEN	13IFVBGF (k) is very lowORNatural mortality (M) is very lowTHENVulnerability is very high14IFVBGF K is lowOR14IFVBGF K is lowORNatural mortality (M) is lowTHENVulnerability is high15IFVBGF K is mediumORNatural mortality (M) is mediumTHENVulnerability is medium16IFVBGF K is highOR17IFGeographic range is restrictedTHENVulnerability is high18IFGeographic range is very restrictedTHENVulnerability is very high19IFFecundity is lowTHENVulnerability is very high20IFSpatial behaviour strength is low 7THENVulnerability is low21IFSpatial behaviour strength is moderateTHENVulnerability is high22IFSpatial behaviour strength is highTHENVulnerability is high	13IFVBGF (k) is very lowOR5, 6, 13, 19, 28, 3314IFVBGF K is lowOR5, 6, 13, 19, 28, 3314IFVBGF K is lowORORNatural mortality (M) is lowTHENVulnerability is high ⁴ 15IFVBGF K is mediumORNatural mortality (M) is mediumTHENVulnerability is medium ⁴ 16IFVBGF K is highORNatural mortality (M) is highTHENVulnerability is low ⁴ 16IFGeographic range is restricted ³ THEN17IFGeographic range is restricted ³ THEN18IFGeographic range is very restrictedTHEN19IFFecundity is low ⁶ THEN20IFSpatial behaviour strength is low ⁷ THEN21IFSpatial behaviour strength is moderateTHEN22IFSpatial behaviour strength is highTHEN23IFSpatial behaviour strength is highTHEN24IFSpatial behaviour strength is highTHEN25IFSpatial behaviour strength is highTHEN24IFSpatial behaviour strength is highTHEN25IFSpatial behaviour strength is highTHEN26IFSpatial behaviour strength is highTHEN27IFSpatial behaviour strength is highTHEN28IFSpatial behaviour strength is highTHEN29IFSpatial behaviour strength is h

Table 2.1.Con't

Attribute	Rule		Conditions		Consequences	Supporting evidence1	Opposing evidence2
8	24	IF	Spatial behaviour is related to feeding	THEN	Vulnerability resulted from	25	
			aggregation		spatial behaviour decreases		
8	25	IF	Spatial behaviour is related to spawning	THEN	Vulnerability resulted from	30, 32	
			aggregation		spatial behaviour increases		

¹ Literature supporting the assertions of the specific rules;

² Literature opposing the assertions of the specific rules;

^{1.2} References: 1. Holden (1973), 2. Holden (1974), 3. Holden (1977), 4. Brander (1981), 5. Hoening & Gruber (1990), 6. Pratt & Casey (1990), 7. Hilborn & Walters (1992), 8. Brown (1995), 9. Pitcher (1995), 10. Pitcher (1997) 11. Jennings *et al.* (1998), 12. Mackinson *et al.* (1997), 13. Russ & Alcala (1998), 14. Smith *et al.* (1998), 15. Walker & Hislop (1998), 16. Jennings *et al.* (1999*a*), 17. Jennings *et al.* (1999*b*), 18. Myers *et al.* (1999), 19. Musick (1999), 20. Stevens (1999), 21. Dulvy *et al.* (2000), 22. Hawkins *et al.* (2000), 23. Stevens *et al.* (2000), 24. Frisk *et al.* (2001), 25. Pitcher (2001*b*), 26. Sadovy (2001), 27. Dulvy & Reynolds (2002), 28. Denney *et al.* (2002), 29. Cardillo (2003), 30. Rowe & Hutchings (2003) 31. Sadovy & Cheung (2003), 32. Sadovy & Domeier (2005);

³ Asymptotic length was used preferentially. However, if asymptotic length was not available, we used maximum length as surrogate;

⁴ Growth rate of fish is represented by the von Bertalanffy growth parameter (VBGF) K. Since natural mortality and von Bertalanffy growth parameter K of fish are highly correlated (Pauly 1980). They were combined using an "OR" operator;

⁵ Geographic range is grossly estimated from the known distribution of fish in Exclusive Economic Zones (EEZs) and Food and Agriculture Organization (FAO) statistical areas. For instance, if a fish species is known to occur in China and in FAO statistical area 61. Its geographic range is represented by the area of the EEZ of China that falls within FAO statistical area 61;

⁶ Strong evidence suggests that high fecundity does not reduce the extinction vulnerability of fishes. However, evidence suggesting that lower fecundity (less than 100) increases vulnerability of fishes is valid. Therefore, the rule relating low fecundity to increased extinction vulnerability is retained. Fecundity is expressed as the minimum number of eggs or pups produced per individual per year;

⁷ Spatial behaviour was defined as groups of fish aggregate together at varying time and spatial scale. Spatial behaviour may be related to spawning, feeding, migration, or defense (schooling and shoaling). The strength of the spatial behaviour is defined by an arbitrary scale that ranges from 0 to 100. The method that assigns strength of spatial behaviour onto the arbitrary scale was described in Appendix 2.3.

2.2.2. System evaluations

We examined the distribution of the fuzzy system output generated from ranges of realistic life history and ecological characteristics input. We extracted from FishBase a list of all marine fishes which, at the time of the query (February 2004), had full records of the life history and ecological characteristic (N = 159). Using the life history and ecological information available for these fishes, we calculated their intrinsic vulnerability based on the fuzzy system.

We evaluated the impacts of individual attributes to the output of the system using a jackknife approach (Sokal & Rohlf 1995), where the calculations of the intrinsic vulnerability were repeated, while excluding one or more attribute(s) each time. If the system outputs were greatly sensitive to the removal of individual attributes, the outputs may also be sensitive to the weighting factors on the attributes. Thus, through this test, we aimed to evaluate our assumption on weighting individual attributes equally. The degree of deviation (*Dev*), represented by the changes in the predicted intrinsic vulnerability, was calculated for each species when attribute j was removed from the system:

 $Dev = R_{T-i} - R_T$

where R is the estimated output from the system with full set of attributes (T) and attributes j being removed. We repeated the analysis by randomly removing increasing number of attributes except maximum length, as maximum length was the most readily available parameter for marine fishes. We repeated the latter 50 times to obtain a distribution of the estimated deviations.

We tested the sensitivity of the system output to different threshold values. We systematically varied the threshold value of the fuzzy expert system and recorded the output for the 159 marine fishes from FishBase. We examined the differences in the system output for different threshold values.

2.2.3. Validity tests on vulnerability estimates

We examined the validity of the intrinsic vulnerability estimated from the fuzzy system using empirical data with three tests that used three independent sets of data in which historical abundance trends of the marine taxa in the datasets were known. We used population decline as an indicator of vulnerability to fishing because it was readily available for a large number of marine fish species. A similar approach had been used in other comparative analysis between life history traits and vulnerability of marine fishes (e.g. Jennings *et al.* 1999 *a*, *b*). Species included in the data sets represent examples from wide geographic and habitat ranges. The three datasets included:

- (1) extinction risk categories of 40 species of marine fishes in the IUCN Red List of threatened species (Baillie *et al.* 2004);
- (2) population trends of 24 species of demersal fishes in the northern North Sea (Jennings *et al.* 1999*a*);
- (3) population trends of 13 species of reef fishes (Scaridae, Serranidae and Lutjanidae) in Fiji [species in Jennings *et al.* (1999b) with at least 15% of their observed population trends explainable by fishing].

We used the goodness-of-fit of the test statistics as an indicator for the accuracy of the intrinsic vulnerability predicted from the explanatory variables. For dataset 1, since the independent variable (IUCN extinction risk categories) is ordinal, logistic regression was used (Agresti 1996). For dataset 2 and 3, linear regression was used. Whenever the required biological parameters for the species were unavailable in the original data sets, we obtained the data for the same species from FishBase (Froese & Pauly 2004).

We repeated the tests using two other selected proxies of extinction vulnerability: (1) whichever life history parameters (maximum or asymptotic length, age at first maturity, longevity or von Bertalanffy growth parameter K) provided the best fit; (2) productivity categories evaluated using the AFS's scheme (see Musick 1999 for details on the methodology). Since AFS's productivity (assumed inverse of vulnerability) is expressed in ordinal categories, we used a Chi-square test for dataset 1 (species from the IUCN Red List), and ANOVA for datasets 2 and 3 (species from Jennings *et al.* 1999 *a*,

b). We compared the intrinsic vulnerability from the fuzzy system with these two proxies using two attributes: (1) predictive ability - represented by the goodness-of-fit with the empirical data, (2) data requirement – the amount and flexibility of data required in the calculation of the proxies.

We conducted an additional test to compare the performance of the expert system with classical logic. We constructed an expert system with attributes and rules that were exactly the same as the fuzzy system. However, classical (Boolean) sets were used instead of fuzzy sets (Table 2.2). Thus, fish species were classified exclusively to a single category for each biological attribute. If the input parameters of a species resulted in multiple conclusions, the final conclusion would be the highest resulting vulnerability category (Musick 1999). We evaluated the vulnerability of the species in the three test data sets using this system and compared the goodness-of-fit to the empirical data with other vulnerability proxies.

Table 2.2. The definitions of classical (Boolean) sets used to classify life history and ecological characteristics into different categories, and the rules that connected them to different level of intrinsic vulnerabilities.

	Life history characteristics and the resulting vulnerability				
Life history characteristics	Low	Moderate	High	Very high	
Maximum length (cm)	$50 \ge L_{max}$	$50 < L_{max} \le 100$	$100 < L_{max} \le 150$	$150 < L_{max}$	
Age at first maturity (year)	$2 \ge T_m$	$2 < T_m < 4$	$4 < T_m \leq 6$	$6 < T_m$	
VBGF parameter K (year ⁻¹)	0.8 < K	$0.5 < K \le 0.8$	$0.2 < K \le 0.5$	$0.2 \ge K$	
Natural mortality rate (year ⁻¹)	0.5 < M	$0.35 < M \le 0.5$	$0.2 < M \le 0.35$	$0.2 \ge M$	
Maximum age (year)	$3 \geq T_{max}$	$3 < T_{max} \le 10$	$10 < T_{max} \le 30$	$30 < T_{max}$	
Geographic range (10^3 km^2)	-	-	$3.2 < Range \leq 5.7$	$3.2 \ge Range$	
Fecundity (egg/pup individual ⁻¹ year ⁻¹)	-	-	$50 < Fec \le 100$	$50 \ge Fec$	
Spatial behaviour strength	$40 \ge SB$	$40 < SB \leq 60$	$60 < SB \leq 80$	80 < SB	

2.3. Results

Based on the input life history and ecological parameters, the fuzzy system estimated the intrinsic vulnerability with associated possibilities. For instance, using the biological parameters available from FishBase, we estimated that Atlantic cod (*Gadus morhua*, Gadidae) has an intrinsic vulnerability of 61 (100 being the most vulnerable) with lower and upper bounds (membership = 0.5) of 48 to 72. It was identified as being highly to very highly vulnerable, with possibility of 0.78 to 0.63 respectively.

Sensitivity analysis showed that the estimated intrinsic vulnerabilities were insensitive to the pre-defined threshold value (Figure 2.3). The estimated intrinsic vulnerabilities varied slightly as we increased the threshold value from 0 to 0.9. Variations in the estimated outputs increased when the threshold value increased to 0.6 and more.

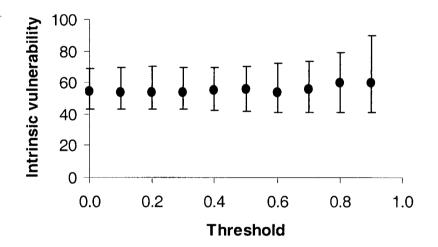


Figure 2.3. Estimated intrinsic vulnerability from the fuzzy logic expert system for the 159 species of marine fishes when threshold value varied from 0 to 0.9. The dots represent the median, while the bars represent the 25% upper and lower quartiles.

Jack-knifing showed that the deviations in the estimated intrinsic vulnerabilities were relatively small for majority of species when individual attributes were removed from the fuzzy system (Figure 2.4a). In most cases, upper and lower quartiles (75% and

25%, respectively) of the deviations in the predicted intrinsic vulnerability were small, within 5 (maximum of 100) relative to the baseline estimates (i.e., all attributes included). However, maximum deviations were up to 20 to 30 for some species. In some cases, deviations were particularly strong when attributes number three and seven were removed (maximum age and spatial behaviour strength, respectively). Removal of attributes three (maximum age), five (geographic range) and six (fecundity) tended to result in unsymmetrical negative bias on the predicted vulnerability, while removal of attribute eight (nature of spatial aggregation) tended to result in positive bias.

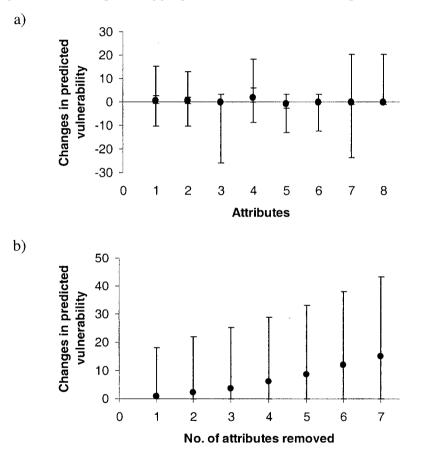


Figure 2.4 Sensitivity of the calculated intrinsic vulnerability to individual attributes incorporated in the fuzzy system evaluated using the jackknife approach (Sokal & Rohlf 1998). The black dots are the median of the deviations of the 159 marine fishes from FishBase when individual (a) attributes were removed, and (b) increasing number of attributes were randomly included (absolute magnitude of changes). The bars are the 25% and 75% quartiles of the deviations (inner bars in Figure 2.4a). The other bars in Figure 2.4a are the maximum and minimum ranges of the deviations.

Deviations of the output from the baseline increased when we randomly removed increasing number of attributes from the system (Figure 2.4b). The median of deviated vulnerability ranged from about 1 (maximum deviation is about 18) when one attribute was randomly removed, to about 12 (maximum deviation is about 42) when only maximum length was used. Predicted vulnerability tended to be under-estimated when only maximum length was considered by the system.

The intrinsic vulnerabilities estimated from the fuzzy system were significantly related to the extinction risk categories of marine fishes in the IUCN threatened species list with better goodness-of-fit than the two other vulnerability proxies (Figure 2.5). Both AFS's scheme and maximum length could not significantly explain the differences in the IUCN categories of the tested species at 5% significant level (AFS's productivity: P = 0.085, L_{max} : 0.0731), while the estimated intrinsic vulnerability could significantly explain them (Intrinsic vulnerability index: P = 0.0253).

Intrinsic vulnerabilities were also significantly related to the population trends of demersal fishes in the North Sea (Jennings *et al.* 1999*a*) with the higher goodness-of-fit (Figure 2.6) than the other proxies. When we considered dragonet (*Callionymus lyra*) and spurdog (*Squalus acanthias*) as outliers, AFS's scheme and individual life history parameters (maximum length and age at first maturity) explained 34% and 28% of the variance, respectively, whereas our fuzzy system explained over 36% of the variance. The relationships remained significant when we included dragonet and spurdog in the analysis; however, its goodness-of-fit was higher than the other two vulnerability proxies by a smaller margin (Figure 2.6).

We did not obtain significant relationships between the three vulnerability proxies and the observed population trends of the Fiji reef fishes based only on the information available from FishBase (Figure 2.7). Lack of life history data meant that we could estimate AFS's productivity for only seven species, preventing us from statistically analyzing the data. There was also no relationship between individual life history parameters (enough data only available for maximum length) and the fuzzy system intrinsic vulnerabilities with the observed population trends (ANOVA p-vaue = 0.142and 0.170, respectively).

A significant relationship between the fuzzy system intrinsic vulnerabilities and the population trends of Fiji reef fishes was shown to occur when we employed supplemental information on occurrence of spawning aggregation available from the global database of the Society for the Conservation of Reef Fish Spawning Aggregation (SCRFA Global Database 2004) (Figure 2.7d). The fuzzy system is then able to explain about 34% of the variance in population trends (ANOVA P = 0.03).

When the fuzzy sets were replaced by classical sets (Table 2.2), the estimated intrinsic vulnerabilities did not correlate with the population trends in the three empirical datasets. The test statistics for the three tests were: marine fishes from the IUCN Red List – Likelihood ratio Chi-square P = 0.206; demersal fishes in the North Sea – ANOVA P = 0.313; reef fishes in Fiji – ANOVA P = 0.133.

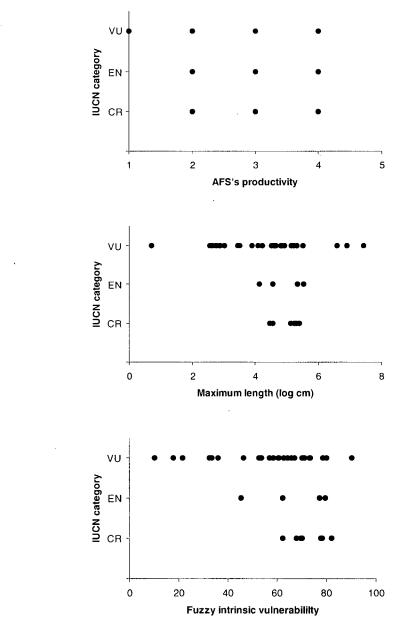


Figure 2.5. Plot of population trends of 40 species of marine fishes listed in the IUCN list of threatened species (Critically Endangered, Endangered and Vulnerable) and (a) AFS's productivity – productivity categories estimated by the AFS scheme (Musick 1999), (b) maximum length (log), and (c) fuzzy system intrinsic vulnerability. We only included species that were categorized by criteria A: reduction in population size (IUCN Species Survival Commission 2001). CR – critically endangered, EN – endangered, VU – vulnerable.

a)

b)

C)

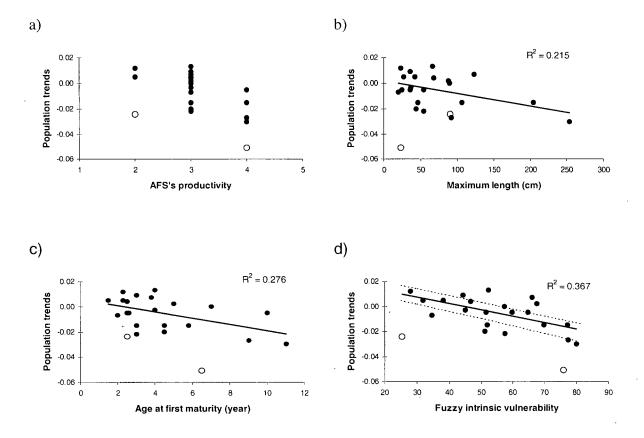


Figure 2.6. Plot of the observed population trends of the 24 species of demersal fish in the North Sea and the proxies of extinction vulnerability: (a) AFS's productivity (ANOVA P = 0.024), (b) maximum length (L_{max}) (ANOVA P = 0.034), (c) age at first maturity (T_m) (ANOVA P = 0.014), (d) fuzzy system intrinsic vulnerability (ANOVA P = 0.004). Population trends refer to the slope of linear relationship between standardized catch rate (number h⁻¹) and time (years). AFS's productivity was expressed in ordinal scale: 1 = high, 2 = medium, 3 = low, 4 = very low. When we included dragonet (*Callionmyrus lyra*) and spurdog (*Squalus acanthias*) (open dots) in the analysis, AFS's productivity was only marginally significant ($R^2 = 0.272$, ANOVA P = 0.042), The goodness-of-fits of age at first maturity and the fuzzy system intrinsic vulnerability became: T_m ($R^2 = 0.207$, ANOVA P = 0.029) and intrinsic vulnerability ($R^2 = 0.246$, ANOVA P = 0.016). The dotted lines represent the upper and lower bounds estimated from the fuzzy system, based on an assumed membership of 0.5.

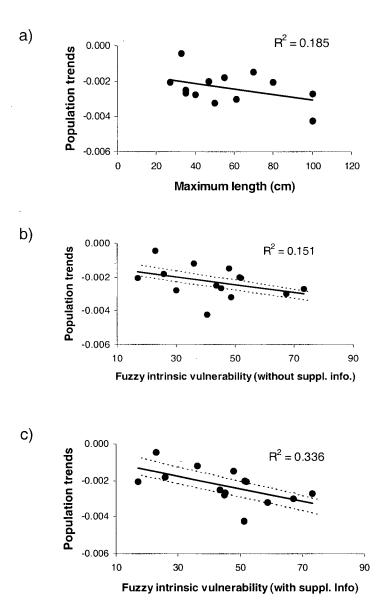


Figure 2.7. Plots between the observed population trends of the 13 species of reef fish in Fiji (a) maximum length (ANOVA P = 0.142), (b) intrinsic vulnerability estimated by the fuzzy system based on information from FishBase only (ANOVA P = 0.170), and (c) intrinsic vulnerability estimated by the fuzzy system with supplementary information from SCRFA Global Database (2004) (ANOVA P = 0.03). Population trends were expressed as the slope of the relationship between biomass and fishing effort (Jennings *et al.* 1999*b*). The dotted lines represent the upper and lower bounds estimated from the fuzzy system based on an assumed membership of 0.5. The lack of the necessary life history data prevented us from analyzing the AFS's productivity.

2.4. Discussion

Comparisons with empirical population abundance trends showed that this fuzzy system could be used to predict the intrinsic vulnerability of marine fishes. It is also a better predictor of rate of population decline than other proxies proposed earlier. The population trends included in the analysis were confounded by factors such as differences in fishing intensities between species. Therefore, they could only be viewed as rough indicators of the vulnerability to fishing. Thus, intrinsic vulnerability is expected to be able to explain only a fraction of the variance in population trends among species. However, the fuzzy system predicted intrinsic vulnerability still explained a considerable proportion of such variance; indeed, the proportions of variance explainable by the predicted intrinsic vulnerability were higher than two suggested proxies of vulnerability. Furthermore, the tests suggest that the use of fuzzy logic in the expert system provides a better predictor of intrinsic vulnerability than a system employing classical logic. These support the validity of the fuzzy system. In addition, the fuzzy system could be applied to species from a wide range of geographic locations, habitats and ecosystem types, and for which different levels of knowledge is available.

We did not account for the number of required input parameters in the comparisons between different vulnerability proxies. The fuzzy system has more attributes than the other proxies. Also, the jackknife analysis suggested that deviations of the outputs increased when attributes were removed from the system. Therefore, its ability to predict vulnerability, and therefore its performance relative to other methods, may decrease when information becomes scarce.

On the other hand, the fuzzy system can provide estimates of intrinsic vulnerability for species with different data availability and can explicitly represent a degree of confidence in the output. In the fuzzy system, the conclusions (level of intrinsic vulnerability) are linked to the inputs concurrently by the heuristic rules. Thus intrinsic vulnerability can still be estimated by the rules fired from the inputs where data are available. The jackknife analysis suggests that the estimated intrinsic vulnerability tends to converge when more attributes are included. Thus the deviation of the estimated output could be reduced by increased data availability and more rules linking the input attributes to intrinsic vulnerability. It is noted that some attributes only relate to either high or low

vulnerability (fecundity, geographic range and type of spatial behaviour), their removals may result in unsymmetrical deviations in the predicted intrinsic vulnerability.

Although removals of attributes result in relatively small deviations of predicted vulnerabilities for the majority of the tested species, some species may have a suite of biological characteristics that render them sensitive to the weighting of particular attribute(s). For instance, by incorporating information on reef fish aggregation from SCRFA Global Database (2004), the fuzzy system greatly increased the goodness-of-fit between the estimated vulnerabilities and the empirical population trends of Fiji's reef fishes. Therefore, weighting of individual rules according to subjective expert judgment (Cox 1999), or availability of evidence supporting the particular rules or attributes (Mackinson 2000) may improve the performance of the system. However, since we defined the attributes and rules from published literature describing a rule (which has been suggested as a weighting factor) does not necessarily reflect the importance of this rule. Future studies may include systematically collating experts' opinions to decide the relative importance of different attributes and thus their weighting factors.

Fecundity may not be a significant attribute to be included in the fuzzy system. Ample evidence suggests that fecundity does not relate to the intrinsic vulnerability of fishes when other life history traits, such as maximum length and age at maturity, are accounted for (see Sadovy 2001 for review). In particular, the notion that highly fecund fish are resilient to fishing has been rejected. Our results suggest that removal of fecundity as an attribute results in small deviations in the predicted intrinsic vulnerability. This appears to support the low importance of the relationship between low fecundity and high vulnerability. On the other hand, we considered all available evidence to develop heuristic rules in the fuzzy system. Also, some literature suggests that low fecundity is a factor causing high intrinsic vulnerability, although majority of them focus on limited group of species (elasmobranchs). Moreover, inclusion of rules that relate low fecundity to high vulnerability makes the system more conservative i.e., the system tends not to underestimate the vulnerability. Therefore, in this thesis, low fecundity (i.e., minimum total fecundity is less than 100 eggs or pups year⁻¹) remained as one of the attributes in the fuzzy system for calculating intrinsic vulnerability of fishes.

The fuzzy system can adapt to new information from both quantitative studies and qualitative experts' knowledge, and enables an integration of local and scientific knowledge (Mackinson & Nøttestad 1998). Currently, some rules in the system are based on literature that does not represent species with full range of life history and ecological traits, and thus these rules were extrapolated from a smaller range of species. Thus the heuristic rules, fuzzy membership functions, and the values that defined them, can be modified based on expert knowledge or newly available information (Cox 1999). The weighting on the rules can also be adjusted when new evidence or experts' opinions are obtained. Therefore, a fuzzy expert system can be particularly useful in facilitating workshop or focus group discussions on the assessment of extinction vulnerability of marine species (see Hudson & Mace 1996). In this case, the discussions and opinions from the experts can act as the knowledge base to revise and update the expert system (Mackinson & Nøttestad 1998; Cox 1999).

The approach described here can facilitate the identification of vulnerable species so that management and conservation efforts can be focused. Current monitoring and management efforts mainly concentrate on commercially important species, which, however, may not necessarily be the most vulnerable. Bycatch and other indirect fishing impacts may threaten non-commercial species (Dulvy et al. 2003). The near extinctions of the Common and Barndoor skates, both low-value bycatch species in bottom trawl fisheries are clear examples (Brander 1981; Casey & Meyers 1998). A large reduction in the abundance of pelagic sharks in the Gulf of Mexico was unnoticed previously because of their relatively low value compared to the tunas; they had life history characteristics which made them highly vulnerable (Baum & Myers 2004). This is particularly true for tropical fisheries where diverse species are caught and resources for monitoring and management are low (Silvestre & Pauly 1997; Johannes 1998; Johannes et al. 2000). The intrinsic vulnerability estimated from the fuzzy system could provide a *priori* indicator on the vulnerability of the species. As such, prioritization of species according to their potential intrinsic vulnerabilities can help to allocate limited research and monitoring resources, and develop more effective fishery management and conservation policies (Dulvy et al. 2004). For instance, Chapter 3 of this thesis applied the fuzzy system presented in this Chapter to evaluate the intrinsic vulnerability a large number of extant marine fishes and found that seamount fishes had significantly higher vulnerability than non-seamount fishes. Therefore, this suggests the need for conservation concerns about the increasing fishery exploitations of seamount assemblages.

In conclusion, we suggest that the fuzzy expert system approach described here is a useful tool to predict intrinsic vulnerability of marine fishes. It may also be easily extended and further improved. Intrinsic vulnerability may be combined with the other, external factors in estimating the total vulnerability of the species. External factors such as fishing intensity, degradation of essential habitat and climate change contribute significantly to the extinction risk associated with each species (Dulvy *et al.* 2003). These external factors, together with intrinsic vulnerability, should be integrated in assessing overall extinction risk. In fact, these external factors can be represented at a higher hierarchical level in the fuzzy system. Rules describing the effects of these external factors, and their synergistic effect with the intrinsic vulnerability, can be incorporated into the fuzzy system through which outputs representing the total vulnerability of the species can be obtained (see Chapter 4). This may provide a decision support tool on local or global extinction risk assessment and categorization such as the IUCN Red List of threatened species of the World Conservation Union or the species listing under the Canada's Species At Risk Act.

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3. INTRINSIC VULNERABILITY IN THE GLOBAL FISH CATCH³

3.1 Introduction

Fishing is a major agent of disturbances to marine ecosystems (Watling & Norse 1998; Pauly *et al.* 2002; Kaiser *et al.* 2003). It has caused a general decline in fish biomass, and placed many marine species under serious conservation concern (e.g. Casey & Myers 1998; Pauly *et al.* 2002; Baum *et al.* 2003; Dulvy *et al.* 2003; Sadovy & Cheung 2003). Among marine fishes that are listed under the IUCN Red List of Threatened Species (Baillie *et al.* 2004), the majority are endangered directly or indirectly by fishing (Dulvy *et al.* 2003).

The life history of a fish species affects its vulnerability to fishing – a feature here called intrinsic vulnerability (Jennings *et al.* 1999b; Reynolds *et al.* 2001; Cheung *et al.* 2005). Generally, species with larger body size (maximum body length or asymptotic length), higher longevity, higher age at maturity, and lower growth rates have higher vulnerability to fishing (Smith *et al.* 1998; Jennings *et al.* 1999a; Jennings *et al.* 1999b; Denney *et al.* 2002; Dulvy & Reynolds 2002). Species with these life history traits are generally less able to sustain fishing mortality, and thus, differences in life history result in structural changes in the exploited fish community (Jennings *et al.* 1999a). In this thesis, a community is defined as the species that occur together in space and time (Fauth *et al.* 1996; Begon *et al.* 2005).

Correlations between life history traits and intrinsic vulnerability to fishing are supported by empirical evidence (Chapter 2). Empirical studies using historical abundance data of exploited fish populations found significant correlations between the rate of population declines (a proxy of vulnerability to fishing) and life history parameters such as maximum body size and age at maturity, but not fecundity (Jennings *et al.* 1998; Jennings *et al.* 1999b). Also, meta-analysis using 54 stock-recruitment timeseries showed that large-sized, late-maturing fishes had strong density-dependence in low abundance but high equilibrium spawner per recruit without exploitation (Goodwin *et al.*

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2006). Analysis including data from other vertebrate groups produced similar conclusions, suggesting that the correlations between life history and population dynamics may be applicable to most vertebrates (Fagan *et al.* 1999). Current evidence suggests that body size is one of the most important factor in determining vulnerability to hunting (Jennings *et al.* 1998; Jennings *et al.* 1999b; Cardillo & Dromham 2001; Reynolds *et al.* 2001; Gaston & Blackburn 2003; Reynolds *et al.* 2005).

The correlations between life history and vulnerability to fishing may explain the serial depletion of fish populations, with fishing activities in heavily exploited areas progressing from large-bodied species that tend to have high vulnerability to species with less vulnerable life histories occurred in heavily exploited areas (Pauly et al. 1998; Pitcher 2001; Pauly et al. 2002; Myers & Worm 2003). More vulnerable species decline faster in abundance given similar fishing rates and thus are more readily over-exploited (Jennings et al. 1998; Jennings et al. 1999b; Reynolds et al. 2001; Cheung et al. 2005; Reynolds et al. 2005). Therefore, the change in relative abundance of vulnerable species can be reflected in the catch composition. In fact, the serial replacement of intrinsically more vulnerable by less vulnerable species may be the reason for the "fishing down marine food webs" phenomenon (Pauly et al. 1998), as fishing generally targets large predatory (often intrinsically more vulnerable) species, but progressively moves to lower trophic level species (often less vulnerable) as the predatory species become overexploited. On the other hand, it has been argued that declines in the relative proportion of predatory species, in some cases, may be the result of a mere expansion of the fisheries to lower trophic level species, without reduction of the catches of predatory species (Essington et al. 2006). Understanding the relationship between intrinsic vulnerability and changes in catch composition may provide insights to this debate.

Different life history traits are evolved to adapt to different environments or habitats (Roff 1984; Beverton 1992; Winemiller & Rose 1992; Charnov 1993; Jensen 1996; Vila-Gispert *et al.* 2002; Winemiller 2005). For instance, many of the coral reef and seamount fishes are thought to be particularly vulnerable to fishing because of life-history traits such as slow growth and late maturation (Koslow *et al.* 2000; Birkeland 2001; Choat & Robertson 2002; Morato *et al.* 2006a). Particularly, coral reef fishes depend strongly on coral reef for refuges. This renders them more vulnerable to direct

and indirect impacts from habitat damages (Pandolfi *et al.* 2003; Wilson *et al.* 2006). Estuarine fishes, on the other hand, have a mixture of life history strategies that are adapted to both fluctuating estuarine environments and more stable marine inshore habitats (Whitfield 1990; Winemiller & Rose 1992; Roessig *et al.* 2004). Their communities include a mixture of diadromous, marine- and freshwater- migratory and estuary resident fishes (Blaber 2000). The relationships between the life history characteristics and the effects of the threats on the estuarine populations may vary widely between species (Reynolds *et al.* 2005). Thus, effects of fishing on structure of coral reef and seamount fishes may be more apparent than on estuarine fish communities.

Given the different characteristics of fish communities in different habitat and the threats of fishing to them, it would be useful to understand the intrinsic vulnerability of fishes in these communities. Also, tracking and comparing the impacts of fishing on these communities over time could help us understand their current conservation status and formulate conservation and fisheries management strategies. Intrinsic vulnerability may be predicted from life history traits (Cheung *et al.* 2005; Reynolds *et al.* 2005) while the effects of fishing on the fish communities may be tracked by evaluating changes in composition of catch over time.

This study attempted to test two hypotheses. (1) We tested if marine fishes that are adapted to different environments have different vulnerabilities to fishing. Based on the life history information available from Fishbase (Froese & Pauly 2004), an index of intrinsic vulnerability to fishing is calculated for all marine fish taxa. Regression analysis is used to evaluate the relationship between the niches and habitats which the fishes inhabit, and their intrinsic vulnerability. (2) We investigated whether changes in species composition of catches are related to the intrinsic vulnerability of the exploited taxa. Finally, we discuss the relative intrinsic vulnerability of fishes and their overall conservation status in the major habitats.

3.2. Methods

3.2.1. Predicting species intrinsic vulnerability

Using the fuzzy logic expert system developed in Chapter 2 (Cheung *et al.* 2005), intrinsic vulnerability index of fishes (the index values ranging from 1 to 100, with 100 being the most vulnerable) were estimated based on the fishes' life history and ecological characteristics. The input variables consisted of traits that were considered to be related to the species intrinsic vulnerability and were obtained from literature review (Cheung *et al.* 2005; Chapter 2). These traits included maximum length, age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality, fecundity (only low fecundity is considered), spatial behaviour and geographic range.

As the operations of the fuzzy logic expert system are detailed in Chapter 2, only a brief description of the system is given here. The expert system classified fishes into different life history categories with different degrees of membership or association (e.g. 'large' maximum length, 'moderate' age at maturity, etc.). The degree of membership or association to each category ranged from 0 to 1 (0 – no association, 1 – full association) and was determined by pre-defined fuzzy logic membership functions (Cheung *et al.* 2005, Chapter 2). The expert system was flexible in terms of data availability. The minimum required input was the maximum length. Rules expressed in IF (predicate)-THEN (conclusion) clauses were used to infer the levels of intrinsic vulnerability. An example of the rule is:

IF maximum length is large THEN intrinsic vulnerability is high

The rules were developed from published literature and expert opinions (Cheung *et al.* 2005; Chapter 2). The degrees of membership of different conclusions (the level of intrinsic vulnerability) were based on the membership to the predicates and were accumulated by the expert system through:

 $Membership_e = Membership_{e-1} + Membership_i (1 - Membership_{e-1})$ eq.3.1 where $Membership_e$ is the degree of membership of the conclusion after combining the conclusions from *e* pieces of rules, and $Membership_i$ is the degree of membership of the conclusion of rule *i*. An index of intrinsic vulnerability was estimated from the mean

values of the conclusions fuzzy membership functions weighted by the degrees of membership to each conclusion category.

3.2.2. Intrinsic vulnerability index of marine fishes

A list of the world marine fishes (n = 15,723) was obtained from FishBase (Froese & Pauly 2004; www.fishbase.org). Their life history and ecological characteristics were obtained from published literature, notably those that were recorded in FishBase. These characteristics include: maximum length, age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality, fecundity (only low fecundity is considered), spatial behaviour and geographic range. To reduce the uncertainty of the predicted vulnerability, species in which total length was the only available life-history parameter were excluded. As a result, the number of species included in the analysis was 1,353.

Marine fishes in the analysis were categorized by according to their association to the four major habitats where fishes may have evolved different sets of life history traits and received different characteristics of threats. The habitat categories are: (1) coral reefassociated, (2) estuarine, (3) seamount and (4) seamount-aggregating fishes. The lists of coral reefs and estuaries-associated species were based on information recorded in FishBase. Seamount fishes are defined as fishes that have been recorded on seamount. Species that aggregate in association with seamounts and similar topographic bathymetric features were categorized as seamount-aggregating fishes (Koslow 1997; Morato *et al.* 2006a). Thus seamount-aggregating fishes are a subset of seamount fishes. Seamount and seamount-aggregating fish were based on the list published by Morato *et al.* (2006a). The average predicted intrinsic vulnerability index of fishes associated to the four habitats were compared using Turkey-Kramer HSD test.

Fishes were also categorized according to their depth range, latitudinal range and positions in the water column. These attributes were considered to be related to the fishes' life history (Macpherson & Duarte 1994; Brown 1995). In general, marine fishes inhabiting deeper environments or with a higher latitudinal range were considered to have larger maximum body size and wider distribution range (Brown & Maurer 1989; Macpherson & Duarte 1994). These traits (maximum body size, in particular) may

then affect the intrinsic vulnerability to fishing. Depth and latitude were represented by the median of the species depth and latitude range and the range sizes, while position in water column was categorized as: (1) demersal, (2) pelagic, (3) benthopelagic, (4) bathypelagic, and (5) bathydemersal. Median depth ranges were log-transformed to correct for the non-linear relationship between depth and intrinsic vulnerability. Information on these attributes was taken from FishBase.

Relationships between the environmental attributes (depth, latitude and ecological niche) and the index of intrinsic vulnerability (V) of fishes were evaluated using a generalized linear model (GLM) (Kutner *et al.* 2005). To test the effects of each of the factors that may correlate with the intrinsic vulnerability, the full GLM model was structured as:

$$V = \alpha + \beta_{Lat} \bullet Lat + \beta_{LatRange} \cdot LatRange + \beta_{Depth} \cdot \log(Depth) + \sum_{i=1}^{5} \beta_{nich,i} \cdot Niche_i + \sum_{j=1}^{4} \beta_{habitat,j} \cdot Habitat_j + \varepsilon$$
eq. 3.2

where α is the average intrinsic vulnerability of all marine fishes, *Lat* is median value of latitudinal range, *LatRange* is the latitudinal range, *Depth* is median of the depth range, *Niche* and *Habitat* are categorical factors representing the positions in water column *i* and habitat types *j*, respectively. *B_{LatRang}*, *B_{Depth}*, *B_{niche}* and *B_{habitat}* are the coefficients for the factors: lattudinal range, median depth range, position in water column and habitat type, respectively. ε is the error term. The significance of the factors was evaluated with t-tests.

As geographic range (closely correlated with latitudinal range) is an attribute in the expert system, it might appear that the dependency of the intrinsic vulnerability index (V) on the latitudinal ranges of the fishes would invalidate the GLM. However, geographic range is positively correlated with maximum body length (Brown 1995). On the contrary, the rules in the expert system stipulated that geographic range and maximum length contribute to intrinsic vulnerability in an opposite way, i.e. vulnerability increases with maximum body size but decreases with distribution range. Here, the GLM explored how such covariation affects the intrinsic vulnerability of fishes to fishing in different environments (e.g. depth and latitude).

3.2.3. Mean intrinsic vulnerability index of catch

Catches of the world from 1950 to 2003 were obtained from the *Sea Around Us* Project (SAUP) global catch database (www.seaaroundus.org). The SAUP catch database was constructed from catch or landing statistics from around the world. The fisheries statistics of the United Nation Food and Agriculture Organization were the major data source. Based on predicted geographic distributions of the exploited organisms and a rule-based model, the original catch data were disaggregated spatially (by 30 min latitude x 30 min longitude cells covering the world's oceans) and taxonomically (Watson *et al.* 2004).

We classified the exploited fishes reported in the catch database (858 taxa) by their associated habitat. In the SAUP catch database, each exploited group (reported as a taxonomically aggregated group by family, genus or species) was given a "habitat affinity" (Appendix 3.1). Exploited group's affinities to the major habitats (coral reef, estuary, seamount, Table 3.1) were expressed as an index that ranged from 0 to 1. The affinity values represented the frequency of occurrence or the relative density of the taxon in the particular habitat. These values had been used to allocate reported annual catches from fisheries statistics (e.g. FAO fisheries statistics) to different area of the world oceans.

The affinities were determined from qualitative descriptions from the published literature, databases such as FishBase and/or through personal communications from experts (Table 3.1). For instance, striped bass (*Morone saxatilis*) prefers estuaries and it also occurs in 'other habitats'; thus, it received a score of 0.75 for estuaries and 0.5 for 'other habitats'. This was repeated for all exploited taxa in the *Sea Around Us* Project global catch database. If specific habitat association information for a group aggregated at a higher taxonomic level (e.g., Genus, Family) was not available, their weighting factors were approximated from the average habitat association values of their composite taxa at a lower taxonomic level (e.g., species). A group may be associated with multiple habitats. The assigned habitat affinity values are available online (www.seaaroundus.org).

Table 3.1. Habitat categories used here, and for which global maps are available in the *Sea Around Us* Project, with some of the terms typically associated with them (in *FishBase* and other sources).

Categories	Terms often used to describe these categories		
Estuary	Estuaries, mangroves, river mouth		
Coral	Coral reef, coral, atoll, reef slope		
Seamounts	Seamounts		
Other habitats	Muddy/sandy/rocky bottom		

The average intrinsic vulnerability index of the taxa in the catch (hereafter called 'average vulnerability of catch') over the past five decades was calculated from the arithmetic mean of the intrinsic vulnerability index of fishes weighted by their annual catch. Firstly, annual catches by exploited fish groups from 1950 to 2003 that had been disaggregated into a world ocean map (represented by 30 min latitude x 30 min longitude cells) were obtained from the Sea Around Us Project database. Secondly, time-series of average vulnerability of catch for all the 858 fish groups with non-zero affinity to coral reef, estuary and seamount-associations were calculated separately. We overlaid global maps of coral reefs (UNEP World Conservation Monitoring Centre, Cambridge, UK), estuaries (Alder 2003) and seamounts (Kitchingman & Lai 2004) onto the spatial catch data. For each habitat and exploited taxon, we calculated the annual catch from areas where the particular habitat occurred. Catches were considered to be originated from a particular habitat if: (a) the catches came from groups that are associated with that habitat, and (b) the catches came from areas where that particular habitat existed. Thirdly, the intrinsic vulnerability index for each of the 858 groups were predicted using the fuzzy expert system (Appendix 3.1). Using these data, the average vulnerability of catch by habitat over the past five decades was calculated. To understand the changes in community structure that led to any observed trends in average vulnerability of catch, surface-plots of intrinsic vulnerability and total catch of fishes against time were created.

3.2.4. Comparison with distributions of globally threatened fishes

Marine fishes that were listed under the IUCN Red List of Threatened Species (Baillie *et al.* 2004) were mapped onto the world ocean map represented by 30 min

latitude x 30 min longitude cells. These included 161 species of fishes that are listed under the vulnerable, endangered and critically endangered categories. Distributions of species were obtained from published literature, maps, and reports. For species without published distribution maps, their distributions were predicted using a rule-based model based on information such as depth and latitudinal range, occurring ocean basins, etc (see Watson et al. 2004 and www.seaaroundus.org for details). The number of red listed species and the time-series of average vulnerability of catch of demersal fishes in each cell was estimated. For each cell in the world ocean map, the slope of the changes in average vulnerability of catch between 1950 and 2003 were estimated using linear regression. Slopes with negative values indicate declines in average vulnerability of catch and otherwise for those with positive values. Correlations between the Red List species number and the slope of the time-series in each spatial cell were then tested using the Kendall correlation test (Kutner et al. 2005). Although the choice of fishes that had been assessed by the Red List was biased (e.g., species that were known to be more vulnerable were more likely to be assessed), the IUCN Red List represented one of the most authoritative global list of threatened marine fishes. It should be useful in revealing largescale general qualitative patterns. The validity of using the IUCN Red List in this analysis is further elaborated in the discussion section.

3.3. Results

3.3.1. Intrinsic vulnerability of fish with different associated habitats

The estimated indices of intrinsic vulnerability of marine fishes varied between habitats (Figure 3.1, Table 3.2). The average intrinsic vulnerability of coral reefassociated and estuarine fishes (43.3 ± 1.2 s.e. and 45.3 ± 1.0 s.e., respectively) had similar level of intrinsic vulnerability (Turkey-Kramer HSD test, P > 0.05). However, coral reef fishes were slightly less vulnerable than all analyzed marine fishes (Turkey-Kramer HSD test, P < 0.05). The predicted intrinsic vulnerabilities of seamount and seamount fishes were significantly higher than coral reef and estuarine fishes (Table 3.2) (Turkey-Kramer HSD test, P < 0.05). Particularly, seamount-aggregating fish, a sub-set of seamount fishes, had the highest average intrinsic vulnerability index among all groups $(63.9 \pm 3.1 \text{ s.e.})$. The average vulnerability index of seamount-aggregating fishes was 63.9 ± 3.1 s.e., and was similar to fishes that were listed under the IUCN Red List of Threatened Species (Figure 3.1).

Table 3.2. Comparisons of intrinsic vulnerability between fishes associated with different habitats. The values represent the difference between the mean intrinsic vulnerability index of the assemblages associated to the habitats listed on the first column and the first row. The asterisk indicated that the pair comparison is significant at 0.05 confidence level in the Turkey-Kramer HSD test (q = 2.574). Seamount-aggregating fishes

Marine fish communities	All	Coral reef	Estuarine	Seamount	Seamount-agg
All		4.10*	2.04	-5.44*	-16.56*
Coral reef	-4.10*		-2.06	-9.54*	-20.67*
Estuarine	-2.04	2.06		-7.41*	-18.61*
Seamount	5.44*	9.54*	7.47*		-11.13
Seamount-agg	16.56*	20.67*	18.61*	-11.13	

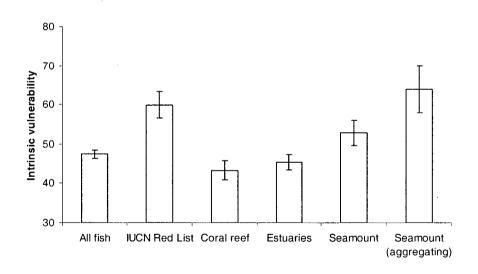


Figure 3.1. Mean intrinsic vulnerability index of marine fishes that are categorized as: coral reef-associated (N = 243), estuaries-associated (N = 381), seamount (172), seamount-aggregating (N = 15), all fish (N = 1,353), species listed under the IUCN Red List (N = 161). The error bars represent 95% confidence limits.

The intrinsic vulnerability index values were significantly related to factors relating to the position in water column, depth and latitudinal ranges (Table 3.3). Fishes occupying the bathypelagic region (i.e., the oceanic zone between 1,000 m to 4,000 m deep) showed significantly lower vulnerability. When position in the water column was the only independent factor considered, bathydemersal fishes had the highest vulnerability index, followed by benthopelagic, then demersal and pelagic fishes. The significance of the position in the water column (except for bathypelagic and bathydemersal fishes) was lost when latitudinal and bathymetric variables were added. The occurrence depth (represented by the log-transformed median of their depth range) and latitudinal range was positively and significantly related to the species' vulnerability index. When positions in water column, depth and latitudinal factors were accounted for, habitat type was only marginally significant in explaining the variations in the vulnerability index. Coral reef-associated, seamount and estuarine fishes did not have significantly different indices, while seamount-aggregating fishes were significantly (5% confidence level) more vulnerable.

Table 3.3. Results of the generalized linear model for the relationships between the environmental attributes (depth, latitude and position in water column) and the index of intrinsic vulnerability of fishes of 1,514 species of marine fishes. This shows fishes in the bathypelagic zone to have significantly lower vulnerability than all fishes in general. Fishes inhabit deeper water, have bigger latitudinal range and are seamount-aggregating have higher vulnerability index.

Factors	Coefficients	Standard error	t-values	Probability> t
Intercept	20.47	2.89	7.074	<0.001**
Pelagic	0.31	2.10	0.149	0.882
Demersal	0.69	1.06	0.653	0.514
Benthopelagic	4.62	2.41	1.912	0.056
Bathypelagic	-28.46	3.11	-9.168	<0.001**
Bathydemersal	6.64	2.39	2.775	0.006**
log(median depth)	4.94	0.46	10.765	< 0.001**
Latitudinal range	0.07	0.02	4.134	<0.001**
Coral reef-associated	-0.84	1.80	-0.467	0.641
Estuarine	2.36	1.79	1.315	0.189
Seamount	-0.23	2.25	-0.102	0.919
Seamount- aggregating	10.85	3.75	2.893	0.004**

** Significant at the 0.01 confidence level

3.3.2. Average intrinsic vulnerability index of catch

The average vulnerability of catches of marine fishes declined from 1950 to 2003 (Figure 3.2). The trends were similar whether all exploited fishes or only coastal fishes were considered (Figure 3.2a). The large fall and rise of average vulnerability of catch mainly resulted from the large catches of Peruvian anchovy (with low vulnerability) catch and its collapse in the 1970s and 1980s. When small pelagic fishes were excluded from the analysis, the average vulnerability of catch declined more smoothly (Figure 3.2b).

The average vulnerability of catches from coral reefs and estuaries declined, while the trend was less clear for seamount fishes (Figure 3.2c-f). The decline was stronger for coral reef-associated fishes (Fig. 2c), from a mean average vulnerability of catch of 50 (out of 100) in 1950 to 40 in the 2000s. Estuarine fishes also showed a consistent decline (Figure 3.2d). When all exploited seamount fishes were considered, average vulnerability of catches fluctuated widely over the past five decades (Fig. 2e). The fluctuations, however, were mainly attributed to the high catch of small pelagic fish. When small pelagic fishes were excluded from the analysis, the average vulnerability of catches for seamount fishes increased consistently from the 1970s to the late 1990s, then levelling from 2000 on (Figure 3.2f).

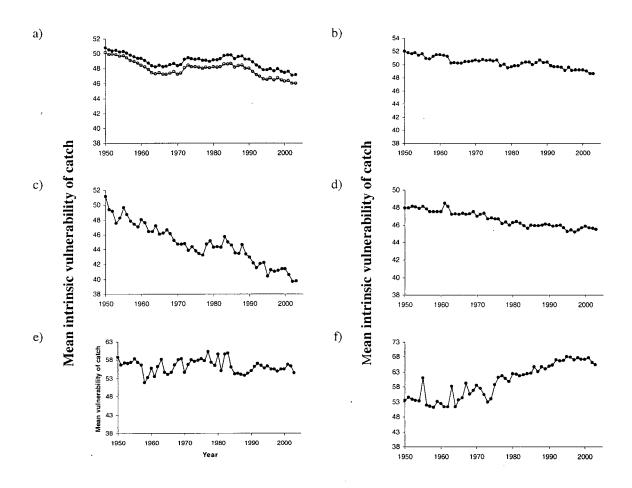


Figure 3.2. Average intrinsic vulnerability index weighted each year by the annual catch of: (a) all exploited fishes (\bullet) and all coastal exploited fishes (\circ); (b) all exploited fishes except small pelagic fishes; (c) coral reef-associated fish communities; (d) estuarine fish communities; (e) seamount fish communities; (f) seamount fish communities (except small pelagics). The average intrinsic vulnerability of the catch can range from 1 to 100. Higher value represents greater vulnerability.

The declines in average vulnerability of catches generally resulted from the slight decrease in catches of more vulnerable species and the increases in catches of low vulnerability species (Figure 3.3). Catches of fishes with intrinsic vulnerability indices of around 60 increased from the 1950s, peaked in the 1990s and appeared to be declining since then (Figure 3a). At the same time, catches of fishes with low vulnerability (vulnerability indices below 60) continued to increase rapidly. When we only included catches of demersal fishes from coastal areas (defined here as less than 50 m deep or within 100 km from the nearest coast), such trends became clearer (Figure 3b, c). In the offshore areas (the complement of coastal areas), highly vulnerable fish catches peaked in the 1980s. On the other hand, the pattern of increasing catches of low vulnerability fishes is less clear. Catches of very high vulnerability fishes (vulnerability index = 70 to 90) showed a stronger increase since the late 1980s (Figure 3 b, d).

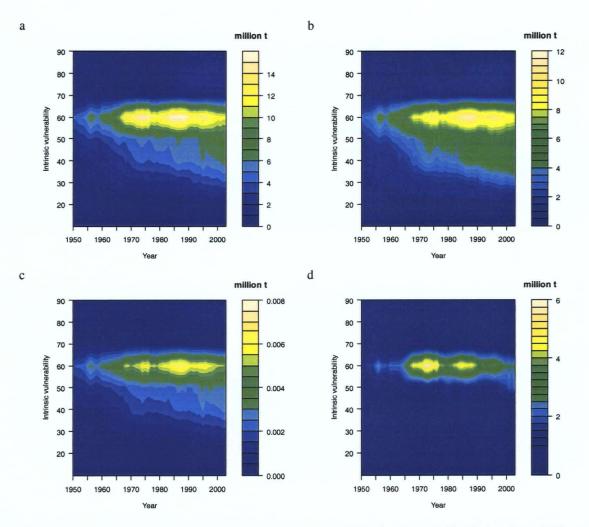


Figure 3.3. Surface plot of catch of fishes with different intrinsic vulnerability index from 1950 to 2003 of (a) all exploited fishes, (b) coastal exploited fishes, (c) coastal demersal fishes, (d) offshore demersal fishes.

3.3.3. Comparing average vulnerability of catch and number of red listed fishes

The map of the global distribution of the number of marine fishes in the IUCN Red List showed that high concentration of red-listed fishes mainly occur along the continental shelf (Figure 3.4). In the world ocean map, where the number of red-listed fishes in each 30 min latitude x 30 min longitude cell was calculated, cells with the highest quartile of the number of red-listed species were all found along the continental shelf. In terms of ocean basins, high concentration of red-listed fishes was observed in the

Indo-Pacific, Northwest Pacific and Northwest and East-central Atlantic (particularly the Caribbean).

The distribution of red-listed marine fishes agrees with the spatial patterns of changes in the average vulnerability of catch. In the world ocean map, most 30 min latitude x 30 min longitude cells in inshore and continental shelf showed declines in average vulnerability of catch from 1950 to 2003. These were also the areas where the bulk of fishes were being caught. The slopes were mostly positive or very small (\pm 0.01) in the cells representing the high seas (i.e. area outside the Exclusive Economic Zones or any national jurisdiction), indicating a slight increase or no change in average vulnerability of catch over the past five decades. Cells with negative slope concentrated more in the Indo-Pacific, Northwest Pacific, North Atlantic and the Caribbean. Kendall correlation test showed that the slopes of average vulnerability of catch and number of fishes listed under the IUCN Red List were significantly and negatively correlated (P < 0.01). This means that more threatened fishes occur in areas where average vulnerability of catch (of demersal fishes) declined from the 1950s to the 2000s.

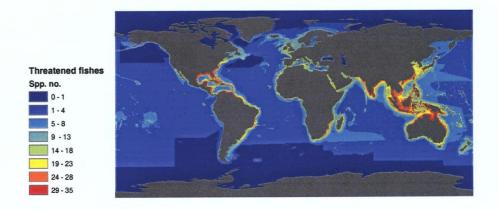


Figure 3.4. Number of marine fishes listed under the IUCN Red List of Threatened Species (Baillie *et al.* 2004) in the world ocean represented by a map with 30 min x 30 min cells.

