

# ECOLOGY AND FISHERIES OF SEAMOUNT ECOSYSTEMS

by

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## ABSTRACT

This thesis explores some fundamental questions about seamount ecology and fisheries. Initially, I characterized the seamount distribution on the Azores Exclusive Economic Zone using two bathymetry datasets. The algorithm developed was able to map and describe 63 large and 332 small seamount-like features in the EEZ of the Azores. The distribution suggests that large proportion of seamounts occur in chains along the Mid Atlantic Ridge, however, few isolated seamounts are also present in the Azores. In clarifying how seamounts affect primary productivity, I show that primary production enhancement is not sufficient to support often-observed large aggregations of fish. My work supports an alternative hypothesis, that a horizontal flux of prey is the key factor in sustaining rich communities living on seamounts. Additionally, the importance of seamounts to some large pelagic fish, marine mammals and seabirds is also demonstrated. In the case of skipjack and bigeye tuna, common dolphin and Cory's shearwater, these species were significantly more abundant in the vicinity of some seamount summits. I found that seamounts may act as feeding stations for some of these visitors. The methodology developed, however, failed to demonstrate seamounts' association for bottlenose dolphins, spotted dolphin, sperm whale, terns, yellow-legged gull, and loggerhead sea turtles. Fisheries exploitation is a major threat to seamount ecosystems, but I am not presently able to quantify the amount of catches taken from seamounts around the world. Instead, I demonstrate that global landings of demersal marine fishes have shifted to deeper water species over the last 50 years, an indirect indication that seamounts have also increased in importance. Moreover, I show that 'deep-water', 'seamount' and 'seamount-aggregating' fish stocks may be at serious risk of depletion, since their life histories render them highly vulnerable to overfishing with little resilience to overexploitation. Finally, ecosystem modelling analyses indicate that sustainable seamount fisheries with tolerable ecosystem impacts can be found only by maximizing an 'ecological' objective function. This suggests that industrial fisheries are not viable on seamounts. However, regulated small-scale artisanal fishing fleets could be sustained by seamount ecosystems.

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## DEDICATION

I'm delighted and excited having the opportunity to dedicate this work to my grandparents Joaquim and Margarida for everything what they mean to me and for what this moment represents for them. I also want to dedicate it to Patrícia and little Matilde, with sincere apologies for the time I have been absent. And to my parents Manuel and Odete and brother Filipe, with no further words. Let me share with the non-Portuguese speaking readers a poem from Fernando Pessoa (1888-1935).

*“É com emoção que dedico este trabalho ao meu avô Joaquim e avó Margarida, por tudo o que eles significam para mim e pelo que este momento representa para eles. Uma dedicação muito especial à Patrícia e à pequenina Matilde, com um pedido sincero de desculpa pelo tempo que estive ausente. E aos meus pais Manuel e Odete e ao irmão Filipe, sem mais palavras.”*

### **Fernando Pessoa** **Mar português**

Ó mar salgado, quanto do teu sal  
São lágrimas de Portugal!  
Por te cruzarmos, quantas mães choraram,  
Quantos filhos em vão rezaram!  
Quantas noivas ficaram por casar  
Para que fosses nosso, ó mar!

Valeu a pena? Tudo vale a pena  
Se a alma não é pequena.  
Quem quer passar além do Bojador  
Tem que passar além da dor.  
Deus ao mar o perigo e o abismo deu,  
Mas nele é que espelhou o céu.

### **Fernando Pessoa** **Portuguese Sea**

Salt-laden sea, how much of all your salt  
Is tears of Portugal!  
For us to cross you, how many sons have kept  
Vigil in vain, and mothers wept!  
Lived as old maids how many brides-to-be  
Till death, that you might be ours, sea!

Was it worth? It is worth while, all,  
If the soul is not small.  
Whoever means to sail beyond the Cape  
Must double sorrow - no escape.  
Peril and abyss has God to the sea given  
And yet made it the mirror of heaven