3.4. Discussion

3.4.1. Intrinsic vulnerability of fish with different associated habitats

This study supports the proposed hypothesis that fish communities differ in intrinsic vulnerabilities as a result of different life histories and ecology. Particularly, the findings agreed with previous conclusions that seamount-aggregating fishes are extremely vulnerable (Koslow 1996; 1997; Morato et al. 2006a). Seamount fish communities consist of demersal and benthopelagic species inhabiting deeper waters. Deepwater fishes, represented here as bathydemersal, are highly vulnerable because of their larger sizes, slower growth and late maturity (Koslow 1996; 1997). Such life history patterns allow them to adapt to the high stability of deepwater environment (Steams 1977). On the contrary, deepwater pelagic (mesopelagic and bathypelagic) fishes are generally small-sized and fast-growing (Childress et al. 1980), and thus have lower intrinsic vulnerability (Rex & Etter 1998). Examples of deepwater demersal and benthopelagic species associated with seamounts include orange roughy (Hoplostethus atlanticus), deepwater oreos (Family: Oreosomatidae) and rockfish (Sebastes spp). Besides their vulnerable life history patterns (Koslow 1996; 1997), these fishes have a high tendency to form aggregations around seamount, which renders them even more vulnerable to exploitation. Although the coral reef assemblages appeared to have low average vulnerability index to fishing, this can be attributed to the large diversity of small-bodied species, which evolved to utilize the many niches provided by the complex coral reef structure (Sale 1977). On the other hand, high species diversity in coral reef communities also means that the absolute number of fish with vulnerable life histories may be considerable. Estuarine fish assemblages consisted of a mixture of freshwaterand marine- migrants and residents (Blaber 2000). Thus the assemblage structures are relatively more volatile. Therefore, the average intrinsic vulnerability of estuarine fishes is statistically similar to all marine fishes.

3.4.2. Intrinsic vulnerability and geographic range

The significant positive relationship between latitudinal range and the vulnerability index suggest that fishes with a large geographic range may be more

vulnerable to fishing. Macroecological theory predicts that geographic range (approximated by latitudinal range here) is positively related to maximum body size, as large-bodied animals tend to be generalists, have higher mobility and require more resources (Gaston 1988; Brown 1995; Brown *et al.* 1996). As body size is positively correlated with intrinsic vulnerability (Dulvy *et al.* 2003; Reynolds *et al.* 2005), vulnerability and latitudinal range are thus correlated. This relationship implies that wide ranging fishes may be more vulnerable to fishing – which contradicts previous conclusions that fishes with large geographic ranges should be less vulnerable. In the fuzzy expert system employed in this study, geographic range was an attribute used to calculate the vulnerability index. However, the 'rule' in the model specified that species with small geographic range and vulnerability relationship obtained from the results should not be an artifact of the model.

3.4.3. Average intrinsic vulnerability of catch

The results from this study support the hypothesis that global fisheries catches were increasingly dominated by less intrinsically vulnerable fishes while more intrinsically vulnerable fishes became over-exploited or depleted. The consistent declines of average vulnerability of catch were generally caused by the reduced catches of more vulnerable species, while catches of less vulnerable fishes increased. This trend was particularly prominent in coastal regions.

The findings agree well with empirical evidence of serial depletion from more vulnerable to less vulnerable species worldwide. Firstly, large declines in abundance of animals in coastal and estuarine ecosystems had been estimated from historical ecosystem reconstructions (Lotze *et al.* 2006). Secondly, empirical evidence at regional scale showed significant relationships between intrinsic vulnerability and changes in community structure because of fishing (Jennings *et al.* 1998; Cheung *et al.* 2005; Cheung, W.W.L. unpublished data). In general, abundances of intrinsically more vulnerable fishes declined faster than those of less vulnerable fishes. In fact, the majority of the currently over-exploited, depleted or collapsed fishery stocks are large demersal

fishes (Grainger & Garcia 1996). Here, these species were shown to have high vulnerability. Moreover, the large-scale depletion of predatory fishes (Baum *et al.* 2003; Christensen *et al.* 2003; Hutchings 2000; Myers & Worm 2003, 2005) and numerous accounts of local extinction of highly vulnerable species (Casey & Myers 1998; Dulvy *et al.* 2003; Sadovy & Cheung 2003; Donaldson & Dulvy 2004) support the hypothesis that the decline in average vulnerability of catch was largely a result of over-exploitation of the more vulnerable fishes. Although catches of extremely vulnerable species also increased (intrinsic vulnerability index \geq 80) recently, particularly those from offshore waters, their contributions to the global catches were relatively small. Current evidence suggests that the increasing exploitations of the offshore deepwater stocks that generally have vulnerable life histories are not sustainable (Morato *et al.* 2006b). The apparent increase in catch was sustained by serial depletions of previously unexploited and inaccessible stocks.

The likelihood of alternative explanations for the observed changes in average vulnerability of catches that were independent of exploited stock status was small. These alternative explanations include changes in market demand and accessibility to fishing grounds. However, a large scale shift in market demand for smaller or less vulnerable fishes independent of the exploited stock status was not apparent in the past five decades. Moreover, changes in accessibility to fishing grounds would have likely affected the catches of fishes similarly across the spectrum of intrinsic vulnerability. On the other hand, the consistent patterns observed in the different habitats and niches and the supporting evidence from empirical studies suggested that the changes in average vulnerability of catch can be contributed mainly to serial depletion of fishes.

Coral reef fishes showed the strongest decline in average vulnerability of catch over the last five decades, thus the more vulnerable reef fishes might have been depleted rapidly. Catches of intrinsically vulnerable reef fishes such as groupers (Serranidae) declined, while those from less vulnerable fishes such as rabbitfishes (Siganidae), goatfishes (Mullidae) and bigeyes (Priacanthidae) increased greatly. As the coral reef fish community is relatively more stable compared to other communities such as estuarine, changes in composition of coral reef fishes resulting from serial depletion of fishes with different vulnerabilities can be detected more easily. On the contrary, the high volatility of estuarine communities may partly explain their weaker decline in the average vulnerability of catch.

This study also showed that high concentrations of threatened fishes occurred in the Indo-Pacific and the Caribbean, where coral reefs were extensive (Bellwood & Hughes 2001; Spalding *et al.* 2004). Together with other direct and indirect threats such as destructive fishing (Jennings & Lock 1996), geographic expansions of the live reef fish trade (Sadovy & Vincent 2002; Sadovy 2005), coastal development, climate change (Pandolfi *et al.* 2003; Birkeland 2004) and data limitations (Sadovy 2005), coral reef habitat should be warranted high conservation attention.

The increasing exploitation of deepwater (Morato *et al.* 2006b) and seamount fishery resources is of concern (Koslow 1997; Koslow *et al.* 2000; Watson & Morato 2004). Seamount assemblages are generally more vulnerability to fishing. Also, fisheries on seamounts are often 'boom-and-bust', i.e., rapidly over-exploiting a seamount soon after their discovery, followed by a move to the next to be discovered, resulting in serial depletions of seamount populations. This might explain the increase in catches of highly vulnerable offshore fishes and the consistent increase in average vulnerability of catch in seamounts. Moreover, the high vulnerability of the seamount communities means that the populations may be over-exploited rapidly once fishing has developed before management plans and regulations are in place (Boyer *et al.* 2001). The sustainability of such fisheries is in doubt (Clark 2001).

The positive spatial correlation between the number of fishes listed under the IUCN Red List and the decline in average vulnerability of catch provided further support for the over-exploitation of more vulnerable stocks. Although fishes that were selected for assessment by the IUCN Red List might have been biased towards the more vulnerable species, this also means that the distribution of the red-listed species reflects the area where intrinsically more vulnerable and currently endangered species were concentrated. Thus the broad-scale patterns of distributions of the Red-listed fishes should be useful in revealing general patterns of threatened species distributions.

The often poor quality of the original catch data should not affect the general conclusion of the analysis. The taxonomic and spatial resolutions of the original data (mainly from FAO) are poor in some regions of the world. This may have limited the

sensitivity of our method to detect changes in average vulnerability of catch (Pauly & Palomares 2005). For example, a mixture of species might have been reported in a single group. These species may have different intrinsic vulnerabilities. As they are aggregated within a single group, their serial depletion would not be detected by the analysis in this study. Also, it is difficult to reveal spatial serial depletion of different populations (e.g. fishing shifts further offshore as inshore stocks are depleted) from landings data reported at country or regional level. Thus we believe that the uncertainty of the data quality can result in underestimation of the decline in the average intrinsic vulnerable of catch over time (Pauly & Palomares 2005).

This study demonstrated the large-scale effects of fishing on structures of fish communities that are related to their intrinsic vulnerability to fishing. Although seamount assemblages showed distinctively higher vulnerability, the nature of threats from fishing shared many similarities with coral reef fishes. This study suggests that the coral reef assemblages in the Indo-Pacific and the Caribbean, deepwater demersal fishes and the seamount-aggregating fishes worldwide are particularly threatened by fishing. If present trends persist, it is likely that the more vulnerable species can be further depleted or, at worst, at risk of extinction. In Chapter 4, I attempted to predict the relative conservation risk of marine fishes from fishing in the world.

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4. AN INDEX THAT EXPRESSES RISK OF SEVERE POPULATION DEPLETION OF MARINE FISH FROM FISHING⁴

4.1. Introduction

Unsustainable fishing is occurring over most of the ocean (Botsford *et al.* 1997; Pauly *et al.* 2002), which poses serious conservation threats to marine taxa (Dulvy *et al.* 2003). Such threats are increasingly being recognized as more cases of severe population depletion or extirpation induced by fishing mortality are documented (Casey & Myers 1998; Dulvy *et al.* 2003; Sadovy & Cheung 2003; Hutchings & Reynolds 2004; Myers & Worm 2005). Although documented marine extinctions are rarer than terrestrial taxa, extirpations (local extinctions) of marine populations are numerous, especially in coastal systems (Carlton 1993; Casey & Myers 1998; Sadovy 2001; Dulvy *et al.* 2003), with extinction following the last extirpation (Pitcher 2001). On the other hand, lack of long-term population data limits the quantification of conservation threats to marine organisms at a global scale (Dulvy *et al.* 2004). Currently, under the IUCN Red List, less than 1% of marine fish species have been evaluated (Baillie *et al.* 2004). Thus developing approaches that allow assessment of extinction risk with limited data is an important step to conservation of marine populations (Dulvy *et al.* 2003).

Conventional methods to assess extinction risk of animals rely strongly on demographic data (Burgman *et al.* 1993); thus their applications to extinction risk assessment of most marine fishes are limited because of a lack of data. Conventional methods can range from diffusion methods to individual-based population models (Boyce 1992; Brook *et al.* 2000; Dulvy *et al.* 2004). These methods require at least time-series data of abundance or an index of abundance. However, such data are generally lacking for the majority of marine fish species except for some exploited populations in well-studied areas (e.g., North America). The data-limitation problem prevents identification of extinction risk for a broad range of populations affected by anthropogenic impacts

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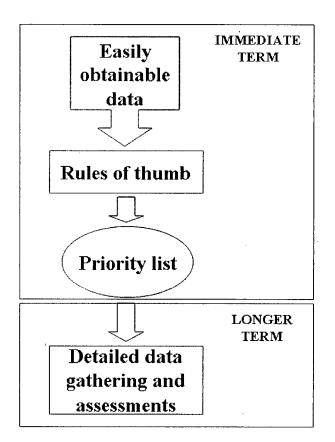
such as fishing. The problem of data-limitation is particularly serious in tropical, developing country fisheries where species diversity is high, but resources for monitoring are low (Pauly 1980; Jennings & Polunin 1996; Johannes 1998).

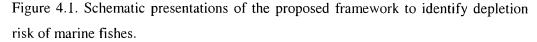
Another obstacle to estimating the extinction risk of marine fishes is the difficulties in determining their minimum viable population size (Reynolds et al. 2005). Three major reasons that have led to this problem. Firstly, experience of contemporary marine extinction is limited (Dulvy et al. 2003). Secondly, population dynamics of marine fishes in small population size are poorly understood. For instance, the extent to which depensation or Allee effect occurs in marine fish populations is not clear. Depensation, termed the Allee effect in the ecology literature (Stephens & Sutherland 1999; Stephens et al. 1999), occurs when fitness (number of offspring per spawner) or per capita growth rate decreases at low population size (Stephens et al. 1999; Petersen & Levitan 2001). Meta-analysis of stock-recruitment data showed that depensation might be uncommon in marine fish (Myers et al. 1995; Liermann & Hilborn 1997). However, reanalysis accounting for the high variance in the original data suggests that it might still be likely that depensation would be more common in marine fishes than previously assumed (Liermann & Hilborn 1997). Thirdly, dynamics of meta-population - spatially separated populations of the same species which interact with each other (Levins 1969) - are poorly studied for most marine fishes. It is difficult to predict extinction risk accurately without understanding the mechanisms of local extinctions and migrations from metapopulations. Thus, here, conservation status of marine fishes was expressed in terms of the risk of severe depletion i.e., the risk that the abundance of the concerned species is reduced to very low level. Although the uncertainty of the true risk of extinction in greatly reduced marine fish population was admitted, it is reasonable to assume that extinction risk increases largely by severe population depletion.

To rapidly assess the relative depletion risk and short-list priority species for detailed assessment, 'rule-of-thumb' approaches were proposed (Fagan *et al.* 2001; Reynolds *et al.* 2001; Dulvy *et al.* 2003; Dulvy *et al.* 2004). Such approaches use easily-obtainable information to approximately identify vulnerable or "priority" species that are in need of immediate conservation attention. For instance, in Chapter 2, the 'rule-of-thumb' approaches were incorporated into a fuzzy logic expert system framework to

provide quantitative predictions of intrinsic vulnerabilities to fishing. The 'rule-of-thumb' approaches are especially useful if their applications are combined with large databases, for instance, FishBase (Froese & Pauly 2004; www.fishbase.org) and the *Sea Around Us Project* database (www.seaaroundus.org), which presents a wide range of fisheries data ranging from spatially disaggregated catch data to prices of fishery catches (Watson *et al.* 2004; Sumaila *et al.* 2007).

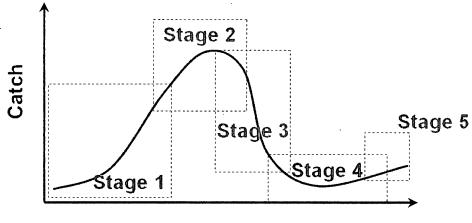
Results obtained from 'rule-of' thumb' approaches can also help focus longer term research on the priority species so that data could be made available for more accurate extinction risk assessments (Figure 4.1).





Among fisheries data, catch time-series are relatively more widely available than data such as absolute abundance or index of relative abundance. Catch time-series can be useful in understanding the overall status of a population (Grainger & Garcia 1996;

Fiorentini *et al.* 1997; Caddy 2004). By definition, a population is under-exploited when a fishery relying on it is developing; in such cases, catch increases as fishing effort increases (Hilborn & Walters 1992). As fishing effort approaches or exceeds maximum productivity, the population becomes over-exploited, and the catch declines, and eventually collapses. A recovery phase may follow if fishing is reduced to a low level (Figure 4.2). Catch time-series had been used as an indicator to reflect the approximate population status at large spatial scale (Grainger & Garcia 1996; Pauly *et al.* 1998; Caddy 2004; Worm *et al.* 2006).



Time

Figure 4.2. Schematic diagram showing the classification of exploitation status of a population based on a catch time-series. Stage 1: under-exploited; Stage 2: fully exploited; Stage 3: over-exploited; Stage 4: depleted; and Stage 5: recovering.

The relationship between catch and population status becomes less tight when there are confounding ecological, environmental, economic and management effects. Firstly, catches can be maintained by spatial changes in fishing effort and targeted subpopulation. In such cases, catch may increase as fishing expands spatially (serial depletion), or catchability increases when a population reduces its range. Also, catches can be reduced by the implementation of more stringent fisheries management policies, while population size may remain roughly constant. Moreover, change in market demand, catch value and costs of fishing may affect the operation of fleets without strong change in population abundance. On the other hand, given that these ecological, environmental and economic data are not available for many targeted fishes and fisheries, we have to rely on catch time-series to identify potentially over-exploited or depleted populations for more detailed analysis.

Apart from the extrinsic factors such as fishing mortality rate, life history and ecology are also important intrinsic factors affecting the depletion risk of marine species (Jennings et al. 1998; Reynolds et al. 2001; Rowe & Hutchings 2003; Cheung et al. 2005; Reynolds et al. 2005). Species with certain features (e.g., large size, late maturation) are less able to withstand high fishing mortalities and thus have a higher risk of extinction than less vulnerable species under similar fishing pressure (Musick 1999). Also, theoretical and empirical studies suggest that fishes with 'periodic' life history characteristics (large size, high longevity, late at maturation and high fecundity) have a high compensation ability (i.e., increase in population growth rate as population size decreases), but a low productivity when their population is greatly reduced. On the other hand, 'opportunistic' fishes (small to medium size, short-lives, early maturation and moderate fecundity) have a low compensation ability, but high productivity at small population size (Winemiller & Rose 1992; Fagan et al. 1999; Rose et al. 2001; Winemiller 2005; Goodwin et al. 2006). Thus fishes with 'periodic' life history characteristics have a low resilience (the ability to recover from disturbance) when populations are over-exploited or depleted, while the 'opportunistic' life history characteristics confer high resilience (Winemiller 2005; Goodwin et al. 2006).

Based on the relationship between the life history and ecology of a species and its vulnerability to fishing, Cheung *et al.* (2005) developed an expert system that predicts the intrinsic vulnerability of marine fishes using simple life history and ecology parameters. These parameters are readily available from easily assessable databases, such as FishBase (www.fishbase.org) (see Chapter 2). This expert system estimates an index of intrinsic vulnerability for each species or populations from one or more of the following parameters: maximum length, age at maturity, longevity, von Bertalanffy growth parameter K, natural mortality rate, fecundity, geographic range and scale of spatial behaviour (e.g., schooling, aggregating, etc.). However, the index of intrinsic vulnerability developed in Chapter 2 can only indicate species' inherent capacity to withstand fishing pressure. To understand the overall risk of depletion, extirpation or

extinction from fishing, we need to understand both the intrinsic vulnerability and the level of fishing exploitation on the exploited species.

Given the above theoretical and empirical bases, we can develop some qualitative relationship between catch time-series, exploitation status, life history and depletion risk of exploited marine fishes. For instance, a consistent decline in catch over a large geographic range after reaching a peak may indicate over-exploitation. While life history traits of the exploited species indicate a high intrinsic vulnerability (or low resilience), the species may likely have high depletion risk when the population is over-exploited. On the other hand, depletion risk may be moderate if the life history of the species confers low intrinsic vulnerability. Developing and collating these qualitative relationships systematically could be useful to evaluate the conservation status of marine fishes to fishing (Jennings *et al.* 1998; Jennings *et al.* 1999; Reynolds *et al.* 2001).

A fuzzy logic expert system could be useful in combining the above qualitative relationships to provide an indicator of depletion risk (see Chapter 2). Fuzzy logic, or fuzzy set theory (Zadeh 1965), allows a subject to be "associated" with one or more set(s) with a gradation of membership defined by fuzzy membership functions, while an expert system is an artificial intelligence system that helps solve problems based on prespecified knowledge-base. The knowledge can be expressed in the form of rules such as:

IF A THEN B

where A is the premise while B is the conclusion (Kasabov, 1996). The actions defined by the rules are 'fired' (= operated) when the degree of membership of the premises exceed certain threshold values. Conflicting rules are allowed to fire jointly. Thus conclusions from a fuzzy logic expert system can be reached from premise(s) with a gradation of truth. Membership can be viewed as a representation of the 'possibility' of association with the particular set (Zadeh 1995; Cox 1999).

Fuzzy set theory is particularly useful because vagueness is a crucial aspect of our knowledge of fishes' biological characteristics, and their relationships with the depletion risk from fishing. Fuzzy expert systems have been proposed and applied to study fisheries and conservation biology (Saila 1996). The applications range from assessing stock-recruitment relationships (Mackinson *et al.* 1999; Chen 2001), predicting fish shoaling

behaviour (Mackinson 2000) and identifying stock structure of fishes (Zhang 1994). They have also been applied to develop an analytical tool to assess conservation threats (Todd & Burgman 1998; Regan & Colyvan 2000) and to assist the IUCN Red List's species assessment (Akçakaya *et al.* 2000). Fuzzy logic was also proposed to be used to assess extinction risks of different Pacific salmon stocks (Tinch 2000).

Here, based on a rule-based fuzzy model, we used readily available catch and life history data to evaluate the relative depletion risk of exploited marine fish. Depletion risk from fishing was defined here as the possibility of severe population depletion (near extirpation) because of fishing and the intrinsic properties of the species.

4.2. Methodology

4.2.1. Analysis of temporal patterns of catch time-series

We analyzed 460 species of marine fish that had at least 10 years of catch timeseries data, and catches of at least 100 tonnes in the United Nations Food and Agriculture Organization (FAO) fishery statistics. Catch time-series were aggregated by 19 FAO statistical areas (a total of 1,313 aggregates). Since catch fluctuations caused by environmental variability (e.g., primary productivity or temperature fluctuations) might mask any trends due to fishing, catch time-series were smoothed with a running average:

$$C'_{y} = \frac{\sum_{t=y'}^{y} C_{t}}{(y-y')}$$
 eq. 4.1

where the averaged catch C' at year y is equal to the average of annual catch from year y'. As smaller species tend to respond more strongly to environmental variability than larger species (Spencer & Collie 1997), the running averages were scaled inversely by species' maximum length (maximum length \leq 30 cm: y - y' = 9 years average, maximum length = 30-90 cm: y - y' = 5 years average, maximum length \geq 90: y - y' = 3 years average). Figure 4 illustrates this for Rainbow sardine and Nassau grouper.

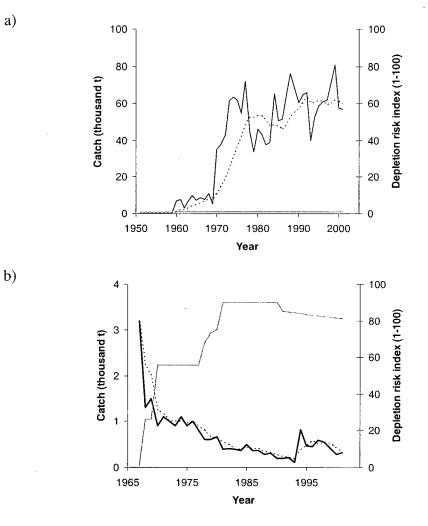


Figure 4.3. Catch time-series (solid black line: original; dotted: smoothed) and the estimated depletion risk index (grey line) for fish with different life history and exploitation patterns. (a) Rainbow sardine (*Dussumieria acuta*) is an example of small pelagic fish with low intrinsic vulnerability and (b) Nassau grouper (*Epinephelus striatus*) is an example of large demersal fish with high intrinsic vulnerability.

Based on the smoothed catch time-series, each population in each year were categorized into different exploitation status. Firstly, the smoothed catch time-series were re-expressed as the ratio of each year's annual catch to the maximum catch in the smoothed time-series. Each data point in the time-series was also classified by its position relative to the maximum catch in the data-series (i.e., before or after the maximum catch

а

is reached). Based on the relative position in the time-series and the ratio to the maximum catch (Table 4.1), each data point was then categorized into exploitation status categories adopted by the FAO: (1) under-exploited, (2) fully exploited, (3) over-exploited, (4) depleted, (5) recovering (Grainger & Garcia 1996). Each data point can belong to multiple categories, each with an associated degree of membership estimated from predefined membership functions for the categories (Table 4.1). The simplest form of membership functions, trapezoidal and triangular, were used:

$$Membership = \frac{x-a}{b-a} \qquad \text{if } a < x < b \qquad \text{eq. 4.2b}$$

$$Membership = 1 if b \le x \le c eq. 4.2c$$

$$Membership = \frac{d-x}{d-c} \qquad \text{if } c < x \le d \qquad \text{eq. 4.2d}$$

where x is the independent variable, and in this case represents the ratio of annual catch to the maximum catch of the time-series. All x values between a and d are in the particular fuzzy set; b and c are the independent variables with maximum membership. For the triangular membership function, b and c are equal (Table 4.1). For instance, the catch of Rainbow sardine (*Dussumieria acuta*) smoothed over nine years in year 1970 is about 11,000 tonnes. This is less than 17% of the maximum smoothed catch (63 thousand tonnes in 1992). Based on the fuzzy member functions in Table 4.1, Rainbow sardine in 1970 was classified as under-exploited with full membership. However, smoothed catch of Nassau grouper in 1970 was 1.2 thousand tonnes, 40% of the maximum catch in 1967. Thus, Nassau grouper was classified as over-exploited and depleted, with memberships of 0.6 and 0.4, respectively (full membership = 1).

Exploitation status	Domain of fuzzy sets in different scenarios ^a Catch relative to maximum in time-series ^b			Position in time-series ^c	Fuzzy membership function ^d
	Conservative	Moderate	Liberal		
Under-exploited	0-1 (0-0.75)	0-0.75 (0-0.5)	0-0.5 (0-0.25)	Before maximum	Trapezoidal
Fully exploited	0.75-1 (1)	0.5-1 (0.75)	0.25-1 (0.5-0.75)	Before maximum	Trapezoidal
Fully exploited	0.5-1 (1)	0.75-1 (1)	-	After maximum	Triangular
Over-exploited	-	-	0.5-1 (0.75-1)	Before maximum	Trapezoidal
Over-exploited	0.1-0.75 (0.5)	0.25-1 (0.75)	0.75-1 (1)	After maximum	Triangular
Depleted	0-0.25 (0.1)	0-0.5 (0.25)	0-0.75 (0.5)	After maximum	Trapezoidal
Recovering	Catch remained	Catch remained	Catch remained	After maximum and after	Trapezoidal
	stable/increasing for	stable/increasing for	stable/increasing for	conditions for 'over-exploited' or	
	at least 3 years	at least 5 years	at least 10 years	'collapsed' occur	

Table 4.1. Categorization of exploitation status based on fishery catch time-series under three scenarios: conservative (minimize overestimation), liberal (minimize under-estimation), and moderate (intermediate).

^a Domain of a set represents its all possible values of an independent variable of a function. Values in parentheses represent the value (or range) of an independent variable with full membership to the set;

^b Estimated from the ratio of catch at year t to the maximum catch (using catch time-series smoothed by running average);

^c Position of data-point in the catch time-series (after running average) relative to the maximum attained catch in the data-series;

^d Types of membership functions assumed in the model. Each year of catch-time series belongs to set(s) of exploitation status with degree of membership to the set(s) determined by the specified fuzzy membership function (trapezoidal and triangular membership functions).

4.2.2. Combining 'rules-of-thumb'

A fuzzy expert system was constructed to predict the depletion risk of marine fishes to fishing (Figure 4.4). The expert system is composed of two stages: the first stage infers intrinsic vulnerability to fishing while the second stage predicts depletion risk from the intrinsic vulnerability (from first stage) and time-series catch data. The structure of the first stage (prediction of intrinsic vulnerability) and its validation are detailed elsewhere (Cheung *et al.* 2005; Chapter 2).

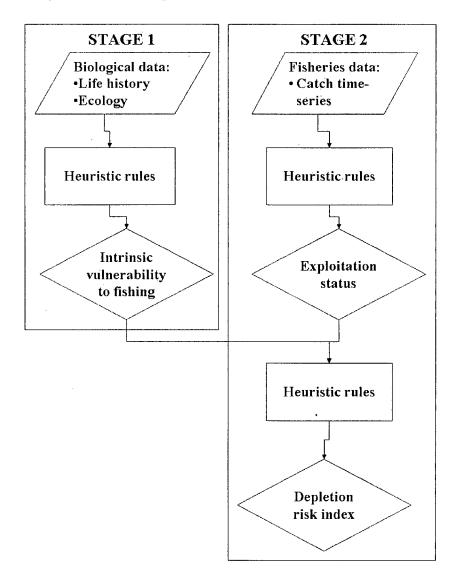


Figure 4.4. Schematic diagram of the structure of a fuzzy expert system to predict depletion risk of marine fishes from fishing.

a. Estimating intrinsic vulnerability

Using the expert system described in (Cheung *et al.* 2005; see Chapter 2) and life history parameters that were available from Fishbase (www.fishbase.org), we estimated the natural resistance to depletion from fishing (i.e., intrinsic vulnerability) for 460 species of exploited marine fishes. The predicted intrinsic vulnerabilities, originally on a scale from 1 to 100, were expressed as ordinal categories (low, moderate, high, very high) with degrees of membership associated with each category according to the life history and ecology of the species. For instance, Rainbow sardine was predicted to have 'low' intrinsic vulnerability with full membership, while Nassau grouper was predicted to have 'high' and 'very high' vulnerability with membership of 0.4 and 0.6, respectively.

b. Inferring depletion risk

Based on sets of heuristic rules, the predicted intrinsic vulnerabilities and exploitation status were combined to infer depletion risk. The heuristic rules were developed from the assumption that the depletion risk of exploited marine fishes increases as populations become fully exploited, over-exploited and depleted (Table 4.2). Depletion risk was categorized into four levels: low, moderate, high, and very high – each representing a set of relative depletion risk that ranged on a scale from 1 to 100 with increasing risk. Heuristic rules that determined the levels of depletion risk were expressed in IF-THEN clauses in which exploitation status and intrinsic vulnerability were the premises, while levels of depletion risk were the conclusions (Table 4.2). For instance, Rainbow sardine has low intrinsic vulnerability (membership = 1) and it was 'under-exploited' in 1970 (membership = 1), following the rule in Table 4.2:

IF intrinsic vulnerability is low and population is under-exploited THEN depletion risk is low.

The membership to the conclusion was calculated from the minimum of the memberships to the premises. Thus Rainbow sardine had low depletion risk with a membership of 1 (full membership) in 1970. Alternative sets of rules were used to the test sensitivity to and validity of the rules (Table 4.2).

Table 4.2. Heuristic rules that relate intrinsic vulnerability and exploitation status (premises) with depletion risk (conclusions). The rules were developed based on the rationale that depletin risk index increased as a population becomes fully exploited, over-exploited and depleted, and related positively with intrinsic vulnerability. Alternative sets of rules representing 'conservative' and 'liberal' estimation of risk were used to test sensitivity to and validity of the assumed rules.

Premises		Conclusions (depletion risk) of scenarios:			
Vulnerability	Status	Conservative	Moderate	Liberal	
Low	Under-exploited	Low	Low	Low & mod.	
	Fully exploited	Low	Low	Mod.	
	Over-exploited	Low	Low & mod.	Mod & high	
	Depleted	Mod	Mod & high	High & v. high	
	Recovering	Low	Low	Mod.	
Moderate	Under-exploited	Low	Low	Low & mod.	
	Fully exploited	Low	Low & mod.	Mod.	
	Over-exploited	Mod.	Mod. & high	High	
	Depleted	High	V. high	V. high	
	Recovering	Low	Low & mod.	Mod.	
High	Under-exploited	Low	Low	Low & mod.	
	Fully exploited	Low & mod.	Mod.	Mod. & high	
	Over-exploited	Mod. & high	High	High & v. high	
	Depleted	High & v. high	V. high	V. high	
- .	Recovering	Low & mod.	Mod.	Mod. & high	
Very high	Under-exploited	Low	Low	Low & mod.	
	Fully exploited	Mod. & high	High	High & v. high	
	Over-exploited	High	High & v. high	V. high	
	Depleted	High & v. high	V. high	V. high	
	Recovering	Mod. & high	High	High & v. high	

When different rules result in the same conclusion, memberships to the conclusion were accumulated using the method (Buchanan & Shortliffe 1984):

Accumulated membership = $Membership_i + Membership_{i+1} \cdot (1 - Membership_i)$

where *Membership*_i is the degree of membership to the conclusion resulted from rule *i*. An index of depletion risk was estimated from the index value of each depletion risk category weighted by their degrees of membership.

Groups		Number of species			
Fishery Importance ^a	Types ^b	With catch data	World total ⁴	Percent represented	Extrapolation ^c
Highly	Pelagics	64	64	100	Included
commercial	Demersals	73	138	54	Included
	Elasmobranchs	3	7	43	Included
Commercial	Pelagics	53	155	34	Included
	Demersals	152	1272	12	Included
	Elasmobranchs	9	117	8	Included
Minor	Pelagics	25	185	14	Included
commercial	Demersals	61	1038	. 6	Included

Table 4.3. Extrapolation from fish species with catch data to all exploited marine fish, by fishery importance and fish types.

1 a – This classification is based on the level of catch in FAO statistics; see FishBase (www.fishbase.org);

13

1

4

165

146

267

44

8

1

1

2

Included

Excluded

Excluded

Excluded

b – Pelagics and demersals include bony fish (teleosts) only;

Elasmobranchs

Elasmobranchs

Pelagics

Demersals

Others

c – Groups that have 5% of less of the species with catch time-series data are excluded in extrapolating the number of world's threatened marine fish.

Depletion risk was estimated for each exploited stock. Catches of each species from each FAO statistical area were considered as being obtained from an independent stock. Thus the 460 species included in this analysis consist of 1,313 'stocks'. To ensure that the predictions from this analysis at the species level are conservative, the depletion risk for each species (group) was estimated from the smallest depletion risk among its stocks.

4.2.3. Comparing the predicted depletion risk with the IUCN categories

We compared the predicted depletion risk with the IUCN Red List threatened categories: (vulnerable, endangered, and critically endangered) using simulated data from a dynamic population model. We selected 21 species of marine fishes with a wide range of intrinsic vulnerability of which estimates of parameters of life history and stockrecruitment functions are available (Myers *et al.* 1999) (Appendix 4.1). For each species, we developed an age-structured population model (Hilborn & Walters 1992), with assumed variability in recruitment, fishing intensity, density dependent change in catchability to fishing (Mackinson et al. 1997). The model was employed to simulate population dynamics for each of the species:

$$N_{a+1,v+1} = N_{a,v} \bullet e^{-(F+M)}$$
 eq. 4.3.

where $N_{a,y}$ is number of age *a* individual at year y, *F* and *M* are fishing and natural mortality rates. Recruitment at time $t(R_t)$ was specified by a Beverton and Holt function:

$$R_t = \frac{\alpha \cdot S_t}{(1 + S_t \cdot \beta)} \cdot e^{\varepsilon(0.\sigma)}$$
eq. 4.4.

where R_t is expressed as a function of the egg production or weight of spawners, α is the maximum annual recruitment per spawner and β determines the degree of density dependence, and S_t is the spawning stock size. Variations of annual recruitment were assumed to be log-normally distributed (mean = 0 and standard deviation = 0.5).

Population was in equilibrium without fishing mortality initially (year 0) from when fishing mortality rate (F) increased at a constant rate each year. The rate of increase in F was randomly chosen for each simulation. Selectivity was assumed to be age-dependent and follow a logistic function:

$$v_a = \frac{a^P}{(t_c^P + a^P)}$$
 eq. 4.5.

where v_a is the probability of capture at age *a*, t_c is the age at 50% capture and *P* is a constant determining the slope of the selectivity curve (*P* = 5 in this analysis).

Time-series of catch (C) and catch-per-unit-effort (CPUE) were generated from each simulation (Hilborn & Walters 1992). In each simulation run, catch and CPUE were calculated from:

$$C = \sum_{a} \frac{F \cdot v_a}{(F \cdot v_a + M)} \cdot N_{a,y} \cdot [1 - e^{-(F \cdot v_a \cdot q + M)}] \cdot w_a \qquad \text{eq. 4.6.}$$

$$CPUE = \frac{C \cdot q'}{F}$$
 eq. 4.7.

where w_a is the weight-at-age, q is the actual catchability coefficient while q' was the assumed catchability coefficient used by the observation model (q' = 0.3). Density-dependence change in catchability was modelled by:

$$q = q^{ib \cdot \epsilon}$$
 if $q < 1$ eq. 4.8.
 $q = 1$ if $q > 1$

(Mackinson *et al.* 1997): *b* is the biomass relative to the unexploited biomass and ε is the uniformly distributed error with values between 0 and 1. Time-series of catch and CPUE were recorded for 100 years of the tested species.

The extinction risk of each population in each simulation was determined using the IUCN Red List criterion E (based on probability of extinction). Probability of quasiextinction of the population was determined in each simulation. Quasi-extinction was defined here as a population declines to reach the point of non-viability (Ginzburg *et al.* 1982; Burgman *et al.* 1993). For each species, the population dynamics described by the above model was run 100 times. Probability of quasi-extinction was measured as the frequency of a population reaching 1/1000 of the unfished equilibrium biomass in the 100 simulations (Punt 2000). We assumed that populations that have been reduced by 99.9% are not viable, thus the estimated quasi-extinction probability is an approximate estimation on the true extinction probability. Therefore; the population was classified as critically endangered, endangered or vulnerability if the probability of quasi-extinction is at least 50% in 10 years or three generations, at least 20% in 20 years or 5 generations, and at least 10% in less than 100 years, respectively (IUCN 2001).

Simultaneously, using the generated catch-per-unit-effort time-series, we estimated the threatened status as defined by the IUCN Red List criterion A – trends of index of abundance (IUCN 2001). The population was categorized as critically endangered, endangered and vulnerable if the CPUE declined by 80%, 50% and 30% in three generations or 10 years, whichever is longer.

In each simulation, depletion risk of each population was also estimated using the expert system developed in this study. The intrinsic vulnerability of each test species was estimated based on the available life history parameters (Table 4.4). At each time-step, the exploitation status was inferred from the catch time-series recorded from the simulation model. Depletion risk was then estimated from the predicted intrinsic vulnerability and exploitation status. Populations were classified as having moderate, high and very high depletion risk if the calculated depletion risk index was above 40, 55 and 70, respectively.

The depletion risk calculated from the expert system was compared with the extinction risk identified by using the IUCN criteria E and A. We considered that the extinction risk identified based on the probability of quasi-extinction (IUCN criteria E) was accurate, while the IUCN criteria A is most widely used to assess extinction risk of marine fishes (Punt 2000). We compared the depletion risk categories and the IUCN categories determined based on criteria A with the threatened categories determined by criteria E. Considering that the depletion risk categories of moderate, high and very high correspond to the IUCN categories of vulnerable, endangered and critically endangered, respectively, we calculated the probability of under- and over- estimating threatened status (Type I and II errors) from predictions of rule-based model presented here using the simulated data from the above population model.

4.2.4. Depletion risk of all exploited marine fishes

To obtain an approximate estimate on the depletion risk of exploited marine fishes globally, we extrapolated the results from our analyses on the 460 selected species to all exploited marine fishes (3,503 species). To correct for biases in our sample towards more vulnerable and targeted species, we grouped species by types (pelagic bony fish, demersal bony fish and elasmobranchs) and fishery importance (highly commercial, commercial, minor commercial) using information available from FishBase (Froese & Pauly 2004). We excluded classes with low sample size (sample to global species number ratio $\leq 5\%$) before we extrapolated the predicted threatened status in each class (Table 4.3).

4.3. Results

Our results showed that depletion risk of the 460 exploited fishes increased rapidly over the past three decades (Figure 4.5). In 2001, about 24% of the evaluated species were associated with a very high depletion risk level (depletion risk index \geq 70), compared to none in the mid 1950s and 4% in 1970. The average depletion risk index of all species in 2001 is about 44. Fishes that are in the very high depletion risk category include gadids, polynemids, haemulids, epinephelids, triglids, dasyatids, while those in moderate depletion risk (depletion risk index around 44) include platycephalids, sciaenids, priacanthids and sparids, etc. Fishes with lower depletion risk include mainly small-bodied clupeids, engraulids, carangids and tetraodontids.

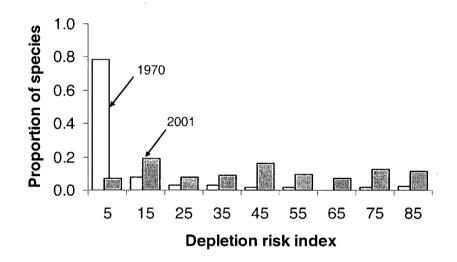


Figure 4.5. Proportion of the 460 species of marine fishes with different classes of calculated depletion risk index in 1970 (open bars) and 2001 (gray bars). The values in the x-axis are the mid-point of the classes.

Comparing the predicted depletion risk index in 2001 among different fish groups, large demersal fish (maximum length ≥ 30 cm) and elasmobranchs had depletion risk index significantly higher than average of all marine fishes, including small demersal and pelagic fishes, at the 95% confidence level (logistic regression, P = 0.003 and 0.022 respectively) (Figure 4.6). Among the 14-28%, 20-56% and 8-24% of the 460 species that were in the "very high", "high" and "moderate" categories in 2001, elasmobranchs (sharks and rays) had the highest proportion in the "moderate" or higher categories (73%), followed by large demersal (61%), large pelagics (48%) and then small pelagic bony fish (36%).

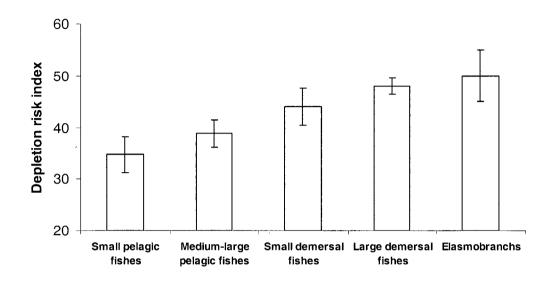


Figure 4.6. Average depletion risk index of different fish groups. Standard errors are indicated by the error bars.

By extrapolating to all exploited marine fish, we found that the proportion of marine fishes that have moderate to very high depletion risk (a depletion risk index over 55) was considerable. Of the 3,503 species of marine fish that FishBase (Froese & Pauly 2004) classifies as being commercially exploited, 500-957 (3-6% of all marine fish), 218-730 (2-3%) and 641-1,763 (5-11%) were categorized as having very high, high and moderate depletion risk, respectively. The statistically non-significant difference between the accuracy of the depletion risk index and the IUCN Red List categories suggests that the very high, high and moderate depletion risk index and the IUCN Red List categories to indicate a species being in the critically endangered, endangered and vulnerable categories, respectively. Thus our results suggest that 3-6%, 2-3% and 5-11% of all marine fishes may be critically endangered, endangered, and vulnerable. This is in the same order of magnitude as for other vertebrates (mammals, birds and amphibians), for which, however, a much higher number of species has been evaluated under the IUCN Red List procedure (Baillie *et al.* 2004) (Figure 4.7).

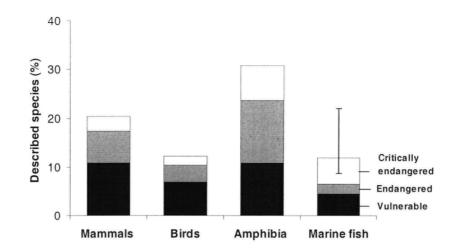


Figure 4.7. Proportion of described mammals, birds, amphibians categorized as critically endangered (white), endangered (grey) and vulnerable (black). Status of mammals, birds and amphibians are obtained from the IUCN Red List (Baillie *et al.* 2004), while the status of marine fish was inferred from our rule-based model. The error bars are the upper and lower 95% confidence limits.

Analyses using the simulated data suggested that the performance of the depletion risk index as a proxy to predict the extinction risk category of fishes is similar to the IUCN Red List criteria A (Figure 4.8). Using threshold depletion risk index values of 70, 55 and 40 to define "critically endangered", "endangered" and "vulnerable" categories, the probabilities of categorizing a species to a category that is lower than the prediction using the IUCN criterion E (based on probability of extinction from the population model) (Type I error) are 0.03, 0.14, 0.36 for the three threatened categories, respectively. The probabilities of assigning a higher threatened status of "critically endangered", "endangered" and "vulnerable" than those predicted from the IUCN criterion E (Type II error) are 0.33, 0.2, and 0.05, respectively. Comparing with the predictions based on the IUCN criterion A, the probability of over-estimating risk (Type II error) from predictions of the depletion risk index was significantly lower than the IUCN criterion A, while probability of under-estimation (Type I error) appeared slightly higher. The relatively higher Type I and Type II errors in predicting the vulnerable and critically endangered

categories, respectively, means that we might underestimate the risk of extirpation of less threatened taxa but overestimate the risk of those that seem to be highly threatened.

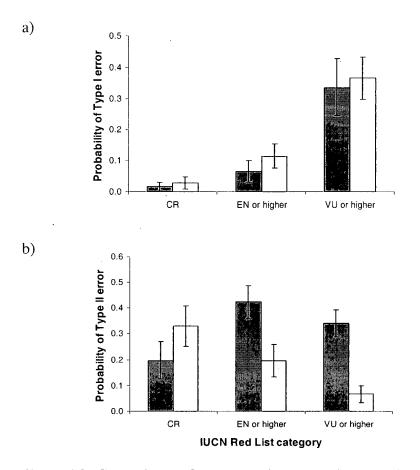


Figure 4.8. Comparisons of Type I and II errors between threatened status predicted by the IUCN Red List procedure (criterion E, solid bars) and the rule-based model (white bars). CR – critically endangered; EN – endangered; VU – vulnerable. The error bars represent the 95% confidence limits, assuming that errors are binomially distributed.

Results from the two extreme sets of criteria and rules that represented conservative and liberal interpretations of depletion risk (Tables 4.1, 4.2) showed that our assumed fuzzy sets and heuristic rules performed best (Figure 4.9). Type I errors did not differ significantly while the 'liberal scenario' performed poorly on Type II error, suggesting that predictions from our 'moderate' scenario were robust to the assumed rules and criteria.

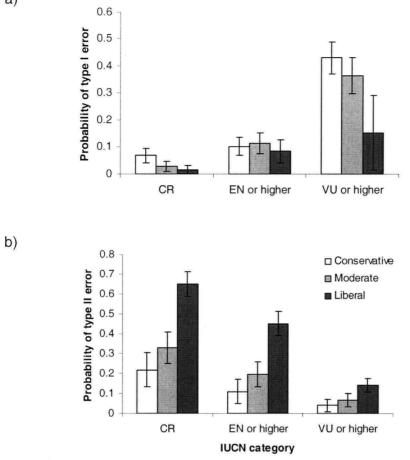


Figure 4.9. Probability of (a) under-estimating (type I) and (b) overestimating (type II) risk using the depletion risk index predicted from conservative (open bars), moderate (default, gray bars) and liberal (dark bars).

a)

4.4. Discussion

Our study shows that the estimated conservation status of marine fish resulting from fishing was consistent with that of other, mainly terrestrial, vertebrates. This is surprising in view of the frequently-expressed notion that marine fish populations should be inherently more resilient than other vertebrates (Hutchings 2001a). However, our findings are supported by abundant empirical evidence. For instance, population parameters such as the intrinsic rate of population increase, and population variability of marine fish were shown to be similar to value for other vertebrates (Fagan *et al.* 2001; Hutchings 2001b). Maximum reproductive potential, a population parameter that reflects the ability to withstand fishery-induced losses, is similar among fish groups, and similar to values among mammals of similar sizes (Myers et al. 1999), while the geographic range of many fish need not render them less vulnerable, given their propensity for range collapse when abundance declines (Pitcher 1997; Jennings et al. 1998; Sadovy 2001; Dulvy et al. 2003). Studies on fish stock recovery after depletions showed that, except for clupeids, recovery rate was generally low (Hutchings & Reynolds 2004). Although known contemporary marine extinction was rare; it might partly a result of poor detection ability (Dulvy et al. 2003).

The rapid increase in our estimated depletion risk over the last three decades coincides with the dramatic expansion of global fisheries (Pauly *et al.* 2002). Over the past few decades, fishes have lost their natural refuges (in the form of inaccessible habitats) owing to improved technology (e.g., GPS, sea-floor mapping, echo-acoustic; (Pauly *et al.* 2002, 2004). Bio-economic factors (e.g. diminishing return from depleted stocks) might not prevent extirpation (or even extinction) as, in some case, market value increased with resource rarity (Sadovy & Cheung 2003). Factors such as government subsidies to fisheries or the lack of alternative livelihood to fisher can maintain fishing effort even if profitability of fishing becomes low or negative (Khan *et al.* 2006; Pauly 2006). Thus depletion of populations across their geographic range should greatly increase their depletion risk.

Vulnerable species such as elasmobranchs and other large predatory fishes, particularly demersal fish should be prioritized for monitoring and conservation. The life

history of elasmobranchs (large-size, late maturation) renders them highly vulnerable to fishing (Stevens *et al.* 2000; Dulvy & Reynolds 2002; Baum *et al.* 2003), while large predatory fish are traditionally targeted by fishing (Pauly *et al.* 1998; Myers & Worm 2003), which contribute to the higher extinction risk in these groups (Hutchings & Reynolds 2004). Our results are also consistent with predictions from simulation modelling that suggest 20-50% of bony fish and 40-100% of sharks might be driven to extinction under a typical fishery removal rate i.e., 40% of the population size removed per year (Myers & Worm 2005). Our results parallel the estimation that 65% of exploited fish and invertebrate taxa have been collpased (>90% decline in reported catches) since 1950 (Worm *et al.* 2006).

Our global estimate for threatened marine species is uncertain. Firstly, because of the poor understanding of the dynamics of fish in small population sizes, the depletion risk index may not represent the 'true' risk of extinction (Dulvy et al. 2004). For instance, the extend of depsensation or allele effects at low population size in marine fishes is uncertain (Myers et al. 1995; Liermann & Hilborn 1997). Future studies on the dynamics of small population size are needed (Pitcher 1998; Dulvy et al. 2003). Secondly, the estimation was dependent on the assumed heuristic relationships and categorization criteria. Also, the structure of catch time-series might be confounded by non-fishery factors (i.e., error in the statistical recording system) and not accurately depict actual fishing yields. Statistical data uncertainties are particularly serious in tropical developing regions and reef fisheries where fishery monitoring was less effective but threats to their high biodiversity were acute (Johannes 1998). Many of the exploited species are not reported explicitly in the catch statistics and thus are excluded from our analysis. Thus our predictions may underestimate the threatened status in these regions. Moreover, indirect effects of fishing, e.g., habitat destruction (Kaiser et al. 2003), ecosystem effects (Jackson et al. 2001), or genetic effects (Law 2000), are not considered in our estimates. Other threats to biodiversity such as climate change (Roessig et al. 2004) were also not accounted for. These factors would likely increase our predicted extinction risk. On the other hand, our sensitivity analysis suggested that estimations from the assumed rules ('moderate' scenario) were robust and preformed best among the various scenarios.

Given the limited available data, accuracy of predictions from our model was similar to the widely applied IUCN Red List criteria.

This study suggested that exploited marine fishes are vulnerable to severe depletion by fishing and their risk of extinction should not be dismissed. Given the current problems of data limitations and the urgent need to increase coverage of extinction risk assessment of marine fishes (Reynolds *et al.* 2005), this study provides a way to roughly evaluate the scope of the threats using currently available data. Hopefully, this would attract attention and further researches on the depletion risk of exploited marine fishes.

Unsustainable fishing has caused extirpations and large historical depletions of abundance of marine fish (Myers & Worm 2003; 2005). Our results suggest these may likely to follow the path of the megafaunal extinction caused by human hunting if the current levels of fishing exploitations are not reduced (Alroy 2001; Pitcher 2001; Pauly *et al.* 2005). The alternative, obviously, is to fish less.

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5. EVALUATING THE STATUS OF EXPLOITED FISHES IN THE NORTHERN SOUTH CHINA SEA USING INTRINSIC VULNERABILITY AND SPATIALLY EXPLICIT CATCH-PER-UNIT-EFFORT DATA⁵

5.1. Introduction

The fishery resources of the northern South China Sea (NSCS) have been heavily exploited in the past and are now in decline (Lu & Ye 2001; Cheung & Pitcher 2006). The reported fishing power of the three major Chinese fishing provinces of Guangzhou, Guangxi and Hainan increased by almost 20 times from 1950 to 2000 (Figure 5.1). At the same time, the total catch landings from NSCS have increased 16 times, from 0.2 million tonnes in the 50s to 3.5 million tonnes in 2002 (Department of Fishery, Ministry of Agriculture, The People's Republic of China 1991, 1996, 2000). During this period, the total catch-per-unit-effort (CPUE) decreased by half. Moreover, the total demersal fishery resources in the NSCS have declined in abundance by about 75% from the unexploited level, a trend which is consistent in both the Gulf of Tonkin and the entire continental shelf of NSCS (Jia *et al.* 2004) (Figure 5.2). In fact, analyses that are based on China's national landing statistics could largely underestimate the true decline given the inaccuracy and known over-reporting in Chinese fisheries statistics (Pang and Pauly 2001; Watson & Pauly 2001).

^{5 5} A version of this chapter has been submitted for publication. Cheung, W. W. L. & Pitcher, T. J. Evaluating the Status of Exploited Taxa in the Northern South China Sea Using Intrinsic Vulnerability and Spatially Explicit Catchper-unit-effort Data. Fisheries Research. [in review].

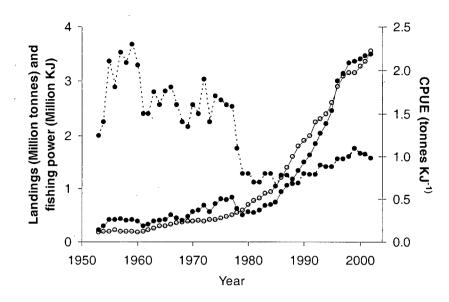


Figure 5.1 Change in landings (left axis, solid line, filled circle), fishing power (left axis, solid line, open circle) and CPUE (right axis, broken line, filled circle) of the three coastal Chinese provinces (Guangdong, Guangxi and Hainan) in the NSCS (Department of Fishery, Ministry of Agriculture, The People's Republic of China 1991, 1996, 2000; Qiu, Y. South China Sea Fisheries Institute, pers. comm.).

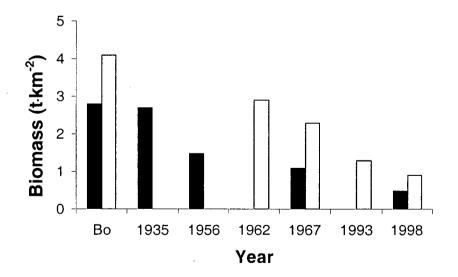


Figure 5.2 Estimated demersal fishery resources in the northern South China Sea. Total demersal biomass declined from the unexploited level (Bo) in Gulf of Tonkin (black bar) and the continental shelf in general (open bar) from the 1930s to 1990s.

Other sources of information such as local fishers' knowledge corroborate this decline of populations of exploited fisheries in the NSCS. For instance, collations of anecdotal fishers' knowledge indicate that a number of populations, particularly those with life history and ecology that make them vulnerable to exploitation, are in a severely depleted state (Sadovy & Cornish 2000; Sadovy & Cheung 2003; Cheung & Sadovy 2004). Given the continued increase in fishery exploitation in the NSCS, more fish populations can be expected to undergo decline and even extirpation in the future (Cheung & Pitcher 2006). Therefore, accurate evaluation of the current status of fisheries in the NSCS is needed in order to properly guide the adjustment of fishing exploitation in this region to non-destructive and more sustainable levels.

5.1.1. Data availability

Assessment of the current status of most exploited species in NSCS is difficult because of poor availability of data (Cheung & Pitcher 2006). Quantitative information such as time-series of abundance indices is virtually non-existent for the majority of exploited fish species. Chinese researchers conducted a number of independent fisheries surveys and assessments (Jia *et al.* 2004); however, most of these data are classified as 'national security documents' and therefore are unavailable for public use (Xiaping Jia, Director of the South China Sea Fisheries Institute, pers. comm.).

More consistent historical time-series data were collected from the NSCS by the Hong Kong government. The Agriculture and Fisheries Department (renamed as Agriculture, Fisheries and Conservation Department in 1998) in Hong Kong carried out catch and effort surveys with fishing vessels operating in NSCS during the 1970s and 1980s. The Hong Kong government's surveys focused on demersal trawlers that were registered in Hong Kong but were allowed to fish in most parts of NSCS, including the inshore Hong Kong waters and the continental shelf (Cheung & Sadovy 2004). These catch and effort data can help reveal the status of exploited fisheries in the NSCS.

Using CPUE data as an index of stock abundance has a number of limitations for evaluating the population status of exploited fisheries. In fisheries stock assessment,

$$B = \frac{C}{fq} = \frac{CPUE}{q}$$
 eq. 5.1

where B is stock abundance, C is catch, f is fishing effort and q is catchability coefficient (Hilborn & Walters 1992). It is often assumed that catchability is a constant, thus stock abundance is proportional to CPUE. However, CPUE may not represent the actual proportion of the fish populations because catchability of different fish species may vary according to stock size, time and space (Hilborn & Walters 1992; Walters 2003). For instance, in some shoaling fish species, population decline may lead to range collapse (Pitcher 1995; Mackinson et al. 1997). These fish may continue to maintain dense schools even the population abundance is reduced by fishing (Pitcher 1997). Thus catches can be maintained even when population size (and effort) decline, through an increase in catchability. Also, catch from fishers targeting fish aggregations or schools may be limited by the time to deplete an aggregations rather than the actual fish population size. This means that catch rate of fishers may not decrease despite the overall drop in the abundance of targeted fisheries (a term known as 'hyperstability') (Walters 2003). Moreover, non-random search for targeted species using accurate and advance fish tracking technology could maintain high catch rate when stock abundance declines and thus severely bias CPUE data (Walters & Martell 2004).

Fish population estimates from CPUE data are also sensitive to the underlying statistical assumptions of the analysis, particularly when the estimate is based on commercial fishing, wherein samplings were spatially non-random (Walters 2003). For instance, fishers may select fishing grounds that maximize their CPUE (Gillis 2003). Thus, if we assume that CPUE in unfished areas is equivalent to the average CPUE of fished areas, we may overestimate the true CPUE of the entire exploited population. On the other hand, assuming very low or zero CPUE for unfished areas could underestimate the true CPUE (i.e., 'hyperdepletion') (Walters 2003). Therefore, in order for CPUE data to accurately reflect actual fish population trends, it is important to find an objective way to determine a realistic potential CPUE in unfished areas.

5.1.2. Intrinsic vulnerability

Proper management of degraded systems such as the NSCS (see Chapter 1) requires understanding of the population status of a wide array of species. However, the

currently available CPUE data from NSCS are biased towards commercially important taxa. Therefore a method for estimating the status of fish populations that can extend the assessment to non-commercial species is needed.

Calculation of intrinsic vulnerability is one way to determine the status of fish populations that are not represented well in survey data (Cheung et al. 2005). Intrinsic vulnerability, defined as the inherent capacity of the species to respond to fishing, is correlated with life history traits such as body length, age at sexual maturation, longevity, etc. (Reynolds et al. 2001; Dulvy et al. 2003; Cheung et al. 2005). Intrinsic vulnerability can be expressed by an index that is predicted using a fuzzy logic expert system based on one or more of the following input parameters: maximum body length, age at sexual maturation, longevity, von Bertalanffy growth parameter K, natural mortality rate, fecundity (only low fecundity is considered), geographic range and a ranking on the type and strength of aggregation behaviour (Cheung et al. 2005; Chapter 2). These input data are relatively easy to obtain for most exploited species from the literature or an online database (e.g., FishBase; www.fishbase.org). The index of fish vulnerability can be applied to fishes from different areas and taxonomic groups and is positively correlated with rate of decline of marine populations. (Cheung et al 2005, Chapter 2). Here this relationship is applied to demersal fish populations in NSCS to evaluate the status of fish populations.

The major steps in this study are (1) evaluating the changes in relative abundance of 17 commercially important demersal fishes in the NSCS, and (2) testing the correlation between the intrinsic vulnerability index and fish population decline. If the correlation between vulnerability index and population decline is significant, then the intrinsic vulnerability index can be applied to evaluate the status of the rest of the exploited demersal fish populations in the region that do not have CPUE data. The possible contributions of fishing, environmental changes and non-fishing anthropogenic impacts (e.g., pollution, coastal development) to the observed changes in NSCS demersal fish populations are discussed.

5.2. Methods

Firstly, spatially explicit CPUE data of 17 commercially exploited demersal taxa in NSCS from 1973 to 1988 were compiled. The data were standardized to evaluate the time-series changes in relative catch rate during this period. Then, intrinsic vulnerabilities of these 17 taxa were estimated and the relationship with changes in CPUE was examined. The estimated vulnerability was then applied to extrapolate the population status of other taxa in the region.

5.2.1. CPUE data

The Hong Kong government conducted surveys between 1973 and 1988 to estimate the catch per unit effort (CPUE) of bottom trawlers (stern and pair trawlers) registered in Hong Kong that fished in the NSCS (Hong Kong Agriculture, Fisheries and Hong Kong Department or AFCD, unpublished data). Fishing effort data were obtained once per week by interviewing skippers to estimate the number of days fishing. These data were spatially agregated into spatial cells of 30 minutes latitude by 30 minutes longitude. Each cell fell within one of the seven major fishing zones in the NSCS (Figure 5.3). Data for the catch composition by weight were obtained from sales vouchers reported in the government wholesale market (Fish Marketing Organization or FMO). For a single trip in which more than one spatial cell were fished, the landed catch was split by the proportion of the total effort spent in each grid (AFCD, unpublished data). The original data existed in hard copy, so they were firstly transcribed into an electronic database for quantitative analysis.

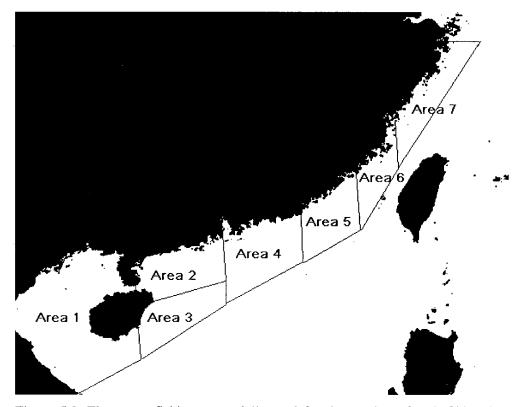


Figure 5.3. The seven fishing areas delineated for the northern South China Sea continental shelf.

Raw data from 17 commercially important demersal taxa, selected because they were well-represented in the landings of commercial trawlers, were compiled for further analyses (Table 5.1). They represented a wide range of different life-history characteristics (and thus intrinsic vulnerability), which facilitated the test of correlations between intrinsic vulnerability and rate of decline. Estimated distribution of fishing effort from the survey between 1973 and 1988 were plotted using ArcGIS 9.0.

Table 5.1. The 17 taxa reported in the catch and effort surveys conducted by the Hong Kong Agriculture and Fisheries Department* and their composite species(s). Only commercial species that are likely to be vulnerable to demersal trawl gears were included.

Reported taxon	Scientific name(s) of component species				
Yellow croaker	Larimichthys crocea				
Slate cod croaker	Protonibea diacanthus				
Other croakers	Sciaenids (except the above)				
Two-spotted red snapper	Lutjanus bohar				
Red snapper	Lutjanus argentimaculatus				
Golden threadfin bream	Nemipterus virgatus				
Flathead	Platycephalids				
Groupers	Epinephelus bruneus				
Scads	Alepes djedaba, Decapterus russelli				
Bigeyes	Priacanthus tayenus, P. marcracanthus				
Lizardfish	Synodontids				
Hairtail	Trichiurus lepterus, T. nanhaiensis				
White pomfret	Pampus argenteus				
Red goatfish	Upeneus molluccensis				
Melon seed	Psenopsis anomala				
Sharks	Hemiscylliids, carcharhinids				
Skates and rays	Daysatis akajei, D. kuhlii, Himantura gerrardi				

* Then the Agriculture, Fisheries and Conservation Department.

5.2.2. Interpolation of CPUE

Estimated CPUE data (measured as kg·day⁻¹·hp⁻¹·metre haul length⁻¹) of each of the 17 taxa from the Hong Kong survey were spatially and temporally interpolated. The fishing vessels that were sampled by the original survey had not fished in the entire study area. Thus, expected catch rate in the unfished areas remained unknown. However, fishing areas selected by the fishers were non-random as fishers might have targeted areas with high stock abundance. In this case, CPUE in unfished areas might be assumed to have very low abundance (e.g., CPUE = 0). On the other hand, it might be possible that area of high stock abundance were not fished because of the costs of fishing, market prices or accessibility of the fishing grounds. Therefore, CPUE in unfished areas might be assumed to have the same level of CPUE as the other fished areas (Walters 2003). However, the assumption of CPUE = 0 in unfished areas may result in underestimation of CPUE in the region while the latter assumption may lead to over-estimation. In fact, CPUE in an area may generally be similar to its immediate surrounding areas. CPUE in one year can also reflect the level of CPUE in preceding years in the same area. Therefore, spatial and temporal interpolation of CPUE from available data in the surrounding areas and successive years should provide better estimates of CPUE than the simple assumptions mentioned above.

It was assumed that CPUE in cells without data (i.e., not fished by the sampled fishing vessels) was dependent on (1) the historical occurrence of the taxa, (2) CPUE in the neighbouring cells and (3) CPUE in the same cell in different years. To decide on the appropriate CPUE in cells (Figure 5.4), the distribution range for each taxa was established from all the cells with positive CPUE in the time-series (1973-1988). If a cell fell within the historical range but was not fished in a particular year, its CPUE was assumed to be equal to the mean of its immediate surrounding cells in the same year (if at least two cells with positive CPUE existed). If the number of surrounding cells with positive CPUE was less than two, then the CPUE from the nearest succeeding year was included in the calculation. However, if the cell was not fished in any succeeding years and no fishing occurred in its surrounding cells either, its CPUE was assumed to be the average for this species in the entire fishing area. These procedures allow the use of all the available information in the dataset to extrapolate CPUE from fisheries-dependent catch and effort surveys.

I repeated the analysis by assuming that CPUE in all cells without data was equal to the average of cells with data at the same year only. The latter was to evaluate how alternative assumption in data treatment would affect the conclusions of this study.

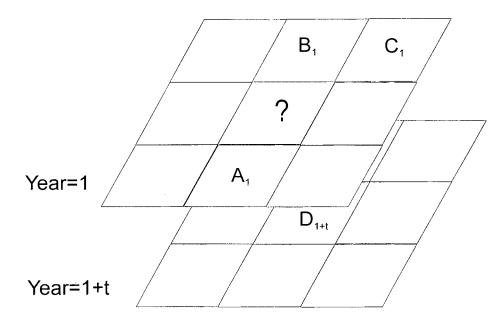


Figure 5.4. Diagram illustrating the interpolation of CPUE for cells without estimate of CPUE. For instance, assuming that the cell marked with '?' falls within the historical range of the taxa, but was not fished at year 1. If CPUE estimates are available for two or more of its immediate surrounding grids (e.g. A1, B1, C1), its CPUE is assumed to be the average of these surrounding cells. However, if CPUE estimate is available for only one of its immediate surrounding grids, CPUE estimate of the same grid and in the nearest succeeding year (D_{1+1}) is included in calculating the average CPUE. Otherwise, CPUE of the cell with '?' is assumed to be the average of the fishing area.

5.2.3. Standardization of CPUE

The original CPUE data were aggregated to reduce the effects of data errors in evaluating the changes of CPUE over time. The original survey method relied solely on the fishing locations reported by fishers in landing sites to estimate catch and effort on a spatial grid map. Thus, the spatial precision of the estimates was limited. Also, the CPUE of a taxon obtained from areas (cells) in close proximity and from the same year might belong to the same sub-population. If so, these data points might be spatially autocorrelated. Thus, the spatial CPUE data were aggregated into the seven fishing zones delineated by the original survey (Figure 5.3). This helps minimize the effects of spatial auto-correlation and low spatial resolution of the data (Agnew *et al.* 2000). The analysis was repeated using the non-aggregated data to evaluate the sensitivity of the results to this procedure. Also, inter-annual variability in catch rates resulting from random error might mask any trends in CPUE. Therefore, analysis of the CPUE data was repeated by aggregating the data into three time periods: (1) 1973-1978, (2) 1979-1983, (3) 1984-1988.

CPUE data were standardized across gear types, fishing areas and time using a generalized linear model (GLM) (Allen & Punsly 1984; Hilborn & Walters 1992; Venables & Ripley 1999; Agnew *et al.* 2000; Maunder 2001; Baum & Myers 2004). CPUE from two gear types were included: stern (otter) trawl and pair trawl. Fishing areas were included in the model to correct for the effects of localized stock depletion. The model included observation error only (Hilborn & Mangel 1997). Previous studies suggest that CPUE data are generally log-normally distributed (Hilborn & Walters 1992; Agnew *et al.* 2000; Maunder 2001). Thus, a log-normal GLM was employed. This assumption was evaluated by comparing the performance of the log-normal GLM with alternative models. The mathematical form of the GLM becomes:

$$\log(U_{i,j,k}) = \log(U_{111}) + \log(\alpha_i) + \log(\beta_j) + \log(\gamma_k) + \varepsilon \qquad \text{eq.5.2}$$

where $U_{i,j,k}$ is the observed CPUE at year or period *i*, by gear *j*, and at fishing area *k*. α , β and γ are effects due to change in stock abundance, difference in fishing gear, and difference in fishing areas, ε is the normally distributed observation error (because of the logarithmic transformation of the variables). The change in the abundance effect (α) between periods provides an estimate of the relative change in standardized CPUE (index of stock abundance) (Hilborn & Walters 1992). Confidence limits of the change in CPUE were obtained from the estimated standard errors of the GLM:

95% confidence intervals =
$$\log(\alpha \pm se \cdot 1.96)$$
 eq.5.3

For each dataset, the assumption that CPUE is log-normally distributed was tested by repeating the GLM analysis with Gaussian distribution. The use of a log-transformation

would be justified if the goodness-of-fit (R^2) from the log-normal GLM was higher than the alternative model.

5.2.4. Intrinsic vulnerability and rate of decline

Indices of intrinsic vulnerability of the 17 taxa were calculated based on their life history and ecology using a fuzzy expert system (Cheung *et al.* 2005; Chapter 2). The life history and ecology data included maximum length, age at first maturity, longevity, von Bertalanffy growth parameter \vec{K} , natural mortality rate, fecundity (only low fecundity, i.e. annual total fecundity ≤ 100 eggs or pups year⁻¹, was considered), geographic range, and an arbitrary score on the strength of their aggregation behaviour (see Chapter 2 for details). These data were obtained from published literature and FishBase (www.fishbase.org) (Table 5.2). The estimated index was in a scale of 1 to 100 (100 being maximum vulnerability). When the taxon was composed of more than one species, its intrinsic vulnerability was assumed to be the median of the vulnerabilities of species belonging to the taxon.

Correlation between CPUE changes and intrinsic vulnerability was tested. The decline in standardized CPUE of the 17 taxa between the mid 1970s and late 1980s was regressed against their estimated indices of intrinsic vulnerability. If the two factors were correlated, the intrinsic vulnerabilities could be used as a rough predictor of relative CPUE decline between fishes that were exploited at similar level.

When the correlation between CPUE changes and intrinsic vulnerability was significant, the relative status of demersal species in NSCS was extrapolated by their estimated index of vulnerability. As demersal trawling was the major fishing activity on the continental shelf of NSCS, it was assumed that demersal and benthopelagic species were subjected to similar level of fishing pressure. Thus, their overall changes in CPUE between the 1970s and 1980s were likely to follow similar relationship between the index of vulnerability and the CPUE changes of the 17 studied taxa. The list of demersal and benthopelagic fishes in NSCS and their life history data were obtained from FishBase (www.fishbase.org). Indices of intrinsic vulnerability were then estimated. Based on the relationships between the intrinsic vulnerability and CPUE change, the status of these fishes could then be predicted.

Taxon	L _{max} (cm)	T _m (year)	T _{max} (year)	K (year ⁻¹)	<i>M</i> (year ⁻¹)	Fecundity* (eggs year ⁻¹)	Spatial behaviour	Geograpahic range (km ⁻²)
Yellow croaker								_
Larimichthys crocea	80	2.3	11	0.27	-	-	80	5,217
Slate cod croaker								
Protonibea diacanthus	150	2	9	0.33	0.83	-	-	24,613
Other croakers								
Atrobucca nibe	45	4.4	19.1	0.15	-	-	-	21,548
Nibea semifasciata	24	-	-	-	-	-	-	5,303
Nibea soldado	60	-	-	-	-	-	-	16,730
Otolithes ruber	90	1.3	5.6	0.51	-	-	-	30,931
Pennahia anea	30	0.6	2.2	1.27	-	-	-	13,889
Pennahia macrocephalus	23	-	-	-	-	-	-	13,116
Two-spotted red snapper								
Lutjanus bohar	90	2	9	0.33	-	-	40	49,090
Golden threadfin bream								
Nemipterus virgatus	35	1.6	6	0.45	-	-	-	18,106
Flathead								
Platycephalus indicus	100	1.5	7	0.41	-	-	-	30,974
Groupers ¹								
Epinephelus bruneus	128	6.6	32	0.09	-	-	-	5,347
Scads								
Alepes djedaba	40	1.2	4.7	0.61	-	-	80	37,652
Decapterus russelli	45	1.1	4.4	0.65	-	50,905	90	35,363
Bigeyes								
Priacanthus tayenus	35	1.1	4.2	0.68	-	-	24	22,529
P. macracanthus	30	0.6	2.2	1.31	-	-	32	24,955

Table 5.2. Data on life history and ecology traits of the 16 taxa reported in the catch and effort survey. Details on each parameter were described in Chapter 2.

Table 5.2 Con't

Taxon	L _{max} (cm)	T _m (year)	T _{max} (year)	<i>K</i> (year ⁻¹)	M (year ⁻¹)	Fecundity	Spatial behaviour	Geograpahic range (km ⁻²)
Lizardfish								
Saurida tumbil	60	1.1	4.4	0.65	-	-	-	26,531
Saurida undosquamis	50	1.1	4.4	0.65	-	-	-	28,037
Synodus variegatus	40	1.7	6.6	0.43	-	-	-	47,761
Trachinocephalus myops	40	0.4	1.8	1.6	-	-	-`	54014
Red snapper								
Lutjanus argentimaculatus	150	3.2	15.2	0.19	· _ ·	-	6	49,979
Hairtail								
Trichiurus lepturus	58.9	1.7	7	0.167	-	-	30	85,613
Trichiurus nanhaiensis	60.2	-	-	0.207	-		-	-
White pomfret								
Pampus argenteus	60	2.8	12	0.24	-	-	95	17,844
Melon seed								
Psenopsis anomala	30	1.4	5.2	0.54	-	-	-	3,861
Sharks								
Chiloscyllium griseum	74	-	-	-	-	-	-	21,001
Chiloscyllium plagiosum	83	-	-	-	-	-	-	19,133
Chiloscyllium punctatum	104	-	-	-	-	-	-	22,629
Skates and rays								
Dasyatis akajei	200	3.3	17.1	0.17	-	10	-	7,544
Dasyatis kuhlii	70	1.4	6.2	0.46	-	-	-	32,146
Himantura gerrardi	200	3.3	17	0.17	-	2	-	18,378
Red goatfish								
Upeneus molluccensis	20	0.8	2.9	0.97	-	111,600	95	29,702

* Fecundity estimates are either not available or over 100 eggs year⁻¹ for most species without fecundity input. The fuzzy expert system does not consider fecundity of over 100 eggs year⁻¹ to have any effect on the intrinsic vulnerability (see Chapter 2).

5.3. Results

5.3.1. Fishing effort distribution

Distributions of fishing efforts of stern and pair trawlers changed from the 1970s to the 1980s (Figure 5.5). During the early 1970s, the effort of stern trawlers distributed mainly along the coast of Guangxi and southern Guangdong provinces. The effort distribution of pair trawlers was similar, but they spread further offshore and to the south around Hainan Island. Since then, effort distributions expanded along the coast. The effort of stern trawlers shifted to northeast in the late 1970s and early 1980s, while the effort of pair trawlers spread slightly eastward to the Taiwan Strait and southward to southern Hainan. Towards the later half of the 1980s, fishing effort of sterns trawlers moved backed to the south, which fished mostly around the Pearl River Estuary and the southwest of Hainan. Distribution of pair trawler efforts remained relatively stable with a slight shift to the south in the late 1980s.

5.3.2. Changes in CPUE

The GLM with time, fishing gears and fish areas as explanatory variables significantly explained the variations of the log-transformed CPUEs for all taxa. The median R^2 from the log-normal GLM of all the taxa was 0.47 (lower and upper quartiles = 0.45 and 0.52, respectively). The log-normal GLM performed considerably better (i.e., higher R^2) than the alternative model with Gaussian error. The median R^2 for the alternative model was only 0.33 (lower and upper quartiles = 0.25 and 0.44, respectively). This supported the use of log-normal transformation in the analysis. Thus, results from the log-normal GLM were used throughout this thesis.

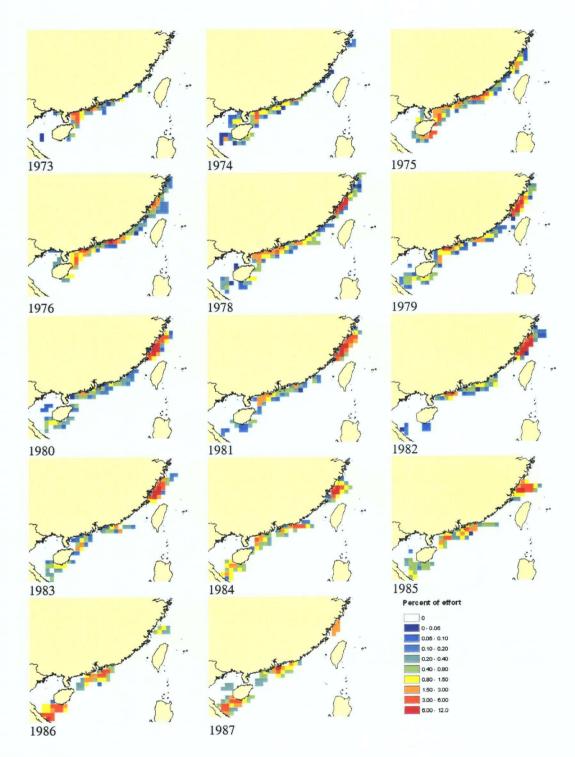


Figure 5.5a

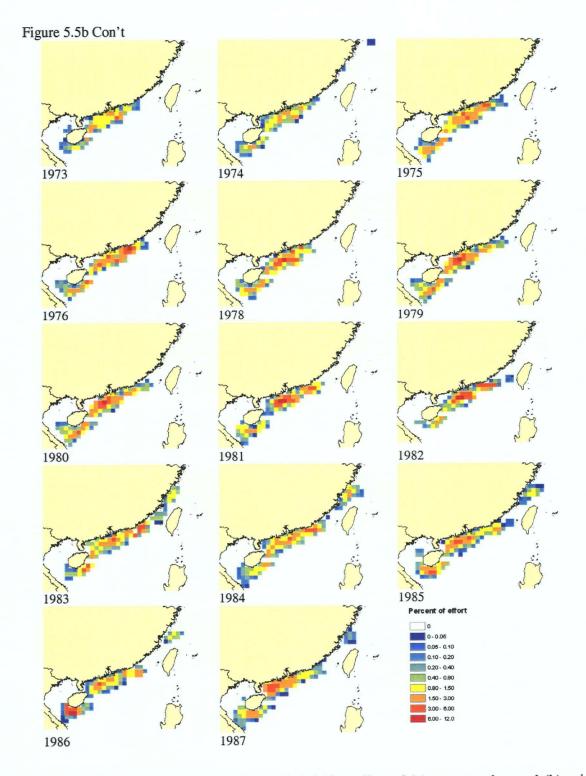


Figure 5.5 Percentage distribution of sampled fishing effort of (a) stern trawlers and (b) pair trawlers from the government survey from 1973 to 1987 (original data records for 1977 and 1988 are missing). The original data were obtained from the Hong Kong government fisheries survey (AFCD, unpublished data).

Among the 17 studied taxa, CPUE of 15 taxa declined by more than 70% on average from the mid 1970s to late 1980s, while the average decline was more than 80% (Figure 5.6a). Skates and rays (Rajidae and Dasyatidae) suffered the greatest decline (99%). Other taxa that showed declines over 85% included yellow croaker, red goatfish, red snapper, slate-cod croaker and sharks, while those with the least decline (<70%) included other croakers, bigeyes, golden threadfin bream and melon seed. Confidence intervals for the estimated declines were generally wide, with average 95% confidence intervals of +26% and -8% from the mean. The most uncertain estimates were other croakers, melon seed, golden threadfin and bigeyes, with the ranges between the upper and lower limits of over 60% (Figure 5.6). The decline of CPUE for all taxa could also be demonstrated from the time-series of standardized CPUE (Figure 5.7). When the standardized CPUE time-series of each of the 17 taxa were linearly regressed, significantly negative slopes were obtained for all cases. CPUE declined by 4% to 16% per year (8% on average) from 1973 to 1988.

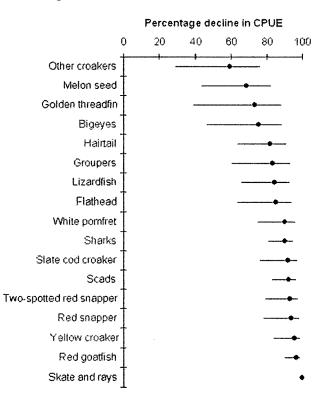


Figure 5.6. Average decline in CPUE of 17 commercially exploited taxa in NSCS from the mid-1970s to late 80s (black dots) estimated from spatially interpolated data. The solid lines mark the 95% confidence intervals.

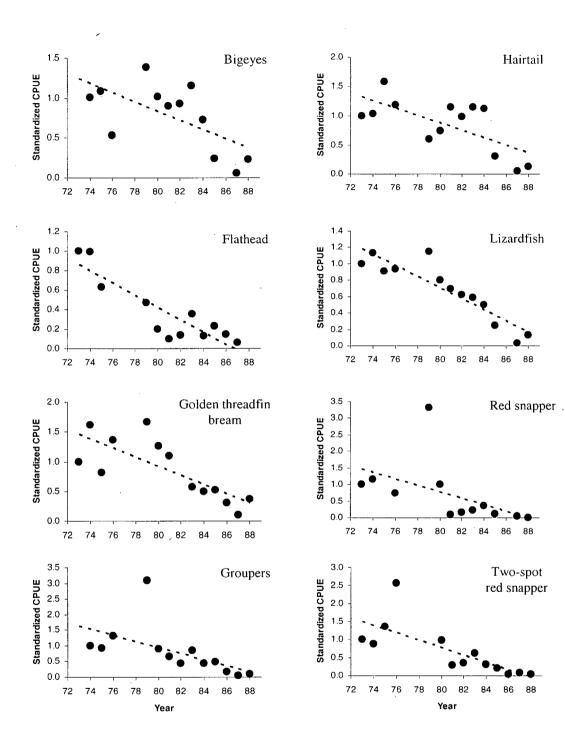
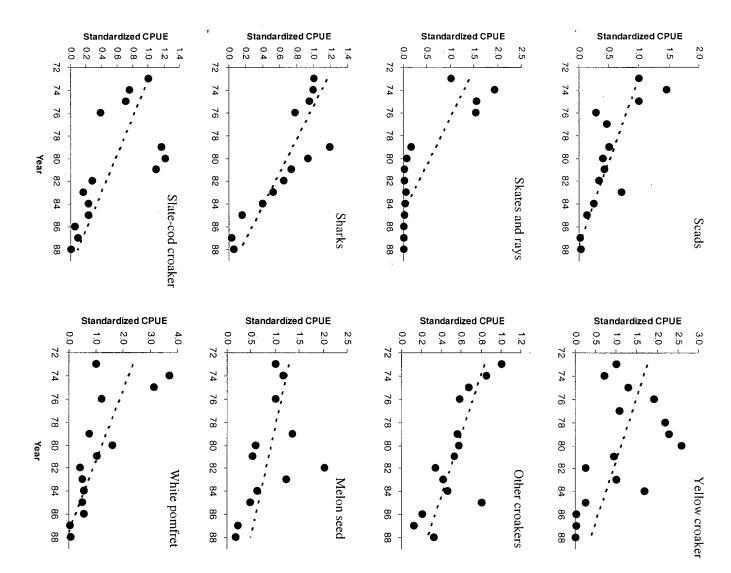


Figure 5.7.

Figure 5.7 con't.



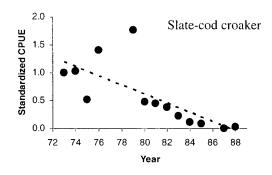


Figure 5.7. Standardized CPUE of demersal fish in the NSCS. Dotted line represents the result from linear regression of the time-series.

Estimated declines in CPUE of some taxa were sensitive to the assumptions of the spatial interpolation (Figure 5.4). When alternative statistical models and assumptions in spatial interpolations were used, the mean declines in CPUE varied by less than 30% for most groups, with the largest CPUE declines occurring in sharks, skates and rays, and slate-cod croaker. However, taxa with smaller declines in CPUE showed high sensitivity to model assumptions, particularly bigeyes, groupers, golden threadfin bream and melon seed (Figure 5.8).

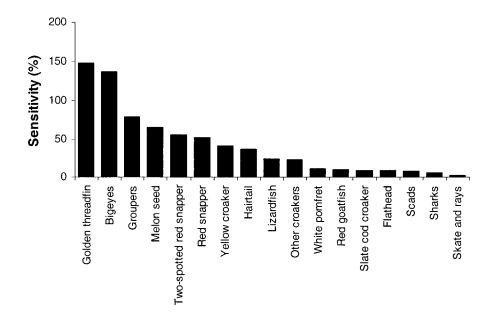


Figure 5.8. Sensitivity of the estimated CPUE decline between the early 1970s and late 1980s from different statistical assumptions in analyzing the spatial data. The sensitivity is represented by the difference between the maximum and minimum estimated change in CPUE.

5.3.3. Intrinsic vulnerability against CPUE changes

The index of intrinsic vulnerability of the 17 taxa ranged from 19 to 65 (most vulnerable = 90). Taxa with the highest vulnerability index were skates and rays, followed by red snapper, yellow croaker and slate-cod croaker. Taxa with the least vulnerability index included bigeyes, other croakers and melon seed. The index of vulnerability was significantly negatively correlated with CPUE change (log-transformed) between the early 1970s and late 1980s (Figure 5.9). Linear regression analysis showed that the indices of vulnerability explained about 50% (adjusted $R^2 = 0.501$) of the variations in CPUE between the 17 taxa (Table 5.3). The slope of the regression line was significantly negative at 95% confidence level (P = 0.001, Table 5.4). The skates and rays group showed the greatest decline among all taxa, but removing it from the analysis did not alter the significance of the relationship. Moreover, correlation between vulnerability and rate of decline continued to be significant when the original spatially disaggregated CPUE data (30' x 30' grids) without interpolation were used (P = 0.005).

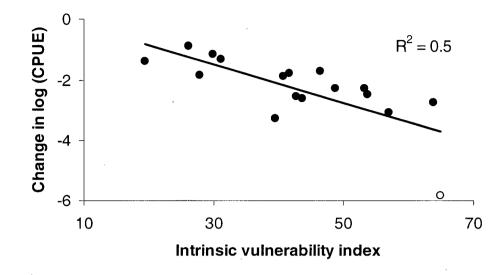


Figure 5.9. Linear regression analysis of change in CPUE (log) and the estimated index of intrinsic vulnerability ($R^2 = 0.5$, P = 0.001). Removal of the data point for skates and rays (open circle) does not affect the significance of the relationship (P = 0.002).

Table 5.3. Analysis of variance (ANOVA) with index of vulnerability and estimated CPUE change being the independent and dependent variables respectively. Df – degree of freedom.

Model	Sum of squares	Df	Mean square	F	Sig
Regression	10.987	1.	10.987	17.087	0.001**
Residual	9.645	15	0.634	-	-
Total	20.632	16	-	-	-

Table 5.4. Linear regression model between the index of intrinsic vulnerability and the estimated CPUE change (n = 17).

Factor	Coefficient	Standard error	t-value	P value	
Intercept	0.407	0.682	0.596	0.560	
Intrinsic vulnerability	-0.0629	0.015	-4.134	0.001**	

5.3.4. Intrinsic vulnerability of demersal and benthopelagic fish in NSCS

An index of intrinsic vulnerability of 176 species (belonging to 62 families) of the demersal and benthopelagic non reef-associated fishes were evaluated. Species with the highest index of vulnerability (= 90) included *Bahaba taipingensis* (Sciaenidae), *Lamiopsis temminckii* (Carcharhinidae), *Carcharhinus hemiodon* (Carcharhinidae), *Eusphyra blochii* (Sphyrnidae), *Hemipristis elongate* (Hemigaleidae) and *Muraenesox cinereus* (Muraenesocidae). Of the 22 species with a vulnerability index over 60, over 50% (n = 12) were elasmobranchs (sharks and rays), while the remaining belonged to the families Sciaenidae, Muraenesocidae, Serranidae, Cynoglossidae and Sparidae.

5.4. Discussion

This study showed that CPUE of the majority of the 17 studied taxa declined greatly in 15 years in the NSCS. Three possible reasons that could explain the declines include the following: (1) increased mortality from fishing, (2) environmental changes, (3) observation error and the non-proportionality of CPUE to abundance. The first two possibilities assume that CPUE is proportional to abundance and the results would then indicate a genuine decline in populations. The third explanation is dependent on the validity of the CPUE assumption as discussed above.

5.4.1. Increased fishing mortality

During the period of 1973 to 1988, nominal fishing effort and fishing power in the region increased 13- and 7-fold, respectively (Department of Fishery, Ministry of Agriculture, The People's Republic of China 1991, 1996, 2000). With improvements in fishing power and technology, fishing extended to most of the area of the NSCS shelf before the 80s. Fishing mortalities of commercially valuable species in the 80s and 90s were estimated to be very high, with exploitation rates (F/Z) ranging from 0.5 to 0.7 for major commercial taxa (Jia *et al.* 2004). At the same time, total demersal biomass in NSCS declined by over 50% from the 60s to the 90s, which agrees with the estimated declines for major demersal groups in this study.

The estimated declines in CPUE also agree well with other estimates on local and global declines in fish abundance. The South China Sea Fisheries Institute (SCSFI) conducted trawl surveys in the Gulf of Tonkin - the south-western part of the NSCS - in 1962 and the 1990s. Estimated density of major commercial species, including the 17 taxa in this study, generally declined by more than 80% during this period⁶. Most species with relatively more vulnerable life history such as sharks and rays, slate-cod, yellow croaker and red snapper, had the greatest declines and species composition became dominated by less vulnerable species (see Chapter 6 for comparisons between possible ecosystem structure in NSCS between the 1970s and 2000s). These species generally have larger body size, later maturation or higher longevity.

Particularly, the collapse of the yellow croaker (*Larimichthys crocea*) has been well documented. It was one of the most important targeted species in China (including Hong Kong, Macau and Taiwan) between the 1950s and early 1980s. Using data independent from the present study, yellow croaker catches from China dropped by 99% from the 1970s to 1990s (Liu & Sadovy, unpublished data), a value that matches the decline in CPUE from this study. Yellow croaker that is currently sold in the market is mostly cultured while the wild-caught yellow croaker has become an expensive delicacy (Liu & Sadovy, unpublished data).

The CPUE decline of red goatfish (*Upeneus moluccensis*) was larger than expected (96%) considering its relatively low intrinsic vulnerability (= 39). This species mainly inhabits coastal muddy substrate where trawling effort is concentrated. Its benthic nature might also make it more vulnerable to demersal trawl gear. These factors were not considered in calculating the index of intrinsic vulnerability and might be a reason for the discrepancy between the observed decline rate and those predicted by the intrinsic vulnerability index.

Declines of vulnerable taxa in NSCS agree with the estimates for average global decline of large predatory fish (Christensen *et al.* 2003; Myers & Worm 2003). Global populations of large predators such as large sharks, skates and rays and large tuna were suggested to have declined at an average rate of 80% in 15 years as a result of over-

⁶ Data from the surveys were classified by the Chinese authorities and thus the exact figures could not be cited in this study (Prof. Jia Xiaping, Director of the South China Sea Fisheries Institute, pers. com.).

exploitation (Myers & Worm 2003). Although validity of the estimated declines to the studied taxa has been contested and alternative estimates yield more conservative declines (Sibert *et al.* 2006), the estimates for the adult populations of these large predators are still dramatic. Also, another study estimated that biomass of high-trophic level fishes in the North Atlantic had declined by two-third from 1950 to 1999. Declines of major demersal fishes that are largely predatory species in NSCS (80-99% in 15 years) fall in the upper extreme of the range of values from these studies.

Further support on the effects of fishing was obtained from ecosystem simulation modelling (Chapter 7). In Chapter 7, changes of NSCS from the early 70s to late 80s were simulated using observed fishing effort changes. By comparing the changes in abundance of ecosystem groups with observed CPUE time-series, the results suggested that fishing alone could cause the observed decline of abundance of exploited fish. The evidence presented above suggests that fishing is likely to be the major factor leading to the decline in CPUE.

5.4.2. Environmental changes

Natural and human-induced environmental changes may also contribute to the decline in resource abundance. These included changes in primary productivity induced naturally by climate variations, or anthropogenically through eutrophication from pollutions, habitat damage and destruction from coastal development and uses of destructive fishing gear (e.g., bottom trawling, blast fishing). For instance, Qiu *et al.* (unpublished manuscript) showed that catches of several commercial taxa in NSCS in the past five decades correlated with climate and environmental variables such as monsoon strength, sea surface salinity, and precipitation, besides fishing. However, taxa that had strong correlations between their catches and environmental factors were mainly small pelagic fish and invertebrates which were not included in this study (Qiu *et al.* unpublished manuscript). Given the general decadal decline in fishery resources in NSCS and commercial taxa in the Gulf of Tonkin, natural environmental fluctuations are likely to be secondary compared to the direct and indirect effects of fishing. The extent to which human-induced environmental changes contributed to the declines has not been quantified. In future studies, proxies for the degree of coastal development or habitat

damage may be included as factors in the analysis to evaluate their relative contributions to the change in CPUE.

5.4.3. Observation error and the non-proportionality of CPUE to abundance

The original survey that collected the catch and effort data was interview-based and fishery-dependent, thus considerable errors were inherent in the CPUE data. Firstly, the survey only covered a sub-set of fishing boats in the region. Fishing performance might differ between fishing boats and skippers. Thus sampling bias may have skewed the estimated change in CPUE. For instance, if fishing boats that performed relatively better (e.g., more experienced skipper, boats with better equipment) were included in interviews during the earlier period, and poorer performing boats in the latter period, the decline in CPUE might be over-estimated. A possible way to diagnose this error is to look at the distribution of reported landings among boats fishing within the same cell and compare the variance between years. Systematic changes in variance structure between years may suggest biases in the standardized CPUE. Since the original CPUE data only included aggregated records from the surveyed skippers or boats, such validation exercise was not possible in this study. Nevertheless, the overall strong trend of CPUE declines shown in this study should not be greatly affected by such uncertainty. Also, the estimated CPUE for different taxa were subjected to similar biases, thus the validity of comparisons between taxa should not be greatly compromised, although the exact values of decline rates for individual taxon should be taken with a grain of salt.

Errors may also have resulted from the spatial interpolation of the CPUE data. Spatial CPUE data depended on where the sampled commercial fishing boats fished, which were non-randomly distributed and had changed during the survey periods. Thus estimating time-series CPUE depended strongly on the assumptions of CPUE in unfished cells. Here, unfished spatial cell was assumed to have similar CPUE as its surrounding cell, and the same area in the next consecutive years. Commonly-used quantitative fishing effort dynamic models such as the ideal free distribution model (Gillis 2003) or the gravity model (Caddy 1975) predict that cells with similar CPUE would be fished at similar rate given similar fishing cost. Thus, it was implicitly assumed in this study that incomplete coverage of all fishing boats in the sample resulted in the absence of data in those cells. As such, cells without CPUE data were given an average CPUE from the surrounding cells or proceeding years. On the other hand, it was possible that the cell with no data had low potential CPUE (perceived by the fishers) in that area and thus were uneconomical for the fishers to fish). This was especially likely when fishing led to range collapse following depletion (Pitcher 1995; Pitcher 1997). However, this assumption may increase the chance of over-estimating the decline in CPUE (i.e., hyper-depletion). Repeating the analysis using alternative assumptions in spatial interpolation suggested that estimated declines of vulnerable species were consistent, while the less vulnerable species were more sensitive to assumptions on spatial interpolation. Therefore, the large declines of vulnerable taxa estimated in this study are based on robust estimates.

Changes in abundance may not be proportional to CPUE. Catchability is likely to increase with improved fishing technology, better boats and experience (Hilborn & Walters 1992). Thus, CPUE may appear to be stable when stock abundance declines. However, since this analysis did not correct for such changes in catchability, the estimated decline in CPUE may actually underestimate the declines in abundance.Overall, although the aforementioned errors may bias the CPUE estimates, they were unlikely to solely explain the strong declines in CPUE obtained from this study. Over-exploitation should be a major reason that explains the declines in CPUE of the 17 taxa.

5.4.4. Status of fishery resources in the NSCS

This study showed that the abundance of traditional food fishes in the NSCS has been severely over-exploited with the abundance index of major food fishes declining by about 80% in slightly over a decade. As fishing effort continued to expand from the 80s to now, abundance is likely to decrease further from the 1980s' level. Large predators such as sharks and rays suffered the most in abundance decline. These agreed with the qualitative descriptions from interviewing fishers in Hong Kong (Cheung & Sadovy 2004), and quantitative results from comparing ecosystem structure between the 70s and 2000s (Chapter 6). This also confirms the analysis of Pang & Pauly (2001).

The rate of decline of the exploited fishes in the NSCS is also consistent with findings elsewhere in the world. Meta-analysis of global declines in predatory fishes (e.g., sharks and tunas) revealed a rate of decline of about 80% within 15 years of exploitation

(Myers & Worm 2003) – an estimate close to the findings here. Moreover, elasmobranchs had previously been shown to be highly vulnerable to exploitation as a result of their life history and ecology (Dulvy *et al.* 2000; Stevens *et al.* 2000). In fact, this analysis suggested that population of skates and rays might have collapsed during the study period and it is highly likely that the populations had little recovery over the past two decades. During the latest survey by the South China Sea Fisheries Institute, elasmobranchs were rarely caught in inshore waters (less than 40 m deep), while the overall catch rate in the 1990s had declined by over 80% comparing to survey conducted in the 1960s (Jia *et al.* 2004).

Using the index of intrinsic vulnerability as a predictor of CPUE decline suggests that other large predatory species may have been depleted at a similar rate. The most vulnerable fish families, as shown from the index of vulnerability, include groupers, large croakers and elasmobranchs among others. These taxa were well represented in fishery catch. Among these groups, some highly vulnerable species such as the Chinese bahaba had already been extirpated or severely depleted (Sadovy & Cheung 2003). Given similarly high fishing pressure on all these species, their status may be similar to the Chinese bahaba. If population status of these vulnerable taxa does parallel the status of the bahaba, further conservation and research efforts from local authorities and the international communities should be dedicated to the NSCS region.

The large decline in demersal fish assemblages should have resulted in considerable changes in ecosystem. In fact, such changes have already been observed along the coast of the NSCS. For instance, the Hong Kong marine ecosystem changed from being dominated with long-lived, *K* selected species to one with mostly small pelagics and benthic invertebrates that have fast turn-over rate (Pitcher *et al.* 2002a; Pitcher *et al.* 2002b; Buchary *et al.* 2003; Cheung & Sadovy 2004). Such changes do not only dissipate direct economic benefits to the society (Chapter 8) but may also adversely affect ecosystem functions (Worm *et al.* 2006). Changes of the NSCS ecosystem between the 1970s and 2000s are evaluated in Chapter 6 of this thesis.

Despite the high vulnerability and the potential conservation concerns of the exploited species, fishery and biological information on these species were insufficient. Catch of almost all of these species were not reported separately as the data are

aggregated into groups. The problem was amplified by the inaccuracy of landing statistics in recent decades (Watson & Pauly 2001). Moreover, fishery and biological studies focused mainly on commercially important species while knowledge on more vulnerable, although less economically important, species was scare. Thus, more resources should be given to conserve and better understand and monitor them. The intrinsic vulnerable index can be used as one of the tool to identify key taxa for conservation and research. However, improved monitoring and more accurate fisheries statistics are still essential for effective management of fisheries resources

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6. ECOSYSTEM MODELLING OF THE NORTHERN SOUTH CHINA SEA FOR THE 1970S AND 2000S

6.1 Introduction

The northern shelf of the South China Sea (NSCS) is a tropical ecosystem with a very diverse fauna and flora (Morton & Blackmore 2001). Over 900 species of fishes (Ni & Kwok 1999), at least five species of marine turtles (Marque, 1990), 8 species of marine mammals (Jefferson *et al.* 1993) and hundreds of invertebrates (Jia *et al.* 2004) have been recorded from the area. The NSCS also features diverse habitats including coral reefs, estuaries, mangroves and seagrass beds (Morton & Blackmore 2001). The NSCS ecosystem provides important fishery resources which are exploited mainly by trawls (demersal, pelagic and shrimp), gillnets, hook and line, purse seine and other fishing gears such as traps. The continental shelf (i.e., areas less than 200 m depth), ranging from 106°53'-119°48' E to 17°10'-25°52' N, falls largely within the Exclusive Economic Zone of the People's Republic of China (PRC), but Vietnam also shares part of the Gulf of Tonkin. This study focuses mainly on the shelf within the Chinese EEZ (Figure 6.1).

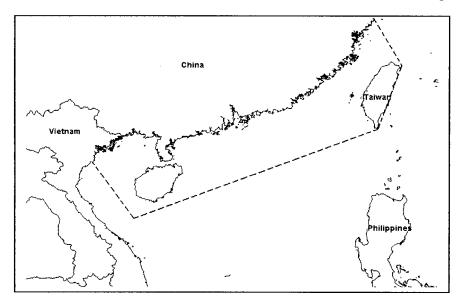


Figure 6.1. Map of the northern South China Sea, emphasizing the study area (from the coast to the broken line). As fishers from the PRC and Vietnam traditionally fish in the Gulf of Tonkin, the PRC and Vietnam governments agreed to establish common fishing zone in the Gulf of Tonkin, at least for a limited period (Vietnam-China Tonkin Gulf Fishing Co-operation Agreement).

Over the past five decades, a dramatic expansion of the fishing fleets, accompanied by mechanization and other technological advancements, has resulted in over-exploitation of fisheries resources (Shindo 1973; Pang & Pauly 2001; Cheung & Sadovy 2004). Following an over 8-fold increase in fishing effort from 1970 to 2000 (Department of Fishery Ministry of Agriculture, The People's Republic of China 1996, 2000), total landings from Chinese fishing fleets in the regions increased from 570,000 to 3,400,000 tonnes. On the other hand, catch-per-unit-effort (CPUE - a rough index of resource abundance) dropped by more than 70% from 1986 to 1998 (Lu & Ye 2001). If over-reporting of landings by China is considered (Watson & Pauly 2001), the decline in catch rates becomes even stronger.

Most traditional large-sized food fish have been depleted and catches are now dominated by small-sized, high turnover rate species (Cheung & Sadovy 2004; Jia *et al.* 2004). In Chapter 5 of this thesis, I found that the CPUE of 17 commercial demersal taxa in the NSCS declined by over 70% from the early 1970s to the late 1980s. In fact, numerous species with high intrinsic vulnerability to exploitation have probably been extirpated locally or regionally by fishing. For instance, the Chinese bahaba (*Bahaba taipingensis*, Sciaenidae), endemic to the coast of China, is nearly extinct (locally and globally) as a result of over-exploitation (Sadovy & Cheung 2003). The previously abundant Red grouper (*Epinephelus akaara*, Serranidae) and some other large reefassociated fishes in Hong Kong have disappeared in commercial catches (Sadovy & Cornish 2000). Non-target species such as skates and rays have also been largely depleted, especially in the heavily fished coastal areas (Sadovy & Cornish 2000; Jia *et al.* 2004). Over-exploitation and extirpation of these species have altered the ecosystem structure in the NSCS. Such ecosystem changes raise serious fishery management and biodiversity conservation concerns.

To properly manage the fisheries resources, restore the ecosystem and conserve the threatened species in the NSCS, it is important to understand the ecosystem effects of fishing (e.g., trophic interactions, bycatch and habitat destruction) (Botsford *et al.* 1997; Pitcher & Pauly 1998; Pitcher 2001; Kaiser *et al.* 2003). Ecosystem modelling is a useful tool for such purposes (Cochrane 2002). It can generate alternative hypotheses about ecosystem structure, and on the interactions among biological groups and with the

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fisheries (Trites *et al.* 1999; Butterworth 2000; Christensen & Walters 2004a). Particularly, comparing models of the past and present ecosystem can reveal changes in ecosystem structure and dynamics, and help diagnose management problems (Buchary *et al.* 2003; Pitcher 2004; Bundy 2005; Pitcher *et al.* 2005). In addition, dynamic ecosystem simulations allow explorations of the effects of fishing, environmental changes, and fishery management policies (Walters *et al.* 1997; Cochrane 2002; Christensen & Walters 2004a). Such models can identify important ecological indicators and critical information gaps for efficient use of limited resources for ecological monitoring and field studies (Walters 2000; Walters *et al.* 2000; Cochrane 2002b; Walters & Martell 2004; Cheung & Pitcher 2006).

Ecopath with Ecosim was used as the modeling approach in this study (Polovina 1984; Pauly *et al.* 2000; Christensen & Walters 2004). Ecopath is a steady-state, massbalance model which can be used to describe a snap-shot of the whole ecosystem at a particular time period. Species, usually those with similar biology and ecology, are aggregated into functional groups to reduce the number of modelled units. The model is governed by the mass-balance principle which is based on two basic equations. The first one ensures balance between production, consumption, predation, fishery, migrations and other mortalities among functional groups:

$$(P/B)_i \cdot B_i \cdot (1 - EE_i) - B_i \cdot (Q/B)_i \cdot DC_{ii} - Y_i - E_i - BA_i = 0$$
 eq. 6.1

The second equation ensures balance between consumption, production and respiration within a group:

$$Q_i = P_i + R_i + GE_i \cdot Q_i \qquad \text{eq. 6.2}$$

where $(P/B)_i$ is the production to biomass ratio; B_i the total biomass; EE_i the ecotrophic efficiency (1- EE_i represents mortality other than predation and fishing); Y_i the total catch; E_i the net migration; BA_i the biomass accumulation of functional group i; $(Q/B)_j$ are consumption to biomass ratio for predator groups j; DC_{ji} is the proportion of group i in the diet of predator groups j; R is respiration while GE is the proportion of unassimilated food (Christensen & Walters 2004). The model maintains mass-balance by solving equations 6.1 and 6.2 for all groups simultaneously. Thus any of the four basic input parameters (B, P/B, Q/B, EE) in each group has to be estimated to ensure mass-balance. Since it is difficult to measure EE empirically, it is usually estimated through the mass-balance process when other input parameters are available. In the case where data for B, P/B or Q/B are unavailable, EE is often assumed to be 0.95 in a heavy exploited ecosystem (Christensen *et al.* 2004).

Ecosystem models of a number of sub-systems of the NSCS have been built. These include models of Hong Kong waters (Buchary *et al.* 2003; Cheung & Sadovy 2004), and coastal waters of the NSCS (10-50 m) between Cambodia and China (Pauly & Christensen 1995b). All of these studies used Ecopath with Ecosim as the modeling platform. Attempt to model the entire NSCS ecosystem have not previously been undertaken.

In this chapter, I attempt to describe the past and present status of the NSCS ecosystem using a mass-balance modelling approach (Ecopath with Ecosim) (Christensen & Walters 2004). Models of the early 1970s and 2000s were constructed based on published literature, unpublished reports from government surveys and global databases. By comparing the structure and dynamics of the past and present systems, I evaluated the ecosystem changes over the past three decades. Parameter uncertainty was addressed through the 'pedigree' of the model, and analyses of its sensitivity.

6.2 Methods

6.2.1. Model structure and parameterization

Using Ecopath, two ecosystem models of the NSCS representing the status in the early 1970s and 2000s (hereafter called the 1970s and 2000s models) were constructed. In the 1970s and 2000s NSCS models, species were aggregated based on their commercial importance, body size, ecology, and the available data. Each model had 38 functional groups composed of 2 primary producers, 10 invertebrates, 21 fishes, 2 marine mammals, 1 marine turtle and 1 seabird groups (Table 6.1). The 8 commercially-important functional groups of fishes included threadfin breams (Nemipteridae), hairtails

(Trichiuridae), pomfrets (Stromateidae), lizardfishes (Synodontidae), groupers (Serranidae), snappers (Lutjanidae), croakers (Sciaenidae), and melon seed (Centrolophidae). Other species were aggregated by their maximum body size (i.e., small \leq 30 cm TL and large > 30 cm TL) and ecology (demersal, pelagic or benthopelagic). To represent the difference in ecology between juvenile and adult stages, some groups with longer life-span were split into juvenile and adult stanzas using the multi-stanza routine (Christensen et al. 2004). These groups included: hairtail, large croakers (> 30 cm TL), large demersal fish (> 30 cm TL) and large pelagic fishes (> 30 cm TL).

Table 6.1. Functional groups and their basic parameters used in the Northern South China Sea ecosystem models for (a) the 1970s and (b) the 2000s states. Values in parentheses were estimated by the model.

Group no.	Functional group	В	P/B	Q/B	EE
1	Phytoplankton	323	399	-	(0.035)
2	Benthic producer	153	11.89	-	(0.020)
· 3	Zooplankton	33.8	32	192	(0.052)
4	Jellyfish	(0.146)	5.00	20.0	0.950
5	Polychaetes	(3.421)	6.75	22.5	0.950
6	Echinoderms	3.065	1.20	3.58	(0.398)
7	Benthic crustaceans	2.649	5.65	26.9	(0.624)
8	Non-ceph molluscs	13.747	3.00	7.00	(0.383)
9	Sessile/other invertebrates	3.114	1.00	9.00	(0.845)
10	Shrimps	(0.422)	5.40	28.9	0.950
11	Crabs	(0.731)	3.00	12.0	0.950
12	Cephalopods	(0.465)	3.10	8.00	0.500
13	Threadfin bream (nemipterids)	1.04	0.74	8.10	(0.469)
14	Bigeyes (priacanthids)	0.318	1.21	11.3	(0.328)
15	Lizard fish (synodontids)	0.30	2.30	5.41	(0.241)
16	Juvenile Hairtail (trichiurids)	0.034	2.30	13.41	(0.329)
17	Adult hairtail (trichiurids)	0.0426	1.50	6.21	(0.327)
18	Pomfret (stromateids)	(0.065)	1.30	6.38	0.950
19	Snappers	(0.014)	1.34	8.98	0.950
20	Adult groupers	0.040	0.85	6.10	(0.375)
21	Croakers (≤ 30 cm)	0.289	2.36	11.28	(0.784)
22	Juvenile large croakers	0.0425	2.36	15.65	(0.913)
23	Croakers (> 30 cm)	0.095	1.43	6.23	(0.541)
24	Demesral fish (≤ 30 cm)	(1.541)	2.70	13.03	0.950
25	Juvenile demersal fish (> 30 cm)	0.112	2.60	15.46	(0.599)
26	Adult demersal fish (>30 cm)	0.195	1.44	6.21	(0.355)
27	Benthopelagic fish	(0.470)	3.00	15.0	0.950
28	Melon seed	0.114	2.24	24.7	(0.964)
29	Pelagic fish ($\leq 30 \text{ cm}$)	(1.050)	2.87	12.22	0.950
30	Juvenile large pelagic fish	0.118	2.87	. 14.37	(0.62)
31	Pelagic fish (> 30 cm)	0.158	0.90	6.28	(0.283)
32	Demersal sharks and rays	0.04	1.26	6.30	(0.364)
33	Pelagic sharks and rays	(0.028)	0.39	1.95	0.500
34	Seabirds	0.0022	0.06	67.76	(0.005)
35	Pinnipeds	0.0046	0.045	14.77	(0.679)
36	Other mammals	0.0158	0.112	10.52	(0.068)
37	Marine turtles	0.0002	0.100	3.50	(0.503)
38	Detritus	100	-	-	(0.017)

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(a) Basic parameters of the 1970s NSCS model

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(b)	Basic	parameters of	f the	2000s	NSCS	model	
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Group no.	Functional group	В	P/B	Q/B	EE
1	Phytoplankton	323	398		(0.010)
2	Benthic producer	153	11.89		(0.010)
3	Zooplankton	9.0	32.0	192	(0.306)
4	Jellyfish	1.53	5.00	20.0	(0.520)
5	Polychaetes	2.24	6.75	22.5	(0.673)
6	Echinoderms	1.98	1.20	3.58	(0.444)
7	Benthic crustaceans	1.43	5.65	26.9	(0.617)
8	Non-ceph molluscs	2.68	3.50	11.7	(0.951)
9	Sessile/other invertebrates	2.61	1.00	9.00	(0.575)
10	Shrimps	(0.194)	7.60	28.94	(0.950)
11	Crabs	(0.368)	3.00	12.0	(0.950)
12	Cephalopods	0.68	3.10	8.00	(0.393)
13	Threadfin bream (nemipterids)	0.26	3.08	15.4	(0.847)
14	Bigeyes (priacanthids)	0.13	3.33	11.3	(0.550)
15	Lizard fish (synodontids)	0.032	1.60	5.407	(0.658)
16	Juvenile Hairtail (trichiurids)	0.015	3.08	14.894	(0.749)
17	Adult hairtail (trichiurids)	0.012	1.47	6.207	(0.545)
18	Pomfret (stromateids)	0.108	3.03	(15.15)	0.950
19	Snappers	(0.0013)	1.75	8.984	0.950
20	Adult groupers	(0.0064)	1.75	6.10	0.950
. 21	Croakers (≤ 30 cm)	0.07	3.30	11.276	(0.958)
22	Juvenile large croakers	0.04	3.30	16.366	(0.564)
23	Croakers (> 30 cm)	0.0094	1.43	6.232	(0.587)
24	Demesral fish (≤ 30 cm)	(0.316)	4.70	23.5	0.950
25	Juvenile demersal fish (> 30 cm)	0.143	3.50	16.144	(0.722)
26	Adult demersal fish (>30 cm)	0.021	2.10	6.207	(0.747)
27	Benthopelagic fish	0.922	3.08	15.42	(0.479)
28	Melon seed	0.070	2.41	24.0	(0.994)
29	Pelagic fish (≤ 30 cm)	1.772	4.26	17.04	(0.740)
30	Juvenile large pelagic fish	0.289	4.26	16.12	(0.622)
31	Pelagic fish (> 30 cm)	0.079	1.40	6.27	(0.759)
32	Demersal sharks and rays	0.001	1.20	6	(0.867)
33	Pelagic sharks and rays	(0.0011)	0.68	3.4	0.950
34	Seabirds	0.0022	0.06	67.759	(0.046)
35	Pinnipeds	0.0046	0.045	14.768	(0.290)
36	Other mammals	0.0158	0.112	10.523	(0.034)
37	Marine turtles	0.0002	0.10	3.50	(0.300)
38	Detritus	100	-	-	(0.005)

Basic model input parameters were estimated from government surveys, published literature, empirical equations and global databases (see Table 6.1 and Appendix 6.1 for detailed descriptions of parameter estimations). Biomasses of most commercially important groups in the 2000s model were estimated based on trawl and acoustic surveys conducted by the South China Sea Fisheries Research Institute (Jia *et al.* 2004). In the 1970s model, their biomasses were back-calculated from the observed changes in relative abundance between the 1970s and 2000s as reported in published literature and government reports (see Appendix 6.1 for details). P/B ratios were based on mortality estimates from length-based studies and empirical equations (Pauly 1980). Q/B ratios were based on local surveys (Xu *et al.* 1994) and the information available from FishBase (Froese & Pauly 2004) (Appendix 6.2).