Translated into English by J.Griffin

## CO-AUTHORSHIP STATEMENT

### CHAPTER 2

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## CHAPTER 5

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## CHAPTER 6

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## CHAPTER 7

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## CHAPTER 1

### INTRODUCTION: SEAMOUNTS AS HOTSPOTS OF MARINE LIFE<sup>1</sup>

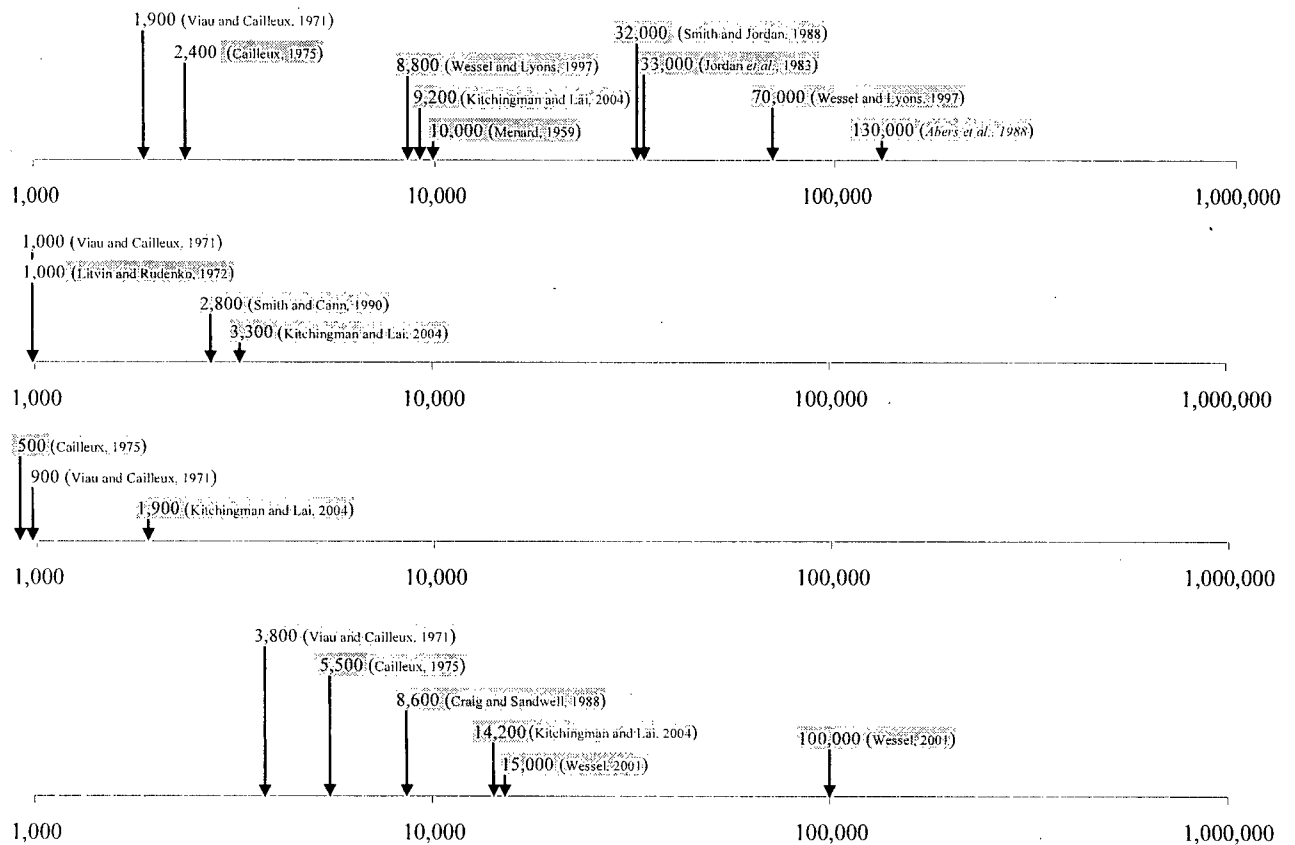
#### 1.1 WHAT ARE SEAMOUNTS?

Seamounts are undersea mountains (usually of volcanic origin) rising from the seafloor and peaking below sea level (Epp and Smoot, 1989). Underwater mountains of heights above 1000 m are considered to be seamounts, those between 500-1000 m as knolls, and those below 500 m as hills (Rogers, 1994). Typically, seamounts are formed by volcanic activity over hotspots in the earth's crust (Epp and Smoot, 1989). Spreading of the sea floor away from these hotspots via plate tectonic movements means that seamounts are often arranged in long chains or clusters that radiate out from such spreading zones (Menard and Dietz, 1951; Menard, 1964). Seamounts can have slopes of up to 60°, much greater than anywhere else in the deep sea, and are often much younger than the surrounding sea floor. A seamount tall enough to break the sea surface is called an oceanic island, e.g., the islands of Hawaii, the Azores and Bermuda were all underwater seamounts at some point in the past.

Though most people may be unaware of it, underwater seamounts are fairly common. Estimates vary largely (Figure 1.1), but studies suggest that there may be from 1.9 to 130 thousand large seamounts, those of heights over 1000 m, in the Pacific Ocean (Viau and Cailleux, 1971; Cailleux, 1975; Jordan *et al.*, 1983; Smith and Jordan, 1988; Abers *et al.*, 1988; Wessel and Lyons, 1997), from 1 to 2.8 thousand the Atlantic Ocean (Viau and Cailleux, 1971; Litvin and Rudenko, 1972; Smith and Cann, 1990) and from 500 to 900 large seamounts in the Indian Ocean (Viau and Cailleux, 1971; Cailleux, 1975).

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<sup>1</sup> A version of this chapter has been published. Morato, T. 2003. Seamounts – hotspots of marine life. ICES Newsletter 40: 4-6. <http://www.ices.dk/marineworld/seamounts.asp>



Numbers of large seamount (> 1km height)

**Figure 1.1** - Number of seamounts large seamount (> 1km height) estimated by various authors and methods, where a) is for the Pacific Ocean, b) for the Atlantic Ocean, c) for the Indian Ocean, and d) for world's oceans. Colours refer to the methods used: yellow is contour maps; orange is wide-beam soundings; green is multi-beam soundings; and blue is satellite altimetry.

The world's number of large seamounts is still unknown, but estimates vary from 3.8 to over 100 thousand (Viau and Cailleux, 1971; Cailleux, 1975; Craig and Sandwell, 1988; Marova, 2000; Wessel, 2001). Global seamount datasets containing information on world's seamount positions are rare, and most larger datasets often only contain data for single oceans (e.g., Fornari *et al.*, 1987; Smith and Jordan, 1988; Epp and Smoot, 1989; Smith and Cann, 1990; Wessel and Lyons, 1997).

Scientific knowledge on seamounts is still very poor and fundamental questions such as how many are out there are still hard to answer. In fact, only a small fraction of the world's seamounts have actually been mapped bathymetrically (Wessel and Lyons, 1997).

## **1.2 CURRENTS AND PRIMARY PRODUCTION AROUND SEAMOUNTS**

Seamounts are said to be hotspots of marine life in the relatively empty open ocean (Rogers, 1994). They tend to enhance water currents (Genin *et al.*, 1986; Boehlert, 1988) and can have their own localized tides, eddies and upwellings (Lueck and Mudge, 1997) where cold deepwater moves up from the deep along the steep sides of the seamount. These patterns may enhance primary production (PP) over and around seamounts due either to uplifting of isotherms into the euphotic zone and introducing biogenes into nutrient-poor water (Genin and Boehlert, 1985; Dower *et al.*, 1992; Odate and Furuya, 1998; Mouriño *et al.*, 2001), or to stabilization of the water column above the seamount, maintaining phytoplankton cells in a suitable light regime, promoting the growth of diatoms, and increasing growth rates and PP (Comeau *et al.*, 1995). For example, Mouriño *et al.* (2001) showed that local increase in chlorophyll *a*, enhanced carbon incorporation rates and changes in phytoplankton species composition were associated with a seamount. Although some investigations have failed to demonstrate persistent high chlorophyll *a* patches over seamounts (Peláez and McGowan, 1986), Mouriño *et al.* (2001) demonstrated that production enhancement effects were subjected to a large degree of spatial and temporal variability both at seasonal and shorter time scales. The effects of seasonality on upwelling may be partially responsible for the large variation in the results and conclusions of seamount studies.

Nevertheless, the hypothesis that seamounts enhance PP is not yet well tested (Table 1.1) and a general procedure to test this hypothesis is still lacking.

### 1.3 SECONDARY PRODUCTION ON SEAMOUNTS: ZOOPLANKTON COMMUNITIES

The biomass of zooplankton is often high over seamounts, but, as for PP, evidence concerning zooplankton features over seamounts is conflicting (Table 1.1). Huskin *et al.* (2001) concluded that mesoscale structures (such as seamounts) influence zooplankton distribution and abundance, although more detailed temporal and spatial studies were said to be required to determine the real influence of them. Fedosova (1974) reported increases in zooplankton abundances over seamounts of 2 to 8 fold, while Huskin *et al.* (2001) reported a 1.6 fold increase. On the other hand, an absence of zooplankton above seamounts due to grazing or other effects were detected in several studies (Genin *et al.*, 1994; Haury *et al.*, 2000), while other studies reported no differences in zooplankton biomass either on or off seamounts (Voronina and Timonin, 1986; Dower and Mackas, 1996). Sime-Ngando *et al.* (1992) reported an increase of ciliate biomass (micro-zooplankton) over seamounts, probably related to seamount-induced physical forcing, which likely generates microhabitats favourable to the growth of opportunistic or physiologically-adapted populations.

Regarding pelagic crustaceans over and around seamounts, two main features have been observed (Vereshchaka, 1994): 1) the rise of lines of equal size, abundances and biomass of the pelagic animals, and 2) the decrease in abundance, biomass and sizes of pelagic animals near the bottom water layer. One of the possible important causes of the decrease in abundance and biomass of pelagic shrimps near the bottom is that they are consumed by benthic and benthopelagic predators. Vereshchaka (1996) concluded that the abundance of pelagic animals decreases while the concentration of benthopelagic predators increases near the seafloor and the role of the former in planktonic communities falls in the near-bottom layer.

**Table 1.1** - Examples of literature supporting or opposing the main hypotheses about seamount ecosystem functioning. Note **this is not a complete list** but some examples only.