The 2000s ecosystem was exploited by six fleets categorized by their fishing gears: pair and stern trawls, shrimp trawl, purse seine, hook and line, gillnet and 'others'; all fishing gears were aggregated into one fishing fleet in the 1970s model. The specifications of fishing sectors in the 2000s model facilitated the identification of optimal fleet configurations through dynamic ecosystem simulations (Chapter 8). However, the limited resolution of catch data by fishing fleets in the 1970s did not allow segregation of catches by fishing fleet types for that period. On the other hand, this did not affect the comparison of ecosystem structures between the 1970s and 2000s as the models only accounted for the total catches by all fishing fleets.

Catches in the 1970s and 2000s model were based on landings statistics reported by the PRC government. However, the PRC landings data have been suggested to be largely over-estimated (Watson & Pauly 2001). The *Sea Around Us* Project (SAUP) provided (www.seaaroundus.org) catch estimates for China that had been adjusted downward based on a meta-analysis of global fisheries catches (Watson & Pauly 2001). Thus the SAUP data were also used to estimate the catches in the two models (Appendix 6.1).

Catches by fishing sectors and functional groups were estimated from national and regional fisheries statistics. Catches from the six fishing sectors in the 2000s model were obtained from the PRC fisheries statistics. The national statistics did not report catch composition by fishing fleets. However, such data were available for Hong Kong fisheries and as fishing vessels and gears used in Hong Kong are typical of those in the NSCS region, species composition by fleets was prorated according to the relative catch compositions of Hong Kong fishing fleets (Pitcher *et al.* 1998) (Table 6.2).

The initial input parameters did not result in a model that met the mass-balance criteria. Thus the input parameters were adjusted iteratively until the model achieved mass-balance i.e., the values of EE of all functional groups were below 1 (Appendix 6.1). The diet composition matrix was the primary parameter adjusted because it was relatively more uncertain than the other input parameters. However, changing the diet composition matrix alone was not enough for the models to achieve mass-balance. Thus the P/B, Q/B and biomass inputs were adjusted based on the relative accuracy of the data sources and the available information. The procedures for defining the relative accuracy of the input parameters are described in a later section.

Table 6.2. Estimated fishery catch $(t \cdot km^{-2})$ by functional groups and gear types in the 1970s and 2000s models. PSt – pair and stern trawl; ShT – shrimp trawl; PS – purse seine; H&L – hook and line; GN – gillnet; Others – other fishing gears; inverts – invertebrates; Ju. – juvenile; Ad. – adult; Dem. – demersal.

	Catches by functional groups (t ⁻ km ⁻²)								
Functional groups	1970s model				2000 mode				
	Total	PSt	ShT	PS	H&L	GN	Others	Total	
Phytoplankton	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000	
Benthic producer	0.0056	0.0000	0.0000	0.0000	0.0000	0.0000	0.0056	0.006	
Zooplankton	0.0100	0.0000	0.0000	0.0065	0.0000	0.0000	0.0883	0.095	
Jellyfish	0.0012	0.0126	0.0000	0.0314	0.0000	0.0000	0.0000	0.044	
Polychaetes	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000	
Echinoderms	0.0039	0.0001	0.0019	0.0000	0.0000	0.0000	0.0001	0.002	
Benthic crustaceans	0.0019	0.0003	0.0388	0.0000	0.0000	0.0000	0.0000	0.039	
Non-ceph molluscs	0.0056	0.0763	0.1800	0.0000	0.0000	0.0000	0.5060	0.762	
Sessile/other inverts	0.0011	0.0001	0.0029	0.0000	0.0000	0.0000	0.0000	0.003	
Shrimps	0.0350	0.0801	0.5760	0.0001	0.0000	0.0000	0.0226	0.679	
Crabs	0.0100	0.0400	0.1000	0.0000	0.0000	0.0421	0.0176	0.200	
Cephalopods	0.0244	0.1530	0.0243	0.0627	0.0009	0.0000	0.0324	0.273	
Threadfin bream	0.0440	0.4590	0.0089	0.0000	0.0651	0.0994	0.0246	0.657	
Bigeyes	0.0350	0.1420	0.0029	0.0000	0.0210	0.0321	0.0080	0.206	
Lizard fish	0.0840	0.0012	0.0015	0.0000	0.0000	0.0166	0.0041	0.023	

Table 6.2 Con't

		(Catches I	oy functi	onal gro	ups (t·kn	n ⁻²)	
Functional groups	1970s model				2000 mode	-		
	Total	PSt	ShT	PS	H&L	GN	Others	Total
Juv. Hairtail	0.0038	0.0206	0.0005	0.0001	0.0000	0.0054	0.0014	0.028
Ad. hairtail	0.0152	0.0047	0.0000	0.0001	0.0009	0.0012	0.0003	0.007
Pomfret	0.0053	0.0809	0.0076	0.0154	0.0299	0.0843	0.0209	0.239
Snappers	0.0053	0.0003	0.0001	0.0001	0.0002	0.0003	0.0001	0.001
Ad. groupers	0.0029	0.0013	0.0003	0.0000	0.0012	0.0049	0.0012	0.009
Croakers (≤ 30 cm)	0.0160	0.0159	0.0117	0.0000	0.0003	0.0027	0.0045	0.035
Juv. large croakers	0.0110	0.0371	0.0033	0.0000	0.0060	0.0168	0.0078	0.071
Croakers (> 30 cm)	0.0440	0.0046	0.0000	0.0000	0.0001	0.0032	0.0001	0.008
Dem. fish (≤ 30 cm)	0.0902	0.0085	0.0760	0.0100	0.0055	0.0262	0.0526	0.179
Juv. Dem. fish (> 30 cm)	0.0288	0.0230	0.2070	0.0100	0.0000	0.0613	0.0152	0.317
Ad. Dem. fish (>30 cm)	0.1150	0.0285	0.0000	0.0000	0.0023	0.0035	0.0009	0.035
Benthopelagic fish	0.0303	0.3420	0.0278	0.0607	0.0010	0.0580	0.1130	0.603
Melon seed	0.0057	0.0284	0.0023	0.0050	0.0000	0.0048	0.0094	0.050
Pelagic fish (≤ 30 cm)	0.1460	0.5120	0.0000	1.0860	0.0000	0.1030	0.6440	2.345
Juv. large pelagic fish	0.0096	0.2080	0.0000	0.0829	0.0000	0.3750	0.0725	0.738
Pelagic fish (> 30 cm)	0.0380	0.0185	0.0000	0.0074	0.0165	0.0333	0.0064	0.082
Dem. sharks and rays	0.0158	0.0006	0.0002	0.0000	0.0000	0.0002	0.0000	0.001
Pelagic sharks and rays	0.0051	0.0002	0.0000	0.0000	0.0002	0.0003	0.0000	0.001
Seabirds	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
Pinnipeds	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
Other mammals	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
Marine turtles	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
Detritus	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
Total	0.8500	2.2990	1.2740	1.3780	0.1510	0.9750	1.6590	7.736

6.2.2. Uncertainty and sensitivity analysis

Uncertainties of the input parameters were specified under a 'pedigree' in the Ecopath with Ecosim package (Christensen *et al.* 2004). The 'pedigree' is a matrix that allowed systematic categorisation of the reliability of the input parameters – specifically the biomass (B); production to biomass ratio (P/B); and the consumption to biomass ratio (Q/B); the diet composition matrix and the catch of each functional group. In the pedigree routine, a coded statement categorizing the origin (data type and associated uncertainty) of a given input was given to each of these parameters. Inputs were rated based on how they had been derived: local data, other locations, 'best guesses', empirical relationships, other Ecopath models, or estimated by the current model. Associated with each of these categories was an index of data quality which ranged from 0 to 1, with 0 being the lowest quality (estimated by the model while solving the mass-balance equations) while 1 being the highest quality (e.g. data from a quantitative study conducted in the study area). By summing across these pedigrees, an index (P) of the overall quality of the input information in Ecopath can be calculated:

$$P = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{I_{ij}}{n}$$
 eq. 6.3

where I_{ij} is the pedigree index for model group *i* and parameter *j*, *n* is the total number of modelled groups. This index summarizes how well the models are rooted in local data (Christensen *et al.* 2004).

The pedigrees were entered for the 1970s and 2000s model based on the source of the data and the author's knowledge on the accuracy of the sources (Table 6.3). The level of confidence corresponded to each pedigree category was based on the default values in Ecopath (Table 6.4). The indices of uncertainty of the 1970s and 2000s models were compared.

Table 6.3. Pedigree categories of the basic parameters used in the Northern South China Sea ecosystem models for (a) the 1970s and (b) the 2000s states.

		Ped	igree categ	gories*	
Functional group	В	P/B	⊂Q/B ⊂	Diet	Catch
Phytoplankton	4	4	N/A	N/A	N/A
Benthic producer	4	5	N/A	N/A	3
Zooplankton	3	4	4	2	3
Jellyfish	3	4	4	2	3
Polychaetes	4	2	2	1	N/A
Echinoderms	4	2	2	1	2
Benthic crustaceans	4	4	2	1	3
Non-ceph molluscs	4	2	2	1	2
Sessile/other invertebrates	4	2	2	1	2
Shrimps	0	4	3	2	3
Crabs	0	2	2	2	2
Cephalopods	0	2	2	2	3
Threadfin bream (nemipterids)	3	3	3	4	3
Bigeyes (priacanthids)	3	3	3	4	3
Lizard fish (synodontids)	3	3	3	4	3
Juvenile Hairtail (trichiurids)	0	1	3	4	3
Adult hairtail (trichiurids)	3	3	3	4	3
Pomfret (stromateids)	0	3	3	4	3
Snappers	0	3	3	4	3
Adult groupers	3	3	3	4	3
Croakers (≤ 30 cm)	3	1	3	4	3
Juvenile large croakers	1	3	3	2	3
Croakers (> 30 cm)	3	3	3	4	3
Demesral fish (≤ 30 cm)	0	3	3	4	3
Juvenile demersal fish (> 30 cm)	0	1	3	2	3
Adult demersal fish (>30 cm)	3	3	3	4	3
Benthopelagic fish	0	3	3	4	3
Melon seed	3	3	3	4	3
Pelagic fish (≤ 30 cm)	0	3	3	4	3
Juvenile large pelagic fish	0	1	3	2	3
Pelagic fish (> 30 cm)	3	3	3	4	3
Demersal sharks and rays	3	3	3	4	3
Pelagic sharks and rays	0	3	3	4	3
Seabirds	2	4	2	2	N/A
Pinnipeds	2	4	$\frac{-}{2}$	2	0
Other mammals	2	4	2	2	Õ
Marine turtles	2	2	2	2	N/A

(a) Pedigree for the basic parameters of the 1970s NSCS model

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		Pedi	igree categ	ories*	
Functional group	В	P/B	⊂Q/B ⊂	Diet	Catch
Phytoplankton	5	7	N/A	N/A	N/A
Benthic producer	4	5	N/A	N/A	3
Zooplankton	4	5	5	2	3
Jellyfish	3	2	2	1	3
Polychaetes	5	2	2	1	N/A
Echinoderms	5	2	2	1	2
Benthic crustaceans	3	4.	2	1	2
Non-ceph molluscs	3	2	2	1	2
Sessile/other invertebrates	4	2	2	1	2
Shrimps	0	4	3	1	3
Crabs	0	2	2	1	3
Cephalopods	4	2	2	3	3
Threadfin bream (nemipterids)	5	7	3	4	3
Bigeyes (priacanthids)	4	7	3	4	3
Lizard fish (synodontids)	5	7.	3	4	3
Juvenile Hairtail (trichiurids)	3	5	3	3	3
Adult hairtail (trichiurids)	4	5	3	3	3
Pomfret (stromateids)	4	5	3	3	3
Snappers .	3	5	3	4	2
Adult groupers	3	5	3	4	2
Croakers (≤ 30 cm)	4	5	3	4	2
Juvenile large croakers	3	5	0	1	0
Croakers (> 30 cm)	3	5	3	4	3
Demesral fish (≤ 30 cm)	3	5	3	4	2
Juvenile demersal fish (> 30 cm)	3	5	0	2	0
Adult demersal fish (>30 cm)	3	5	3	4	2
Benthopelagic fish	4	5	3	4	2
Melon seed	4	5	3	4	3
Pelagic fish (\leq 30 cm)	4	5	3	4	2
Juvenile large pelagic fish	2	5	0	0	0
Pelagic fish (> 30 cm)	4	7	3	4	2
Demersal sharks and rays	3	5	0	1	2
Pelagic sharks and rays	3	5	3	1	2
Seabirds	2	1	2	1	0
Pinnipeds	2	1	2	2	0
Other mammals	2	1	2	2	0
Marine turtles	2	2	2	2	N/A

(b) Pedigree for the basic parameters of the 2000s NSCS model

* For biomass: 1-estimated by model; 2-from other model; 3-guesstimate; 4-approximate or indirect method; 5-sampling-based, low precision; 6-sampling-based, high precision; for P/B and Q/B ratios: 4-empirical equation; 5-similar group/species system; similar system; 6-similar group/species, same system; 7-same group/species, similar system; 8-same group/species, same system; for diet composition: 1-general knowledge of related groups/species; 2-from other model; 3-general knowledge for same group/species; 4-qualitative diet composition study; 5-quantitative but limited diet composition study; 6-quantitative, detailed diet composition study; for catch: 1-guessitimate; 2-from other model; 3-FAO statistics; 4-national statistics; 5-local study; low precision/incomplete; 6-local study; high precision/complete; N/A-Not applicable.

Table 6.4. Pedigree indices of the basic parameters used in the Northern South China Sea ecosystem models for (a) the 1970s and (b) the 2000s states.

		Р	edigree in	dex	
Functional group	В	P/B	Q/B	Diet	Catch
Phytoplankton	0.00	0.60			
Benthic producer	0.00	0.70			0.50
Zooplankton	0.00	0.60	0.60	0.20	0.50
Jellyfish	0.00	0.60	0.60	0.20	0.50
Polychaetes	0.00	0.20	0.20	0.00	
Echinoderms	0.00	0.20	0.20	0.00	0.20
Benthic crustaceans	0.00	0.60	0.20	0.00	0.50
Non-ceph molluscs	0.00	0.20	0.20	0.00	0.20
Sessile/other invertebrates	0.00	0.20	0.20	0.00	0.20
Shrimps	0.00	0.60	0.50	0.20	0.50
Crabs	0.00	0.20	0.20	0.20	0.20
Cephalopods	0.00	0.20	0.20	0.20	0.50
Threadfin bream (nemipterids)	0.00	0.50	0.50	0.70	0.50
Bigeyes (priacanthids)	0.00	0.50	0.50	0.70	0.50
Lizard fish (synodontids)	0.00	0.50	0.50	0.70	0.50
Juvenile Hairtail (trichiurids)	0.00	0.10	0.50	0.70	0.50
Adult hairtail (trichiurids)	0.00	0.50	0.50	0.70	0.50
Pomfret (stromateids)	0.00	0.50	0.50	0.70	0.50
Snappers	0.00	0.50	0.50	0.70	0.50
Adult groupers	0.00	0.50	0.50	0.70	0.50
Croakers (≤ 30 cm)	0.00	0.10	0.50	0.70	0.50
Juvenile large croakers	0.00	0.50	0.50	0.20	0.50
Croakers (> 30 cm)	0.00	0.50	0.50	0.70	0.50
Demesral fish (≤ 30 cm)	0.00	0.50	0.50	0.70	0.50
Juvenile demersal fish (> 30 cm)	0.00	0.10	0.50	0.20	0.50
Adult demersal fish (>30 cm)	0.00	0.50	0.50	0.70	0.50
Benthopelagic fish	0.00	0.50	0.50	0.70	0.50
Melon seed	0.00	0.50	0.50	0.70	0.50
Pelagic fish (≤ 30 cm)	0.00	0.50	0.50	0.70	0.50
Juvenile large pelagic fish	0.00	0.10	0.50	0.20	0.50
Pelagic fish (> 30 cm)	0.00	0.50	0.50	0.70	0.50
Demersal sharks and rays	0.00	0.50	0.50	0.70	0.50
Pelagic sharks and rays	0.00	0.50	0.50	0.70	0.50
Seabirds	0.00	0.60	0.20	0.20	
Pinnipeds	0.00	0.60	0.20	0.20	0.10
Other mammals	0.00	0.60	0.20	0.20	0.10
	0.00	0.00	0.20	0.20	0.10

0.00

Marine turtles

0.20

0.20

0.20

(a) Pedigree indices for the basic parameters of the 1970s NSCS model

(b) Pedigree for the basic parameters of the 2000s NSCS model

		Pedigree index						
Functional group	В	P/B	Q/B	Diet	Catch			
Phytoplankton	1.00	1.00	N/A	N/A	N/A			
Benthic producer	0.70	0.70	N/A	N/A	0.50			
Zooplankton	0.70	0.70	0.70	0.20	0.50			
Jellyfish	0.40	0.20	0.20	0.00	0.50			
Polychaetes	1.00	0.20	0.20	0.00	N/A			
Echinoderms	. 1.00	0.20	0.20	0.00	0.20			
Benthic crustaceans	0.40	0.60	0.20	0.00	0.20			
Non-ceph molluses	0.40	0.20	0.20	0.00	0.20			
Sessile/other invertebrates	0.70	0.20	0.20	0.00	0.20			
Shrimps	0.00	0.60	0.50	0.00	0.50			
Crabs	0.00	0.20	0.20	0.00	0.50			
Cephalopods	0.70	0.20	0.20	0.50	0.50			
Threadfin bream (nemipterids)	1.00	1.00	0.50	0.70	0.50			
Bigeyes (priacanthids)	0.70	1.00	0.50	0.70	0.50			
Lizard fish (synodontids)	1.00	1.00	0.50	0.70	0.50			
Juvenile Hairtail (trichiurids)	0.40	0.70	0.50	0.50	0.50			
Adult hairtail (trichiurids)	0.70	0.70	0.50	0.50	0.50			
Pomfret (stromateids)	0.70	0.70	0.50	0.50	0.50			
Snappers	0.40	0.70	0.50	0.70	0.20			
Adult groupers	0.40	0.70	0.50	0.70	0.20			
Croakers (≤ 30 cm)	0.70	0.70	0.50	0.70	0.20			
Juvenile large croakers	0.40	0.70	0.00	0.00	0.10			
Croakers (> 30 cm)	0.40	0.70	0.50	0.70	0.50			
Demesral fish (≤ 30 cm)	0.40	0.70	0.50	0.70	0.20			
Juvenile demersal fish (> 30 cm)	0.40	0.70	0.00	0.20	0.10			
Adult demersal fish (>30 cm)	0.40	0.70	0.50	0.70	0.20			
Benthopelagic fish	0.70	0.70	0.50	0.70	0.20			
Melon seed	0.70	0.70	0.50	0.70	0.50			
Pelagic fish (≤ 30 cm)	0.70	0.70	0.50	0.70	0.20			
Juvenile large pelagic fish	0.00	0.70	0.00	0.00	0.10			
Pelagic fish (> 30 cm)	0.70	1.00	0.50	0.70	0.20			
Demersal sharks and rays	0.40	0.70	0.00	0.00	0.20			
Pelagic sharks and rays	0.40	0.70	0.50	0.00	0.20			
Seabirds	0.00	0.10	0.20	0.00	0.10			
Pinnipeds	0.00	0.10	0.20	0.20	0.10			
Other mammals	0.00	0.10	0.20	0.20	0.10			
Marine turtles	0.00	0.20	0.20	0.20	N/A			

To test the sensitivity of the Ecopath estimated parameters, two approaches were used. Firstly, input parameters, including biomass, P/B and Q/B ratios and EE, were varied (increased or decreased) by up to 50%. Changes of the output parameters relative to the initial values were noted. This approach tested sensitivity of the model estimates to the major input parameters except diet composition and catches. Secondly, a perturbation analysis (Bundy *et al.* 2005) was conducted using the 'Autobalance routine' (Kavanagh *et al.* 2004) of Ecopath. In this routine, values of the input parameters of the NSCS models were randomly selected from statistical distributions predefined in the 'pedigree' (Christensen *et al.* 2004). This was repeated until the combination of parameter values resulted in a mass-balanced model (i.e., ecotrophic efficiency of all functional group is positive and less than 1). The sampling and balancing of the models was repeated 30 times and parameter values from each mass-balanced model, confidence limits for all input and output parameters of the 1970s and 2000s NSCS models could be estimated.

6.3 Results

6.3.1. Biomass changes

The models indicated a large change in ecosystem structure (Figure 6.2). Total biomass of consumer groups (i.e., excluding primary producers and detritus) in the 1970s $(67.6 \text{ t} \text{ km}^{-2})$ was 2.5 times higher than in the 2000s (27 t km⁻²). Biomasses of functional groups lower in the trophic level increased from the 1970s. These groups included mainly jellyfish, pelagic, small-bodied and juvenile fishes. Biomass of most other groups, particularly the demersal fishes, decreased by an average of 60% from the 1970s level. Groups with the largest declines included sharks and rays, large demersal fish, snappers, groupers, large croakers, lizardfish and hairtail.

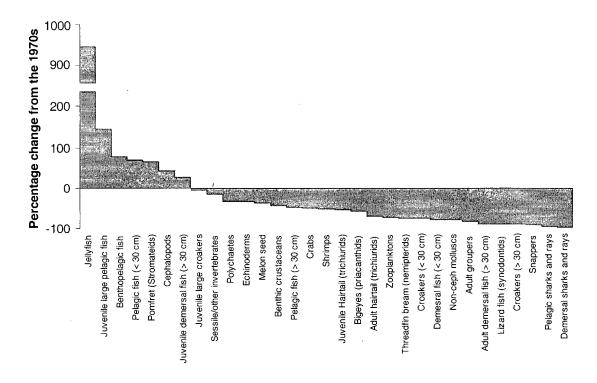


Figure 6.2. Percentage change in biomasses between the 1970s and the 2000s NSCS models.

The models also showed a shift from a demersal-dominant to pelagic-dominant system between the 1970s and the 2000s (Figure 6.3). When pelagic, benthopelagic and demersal feeders were grouped together, biomasses of pelagic and benthopelagic groups increased significantly by about 1.6 times from the 1970s level. On the other hand, biomass of demersal groups declined by more than 60% (Figure 6.3a). Thus, the ratio of total demersal to total pelagic biomass (including fish and invertebrates) declined from 15:1 in the 1970s to 3.7:1 in the 2000s. Moreover, total throughput, a measure of biomass going into and out of a group, increased by 1.8 times for the pelagic fish groups. On the other hand, total throughput of demersal fish groups declined by 2.5 times from the 1970s to 2000s (Figure 6.3b). Energy flows in the 2000s system were mainly through the pelagic groups, which were 3 times the total energy flows of demersal groups. However, 30 years ago, flows of demersal groups were higher than the pelagic groups.

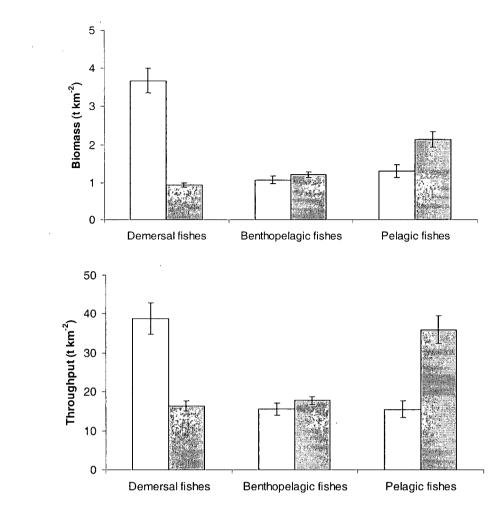


Figure 6.3. Comparisons of (a) biomass and (b) throughput of demersal, benthopelagic and pelagic fish groups in the 1970s (open bars) and 2000s (gray bars) NSCS models. The error bars represent the standard errors generated from the perturbation analysis (N = 30).

The proportion of invertebrates in the total landings of the NSCS increased substantially from the 1970s to the 2000s. The ratio of landings of fishes to invertebrates in the NSCS declined largely from 24:1 to 4:1 since the 1970s, after a period of rapid increase in fish landings between the 1950s and 1970s (Department of Fishery, PRC 1996, 2000) (Figure 6.4). The landings included the Chinese official reported landings from the three provinces that fished in the NSCS (Guangzhou, Guangxi and Hainan).

a)

b)

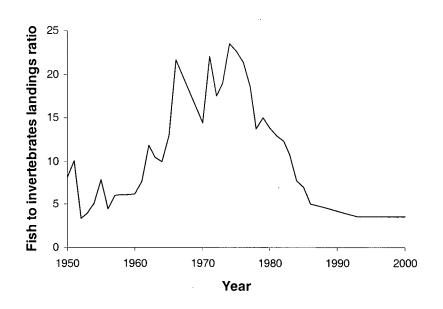


Figure 6.4. Ratio of fishes to invertebrates landings from NSCS from 1950 to 2000.

For the demersal groups, benthic invertebrates became dominant in NSCS in the 2000s. Although biomass of invertebrates (shrimps, crabs, benthic crustaceans, etc.) decreased by almost 30%, the ratio of demersal invertebrates to demersal fish biomass increased 2.8 fold from the 1970s to 2000s. This showed an increase in the proportion of invertebrates in the demersal system despite a decline in the overall demersal biomass.

The proportion of low trophic level demersal groups increased substantially in the 2000s. Overall, total biomass from all trophic levels declined from the 1970s to the 2000s (Figure 6.5). Biomass of trophic level 2 to 3 dropped greatly because of the substantial decrease in biomass of benthic invertebrates such as crustacean and echinoderms. While the majority of the demersal groups in trophic level 3 to 4 decreased strongly (>70%), the biomass of benthopelagic and pelagic groups with this trophic level increased. As such, only a moderate decline in biomass of groups in trophic level 3 to 4 was observed. When only demersal groups were considered, the decline in total biomass of trophic level 3 to 4 was greater than in the lower trophic levels. Decline in abundance of pelagic sharks and rays was responsible for the drop in biomass of functional groups with trophic levels higher than 4.

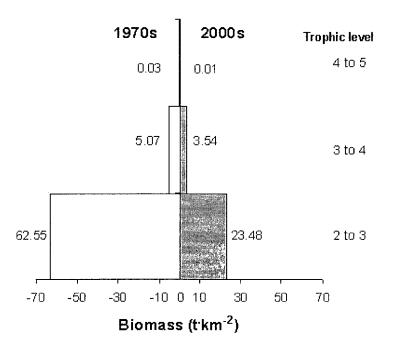


Figure 6.5. Biomasses by trophic level of the 1970s and 2000s NSCS models.

6.3.2. Mortalities

The mortality of the functional groups changed substantially between the two periods. Generally, fishing mortalities of functional groups in the 2000s model were much higher than the 1970s model. Total mortalities of fish groups increased by 15 times on average from the 1970s to 2000s (Table 6.5). This was a logical consequence of the dramatic increase in fishing effort over the past three decades. Changes in predation mortalities between the two time periods varied between groups. Predation mortalities of juvenile and small fish groups decreased because of the decline in abundance of their predators. However, predation mortalities of large fish groups increased slightly, which might be attributed to the declines in average body size and age of the groups. Smallersize and younger fishes should generally have higher predation mortalities. Table 6.5. Estimated fishing (F), natural (M) and other mortalities (M_0) of the 1970s and 2000s NSCS models.

······································	1	970s mod	el	2000s model			
Functional group	F	Μ	Mo	F	Μ	Мо	
Phytoplankton	0.00	14.10	385.00	0.00	3.79	394.00	
Benthic producer	0.00	0.24	11.65	0.00	0.12	11.80	
Zooplankton	0.00	1.67	30.33	0.01	9.77	22.20	
Jellyfish	0.01	4.74	0.25	0.03	2.57	2.40	
Polychaetes	0.00	6.41	0.34	0.00	4.54	2.21	
Echinoderms	0.00	0.48	0.72	0.00	0.53	0.67	
Benthic crustaceans	0.00	3.52	2.13	0.03	3.46	2.16	
Non-ceph molluscs	0.00	1.15	1.85	0.29	3.05	0.17	
Sessile/other invertebrates	0.00	0.84	0.16	0.00	0.57	0.43	
Shrimps	0.08	5.05	0.27	3.49	3.73	0.38	
Crabs	0.01	2.84	0.15	0.54	2.31	0.15	
Cephalopods	0.05	1.50	1.55	0.40	0.82	1.88	
Threadfin bream (nemipterids)	0.04	0.31	0.39	2.53	0.18	0.47	
Bigeyes (priacanthids)	0.11	0.29	0.81	1.62	0.21	1.50	
Lizard fish (synodontids)	0.28	0.27	1.75	0.73	0.52	0.55	
Juvenile Hairtail (trichiurids)	0.11	0.64	1.54	1.86	0.45	0.77	
Adult hairtail (trichiurids)	0.36	0.13	1.01	0.58	0.23	0.67	
Pomfret (stromateids)	0.08	1.15	0.07	2.21	0.67	0.15	
Snappers	0.38	0.90	0.07	0.78	0.88	0.09	
Adult groupers	0.07	0.25	0.53	1.39	0.28	0.09	
Croakers (≤ 30 cm)	0.06	1.80	0.51	0.50	2.66	0.14	
Juvenile large croakers	0.26	2.00	0.21	1.77	0.19	1.44	
Croakers (> 30 cm)	0.46	0.41	0.66	0.84	0.10	0.59	
Demesral fish (≤ 30 cm)	0.06	2.51	0.14	0.57	3.90	0.24	
Juvenile demersal fish (> 30 cm)	0.26	1.40	1.04	2.21	0.51	0.97	
Adult demersal fish (>30 cm)	0.59	0.02	0.93	1.70	0.07	0.53	
Benthopelagic fish	0.06	2.79	0.15	0.65	0.92	1.61	
Melon seed	0.05	2.11	0.08	0.71	1.68	0.01	
Pelagic fish (≤ 30 cm)	0.14	2.58	0.14	1.32	1.51	1.43	
Juvenile large pelagic fish	0.08	1.63	1.16	2.55	0.09	1.62	
Pelagic fish (> 30 cm)	0.24	0.01	0.65	1.04	0.02	0.34	
Demersal sharks and rays	0.40	0.06	0.80	0.98	0.06	0.16	
Pelagic sharks and rays	0.18	0.02	0.20	0.62	0.03	0.03	
Seabirds	0.00	0.00	0.06	0.00	0.00	0.06	
Pinnipeds	0.03	0.00	0.01	0.01	0.00	0.03	
Other mammals	0.01	0.00	0.10	0.00	0.00	0.11	
Marine turtles	0.05	0.00	0.05	0.03	0.00	0.07	

6.3.3. System index

System indices obtained from the models suggested that the ecosystem changed considerably from the 1970s to the 2000s (Table 6.6). Total catch from the NSCS ecosystem increased from 0.85 to 7.35 t km⁻² during this period. Mean trophic level of catch in the 1970s, calculated from the average trophic level of the functional groups weighted by their total annual catches, declined from 3.19 to 2.85. In the 1970s,

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functional groups with trophic level lower than 3 contributed only 31% to the total catch. However, in the 2000s, 71% of the catch came from these groups. Thus, although total catches increased, lower trophic level groups contributed a higher fraction of the catch.

The system indices derived from Odum's attributes of ecosystem maturity (Odum 1969; Christensen 1995) indicated that the 1970s system had higher ecosystem maturity than the 2000s system. The ratio of total primary production to total respiration of the system increased 3-fold between the 1970s and 2000s. Also system overhead, an index that is positively related to the system's reserved strength, and hence to its resilience to unexpected perturbations (Ulanowicz 1986), decreased substantially from the 1970s to the 2000s. Total consumption and respiratory flows, and the resulting total system throughput in the 1970s model were higher than the 2000s model. Total consumption and respiratory flows are measures of the total biomass flows through consumption and respiration of all the functional groups (except detritus) in the system.

Average trophic transfer efficiency of the system, calculated from the geometric mean of the transfer efficiency of all trophic levels, was lower in the 1970s model (from 6.6% in the 70s to 10.2% in the 2000s). Transfer efficiency of each trophic level was estimated from the proportion of input that was transferred to the next trophic level. In general, trophic transfer efficiency declined with higher trophic level (Christensen & Pauly 1995). Thus the lower transfer efficiency in the 1970s relative to the 2000s level might indicate that the flows in higher trophic level constituted a large fraction of the total throughput in the 1970s than the 2000s. This paralleled the 8-fold increase in gross efficiency of the system (ratio of catch to net primary production) between the 1970s and 2000s (Table 6.6).

System index	1970s	2000s
Sum of all consumption (t·km ⁻²)	6,869	1,994
	(s.e. = 187)	(s.e. = 32)
Sum of all exports (t·km ⁻²)	127,037	129,132
•	(s.e. = 1,561)	(s.e. = 916)
Sum of all respiratory flows (t•km ⁻²)	3,659	1,242
	(s.e. = 100)	(s.e. = 20)
Sum of all flows into detritus (t·km ⁻²)	129,187	129,751
	(s.e. = 1,532)	(s.e. = 906)
Total system throughput (t·km ⁻²)	266,752	262,118
· · · · · · · · · · · · · · · · · · ·	(s.e. = 2,976)	(s.e. = 1,800)
Sum of all production (t·km ⁻²)	131,881	130,725
	(s.e. = 1,505)	(s.e. = 906)
Mean trophic level of catch	3.19	2.85
	(s.e. = 0.003)	(s.e. = 0.003)
Gross efficiency (catch/net primary production)	7x10 ⁻⁶	5.6x10 ⁻⁵
	$(s.e. = 9.5 \times 10^{-8})$	$(s.e. = 4.3 \times 10^{-7})$
Total primary production/total respiration	35.72	104.99
	(s.e. = 1.67)	(s.e. = 2.17)
Total primary production/total biomass	240.4	259.2
	(s.e. = 1.67)	(s.e. = 1.61)
Connectance index	0.317	0.303
	$(s.e. = 8.5 \times 10^{-5})$	$(s.e. = 7.7 \times 10^{-5})$
System omnivory index	0.185	0.181
	(s.e. = 0.001)	$(s.e. = 9.1 \times 10^{-4})$
Pedigree index	0.393	0.417

Table 6.6. Estimated system indices of the 1970s and 2000s models. Standard errors (s.e.) estimated from the perturbation analysis (N = 30) were noted in the parentheses.

The primary production required (PPR) for consumption by the functional groups and for the fisheries changed between the 1970s and 2000s (Figure 6.6). PPR was calculated from all the flows from primary production (trophic level = 1) required to support the higher trophic levels or the fisheries (Pauly & Christensen 1995a). The PPR for consumption by animals in the NSCS ecosystem decreased by 75% from the 1970s (19,926 +/- s.e. 3,098 t·km⁻²) to the 2000s (5,090 +/- s.e. 130 t·km⁻²) (Figure 6.6a). However, PPR for fisheries increased by about 78% (from 431 +/- s.e. 95 t·km⁻² to 769 +/- s.e. 37 t·km⁻²) (Figure 6.6b). Thus, the ratio between PPR for fisheries and PPR for consumption increased greatly from 1:46 to 1:6.6 during this period (Figure 6.6c). In other words, in the 2000s, a higher fraction of the total biomass flows from primary production was required to support the fisheries, relative to those consumed by the organisms in the higher trophic levels (except human). However, the PPR per unit of catch decreased by 80% from 507 to 99 (+/- s.e. 4.7) over the three decades. This indicated that a greater proportion of catch in the 2000s were made up of the lower trophic level species. These species required less energy from primary production per unit of biomass. Based on the estimated PPR generated from alternative input parameters (resulting from the perturbation analysis), the values of the above indicators were significantly different between the 1970s and the 2000s model (P<0.05).

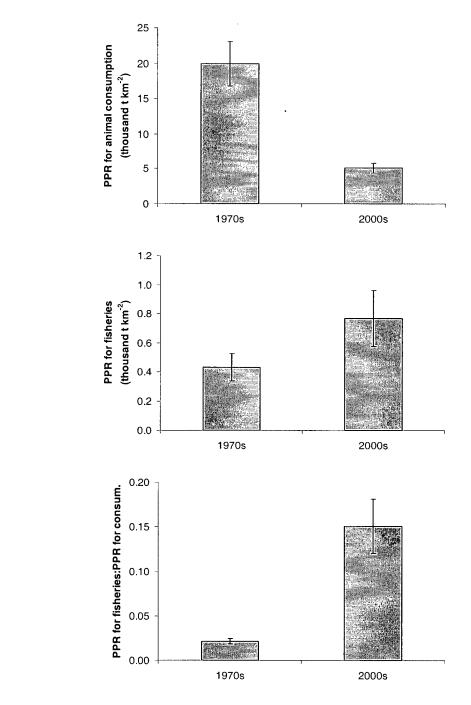


Figure 6.6. Primary production required (PPR) in the 1970s and 2000s models to support (a) consumption by predators (excluding fishing), (b) by fisheries, (c) ratio of fisheries to consumptions. The error bars represent the standard errors generated from the perturbation analysis (N = 30).

a)

b)

c)

6.3.4. Uncertainty and sensitivity analysis

The input parameters for the 1970s model were estimated from less certain sources than the 2000s model. Based on the assigned pedigree matrices, the estimated index of uncertainty from the 2000s model was slightly higher than the 1970s model. Pedigree index of the 2000s and 1970s model was 4.1 and 3.9, respectively. This indicated that parameter values of the 2000s model were based on slightly more reliable sources than the 1970s model. Data sources for the 2000s model were mainly surveybased, while many of the input parameters for the 1970s model were indirectly estimated from global databases and empirical formulae. In our pedigree analysis, the latter are regarded as having lower reliability than survey-based data.

The estimated parameters were sensitive to the input parameters within a functional group, while the outputs were generally robust to parameters from other functional groups (Table 6.7). For instance, when one input parameter of a functional group was reduced by 50%, the output parameters of that group may vary by more than 90%. This was expected as the input parameters of a functional group (e.g., P/B, Q/B, EE) are tightly linked with each other. Excluding this within-group effect, the estimated parameters were reasonably robust to changes in input parameter values of other functional groups in the 2000s model. A 50% change in input parameter values led to, on average, 10% change in the output values (25% and 75% quartile = 4.3% - 13%). The most sensitive sets of parameters were the effect of the assumed ecotrophic efficiency (EE) of small demersal fish groups on the estimated EEs of benthic crustaceans and melon seed, and the biomass of snappers.

The 1970s model was more sensitive to the input parameter values, even when within-group effects were excluded. The effects of P/B and EE of pelagic sharks on the estimated EE of seabirds were most sensitive among all parameter sets, with a maximum change of over 200% in the seabird EE when the input parameters of pelagic sharks and rays changed by 50%. Other more sensitive pairs of input/output parameters included small pelagic fish/juvenile pelagic fish, small demersal fish/melon seed, and cephalopods/pomfret. These indicated the higher uncertainties associated with the estimated parameters of the 1970s model.

Results from the perturbation analysis showed that the system estimates of the 1970s and 2000s models were robust to the uncertainty of the input parameters. Based on the alternative model parameters (N = 30 for each model) generated from the perturbation analysis, the confidence intervals of the system indices presented in this study (e.g., system throughput, primary production required by the fisheries) were narrow for both models. The coefficient of variation of these system indices were generally within 30%.

				Sens	itivity l	by grou	p (aver	age cha	inge in	estimat	ions)	
No	Perturbing group	Perturbations	1	2	3	4	5	6	7	8	9	10
1	Phytoplankton	Reduce by 50%	1.00									
		Increase by 50%	0.33									
2	Benthic producer	Reduce by 50%		1.00								
		Increase by 50%		0.33								
3	Zooplankton	Reduce by 50%	0.50		1.00							
		Increase by 50%	0.50		0.33							
4	Jellyfish	Reduce by 50%			0.22	4.31						
		Increase by 50%			0.04	0.50						
5	Polychaetes	Reduce by 50%					1.00					
		Increase by 50%					0.33					
6	Echinoderms	Reduce by 50%		0.08				0.59			0.21	
		Increase by 50%		0.08				0.25			0.21	
7	Benthic crustaceans	Reduce by 50%		0.15			0.09		1.00	0.18		
		Increase by 50%		0.15			0.09		0.33	0.18		
8	Non-cephalopods mollusks	Reduce by 50%		0.20	0.04		0.22			0.97	0.18	
		Increase by 50%		0.20	0.04		0.22			0.32	0.18	
9	Sessile/other invertebrates	Reduce by 50%			0.15						1.00	
		Increase by 50%			0.15						0.33	
10	Shrimps	Reduce by 50%					0.06					1.0
		Increase by 50%					0.03					0.3
11	Crabs	Reduce by 50%		0.06			0.09	0.06		0.07		0.1
		Increase by 50%		0.02			0.04	0.02		0.03		0.0
12	Cephalopods	Reduce by 50%			0.12	0.34		0.26	0.09	0.08		0.1
		Increase by 50%			0.04	0.12		0.09	0.03	0.02		0.0
13	Threadfin bream (nemipterids)	Reduce by 50%			0.03	0.05	0.05	0.10	0.13	0.13		0.0
		Increase by 50%			0.03	0.05	0.05	0.10	0.13	0.13		0.0
14	Bigeyes (priacanthids)	Reduce by 50%				0.05	0.04		0.07			0.0
		Increase by 50%				0.05	0.04		0.07			0.07

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 Table 6.7. Sensitivity of the estimated parameters when input parameters value were varied

Table 6.7a Con't

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	Functional group			Sens	sitivity	by grou	p (aver	age cha	inge in	estimat	tions)	
No		Perturbations	1	2	3	4	5	6	7	8	9	10
15	Lizard fish (synodontids)	Reduce by 50%			0.03	0.06			0.06			0.09
		Increase by 50%			0.03	0.06			0.06			0.09
18	Pomfret (stromateids)	Reduce by 50%				0.44						
		Increase by 50%				0.21						
21	Croakers (\leq 30 cm)	Reduce by 50%			0.04			0.05	0.06			0.13
		Increase by 50%			0.04			0.05	0.06			0.13
22	Juvenile large croakers	Reduce by 50%										
		Increase by 50%										
23	Croakers (> 30 cm)	Reduce by 50%				0.05						
		Increase by 50%				0.05						
24	Demesral fish (≤ 30 cm)	Reduce by 50%		0.07	0.18	0.49	0.15	0.08	0.53	0.20	0.09	0.35
		Increase by 50%		0.02	0.08	0.20	0.06	0.03	0.22	0.08	0.04	0.15
26	Adult demersal fish (> 30 cm)	Reduce by 50%							0.05			
		Increase by 50%							0.05			
27	Benthopelagic fish	Reduce by 50%			0.09							0.09
		Increase by 50%			0.04							0.04
28	Melon seed	Reduce by 50%				0.04						
		Increase by 50%				0.04						
29	Pelagic fish (≤ 30 cm)	Reduce by 50%			0.14					0.07		0.18
		Increase by 50%			0.06					0.03		0.08
33	Pelagic sharks and rays	Reduce by 50%				0.17						
		Increase by 50%				0.06						
36	Other mammals	Reduce by 50%				0.03						
		Increase by 50%				0.03						

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Table 6.7a Con't

	Functional group			1	Sensitiv	ity by g	roup (a	verage c	hange in	estimatio	ns)		
No.		Perturbations	21	22	23	24	25	26	27	28	29	30	
12	Cephalopods	Reduce by 50%							0.10	0.08	0.36	0.29	
		Increase by 50%							0.03	0.03	0.13	0.10	
13	Threadfin bream (nemipterids)	Reduce by 50%				0.12	0.04		0.07	0.09	~		
		Increase by 50%				0.12	0.04		0.07	0.09			
14	Bigeyes (priacanthids)	Reduce by 50%	0.23	0.39		0.11	0.25			0.06			
		Increase by 50%	0.23	0.39		0.11	0.25			0.06			
15	Lizard fish (synodontids)	Reduce by 50%	0.08			0.10	0.04			0.07	0.09	0.07	
		Increase by 50%	0.08			0.10	0.04			0.07	0.09	0.07	
16	Juvenile Hairtail (trichiurids)	Reduce by 50%	0.04						0.03				
		Increase by 50%	0.04						0.03				
20	Adult groupers	Reduce by 50%					0.04						
		Increase by 50%					0.04						
21	Croakers (≤ 30 cm)	Reduce by 50%	1.00			0.05			0.14	0.05	0.07	0.05	
		Increase by 50%	0.33			0.05			0.14	0.05	0.07	0.05	
22	Juvenile large croakers	Reduce by 50%	0.06	1.00									
	C C	Increase by 50%	0.06	0.33									
23	Croakers (> 30 cm)	Reduce by 50%			1.00								
		Increase by 50%			0.33								
24	Demesral fish (≤ 30 cm)	Reduce by 50%				0.92	0.37		0.20	0.62	0.08	0.07	
		Increase by 50%				0.27	0.16		0.08	0.26	0.03	0.03	
25	Juvenile demersal fish (> 30 cm)	Reduce by 50%					1.00						
		Increase by 50%					0.33						
26	Adult demersal fish (> 30 cm)	Reduce by 50%			0.24			1.00					
		Increase by 50%			0.24			0.33					
27	Benthopelagic fish	Reduce by 50%							0.80	0.07	0.24	0.19	
		Increase by 50%							0.25	0.03	0.11	0.08	
28	Melon seed	Reduce by 50%								0.99			
		Increase by 50%								0.33			
29	Pelagic fish (\leq 30 cm)	Reduce by 50%							0.10	0.16	0.84	0.79	
	• · · · ·	Increase by 50%							0.04	0.07	0.26	0.34	

Table 6.7a Con't

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	Functional group	Sensitivity by group (average change in estimations)											
No.		Perturbations	21	22	23	24	25	26	27	28	29	30	
30	Juvenile large pelagic fish	Reduce by 50%							0.04			0.98	
		Increase by 50%							0.04			0.33	
31	Pelagic fish (> 30 cm)	Reduce by 50%									0.08	. 0.08	
	-	Increase by 50%									0.08	0.08	
33	Pelagic sharks and rays	Reduce by 50%							0.10	0.08	0.11	0.13	
		Increase by 50%							0.02	0.01	0.04	0.04	
34	Seabirds	Reduce by 50%										0.04	
		Increase by 50%										0.04	

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Table 6.7a Con't

		Sensitivity by group (average change in es										
No.	Functional group	Perturbations	31	32	33	34	35	36	37			
31	Pelagic fish (> 30 cm)	Reduce by 50%	1.00									
		Increase by 50%	0.33									
32	Demersal sharks and rays	Reduce by 50%		0.64								
		Increase by 50%		0.23								
33	Pelagic sharks and rays	Reduce by 50%			1.55	1.69						
		Increase by 50%			0.35	0.56						
34	Seabirds	Reduce by 50%				1.00						
		Increase by 50%				0.33						
35	Pinnipeds	Reduce by 50%					1.00					
		Increase by 50%					0.33					
36	Other mammals	Reduce by 50%						1.00				
		Increase by 50%						0.33				
37	Marine turtles	Reduce by 50%							1.00			
		Increase by 50%							0.33			

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(b) The 2000s model

			Sensitivity by group (average change in estimations)											
No.	Functional group	Perturbations	1	2	3	4	5	6	7	8	9	10		
1	Phytoplankton	Reduce by 50%	1.00											
	,	Increase by 50%	-0.33											
2	Benthic producer	Reduce by 50%		1.00										
		Increase by 50%		-0.33										
3	Zooplankton	Reduce by 50%	-0.49		1.00									
		Increase by 50%	0.49		-0.33									
4	Jellyfish	Reduce by 50%			-0.16	0.28								
		Increase by 50%			0.16	-0.01								
5	Polychaetes	Reduce by 50%					1.00							
		Increase by 50%					-0.33							
6	Echinoderms	Reduce by 50%		-0.10				0.47			-0.24			
		Increase by 50%		0.10				-0.11			0.24			
7	Benthic crustaceans	Reduce by 50%		-0.16			-0.10		1.00	-0.17				
		Increase by 50%		0.16			0.10		-0.33	0.17				
8	Non-cephalopods mollusks	Reduce by 50%		-0.13			-0.15			0.97	-0.10			
		Increase by 50%		0.13			0.15			-0.32	0.10			
9	Sessile/other invertebrates	Reduce by 50%			-0.08						1.00			
		Increase by 50%			0.08						-0.33			
10	Shrimps	Reduce by 50%					0.03					1.00		
		Increase by 50%					0.00					-0.33		
11	Crabs	Reduce by 50%					0.06			0.03		0.08		
		Increase by 50%					-0.01			0.00		-0.01		
12	Cephalopods	Reduce by 50%						-0.17	-0.07					
		Increase by 50%						0.17	0.07					
13	Threadfin bream (nemipterids)	Reduce by 50%					-0.05	-0.06	-0.12	-0.11		-0.04		
		Increase by 50%					0.05	0.06	0.12	0.11		0.04		

Table	6.7b	Con'	t.

		Sensitivity by group (average change in estimations)										
No.	Functional group	Perturbations	1	2	3	4	5	6	ັ 7	8	9	10
14	Bigeyes (priacanthids)	Reduce by 50%							-0.06			-0.04
	·	Increase by 50%							0.06			0.04
18	Pomfret (stromateids)	Reduce by 50%				-0.10						
		Increase by 50%				0.10						
21	Croakers (\leq 30 cm)	Reduce by 50%										-0.04
		Increase by 50%										0.04
24	Demesral fish (≤ 30 cm)	Reduce by 50%					0.13		0.45	0.15	0.08	0.23
		Increase by 50%					-0.04		-0.12	-0.04	-0.02	-0.06
25	Juvenile demersal fish (> 30 cm)	Reduce by 50%	· .						-0.06			
		Increase by 50%							0.06			
27	Benthopelagic fish	Reduce by 50%		-0:06	-0.04				-0.07			
		Increase by 50%		0.06	0.04				0.07			
29	Pelagic fish (≤ 30 cm)	Reduce by 50%			-0.13							
		Increase by 50%			0.13							
30	Juvenile large pelagic fish	Reduce by 50%									-0.04	
		Increase by 50%									0.04	

Table 6.7b Con't.

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				Sensitivity by group (average change in estimations)								
No.	Functional group	Perturbations	11	12	13	14	15	16	17	19	20	
11	Crabs	Reduce by 50%	1.00									
		Increase by 50%	-0.33									
12	Cephalopods	Reduce by 50%	-0.13	0.53								
		Increase by 50%	0.13	-0.14								
13	Threadfin bream (nemipterids)	Reduce by 50%			1.00					-0.06		
		Increase by 50%			-0.33					0.06		
14	Bigeyes (priacanthids)	Reduce by 50%	-0.12			0.98				-0.05		
		Increase by 50%	0.12			-0.33				0.05		
15	Lizard fish (synodontids)	Reduce by 50%					0.62					
		Increase by 50%					-0.20					
16	Juvenile Hairtail (trichiurids)	Reduce by 50%					-0.11	0.97				
		Increase by 50%					0.11	-0.32				
17	Adult hairtail (trichiurids)	Reduce by 50%					-0.04		0.63			
		Increase by 50%					0.04		-0.20		·	
18	Pomfret (stromateids)	Reduce by 50%										
		Increase by 50%										
19	Snappers	Reduce by 50%								1.00		
		Increase by 50%								-0.33		
20	Adult groupers	Reduce by 50%									1.01	
		Increase by 50%									-0.33	
24	Demesral fish (≤ 30 cm)	Reduce by 50%	0.24							0.47		
		Increase by 50%	-0.07							-0.13		
27	Benthopelagic fish	Reduce by 50%	-0.07	-0.05								
		Increase by 50%	0.07	0.05								
31	Pelagic fish (> 30 cm)	Reduce by 50%							-0.05			
	÷ · ·	Increase by 50%							0.05			
36	Other mammals	Reduce by 50%							-0.05	-0.08		
		Increase by 50%							0.05	0.08		

Table 6.7b Con't.

				Sensitivity by group (average change in estimations)								
No.	Functional group	Perturbations	21	22	23	24	25	26	27	28	29	30
12	Cephalopods	Reduce by 50%	,								-0.09	
		Increase by 50%									0.09	
13	Threadfin bream (nemipterids)	Reduce by 50%				-0.16				-0.06		
		Increase by 50%				0.16				0.06		
14	Bigeyes (priacanthids)	Reduce by 50%	-0.20			-0.14	-0.05			-0.04		
		Increase by 50%	0.20			0.14	0.05			0.04		
16	Juvenile Hairtail (trichiurids)	Reduce by 50%	-0.05									
		Increase by 50%	0.05									
21	Croakers (\leq 30 cm)	Reduce by 50%	1.00									
		Increase by 50%	-0.33									
22	Juvenile large croakers	Reduce by 50%	-0.07	1.00								
		Increase by 50%	0.07	-0.33								
23	Croakers (> 30 cm)	Reduce by 50%			1.00							
		Increase by 50%			-0.33							
24	Demesral fish (\leq 30 cm)	Reduce by 50%				1.18	0.08		0.08	0.42		
		Increase by 50%				-0.35	-0.02		-0.02	-0.11		
25	Juvenile demersal fish (> 30 cm)	Reduce by 50%					0.98					
		Increase by 50%					-0.33					
26	Adult demersal fish (> 30 cm)	Reduce by 50%						1.00				
		Increase by 50%						-0.33				
27	Benthopelagic fish	Reduce by 50%							0.91	-0.04	-0.12	
		Increase by 50%							-0.30	0.04	0.12	
28	Melon seed	Reduce by 50%								1.00		
		Increase by 50%								-0.33		

Table 6.7b Con't.

		Sensitivity by group (average change in estimations)										
No.	Functional group	Perturbations	21	22	23	24	25	26	27	28	29	30
29	Pelagic fish (\leq 30 cm)	Reduce by 50%									1.00	
		Increase by 50%									-0.33	
30	Juvenile large pelagic fish	Reduce by 50%							-0.10	-0.08		1.00
		Increase by 50%							0.10	0.08		-0.33
34	Seabirds	Reduce by 50%	-0.04									
		Increase by 50%	0.04					•				
35	Pinnipeds	Reduce by 50%	-0.04									
		Increase by 50%	0.04									
36	Other mammals	Reduce by 50%			-0.04							
		Increase by 50%			0.04							

Table 6.7b Con't.

			Sensitivity by group (average change in estimations)							
No.	Functional group	Perturbations	31	32	33	34	35	36	37	
31	Pelagic fish (> 30 cm)	Reduce by 50%	1.00							
		Increase by 50%	-0.33							
32	Demersal sharks and rays	Reduce by 50%		0.94						
		Increase by 50%		-0.31						
33	Pelagic sharks and rays	Reduce by 50%			1.05					
		Increase by 50%			-0.34					
34	Seabirds	Reduce by 50%				1.00				
		Increase by 50%				-0.33				
35	Pinnipeds	Reduce by 50%					1.00			
		Increase by 50%					-0.33			
36	Other mammals	Reduce by 50%						1.00		
		Increase by 50%						-0.33		
37	Marine turtles	Reduce by 50%	`						1.00	
		Increase by 50%							-0.33	

6.4. Discussion

This study showed that the NSCS ecosystem underwent great change between the 1970s and the 2000s. Particularly, the ecosystem had changed from being dominated by demersal species to a heavily-exploited system dominated by pelagic species with a high turn-over rate. Such changes have been observed in other exploited ecosystems such as the Gulf of Carpentaria in Australia (Harris & Poiner 1991), northeastern coast of the United States (Link & Brodziak 2002), and the Mediterranean and Black Seas (de Leiva Morena *et al.* 2000). Two possible hypotheses that may explain such changes are: (1) increased fishing effort especially by bottom trawlers increased fishing mortality of benthic and demersal groups; (2) eutrophication enhanced the productivity of the benthopelagic and pelagic groups.

Both of these hypotheses may have contributed to the observed ecosystem changes but there is more evidence to support the hypothesis related to fishing. In the NSCS, a large fraction of the region's increase in nominal fishing effort (over 8-folds in the past five decades) was from the demersal trawl sectors (Lu & Ye 2001). The detrimental effects of bottom trawling on benthic and demersal communities are well known (Sainsbury et al. 1997; Watling & Norse 1998). Moreover, fishing power and technology also improved dramatically, e.g. the widespread use of global positioning system, acoustic fish finder (Cheung & Sadovy 2004). The technological improvement enabled trawling in most part of the NSCS continental shelf. Thus, the increased fishing effort of bottom trawlers might have largely increased the fishing mortalities of the demersal groups. These factors might have contributed to the heavier depletion of demersal resources relative to the benthopelagic and pelagic groups (Chapter 5). The latter were generally less catchable by the demersal gears. Growing populations, increased agriculture and industrial development in China and neighboring countries increased the run-offs of nutrients and organic pollutants into the coastal area and continental shelf of the NSCS (Morton & Blackmore 2001). These were suggested to be the cause of the increased incidence of harmful algal blooms in some coastal regions (Lam & Ho 1989; Huang & Qi 1997). However, due to the lack of consistent time-series data, the effects of changes in primary productivity on the NSCS continental shelf

ecosystem could not be shown (Chapter 7). When better time-series data of primary productivity are available in the future, it will be possible to evaluate the relative contributions of these two effects.

Fisheries became increasingly dependent on lower trophic level species. This agreed with the decreasing ratio of fish to invertebrate landings in the NSCS during the same period. Such changes may be explained either by the shift in target species following the increase in shrimp trawl effort that targeted primarily benthic invertebrates, or genuine changes in ecosystem structure. Results from this study suggested that the latter was the likely explanation of the estimated changes. This agrees with previous studies that showed depletion of large predatory demersal fishes in the NSCS (Chapter 5) and elsewhere in the South China Sea (Christensen 1998; Pitcher & Pauly 1998). When time-series of catch or landing data by fishing sectors in the region become available, the relative contribution of the gear-change effect on the declining trophic level of catch can be better understood.

Ecosystem maturity generally declined between the 1970s and 2000s with the depletion of the older, long-lived species that had accumulated large amounts of biomass when the system was relatively underexploited. This is reflected by comparing various system indices against Odum's attributes of ecosystem maturity (Odum 1969; Christensen 1995). For instance, the 1970s system had a more balanced production to respiration ratio, smaller system production to biomass ratio, more diverse trophic network and higher system overheads. The more mature 1970s ecosystem should be more stable and resilience to perturbations (Vasconcellos *et al.* 1997). Such perturbations may include environmental variability and anthropogenic changes e.g., climate change.

The reduced stability of the 2000s ecosystem, the increased dominance of the pelagic system and the increased dependence on lower trophic level species by the fisheries might increase the volatility of the ecosystem and fisheries (Pauly *et al.* 1998). Population dynamics of fishes that are small-bodied, fast growing and with high fecundity are often strongly affected by the environment (Winemiller 2005) and have large inter-annual variability (Spencer & Collie 1997). Particularly, as intensive fishing had removed a large proportion of the adult biomass, the populations were dominated by

juveniles. Such truncation of age-class in fish populations may further intensify the variability of populations (Hsieh *et al.* 2006). Increased variability of catches due to the stock variabilities might have considerable socio-economic impacts to the fishing communities. Particularly, fishing fleets that build up fishing capacity during the 'good' fishing years may suffer from economic hardship when environmental factors reduce fishery productivity.

Restoring the 2000s system back to a state with abundant predatory and demersal species may be beneficial ecologically and economically (Pitcher & Pauly 1998; Pitcher 2004). Ecologically, restoration prevents depletion, extirpation or even extinction of some vulnerable species that have been heavily fished in the NSCS. A restored system would have higher ecosystem maturity, stability and resilience, which would helps dampen out the impacts of environmental variability (Peterson et al. 1998; Hsieh et al. 2006). This is especially important as global climate change may further increase environmental fluctuations in the future (Roessig et al. 2004). Economically, as many of the commercially valuable species were strongly over-exploited, the potential economic productivity from these resources were dissipated (Gordon 1954). Restoration can increase stock abundance and improve the profitability of the fisheries. On the other hand, as over-exploitation by fishing appears to be the major driver of ecosystem changes in the NSCS, any restoration effort would likely require reduction of the current level of fishing effort. Thus fishers may suffer from short-term social (jobs) and economic difficulties. Moreover, restoration, conservation and fisheries management measures are sometimes costly to implement. Assessments of trade-offs between ecological and socio-economic objectives in the NSCS are useful to determine viable policy options (Chapter 8).

Parameters values were estimated with higher certainty in the 2000s model than the 1970s model. Input parameter values of this model such as biomass and mortalities were mainly from the latest survey carried out by the Chinese research institute (Jia *et al.* 2004). Data obtained from these studies were relatively more accurate. On the other hand, parameter values of the 1970s were mostly estimated from indirect methods. For instance, the biomass of the fish groups in the 1970s were back calculated from the changes in catch rates between different periods, while gross assumptions were made for estimating the P/B ratios. Moreover, the 1970s model was more sensitive to the uncertain parameters

as the leverages of individual input parameter values to the outputs were higher in the 1970s model. Biomasses of the high trophic level groups were generally large in the 1970s model. Also, predation mortalities constituted a relatively higher proportion to total mortalities in the 1970s system. Thus relatively small change in parameter values such as biomass and Q/B ratio strongly increased total consumption or production, which resulted in a large influence on the mortalities of their prey and competitors.

This situation could be improved by replacing or validating the indirectly estimated input parameters with more precise survey-based estimates. Although large-scale surveys in the NSCS were carried out by the Chinese authorities during the 1960s, 1970s and 1980s, the data are classified by the authorities and not available for use during the course of this study. Declassification of these data could greatly improve the understanding on the changes of the ecosystem, which could help provide more sensible resource assessments and management policy options.

On the other hand, the comparisons of the NSCS ecosystem in the two time periods were robust to alternative ecosystem states generated based on the uncertainties of the parameters. This was shown by the generally small coefficient of variation of the system indices estimated based on the perturbation analysis. In addition, in Chapter 7 of this thesis, the validity of the two models was assessed through fitting time-series relative abundance data using the dynamic Ecosim simulation model. This analysis demonstrates that estimated changes in biomasses from simulations based on the initial parameters generated by the 1970s model agreed reasonably with observed data. Therefore, the conclusions from this study should be valid, although the absolute values of the estimates may be uncertain.

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7. A DEPLETION INDEX AS AN INDICATOR OF BIODIVERSITY STATUS IN ECOSYSTEM SIMULATION MODEL

7.1 Introduction

The impacts of fishing on both targeted species and their ecosystem can be accounted for using ecosystem-based approach to fisheries assessment (EBM). During the past decade, EBM has become widely advocated (Pitcher & Pauly 1998; Hall 1999; Pope & Symes 2000; Pitcher 2001; Pauly *et al.* 2002; Hall & Mainprize 2004; Pikitch *et al.* 2004; Jennings 2005). Governments throughout the world have declared their support through the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem, and various national instruments. Numerous authors have proposed and discussed various tools and approaches (ecological, economic, managerial) to put the EBM concept in operation (Sainsbury *et al.* 2000; Sainsbury & Sumaila 2003; Hilborn 2004; Browman & Stergious 2005; Jennings 2005; Zeller & Pauly 2005). Examples of these tools and approaches include the use of indicators in fisheries management framework to evaluate the state of ecosystem and decide appropriate management actions (Link *et al.* 2002; Jennings 2005; Livingston *et al.* 2005) and developing ecosystem models to explore the effects of fishing and management policies (Pauly *et al.* 2000; Pitcher *et al.* 2005).

Ecosystem simulation modelling is a useful tool to evaluate the effects of fishing and fisheries management policies on ecosystems. Various modelling approaches have tried to simulate interactions between organisms and fisheries, over a range of different assumptions and complexity (Fulton *et al.* 2003). One of the more widely used approaches is Ecopath with Ecosim, or EwE (Walters *et al.* 1997; Pauly *et al.* 2000). Ecopath is a mass-balance model which can be used to describe a snap-shot of the whole ecosystem at a particular time period. Species, usually those with similar biology, are aggregated into functional groups to reduce the number of state variables (see Chapter 6 for details of Ecopath modelling). Ecosim is a dynamic simulation model which simulates changes in the ecosystem that is described in Ecopath. It estimates changes in biomass of functional groups in the ecosystem as functions of abundance of other functional groups and time-varying harvest rates, taking into account predator-prey interactions and foraging behaviors (Walters *et al.* 1997; Pauly *et al.* 2000). Ecosim is governed by the basic equations:

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i$$
eq. 7.1

and

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + a_{ij} \cdot B_j}$$
eq. 7.2

where dB_i/dt gives the growth rate of group *i* in terms of its biomass; g_i is growth efficiency; *M* and *F* are natural and fishing mortalities; *I* and *e* are immigration and emigration rates; C_{ji} is the consumption of organism *j* by organism *i*, *v* and *v'* represent rates of behavioural exchange between invulnerable and vulnerable states; and a_{ij} represents rate of effective search by predator *j* for prey type *i*. The behaviours of functional groups in dynamic simulations are heavily affected by the 'vulnerability factor' – a scaling factor of *v* which determines the foraging behavior of the functional groups in predator-prey interactions (Walters *et al.* 1997; Walters & Martell 2004).

Applications of ecosystem modelling tools to evaluate impacts of fishing on biodiversity are often limited. This is because population dynamics at the species level are difficult to represent explicitly in the models. Hence, in models, the large degree of structural complexity in marine ecosystems is usually simplified or approximated in models. Species with similar functional roles or trophic level are aggregated into a functional group (Fulton *et al.* 2003). This enables better model performance by reducing the number of required parameters and increasing computational efficiency (Fulton *et al.* 2003). For instance, the northern South China Sea (NSCS) models aggregated thousands of species into 38 functional groups (Chapter 6). On the other hand, aggregations may compromise the resolution of the model and reduce the accuracy of the results (Fulton *et al.* 2003; Pinnegar *et al.* 2005).

Aggregations in ecosystem models also mask the differential responses of species within a functional group that may have different intrinsic vulnerability to fishing and consequently a different rate of decline when they are fished (Jennings *et al.* 1999a,b;

Chapters 2 and 5). However, such variations need to be considered in models with aggregated functional groups. This is critical particularly with vulnerable species in a functional group where the threat of over-exploitation may not be evident when they are grouped with numerous other species.

Knowledge about intrinsic vulnerabilities of marine fishes within functional groups can be used to predict species' responses to fishing. Intrinsic vulnerability of fishes is shown to be correlated with their rate of population decline under fisheries exploitation (Jennings *et al.* 1999a, b; Chapters 2 and 5). Therefore, when an ecosystem simulation model predicts that the abundance of a functional group (representing multiple species) is driven down by fishing, species with higher intrinsic vulnerability should decline at a faster rate than those with lower vulnerability. By accounting for the relative intrinsic vulnerability of species within a functional group, we could predict species' relative rates of decline based on the dynamics at the functional group level. Cheung *et al.* (2005) (Chapter 2) developed an index that quantified the relative intrinsic vulnerability of fishes using the species' life history and ecology.

Other indices have been suggested as biodiversity indicators for ecosystem modelling. The two indices that have been incorporated in the EwE software are the diversity index (Q-90) and the mean trophic level of catch (or the marine trophic index, MTI). The Q-90 index is a variant of the Q-index developed by Kempton and Taylor (1976) which indicates the diversity of functional groups in an ecosystem. It is calculated from the slope of the cumulative functional group abundance curve between the 10th and 90th percentiles (see Ainsworth and Pitcher 2005 for details). The index represents both functional group richness and evenness. The MTI is calculated from the average of the trophic level of species weighted by their annual catch (Pauly *et al.* 1998). MTI declines when catches of higher tropic level species (usually more intrinsically vulnerable) decline because of their over-exploitations while species lower in the food web (usually less vulnerable) dominate in the catch. Such decline in MTI indicates deteriorating conservation status. In fact, the MTI is considered a major indicator of marine biodiversity by the IUCN-World Conservation Union (Butchart *et al.* 2004; Pauly & Watson 2005).

This study describes a model that combines simulation modelling with the intrinsic vulnerability of the species to predict the effects of fishing and different fisheries management strategies at the species level. Ecosim simulations using the NSCS Ecopath model (described in Chapter 6) were used as a case study to test this depletion index. The 2000s NSCS ecosystem has been largely depleted compared to the ecosystem in the 1970s (Chapters 5 & 6). Also, the ecosystem has changed from a demersal-dominated to a pelagic-dominated system. To validate the NSCS model for testing the index, the 1970s NSCS model was fitted with historical time-series catch-per-unit effort data (from Chapter 5). The estimated parameters were then transferred to the 2000s model. The validity of the depletion index was studied by evaluating the correlations between the depletion index and other previously used biodiversity indices.

7.2. Methods

7.2.1. Depletion index

A depletion index (DI) was developed to represent the possible responses of a species as a member of a single functional group in an ecosystem model. The DI was based on the assumption that intrinsically more vulnerable species aggregated within a functional group should decline faster than the less vulnerable species. Thus, the DI was calculated from prior knowledge of the intrinsic vulnerability, population status of the functional group at starting year and the estimated changes in functional group biomasses. Intrinsic vulnerability was represented by the index developed in Cheung *et al.* (2005) (Chapter 2) while population status was expressed as the ratio of current to unexploited biomass.

The relationships between intrinsic vulnerability, population status, biomass change and depletion levels were governed by sets of rules (Table 7.1). The rules represented qualitative descriptions of how depletion risks were inferred from indices, i.e., the higher the intrinsic vulnerability and the larger the decline in biomass of the functional group, the higher the DI. In principle, the rule matrix is similar to other decision matrices, e.g., the 'traffic light' approach (Caddy 2002) or a 'Consideration Matrix' suggested for the management of cod and haddock (FRCC 2002). These

approaches are systems of status indicators, reference-limits, and corresponding actions which implicitly infer risk of over-exploitation or depletion (and thus leads to management actions) based on pre-specified rules. There are attempts to implement the traffic light approach in a fuzzy logic system (Silvert 2001).

The levels of intrinsic vulnerability, biomass decline and DI were represented by fuzzy membership functions (Figure 7.1). Fuzzy membership functions are mathematical functions that determine the degree of membership to different heuristic categories based on the input parameters. As prior knowledge about the choice of fuzzy membership functions for the input attributes was lacking, the simplest forms were employed: trapezoid membership functions at the upper and lower limits and triangular membership functions at intermediate positions on the axis. Other options include membership functions having a sigmoid, gamma, or irregular shapes (Cox 1999), which may be explored to test whether their uses are justified.

The memberships to different levels of depletion were calculated from the levels of biomass decline and the intrinsic vulnerability of the species. The memberships to different levels of biomass decline were estimated based on the predicted change in functional group biomass from the simulation model. The predicted biomass changes became the independent variable of the respective fuzzy membership functions (Figure 7.1a). These membership functions then provided the memberships to different levels of depletion. For instance, Chinese bahaba (*Bahaba taigingensis*) belongs to the group 'large croakers' in the NSCS models (Chapter 6). Based on its life history and ecology, its intrinsic vulnerability was estimated to be very high, with a degree of membership of 0.5. If the Ecosim model predicted that biomass of 'large croakers' declined by 84% relative to the starting biomass, based on the fuzzy membership functions specified in Figure 7.1a, the memberships to 'high' and 'very high' biomass decline would be 0.55 and 0.45, respectively. Based on the pre-defined rules (Table 7.1):

IF intrinsic vulnerability is very high (0.5) and decline in biomass is large (0.55)THEN depletion is high (0.5)

IF intrinsic vulnerability is very high (0.5) and decline in biomass is very large (0.45) THEN depletion is very high (0.45)

		Decline in abundance of species within group (relative to B_0)*									
		Very low	Low	Moderate	High	Very high	Extremely high				
	Low	Minimum DI	Minimum DI	Very low DI	Low DI	Low DI	High/Very high DI				
Intrinsic	Moderate	Minimum DI	Very low DI	Low DI	Low DI	Moderate DI	Very high DI				
vulnerability	High	Minimum DI	Low DI	Low DI	Moderate DI	High DI	Very high DI				
	Very high	Minimum DI	Low DI	Moderate DI	High DI	Very high DI	Very high DI				

Table 7.1. Heuristic rules for the relationship between intrinsic vulnerability, relative abundance and the depletion index (DI).

* Default decline in population is calculated as biomass at t_1 /biomass at t_0 , where t_0 is the starting time of the simulation. However, if knowledge on unfished biomass (B_o) is known, the starting biomass can be replaced by B_o .

Predicates

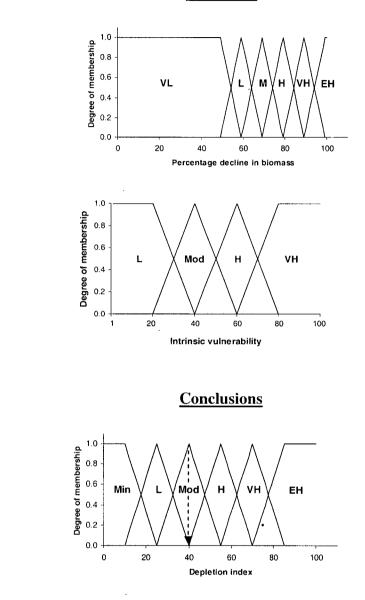


Figure 7.1. Fuzzy membership functions for the inputs: (a) predicted decline in functional group biomass; (b) estimated intrinsic vulnerability of the species; and (c) output: depletion index. The upper two figures (a and b) are fuzzy membership functions for the predicate while the lower figure (b) is fuzzy membership functions for the conclusions. Each attribute are categorized into different levels based on the fuzzy membership functions: VL - very low; L - low; M - medium; H - high; VH - very high; EH - extremely high; Mod - moderate; Min - minimum. The broken line in Figure c indicates the centroid of the 'moderate' fuzzy membership function.

a)

b)

c)

Chinese bahaba would have memberships to 'high depletion risk' and 'very high depletion risk' of 0.5 and 0.45, respectively (values in parentheses are the degree of memberships). The memberships of the conclusion (levels of depletion) were calculated from the minimum of the memberships to their predicates (i.e., biomass decline and intrinsic vulnerability) (Zadeh 1965).

We obtained the degree of membership of the final conclusions by combining the conclusions from each heuristic rule. Membership of the conclusion from each rule was combined using the knowledge accumulation method from Buchanan and Shortliffe (1984):

$$Membership_e = Membership_{e-1} + Membership_i \cdot (1 - Membership_{e-1})$$
 eq. 7.3

where $Membership_e$ is the degree of membership of the conclusion after combining the conclusions from *e* pieces of rules, and $Membership_i$ is the degree of membership of the conclusion of rule *i*.

DI was then calculated from the average of the centroids of each output fuzzy membership function weighted by the membership associated with each conclusion (i) (Figure 7.1):

$$DI = \frac{\sum_{i=1}^{5} Centroid_{i} \cdot membership_{i}}{\sum_{i=1}^{5} membership_{i}}$$
eq. 7.4

In a triangular membership function, the centroid was assumed to be the input variables corresponding to the peak of the triangle. For a trapezoid membership function, the centroid was assumed to be the mid-point between the two ends of the plateau. Following the example of the Chinese bahaba, the estimated DI was 80 (scale from 1 to 100, maximum depletion index = 100).

I programmed the calculation of the DI using Visual Basic 6 and incorporated this sub-routine into the EwE modelling software. By specifying the lists of species within the functional group of a particular Ecopath model, this new routine automatically obtained the required life history parameters for each species from FishBase and calculated the intrinsic vulnerability indices based on the available inputs. Specifically, the species composition and their life history information (maximum body length with, if available, the von Bertalanffy growth parameter K, natural mortality rate, age-at-maturity, longevity, fecundity, spatial aggregation strength and geographic range) (see Chapter II for details) was based on the information available from FishBase (Froese and Pauly 2004, www.fishbase.org). Secondly, this list (442 species of fishes) was uploaded into the newly developed routine in Ecosim (Appendix 7.1). When the Ecosim simulation was run, the routine calculated the DI of the functional group for each time-step (see Appendix 7.1 for screenshots of the interface). Thus the DI can be used as an indicator of the conservation status of marine fishes in Ecosim. The use of this index in policy optimization routine of Ecosim is discussed in Chapter 8.

7.2.2. Validation with the NSCS model

a. Time-series fitting

The 2000s NSCS model described in Chapter 6 was used to test the DI. This model has 38 functional groups and six fishing fleet. To run the model in Ecosim, one of the most important input parameters was the vulnerability parameter that determined the form of the predator-prey relationships. However, the vulnerability parameter in Ecosim cannot be measured empirically. Therefore, it was estimated from fitting the simulation model to time series of the observed index of abundance (CPUE).

To estimate the vulnerability parameters, standardized CPUE data from 1973 to 1988 for 17 commercially exploited taxa (Chapter 5) were fitted to Ecosim dynamic simulations using the 1970s NSCS model. Firstly, changes in the ecosystem groups in the 1970s model were simulated using nominal fishing effort from 1973 to 1988 (total engine power of boats in the NSCS (Department of Fishery Ministry of Agriculture, People's Republic of China, 1996). Then vulnerability factors by prey groups were varied iteratively using a numerical search routine to minimize the sum-of-square error between the observed and predicted abundance trends (Christensen *et al.* 2004). Basic Ecopath input parameters were also adjusted based on their estimated ranges to improve the fit. The estimated vulnerability factors were then transferred to the 2000s model.

Phytoplankton biomasses were varied iteratively to evaluate the possibility of the ecosystem being driven by variations in primary production. After estimating the vulnerability factors by time-series fitting, phytoplankton biomasses in each simulation time-step were varied until the sum-square-error between the observed catch rates data and the simulation results was minimized. Primary productivity and fisheries production in the NSCS were suggested to be partially dependent on environmental factors driven by the winter monsoon (Qiu et al. South China Sea Fisheries Institute, unpublished data; Le and Ning 2006). The duration (in hours) of the strong winter monsoon signals in winter the Kong (from November to March) issued by Hong Observatory (http://www.hko.gov.hk) was used as an index of the strength of the monsoon. The same index was compared with the estimated primary production anomalies from the model to identify any correlation between the two.

b. Relationship between system indicators

Changes to the NSCS ecosystem were simulated in Ecosim and the DI was calculated for each simulation. To calculate the depletion index, firstly, a list of the major species that were likely to be represented in the catches was prepared. Then, using the NSCS model that had been fitted with time-series CPUE data, changes of the NSCS ecosystem in 30 years were simulated with over 180 different combinations of fishing efforts of the six fisheries sectors. For each simulation, the average DI was calculated from:

$$DI = \frac{\sum_{i}^{N} DI'_{i}}{N}$$
 eq. 7.5

where DI'_i is the depletion index of species \underline{i} . N^{\sim} is the total number of species in the functional group specified in the simulation model. For each of the 180 simulations, the Q-90 and MTI were also calculated from the simulation results. Correlations of the DI with the Q-90 and MTI were calculated.

c. Sensitivity analysis

The sensitivity of the calculated DI to vulnerability factors in Ecosim and the rule matrix in calculating the DI was tested. The vulnerability factors are scaling parameters in the Ecosim dynamic simulation model which determine the degree of predator-prey interactions by determining the rate of transfer from a pool of invulnerable prey to a pool of prey vulnerable to predation (Walters et al. 1997; Walters & Martell 2004). Ecosim simulations are generally sensitive to the vulnerability factors. Thus, in this study, simulations were repeated with three different assumptions of vulnerability factors. The assumptions represented top-down (vulnerability factors = 10), bottom-up (vulnerability factors = 1) and 'mixed' (vulnerability factors proportional to the trophic level of prey $(1 + 1)^{1/2}$ groups) controlled ecosystem. The relatively extreme bottom-up and top-down assumptions of predator-prey interactions were used to test the responses of the DI under these extreme assumptions. Moreover, a major assumption in calculating the DI was the rule matrix that determined the relationship between the intrinsic vulnerability, functional group abundance and the depletion levels. Therefore, the analysis was repeated with alternative rule matrices representing 'conservative' and 'liberal' rule sets. The effects of varying these parameters on the calculated DI and its relationship with other indicators were evaluated.

			Decline in ab	undance of speci	es within group	(relative to $B_o)^*$	
		Very low	Low	Moderate	Large	Very large	Extremely large
	Low	Minimum DI	Minimum DI	Minimum DI	Very low DI	Very Low DI	Low/Moderate DI
Intrinsic	Moderate	Minimum DI	Minimum DI	Very low DI	Very Low DI	Low DI	High DI
vulnerability	High	Minimum DI	Very Low DI	Very Low DI	Low DI	Moderate DI	High DI
	Very high	Minimum DI	Very Low DI	Low DI	Moderate DI	High DI	High DI
			Decline in ab	undance of speci	es within group	(relative to B _o)*	
		Very low	Low	Moderate	Large	Very large	Extremely large
	Low	Minimum DI	Minimum DI	Very low DI	Low DI	Low DI	High/Very high DI
Intrinsic	Moderate	Minimum DI	Very low DI	Low DI	Low DI	Moderate DI	Very high DI
vulnerability	High	Minimum DI	Low DI	Low DI	Moderate DI	High DI	Very high DI
	Very high	Minimum DI	Low DI	Moderate DI	High DI	Very high DI	Very high DI

Table 7.2. Alternative heuristic rules that describe the relationship between intrinsic vulnerability, relative abundance and the depletion index (DI) representing the more optimistic (upper table) and pessimistic (lower table) scenarios.

Default decline in population is calculated as biomass at t_{0+1} /biomass at t_0 , where t_0 is the starting time of the simulation. However, if knowledge on unfished biomass (B_o) is known, the starting biomass can be replaced by B_o .

7.3. Results

7.3.1. Time-series fitting

Simulated biomasses from the fitted model generally matched with the observed relative biomass trends (Figure 7.2). The total sum-of-square error was minimized to around 77.9 from over 1,000 after varying the vulnerability factors iteratively. However, the model could not emulate some of the large fluctuations in the observed relative biomass time-series of some groups (e.g., large croakers, threadfin breams, pomfrets). The high variability of the CPUE data was likely a result of the high uncertainty of the CPUE estimations due to the original data collection methodology (see Chapter 5 for details).

The sum-of-square error increased substantially when vulnerability factors were assumed to be bottom-up (vulnerability factors = 1), top-down (vulnerability factors = 10) or proportional to the trophic level of prey groups throughout the system, which were estimated to be 122, 2266 and 1980, respectively (Figure 7.3). Particularly, under these alternative rule assumptions, the model failed to reproduce the rapid decline in CPUE in the 1980s for the major commercial groups such as the threadfin breams, bigeye, cephalopods and small croakers.

Varying the phytoplankton biomasses improved the goodness-of-fit. The sum-ofsquare error was reduced by about 35%. However, the predicted phytoplankton biomass anomalies did not correlate with the index of monsoon strength (Figure 7.4). In fact, the short time-series (16 years) available limited the utility of simulation results for evaluating the possible ecosystem effects of primary production variations.

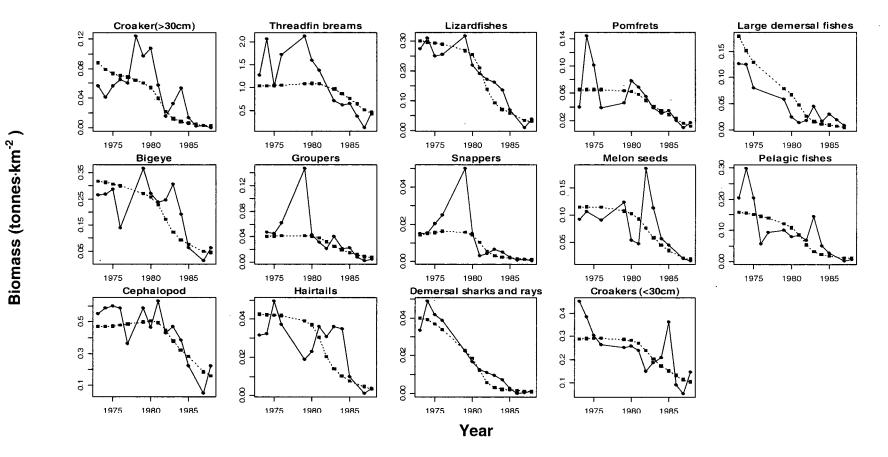
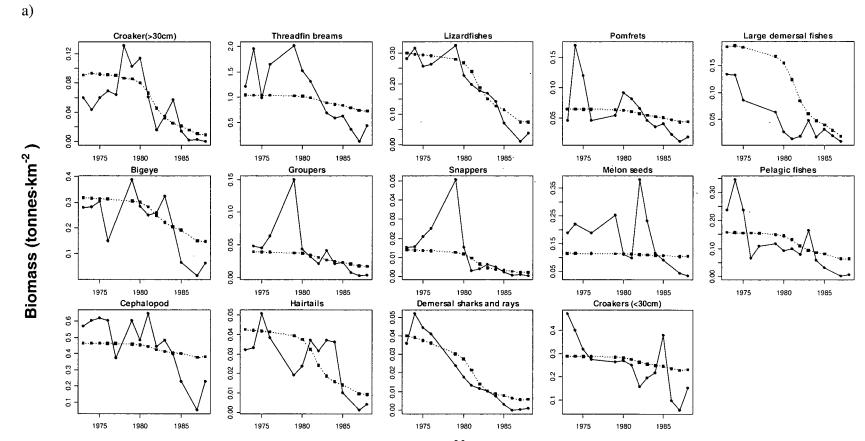


Figure 7.2. Time-series of the observed relative biomasses (solid lines) and predicted biomasses (broken lines) of the 14 functional groups in the northern South China Sea model. The observed relative biomasses are CPUE estimated from survey (Chapter 5) and has been scaled by the model to obtain the best fit with the predicted biomasses. The total sum-of-square error between the predicted and observed data is 78.



Year

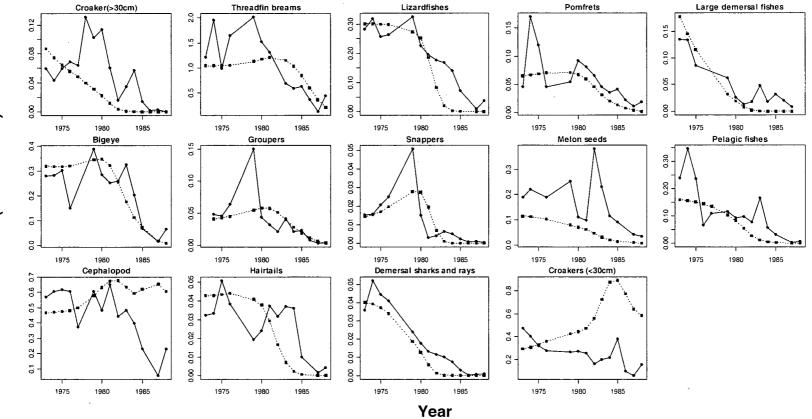
Figure 7.3.

230

-



Biomass (tonnes·km⁻²)





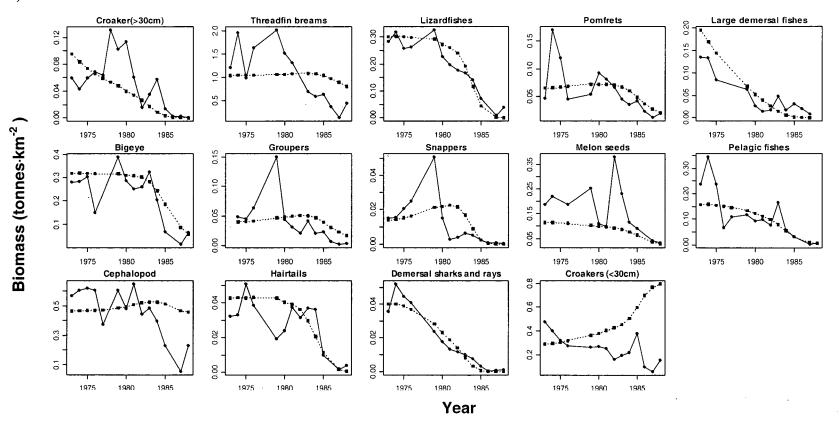


Figure 7.3. Time-series of the observed relative biomasses (solid lines) and predicted biomasses (broken lines) of the 14 functional groups in the northern South China Sea model, assuming that the ecosystem is: (a) bottom-up (assuming 'vulnerability factor' = 1), (b) top-down (assuming 'vulnerability factor' =10) and (c) 'mixed' (assuming 'vulnerability factor' is proportional to the group's trophic level). The sum-of-square error between the predicted and observed data of the bottom-up, top-down and "mixed" assumptions are 122, 2266 and 1980, respectively.

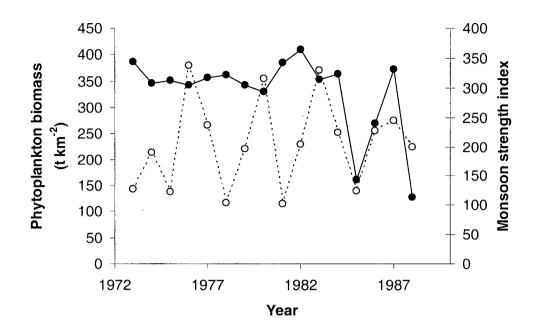


Figure 7.4. Comparison between the predicted phytoplankton biomass (solid dots) from fitting the NSCS ecosystem model with time-series catch rate data and the observed winter monsoon strength index (open circles).

7.3.2. Depletion index (DI)

The estimated DI was correlated with the biomasses of predatory or highly vulnerable groups (e.g., sharks and rays), particularly those that had been depleted (Figure 7.5). In the NSCS model, simulations with low DI (= 7.8) had large increases in biomasses of intrinsically vulnerable or previously depleted groups, such as the sharks and rays, groupers, threadfin breams and croakers. On the contrary, these groups were greatly depleted in the ecosystem with relatively high DI (= 51.5). The system with moderate DI (= 25.3) fell within these two extremes. Therefore, the DI calculated from the simulation results could largely represent the general conservation status of the ecosystem.

Under different scenarios of fishing effort, the resulting DI was significantly and negatively correlated with the Q-90 index (Kendall's correlation test, correlation coefficient = 0.87, p<0.01) and the marine trophic index (MTI, Kendall's correlation test,

correlation coefficient = -0.72, p<0.01) (Figure 7.6). Correlations between the depletion index, Q-90 and the MTI remained strong and significant under different the assumptions in the heuristic rules matrix (Kendall's tests, p<0.01) (Figure 7.7), although correlations between the indicators were slightly lowered. Moreover, the absolute values of the depletion index changed with different sets of rule. A more conservative set of rules lowered the predicted DI while the more liberal set of rules increased the predicted DI. The changes in absolute values would not affect the validity of using the depletion index provided that a consistent set of rules was used throughout the analysis.

Varying the assumptions about vulnerability in Ecosim had stronger effects on the relationship between DI and the Q-90 index (Figure 7.8). When the NSCS ecosystem was assumed to be bottom-up or 'mixed' controlled (i.e., vulnerability factors of all predatorprey interactions were set to be 1 and proportional to the trophic level of prey groups, respectively), the relationship of DI with the MTI and Q-90 index remained significant and strong (Kendall's correlation test, p<0.01; correlation coefficients = 0.80 and 0.52, respectively for the bottom-up assumption and 0.95 and 0.95, respectively for the 'mixed' assumption). However, when the system was assumed to be top-down controlled, i.e., vulnerability factors were set to be 10, the plot between the MTI and DI became more scattered, although the correlation was significant (Kendall's correlation test, p<0.01, cor

The estimated DI was able to track the changes in the conservation status of the NSCS ecosystem (Figure 7.9). When changes in the NSCS ecosystem due to linear increase in the fishing effort of all sectors from the *status quo* were projected for 30 years, the DI increased over time. The increase in DI indicated a deterioration of the conservation status of the ecosystem. On the contrary, with linear decline in fishing effort from the *status quo*, the DI decreased consistently, indicating an improvement in conservation status.

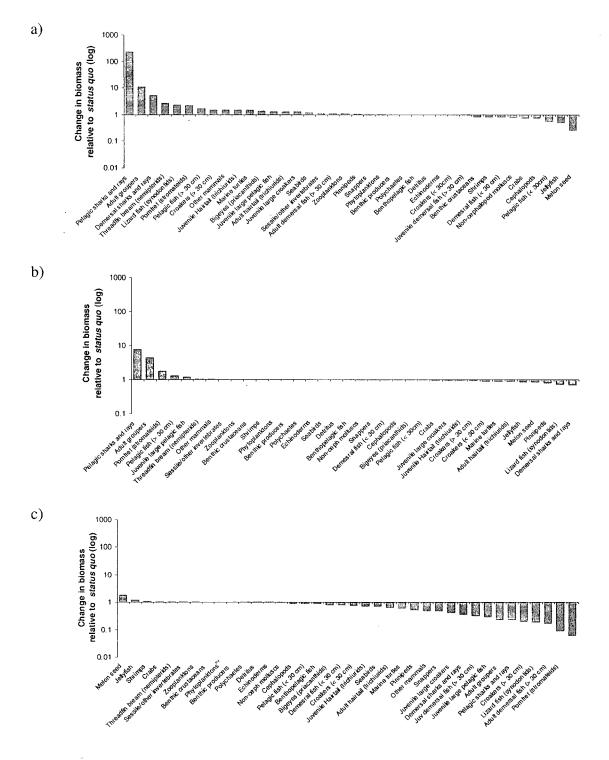


Figure 7.5. Simulated changes in biomass of the 37 functional groups of living organisms in the NSCS model relative to the *status quo* (Ecopath base) (log-transformed) when the estimated depletion index is (a) low, DI = 7.8, (b) medium, DI = 25.3 and (c) high, DI = 51.5.

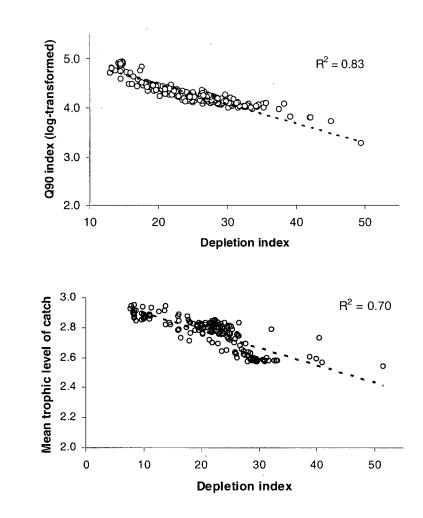


Figure 7.6. Comparisons of the depletion index with published ecological indices (a) Q-90 index (Ainsworth and Pitcher 2006) and (b) mean trophic level of catch (Pauly *et al.* 1998). The dotted lines represent the results of linear regression between the two indices.

a)

b)

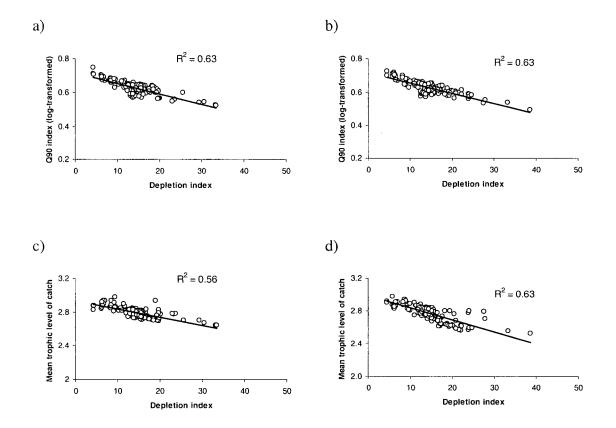


Figure 7.7. Correlations between (a, b) Q90 biodiversity index and (c, d) mean trophic level of catch with the depletion index using (a, c) conservative rule matrix and (b, d) liberal rule matrix.

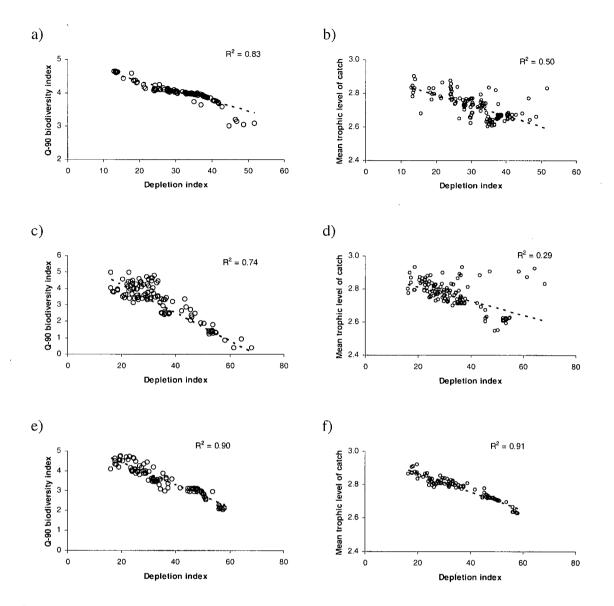


Figure 7.8. Correlations between (a, c, e) Q90 biodiversity index and (b, d, f) mean trophic level of catch with the depletion index calculated from simulations by assuming: (a, b) bottom-up ecosystem control, i.e. vulnerability factors = 1, (c, d) top-down ecosystem control, i.e. vulnerability factors = 10, and (e, f) 'mixed' ecosystem control, i.e. vulnerability factors are proportional to the trophic level of prey groups.

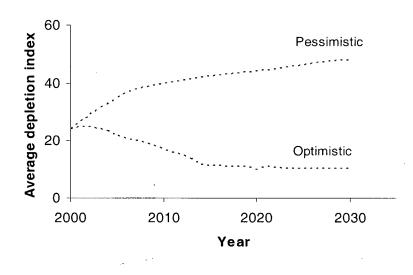


Figure 7.9. Predicted average depletion index of the NSCS ecosystem from 2000 to 2030. The pessimistic scenario assumes a 3-fold linear increase in fishing effort from 2000 to 2030 while the optimistic scenario assumes a linear decrease in fishing effort to a quarter of the 2000 level in 2030.

7.4. Discussion

The depletion index presented in this study provided a means to evaluate conservation status at the species level through ecosystem simulation modelling. The DI accounts for the life history and ecology of the composite species within a functional group. Also, the rule matrix was developed from well-established empirical trends. These provided the biological rationale to the calculation of the index.

The DI was able to indicate the conservation status of the species in all test cases. Firstly, predictions from the DI were consistent with other biodiversity indicators (the Q-90 and MTI). Secondly, the DI calculated from the simulation results matched with the overall conservation status as indicated by the increase in biomass of depleted and vulnerable groups predicted by the ecosystem simulation models when DI was low and *vice versa*. For instance, a high DI was predicted for a highly depleted ecosystem with fishing pressure. A low DI was predicted for an ecosystem with low fishing pressure that was lightly depleted. These results demonstrate that the DI can be a valid indicator of the conservation status of an ecosystem.

The DI was robust to major assumptions in the calculation of the index. A major assumption in the calculation of DI was the rule matrix. This matrix determined how the input parameters (intrinsic vulnerability and decline of functional group abundance) were related to the outputs (depletion risk of the species within a functional group). Sensitivity analysis showed that the estimated DI was robust to this assumption. In fact, the critical factor in determining the rule matrix is to capture the positive relationship between the intrinsic vulnerability of a species, the rate of decline of the functional group biomass and the resulting depletion risk of the species. The exact form of the rules had a small effect on the relative level of the DI. The DI was also robust to uncertainties in the ecosystem model. The performance of the DI remained good when different trophic controls (vulnerability factors in Ecosim) were assumed. Calculations of DI were applied to fish groups only, but results of this study demonstrate that the DI is a valid and stable indicator of the conservation status of the ecosystem.

The DI was based on easily obtainable information available from open-access online databases and may potentially be applied to most marine ecosystems. In fact, the required biological information for calculating the index is readily available from FishBase (www.fishbase.org). The list of species within the functional groups can be compiled from the species database in FishBase. Also, the new sub-routine developed in this study can automatically extract the required biological parameters from a FishBase database. Moreover, the intrinsic vulnerability index, a key parameter in calculating the DI, will soon be made available as a standard index in FishBase (Froese, R. IFM-Geo-Mar, Kiel, Germany, pers. comm.).

The validity of the predictions from the NSCS model was supported by fitting the model with time-series of catch rates. Although some variations in the data could not be explained by the model, such variations mainly resulted from data uncertainty and environmental changes. The original time-series data were collected using low-accuracy methodology (based on fisher interviews at fishing ports). Therefore, the time-series data should have high inherent uncertainty and variations. Secondly, the NSCS is strongly

influenced by the monsoon (Morton & Blackmore 2001). The seasonal variation of ocean currents driven by the monsoon may explain the fluctuations in the catch rates of some taxa. However, the time-series (16 years) was too short for any meaningful time-series analysis to evaluate the correlations between the data and potential environmental drivers. Such analysis could be done when more consistent data are collected in the future. Given these uncertainties, the model successfully reconstructed the average trends of the CPUE time-series included in the analysis. Thus the model was believed to provide reasonable predictions of ecosystem changes and could be used as a reference model to test the DI.

The DI was applied to fish groups only, but its application can be extended to other marine fauna. The DI bases strongly on the index of intrinsic vulnerability to fishing which is developed from life history theory (Chapter 2). As life history theory is generally invariant to a wide range of fauna (from mammals to invertebrates) (Charnov 1993; Charnov & Downhower 2002), correlates between life history and vulnerability to fishing in non-fish marine animals should be similar to those in fishes. Also, the inputs for calculating the intrinsic vulnerability index and DI (e.g., maximum body size, age at maturity and longevity) are available for non-fish groups. The DI should be applicable to a wide range of marine fauna. Future studies can compare the predictions from the indices with empirical data to test the applicability of the indices to non-fish groups.

In summary, the DI is proved to be a valid indicator for evaluation of the conservation status of fish species in models with highly aggregated groups. The DI helps to overcome a fundamental difficulty in addressing the conservation concerns at the species level while evaluating the changes at the ecosystem level. This is particularly useful in understanding the trade-offs between objectives that focus on the species level (e.g., conservation of vulnerable species) and those that focus on the ecosystem level (e.g., economic benefits from the ecosystem). Applications of the DI in evaluating various policy trade-offs in the NSCS are documented in Chapter 8. Here, an EwE model of the NSCS was used as operating model to test the indicator. However, potential applications of this index should not be restricted to the EwE modelling approach. Instead, it can be applied to other types of ecosystem models in which species are aggregated in functional groups. Moreover, the DI should be applicable to other non-fish marine taxa. Therefore,

the DI enhances the use of ecosystem models in development of ecosystem-based fisheries management.

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7.5. References

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8. TRADE-OFFS BETWEEN CONSERVATION AND SOCIO-ECONOMIC OBJECTIVES IN MANAGING A TROPICAL MARINE ECOSYSTEM⁷

8.1. Introduction

Conservation of marine species that are threatened by fishery exploitation is a growing concern. Over the past few decades, over-exploitation of fishery resources has caused depletion, or extirpation in some extreme cases, of marine populations (Pauly *et al.* 2002; Dulvy *et al.* 2004; Hilborn *et al.* 2004a). The need to conserve these populations is being formally recognized by international and national treaties and legislations. Developing fishery management policy that conserves marine biodiversity is an important step towards addressing the above problems.

A challenge to managing exploited marine ecosystems is the trade-offs between ecological, social and economic objectives. A trade-off can be thought of as giving up some of one thing to get more of something else. Given a set of alternative allocations or system configurations, a system is considered to be in Pareto-optimum if improvement in any one individual's benefits results in a reduction in benefits to others. The Pareto-frontier is the set of system configurations that are all in Pareto-optimum (Baumol *et al.* 1998). Examples of the Pareto-frontier of a trade-off between two objectives are shown in Figure 8.1. Points located within the Pareto-frontier are inefficient or sub-optimal, because one objective can be improved without causing a reduction in the other. Thus, evaluation of the trade-off relationships can help reveal the 'efficiency' of the fisheries in achieving specified management objectives, and the costs and benefits of policy decisions that change the position on a trade-off state-space diagram.

⁷ A version of this chapter has been submitted for publication. Cheung, W. W. L. & Sumaila, U. R. Trade-offs between Conservation and Socio-economic Objectives in Managing a Tropical Marine Ecosystem. *Ecological Economics[in review]*.

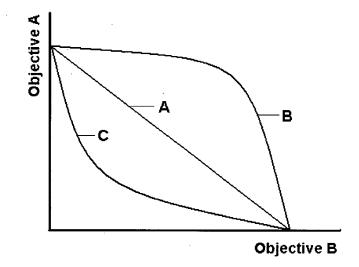


Figure 8.1. Possible trade-off relationships between two fisheries management objectives: (A) linear, (B), convex, and (C) concave (Walters & Martell 2004).

A wide range of trade-offs can be found in fishery management. Among these, trade-offs between ecological and socio-economic objectives are particularly important (Walters & Martell 2004). On one hand, catch may have to be reduced to minimize the risk of stock collapse in the long term (Hilborn *et al.* 2004b). On the other hand, catch should be maximized in the short term to provide economic rent and maintain the livelihoods of the fishing communities.

The trade-offs between conservation and socio-economic objectives are especially complex in a multi-species or ecosystem context. Most conventional resource management approaches aim to maximize the long term sustainable yield of the resources being targeted (Rosenberg *et al.* 1993; Pitcher 1998). However, most fisheries (particularly tropical multi-species fisheries) catch a mixture of species and stocks with different productivity. Thus, the fishing effort required to achieve the maximum sustainable yield may over-exploit, deplete or even extirpate some of the least productive species or stocks, while the most productive stocks may be under-exploited. Particularly,

if the fisheries are open access or if illegal fishing is prevalent, the ecosystem may be fished to a bionomic equilibrium (BE) – the point at which the total revenue from fishing is just enough to cover the total cost (Figure 8.2). At *BE*, the less productive species/stocks may be over-exploited or extirpated (Walters *et al.* 2005) (Figure 8.2). To restore and conserve over-exploited and vulnerable species, fisheries management may need to consider the trade-off between exploitation of species that are not trophically linked, but which have different productivity and are targeted by the same fisheries.

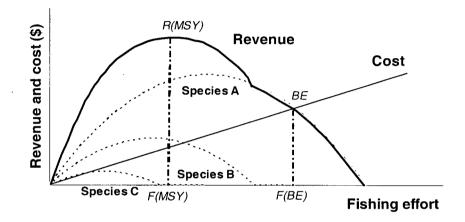


Figure 8.2. Schematic diagram comparing revenue and cost that can theoretically be obtained from a multi-species fishery (without tropic interaction between the species) (Sparre & Venema 1998). The broken lines represent the hypothetical fishery revenue from catching the three species: Species A, B, C have high, medium and low productivity, respectively. Total revenue is represented by the solid line. The shape of this curve is due to the disappearance of less productive species as fishing effort increases. The fishing effort, F(MSY), that achieves the revenue at Maximum Sustainable Yield R(MSY) for all three species leads to under-exploitation of Species A, over-exploitation of Species B and extirpation of Species C. Unregulated fisheries (fishing effort at *BE*) leads to the over-exploitation of all species, with the less productive Species B and C extirpated. Fisheries subsidies generally lower the cost of fishing, thus reduces the slope of the cost line and increases the open access equilibrium effort, F(BE).

The trade-off becomes more complicated when trophic linkages between the species or stocks are considered explicitly. For instance, the recovery of predatory, charismatic or less productive species may reduce the productivity of their commercially valuable prey. The release from predation pressure from cod on commercially valuable

benthic crustaceans in the Northwest Atlantic following the northwest Atlantic cod collapse is a good example (Worm & Myers 2003). Moreover, following the depletion of a predator by fishing, the increased productivity of prey that feed on the juveniles of the preys' predators may prevent recovery of the depleted predators (Walters & Kitchell 2001). A more holistic approach would help understand the trade-offs between different management objectives at the ecosystem level.

Trade-offs between social values (e.g., as a source of livelihoods) and conservation or economic values of the fisheries may be acute. Particularly, when the ecosystem has been over-exploited, most management policies aimed at restoration of depleted populations or improvement of the profitability of fisheries would require reduction of fishing capacity. The associated social problems may be more serious in developing countries where alternative livelihoods for fishers are lacking and the social benefit system is not well-developed. Therefore, to make well-informed policy decisions, policy makers and the public need to understand the costs and benefits associated with such trade-offs.

Understanding the trade-offs between conservation and socio-economic benefits are of considerable interest in the northern South China Sea (NSCS), which is defined as the continental shelf (less than 200 m depth) ranging from 106°53'-119°48' E to 17°10'-25°52' N. It falls largely within the Exclusive Economic Zone of the People's Republic of China, but Vietnam also shares part of the Gulf of Tonkin (Chapter 1). It is a tropical ecosystem where coral reefs, estuaries, mangroves, seagrass beds and others, provide habitats for a rich array of species (Morton & Blackmore 2001).

Rapid expansion of fisheries in the region has resulted in depletion of most fishery resources and loss of biodiversity. From 1978 to 2000, the number of mechanized fishing boats from Guangdong, Guangxi and Hainan – the three provinces bordering the coast of the NSCS - increased from 8,109 to 79,249 (Department of Fisheries, Ministry of Agriculture, People's Republic of China 1991, 1996, 2000). Although NSCS fisheries appear to have a reasonably comprehensive set of legislation and regulations, the high level of illegal fishing (e.g., fishing without a license) may have driven the system towards bionomic equilibrium (BE). Some vulnerable species, such as the Chinese

bahaba (*Bahaba taipingensis*) and Red grouper (*Epinephelus akaara*), were extirpated locally while numerous other species were depleted or over-exploited (Sadovy & Cornish 2000; Cheung & Sadovy 2004). Previous modelling analysis suggested that approximately 20% of fishing grounds should be closed to fishing and fishing effort should be reduced at an annual rate of 5% for 30 years in order for the NSCS ecosystem to recover (Cheung & Pitcher 2006). However, the cited study did not evaluate the socio-economic implications of the suggested policy initiatives and its cost-effectiveness.

8.1.1. Buy-back as means to restructure fishing fleets

Fishing vessel or license buy-back has been proposed as a means to reduce fishing capacity and restructure fishing fleets to achieve specific management objectives (Cunningham & Gréboval 2001). This is a financial mechanism designed to buy fishing vessels or licences from fishers or fishing firms in order to reduce fishing effort and capacity. Various factors, however, may render a buy-back scheme ineffective in removing fishing capacity (Cunningham & Gréboval 2001). For instance, the bought-out fishing capacity may seep back into the fishery through improved technology, increased fishing knowledge and experience. Also, if fishers expect a buy-back scheme to be implemented in the near future, they may build up excessive capacity in anticipation of the buy-back program (Clark *et al.* 2005).

Internalizing the cost of a buy-back through a 'fisher-paid' scheme may improve its effectiveness (Clark *et al.* 2005). Conventional economic theory predicts that, for an over-exploited system, the net benefits from the system should increase if fishing capacity is reduced to a level that produces the highest rent (largest positive difference between the total revenue and cost) or Maximum Economic Rent (MER) (Gordon 1954). It has been suggested that benefits gained by fishers who remain in the fisheries can be used, through taxation, for instance, in vessel buy-back schemes (Pauly *et al.* 2002; Clark *et al.* 2005). This paper attempts to identify the trade-offs between conservation and socio-economic objectives in managing a tropical marine ecosystem exploited by multispecies fisheries. Moreover, the possibility of using vessel buy-backs to achieve conservation goals is assessed.