Hypotheses	Supporting evidence	Opposing evidence	Judgment
Enclosed circulation cells around seamounts (Taylor columns)	17, 22, 32, 34, 52	35	Tested and supported by data
Increased phytoplankton biomass and primary productivity	7, 19, 26, 40, 48	10, 54	Not fully tested
Increased zooplankton biomass (micro and meso)	4, 5, 20, 35, 37, 47, 53, 55, 58	11, 14, 24, 29, 42	Not fully tested
Increased fish larvae biomass	46	21, 56	Not fully tested
Increased micronekton biomass	13, 31	25, 28, 57	Not fully tested
Increased demersal and pelagic fish biomass	6		Tested and supported by data
Tuna aggregations	18, 41, 43, 45		Not fully tested
Swordfish aggregations	49		Not tested
Increased occurrence of sharks	16, 38		Not tested
Increased occurrence of cephalopods		52	Not fully tested
Increased occurrence of marine mammals	22		Not tested
Increased occurrence of seabirds	27, 30		Not tested
Increased occurrence of sea-turtles	60		Not tested
Increased occurrence of corals and other epibenthic megafauna	9, 15	15	Not fully tested
High endemism	12, 36, 39, 44, 61	50, 59	Not fully tested
Increased demersal and pelagic fish biomass are supported by:			
bottom trapping of migrating zooplankton	3, 24, 31, 33, 51		Not fully tested
horizontal flux of non-migrating zooplankton	8, 9, 33		Not fully tested
locally enhanced primary production	1, 2, 6		Not fully tested

1) Uda and Ishino, 1958; 2) Hubbs, 1959; 3) Isaacs and Schwartzlose, 1965; 4) Simpson and Heydorn, 1965; 5) Fedosova, 1974; 6) Uchida and Tagami, 1984; 7) Genin and Boehlert, 1985; 8) Tseitlin, 1985; 9) Genin *et al.*, 1986; 10) Peláez and McGowan, 1986; 11) Voronina and Timonin, 1986; 12) Wilson and Kaufman, 1987; 13) Boehlert, 1988; 14) Genin *et al.*, 1988; 15) Kaufman *et al.*, 1989; 16) Klimley *et al.*, 1988; 17) Brink, 1990; 18) Fonteneau, 1991; 19) Dower *et al.*, 1992; 20) Sime-Ngando *et al.*, 1992; 21) Boehlert and Mundy, 1993; 22) Reeves and Mitchell, 1993; 23) Freeland, 1994; 24) Genin *et al.*, 1994; 25) Vereshchaka, 1994; 26) Comeau *et al.*, 1995; 27) Haney *et al.*, 1995; 28) Vereshchaka, 1995; 29) Dower and Mackas, 1996; 30) Monteiro *et al.*, 1996; 31) Vereshchaka, 1996; 32) Goldner and Chapman, 1997; 33) Koslow, 1997; 34) Lueck and Mudge, 1997; 35) Mullimeaux and Mills, 1997; 36) Parin *et al.*, 1997; 37) Saltzman and Wishner, 1997; 38) Hazin *et al.*, 1998; 39) Koslow and Gowlett-Holmes, 1998; 40) Odate and Furuya, 1998; 41) Holland *et al.*, 1999; 42) Haury *et al.*, 2000; 43) Itano and Holland, 2000; 44) Richer de Forges *et al.*, 2000; 45) Sibert *et al.*, 2000; 46) Dower and Perry, 2001; 47) Huskin *et al.*, 2001; 48) Mouriño *et al.*, 2001; 49) Sedberry and Loefer, 2001; 50) Fock *et al.*, 2002a; 51) Fock *et al.*, 2002b; 52) Diekmann and Piatkowski, 2004; 53) Fock *et al.*, 2004; 54) Genin, 2004; 55) Martin and Nellen, 2004; 56) Nellen and Ruseler, 2004; 57) Pusch *et al.*, 2004; 58) Schnack-Schiel and Henning, 2004; 59) Tracey *et al.*, 2004; 60) Dellinger, 2005; 61) Vereshchaka, 2005.



Another example of high zooplankton abundance over seamounts was reported by Dower and Perry (2001) who found a high abundance of larval rockfish over Cobb Seamount (SW of Vancouver Island, Canada). They suggested that a persistent clockwise eddy, consistent with a stratified Taylor cone, plays a critical role in retaining larval rockfish and may contribute to the process of self-recruitment.

#### **1.4 SEAMOUNT BENTHIC COMMUNITIES**

On the seamount floor there are often rich communities dominated by suspension feeders, e.g., gorgonians and other corals (Richer de Forges *et al.*, 2000; Ohkushi and Natori, 2001; Koslow *et al.*, 2001), that may be particularly susceptible and sensitive to disturbance by trawling (Probert *et al.*, 1997; Koslow *et al.*, 2001). Enhanced currents and steep slopes expose the volcanic rocks and favour the growth of suspension feeders in these benthic seamount communities (Genin *et al.*, 1986; Grigg *et al.*, 1987; Wilson and Kaufmann, 1987; Rogers, 1994), in contrast to the deposit feeders typical of most deep-sea benthos.

The abundance and biomass of benthic organisms on some seamounts was, however, observed to be very low when compared to other hard bottom habitats at similar depths (Grigg *et al.*, 1987; Gillet and Dauvin, 2000). Though the diversity and exceptionally localized distribution of species living in these communities are acknowledged (Richer de Forges *et al.*, 2000), their biology and life history remain poorly studied, except for some indications that some of these species may be extremely long-lived, e.g., up to maximum ages of over 100 years (Grigg, 1993).

#### **1.5 SEAMOUNT FISHES**

Seamounts have received much attention mainly because of the presence of substantial aggregations of forage fishes in mid- and deep-water (Boehlert and Sasaki, 1988; Rogers, 1994; Koslow, 1996, 1997; Koslow *et al.*, 2000), which became the prime target of a highly technological fishery.

What are “seamount fishes”? This is a simple question, yet the answer remains elusive. The designation of “seamount fishes” or seamount species has been widely employed (e.g. Koslow, 1996; Probert *et al.*, 1997; Probert, 1999; Koslow *et al.*, 2000; Fock *et al.*, 2002a; Tracey *et al.*, 2004), but the criteria used in identifying those taxa are rarely defined. Pioneering work on seamounts focused on the intriguing question: what species inhabit individual banks and seamounts? Since then, a large number of studies have described the fish fauna inhabiting these features. The results of early studies have been summarised in a number of reviews (e.g., Wilson and Kaufman, 1987; Rogers, 1994; Froese and Sampang, 2004).

The question is how can we appropriately classify those fishes that live in association with seamounts from those more typical of other habitats, or that span both. Most species appear to occupy a range of habitats. Many fish species occur on seamounts or congregate over their summits to feed due to enhanced levels of planktonic production, hydrographic retention mechanisms such as eddies, or being able to remain close to the bottom yet reach shallower depths (Tseytlin, 1985; Genin *et al.*, 1988; Koslow, 1997). This may be the case for some commercially important species of deepwater fish, such as orange roughy, *Hoplostethus atlanticus*, pelagic armorhead, *Pseudopentaceros wheeleri*, oreosmatids, e.g. *Allocyttus niger* and *Pseudocyttus maculatus*, and alfonsinos, *Beryx* spp., as well as for some sharks (Klimley *et al.*, 1988; Hazin *et al.*, 1998), tunas (Holland *et al.*, 1999; Itano and Holland, 2000; Sibert *et al.*, 2000) and other large pelagic predators (Ward *et al.*, 2000; Sedberry and Loefer, 2001).

A range of fish species sporadically aggregate around shallow seamounts mainly for spawning; for instance, reef-associated fish like serranids (*Mycteroperca rosacea*, *Paranthias colonus*) and jacks (*Caranx sexfasciatus*, *Seriola lalandi*) (Sala *et al.*, 2003). Recently, Tsukamoto *et al.* (2003) found that the spawning site of the Japanese eel (*Anguilla japonica*) in the western North Pacific appears to be near three seamounts, 2000-3000 km away from their freshwater habitats. Further examples are the deep-bodied species of the orders Zeiformes (mainly the genera *Antigonia*, *Capros*, *Zenopsis* and *Cyttopsis*) and

Syngnathiformes (in particular the genus, *Macroramphosus*), which are the dominant fishes (<500 m depth) of the Great Meteor seamount, a large, isolated, flat-topped feature in the central eastern Atlantic (Fock *et al.*, 2002a). These fish are also the main prey of large demersal predators inhabiting the slopes of the Azores islands and seamounts (Morato *et al.*, 1999, 2000, 2001, 2003). However, as well as occurring on seamount features, in some areas they are among the most abundant fishes from adjacent continental shelves.

Coral reef scientists faced exactly the same problem when trying to provide a definition of “reef fishes” (see Choat and Bellwood, 1991; Bellwood, 1996; Bellwood, 1998; Robertson, 1998). They first tried to find potential taxonomic and ecological characteristics that could distinguish coral fish assemblages from other fish assemblages (Choat and Bellwood, 1991). They also proposed a consensus list of fish families that would better describe, not define, a coral reef assemblage (Bellwood, 1996). They concluded from this list that most reef fishes are characteristic of, but not restricted to, coral reefs (Bellwood, 1996). Coral reef scientists are still debating the meaning of reef fishes, and apparently they can only agree on the tautological definition of reef fishes: those that live on coral reefs.

The definition of “seamount fishes” may be similar and involve the same redundancy with trying to define a functional type of label that applies only in part to the ecology of the species: seamount fishes are those individual fishes that live on seamounts.