8.2. Methods

The analyses in this study were based on dynamic simulation models using Ecopath with Ecosim, or EwE (Christensen & Walters 2004a). An ecosystem model of the NSCS was used as a case study to evaluate the trade-offs between different objectives in managing tropical multi-species fisheries. Multi-objective decision analysis was applied in order to identify and display policy trade-offs under conflicting objectives (Enriquez-Andrade & Vaca-Rodriguez 2004). Particularly, EwE incorporates formal numerical optimization routines to search for optimal fishing fleet configurations that maximize the benefits under stated management objectives (see below for details). Fishing efforts that would maximize the benefits to specified conservation, economic and social objectives were estimated. The possible trade-offs between the objectives were then mapped out quantitatively. Finally, strategies to facilitate fishing fleet restructuring to achieve the management goals were discussed.

8.2.1. Ecopath with Ecosim modelling

The NSCS ecosystem model represents a hypothesis of the ecosystem structure in the early 2000s (see Chapter 6). The Ecopath model consists of 38 functional groups with six fishing fleets characterized by their gears (stern and pair trawl, shrimp trawl, purse seine, gillnet, hook and line, and others). The model had been fitted with time-series survey data (see Chapter 7). This supports the validity of using the NSCS model in Ecosim dynamic simulations.

Ecosim is a dynamic model which simulates changes in ecosystems that have been described with Ecopath (Walters *et al.* 1997). It estimates changes of biomass among functional groups in the ecosystem as functions of abundance of other functional groups and time-varying catch rates, taking into account predator-prey interactions and foraging behaviors (Walters *et al.* 1997; Pauly *et al.* 2000). Ecosim is governed by the basic equations:

$$\frac{dB_i}{dt} = g_i \sum_{j} C_{ji} - \sum_{j} C_{ij} + I_i - (M_i + F_i + e_i)B_i$$
 eq. 8.1

and

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + a_{ij} \cdot B_j}$$
eq. 8.2

where equation 8.1 gives the rate of change of biomass of functional group *i*, g_i is growth efficiency, *M* and *F* are natural and fishing mortalities, *I* and *e* are immigration and emigration rates, C_{ji} is the consumption of group *j* organisms by group *i* organism, *v* and *v*' parameters represent rates of behavioral exchange between invulnerable and vulnerable states and a_{ij} represents rate of effective search by predator *j* for prey type *i*. The behaviours of functional groups in dynamic simulations are heavily affected by the 'vulnerability factor' – a scaling factor of *v* which determines the foraging behavior of the functional groups in predator-prey interactions (Walters *et al.* 1997; Walters & Martell 2004). The 'vulnerability factors' in the NSCS model were estimated from empirically observed catch-per-unit-effort data (see Chapter 7). Alternative 'vulnerability factors' representing a complete 'bottom-up' (vulnerability factor = 1), 'top-down' (vulnerability factor = 10) controlled ecosystem (Christensen *et al.* 2004) and 'mixed' (i.e. vulnerability factors proportional to the trophic level of the prey groups) (Cheung *et al.* 2002) were used to test the sensitivity of the analysis to these settings.

8.2.2. Policy optimization

The policy optimization routine in Ecosim (Christensen & Walters 2004b) was used to identify the optimal fishing efforts that maximize the benefits from the NSCS given the specific policy objectives. This analysis included four policy objectives:

(a) Maximizing economic rent

Economic rent is represented by the net present value (NPV) of the flow of profits from the different fisheries over time. NPV of the profits was calculated by taking the difference between landed values and cost, and discounting this over time with a specified discount rate, i.e.,

$$NPV = \sum_{i=0}^{m} \sum_{j=1}^{n} \left[\left(\sum_{k=1}^{q} Y_{ijk} \cdot P_{jk} \right) - C_{j} \right] \cdot \left(1 + \delta\right)^{-i}$$
eq. 8.3

where Y and P are the annual catch and price of species k, C is the total cost of fishing of fishery sector j, i is number of years from the present to the end of the time horizon of the analysis and δ is the discount rate. The discount rate applicable in China was assumed to be 3%, calculated from the interest rate of 9-year Chinese government bonds from 2000-2004 (http://www.chinabond.com.cn). Alternative discount rates of 1% and 5% were used to test the sensitivity of results to this assumption.

Since accurate economic data for the fisheries were not available from China, data from Hong Kong were assumed to be reasonable for the NSCS region. Fishing boats registered in Hong Kong were generally similar to those non-Hong Kong boats in mainland China in recent years. In fact, most new fishing boats in Hong Kong were built in China (Sumaila *et al.* in press). Also, Hong Kong fishers reported that wholesale prices were similar between landing ports (Several members, Aberdeen Fishermen Association, Hong Kong, pers. com.). Skippers of fishing boats in Hong Kong, particularly the trawlers, mostly employ workers and purchase supplies from the Mainland (Sumaila *et al.* in press). Thus, the cost of fishing in the NSCS continental shelf in the 2000s between the fleets from Hong Kong and China should be similar (Table 8.1). All values in HK\$ were converted to US\$ by assuming the fixed exchange rate of US\$ 1 = HK\$ 7.785.

Fishing fleets	Total landed value (US\$ thousand km ⁻²)	Total cost (US\$ thousand km ⁻²)	Profitability (%)
Stern & Pair trawl	2.86	2.64	7.69
Shrimp trawl	15.91	10.02	28.07
Purse seine	1.07	0.77	37.02
Hook and line	0.31	0.29	6.45
Gillnet	2.12	2.03	4.23
Others	2.03	1.19	41.60

 Table 8.1. Landed value, total cost and profitability of the six fishing fleets in the 2000s

 NSCS ecosystem model.

(b) Employment

Employment was measured by the number of jobs that could be generated from the fisheries. Data on the average total amount spent on wages by each fishing sector, and the total value of the catches of Hong Kong fishing fleets were obtained from the Hong Kong government (Agriculture, Fisheries and Conservation Department, Hong Kong, unpublished data). The ratios of wage to landed values in a year between fishing fleets in Hong Kong and the Mainland were assumed to be similar. The amount spent on wages per unit of catch value was calculated and used as a proxy of the amount of employment provided by each fishery sector (Table 8.2).

Fishing fleet	Number of jobs ¹
Stern and pair trawls	2
Shrimp trawl	2
Purse seine	3
Hook and line	6
Gillnet	3
Others	2

Table 8.2. The estimated relative jobs per value for the six fishingfleets in the NSCS ecosystem model.

1. Estimated number of jobs per catch value was relative between fishing fleet. The relative number of jobs were used in the optimization analysis, thus the absolute values were not important in the trade-off analysis.

(c) Ecosystem structure

Two aspects of ecosystem structure were evaluated: (1) ecosystem maturity (Odum 1969) – measured by the longevity-weighted biomass of all functional groups in the model (Christensen & Walters 2004b), (2) biomass diversity – measured by a relative index calculated from a modified Kempton's Q (Q_{90}) index (Kempton & Taylor 1976; Ainsworth & Pitcher 2006). Average longevity was approximated by the biomass to production ratio of the groups. Thus, ecosystem maturity can be maximized by increasing the biomass of long-lived groups. The Q-90 index, a variant of the Q-index developed by Kempton and Taylor (1976), indicates the diversity of the functional groups in an ecosystem. The Q-90 index is calculated from the slope of the cumulative functional group abundance curve between the 10 and 90 percentile (Ainsworth & Pitcher 2006).

(d) Conservation of vulnerable species

An index called the Depletion Index (DI) that had been developed to represent the relative degree of species depletion by fishing in ecosystem simulation modelling was used as a performance indicator of conservation status. Detailed methodology for

calculating the DI is reported separately in Chapter 7. In brief, to calculate the DI, firstly, list of species within the aggregate groups were uploaded to a sub-routine specifically developed to calculate the DI in Ecosim (see Chapter 7). Then, life history parameters for each species were obtained from FishBase (www.fishbase.org). These parameters included: maximum body length, maximum length, age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality, fecundity (only low fecundity is considered), spatial behaviour and geographic range. The life history data were combined with simulated changes in the abundance of the aggregate groups in the ecosystem model using a rule-based expert system (Chapter 7). The expert system then estimated the DI for each aggregate group. The DI ranges from 1 to 100, with 100 indicating the most severe population depletion. The DI was validated and shown to be robust to its major assumptions in comparing the relative conservation status between alternative ecosystem states (Chapter 7).

The average DI of all the specified species in the ecosystem model was used as a proxy for the conservation status of the ecosystem. The proxy ($Func_{DI}$) is calculated from:

$$Func_{DI} = 100 - \frac{\sum_{i=1}^{N} DI_{i}}{N}$$
eq. 8.4

where DI_i is the depletion index of species <u>i</u>. N is the total number of specified species.

The policy search routine employs a multi-criterion non-linear numerical search method (Fletcher 1964; Fletcher & Reeves 1964). It iteratively varies fishing efforts (by fleets) and simulates the changes in fisheries and the ecosystem accordingly until the objective function is maximized. The objective function is calculated from the weighted-sum of the indices that represent the above policy objectives:

 $Func_{Total} = w_{Econ} \bullet NPV + w_{employment} \bullet Employment + w_{e \cos ystem} \bullet Ecol(i)$ eq. 8.5 where

$$Ecol(i) = \begin{cases} ecosystem maturity = (\sum_{i=1}^{n} \frac{B}{P_{i}} \bullet B_{i}) \\ functional group diversity = Q_{90} \\ Ecol(i = Conservation status) = Func_{Di} \end{cases}$$

where w is the weighting factor for objectives specified in the subscript, *NPV* is the net economic value (calculated from eq. 8.3), B and P are the biomass and biomass production of functional group i, respectively.

Trade-offs between policy objectives were evaluated by running the policy search routine with different weighting factors for each objective. Particularly, the trade-offs between conservation of vulnerable fish species and socio-economic objectives were plotted. To ensure the numerical optimization routine had not become trapped by local maxima, each optimization was initiated with random fishing fleet efforts and repeated a number of times (Christensen & Walters 2004b). Benefits in conservation status (expressed as average DI of the ecosystem) from the optimal policies were plotted against other policy objectives. The optimal solutions identified by the optimization routine were approximated as the Pareto-frontier of the trade-offs.

8.2.3. Cost of fleet restructuring

The cost of restructuring the fishing fleets to achieve the Pareto-optimum outcome was estimated by evaluating the cost of a hypothetical buy-back scheme. The cost of buying-back one unit of fishing effort was calculated by treating the fisheries as a small business (Walters *et al.* in press). Since the theoretical buy-back scheme was assumed to happen once at time-step = 0 in the simulation, the buy-back price was calculated by multiplying the revenue per unit effort (R_i) for each fishing sector *i* by 5 times (Walters *et al.* in press). The total buy-back cost (*cB*) required to achieve the management goal was calculated by multiplying the required reduction in fishing effort for each sector *i* (ΔK_i) by the per unit effort buy-back price:

$$cB = \sum_{i=1}^{6} \Delta K_i \cdot R_i \cdot 5 \qquad \text{eq. 6}$$

where $\Delta K_i \ge 0$

The above approach is usually used to value small businesses (Desmond & Marcello 1987), which is appropriate here because most of the fishing enterprises in the Northern South China Sea can be classified as small businesses (Desmond & Marcelo, 1987; Walters *et al.* in press). Also, it is assumed that fleet capital is perfectly non-malleable while human capital is malleable (Clark *et al.* 1979; Clark *et al.* 2005). Therefore, fishers were able to move to other job sectors, and in fact, the PRC authorities have been offering retraining programmes to facilitate switching to other sectors, e.g. aquaculture (Qiu, Y, South China Sea Fisheries Institute, pers. comm.). Thus, the buy-out of human capital is not included in the calculation.

8.3. Results

8.3.1. The Pareto-frontiers

A convex-shaped Pareto-frontier was obtained from the trade-off between net present value of benefits from the fisheries and the average depletion risk of the system (Figure 8.3). The shape of the Pareto-frontier was approximated by a quadratic function. The maximum NPV of benefits (of about US\$ 180,000 km⁻²) from the fisheries over 30 years was achieved at a system state with a depletion index of 27. Further improving the conservation status (reducing the depletion index from 27) reduced the maximum benefits from the fisheries. At a depletion index of 20, the marginal decrease in the NPV of benefits was US\$ 5,600,000 km⁻² per depletion index, while the rate of decrease was more than doubled at a depletion index of 10.

The multi-criteria policy optimization routine could not find any 'optimal' solution when DI was over 27. In other words, any combinations of fishing fleet structure that result in a depletion index of over 27 are sub-optimal in economic and conservation

objectives. Thus, increasing the DI from an index of 27 would reduce the maximum NPV of benefits from the fisheries.

The state of the NSCS fisheries in the 2000s was sub-optimal in terms of both conservation and economic objectives (Figure 8.3). Therefore, by definition, the conservation status (indicated by the DI) could be improved without reducing the economic benefits and *vice versa*. Under the *status quo* of the 2000s and a discount rate of 3% over a 30-year time horizon, the estimated average depletion index of the ecosystem was around 34 and the net present value of the profits was US\$ 117,000 km⁻². Based on the predicted trade-off frontier, reducing the average depletion index of the system from the *status quo* level (34.3) to 15 should not compromise the maximum net economic benefits from the fisheries. Moreover, restructuring the fishing fleets could increase the maximum economic benefits from the *status quo* by over 50% (Figure 8.3).

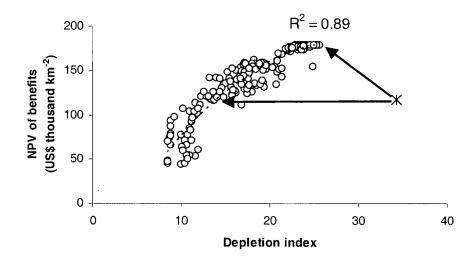


Figure 8.3. Pareto-frontier between the net present value of benefits (profit) of the fisheries and the estimated depletion index assuming a 3% discount rate and an exchange rate between US\$ and HK\$ of 7.785. The equation of the fitted function is: $Y = -0.31x^2 + 17.66x - 69.48$ where Y is the net present value (NPV) of benefits from the fisheries and x is the depletion index. The position of the *status quo* on the trade-off space is marked by an asterisk. The area enclosed by arrows shows the potential improvement from the *status quo* in which neither conservation nor economic benefits would have to be reduced to achieve an increase in the other.

The Pareto-frontier between the depletion index and the social benefits (number of jobs) from the fisheries was approximated by a linear relationship (Figure 8.4). Improving the conservation status (i.e., reducing the DI) from the *status quo* led to an approximately linear decline in the number of jobs provided by the fisheries. For instance, reducing the depletion index from 30 to 10 halved the number of jobs provided by the fisheries the relative number of jobs, conservation performance has to be reduced.

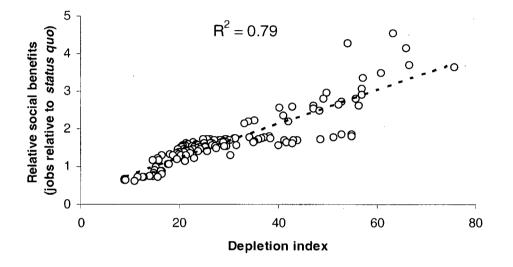


Figure 8.4. Trade-off relationship between social (expressed in number of jobs created relative to the *status quo*) and conservation (depletion index) objectives. The relationship is approximated by a linear function: Y = 0.05x + 0.32 ($R^2 = 0.79$).

The relationship between ecosystem maturity and economic benefits was sigmoid-shaped (Figure 8.5a). Economic profits of the fisheries remain relatively constant at around US\$ 180,000 km⁻² as relative ecosystem maturity index increased from 11 to 12.2 (region of economic stability). However, increasing the index from 12.2 to 12.5 led to a decline in the net economic profits of almost US\$ 200,000 km⁻². Further improvement in ecosystem maturity led to a rapid drop in economic benefits which turned a net gain into a large net loss of over US\$ 1,200,000 km⁻². This represents a region of economic collapse. Therefore, the highest ecosystem maturity level that could be achieved by keeping the net economic benefits at the same level as the *status quo* was about 12.

The shape of the trade-off frontier between the net economic benefits and the Q-90 biodiversity index is similar to the one with ecosystem maturity (Figure 8.5b). As the Q-90 index increased from 4, the maximum NPV of the net benefits from the fisheries decreased gradually. However, when the Q-90 index increased to over 4.7, the maximum NPV of benefits dropped rapidly from over US\$ 130,000 km⁻² to below US\$ 50,000 km⁻². The maximum net benefits remain relatively constant when the Q-90 index increased from 4.8.

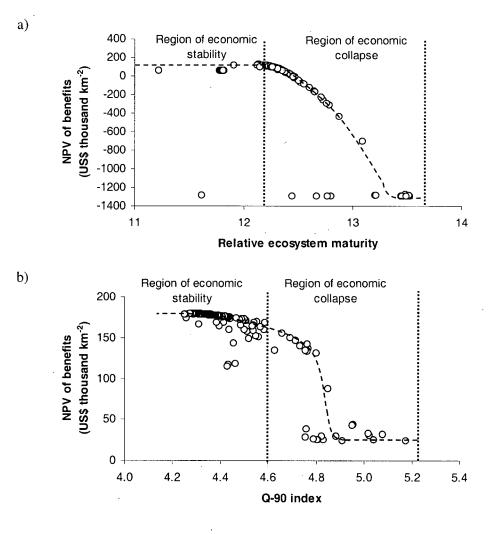


Figure 8.5. The approximated Pareto-frontiers between the net present value of benefits and (a) relative ecosystem maturity, and (b) Q-90 biodiversity index. The horizontal broken line in (a) represents zero net benefit (i.e., points below the dotted line represent fisheries operating at a loss). The vertical dotted lines delineate the regions regions of economic stability and collapse.

8.3.2. Ecosystem structures

The biomass of most vertebrate groups increased when policy objectives focused primarily on conservation (Figure 8.6). The biomass of pelagic sharks and rays show the largest increases of over 400% in 30 years. Such dramatic biomass appears possible given the severely depleted state of the pelagic sharks and rays group (Chapter 5). This is followed by other targeted demersal fish groups such as the groupers, demersal sharks and rays, lizardfish and threadfin breams with more than 10-fold increases in biomasses from the 2000s level (Figure 8.6a). Moreover, abundance of charismatic fauna such as seabirds, marine turtles and marine mammals also increased. Conversely, biomasses of invertebrates (e.g., jellyfish, shrimps and crabs) and small fishes declined. The declines were mainly caused by the increased predation mortalities because of increased predator abundance (Figure 8.6a).

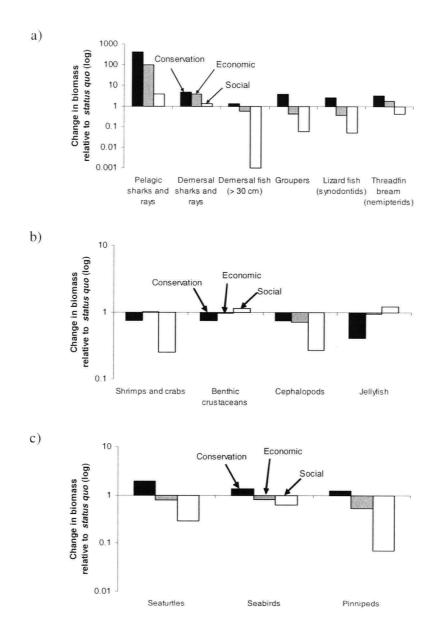


Figure 8.6. Estimated changes in biomass of: (a) fishes, (b) invertebrates and (c) charismatic megafauna from the *status quo* (2000s NSCS model) after 30-year simulation with maximized conservation (black bars), economic (grey bars) and social (open bars) objectives.

Policy focusing heavily on maximizing economic benefits led to further depletion of many functional groups although the biomass of some target groups increased slightly (Figure 8.6b). Many targeted demersal fish groups (e.g., lizard fish, groupers, adult demersal fish, hairtail, small and large croakers, etc) and charismatic fauna (pinnipeds, sea turtles and seabirds) decreased by 20% to 70% from the 2000s level. The biomass of benthic invertebrates, jellyfishes and pelagic fishes increased slightly. Also, biomass of some targeted groups such as threadfin bream and pomfret and the heavily depleted sharks and rays increased.

The model predicted very high level of depletion when policy objectives focused only on maximizing the number of jobs (social objective) (Figure 8.6c). Most of the demersal groups were depleted to less than 30% of the *status quo* biomass. Some groups were fished to near extinction (Adult demersal fish). The less-affected groups included benthic invertebrates, jellyfish and pelagic fishes.

8.3.3. Restructuring the fishing fleets

Moving from the *status quo* to the Pareto-optimum solutions requires restructuring the fishing fleets (Figure 8.7). To improve the conservation status from the *status quo* level (depletion index = 34), fishing effort of the pair and stern trawl sector and the gillnet fleet was reduced in most scenarios. The effort of most fishing sectors decreased in scenarios with a heavy focus on conservation status. An exception was the purse seine fleet which achieved an increase in effort (Figure 8.7). To maximize the net economic benefits, fishing effort of the 'others' fleet increased as much as 4.5 times the *status quo* level. This is due to the high profitability of this fleet. Effort by the shrimp trawlers remained the same, while efforts from the other fleet decreased (Figure 8.7). When heavy weight was put on the social objective (i.e., maximizing the number of jobs provided by the fisheries), fishing effort by most fleets, except the stern and pair trawls and the gillnet fleets, was increased (Figure 8.6). In particular, the shrimp trawl sector experienced an almost 14 times increase in fishing effort from the *status quo* level.

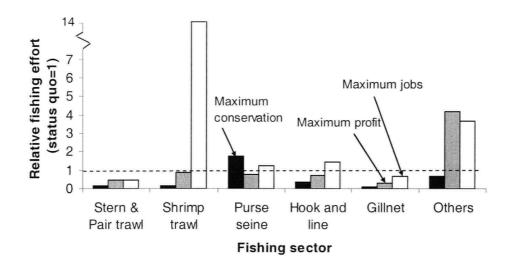


Figure 8.7. Relative fishing effort of the six fishing sectors required to achieve the best conservation status (depletion index <10) (black bars), the highest net economic benefits (30 year time-horizon, 3% discount rate) (grey bars) and the maximization of social benefits (number of jobs) (white bars). The dotted line represents the fishing effort level at *status quo*.

8.3.4. Buy-back cost

To move the fishery from its current Pareto inefficient state under the *status quo* to the Pareto-frontier, the estimated cost of a buy-back scheme increased exponentially as the depletion index of the NSCS ecosystem decreased (i.e., improvement in conservation status) (Figure 8a). When fishers who remain active are paid for the cost of buy-back (cost internalization), profits remained higher than the *status quo* level for a slight improvement in conservation status (Figure 8b). Internalization of the buy-back cost was calculated by subtracting the NPV of net profits by the buy-back cost required to restructure the fishing fleets to achieve the optimal points (Munro & Sumaila 2002). With the internalized buy-back cost, the overall shape of the frontier remained convex. The fisheries could potentially achieve higher profits relative to the *status quo* if the DI was above 17. However, further reduction of the DI reduced the profits from the *status quo* level. The fisheries would be running at a loss if the DI were to be reduced to below 10.

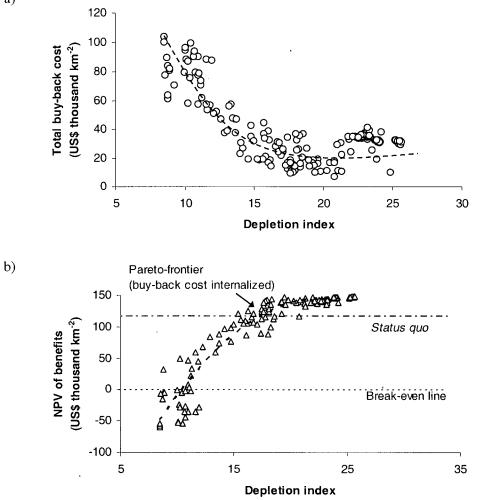


Figure 8.8. The (a) estimated buy-back cost to reduce fishing capacity in order to achieve the Pareto-optimal outcome and (b) the estimated Pareto-frontier after internalizing the cost of buy-back to achieve the Pareto-optimum. The upper and lower horizontal lines represent the net present value of benefits (using 3% discount rate over 30-year time horizon), and the break-even point (zero discounted profit), respectively.

8.3.5. Sensitivity analysis

While absolute values varied, the shapes of the Pareto-frontiers are similar under different discount rate scenarios (Figure 8.9). As expected, a higher discount rate reduced the net present value of profits from the fisheries. NPV of profits started to decline rapidly when the DI of the ecosystem was reduced to below 25. Moreover, the steepness

a)

of the decline in profits increased with higher discount rate. In general, the trade-off of relative economic and conservation benefits was qualitatively robust to the discount rates used in this study (1% to 5%).

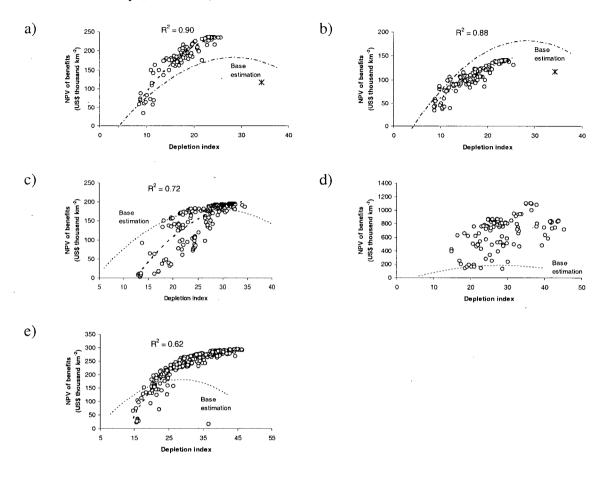


Figure 8.9. The estimated Pareto-frontiers between the net present value of benefits and the calculated depletion index under (a) annual discount rates = 1%, (b) annual discount rates = 5%, (c) bottom-up controlled (vulnerability parameters = 1), (d) top-down controlled (vulnerability parameters = 10) and (e) vulnerability parameters proportional to the trophic level of prey groups. The 'base estimation' (discount rate = 3% and vulnerability parameters estimated from fitting with time-series data, Chapter 7) was included in the figures for comparisons. The data points in (a), (b), (c) and (e) were fitted with quadratic functions. The results from (d) were too scattered to fit an assumed relationship.

The estimated 'optimal' solutions varied considerably when the entire system was assumed to be either bottom-up (vulnerability factor = 1), top-down (vulnerability factor = 10) or 'mixed' (vulnerability factor proportional to trophic level of the prey groups) controlled (Figure 8.9). When the ecosystem was assumed to be bottom-up controlled, the Pareto-frontier between economic profits and conservation status became closer to a linear relationship. Also, when the DI was less than 30, the estimated NPV of profits was lower than that from scenarios with vulnerability parameters obtained from time-series fitting ('base estimation'). Otherwise, higher profits were predicted. Under the top-down controlled assumption, plot of estimated maximum achievable conservation and economic benefits was scattered. The estimated NPV of profits from both top-down and 'mixed' controlled ecosystem were generally higher than that from the 'base case'.

8.4. Discussion

8.4.1. Trade-offs between policy objectives

This study has revealed the possible trade-offs between conservation, economic and social objectives in fisheries management in the NSCS. The trade-off analyses show that NSCS fisheries in the 2000s are in a sub-optimal state in terms of achieving conservation and economic objectives. The fisheries had depleted most commercial stocks (Chapters 6 and 7) and largely dissipated the potential economic benefits that could be obtained from an optimally-exploited ecosystem. This agrees with conventional economic theory in which over-capitalization leads to over-exploitation and dissipation of potential economic benefits (Gordon 1954). Thus, the *status quo* of the NSCS fisheries should have room to improve its conservation status without compromising the overall economic benefits from the fisheries. Such an improvement could be achieved by reducing the effort of fleets that have large impacts on intrinsically vulnerable stocks, while contributing low economic benefits (e.g., stern and pair trawlers, which have low profit margins relative to other sectors because of their larger fuel consumption and labour cost). Therefore, well-designed conservation policies aiming for a moderate improvement in conservation status should also improve the net economic benefits from the fisheries. However, the major problem is the transaction costs (economic and social) that are required to reduce excess fishing capacity.

The trade-offs between conservation and socio-economic objectives will become severe when policy targets a high conservation status. Largely improving conservation status (reduce risk of depletion, increase biodiversity and ecosystem maturity) would require restoring and protecting over-exploited and intrinsically vulnerable species. This would also reduce the catch of the less vulnerable or more productive species (Hilborn *et al.* 2004c; Walters & Martell 2004). For instance, fishing effort in the shrimp trawl sector was largely reduced when the management goal focused on conservation. Because shrimp trawlers targeted highly-valuable benthic invertebrates (e.g., mantis shrimp) and were among the most profitable fleets in the NSCS (Cheung and Sadovy 2004), reducing their effort substantially lowered the net economic benefits from the fisheries. Moreover, recovery of predatory species, particularly, the large demersal fishes, increased the predation mortality of their valuable invertebrate prey and reduced their productivity. This may result in severe trade-offs between conservation and socio-economic objectives.

Trade-offs between restoring predatory species and loss of fisheries productivity have occurred in other ecosystems. For instance, following the collapse of the Northeast Altantic cod (*Gadus morhua*) stocks, lucrative invertebrate fisheries, such as lobster, crabs and shrimp, bloomed. There was a concern that restoring the cod stocks would negatively affect the economic values of the fisheries because of the reduced productivity of the invertebrates stocks that this may entail (Worm & Myers 2003). Also, salmon fisheries along the coast of British Columbia were reduced to protect a number of less productive salmon stocks that were considered endangered, foregoing potential catches from other more productive salmon stocks (Walters & Martell 2004). Similar trade-offs occurred in the central Pacific Ocean where longline fisheries captured both yellowfin tuna (*Thunnus albacares*) and relatively less productive blue sharks (*Prionace glauca*) (Schindler *et al.* 2002).

In the past few decades, NSCS fisheries appear to have developed with a strong focus on social benefits (i.e., maximizing the number of jobs). In the late 1980s, fishing firms previously owned by the state were privatized in the People's Republic of China

(PRC). The majority of the fisheries were operated by small units in the 2000s, with many of the fishers previously unemployed workers or farmers (Jia, S.P., Director of the PRC South China Sea Fisheries Institute, pers. comm.). Although the nominal fishing effort was theoretically restricted through a licensing system, the fisheries were grossly over-capitalized. Also, illegal fishing (fishing without proper licenses) was common in the region (Yang 2001). Thus, it was inevitable that the fisheries resources were over-exploited, with accompanying large depletion and extirpation of targeted fish stocks in the region (see Chapter 5).

Fishers maintained their income from fishing by targeting species further down the food web and, in some cases, using destructive fishing methods. The coastal trawl sectors catch mostly juveniles, small fishes and invertebrates that are more resilient to fishing. Benthic invertebrates such as shrimps and crabs have high market prices. Also, the booming mariculture of predatory fishes (e.g., groupers) in China has created a large demand for small and juvenile fishes used as feed (Chau 2004; Cheung & Sadovy 2004; Funge-Smith et al. 2005). Moreover, destructive fishing methods such as fishing with dynamite or trawl nets with high-voltage electric current have been used (Sumaila et al. in press). Fishers in the region generally have low education levels and limited employment opportunities other than fishing. Therefore, they have few alternatives to fishing harder on the remaining resources. These are clear symptoms of Malthusian overfishing – a situation in which overfishing is driven by poverty, population growth and lack of alternative livelihoods (Pauly 1993, 2006; Teh & Sumaila, in press). This can be the major reason for the largely sub-optimal state of NSCS fisheries in the Paretofrontier between net economic benefits and conservation. This study suggests that if fishing continues to serve as a source of new job opportunities, the ecosystem is likely to be further depleted. On the other hand, reducing effort without a proper programme to help fishers find alternative livelihoods may create considerable social problems.

8.4.2. Economics of restructuring the fishing fleets

A buy-back scheme may potentially reduce fishing capacity and reduce the direct economic impact on the fishing communities resulting from the management policies.

However, this study shows that the cost of a buy-back scheme may increase exponentially with the targeted conservation status. Who should pay the cost?

Buy-back schemes that are paid for by the remaining fishers might be implemented through taxation or license fees (Munro & Sumaila 2002; Clark *et al.* 2005). This approach helps to internalize the environmental externalities of fishing. An underlying assumption is that the net economic benefits from the fisheries would increase in the future. Therefore, fishers who would benefit from the conservation policy should contribute to the cost of fleet re-organization. This study showed that the increase in net benefits would only be sufficient to pay for the buy-back cost to achieve a moderate conservation level in the NSCS. Given the highly depleted NSCS ecosystem, it appears that a moderate conservation level might not allow sufficient recovery of some vulnerable and highly depleted groups.

Public funds through government or non-governmental organizations might be needed if a high conservation level were to be targeted. Besides commercial fishers, society in general could also obtain benefits from a restored ecosystem, directly (e.g., through ecotourism, recreational fishing, etc) and indirectly (e.g., through increased nonmarket value, restored ecosystem function, etc.) (Costanza *et al.* 1998; Balmford *et al.* 2002; Berman & Sumaila 2006; Worm *et al.* 2006). A cost benefit analysis of the private and societal sectors is a possible way to evaluate the potential sharing of costs between these two groups. A study focusing on market values was conducted for the Hong Kong marine ecosystem. It showed that conservation policies could provide several times more economic benefits to society than the fishing sectors (Sumaila *et al.* in press). Therefore, it may be reasonable for society to share part of the cost of conservation.

So far, buy-back schemes have been assumed to be perfectly effective, i.e., buying-out each fishing unit resulted in equivalent reduction in fishing effort – an assumption that is hardly true in reality. Fisheries often have latent effort (Brodziak *et al.* 2004). For instance, fishers may hold valid fishing licenses, but not practice fishing for reasons such as fishing being unprofitable, or the opportunity cost of fishing being high. These fishers may become active when profitability of the fisheries increases. Also, if the buy-back scheme is expected by the fishers before the scheme is implemented,

investments in fishing capacity would possibly increase substantially, as any excessive fishing capacity would likely be bought out when the buy-back scheme is in effect (Clark *et al.* 2005). Moreover, fishing effort may seep back into the fisheries through improved fishing technology and power, increased fishing time, etc. Therefore, buying out fishing vessels may not reduce fishing effort proportionally. Moreover, effective regulation and monitoring of fishing effort is essential. However, these are weak in the NSCS. In fact, a review of previous experiences of fishing vessel buy-back programmes, such as the British Columbia and Washington State salmon fisheries, Australian northern prawn fishery, the Canadian Atlantic groundfish fishery, concludes that such programmes are generally not an effective way to reduce fishing capacity (Holland *et al.* 1999). Thus, although this study shows that a buy-back scheme to reduce fishing capacity is economically sound, the PRC government should carefully consider its practical feasibility and effectiveness. It appears that a priority for the PRC government is to improve monitoring, surveillance and control of its fisheries, and develop alternative livelihoods for fishers.

Other means of reducing fishing capacity may be through removal of subsidies given to the fisheries. The PRC government is subsidizing fisheries (non-fuel subsidies amount to US\$ 1.3 billion annually) (Khan *et al.* 2006; Sumaila *et al.* 2006). Therefore, removal of subsidies may lower the profitability of fishing and thus discourage continued investment in maintaining or increasing fishing capacity. However, social problems may still be created because of the lack of alternative livelihoods for the fishers. Clearly, viable alternative livelihood programmes for the fishing communities are essential for the success of fisheries management and conservation measures.

8.4.3. Model assumptions and uncertainties

A key parameter uncertainty was the predator-prey vulnerability factors. Here, observed time-series catch rate data were used to estimate the vulnerability factors, which provided some empirical support to the model (Chapter 7). However, the results were very sensitive to the vulnerability factor settings, particularly if a top-down controlled system was assumed. A top-down controlled system predicted large fluctuations in biomass of prey and predator groups. Such unrealistic predictions led to highly scattered

estimates from the multi-criteria policy optimization routine. Thus, extreme top-down control assumptions in the simulations may be invalid. When time-series abundance data in the NSCS are available in the future, the model can be further validated by comparing the observed trends with the model predictions.

The effects of other (non-fishing) anthropogenic changes, economic and environmental fluctuations were not included in the model. Oceanographic and other physical changes (e.g., coastal nutrient inputs) may have considerable effects on the NSCS ecosystem. Also, following the rapid economic development of China, anthropogenic disturbance such as reclamation and pollution may significantly affect the ecosystem (Zhang *et al.* 2002; An & Hu 2006). These factors are likely to have negative effects on the benefits from conservation policies. However, limited historical time-series data prevented the analysis of the effects of these factors. There is a need to better understand the effects of environmental and non-fishing anthropogenic factors on the ecosystem dynamics in the NSCS. In addition, the costs of fishing and prices of catch are assumed to be constant, which may vary as the ecosystem and market conditions change in reality. Accurate economic data of the NSCS fisheries, such as cost profiles of different fishing fleets, were also limited. These may render the absolute values of benefits and costs calculated from the ecosystem model uncertain.

One of the major assumptions in the multi-criteria optimization analysis is that all fishing fleets cooperate to maximize the overall benefits of the fisheries. Thus, in some scenarios, benefits of some fishing sectors were maximized at the expense of other sectors. Although this assumption may affect the optimal fleet structures, the overall trade-off relationships revealed from the present analyses should remain valid. On the other hand, the evaluations of trade-offs and allocations of resources between different fishing sectors is an important topic and should be areas for future studies.

The aim of this study was to quantify the potential trade-offs between conservation and other socio-economic objectives. The NSCS ecosystem has been greatly depleted by fishing and is considered to be currently in a sub-optimal state both in terms of ecological and economic objectives. We believe that the findings in this paper should be generally applicable to other tropical marine ecosystems, as the symptoms of

Malthusian and ecosystem overfishing are commonly observed, particularly in developing countries (Pauly 1993, 2006; Teh & Sumaila in press). To prevent more degradation and extirpations, and improve economic benefits from exploiting these ecosystems, restructuring the fishing fleets is urgently needed. However, fishing communities might oppose a restoration policy because of the inevitable need to reduce fishing capacity in the short term. Moreover, the restructuring of fishing fleets and the unbalanced share of costs and benefits may create tension among fishing sectors (Cheung and Sadovy 2004). Understanding the trade-offs between management objectives may allow the stakeholders and the public to hold informed discussions on future management policies. It is also important to develop alternative livelihoods for fishers that may be affected by fisheries management and conservation policies in order to facilitate the transition to sustainable fishing.

8.5. References

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9. CONCLUSIONS

9.1. General summary

In the first chapter of this thesis, the case of the disappearance of the Chinese bahaba (*Bahaba taipensis*) along the coast of China was discussed (Sadovy & Cheung 2003). In fact, given the sustained high fishing pressure in the South China Sea (and globally in most of the oceans), the Chinese bahaba is not likely to be an isolated case. Then, how can we identify fishes that are in a similar situation and reduce the threat from fishing in a timely fashion? The major aim of this thesis was to provide answers to this question. The issue was addressed by following the analytical framework described in Chapter 1: (i) using approaches that can be applied under data-limited conditions to identify species that are more vulnerable to extirpation (or extinction), and regions that are associated with higher risk of population depletion or extirpation (Chapters 2, 3 and 4); (iii) assess the status of the ecosystem and its associated species (Chapters 5 and 6); and (iv) explore the effects of fisheries management policies and identify socio-economically viable conservation and fisheries management options (Chapters 7 and 8).

The fuzzy logic expert system developed in Chapter 2 provided an intrinsic vulnerability index that correlated significantly with observed population declines in different areas and ecosystems. Such correlation was higher than those from other vulnerability indicators that had previously been proposed e.g., the approach adopted by the American Fisheries Society (Musick 1999) and individual life history traits (e.g., Jennings *et al.* 1998). The fuzzy expert system had the additional advantages of flexible requirements for input data and ease of incorporating new knowledge. The system could quantitatively and consistently assess the relative vulnerability of wide ranges of marine fishes and identify priority species for protection and further studies using readily available life history parameters, such as those in FishBase (www.fishbase.org). This index was applied to the analyses in most chapters of this thesis.

Using the intrinsic vulnerability index developed in Chapter 2, the differences among marine fishes in different habitats, latitudinal and depth zones were evaluated. The

study found that deepwater demersal fishes, particularly those aggregating around seamounts, had higher intrinsic vulnerability to fishing. Moreover, when the average intrinsic vulnerability indices of species weighted by their annual catch over the past 50 years were calculated for coral reef, estuary and seamount fish communities, a consistent decline became apparent in coral reefs and estuaries, while the opposite was observed in seamounts. When coral reef and estuarine communities were compared, decline in average vulnerability of fishes in the catch was much stronger in coral reefs. Catches from coral reefs have been increasingly dominated by low intrinsic vulnerability species, while the highly vulnerable species have been rapidly depleted. Moreover, an increasing average vulnerability of fishes in the catch was observed in seamounts, where the highly vulnerable species have been serially depleted in recent years (Koslow 1997; Clark 2001; Roberts 2002). Estuarine fish communities consist of a mixture of freshwater- and marine- migrants and residents (Blaber 2000). Thus community structure is more volatile, which may explain the weaker decline in average vulnerability of catch. The link between average vulnerability of catches and status of fish communities agrees with the correlation between the number of fishes listed under the IUCN Red List of Threatened Species and the rates of decline of mean vulnerability of catches. These findings quantitatively revealed patterns of changes in fish community structure in coral reef, estuary and seamount since 1950. Also, the results showed that changes in the structure of these fish communities were closely related to the species' intrinsic vulnerability.

An analytical approach to predict the depletion risk of exploited fishes from fishing using life history and catch time-series data was developed and applied to analyze the conservation status of marine fishes globally (Chapter 4). The study found that a considerable proportion of the exploited fishes had moderate, high or very high risk of population depletion. The proportion of species that had at least moderate depletion risk increased greatly over the past 50 years, particularly large-bodied demersal fishes and elasmobranchs. These results agreed with the conclusions from Chapters 2 and 3. The proportion of species facing moderate to very high depletion risk from fishing was comparable to other vertebrate groups. Thus, this chapter showed that the scale of the conservation problems faced by marine fishes might be similar to those of other

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terrestrial vertebrates. This chapter, together with Chapters 2 and 3, highlighted the need to incorporate conservation plans into fisheries management.

The Northern South China Sea (NSCS) ecosystem was used as a case study to evaluate the conservation concerns resulting from fishing (Chapter 5). The NSCS was heavily exploited by fishing, but baseline data were limited. Using standardized timeseries CPUE data of demersal trawlers from 1973 to 1988, it was shown that the relative abundance of most of these species declined by over 70% over the 15-year period. Relative abundance of some intrinsically vulnerable species (e.g., sharks, rays and yellow croaker) declined by an average of over 90%. The rate of decline was significantly correlated with the species' predicted intrinsic vulnerability. Using the predicted intrinsic vulnerability, this study suggested that many exploited fish species in the NSCS might be threatened by fishing. This is in accord with the global predictions of depletion risk of marine fishes in Chapter 4.

To understand the impacts of fishing in the NSCS at the ecosystem level, past (the early 1970s) and present (the 2000s) status of the NSCS ecosystem was evaluated using the Ecopath with Ecosim modelling approach (Chapter 6). The models indicated a large decline in system biomass. Also, biomass and energy flows of the demersal groups reduced greatly from the 1970s to the 2000s, resulting in a shift from being a demersal-dominated to a pelagic-dominated system. Moreover, most of the primary production that had originally been consumed by marine organisms through the foodweb went to capture fisheries. This showed that intensive and ill-managed fishing does not only directly threaten vulnerable species (Chapter 5), but also exerted large ecosystem impacts that indirectly threatened other non-target species.

Based on the Ecopath with Ecosim dynamic simulation models developed in Chapter 6 and validated in Chapter 7, trade-offs between conservation and socioeconomic objectives of fisheries management in the NSCS were evaluated. The depletion index developed and validated in Chapter 7 was used as an indicator of conservation status. Using a numerical optimization routine, this study identified convex paretofrontiers in the trade-offs between conservation and socio-economic objectives. The 2000s NSCS ecosystem was sub-optimal for achieving either conservation or economic objectives. Thus improvement in both the conservation status and the net present value of benefits from the fisheries could be made by restructuring the fishing fleets. However, this would require reduction of fishing capacity and the number of jobs provided by the fisheries. Under the current socio-economic situation in China, such changes might lead to considerable social problems. A buy-back scheme that is funded by the fishing industry might be possible, as the buy-back cost could be offset by the higher profit expected from improved management. However, public funds would be required if a higher conservation target were to be achieved. This might be justified by the direct or indirect benefits to society that could be provided by a well-conserved ecosystem. On the other hand, social problems associated with the lack of alternative livelihood for fishers might hinder any management and restoration plans. The livelihood problems appeared to be a priority for improving fisheries management and conservation policies in the NSCS.

9.2. Applications and recommendations

It is important to ensure proper management and conservation of marine ecosystem and species that are particularly vulnerable to fishing. These vulnerable species may include those that are targeted by fisheries and bycatch. The need for such efforts can be supported by a number of reasons. Firstly, loss of marine biodiversity may have significant socio-economic implications (Chapin III et al. 2000). The depletion or extirpation of valuable exploited species may result in direct economic losses. These can result in large repercussion to the fishing industries and the community depending on the resources. For example, the depletion of Atlantic cod (Gadus morhua, Gadiidae) and the subsequent moratorium on the Canadian cod fisheries resulted in extensive socioeconomic problems to the fishing communities. Secondly, loss of biodiversity may directly or indirectly affect the functioning of the ecosystem (Loreau et al. 2001; Worm and Duffy 2003; Worm et al. 2006) and can alter the productivity of the ecosystem and the recovery of depleted species. Removal of keystone species, which include species that are critical to the ecological function of a community or habitat in their current states (Zacharias and Roff 2001), can result in state shift in marine ecosystem. For instance, the removal of sea otters in the Aleutian Archipelago resulted in sea urchin population

expansion, which virtually excluded fleshy macroalgae such as kelp and greatly affected their associated communities (Tegner and Dayton 2000). Moreover, biodiversity can be positively correlated with stability and resilience of an ecosystem (Tilman and Downing 1994; Tilman 1996; Tilman et al. 1997; Scheffer et al. 2001; Worm et al. 2006). For instance, in this thesis, I demonstrated that the depletion of the intrinsically vulnerable, predatory species (both targeted and non-targeted species) such as sharks, rays, largebodied sciaenids and groupers in the NSCS had lead to the dominance of less vulnerable species with generally high population turn-over rate (e.g., small pelagic and juvenile fishes, and invertebrates). Populations of the latter are generally more variable (Spencer & Collie 1997) and their dominance reduces the stability of the ecosystem. The NSCS fisheries are currently supported by fishing for these high turn-over species. The resulted increase in variability of catches due to the stock variabilities might have considerable socio-economic impacts to the fishing communities. Particularly, fishing fleets that build up fishing capacity during the 'good' fishing years may suffer from economic hardship when environmental factors reduce fishery productivity. Given that losses of species diversity may be irreversible and can have large socio-economic consequences, based on the precautionary principle, instead of protecting only the valuable fishery targeted species, we should aim to conserve the full spectrum of species in the ecosystem (Worm & Duffy 2003), particularly those that are more vulnerable to fishing.

The analytical approaches developed in this thesis may allow conservation assessment to cover a wider range of marine fishes. Currently, only a small proportion of marine fishes have been assessed by the IUCN Red List criteria (Baillie *et al.* 2004). A major obstacle that hindered the assessments was data limitation (Dulvy *et al.* 2003). The analytical approaches developed in this study (e.g., intrinsic vulnerability index) and elsewhere (Dulvy *et al.* 2003; Reynolds *et al.* 2005) can facilitate rapid assessment of the relative conservation status of fishes with limited data. Thus, fisheries managers or conservation practitioners can make use of these approaches to understand the status of the ecosystem of concern and identify priority areas and species for conservation planning and undertaking more detailed assessment (e.g., the IUCN threatened species assessment). In fact, the intrinsic vulnerability index will become a standard parameter for most species in FishBase in 2007 (Rainer Froese, IFM-Geo-Mar, Kiel, Germany, pers. comm.). This should facilitate the utilization of this index for research, conservation planning and fisheries management.

Particularly, the use of fuzzy expert system enabled integration of local and scientific knowledge and adaptation to new knowledge (Mackinson & Nøttestad, 1998). The fuzzy expert systems presented in this thesis allowed better use of available information to predict intrinsic vulnerability and depletion risk of marine fishes and ecosystems. Moreover, the heuristic rules, fuzzy membership functions, and the defining values, can be modified based on expert knowledge or newly available information (Cox, 1999). The weighting on the rules can also be adjusted when new evidence or experts' opinions are obtained. The fuzzy expert system, and the indices developed from it, are particularly useful in data limited situations, e.g., tropical fisheries where diverse species are caught and resources for monitoring and management are low (Silvestre & Pauly 1997; Johannes 1998; Johannes *et al.* 2000). This may provide a decision support tool on local or global extinction risk assessment and categorization such as the IUCN Red List of threatened species of the World Conservation Union or the species listing under Canada's Species At Risk Act.

Deepwater demersal and seamount, as well as coral reef fish assemblages should warrant high conservation concerns. The many threats to coral reef ecosystems (e.g., overfishing, habitat destruction, climate change) have been well understood (Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Birkeland 2004). However, fishing in the deep seas (including the continental slope) and seamount ecosystems have only been recognized as a major concern recently (Pankhurst 1999; Koslow *et al.* 2000; Roberts 2002; Morato *et al.* 2006b). This thesis has quantitative showed the high intrinsic vulnerability of demersal deepwater fishes and seamount-associated fishes to fishing. It has also shown that these species have been increasingly exploited (Chapter 3). As many of the deepsea and seamount species occur in the high seas, international conservation efforts are necessary. On the other hand, although protection and conservation of these species and their vulnerable habitats (e.g., deepwater coral) are advocated by conservation groups and scientists, international conservation actions are lacking. Results from this thesis demonstrated an urgent need to increase international conservation efforts.

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In addition to the conventional approaches to assessment of target species, assessments should expand to non-target species and the ecosystem. Even if conventional management goals such as the Maximum Sustainable Yield (MSY) are achieved, non-target species that are biologically more vulnerable to fishing can be susceptible to over-exploitation (Walters *et al.* 2005). In this thesis, through analyses of intrinsic vulnerability and depletion risk from life history and fisheries data, and an empirical case study of the NSCS, the elasmobranchs (sharks and rays) were clearly shown to be intrinsically vulnerability and had been largely depleted by fishing. Sharks and rays are bycatch of many fisheries, e.g., the bycatch of blue shark (*Prionace glauca*) from the tuna and swordfish longline fisheries in the Central Pacific Ocean, North Atlantic Ocean and Mediterranean Sea. (e.g., Buencuerpo & Moron 1998; Schlinder *et al.* 2002). This problem is also illustrated in tropical multi-species fisheries such as the high bycatch rate of shrimp trawling (Andrew & Pepperell 1992). The index can improve understanding on intrinsic vulnerabilities of bycatch species, and therefore, should be a useful tool to reveal potential impacts of the bycatch.

Moreover, fishing may affect ecosystem dynamics and functions (Pitcher & Pauly 1998; Worm *et al.* 2006). The analytical tools presented in this study (e.g., ecosystem modelling) should be useful to facilitate the assessments on the effects of fishing on the non-target species and ecosystem. These tools can be combined with alternative management goals such as the 'Optimal Restorable Biomass' – an optimized form of historical ecosystem – proposed by Ainsworth (2006) to achieve ecosystem-based management objectives.

As fisheries management involves a multitude of objectives (e.g. ecological, economic, social), the trade-offs of benefits and costs between the different objectives should be evaluated and presented to the decision makers and stakeholders. Ideally, consensus on the desirable set of management objectives could be made from informed discussions among stakeholders. Fisheries managers could then develop management tactics that could effectively achieve the management goals (Cochrane 2002) such as the 'Optimal Restorable Biomass' mentioned previously (Pitcher 2005; Ainsworth 2006).

Particularly, in the NSCS, effective management and conservation actions are urgently needed. This thesis clearly showed that the fisheries resources in the NSCS are heavily over-exploited and that the fisheries contributed largely to the adverse ecosystem changes. A major root cause of this problem is Malthusian overfishing (Pauly 1993, 2006): unemployed workers and farmers moved to the coast and became fishers (Huang & Guo 2001), many of them fishing illegally (e.g., without fishing license) (Pang and Pauly 2001). In the NSCS, with the depletion of fisheries resources (Chapters 5 and 6) and the lack of alternative livelihood, destructive fishing methods (e.g., fishing with dynamite, electric net) were sometimes employed, leading to further depletion. Any measures that improve the ecological and economic benefits of fisheries would involve effort reduction and loss of fisheries-related jobs (Chapter 8). Thus, it is critical for the PRC government to help develop sustainable alternative livelihoods for potentially displaced fishers. The government provided funding to help fishers develop alternative livelihoods in aquaculture, distant water fishing, tourism and other land-based industries⁸. However, the PRC government should also carefully consider whether some of the current alternative livelihood programmes for fishers are ecologically and economically sustainable.

The PRC government should also improve monitoring, surveillance and control (MSC) of fishing effort. This thesis showed that a buy-back scheme funded by the fishing industry could be an economically viable option to facilitate reduction in fishing capacity. However, the effectiveness of any buy-back scheme relies heavily on the ability to monitor and control fishing effort. MSC is weak in China and strengthening this area is a pre-requisite for improvements from the *status quo*. The ecosystem models developed in this thesis can be used as an operating model to test the performance of different monitoring and management system through 'closed loop' analysis (*a.k.a.* Management Strategy Evaluation framework) (Watlers 1998; Smith *et al.* 1999; Plaganyi & Butterworth 2004).

9.3. Limitations and future improvements

The extent and accuracy of the analyses in this thesis was partly limited by our current understanding on the biology of extinction of marine fishes. Conservation risks of

⁸ News article (Chinese). China Report 5 December 2005.

http://big5.chinabroadcast.cn/gate/big5/gb.cri.cn/41/2003/12/05/108@13466.htm

marine fishes (particularly the highly fecund commercial species) have only become seriously recognized in recent decades (Sadovy 2001; Dulvy *et al.* 2003). Although knowledge about the extinction biology of fishes is growing rapidly, a number of key issues and questions are still being researched (Reynolds *et al.* 2005). For instance, the dynamics of fish populations in small population size are still poorly understood and it is difficult to determine the minimum viable population size for most marine fishes. Future studies on the dynamics of fish at small population size are needed (Pitcher 1998; Dulvy *et al.* 2003). Also, the responses of marine fishes to other environmental and anthropogenic changes such as climate change (Roessig *et al.* 2004; Perry *et al.* 2005) and genetic effects from fishing (Law 2000) are being studied. Further understanding on these factors would improve the predictions of extinction risk for marine fishes. Thus the expert system developed here should be updated regularly to incorporate new knowledge in these areas.

Although the analytical approaches developed here allowed rapid assessment of intrinsic vulnerability and depletion risk under data-limited situation, good data are necessary to improve our understanding on the threats of fishing, human and environmental changes to marine fishes. Data limitations are particularly serious in tropical developing regions and reef fisheries where fishery monitoring is less effective but threats to their high biodiversity are acute (Johannes 1998). For instance, the life history parameters of many fishes in the NSCS are unknown. Also, catch or landings data are available only for a few commercial species, and many species are not reported explicitly in the catch. Better monitoring systems should be developed to improve the collection of basic biology and fisheries data.

The problem of data limitation is serious in the NSCS. Fisheries statistics from the PRC government are suggested to be inaccurate, especially those in recent decades (Pang & Pauly 2001, Watson & Pauly 2001). Although government and research institutes in China have conducted sporadic surveys in the NSCS, access to the data was generally restricted by the government (Jia, S.P., Director of the South China Sea Fisheries Institute, pers. comm.). Therefore, this thesis relied on the available data from past surveys conducted by the Hong Kong government. However, the temporal coverage of the data was short (from the mid-1970s to the late 1980s only), and the accuracy was limited

because of the survey methodology. These affected the accuracy of the study results. It would be helpful to all if the Chinese authorities allowed legitimate researchers to access their past survey data so that the status of the NSCS ecosystem and the dynamics of its changes can be better understood. Moreover, if monitoring could be improved in the future, the collected data could be used to validate the predictions (e.g., through Ecosim modelling) from this thesis. On the other hand, meta-analysis and global databases could be used for studies in cases with limited data.

Uncertainties associated with the Ecopath with Ecosim approach have been reviewed in detail (Plaganyi & Butterworth 2004). Some of the stated uncertainties have been addressed in this study, while the remaining may be addressed through future development of the Ecopath with Ecosim programme:

• Functional group aggregations

Specification of the structure of the NSCS ecosystem model may affect the model predictions (Fulton *et al.* 2003; Pinnegar *et al.* 2005). The current model structure (i.e., specifications of the functional groups) was determined based on the characteristics of the NSCS ecosystem, the objectives of the study, and the available data (Chapter 4). Moreover, the model provided reasonable agreement with historical time-series data (Chapter 7). When more data on the biology, ecology and fisheries of the NSCS become available, it would be useful to test the sensitivity of the model predictions to different functional group structures.