There is a group of fish species, however, living on (or visiting) seamounts that have raised much attention because of their high abundance and good flesh quality: they include orange roughy, pelagic armorhead and alfonsinos. These fish aggregate on top and around seamounts and have been object of intense exploitation since the late 1970's. The discovery of these commercially important aggregations of deepwater fish species on seamount features have changed the idea that significant commercial fisheries would never develop in the deep sea due to scarcity at those depths and poor palatability of fish flesh. Koslow (1996, 1997) explored the differences of fish species aggregating on seamounts from those generally considered typical of the deep-sea environment. By addressing this problem in an energetic

perspective (see below), he concluded that fish species that aggregate around seamounts appeared to form a distinct guild. He found that these fishes differ markedly from other deep-water species in their relatively high levels of food consumption and energy expenditure, low growth and productivity and a robust body composition and body plan suited for strong swimming currents. Koslow called them “seamount-associated fishes” or “seamount-aggregating fishes” (Koslow, 1996; Koslow *et al.*, 2000).

For the propose of this thesis we will consider: 1) “seamount fishes” as those individual fishes that live on seamounts; and 2) “seamount-aggregating fishes” as those species that form large aggregations around these features and that are the main target for fisheries that develop around seamounts.

Numerous studies have described the species richness and diversity of fish fauna on seamounts. Wilson and Kaufman (1987) reviewed seamount biota worldwide and reported about 450 fishes collected from more than 60 seamounts. Rogers (1994) provided a list of 77 commercial species fished on seamounts. Since then, more detailed studies of certain seamounts and seamount chains provide more comprehensive species lists, especially with an increase in exploratory fishing in the last two decades (e.g., Parin *et al.*, 1997; Koslow and Gowlett-Holmes, 1998; Grandperrin *et al.*, 1999; Fock *et al.*, 2002a; Moore *et al.*, 2003; Clark and Roberts, 2003; Tracey *et al.*, 2004). Froese and Sampang (2004) compiled a list of fish that have been reported on seamounts, and found 535 fish species recognized as seamount fishes. Based on the best available information, I collated species lists for fishes that occur or aggregate in and around seamounts. “Seamount fishes” are defined as fish that have been reported as occurring on seamounts, even if rare. A total of 798 species of marine fishes were classified as “seamount fishes” (see Appendix 1).

I now have the most comprehensive checklist of seamount fishes, even if incomplete. The number of known seamount fishes represents about 2.8% of the total number of known fish species and belong to 165 families (32% of the 515 known). Although the number of known seamount fishes is comparatively small, because they encompass a third of fish families,

about half of the orders and many unique adaptations, they represent a relatively large and unique portion of fish biodiversity (Froese and Sampang, 2004). Currently recognized seamount fishes have different habitat preferences (associations). Forty-three species are pelagic, 94 are reef-associated, 118 demersal, 68 benthopelagic, 223 bathypelagic, and 252 bathypelagic. A large portion of the seamount fish community is composed by deep-sea fishes, but many shallow water species are also known to occur on these features. According to Froese and Sampang (2004), only 6 seamount fishes are included in the 2000 IUCN Red List (Hilton-Taylor, 2000): *Sebastes paucispinis* is listed as 'critically endangered', *Sphoeroides pachygaster* and *paucispinis* are listed as 'vulnerable', and *Squalus acanthias*, *Dalatias licha* and *Prionace glauca* are listed as 'lower risk, near threatened.' Other seamount fishes have not been evaluated so far.

The second category of fish species living on seamounts considered for the purpose of this chapter is the "seamount-aggregating fish". A list of 23 fishes was compiled (Table 1.2). I acknowledge that this list is preliminary and its completeness and accuracy will improve as we gain more knowledge about the ecology of seamount and deepwater fish species. Some of the most well known representatives of this group include the deep-water fishes: orange roughy, alfiosinos (*Beryx splendens* and *B. decadactylus*), Patagonian toothfish (*Dissostichus eleginoides*), oreos, pelagic armourhead, several species of rockfishes (*Sebastes* spp.) (Koslow, 1996; Koslow *et al.*, 2000) and probably roundnose grenadier (*Coryphaenoides rupestris*) (Vinnichenko, 2002a). These species are the main target of the large-scale fisheries that occurs on top and around seamounts.

These fish aggregations are supported in the otherwise food-poor deep sea by the enhanced flux of prey organisms past the seamounts and the interception and trapping of vertical migrators by the uplifted topography (Tseytlin, 1985; Genin *et al.*, 1988; Koslow, 1997). It has long been held, however, that the high biomass of fish on seamounts result, at least in part, from locally enhanced primary production and the subsequent bottom-up transfer of this energy to higher trophic levels in seamount food chains (Uda and Ishino, 1958; Hubbs, 1959; Uchida and Tagami, 1984).

**Table 1.2** - List of species considered as “seamount-aggregating” fishes.

Species	Aggregation	Reference
<i>Alepocephalus bairdii</i>	Maybe	6, 11
<i>Allocyttus niger</i> <sup>a</sup>	True	3, 4
<i>Allocyttus verrucosus</i> <sup>a</sup>	Maybe	12
<i>Aphanopus carbo</i> <sup>b</sup>	True	10
<i>Beryx decadactylus</i>	True	4, 9
<i>Beryx splendens</i>	True	3, 4, 7, 9
<i>Coryphaenoides rupestris</i>	True	8, 5
<i>Dissostichus eleginoides</i>	True	4
<i>Epigonus telescopus</i> *	True	10, 5
<i>Hoplostethus atlanticus</i>	True	3, 4, 8, 5
<i>Hoplostethus mediterraneus</i>	Maybe	6
<i>Lepidion eques</i> *	Maybe	6
<i>Mora moro</i>	Maybe	6
<i>Neocyttus rhomboidalis</i> *, <sup>a</sup>	Maybe	11
<i>Pseudocyttus maculatus</i> <sup>a</sup>	True	3, 4
<i>Pseudopentaceros richardsoni</i>	True	9
<i>Pseudopentaceros wheeleri</i> *	True	2, 3, 4
<i>Sebastes entomelas</i> *, <sup>c</sup>	Maybe	1
<i>Sebastes helvomaculatus</i> *, <sup>c</sup>	Maybe	1
<i>Sebastes marinus</i>	True	5
<i>Sebastes mentella</i>	True	8
<i>Sebastes paucispinis</i> <sup>c</sup>	Maybe	1
<i>Sebastes ruberrimus</i> <sup>c</sup>	Maybe	1

\* intrinsic vulnerability index not estimated due to the lack of sufficient parameters. a) forming large shoals over rough ground near pinnacles and canyons; b) not a typical “seamount-aggregating” fish (sensu Koslow, 1996); c) juveniles form large schools. References: 1) Parker and Tunnicliffe, 1994; 2) Rogers, 1994; 3) Koslow, 1996; 4) Koslow *et al.*, 2000; 5) Hareide and Garnes, 2001; 6) Piñeiro *et al.*, 2001; 7) Ramos *et al.*, 2001; 8) Shibanov *et al.*, 2002; 9) Vinnichenko, 2002a; 10) Vinnichenko, 2002b; 11) Allain *et al.*, 2003; 12) Fishbase - Froese and Pauly, 2003.

Studies of fish composition on seamounts have often reported high levels of endemism, exceeding 40% in one case (e.g. Wilson and Kaufmann, 1987; Parin *et al.*, 1997; Richer de Forges *et al.*, 2000; Froese and Sampang, 2004). However, estimates can be variable, and some studies have found little evidence of endemic seamount fish species. For example, none of the fish species recorded by Tracey *et al.* (2004) on New Zealand seamounts were regarded as endemic to any seamount, seamount chain, or even the region. However, the data were from fish trawls designed to capture relatively large-sized fishes, and these fish will generally tend to have wider distributions. Small sampling gear used off Tasmania revealed previously unknown, and probably endemic, species of *Paralaemonena* (Family Moridae), and *Cataetys* (Family Bythitidae) (Koslow and Gowlett-Holmes, 1998). The number of seamount endemic species or the number of fish that lives only on seamounts is still not known. Froese and Sampang (2004) speculated that of the 535 seamount fishes they identified, 62 species are reported from only one seamount, suggesting a high rate of endemism. Generally, species accounts from seamounts focus on just the samples collected from the seamount features, and studies have not considered how specific the species composition is to seamounts.

#### **1.6 SEAMOUNT VISITORS: LARGE PELAGIC FISH, CEPHALOPODS, MARINE MAMMALS, AND SEABIRDS**

While the importance of seamounts for bottom fishes is very well documented (see above), the importance for large pelagic or visiting organisms has been poorly tested (see Table 1.1). However, it has been hypothesised that there are higher abundances of some “visiting” animals, such as tuna, sharks, billfishes, marine mammals, sea-turtles and even seabirds, over seamounts but this has been based on sparse records, warranting further examination.

Sharks appear to be attracted to seamounts as demonstrated by Klimley *et al.* (1988), who showed that hammerhead sharks remained grouped at a seamount in the Gulf of California (Mexico) during the day and moved separately into the surrounding pelagic environment at night. Hazin *et al.* (1998) showed that catches of gray sharks were significantly higher

around seamounts, mainly in those with summits of about 300m and low-sloping depth profiles. The reasons for these aggregations are not clear, but Hazin *et al.* (1998) assumed that seamounts were used by some sharks as feeding stations.

It is known by fishermen and researchers that large biomasses of tuna are sometimes concentrated on seamounts (Fonteneau, 1991; Holland *et al.*, 1999; Itano and Holland, 2000; Sibert *et al.*, 2000). Several thousand tons of tuna can be taken yearly on some remote seamounts, while other seamounts closer to land are apparently always poor in tuna, even when they are located in regular fishing areas (Fonteneau, 1991). It is possible that seamounts act both as feeding stations and as orientation points in the larger-scale movement patterns of these fish (Holland *et al.*, 1999). The navigation role might explain why remote seamounts aggregate more tuna than seamounts located closer to land masses, as noticed by Fonteneau (1991). Swordfish and other billfishes appear also to be attracted to complex high-relief bottom structures. For example, swordfish that moved away from the Charleston Bump were frequently found associated with seamounts, submarine canyons, and with thermal fronts of the northern wall of the Gulf Stream (Sedberry and Loefer, 2001).