• Steady-state assumption

The NSCS ecosystem in two time periods (the 1970s and 2000s) was constructed to reveal changes in biological and ecological parameters over time (Bundy 2001). However, the long-term changes of some biological and fisheries parameters (e.g. consumption rate, fishing cost, landing prices, etc) could not be reflected in the dynamic simulations. Modification of the modelling approach to incorporate systematic changes of some of these parameters in dynamic simulations may allow analysis on the sensitivity of the model predictions to such changes.

Prey selection by predators

Prey selection in the current NSCS model was specified by a diet composition matrix that reflected the proportion of biomasses of different prey items in the predators' diet. Accurate diet composition data are difficult and costly to collect (Hyslop 1980; Cortés 1997). Particularly, prey items that form a tiny proportion of the predators' diet (e.g., juvenile fishes) are easily missed in determining the diet composition matrix. However, such predator-prey linkages may control important ecosystem dynamics (Walters & Martell 2004). Alternative specification of diet composition can be expressed as a function of predators' grip-sizes, prey body-sizes and availabilities (Fulton *et al.* 2003). Currently, such a 'size-based' approach to specification of diet composition in ecosystem model is being developed for Ecopath with Ecosim (Cameron Ainsworth, Fisheries Centre, University of British Columbia, pers. comm.). It would be useful to cross-validate the results from the current diet composition matrix in Ecopath with this newly developed approach.

• The vulnerability settings (foraging arena theory)

One of the most important components in Ecosim modelling is the vulnerability parameters that determine the foraging behaviour and predator-prey interactions in the ecosystem model (Walters & Juanes 1993; Walters *et al.* 1997). Chapters 7 and 8 and other previous studies (Hollowed *et al.* 2000) indicated that predictions from Ecosim were sensitive to the vulnerability parameters. Some have suggested that modelling predator-prey relationships through explicit specification of functional responses may perform better than the foraging arena model in Ecosim (Koen-Alonso & Yodzis 2005). However, these studies mainly criticized the assumption of either top-down or bottom-up trophic control (high or low vulnerability parameters, respectively) throughout the ecosystem. Here, each prey group's vulnerability parameter was estimated by fitting the model with time-series CPUE data. This represents a more systematic approaches in representing the vulnerability parameters. Moreover, alternative approaches in representing

trophic control may be developed in the future to generate alternative hypothesis on ecosystem changes.

In addition, a new version (version 6) of the Ecopath with Ecosim programme is being developed. One of the characteristics of this version is to allow users to incorporate alternative sub-routines in the model (e.g., incorporating alternative trophic control routine) (Villy Christensen, Fisheries Centre, University of British Columbia, pers. comm.). The potential flexibility to incorporate user-defined sub-routines greatly widens the possibility of testing the effects of alternative model assumptions and structures (e.g., on recruitment, compensation and considerations of long-term life history changes).

9.4. Final conclusions

The various analytical approaches developed in this thesis can improve our understanding of the intrinsic vulnerability and depletion risk of marine fishes to fishing. Currently, the IUCN Red List assessment – the authority on extinction risk assessment – covers only a small proportion of marine fishes compared to other vertebrate groups. A major problem that prevents assessing a wider range of marine fish species is insufficient data. Thus, the true scale of conservation problems associated with fishing remains inaccessible. The analytical approaches developed here can provide rapid conservation risk assessments with limited data and inform conservation practitioners, policy makers and the public for conservation actions.

Using analytical approaches and ecosystem modelling developed in this thesis, conservation and socio-economic problems associated with over-exploitation in the NSCS have been identified. The results could allow policy makers, fishers, fisheries managers and the public to realize the seriousness of the problems and inform them about the cost and benefits of managing fisheries under alternative objectives. These should facilitate discussions between management authorities and stakeholders to decide on fisheries management and conservation policies in the future. These approaches should be applicable to fisheries assessments in other regions, especially in areas where species diversity is high but available data and resources for researches are limited.

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APPENDICES

2.1 Development of the fuzzy expert system

We collated known relationships between life-history and ecological characteristics to intrinsic vulnerability from the published literature (Table A2.1), excluding those overwhelmingly disproved by empirical data. For instance, high fecundity had been suggested to be associated with low vulnerability. However, both theoretical and empirical studies lately do not support such relationship (see Table A2.1 for the list of evidence). Thus the rules relating high fecundity and low vulnerability are excluded from the system.

The published relationships were transformed into IF-THEN rules relating life history and ecological characteristics to the four vulnerability categories (Table A2.1). Firstly, we transformed the input biological attributes into verbal categories, defined by fuzzy sets (Figure A2.1), and based on an existing vulnerability categorization scheme: AFS's scheme (Musick 1999a) and scheme proposed by Rainer Froese and is presented in FishBase (Rainer Froese, IFM-Geo-Mar, Kiel, Germany, pers. comm.). However, studies reported in Table A2.1 may not represent the full range of each trait for marine fishes. Thus we have to extrapolate the reported qualitative relationships between biology/ecology and vulnerability to fishes with wider range of traits. As prior knowledge about the choice of fuzzy membership functions for the input attributes was lacking, we employed the simplest forms: trapezoid membership functions at the upper and lower limits and triangular membership functions at intermediate positions on the axis. Other options include membership functions in sigmoid, gamma, and irregular shapes (Cox 1999) which may be explored if their uses are justified by experts.

Trapezoid and triangular membership functions can be defined by values of independent variables that give minimum (0) and maximum (1) memberships. These values are modified from AFS's scheme; maximum length, geographic range and spatial behavior strength were not included and so, for consistency with other attributes, we classified each of them with four verbal categories (only two categories of geographic range are associated with rules). We defined the membership functions for maximum length and geographic range from the lower quartile, median, and upper quartile of each attribute from all marine fishes recorded in FishBase (over 15,000 species) (Froese & Pauly 2004). Membership functions of spatial behavior strength were defined by arbitrary values (Appendix 2.3). For all the fuzzy membership functions, I assumed high degree of overlap between fuzzy sets. This assumption reflects our uncertainty on the exact

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relationship between the premises (the biological and ecological characteristics) and the conclusion (intrinsic vulnerability) (Kosko 1993).

We defined four verbal categories referring to the levels of intrinsic vulnerability: (1) very high vulnerability, (2) high vulnerability, (3) moderate vulnerability and (4) low vulnerability. These verbal categories were defined by fuzzy sets on an arbitrary 'intrinsic vulnerability' scale from 1 to 100. Without prior knowledge, we assumed the simplest forms of fuzzy membership function: trapezoid and triangular membership functions. A trapezoid membership function was used for the 'very high vulnerability' and the 'low vulnerability' categories, while symmetric triangular membership functions were used for the other two categories (Figure A2.2).

We assumed the minimum membership in the premises (conditions) required to fire the rules (threshold value) to be 0.2. This means that we considered the premises to be totally false unless they had membership of trueness of 0.2 or more. Thus the system screens out premises that have very low degree of membership. We evaluated the sensitivity of the system outputs to different threshold values.

We made an initial assumption of equal weighting with 0.5 for all rules. The weighting factor represents the level of belief associated with the rule. Thus a weighting factor of 0.5 means we have 50% of belief to the validity of the rule. That is:

$$Membership_{conclusion} = Membership_{premise} \bullet CF \qquad eq. A2.1$$

where CF represents the weighting factor. Thus the conclusion of a particular rule can only have a maximum degree of membership of 0.5 to its fuzzy set. We tested the validity of the equal weighting assumption using a jackknife approach.

We obtained the degree of membership of the final conclusions (four levels of intrinsic vulnerability) by combining the conclusions from each heuristic rule. Membership of the conclusion from each rule was combined using the knowledge accumulation method in (Buchanan & Shortliffe 1984):

$$Membership_{e} = Membership_{e-1} + Membership_{i} \bullet (1 - Membership_{e-1})$$
 eq. A2.2

where $Membership_e$ is the degree of membership of the conclusion after combining the conclusions from *e* pieces of rules, and $Membership_i$ is the degree of membership of the conclusion of rule *i*.

2.2. Operation of the fuzzy system

a. Fuzzification

Fuzzification is a process that determines the degree of membership to the fuzzy set based on the fuzzy membership function. We input the life history and ecological parameters into the fuzzy system. The input parameters were categorized into the different verbal categories (e.g. *large* maximum size, *low* value of von Bertalanffy growth parameter K) with the corresponding membership based on the pre-defined fuzzy membership functions (Figure 2.2). Categories with membership exceeding the threshold values would fire the corresponding rules. For example, for a fish species with maximum body length of 68 cm, the input parameters would correspond to "medium body size" and "large body size" with membership of 0.7 and 0.3 respectively (*threshold value* = 0.2) (Figure 2.1).

b. Rule firing and fuzzy reasoning

All premises with membership exceeding the threshold values (*Membership*_{ant}) triggered the fuzzy system to fire their corresponding rules. Following the example used in the fuzzification sessions, the rules:

IF fish maximum body size is medium, THEN intrinsic vulnerability is moderate

IF fish maximum body size is *large*, THEN intrinsic vulnerability is *high*

would be fired. When several rules with the same conclusion were fired, the conclusions were combined and accumulated using the method of Buchanan and Shortliffe (1984).

c. Defuzzification

Defuzzification refers to the reduction of a range of conclusions with different membership to a single point output. The conclusions reached from the rules were defuzzified based on the output fuzzy membership functions. Defuzzification was based on the centroid weighted-average method (Cox, 1999), i.e., the output intrinsic vulnerability factor was calculated from the average of the supremums of each output fuzzy membership function weighted by the membership associated with each conclusion. In a triangular membership function, the supremum is equivalent to the intrinsic vulnerability factor with the highest membership (peak of the triangle). For trapezoid membership function, the supremum was assumed to be the mid-point between the two ends of the plateau. The upper and lower bounds of the output were estimated by using the smallest and largest intrinsic vulnerability factors that fall within the particularly fuzzy sets at the specified membership level, instead of using the supremums. They represent the range of intrinsic vulnerability that falls within the pre-specified membership of the conclusion fuzzy membership functions. Therefore,

Intrinsic vulnerability =
$$\frac{1}{\sum_{i=1}^{4} Membership_i} \cdot \left(\sum_{i=1}^{4} Membership_i \cdot Sup_i\right)$$
 eq. A2.3

$$Bounds_{U/L} = \frac{1}{\sum_{i=1}^{4} Membership_i} \cdot \left(\sum_{i=1}^{4} Membership_i \cdot f_i(ML_{U/L})\right)$$
eq. A2.4

where Sup_i is the supremums of conclusion fuzzy membership functions *i*, and f(ML) is the estimated upper or lower bounds (*U* and *L* respectively) of the conclusion fuzzy membership functions at the specified membership level (*ML*).

2.3 Assignment of strength of spatial behaviour of fish

We obtained qualitative descriptions on the spatial behaviour of the fish from FishBase. We looked for keywords that verbally describe the spatial behaviour of fish (Table A 2.1). We assumed a baseline spatial behaviour strength of 1 for species forming groups or colonies, 40 for aggregations and shoals and 80 for schools (Pitcher 2002). The baseline spatial behaviour strength (B) was then adjusted by a multiplication factor (A) based on their verbal descriptions (Table A 2.1). That is:

$$S = B \cdot (1 + A_1 + A_2 + \dots A_n)$$
 eq. A2.5

where S is the total spatial behaviour strength (0 to 100) of the species. If S is above 100, it is rounded to 100. n is the number of verbal terms included. Moreover, if spatial behaviour only occurs in either juvenile or adult stage, the total spatial strength was divided by two.

For example, *Callionymus limiceps* (Round-headed dragonet) is described as "usually in small aggregations" in FishBase. The baseline spatial behaviour strength for 'aggregation' is 40, the multiplication factors for 'usually' and 'small' are 40% and -40% respectively. Therefore, the spatial behaviour strength is calculated as:

$S = (1 + 40\% - 40\%) \cdot 40 = 40$

Table A 2.1. Keywords that verbally describe the strength of spatial behaviour and their corresponding multiplication factors.

Verbal descriptions	Multiplication % (A)
Usually Solitary/Pair	-40
Occasionally/Sometimes/Alternately/May/Probably/Loose/small	-40
Sometimes Solitary/Pair	-20
Presumably/Apparently	-20
Frequently/Often	20
Commonly/Usually/Large/Dense	40

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Family	Pristidae	Sawfishes	88
	Squatinidae	Angel sharks	80
	Anarhichadidae	Wolffishes	78
	Carcharhinidae	Requiem sharks	77
		Hammerhead, bonnethead,	
	Sphyrnidae	scoophead shark	77
	Macrouridae	Grenadiers or rattails	75
	Rajidae	Skates	72
	Alepocephalidae	Slickheads	71
	Lophiidae	Goosefishes	70
	Torpedinidae	Electric rays	68
	Belonidae	Needlefishes	67
	Emmelichthyidae	Rovers	66
	Nototheniidae	Cod icefishes	65
	Ophidiidae	Cusk-eels	65
	Trachichthyidae	Slimeheads	64
	Channichthyidae	Crocodile icefishes	63
	Myliobatidae	Eagle and manta rays	63
	Squalidae	Dogfish sharks	62
	Congridae	Conger and garden eels	60
	Serranidae	Sea basses, groupers, etc.	60
	Exocoetidae	Flyingfishes	59
	Malacanthidae	Tilefishes	58
	Scorpaenidae	Scorpionfishes or rockfishes	58
	Polynemidae	Threadfins	56
	Triakidae	Houndsharks	56
	Istiophoridae	Billfishes	55
	Petromyzontidae	Lampreys	55
	Rhinobatidae	Guitarfishes	55
	Bramidae	Pomfrets	53
	Lethrinidae		53
	Muraenidae	Emperors or scavengers	
	Scombridae	Moray eels	53
		Mackerels, tunas, bonitos	52
	Scyliorhinidae	Cat sharks Herrings, shads, sardines,	52
	Clupeidae	menhadens	51
	Lutjanidae	Snappers	51
	Labridae	Wrasses	50
	Labridae		50 50
	Pomacanthidae	Trumpeters	
		Angelfishes Butterfishes	50
	Stromateidae		50
	Moridae	Morid cods	49
	Mugilidae	Mullets	49
	Oreosomatidae	Oreos	49
	Scophthalmidae	Scophthalmidae	49

3.1. Intrinsic vulnerability index of fish taxa represented in the global catch, based on the Sea Around Us database (www.seaaroundus.org).

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Family	Pleuronectidae	Righteye flounders	48
	Scaridae	Parrotfishes	48
	Batrachoididae	Toadfishes	47
	Sciaenidae	Drums or croakers	47
	Zeidae	Dories	47
	Carangidae	Jacks and pompanos	46
	Cottidae	Sculpins	.46
	Platycephalidae	Flatheads	46
	Soleidae	Soles	46
	Ammodytidae	Sand lances	45
	Centrolophidae	Medusafishes	45
	Echeneidae	Remoras	45
	Scomberesocidae	Sauries	45
	Sparidae	Porgies	45
	Engraulidae	Anchovies	44
	Haemulidae	Grunts	43
	Mullidae	Goatfishes	43
	Chlorophthalmidae	Greeneyes	42
	emerephinandae	Spadefishes, batfishes and	12
	Ephippidae	scats	42
	Trichiuridae	Cutlassfishes	42
	Ariidae	Sea catfishes	40
	Cynoglossidae	Tonguefishes	40
	Dasyatidae	Stingrays	40
	Sillaginidae	Smelt-whitings	40
	Trachinidae	Weeverfishes	40
	Atherinidae	Silversides	39
		Threadfin breams, Whiptail	
	Nemipteridae	breams	39
	Triglidae	Searobins	38
	Balistidae	Triggerfishes	37
	Salmonidae	Salmonids	36
	Tetraodontidae	Puffers	36
		Boxfishes (cowfish and	
	Ostraciidae	trunkfish)	33
		Surgeonfishes, tangs,	
	Acanthuridae	unicornfishes	31
	Myctophidae	Lanternfishes	31
		Slimys, slipmouths, or	20
	Leiognathidae	ponyfishes	30
	Gobiidae	Gobies	29
	Bothidae	Lefteye flounders	28
	Caproidae	Boarfishes	28
	Centriscidae	Snipefishes and shrimpfishes	28
	Holocentridae	Squirrelfishes, soldierfishes	28
	Gerreidae	Mojarras	22
	Synodontidae	Lizardfishes	22

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Family	Ambassidae	Asiatic glassfishes	21
	Apogonidae	Cardinalfishes	10
Genus	Muraenesox	Conger eels	90
	Mycteroperca	Grouper	89
	Alopias	Thresher	79
	Dissostichus	Toothfish	79
	Anarhichas	Wolffish	78
	Macrourus	Grenadier	78
	Isurus	Mako	76
	Molva	Ling	76
	Callorhinchus	Elephantfish	75
	Genypterus '	Cusk-eel	75
	Gymnura	Gymnura	75
	Lophius	Angler/Monk fishes	75
	Dasyatis	Stingrays	73
	Macruronus	Grenaiders	73
	Raja	Rays	72
	Bathyraja	Skates	70
	Salvelinus	Charr	70
	Torpedo	Torpedo	68
	Trachinotus	Pompanos	68
	Tylosurus	Needlefishes	67
	Etmopterus	Lanternsharks	66
	Thunnus	Tuna	64
	Austroglossus	Southern soles	63
	Epinephelus	Groupers	63
	Sphyraena	Barracudas	62
	Squalus	Squalus	62
	Trachurus	Cutlass fishes	62
	Argentina	Argentines	61
	Pseudotolithus	Croakers	61
	Scorpaena	Scórpionfish	61
	Beryx	Alfonsinos	60
	Chirocentrus	Wolf herring	60
	Hydrolagus	Chimaeras	60
	Lepidorhombus	Megrims	60
	Merluccius	Hakes	59
	Micropogonias	Western croakers	59
	Chrysoblephus	Seabreams	58
	Sebastes	Redfishes	58
	Caranx	Jacks	57
	Rhinobatos	Guitarfish	57
	Lithognathus	Lithognathus	56
	Lutjanus	Snappers	56
	Mustelus	Smooth-hounds	56
	Nemadactylus	Porae	55

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Genus	Seriola	Amberjacks	55
	Trigla	Gurnards	55
	Centropomus	Snooks	53
	Pagellus	Pandoras	53
	Scyliorhinus	Lesser catsharks	53
	Dentex	Seabreams (Dentex spp)	52
	Pampus	Silver pomfrets	52
	Paralichthys	American flounders	52
	Epigonus	Cardinalfishes	51
	Hemiramphus	Halfbeaks	51
	Scomberoides	Queenfishes	51
	Solea	Soles	51
	Alosa	Shads	50
	Caesio	Fusiliers	50
	Cynoscion	Weakfishes	50
	Diplodus	Seabreams (Diplodus spp)	50
	Salmo	Salmons	50
	Scomberomorus	Seerfishes	50
	Seriolella	Barrelfishes	50
	Trachipterus	Deaf fishes	50
	Coregonus	Whitefishes	49
	Phycis	Gunnels, forkbeards	49
	Batrachoides	Toadfish	47
	Calamus	Porgies	47
	Kyphosus	Sea chubs	47
	Rhinochimaera	Rhinochimaera	47
	Ammodytes	Spookfishes	45
	Prionotus	Sandlances	45
	Rastrelliger	Indo-Pacific mackerels	45
	Sardinella	Sardine	45
	Dicentrarchus	European/spotted seabass	44
	Mullus	Goatfishes	44
	Oncorhynchus		44
	Gymnocranius	Pacific salmon	
	Platax	Large-eye breams	42
		Batfishes	42
	Terapon	Trumpeters	42
	Harengula	Herring	41
	Pagrus	Seabreams (Pagrus spp)	41
	Stolephorus	Anchovies	41
	Lycodes	Eelpouts	40
	Peprilus	Harvestfishes	40
	Menticirrhus	Kingcroakers	39
	Nemipterus	Threadfin breams	39
	Rhodichthys	Rhodichthys	39
	Siganus	Rabbitfishes	39
	Microchirus	Microchirus	38
	Plotosus	Eel catfishes	36

Taxonomic level	Taxon	Common name	Intrinsic vulnerability
Genus	Cantherhines	Filefishes	35
	Rhombosolea	Flounders	35
	Trematomus	Antarctic rockcods	35
	Spicara	Picarels	34
	Serranus	Groupers	32
	Uranoscopus	Stargazers	32
	Leiognathus	Pony fishes	30
	Notoscopelus	Notoscopelus	30
	Gobius	Gobies	29
	Muraenolepis	Moray cods	27
	Myoxocephalus	Sculpins	27
	Priacanthus	Bigeyes	27
	Upeneus	Goatfishes (Upeneus spp)	27
	Auxis	Frigate tuna	26
	Decapterus	Scads	26
	Gaidropsarus	Rocklings	24
	Sphoeroides	Puffers	23
	Gerres	Morrajas	22
	Hypomesus	Hypomesus	20
	Scatophagus	Scats	10
	Scolopsis	Monocle breams	10
Species	Centrophorus granulosus	Gulper shark	90
•	Centrophorus squamosus	Leafscale gulper shark	90
	Lampris guttatus	Opah	90
	Lepidocybium flavobrunneum	Escolar	90
	Lichia amia	Leerfish	90
	Muraenesox cinereus	Daggertooth pike conger	90
	Oxynotus centrina	Angular roughshark	90
	Regalecus glesne	King of herrings	90
	Ruvettus pretiosus	Oilfish	90
	Somniosus microcephalus	Greenland shark	90
	Somniosus pacificus	Pacific sleeper shark	90
	Dipturus laevis	Barndoor skate	87
	Dipturus batis	Blue skate	86
	Dipturus oxyrinchus	Longnosed skate	86
	Megalops atlanticus	Tarpon	84
	Megalops cyprinoides	Indo-Pacific tarpon	84
		-	
	Carcharhinus brachyurus	Copper shark	83
	Carcharhinus obscurus	Dusky shark	83
	Petrus rupestris	Red steenbras	82
	Squatina argentina	Argentine angelshark	80
	Squatina squatina	Angelshark	80
	Alopias superciliosus	Bigeye thresher	79
	Alopias vulpinus	Thintail thresher	79
	Dissostichus eleginoides	Patagonian toothfish	79
	Dissostichus mawsoni	Antarctic toothfish	79

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Ginglymostoma cirratum	Nurse shark	79
	Anarhichas lupus	Wolf-fish	78
	Anarhichas minor	Spotted wolffish	78
	Carcharhinus falciformis	Silky shark	77
	Carcharhinus limbatus	Blacktip shark	77
	Centroscyllium fabricii	Black dogfish	77
	Deania calcea	Birdbeak dogfish	77
	Lepidopus caudatus	Silver scabbardfish	77
	Notorynchus cepedianus	Broadnose sevengill shark	77
	Prionace glauca	Blue shark	77
	Sphyrna lewini	Scalloped hammerhead	77
	Sphyrna zygaena	Smooth hammerhead	77
	Isurus oxyrinchus	Shortfin mako	76
	Isurus paucus	Longfin mako	76
	Aphanopus carbo	Black scabbardfish	75
	Argyrosomus hololepidotus	Southern meagre	75
	Argyrosomus regius	Meagre	75
	Coryphaenoides rupestris	Roundnose grenadier	75
	Lota lota	Burbot	75
	Molva dypterygia	Blue ling	75
	Molva molva	Ling	75
	Reinhardtius stomias	Arrowtooth flounder	75
	Conger orbignyanus	Argentine conger	73
	Rexea solandri	Silver gemfish	73
	Callorhinchus capensis	Cape elephantfish	73 72
	Callorhinchus milii	Ghost shark	72
	Centroscymnus coelolepis	Portuguese dogfish	72
	Centroscymnus coetotepis Centroscymnus cryptacanthus	Shortnose velvet dogfish	72
	Conger oceanicus	American conger	72
	-	American angler	72
	Lophius americanus	Cape monk	72
	Lophius vomerinus Baia microscollata	•	72
	Raja microocellata Tataaha waadaa aldi	Small-eyed ray	
	Totoaba macdonaldi	Totoaba Dairda amaath baad	72
	Alepocephalus bairdii	Bairds smooth-head	71
	Argyrozona argyrozona	Carpenter seabream	71
	Macruronus magellanicus	Patagonian grenadier	71
	Macruronus novaezelandiae	Blue grenadier	71
	Mola mola	Ocean sunfish	71
	Pseudosciaena crocea	Croceine croaker	71
	Bathyraja eatonii	Eatons skate	70
	Genypterus blacodes	Pink cusk-eel	70
	Gobionotothen gibberifrons	Humped rockcod	70
	Lepidonotothen squamifrons	Grey rockcod	70
	Macrourus berglax	Onion-eye grenadier	70
	Macrourus whitsoni	Whitsons grenadier	70
	Salvelinus alpinus	Charr	70
	Dalatias licha	Kitefin shark	69

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Eleutheronema tetradactylum	Fourfinger threadfin	69
	Genypterus chilensis	Red cusk-eel	69
	Leucoraja circularis	Sandy ray	69
	Leucoraja fullonica	Shagreen ray	69
	Polyprion americanus	Wreckfish	69
	Polyprion oxygeneios	Hapuka	69
	Raja clavata	Thornback ray	69
	Raja undulata	Undulate ray	69
	Gnathanodon speciosus	Golden trevally	68
	Hippoglossus hippoglossus	Atlantic halibut	68
	Hippoglossus stenolepis	Pacific halibut	68
	Lobotes surinamensis	Atlantic tripletail	68
	Channichthys rhinoceratus	Unicorn icefish	67
	Lepidopsetta bilineata	Rock sole	67
	Chaenocephalus aceratus	Blackfin icefish	66
	Emmelichthys nitidus nitidus	Redbait	66
	Lamna nasus	Porbeagle	66
	Ophiodon elongatus	Lingcod	66
	Orthopristis chrysoptera	Pigfish	66
	Scomberesox saurus saurus	Atlantic saury	66
	Lophius piscatorius	Angler	65
	Stereolepis gigas	Giant sea-bass	65
	Carcharodon carcharias	Great white shark	64
	Champsocephalus gunnari	Mackerel icefish	64
	Hoplostethus atlanticus	Orange roughy	64
	Makaira mazara	Indo-Pacific blue marlin	64
	Notothenia coriiceps	Yellowbelly rockcod	64
	Notothenia rossii	Marbled rockcod	64
	Orcynopsis unicolor	Plain bonito	64
	Pogonias cromis	Black drum	64
	-	Giant African threadfin	64
	Polydactylus quadrifilis		64
	Pterogymnus laniarius The man ani antalia	Panga seabream	
	Thunnus orientalis	Pacific bluefin tuna	64
	Xiphias gladius	Swordfish	64
	Atractoscion aequidens Atractoscion nobilis	Geelbeck croaker	63
		White weakfish	63
	Centroberyx affinis	Redfish	63
	Cheimerius nufar	Santer seabream	63
	Elagatis bipinnulata	Rainbow runner	63
	Epinephelus aeneus	White grouper	63
	Epinephelus flavolimbatus	Yellowedge grouper	63
	Epinephelus goreensis	Dungat grouper	63
	Epinephelus nigritus	Warsaw grouper	63
	Epinephelus niveatus	Snowy grouper	63
	Epinephelus tauvina	Greasy grouper	63
	Spondyliosoma cantharus	Black seabream	63
	Thunnus maccoyii	Southern bluefin tuna	63

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Thunnus tonggol	Longtail tuna	63
	Eopsetta jordani	Petrale sole	62
	Epinephelus marginatus	Dusky grouper	62
	Lateolabrax japonicus	Japanese seaperch	62
	Leucoraja naevus	Cuckoo ray	62
	Macquaria ambigua	Golden perch	62
	Makaira indica	Black marlin	62
	Makaira nigricans	Atlantic blue marlin	62
	Squalus acanthias	Piked dogfish	62
	Thunnus alalunga	Albacore	62
	Anoplopoma fimbria	Sablefish	61
	Argyrops spinifer	King soldierbream	61
	Galeorhinus galeus	Tope shark	61
	Plectorhinchus mediterraneus	Rubberlip grunt	61
	Pseudotolithus senegallus	Law croaker	61
	Scorpaena scrofa	Largescaled scorpionfish	61
	Thyrsites atun	Snoek	61
	Alectis alexandrinus	African threadfish	60
	Beryx decadactylus	Alfonsino	60
	Chirocentrus dorab	Dorab wolf-herring	60
	Conger conger	European conger	60
	Conger myriaster	Whitespotted conger	60
	Euthynnus affinis	Kawakawa	60
	Euthynnus alletteratus	Little tunny	60
	Euthynnus lineatus	Black skipjack	60
	Hydrolagus novaezealandiae	Dark ghost shark	60
	Megalaspis cordyla	Torpedo scad	60
,	Mycteroperca venenosa	Yellowfin grouper	60
	Mycteroperca xenarcha	Broomtail grouper	60
	Paralonchurus peruanus	Peruvian banded croaker	60
	Paristiopterus labiosus	Giant boarfish	60
	Pseudopercis semifasciata	Pigletfish	60
	Reinhardtius evermanni	Kamchatka flounder	60
	Reinhardtius hippoglossoides	Greenland halibut	60
	Rhabdosargus globiceps	White stumpnose	60
	Semicossyphus pulcher	California sheephead	60
	Stenotomus chrysops	Scup	60
	Thunnus albacares	Yellowfin tuna	60
	Thunnus atlanticus	Blackfin tuna	60
	Thunnus obesus	Bigeye tuna	60
	Thunnus thynnus	Northern bluefin tuna	60
	Cheilopogon agoo	Japanese flyingfish	59
	Helicolenus dactylopterus		
	dactylopterus	Blackbelly rosefish	59
	Larimichthys polyactis	Yellow croaker	59
	Merluccius australis	Southern hake	59
	Merluccius capensis	Shallow-water Cape hake	59
	Pleuronectes platessus	European plaice	59

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Pleuronectes quadrituberculatus	Alaska plaice	· 59
	Rhomboplites aurorubens	Vermilion snapper	59
	Gadus macrocephalus	Pacific cod	58
	Lates calcarifer	Barramundi	58
	Lopholatilus chamaeleonticeps	Great northern tilefish	58
	Merluccius senegalensis	Senegalese hake	58
	Mugil liza	Liza	58
	Pollachius pollachius	Pollack	58
	Pollachius virens	Saithe	58
•	Sebastes entomelas	Widow rockfish	58
	Sebastes flavidus	Yellowtail rockfish	58
	Sebastes melanops	Black rockfish	58
	Sebastes mentella	Deepwater redfish	58
	Sebastes viviparus	Norway redfish	58
	Amblyraja georgiana	Antarctic starry skate	57
	Amblyraja radiata	Thorny skate	57
	Brotula barbata	Bearded brotula	57
	Caranx ruber	Bar jack	57
	Liza saliens	Leaping mullet	57
	Merluccius gayi peruanus	Peruvian hake	57
	Merluccius merluccius	European hake	57
	Rachycentron canadum	Cobia	57
	Mustelus mustelus	Smooth-hound	56
	Theragra chalcogramma	Alaska pollack	56
	Austroglossus microlepis	West coast sole	55
	Austroglossus merotepis Austroglossus pectoralis	Mud sole	55
	Epinephelus analogus	Spotted grouper	55
	· · ·		• 55
	Epinephelus morio Ethmidium maculatum	Red grouper	
		Pacific menhaden	55
	Katsuwonus pelamis	Skipjack tuna	55
	Nemadactylus macropterus	Tarakihi	55
	Petromyzon marinus	Sea lamprey	55
	Pomatomus saltator	Bluefish	55
	Trigla lyra	Piper gurnard	55
	Brosme brosme	Tusk	54
	Caranx rhonchus	False scad	54
	Cetorhinus maximus	Basking shark	54
	Elops lacerta	West African ladyfish	54
	Elops saurus	Ladyfish	54
	Morone americana	White perch	54
	Morone saxatilis	Striped sea-bass	54
	Mycteroperca phenax	Scamp	54
	Nibea mitsukurii	Nibe croaker	54
	Rhinobatos percellens	Chola guitarfish	54
	Rhinobatos planiceps	Pacific guitarfish	54
	Sarda orientalis	Striped bonito	54
	Sardinops sagax	South American pilchard	54

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Sebastes alutus	Pacific ocean perch	54
	Sebastes capensis	False jacopever	54
	Sebastes paucispinis	Bocaccio	54
	Tautoga onitis	Tautog	54
	Trachinotus blochii	Snubnose pompano	54
	Trachinotus carolinus	Florida pompano	54
	Albula vulpes	Bonefish	53
	Brama brama	Atlantic pomfret	53
	Caranx crysos	Blue runner	53
	Caranx hippos	Crevalle jack	53
	Centropomus undecimalis	Common snook	53
	Clupea harengus	Atlantic herring	53
	Clupea harengus membras	Baltic herring	53
	Clupea pallasii	Pacific herring	53
	Girella nigricans	Opaleye	53
	Girella tricuspidata	Luderick	53
	Holtbyrnia anomala	Bighead searsid	53
	Lethrinus atlanticus	Atlantic emperor	53
	Lithognathus lithognathus	White steenbras	53
	Lithognathus mormyrus	Striped seabream	53
	Merluccius hubbsi	Argentine hake	53
	Mora moro	Common mora	53
	Mustelus henlei	Brown smooth-hound	53
	Mustelus lenticulatus	Spotted estuary smooth-hound	53
	Mustelus schmitti	Narrownose smooth-hound	53
	Mycteroperca bonaci	Black grouper	53
	Mycteroperca microlepis	Gag	53
	Myxine glutinosa	Hagfish	53
	Paralabrax humeralis	Peruvian rock seabass	53
	Sarda chiliensis lineolata	Pacific bonito	53
		Red drum	53
	Sciaenops ocellatus Scomber australasicus	Blue mackerel	53
	Sebastolobus alascanus	Shortspine thornyhead	53
	Dentex dentex	Common dentex	52 52
	Eleginops maclovinus	Patagonian blennie	52 52
	Gadus morhua	Atlantic cod	52
	Gadus ogac	Greenland cod	52
	Kathetostoma giganteum	Giant stargazer	52
	Pagellus bogaraveo	Blackspot seabream	52
	Pampus argenteus	Silver pomfret	52
	Paralichthys californicus	California flounder	52
	Pleuragramma antarcticum	Antarctic silverfish	52
	Scyliorhinus canicula	Smallspotted catshark	52
	Scyliorhinus stellaris	Nursehound	52
	Seriola quinqueradiata	Japanese amberjack	52
	Dentex angolensis	Angola dentex	51
	Epigonus telescopus	Bulls-eye	51

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit	
Species	Galeus melastomus	Blackmouth catshark	51	
	Hemiramphus brasiliensis	Ballyhoo	51	
	Isacia conceptionis	Cabinza grunt	51	
	Lepidotrigla dieuzeidei	Spiny gurnard	51	
	Melamphaes leprus	Melamphaes leprus	51	
	Merluccius gayi gayi	South Pacific hake	51	
	Pagellus erythrinus	Common pandora	51	
	Scomber japonicus	Chub mackerel	51	
	Scomber scombrus	Atlantic mackerel	51	
	Scophthalmus maximus	Turbot	51	
	Strangomera bentincki	Araucanian herring	51	
	Trachurus murphyi	Inca scad	51	
	Trachurus picturatus	Blue jack mackerel	51	
	Acanthocybium solandri	Wahoo	50	
	Antimora rostrata	Blue antimora	50	
	Chimaera monstrosa	Rabbit fish	50	
	Clupeonella cultriventris	Black Sea sprat	50	
	Coryphaena hippurus	Common dolphinfish	50	
	Diplodus cervinus cervinus	Zebra seabream	50	
	Galeoides decadactylus	Lesser African threadfin	50	
	Lophius budegassa	Black-bellied angler	50	
	Lophius vaillanti	Shortspine African angler	50	
	Pseudopleuronectes americanus	Winter flounder	50	
	Pseudopleuronectes herzensteini	Littlemouth flounder	50	
	Salilota australis	Tadpole codling	50 50	
	Sarpa salpa	Salema	50 50	
	Seriola dumerili	Greater amberjack	50	
	Seriola lalandi	Yellowtail amberjack	50 50	
	Trachurus declivis	Greenback horse mackerel	50	
		Cunene horse mackerel		
	Trachurus trecae Zanongia conchifer		50 50	
	Zenopsis conchifer	Silvery John dory	50	
	Zenopsis nebulosus	Mirror dory	50	
	Acanthistius brasilianus	Sea bass	49	
	Alosa aestivalis	Blueback shad	49	
	Aloša alosa	Allis shad	49	
	Alosa fallax	Twaite shad	49	
	Alosa pontica	Pontic shad	49	
	Alosa sapidissima	American shad	49	
	Atrobucca nibe	Longfin kob	49	
	Coregonus albula	Vendace	49	
	Dentex macrophthalmus	Large-eye dentex	49	
	Epinephelus guttatus	Red hind	49	
	Epinephelus striatus	Nassau grouper	49	
	Genypterus capensis	Kingklip	49	
	Genypterus maculatus	Black cusk-eel	49	
	Mallotus villosus	Capelin	49	
*	Mugil cephalus	Flathead mullet	49	

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Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Mugil_soiuy	So-iuy mullet	49
	Parona signata	Parona leatherjacket	49
	Phycis blennoides	Greater forkbeard	49
	Phycis phycis	Forkbeard	49
	Pseudochaenichthys georgianus	South Georgia icefish	49
	Raja asterias	Starry ray	49
	Raja montagui	Spotted ray	49
	Sardina pilchardus	European pilchard	49
	Sebastes marinus	Ocean perch	49
	Seriolina nigrofasciata	Blackbanded trevally	49
	Trachurus symmetricus	Pacific jack mackerel	49
	Brevoortia aurea	Brazilian menhaden	48
	Brevoortia pectinata	Argentine menhaden	48
	Cynoscion analis	Peruvian weakfish	48
	Cynoscion regalis	Gray weakfish	48
	Lutjanus purpureus	Southern red snapper	48
	Merluccius bilinearis	Silver hake	48
	Merluccius polli	Benguela hake	48
	Merluccius productus	North Pacific hake	48
	Parophrys vetula	English sole	48
	Pseudophycis bachus	Red codling	48
	Pteroscion peli	Boe drum	48
	Salmo salar	Atlantic salmon	48
	Salmo trutta trutta	Sea trout	48
	Sarda chiliensis chiliensis	Eastern Pacific bonito	48
	Sarda sarda	Atlantic bonito	48
	Sciaena gilberti	Sciaena gilberti	48
	Sciaena umbra	Brown meagre	48
	Scomberomorus guttatus	Indo-Pacific king mackerel	48
	Selaroides leptolepis	Yellowstripe scad	48
	Seriolella brama	Common warehou	48
	Sparisoma cretense	Parrotfish	48
	Tautogolabrus adspersus	Cunner	48
	Tenualosa ilisha	Hilsa shad	48
	Tenualosa toli	Toli shad	48
	Acanthopagrus latus	Yellowfin seabream	47
	Acanthopagrus schlegeli	Black porgy	47
	Brevoortia patronus	Gulf menhaden	47
	Brevoortia tyrannus	Atlantic menhaden	47
	Kyphosus cinerascens	Blue seachub	47
	Melanogrammus aeglefinus	Haddock	47
	Paralichthys dentatus	Summer flounder	47 47
	Paralichthys olivaceus	Bastard halibut	47
	Percophis brasiliensis	Brazilian flathead	47 47
	Pomadasys jubelini		47 47
	Pomaaasys jubenni Pseudocaranx dentex	Sompat grunt White trevelly	
	Pseudocaranx aentex Pseudotolithus elongatus	White trevally Bobo croaker	47 47

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Pseudotolithus senegalensis	Cassava croaker	47
	Rhinochimaera atlantica	Spearnose chimaera	47
	Scomberomorus maculatus	Spanish mackerel	47
	Scomberomorus sierra	Pacific sierra	47
		West African Spanish	
	Scomberomorus tritor	mackerel	47
	Selene dorsalis	African moonfish	47
	Selene setapinnis	Atlantic moonfish	47
	Seriolella caerulea	White warehou	47
	Seriolella porosa	Choicy ruff	47
	Seriolella punctata	Silver warehou	47
	Zeus faber	John dory	47
	Etrumeus teres	Round herring	46
	Etrumeus whiteheadi	Whiteheads round herring	46
	Glyptocephalus cynoglossus	Witch	46
	Glyptocephalus zachirus	Rex sole	46
	Istiophorus albicans	Atlantic sailfish	46
	Istiophorus platypterus	Indo-Pacific sailfish	46
	Parastromateus niger	Black pomfret	46
	Platichthys flesus	Flounder	46
	Platycephalus indicus	Bartail flathead	46
	Psettichthys melanostictus	West American sand sole	46
	Rhizoprionodon terraenovae	Atlantic sharpnose shark	46
	Scomberomorus brasiliensis	Serra Spanish mackerel	46
	Scomberomorus cavalla	King mackerel	46
	Scomberomorus lineolatus	Streaked seerfish	46
	Scorpaenichthys marmoratus	Cabezon	46
	Sebastes goodei	Chilipepper	46
	Sebastes pinniger	Canary rockfish	46
	Sprattus fuegensis	Falkland sprat	46
	Sprattus sprattus	European sprat	46
	Sprattus sprattus balticus	Baltic sprat	46
	Tetrapturus angustirostris	Shortbill spearfish	46
	Tetrapturus pfluegeri	Longbill spearfish	46
	Trachurus lathami	Rough scad	46
	Trachurus mediterraneus	Mediterranean horse mackerel	46
	Trachurus trachurus	Atlantic horse mackerel	46
	Ammodytes personatus	Pacific sandeel	45
	Archosargus probatocephalus	Sheepshead seabream	45
	Boops boops	Bogue	45
	Caulolatilus chrysops	Atlantic goldeye tilefish	45
	Caulolatilus princeps	Ocean whitefish	45
	Cetengraulis edentulus	Atlantic anchoveta	45
	Cetengraulis mysticetus	Pacific anchoveta	45
	Cololabis saira	Pacific saury	45
	Hyperoglyphe antarctica	Antarctic butterfish	45
	Hyperoglyphe bythites	Black driftfish	45
	Joturus pichardi	Bobo mullet	45

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Lutjanus campechanus	Northern red snapper	45
	Micromesistius australis	Southern blue whiting	45
	Micromesistius poutassou	Blue whiting	45
	Ocyurus chrysurus	Yellowtail snapper	45
	Pagellus acarne	Axillary seabream	45
	Pagellus bellottii bellottii	Red pandora	45
	Pleurogrammus azonus	Okhostk atka mackerel	45
	Pleurogrammus monopterygius	Atka mackerel	45
	Pterothrissus belloci	Longfin bonefish	45
	Rastrelliger brachysoma	Short mackerel	45
	Rastrelliger kanagurta	Indian mackerel	45
	Sardinella brasiliensis	Brazilian sardinella	45
	Solea senegalensis	Senegalese sole	45
	Solea solea	Common sole	45
	Spratelloides gracilis	Silverstriped round herring	45
	Tetrapturus albidus	Atlantic white marlin	45
	Tetrapturus audax	Striped marlin	45
	Engraulis anchoita	Argentine anchoita	44
	Engraulis capensis	Cape anchovy	44
	Engraulis encrasicolus	European anchovy	44
	Engraulis japonicus	Japanese anchovy	44
	Engraulis mordax	Californian anchovy	44
	Engraulis ringens	Anchoveta	44
	Mullus barbatus	Red mullet	44
	Mullus surmuletus	Striped red mullet	44
	Opisthonema libertate	Pacific thread herring	44
	Opisthonema oglinum	Atlantic thread herring	44
	Psettodes belcheri	Spottail spiny turbot	44
	Psettodes bennettii	Spiny turbot	44
	Psettodes erumei	Indian spiny turbot	44
	Sardinella maderensis	Madeiran sardinella	44
	Trachurus capensis	Cape horse mackerel	44
	Trachurus japonicus	Japanese jack mackerel	44
	Alosa mediocris	Hickory shad	43
	Alosa pseudoharengus	Alewife	43
	Brachydeuterus auritus	Bigeye grunt	43
	Cyclopterus lumpus	Lumpsucker	43
	Sardinella aurita	Round sardinella	43
	Atherina boyeri	Big-scale sand smelt	42
	Belone belone belone		42
	Dicentrarchus labrax	Garpike European seabass	42
		-	
	Dicentrarchus punctatus	Spotted seabass	42
	Herklotsichthys quadrimaculatus	Bluestripe herring	42
	Lepidorhombus boscii	Fourspotted megrim	42
	Lepidorhombus whiffiagonis	Megrim	42
	Lutjanus argentimaculatus	Mangrove red snapper	42
	Lutjanus argentiventris	Yellow snapper	42

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Lutjanus synagris	Lane snapper	42
	Sardinella gibbosa	Goldstripe sardinella	42
	Sardinella lemuru	Bali sardinella	42
	Sardinella longiceps	Indian oil sardine	42
	Sardinella zunasi	Japanese sardinella	42
	Scophthalmus aquosus	Windowpane	42
	Scophthalmus rhombus	Brill	42
	Trichiurus lepturus	Largehead hairtail	42
	Chrysophrys auratus	Squirefish	41
	Coregonus lavaretus	Common whitefish	41
	Dicologlossa cuneata	Wedge sole	41
	Dorosoma cepedianum	American gizzard shad	41
	Merlangius merlangus	Whiting	41
	Oncorhynchus tshawytscha	Chinook salmon	41
	Pagrus auriga	Redbanded seabream	41
	Pagrus caeruleostictus	Bluespotted seabream	41
	Pagrus pagrus	Common seabream	41
	Sparus auratus	Gilthead seabream	41
	Umbrina canariensis	Canary drum	41
	Urophycis brasiliensis	Brazilian codling	41
	Urophycis chuss	Red hake	41
	Urophycis tenuis	White hake	41
	Chaenodraco wilsoni	Spiny icefish	40
	Chionodraco rastrospinosus	Ocellated icefish	40
	Coregonus huntsmani	Atlantic whitefish	40
	Coregonus oxyŕinchus	Houting	40
	Dasyatis akajei	Red stingray	40 40
	Dasyatis pastinaca	Common stingray	40 40
	Dentex canariensis	Canary dentex	40 40
		Congo dentex	40 40
	Dentex congoensis Eleginus gracilis	Saffron cod	40 40
	Eleginus navaga Galaishthan falisana	Navaga White house	40
	Galeichthys feliceps	White baggar	40
	Hyporhamphus ihi	Garfish	40
	Hyporhamphus sajori	Japanese halfbeak	40
	Lepidorhynchus denticulatus	Thorntooth grenadier	40
	Limanda aspera	Yellowfin sole	40
	Microstomus kitt	Lemon sole	40
	Microstomus pacificus	Dover sole	40
	Peprilus simillimus	Pacific pompano	40
	Pomadasys argenteus	Silver grunt	40
	Pomadasys incisus	Bastard grunt	40
	Pontinus kuhlii	Offshore rockfish	40
	Pseudopentaceros richardsoni	Pelagic armorhead	. 40
	Stromateus fiatola	Blue butterfish	40
	Trachinus draco	Greater weever	40
	Nemipterus virgatus	Golden threadfin bream	39

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Ethmalosa fimbriata	Bonga shad	38
	Oncorhynchus keta 🥤	Chum salmon	38
	Oncorhynchus masou masou	Cherry salmon	38
	Oncorhynchus mykiss	Rainbow trout	38
	Oncorhynchus nerka	Sockeye salmon	38
	Psenopsis anomala	Melon seed	. 38
	Takifugu vermicularis	Takifugu vermicularis	38
	Argentina silus	Greater argentine	37
	Argentina sphyraena	Argentine	37
	Citharichthys sordidus	Pacific sanddab	37
	Cynoscion nebulosus	Spotted weakfish South American striped	37
	Cynoscion striatus	weakfish	37
	Labrus bergylta	Ballan wrasse	37
		Narrow-barred Spanish	
	Scomberomorus commerson	mackerel	37
	Labrus merula	Brown wrasse	37
	Scomberomorus niphonius	Japanese Spanish mackerel	37
	Scomberomorus regalis	Cero	37
	Centropristis striata	Black seabass	36
	Chelidonichthys cuculus	East Atlantic red gurnard	36
	Chelidonichthys lucerna	Tub gurnard	36
	Pegusa lascaris	Sand sole	36
	Chelidonichthys capensis	Cape gurnard	35
	Chelidonichthys gurnardus	Grey gurnard	35
	Chelidonichthys kumu	Bluefin gurnard	35
	Chelidonichthys lastoviza	Streaked gurnard	35
	Chloroscombrus chrysurus	Atlantic bumper	35
	Chloroscombrus orqueta	Pacific bumper	35
	Clupanodon thrissa	Chinese gizzard shad	35
	Diplodus sargus sargus	White seabream	35
	Macrodon ancylodon	King weakfish	35
	Patagonotothen brevicauda	6	
	brevicauda	Patagonian rockcod	35
	Patagonotothen ramsayi	Patagonotothen ramsayi	35
	Pentanemus quinquarius	Royal threadfin	35
	Boreogadus saida	Polar cod	34
	Diplodus puntazzo	Sharpsnout seabream	34
	Normanichthys crockeri	Normans camote	34
	Oncorhynchus gorbuscha	Pink salmon	34
	Oncorhynchus kisutch	Coho salmon	34
	Spicara maena	Blotched picarel	34
	Genyonemus lineatus	White croaker	33
	Lepidoperca pulchella	Orange perch	33
	Limanda ferruginea	Yellowtail flounder	33
	Limanda limanda	Dab	33
	Oblada melanura	Saddled seabream	33
	Trisopterus esmarkii	Norway pout	33

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Trisopterus luscus	Pouting	33
	Trisopterus minutus	Poor cod	33
	Arctoscopus japonicus	Sailfin sandfish	32
	Otolithes ruber	Tiger-toothed croaker	32
	Pennahia argentata	White croaker	32
	Stephanolepis cirrhifer	Thread-sail filefish	32
	Thyrsitops lepidopoides	White snake mackerel	32
	Uranoscopus scaber	Atlantic stargazer	32
	Cheilodactylus variegatus	Peruvian morwong	31
	Ilisha africana	West African ilisha	31
	Ilisha elongata	Elongate ilisha	31
	Lampanyctodes hectoris	Hectors lanternfish	31
	Nemadactylus bergi	White morwong	31
	Zoarces americanus	Ocean pout	31
	Zoarces viviparus	Viviparous blenny	31
	Maurolicus muelleri	Pearlsides	30
	Osmerus eperlanus	European smelt	30
	Osmerus mordax mordax	Atlantic rainbow smelt	30
	Arripis georgianus	Australian ruff	29
	Arripis trutta	Eastern Australian salmon	29
	Gobius niger	Black goby	29
	Hippoglossoides elassodon	Flathead sole	29
	Hippoglossoides platessoides	American plaice	29
	Menticirrhus littoralis	Gulf kingcroaker	29
	Menticirrhus saxatilis	Northern kingcroaker	29
	Pleuronichthys decurrens	Curlfin sole	29
		West African goatfish	29
	Pseudupeneus prayensis	Eulachon	29
	Thaleichthys pacificus Balistes carolinensis		29
	•	Grey triggerfish	
	Macroramphosus scolopax	Longspine snipefish	28
	Muraenolepis microps	Smalleye moray cod	27
	Parapercis colias	Blue cod	27
	Priacanthus macracanthus	Red bigeye	27
	Synagrops japonicus	Japanese splitfin	27
	Ariomma indica	Indian ariomma	26 26
	Hypoptychus dybowskii	Korean sandeel	26
	Pterygotrigla picta	Spotted gurnard	26
	Pterygotrigla polyommata	Latchet	26
	Auxis rochei rochei	Bullet tuna	25
	Auxis thazard thazard	Frigate tuna	25
	Conodon nobilis	Barred grunt	25
	Micropogonias furnieri	Whitemouth croaker	25
	Micropogonias undulatus	Atlantic croaker	25
	Anchoa hepsetus	Broad-striped anchovy	24
	Anchoa mitchilli	Bay anchovy	24
	Glossanodon semifasciatus	Deepsea smelt	24
	Konosirus punctatus	Konoshiro gizzard shad	24

Taxonomic level	Taxon	Common name	Intrinsic vulnerabilit
Species	Microgadus proximus	Pacific tomcod	24
	Microgadus tomcod	Atlantic tomcod	24
	Umbrina canosai	Argentine croaker	24
	Umbrina cirrosa	Shi drum	24
	Mene maculata	Moonfish	23
	Sphoeroides maculatus	Northern puffer Common two-banded	23
	Diplodus vulgaris	seabream	22
	Harpadon nehereus	Bombay-duck	22
	Diplodus annularis	Annular seabream	21
	Diplodus argenteus argenteus	South American silver porgy	21
	Saurida tumbil	Greater lizardfish	21
	Saurida undosquamis	Brushtooth lizardfish	21
	Hypomesus pretiosus	Surf smelt	20
	Leiostomus xanthurus	Spot croaker	20
	Diplophos maderensis	Diplophos maderensis	19
	Lactarius lactarius	False trevally	19
	Peprilus alepidotus	Harvestfish	19
	Peprilus triacanthus	American butterfish	19
	Pellona ditchela	Indian pellona	18
	Leucoraja erinacea	Little skate	17
	Leucoraja garmani	Freckled skate	17
	Meuschenia scaber	Velvet leatherjacket	17
	Diplectrum formosum	Sand seabass	16
	Decapterus maruadsi	Japanese scad	15
	Decapterus russelli	Indian scad	15
	Selar crumenophthalmus	Bigeye scad	15
	Ciliata mustela	Fivebeard rockling	14
	Anodontostoma chacunda	Chacunda gizzard shad	10
	Apogon pseudomaculatus	Twospot cardinalfish	10
	Astronesthes micropogon	Astronesthes micropogon	10
	Bregmaceros mcclellandi	Spotted codlet	10
	Centrobranchus nigroocellatus	Roundnose lanternfish	10
	Dussumieria acuta	Rainbow sardine	10
	Dussumieria elopsoides	Slender rainbow sardine	10
	Ectreposebastes imus	Midwater scorpionfish	10
	Gonostoma atlanticum	Atlantic fangjaw	10
	Hilsa kelee	Kelee shad	10
	Menidia menidia	Atlantic silverside	10
	Symbolophorus veranyi	Large scale lantern fish	10
	Taaningichthys minimus	Taaningichthys minimus	10
	Uncisudis longirostra	Uncisudis longirostra	10

Appendix 4.1. Life history and recruitment parameters of the 21 species of marine fish that are used to simulate time-series of catch, catch-per-unit-effort and abundance through an age-structured population model. Parameters on L_{inf} – Asymptotic length, t_m – age at first maturity, t_{max} – longevity, K – von Bertalanffy growth parameter K, t_o – theoretical age at zero body length, M – instantaneous natural mortality rate, Fecundity – annual fecundity.

	T	4		V	4	М	Es sur diter	
Scientific name	L _{inf}	$\mathbf{t}_{\mathbf{m}}$	t _{max}	K (year ^{·1})	t_{o}	M (year ⁻¹)	Fecundity (eggs per female)	Vulnerability ¹
	(cm)	(year)	(year)		(year)			
Alosa pseudoharengus	41.7	3.6	14.4	0.20	-0.63	0.41	37932	43.33
Alosa sapidissima	78.5	4.7	20.6	0.14	-0.78	0.21	75864	62.87
Brevoorita patronus	38.9	4.7	18.9	0.15	-1.06	0.39	27569	47.5
Brevoortia tyrannus	51.0	2.1	8.4	0.34	-0.45	0.55	154849	34.18
Clupea harengus	30.0	3.5	11.0	0.35	0	0.27	37100	40.65
Coilia dussumieri	25.0	0.6	2.3	1.21	-0.14	2.08	2237	10.00
Engraulis encrasicolus	25.0	2.3	8.8	0.32	-0.55	0.59	16125	32.24
Engraulis mordax	31.0	2.3	8.5	0.33	-0.56	0.64	3417	32.72
Gadus morhua	105.0	2.2	25.0	0.19	0	0.23	4287500	53.82
Lutjanus campechanus	94.1	3.7	16.9	0.17	-0.73	0.31	27943	51.98
Melanogrammus aeglefinus	75.5	2.7	12.0	0.24	-0.54	0.27	318206	50.06
Merluccius hubbsi	98.0	3.3	15.1	0.19	-0.64	0.23	28620	52.83
Morone saxatilis	203.4	11.2	57.9	0.05	-2.10	0.09	250999	86.21
Reinhartius hippoglossoides	82.9	10.9	48.2	0.06	-1.81	0.10	45167	74.95
Sardinops sagax	30.0	1.7	6.6	0.43	-0.38	0.80	25496	27.29
Solea vulgaris	42.4	1.8	7.3	0.39	-0.38	0.57	59161	31.32
Spratus spratus	13.0	1.2	4.0	0.70	-0.29	1.08	5478	20.03
Stenotomus chrysops	38.5	2.6	10.5	0.27	-0.58	0.47	6767	37.54
Stizostedion vitreum	107.0	12.1	57.5	0.05	-2.49	0.09	168739	78.77
Thunnus albacares	183.9	2.3	11.6	0.25	-0.41	0.36	647723	56.08
Trachurus trachurus	54.3	5.1	22.0	0.13	-1.12	0.25	103888	59.23

I - Estimated using the expert system developed in Chapter 2.

2 - Based on estimates in Myers et al. (1999).

6.1 Parameterizations of the 1970s and 2000s model

6.1.1 Phytoplankton

Phytoplankton communities in the NSCS were dominated by diatoms (over 97% in numbers during a survey in the late 1990s), followed by dinoflagellates and other groups (Jia *et al.* 2004).

Biomass and P/B ratio of phytoplankton in the 2000s model were estimated from survey data. The survey estimated chlorophyll *a* concentration by depth in each season. A phytoplankton cell was assumed to consist of an average of 1% (0.5-1.5%) of chlorophyll *a* by weight (Ahlgren 1970). Thus the average depth-integrated chlorophyll *a* concentration was converted to wet weight of biomass using a conversion factor of 100. (Table A6.1). The estimated biomass amounted to 323 t·km⁻² (215 – 646 t·km⁻²). The value is within the range of phytoplankton biomasses reported in Pauly and Christensen (1995a) (13-730 t·km⁻²).

		Estimated Chl	orophyll a density	$(mg Chl.a \cdot m^{-3})$	
Depth	Spring	Summer	Autumn	Winter	Average
(m)					
0	0.10	0.22	0.38	0.50	0.30
20	0.15	0.25	0.35	0.50	0.31
40	0.23	0.32	0.29	0.41	0.31
60	0.22	0.31	0.22	0.31	0.27
80	0.16	0.29	0.16	0.23	0.21
100	0.08	0.20	0.10	0.15	0.13
150	0.01	0.05	0.05	0.05	0.04
200	0.01	0.03	0.03	0.03	0.03
	De	pth-integrated Chlo	rophyll a density (r	ng <i>Chl.a</i> •m ⁻²)	32.26
·		Estimated	l phytoplankton bio	mass (t•km ⁻²)	323

Table A6.1. Estimation of phytoplankton biomass in the NSCS (Jia et al. 2004).

By summing up the estimated daily phytoplankton production in each season in the late 1990s, I estimated the annual phytoplankton production to be 14,290 t·km⁻² year⁻¹. Assuming 1 g C = 9 g (range = 8-10 g) wet weight (Pauly & Christensen 1995a), the estimated annual total production in wet weight was 128,608 t·km⁻² year⁻¹. Thus the P/B ratio of phytoplankton was estimated to be 399 (177 – 665) year⁻¹.

As independent estimates of biomass and P/B ratio in the 1970s were not available, they are assumed to be the same as the 2000s model.

6.1.2. Benthic producer

Benthic producer consists of benthic algae. Biomass and P/B ratio were based on the values reported in Pauly and Christensen (1995a), i.e., 153 t·km⁻² and 11.9 year⁻¹. Since I found no evidence of large changes in biomass of this group over the past few decades, I assumed that the biomass and P/B ratio were the same in the 1970s and 2000s models.

Catch in the 2000s and the 1970s models were estimated from national landings statistics from Guangdong, Guangxi and Hainan provinces in 2000 and 1973. The group 'algae' amounted to 0.045 t·km⁻² and 0.0056 t·km⁻² in 2000 and 1973, respectively.

6.1.3. Zooplankton

Zooplankton biomasses in the three regions in the NSCS: Pearl River Estuary, western Guangdong, and eastern Hainan were estimated to be 10.4, 9.8 and 6.9 t·km⁻², respectively (South China Sea Fisheries Institute, unpublished data). The average was used as the zooplankton biomass in the 2000s model (Average = 9 t·km⁻²; range: 6.9 – 10.4 t·km⁻²). P/B and Q/B ratios were assumed to be the same as the value used in the South China Sea (50-200 m) ecosystem model (Pauly & Christensen 1995b).

The biomass of zooplankton in NSCS decreased from 104.6 mg m⁻³ in 1978-1979 to 22.0 mg m⁻³ in the late 1990s (South China Sea Fisheries Institute, unpublished data). Thus biomass of zooplankton in the 1970s model was increased by 3.8 times from the 2000s model, which became 33.8 t·km⁻². P/B and Q/B ratios were assumed to be the same between years.

Catches in the 2000s and 1970s models were based on national landings statistics from Guangdong, Guangxi and Hainan provinces in 2000 and 1972 (data point only available in the early 1970s), in which the group 'Mo shrimp' (*Acetes* spp.) amounted to $0.095 \text{ t}\cdot\text{km}^{-2}$ and $0.01 \text{ t}\cdot\text{km}^{-2}$, respectively.

6.1.4. Jellyfish

The jellyfish group consists of medusae of the phylum Cnidaria. Based on trawl survey conducted in Hong Kong in 1982-83, biomass of jellyfish in the early 1980s was estimated to be about 1.529 t-km^{-2} . Since extrapolation of this estimate to the entire NSCS may not be valid, biomass was left to be estimated by assuming ecotrophic efficiency of 0.95 in both the 1970s and 2000s models. Local estimates for P/B and Q/B ratios are not available. Thus estimates from the Gulf of Thailand (P/B = 5 year⁻¹, Q/B = 20 year⁻¹) - the closest region where estimates were available – were used in both the 1970s and 2000s models.

Catches were based on national landings statistics. There is no reported landing of jellyfish in 2000 and 1973. However, jellyfish should have been caught and landed in both periods (Jiahua Cheng, East China Sea Fisheries Institute, pers. comm.). Thus I used the 1993 and 1977 landings, the closest years when landings data are available, as approximate estimates of jellyfish landings in the 2000s and 1970s' (0.044 t·km⁻² and 0.0012 t·km⁻², respectively).

6.1.5. Benthos

Benthos is sub-divided into five functional groups: polychaetes, echinoderms, benthic crustaceans (excluding shrimps and crabs), non-cephalopod molluscs, and sessile/other invertebrates. Their biomasses in the 2000s model were estimated from survey conducted in 1998 -2000 (Jia *et al.* 2004) (Table A6.2). Local estimates on P/B and Q/B ratio for these groups were not available, thus I used estimates from other similar systems. Based on estimates for the southern Gulf of Mexico, Q/B ratio of polychaetes in the 2000s model is 22.5 year⁻¹ (Chavez *et al.* 1998). P/B ratio was estimated by assuming a P/Q ratio of 0.3. P/B of echinoderms was assumed to be 1.2 year⁻¹ based on estimates from the Caribbean coral reef (Opitz 1993) while Q/B was 3.58 year⁻¹ (Pauly *et al.* 1993). P/B of benthic crustaceans was 5.65 year⁻¹, the same as the estimated total mortality of *Oratosquilla* spp. from Hong Kong (Pitcher *et al.* 1998), while Q/B was 26.9 year⁻¹ (Opitz 1996). Based on estimates from the Gulf of Thailand (Christensen & Walters 2004b), P/B of non-cephalopod molluscs was 3 year⁻¹. Q/B was

assumed to be 7 year⁻¹ (Opitz 1993). Based on estimates for sessile invertebrate in the Caribbean coral reef (Opitz 1993), P/B and Q/B of sessile/other invertebrates was assumed to be 1 year⁻¹ and 9 year⁻¹, respectively. Biomass estimates of benthos in the 1970s model were based a survey along the Guangdong coast in the late 1970s, while P/B and Q/B ratio were assumed to be similar in the two periods.

Table A6.2. Survey estimated biomass for polychaetes, echinoderms, benthic crustaceans, noncephalopod molluscs, and sessile/other invertebrates in the NSCS in the late 1990s (Jia *et al.* 2004).

Functional groups	Biomass (t·km ⁻²)		
Polychaetes	2.24		
Echinoderms	1.98		
Benthic crustaceans	1.43		
Non-cephalopod molluscs	2.68		
Sessile/other invertebrates	2.61		

Echinoderms were caught in the NSCS but were not reported as a separate group in the national catch statistics. Thus catch estimates from the *Sea Around Us* Project catch database was used, which amounted to 0.0019 t·km⁻² and 0.0039 t·km⁻² for the 2000s and 1970s models, respectively. Catch of benthic crustaceans was obtained from reported landings of 'crustacean' in the national statistics, subtracted by the landings of shrimps and crabs to avoid double-counting (see below). Thus the catch estimates in the 2000s and 1970s models were 0.039 t·km⁻² and 0.0019 t·km⁻², respectively. Noncephalopod molluscs were based on the group 'molluscs' and catches were estimated from national fisheries statistics subtracted by the estimated catch of cephalopods (0.763 t· km⁻² and 0.0056 t·km⁻² in the 2000s and 1970s model, respectively).

6.1.6. Shrimps

Based on trawl survey conducted in the late 1990s, biomass of shrimps in the NSCS was estimated to be 0.013 t·km⁻². However, because of the low catchability of shrimps by the survey trawl nets, the biomass of shrimps was likely to be under-estimated.

Thus biomasses of shrimps in the 1970s and 2000s models were left to be estimated by the model by assuming *EE*. P/B ratio in the 2000s was based on the averaged total mortality estimates of *Metapenaeopsis palmensis* and *M. barbata* from Hong Kong (7.60 year⁻¹) (7.1 – 8.1 year⁻¹), while estimates for the past model was estimated from assuming that fishing mortality rate was half of their natural mortality rate. Assuming that M = 3.6 year⁻¹ (Pitcher *et al.* 1998), P/B ratio for the 1970s model was 5.4 year⁻¹. Q/B ratios of penaeid shrimps were based on the estimates available from Pauly *et al.* (1993). Landings of shrimp were estimated based on national statistics.

6.1.7. Crabs

The late 1990s trawl survey estimated biomass of crabs in the NSCS to be 0.0045 t·km⁻² (Jia *et al.* 2004). This was subsequently found to be too low to support the fisheries and predation specified in the 2000s model. Also, biomass data of crabs in the 1970s were not available. Thus biomasses in the 1970s and 2000s models were estimated by assuming ecotrophic efficiency equalled 0.95. P/B and Q/B ratios in the 1970s model were assumed to be similar to the Gulf of Thailand during that period (3 year⁻¹ and 12 year⁻¹ respectively). I increased the P/B ratio in the 2000s model to 4 year⁻¹ to reflect the higher exploitation rate. Landings of crab was based on the national fisheries statistics.

6.1.8. Cephalopods

In NSCS, *Loligo* squid was the dominant group of cephalopod, consisting of *Loligo edulis* and *L. chinensis*. Estimated *Logilo* squid biomasses from acoustic and trawl surveys in the late 1990s were 1.24 t·km⁻² and 0.13 t·km⁻², respectively (Jia *et al.* 2004). Report from the surveys suggested that the actual biomass of *Loligo* squid in NSCS might probably lie between these two values. Thus I used their average (0.68 t·km⁻²) as the biomass estimate for the cephalopods in the 2000s model. Biomass in the 1970s model was estimated by assuming *EE* to be 0.95. P/B and Q/B ratios were assumed to be the same as the cephalopods group in the Gulf of Thailand (Christensen & Walters 2004).

Cephalopod landings were not reported in the 2000s period. Thus catch estimates of the NSCS region were obtained from the *Sea Around Us* Project catch database (www.seaaroundus.org), which amounted to 0.273 t·km⁻². Catches of cephalopods in the 1970s model was based on the reported landings from the national fisheries statistics in 1973 (0.0244 t·km⁻²).

6.1.9. Threadfin bream (nemipterids)

This group consists of fish from the family Nemipteridae, including *Nemipterus virgatus*, *N. bathybius* and *N. japonicus*. Based on acoustic survey in the late 1990s, biomass of nemipterids in NSCS was estimated to be $0.26 \text{ t}\cdot\text{km}^{-2}$. This was used in the 2000s model. P/B ratio, approximated by the total mortality rate, was estimated to be 3.08 year⁻¹ (Wang *et al.* 2004). Q/B ratio was estimated from empirical equations (Palomares & Pauly 1998).

Compared to the 1990s survey, catch rate of *N. virgatus* in the NSCS dropped by about 72% from a 1962 survey (Jia *et al.* 2004) while catch rate of *N. bathybius* dropped by 68%-88.2% (averaged 78%) from an early 1990s survey (Jia *et al* 2004). Based on the average between the two estimates, I assumed that biomass of nemipterids (assuming that abundance was roughly proportional to catch rate) declined approximately by 75% from the 1970s to late 1990s. Thus biomass in the 1970s model was estimated to be 1.04 t·km⁻². Fishing mortality rate in the 1970s was estimated from the exploitation rate (catch/biomass). With an estimated total catch of 0.062 t·km⁻², total mortality rate was estimated to be 0.74 year⁻¹ (M = 0.68 year⁻¹, Wang *et al.* 2004). Q/B ratio was assumed to be stationary between years. Catch data in the 2000s and 1970s were obtained from national landings statistics.

6.1.10. Bigeyes (priacanthids)

Bigeyes consists of fishes from the family Priacanthidae. Acoustic and trawl surveys estimated that the biomass of Bigeyes in the late 1990s was 0.245 t·km⁻² and 0.009 t·km⁻², respectively. The average of the two estimates was used as the biomass in the 2000s model (0.127 t·km⁻²). P/B ratio in the 2000s model was estimated from the total mortality rates (3.33 year⁻¹) (Sun & Qiu 2004), Q/B ratio was estimated from an empirical equation (Palomares and Pauly 1998).

Catch rates of priacanthids in the late 1990s was only 40% of the 1962 level (South China Sea Fisheries Institute, unpublished data). Assuming that change in biomass was proportional to catch rate, estimated biomass in the 1970s was 0.318 t·km⁻². Fishing mortality rate in the 1970s was approximated from the exploitation rate calculated from the total catch (0.025 t·km⁻²) and biomass. The estimated total mortality rate was 1.21 year⁻¹ (M = 1.13 year⁻¹) (Sun and Qiu 2004). Q/B ratio was assumed to be stationary between years.

Landings of bigeyes in 2000 were not reported in the national fisheries statistics. However, bigeyes were reported to represent about 2.31% and 1.79% in weight in the catch of the late 1990s and the 1970s fishing surveys in the NSCS, respectively (South China Sea Fisheries Institute, unpublished data). Based on the total landings reported in the national statistics, catch of bigyeyes in the 2000s and 1970s models were estimated to be 0.207 t·km⁻² and 0.035 t·km⁻², respectively.

6.1.11. Lizardfish (synodontids)

Fishes of the family Synodontidae are included in this group. The major species in the NSCS include *Saurida tumbil* and *S. undosquamis*. Based on fishing survey in the late 1990s, total biomass of these two species was estimated to be 0.0318 t·km⁻². Total mortality rates of the lizardfish in the NSCS continental shelf and Gulf of Tonkin were estimated to be 1.42 and 1.78 year⁻¹, respectively (Shu & Qiu 2004). Their average was used as the P/B ratio in the 2000s model. Q/B ratio was estimated from an empirical equation (Palomares and Pauly 1998).

Since a historical biomass trend for lizardfish was not available, its biomass in the 1970s model was estimated indirectly. Estimated total demersal fish biomass in the NSCS declined by 30.8% from the early to late 1990s (South China Sea Fisheries Institute, unpublished data). Moreover, standardized catch rate of lizardfish by Hong Kong trawlers declined by 69% from the 1970s to the late 1980s (Chapter 5). Biomass in the 1970s was then back-calculated from the 1980s and 1990s (0.149 t·km⁻²). Fishing mortality rate in the 1970s was approximated from the exploitation rate calculated from the total catch (0.024 t·km⁻²) and biomass. The total mortality rate was estimated to be

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0.79 year⁻¹ (M = 0.63 year⁻¹) (Shu & Qiu 2004). This was later found to be too low to support predation and catches on this group. Thus I increased the P/B ratio slightly to 0.85 year⁻¹. Q/B ratio was assumed to be the same between the 1970s and 2000s.

Landings of lizardfish in the late 1990s and early 2000s were not available from the national statistics. Thus catch in the 2000s and 1970s models were estimated based on the SAUP database ($0.086 \text{ t}\cdot\text{km}^{-2}$ and $0.084 \text{ t}\cdot\text{km}^{-2}$, respectively).

6.1.12. Hairtails (trichiurids)

This group is composed of fishes from the family Trichiuridae. This group has been seriously over-exploited and is now dominated by juvenile (age 1 or less) fishes (South China Sea Fisheries Institute, unpublished data). I segregated this group into two multi-stanza groups – juvenile (age less than 18 months) and adult using the multi-stanza routine in Ecopath (Table A6.3) (Christensen & Walters 2004). In the late 1990s, biomass of *Trichiurus lepturus* – a dominant species of this group in the NSCS – was estimated to be 0.015 t·km⁻² by trawl survey (South China Sea Fisheries Institute, unpublished data). Since catch of *T. lepturus* was mainly composed of juvenile fish (Jia *et al.* 2004), I allocated the entire estimated biomass to the juvenile stage, and I used the multi-stanza routine to estimate the adult stage biomass.

Biomass of the adult stage in the 1970s was back calculated from the estimated biomass in the 1990s. By assuming a 65% decline in biomass from the 1970s to the late 1980s (see Chapter 5), and a 30.8% decline from the early to late 1990s (assuming that biomass of trichiurids declined at the same rate as the overall demersal resources) (Jia *et al.* 2004), the biomass in the 1970s was estimated to be 0.0426 t·km⁻².

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Table A6.3. Growth and recruitment parameter values for groups that consist of multi-stanza in the 1970s and 2000s models.

Groups	No. of stanza	von Bertalanffy growth parameter <i>K</i> (year ⁻¹)	Recruitment power	W _{maturity} /W _{inf}
Hairtails (trichiurids)	2	0.41 ¹	1^2	0.0007^{1}
Croakers (> 30 cm)	2	0.36^{3}	1^2	0.15^{4}
Demersal fish (> 30 cm)	2	0.31 ⁵	1^{2}	0.13 ⁵
Pelagic fish (> 30 cm)	2	0.59 ⁶	12	0.136

¹ Values reported in Fishbase (www.fishbase.org);

² Default value ;

³ Based on 26 stocks of large croakers in the NSCS;

⁴ Based on 59 stocks of large croakers in the NSCS;

⁵ Based on 33 species of large demersal fish in the NSCS;

⁶ Based on 23 species of large pelagic fish in the NSCS.

Hairtails were found to be relatively under-exploited in the 1970s compared to the 2000s (Chapter 5). The P/B ratio was thus approximated as 2 times the natural mortality rate, and P/B of the adult stage hairtails in the 1970s was estimated to be 1.08 year⁻¹.

Landings of hairtail reported in the national statistics in 2000 was 227,202 t. However, an independent survey estimated a maximum annual fishery catch of hairtail from the NSCS of only 13,000 t (South China Sea Fisheries Institute, unpublished data). Because of the higher unreliability of the national statistics and the possibility of overreporting (Watson & Pauly 2001), the latter estimate (13,000 t) was used in the 2000s model. Since the majority of the hairtails caught in the 2000s were reported to be juveniles (< 1 year), I assumed that 80% of the total hairtail catch in weight was from the juvenile stanza. This resulted in estimated catches of 0.028 t·km⁻² and 0.007 t·km⁻² for the juvenile and adult stanza, respectively. As landings statistics in the1970s were more reliable (Qiu, Y. South China Sea Fisheries Institute, pers. comm.), it was used in the 1970s model (0.019 t·km⁻²). Since hairtails in the 1970s were only moderately exploited and the fishery targeted mostly adults, I assumed that 80% of the catch was from the adult stanza.

6.1.13. Pomfrets (stromateids)

Members of this group are fish from the family Stromateidae. Based on an acoustic survey in the late 1990s, the estimated total biomass of stromateids, ariommids, nomeis and formionids in the late 1990s was 0.43 t·km⁻². As information on the relative composition among these groups was not available, I assumed that the estimated biomass was evenly distribution among the groups. Thus biomass of pomfrets was estimated to be 0.108 t·km⁻². Changes in biomass of this group from the 1970s to 2000s were reported to be similar to trends of overall resource changes. Estimated demersal fishery resources in the NSCS in this period declined by approximately 59%. Thus the estimated biomass of this group in the 1970s model was 1.03 t·km⁻².

Estimates of total mortality or exploitation rates were mainly available for demersal or pelagic species, but not benthopelagic species. Thus P/B ratios in the 1970s and 2000s models were left to be estimated by the model, assuming P/Q ratio of 0.2. Q/B ratio was calculated from an empirical equation (Palomares & Pauly 1998) and assumed to be similar in both models. Catches in the 2000s and 1970s were based on national statistics (0.230 t·km⁻² and 0.0053 t·km⁻²).

6.1.14. Snappers

Members of this group are from the family Lutjanidae. Biomass estimates were not available for the 1970s and 2000s. Thus biomasses of snappers in the 1970s and 2000s models were estimated by assuming EE (= 0.95). Natural mortality rate was estimated from Pauly's empirical equation (Pauly 1980). Since independent estimates of fishing mortality were not available, I assumed that the group was under similar exploitation rate (E = F/Z) as the other exploited demersal fish groups. Based on the average E of 0.62 for demersal fish groups in the NSCS (South China Sea Fisheries Institute, unpublished data) and substituting Z = F+M into the equation, total mortality was roughly estimated to be 1.75 year⁻¹. Populations of snappers was assumed to be under-exploited in the 1970s, thus I assumed F = M and Z = 2M. The total morality rate calculated from this method was 1.24 year⁻¹. Q/B ratios were calculated from an empirical equation (Palomares & Pauly 1998).

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Since landings of snappers were not reported in the national statistics in the 2000s, estimates from the SAUP database were used in the model (0.001 t·km⁻²). Landings statistics were available in the 1970s, which amounted to 0.0053 t·km⁻².

6.1.15. Groupers

Members of this group are from the family Serranidae. Biomass estimates were not available and thus they were estimated in the models by assuming *EE* to be 0.95. Natural mortality rate was estimated to be 0.67 year⁻¹ from Pauly's empirical equation. Since independent estimates of fishing mortality were not available, I assumed that the group was under similar exploitation rate (E = F/Z) as other major exploited demersal fish groups (E = 0.62, South China Sea Fisheries Institute, unpublished data) and substituting Z = F+M into the equation, total mortality was roughly estimated to be 1.75 year⁻¹. Populations of groupers were assumed to be fully-exploited in the 1970s. Thus I assumed F = M and Z = 2M (total morality = 1.24 year⁻¹). Q/B ratios were calculated from an empirical equation and assumed to be the same in the 1970s and 2000s models. Landings in 2000 and 1973 reported in the national statistics were 0.089 t·km⁻² and 0.0029 t·km⁻², respectively.

6.1.16. Melon seed

Melon seed, or *Psenopsis anomala*, is a benthopelagic fish. Biomass in the late 1990s was estimated from the average between the biomass estimates from a trawl survey and an acoustic survey $(0.00091 - 0.11 \text{ t·km}^{-2})$ (Jia *et al.* 2004). However, this value was later found to be too small to support the catch and predations. Thus the biomass was adjusted upward slightly to become 0.07 t·km⁻². P/B in the 2000s was estimated from the total mortality rate of *P. anomala* (2.41 year⁻¹) (South China Sea Fisheries Institute, unpublished data). Between the 1970s and 2000s, fishery resources in the NSCS declined by approximately 59% (Jia *et al.* 2004). Based on the estimated biomass in the 2000s model, the estimated biomass of melon seed in the 1970s model was estimated to be 0.114 t·km⁻². P/B in the 1970s was assumed to be twice the natural mortality rate while

Q/B was estimated from an empirical equation. Catches were based on the national fisheries statistics.

6.1.17. Small croakers

Members of this group are of the family Sciaenidae, with total length less than or equal to 30 cm. Commercially important species include Agyrosomus spp. and Pennahia spp. Based on an acoustic survey in the late 1990s (Jia et al. 2004), biomass of commercially important small croakers in the NSCS was estimated to be 0.0368 t km⁻². However, based on a trawl survey, biomass of *Pennahia* (Agyrosomus) argentatus in the same time period was already 0.392 t·km⁻². This group was reported to have been severely over-exploited and age 1 fish dominated the population (South China Sea Fisheries Institute, unpublished data). Given that the annual catch of this group was estimated to be about 0.003 t km⁻² only, the acoustic survey estimated biomass should be more reasonable. The ratio of commercial to non-commercial demersal fish in the NSCS was about 1:0.9 (Jia et al. 2004). Scaling the biomass of commercially important Agyrosomus spp and Pennahia spp. with this ratio, total biomass of small croakers in the 2000s model was estimated to be 0.07 t·km⁻². Total mortality rate of Pennahia (Agyrosomus) argentatus in 1992-93 was estimated to be 3.3 year⁻¹ (Yuan, South China Sea Fisheries Institute, unpublished data). Since a similar estimate was not available for recent years, the 1992-93 estimate was used as P/B ratio in the 2000s model.

Biomass in the 1970s model was estimated from the biomass estimate for the 2000s model. Catch rates of *Pennahia* (*Agyrosomus*) *argentatus* by trawlers halved from 0.4 kg h⁻¹ to 0.2 kg h⁻¹ in the mid 1980s and the late 1990s, respectively (Jia *et al.* 2004). From the early 1970s to the mid 1980s, its biomass declined by about 52% (Chapter 5, estimated from the average of white croaker and other croakers). Assuming that catch rate was proportional to abundance, biomass in the 1970s was estimated to be 0.29 t·km⁻². A direct estimate of total mortality in the 70s period was not available. Since exploitation of this group should be moderate, fishing mortality rate was assumed to be the same as the natural mortality rate. Thus a total mortality rate of 2.36 year⁻¹ for the 1970s model was used. Q/B ratios of the 1970s and 2000s models were derived from an empirical

equation. Catch of small croakers in the 1970s model was based on the reported landings in 1973 (0.0197 t·km⁻²). Catches of small croakers in the 2000s were calculated from the estimated biomasses and fishing mortality rates (0.035 t·km⁻²).

6.1.18. Large croakers

Large croakers are sciaenids with maximum total length of more than 30 cm. This group was seriously over-exploited, and is currently composed of mostly juveniles. This group was divided into two stanzas which were ontogenically linked through the multi-stanza routine (Christensen *et al.* 2004). The first stanza represented sexually immature fish (less than 24 months old), while the second stanza represented fishes older than 24 months. The parameter values for the multi-stanza routine were obtained from FishBase (www.fishbase.org) (Table A6.3).

Biomass of the adult stanza was estimated from catch composition of bottom trawls and the total demersal biomass in the NSCS. Landings of stern and bottom trawls from Hong Kong were reported to have an average of 1.5% of large croakers (Agriculture, Fisheries and Conservation Department, Hong Kong unpublished data). Because of the low value of juvenile croakers, they were usually landed as "mixed fish" instead of "croakers". The average proportion of adult croakers in the landings of croakers was assumed to represent its relative abundance in the demersal fishery resources of the NSCS. Total demersal resources in the NSCS in the late 1990s were estimated to be 0.64 t·km⁻² (Jia *et al.* 2004). Thus biomass of adult croakers was estimated to be 0.0094 t·km⁻². Total demersal biomass in the NSCS declined by 30.8% from the 80s to late 90s while catch rate of commercially important large croakers declined by an average of 85.5% from the 70s to 80s. Assuming that biomass of adult large croakers followed these trends, biomass in the 1970s model was estimated to be 0.095 t·km⁻².

P/B ratio in the 2000s model was estimated from natural mortality rate, catch and biomass. Fishing mortality rate of adult large croakers in the 2000s was estimated to be 0.67 year⁻¹ (Jia *et al.* 2004). Based on Pauly's empirical equation, natural mortality rate was estimated to be 0.76 year⁻¹, therefore the total mortality rate was 1.43 year⁻¹. Since large croakers were already heavily exploited in the 70s, I assumed that P/B ratio in the

1970s model was the same as in the 2000s model. P/B ratios of juvenile croakers in both models were assumed to be the same as small croakers. Q/B ratio of adult croakers was estimated from an empirical equation.

Based on the above parameter values, the multi-stanza routine estimated the biomass and Q/B ratio of juvenile large croakers to be $0.072 \text{ t}\cdot\text{km}^{-2}$ and 16.47 year⁻¹ in the 2000s model, and 0.051 t $\cdot\text{km}^{-2}$ and 15.48 year⁻¹ in the 1970s model respectively.

Landings of yellow croaker (*Larimichthys crocea*), a commercially important large croaker, was reported to be 0.079 t·km⁻² in 2000 in the national statistics. As the majority of the catch was dominated by juvenile fish (<1 year), 90% of the landings was assumed to be juveniles. As catch of this group in 1973 was not reported in the national statistics, estimates were based on the SAUP database (0.055 t·km⁻²). In the 1970s model, 80% of the catch was assumed to be adults.

6.1.19. Small demersal fish

This group consists of demersal fish with maximum total length less than or equal to 30 cm (except those that have been included in other functional groups). Estimates of total biomasses of small demersal fish in the 1970s and 2000s were not available, so it was estimated by assuming *EE* to be 0.95. P/B ratio in the 2000s model was estimated from natural mortality rate (1.8 year⁻¹, averaged from species with available estimates using Pauly's empirical equation) and an averaged exploitation rate (F/Z) of 0.62 in the NSCS (thus Z = 4.7 year⁻¹). In the 1970s model, as small demersal fish were only moderately exploited, fishing and natural mortality rate of 2.7 year⁻¹. Q/B ratios in both models were estimated from an empirical equation. Catch of this group in the 2000s and 1970s were based on the SAUP database (0.179 t·km⁻² and 0.0902 t·km⁻² respectively).

6.1.20. Large demersal fish

This group consists of demersal fish with maximum total length greater than 30 cm (except those that have been included in other functional groups). This group was divided into two stanza. The adult stanza represents fish older than 18 months.

Biomass was estimated from commercial catch composition and estimated total demersal resources in the NSCS. Large demersal fish contributed about 25% to the total catch of bottom trawls. Based on the estimated total demersal fishery resources, biomass of large demersal fish was estimated to be 0.64 t·km⁻². Since the late 1990s, the majority of large demersal fish stocks had been over-exploited and juveniles (age 1-2) dominated the populations. Thus I assumed that 90% of the biomass was from the juvenile stanza (below age 2) (i.e., 143 t·km⁻²).

In the 2000s model, juvenile large demersal fish were assumed to have similar natural mortality rates as the small demersal fish, while fishing mortality rate was estimated to be 1.68 year⁻¹. Thus the P/B of juvenile large demersal fish in the 2000s was estimated to be 3.5 year⁻¹. P/B ratio of adult large demersal fish was obtained from the estimated natural mortality rate (0.8 year⁻¹) and the averaged exploitation rate (F/Z) of exploited species in the NSCS in the late 90s. This resulted in a P/B ratio of 2.1 year⁻¹. Q/B ratio was estimated from an empirical equation. Based on the other basic parameter values for the multi-stanza routine, biomass of adult large demersal fish was estimated to be 0.015 t·km⁻².

In the 1970s model, average demersal fishery resources in the 1970s was estimated to be 1.51 t·km⁻². Large demersal fish represented about 26% of the catch of bottom trawls in 1973 (Agriculture, Fisheries and Conservation Department, Hong Kong, unpublished data). Assuming that this represents the relative abundance of this group in the demersal fisheries resources, biomass of large demersal fish in the 1970s was estimated to be 0.39 t·km⁻². Since the group was relatively under-exploited in the 1970s, I assumed that the adult stanza represented 50% of the estimated biomass. Based on the estimated biomass and catch (0.144 t·km⁻²) of adult large demersal fish, fishing mortality was roughly estimated to be 0.74 year⁻¹. Thus P/B ratio of adult stanza was 1.54 year⁻¹ (M = 0.8 year⁻²). P/B ratio of juvenile stanza was assumed to be the same as small demersal

fish. Q/B ratio was estimated from an empirical equation. Multi-stanza parameters follow those in the 2000s model (Table A6.3).

Catches in the 2000s and 1970s models were based on the SAUP database (0.351 $t \cdot km^{-2}$ and 0.144 $t \cdot km^{-2}$, respectively). Since catch of this group was dominated by juvenile fish in the late 1990s, I assumed 90% of the catch was from the juvenile stanza. However, the adult stanza should have dominated the catch in the 1970s, thus I assumed 80% of the catch was from adult stanza in the 1970s model.

6.1.21. Small benthopelagic fish

This group consists of benthopelagic fish with maximum total length less than or equal to 30 cm. Benthopelagic fish was defined as fish living and feeding near the bottom as well as in mid-water or near the surface (FishBase: www.fishbase.org).

Natural mortality rates of fishes in this group were estimated by using Pauly's empirical equation. The average natural mortality rate from the member species was 1.54 year⁻¹. Exploitation rate (F/Z) in the 2000s was estimated to be about 0.55 (South China Sea Fisheries Institute, unpublished report). Thus total mortality rate was approximately 3.08 year^{-1} . Q/B ratio was estimated from a P/Q ratio of 0.2. As a biomass estimate was not available, it was estimated by assuming *EE* to be 0.95.

For the 1970s model, biomass was estimated by assuming *EE* to be 0.95. As the group was only lightly exploited in the 1970s, fishing mortality rate was assumed to be half the natural mortality rate. Thus P/B ratio was estimated to be 2.31 year⁻¹. Q/B was estimated from an assumed P/Q ratio of 0.2. Catches of this group in the late 1990s and early 1970s were estimated based on the SAUP database (0.643 t·km⁻² and 0.0023 t·km⁻² respectively).

6.1.22. Large benthopelagic fish

This group consists of fish with maximum total length of more than 30 cm. Biomass was estimated by assuming *EE* to be 0.95. Natural mortality rate estimated from Pauly's empirical equation was 0.86 year⁻¹. Exploitation rate (F/Z) in the 2000s was estimated to be about 0.55 (South China Sea Fisheries Institute, unpublished report). Thus total mortality rate was estimated to be 1.91 year⁻¹. Q/B ratio was estimated from an empirical equation.

For the 1970s model, biomass was of large benthopelagic fish estimated by assuming *EE* to be 0.95. As the group was only lightly exploited in the 1970s, fishing mortality rate was assumed to be half of the natural mortality rate, thus P/B ratio was estimated to be 1.29 year⁻¹. Q/B ratio was assumed to be the same between the 1970s and 2000s. Catches in the two periods were based on the SAUP database (0.0079 t·km⁻² and 0.0053 t·km⁻², respectively).

6.1.23. Small pelagic fish

This group consists of pelagic fish with maximum total length of less than or equal to 30 cm. In the late 1990s, total biomass of commercially valuable small pelagic fish, including sardine, thryssa, anchovy, etc. was estimated to be $1.47 \text{ t}\cdot\text{km}^{-2}$ (Agriculture, Fisheries and Conservation Department, Hong Kong unpublished data). The ratio of commercial to non-commercial pelagic nekton biomass was estimated to be 4.9:1 (Jia *et al.* 2004). Based on this ratio, small pelagic fish biomass was estimated to be $1.77 \text{ t}\cdot\text{km}^{-2}$.

Based on Pauly's empirical equation, natural mortality rate of small pelagic fish was 1.91 year^{-1} . Assuming that this group had similar exploitation rate (F/Z) as *Decapterus maruadsi* in the late 1990s (0.55), total mortality rate was estimated to be 4.26 year^{-1} . Q/B ratio was estimated from empirical equation.

A biomass estimate of small pelagic fish in the 1970s was not available, thus it was estimated by the model by assuming EE to be 0.95. As the group was only lightly exploited in the 70s, fishing mortality rate was assumed to be half the natural mortality rate. Thus the P/B ratio was estimated to be 2.87 year⁻¹. Q/B ratio was assumed to be the same between the 1970s and 2000s.

Catch of this group was estimated from the landings of the commercially important small pelagic taxa (anchovy and sardine) reported in the national statistics $(2.344 \text{ t·km}^{-2})$. However, such data were not reported in the early 1970s. Thus catch in the 1970s model was based on the SAUP data (0.146 t·km⁻²).

6.1.24. Large pelagic fish

This group consists of demersal fish with maximum total length greater than 30 cm (except those that have been included in other functional groups). It was divided into two stanzas. The adult stanza represented fish older than 18 months. Based on acoustic survey, biomass of commercially valuable large pelagic fishes (e.g. scombrids) in the late 1990s was about 0.079 t·km⁻². Based on Pauly's empirical equation, natural mortality rate of large pelagic fish was 0.59 year⁻¹. Assuming that this group had similar exploitation rate (F/Z) as *Decapterus maruadsi* in the late 1990s (0.55), total mortality rate was estimated to be 1.31 year⁻¹ (Cheng & Qiu 2003). Q/B ratio was estimated from an empirical equation. For the juvenile stanza, P/B ratio was assumed to be the same as small pelagic fish. Based on the multi-stanza routine, its biomass and Q/B ratio were estimated to be 0.242 t·km⁻² and 16.08 year⁻¹ respectively.

For the 1970s model, biomass of large pelagic fish was suggested to have declined by more than 90% from the 1950s to 1990s (Cheung & Sadovy 2004). Assuming that biomass of this group declined by approximately 50% from the 1970s to 1990s (upper and lower limits are 90% and 10% respectively), biomass of the adult stanza in the 1970s model was estimated to be 0.158 t·km⁻². As the group was only lightly exploited in the 70s, fishing mortality rate was assumed to be half the natural mortality rate. Thus P/B ratio was estimated to be 0.9 year⁻¹. Q/B was assumed stable in the two periods.

Catch of this group was calculated based on landings of commercially important large pelagic taxa. In the 2000s model, since the majority of the catches were juveniles, I assumed that 90% of the catch was from the juvenile stanza. However, such data were not reported in the early 1970s. Thus catch was based on the SAUP data (0.048 t·km⁻²). As the group was only moderately exploited in the 1970s, I assumed 80% of the catch was from the adult stanza.

6.1.25. Sharks and rays

Elasmobranchs were divided into demersal and pelagic groups. Demersal sharks and rays represented about 0.1% of bottom trawlers' catches in the late 1980s. This was assumed to represent the relative abundance of demersal elasmobranchs relative to the total demersal biomass in the late 1990s. Thus biomass was estimated to be about 0.001 t km⁻². However, this biomass level was found to be too low to support the fishery. Thus it was left to be estimated by the model by assuming an *EE* of 0.95. Since pelagic sharks and rays were ill-represented in demersal trawls, its biomass could not be estimated from the catch composition of demersal trawlers. The biomass of this group in the 1970s was estimated by assuming *EE* to be 0.5. A report in the late 1990s suggested that demersal sharks and rays mostly consisted of small species in the NSCS (Jia *et al.* 2004). The natural mortality rates of the demersal and pelagic groups estimated from Pauly's empirical equation were about 0.84 year⁻¹ and 0.26 year⁻¹. Assuming an averaged exploitation rate (F/Z) of 0.62 in the NSCS, total mortality rates of the demersal and pelagic groups were estimated to be 2.2 year⁻¹ and 0.68 year⁻¹, respectively. Q/B ratios were estimated by assuming P/Q ratios to be 0.2.

Catch composition of bottom trawls in the 1970s consisted of about 1% of demersal sharks and rays. Based on total estimated demersal resources of 1.51 t·km⁻² in that period, biomass of demersal sharks and rays in the 1970s model was estimated to be 0.015 t·km⁻². Biomass of pelagic sharks and rays was estimated by the model with an assumed *EE* of 0.5.

As the group was lightly exploited in the 1970s, fishing mortality rate was assumed to be half the natural mortality rate, thus P/B ratios of the demersal and pelagic groups become 1.26 year⁻¹ and 0.39 year⁻¹, respectively. Q/B ratios were estimated by an assumed P/Q ratio of 0.2. Catch of demersal and pelagic sharks and rays in the late 1990s and the 1970s were based on the SAUP database.

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6.1.26. Seabirds, pinnipeds, other mammals and marine turtles

Since parameters for these groups were not available for the whole modeled region, the input parameter values were assumed to be the same as an ecosystem model of Hong Kong waters (Buchary *et al.* 2003; Cheung and Sadovy 2004; Pitcher *et al.* 2002).

6.1.27. Detritus

Information regarding detritus biomass in the NSCS was unavailable. Since the model was generally insensitivity to detritus biomass, biomasses of detritus in the 1970s and 2000s models were assumed to be $100 \text{ t}\cdot\text{km}^{-2}$.

6.2. Diet composition matrices of the 1970s and 2000s NSCS models

	Predators			
Preys	Zooplanktons	Jellyfish		
Phytoplanktons	0.700			
Zooplanktons		0.900		
Jellyfish		0.080		
Pelagic fish (≤ 30 cm)		0.019		
Juvenile large pelagic fish		0.001		
Detritus	0.300			
Sum	1.000	1.000		

			Predators		
Preys	Polychaetes	Echinoderms	Benthic crustaceans	Non-ceph molluscs	Sessile/other invertebrates
Phytoplanktons		0.003	0.070	0.070	
Benthic producers		0.554	0.151	0.151	
Zooplanktons		0.003	0.050	0.050	0.600
Polychaetes		0.022	0.054	0.100	
Echinoderms		0.059			
Benthic crustaceans		0.003			
Non-ceph molluscs		0.056	0.080	0.010	
Sessile/other					
invertebrates		0.100	0.001	0.010	
Shrimps					
Detritus	1.000	0.200	0.594	0.609	0.400
Sum	1.000	1.000	1.000	1.000	1.000

Preys	Shrimps	Crabs
Phytoplanktons	0.027	
Benthic producers	0.125	0.200
Zooplanktons	0.193	
Polychaetes	0.121	0.240
Echinoderms		0.010
Benthic crustaceans		0.020
Non-ceph molluscs		0.140
Sessile/other		
invertebrates		0.010
Shrimps		0.050
Detritus	0.534	0.330
Sum	1.000	1.000

Predators

	Predators
Preys	Cephalopods
Zooplanktons	0.46600
Echinoderms	0.06200
Benthic crustaceans	0.12500
Non-ceph molluscs	0.06800
Shrimps	0.00500
Crabs	0.05000
Cephalopods	0.04300
Threadfin bream (nemipterids)	0.00010
Lizard fish (synodontids)	0.00010
Juv Hairtail (trichiurids)	0.00010
Pomfret (stromateids)	0.01000
Snappers	0.00001
Adult groupers	0.00001
Demesral fish (≤ 30 cm)	0.00005
Benthopelagic fish	0.01300
Melon seed	0.00100
Pelagic fish (≤ 30 cm)	0.15600
Juvenile large pelagic fish	0.00010

	Predators					
Preys	Threadfin bream (nemipterids)	Bigeyes (priacanthids)	Lizard fish (synodontids)			
Phytoplanktons	0.015					
Zooplanktons	. 0.120	0.322				
Polychaetes	0.173	0.086				
Echinoderms	0.030		·			
Benthic crustaceans	0.156	0.084				
Non-ceph molluscs	0.384	0.015				
Sessile/other invertebrates		0.003				
Shrimps	0.005	0.007	0.190			
Crabs	0.001	0.136				
Cephalopods		0.005	0.092			
Threadfin bream (nemipterids)		0.014	0.050			
Bigeyes (priacanthids)	0.001	0.008	0.038			
Lizard fish (synodontids)			0.019			
Adult groupers			0.002			
Croakers (≤ 30 cm)		0.060				
Juv large croakers		0.001	0.004			
Demesral fish (≤ 30 cm)	0.099	0.239	0.198			
Juv demersal fish (> 30 cm)		0.020				
Benthopelagic fish	0.015					
Melon seed	0.001					
Pelagic fish (≤ 30 cm)			0.407			

	Predators			
	Juv Hairtail	Adult hairtail	Pomfret	
Preys	(trichiurids)	(trichiurids)	(stromateids)	
Phytoplanktons			0.010	
Zooplanktons	0.107	0.040	0.375	
Jellyfish			0.478	
Polychaetes	0.008		0.020	
Echinoderms	0.015		0.002	
Benthic crustaceans	0.031	0.010	0.002	
Non-ceph molluscs			0.023	
Sessile/other invertebrates			0.024	
Shrimps	0.092	0.050		
Crabs	0.005	0.010	0.024	
Cephalopods	0.153	0.100	0.008	
Threadfin bream (nemipterids)	0.046	0.034		
Bigeyes (priacanthids)				
Lizard fish (synodontids)	0.034	0.035		
Juv Hairtail (trichiurids)	0.010	0.010		
Adult hairtail (trichiurids)		0.010		
Adult groupers				
Croakers (≤ 30 cm)	0.096	0.070		
Juv large croakers	0.008			
Demesral fish (≤ 30 cm)	0.236	0.142		
Juv demersal fish (> 30 cm)				
Benthopelagic fish	0.150	0.099	0.013	
Melon seed	0.009	0.001	0.001	
Pelagic fish (≤ 30 cm)		0.389	0.020	

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		Predators				
		Adult	Croakers	Juv large	Croakers	
Preys	Snappers	groupers	(≤ 30 cm)	croakers	(> 30 cm)	
Zooplanktons	0.0500		0.3140	0.3140	0.2230	
Jellyfish					0.0090	
Polychaetes	0.0100		0.0550	0.1200		
Echinoderms			0.0420	0.1000		
Benthic crustaceans	0.1000	0.1720	0.2020	0.2460	0.3400	
Non-ceph molluscs	0.0500	0.0460	0.0070	0.0070	0.0090	
Sessile/other invertebrates			0.0020	0.0110		
Shrimps	0.0500	0.0840	0.1300	0.1000		
Crabs	0.0500	0.0910	0.0010	0.0010	0.0010	
Cephalopods		0.0840				
Threadfin bream (Nemipterids)	0.0100				0.0090	
Bigeyes (Priacanthids)					0.0020	
Lizard fish (Synodontids)				•	0.0020	
Pomfret (Stromateids)					0.0280	
Snappers		0.0001				
Adult groupers		0.0009				
Croakers (≤ 30 cm)				0.0500	0.0070	
Juv large croakers			0.0010			
Croakers (> 30 cm)						
Demesral fish (≤ 30 cm)	0.6800	0.4570	0.0940	0.0500	0.1250	
Juv demersal fish (> 30 cm)		0.0550			0.0003	
Adult demersal fish (> 30 cm)		0.0090			0.0010	
Benthopelagic fish			0.1000		0.1140	
Melon seed			0.0010		0.0130	
Pelagic fish (≤ 30 cm)			0.0500		0.1170	

	Predators				
	Demesral fish	Juv demersal	Adult demersal	Benthopelagic	
Preys	(≤ 30 cm)	fish (> 30 cm)	fish (> 30 cm)	fish	
Phytoplanktons	0.0130	0.0130		0.1459	
Benthic producers	0.0300	0.0300		0.1459	
Zooplanktons	0.3020	0.4244	0.0840	0.4705	
Jellyfish	0.0090	0.0090	0.0010		
Polychaetes	0.0890	0.0901	0.0470	0.0290	
Echinoderms	0.0020	0.0020	0.0150		
Benthic crustaceans	0.2200	0.2653	0.4380	0.0490	
Non-ceph molluscs	0.1210	0.0511	0.1370	0.0190	
Sessile/other invertebrates	0.0100	0.0410			
Shrimps	0.0270	0.0020	0.0020		
Crabs	0.0250	0.0010	0.0010	0.0100	
Cephalopods	0.0040	0.0090	0.0100	0.0060	
Threadfin bream (nemipterids)			0.0100		
Bigeyes (priacanthids)			0.0100		
Lizard fish (synodontids)			0.0100		
Juv Hairtail (trichiurids)			0.0100		
Snappers	0.0001				
Adult groupers			0.0050		
Croakers (≤ 30 cm)			0.0100		
Juv large croakers	0.0001	0.0010	0.0004		
Croakers (> 30 cm)			0.0004		
Demesral fish (≤ 30 cm)	0.0250	0.0050	0.1940		
Juv demersal fish (> 30 cm)	0.0030	0.0050			
Benthopelagic fish	0.0110		0.0070	0.0090	
Melon seed	0.0070		0.0010	0.0010	
Pelagic fish (≤ 30 cm)		0.0090	0.0070	0.0859	
Detritus	0.1010	0.0420		0.0290	

	Predators				
Preys	Melon seed	Pelagic fish (≤ 30 cm)	Juvenile large pelagic fish	Pelagic fish (> 30 cm)	
Phytoplanktons	0.0190	0.2200	0.0630	0.0110	
Benthic producers			0.0760		
Zooplanktons	0.8860	0.7520	0.5890	0.4580	
Jellyfish					
Polychaetes	0.0380	0.0210	0.0160	0.0110	
Echinoderms					
Benthic crustaceans			0.0060	0.0580	
Non-ceph molluscs		0.0060	0.0550	0.0090	
Sessile/other invertebrates	0.0190	0.0010	0.0230	0.0060	
Shrimps			0.0006		
Crabs					
Cephalopods	0.0190		0.0030	0.0180	
Juv Hairtail (trichiurids)				0.0005	
Adult hairtail (trichiurids)				0.0020	
Pomfret (stromateids)	0.0030				
Croakers (≤ 30 cm)				0.0050	
Juv large croakers				0.0002	
Demesral fish (≤ 30 cm)	0.0030				
Benthopelagic fish	0.0100		0.0600	0.0400	
Melon seed			0.0060	0.0040	
Pelagic fish (≤ 30 cm)	0.0030		0.0300	0.3750	
Detritus			0.0730	0.0020	

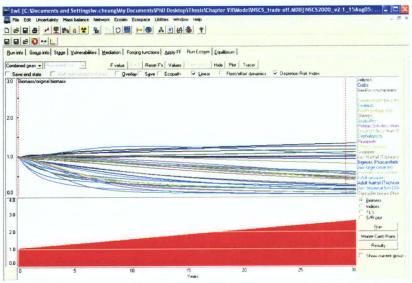
Predators

	Predators							
Preys	Demersal sharks and rays	Pelagic sharks and rays	Seabirds	Pinnipeds	Other mammals	Marine turtles		
Phytoplanktons				· · · · · · · · · · · · · · · · · · ·		0.0005		
Benthic producers			0.1198			0.4000		
Zooplanktons	0.0860		0.0030		0.0040	0.2380		
Polychaetes			0.2086					
Echinoderms			0.0030		0.0350	0.0110		
Benthic crustaceans	0.3600		0.0190			0.0110		
Non-ceph molluscs	0.1150	0.0006	0.1357		0.0350	0.0110		
Shrimps	0.0700		0.0479	0.0380		0.0090		
Crabs	0.0520	0.0010	0.0010	010200	0.0001	0.0110		
Cephalopods		0.2420	0.1148	0.2700	0.0800	0.0180		
Threadfin bream		0.2.20	0.11.0	0.2700	0.0000	0.0100		
(nemipterids)	0.0050				0.0200	0.0050		
Bigeyes (priacanthids) Lizard fish	0.0050				0.0190	0.0050		
(synodontids)	0.0410				0.0050	0.0009		
Juv Hairtail (trichiurids)	0.0110	0.0010			0.0100	0.0500		
Adult hairtail						0.0500		
(trichiurids)		0.0010			0.0060	0.01(0		
Pomfret (stromateids)	0.0001	0.0660			0.0630	0.0160		
Snappers	0.0001				0.0020	0.0006		
Adult groupers	0.0050	0.0100	0 1 1 10		0.0040	0.0006		
Croakers (≤ 30 cm)	0.0170	0.0130	0.1148	0.2500	0.0140	0.0040		
Juv large croakers	0.0030			0.0030	0.0002	0.0001		
Croakers (> 30 cm)	0.0020			0.0030	0.0040			
Demesral fish (≤ 30 cm) Juv demersal fish	0.1860			0.3080	0.0300	0.0070		
(> 30 cm)	0.0070			0.1130	0.0060	0.0820		
Adult demersal fish								
(> 30 cm)	0.0010			0.0130	0.0010	0.0090		
Benthopelagic fish	0.0270	0.1790	0.1068		0.1690	0.0430		
Melon seed	0.0070	0.0260	0.0080		0.0330			
Pelagic fish (≤ 30 cm) Juvenile large pelagic		0.4320			0.4040	0.0660		
fish		0.0250	0.1148	0.0010	0.0450	0.0009		
Pelagic fish (> 30 cm)		0.0050		0.0010	0.0110			
Demersal sharks and								
rays	0.0100	0.0001						
Pelagic sharks and rays		0.0090						
Seabirds		0.0001						
Pinnipeds		0.0001						
Other mammals		0.0001						
Marine turtles		0.0001						
Detritus			0.0030					

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7.1. Screenshots of an interface for calculating the depletion index in Ecosim.



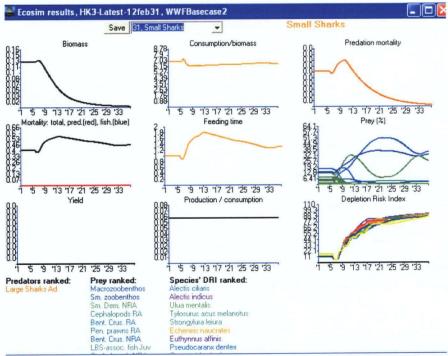
a. A check box 'Depletion Risk Index' was added to the 'Run Ecosim' panel in Ecosim. User needs to check the box to set up the input parameters and calculate the depletion index from the simulation results. An input parameter form will appear after checking the box.

	Designed		
Lg. Dem. NRA. Juv	▼ Parameters		Edit
	Lmax (cm)	1.4.77	
Leiognathus splendens	Tm (year)	1	
Paraplagusia bilineata Stephanolepis cirrhifer Istigobius hoshinonis	T max (year)	2.3	
Bothus myriaster Carangoides praeustus	von Bertalanffy growth K	0.98	
Acanthogobius flavimanus Tridentiger trigonocephalus	Natural mortality (year^-1)	2.59	
Istigobius campbelli Upeneus sulphureus Pentaprion longimanus	Fecundity (egg per year)		
Leiognathus bindus Leiognathus elongatus	Spatial behaviour strength	80	
Leiognathus leuciscus Leiognathus splendens	Aggregation	Г	
Secutor insidiator	Feeding	Г	
Gazza minuta Polydactylus sextarius	Spawning	Г	
Add Delete	Geographic range		
Add Delete	EEZ area (km^2)	32958	
View rules	Coastline (km)	219466	

b. This forms allow the user to open the species lists and connect to a database (extracted from FishBase) from which the life history and ecology parameters required to calculate the depletion index will be automatically extracted.

Biomass decline	VLw	VLw	VLw	Lw	Lw	Lw	Mod	-
Rel.F/Int. Vul.	Lw	Ave	Hg	Lw	Ave	Hg	Lw	F
Low	0	0	0	0	0	0	0	1
Mod	0	0	0	0	1	1	1	2
High	0	0	0	1	2	2 3	2	2
VHigh	0	0	1	1	2	3	2	2
								•
					Vie	w rules	Default	
					Vie	w rules	Default	

c. Users can vary the rule matrix that is used to calculate the depletion index.



d. After setting up the input parameters, users can run Ecosim to simulation changes in the ecosystem. The depletion risk estimated of each species within a functional will be recorded and can be displayed in one of the Ecosim graphical display form. The figure for depletion index is located in the lower right corner. The list of species within the functional in descending order of depletion risk is also displayed in the lower right panel.

	Group	Average risk	Species no.	High risk species no
1	Pen. prawns RA	42.3	3	2
2	Cephalopods NRA	81.7	3	3
3	Cephalopods RA	5	10	0
4	LBS-assoc. fish Ad	87	6	6
5	Sm. Dem. RA	85.5	2	2
6	Sm. Dem. NRA	46.9	35	1
7	Med. Dem. RA	89.9	52	52
8	Med. Dem. NRA	81.3	17	17
9	Lg. Dem. RA. Ad	88	9	9
10	Lg. Dem. NRA. Juv	81.4	309	309
11	Sm. Pelagics	88.4	197	197
12	Med. Pelagics	83.5	27	27
13	Lg. Pelagics Ad	81.5	19	19
14	Small Sharks	84.6	43	43
15	Large Sharks Juv.	90.5	61	61
16	Large Sharks Ad.	92.5	3	3
	TOTAL	82.2	796	41

e. The average depletion index ('Average risk') of the species within a functional group ('Group) at a particular time-step of the simulation can be displayed.

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