Cephalopods may drift passively over and around seamounts and be subject to predation (Nesis, 1986). The author suggested that this link might be one of the reasons for the high abundance of benthic and demersal fish species on certain seamounts. Cephalopod fauna of seamounts may consist of four main components (Nesis, 1986): 1) bottom and near-bottom species that reside there permanently (e.g., genera *Froekenia*, *Danoctopus* and *Scaeurgus*); 2) pelagic species that descend to or near the bottom to spawn, and including either those that maintain themselves constantly in midwater above or near seamounts, or those that migrate actively to seamounts for sexual maturation (e.g., genera *Ornithoteuthis*, some *Todarodes*, *Lycoteuthis*); 3) mesopelagic species that may migrate vertically and descend to the bottom during the daytime (e.g., Enoploteuthidae and Octopoteuthidae); and 4) non-migrating pelagic species that permanently inhabit the water column (Mastigoteuthidae, Vampyroteuthidae, Cranchiidae).



Although several works have correlated marine mammals occurrence with complex and steep topographies (e. g. Schoenherr, 1991; Balcomb, 1989; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; Hastie *et al.*, 2004; Yen *et al.*, 2004) the literature addressing their association with seamounts is scarce. Reeves and Mitchell (1993) noticed that when in pelagic areas Baird's beaked whales (*Berardius bairdii*) are observed close to submarine escarpments and seamounts.

Seabird density and biomass has been reported to be higher around seamounts when compared to adjacent areas (Haney *et al.*, 1995; Monteiro *et al.*, 1996). Haney *et al.* (1995) showed that seabird biomass was eight times higher within a 30-km radius centred on a seamount summit. The authors attributed seabird aggregation observed at the seamount to be related to an increase of food availability.

### **1.7 SEAMOUNT FISHERIES AND OTHER THREATS**

The steady and steep decline of global catches since the 1980s (Watson and Pauly, 2001) alludes to the fact that the world's fisheries resources are in serious danger of depletion (e.g. Pauly and Christensen, 1995; Pauly *et al.*, 1998; Pitcher, 2001; Pauly *et al.*, 2002), undoubtedly due to poor management practices and increased fishing pressure (Ludwig *et al.*, 1993). Unsustainable fishing practices along with an excessive level of investment in fishing capacity have resulted in serious stock depletion on most continental shelves, thus creating new pressures on alternative fishing grounds (Pauly *et al.*, 2002).

Fisheries are evidently expanding offshore (e.g., Christensen *et al.*, 2003; Myers and Worm, 2003; Pauly *et al.*, 2003) and into deeper waters (Koslow *et al.*, 2000; Garibaldi and Limongelli, 2003; FAO, 2004; Gianni, 2004). The expansion into offshore areas has been well documented, (for example, fisheries targeting oceanic tuna, billfishes and their relatives covered the world ocean by the early 1980s; Myers and Worm, 2003), but the extension into deeper waters is less well analysed. While many local examples of fisheries expansion into deeper waters have been reported (e.g., some European, Soviet, U.S.A., Canada, New

Zealand and Australian fishing fleets: see references in Hopper, 1995; Moore, 1999; Koslow *et al.*, 2000; Roberts, 2002), we still lack a global quantitative analysis. Seamounts are also among those "newly" targeted ecosystems that, since the second half of the 20th century, have been intensively fished (Rogers, 1994; Koslow *et al.*, 2000).

Deepwater fisheries in general and seamounts fisheries in particular usually exhibit a boom and bust sequence, crashing within about ten years of their initial development. This was the case of the orange roughy (*Hoplostethus atlanticus*) fisheries off New Zealand (Clark, 1995; Clark, 1999; Clark *et al.*, 2000), Australia (Wayte and Bax, 2001; Lack *et al.*, 2003), Namibia (Boyer *et al.*, 2001; Branch, 2001) and even in the North Atlantic (Branch, 2001), the pelagic armourhead (*Pseudopentaceros wheeleri*) fisheries over seamounts in international waters off Hawaii (Boehlert and Genin, 1987), and the blue ling (*Molva dipterygia*) fisheries in the North Atlantic (Bergstad *et al.*, 2003; Devine *et al.*, 2006). As seamounts are rapidly depleted, the continued existence of a fishery depends upon the continuing discovery of unexploited seamounts with large fish aggregations.

The species targeted by fisheries at seamounts have a very low overall abundance, but aggregate at seamounts as part of their life cycle strategy, e.g., for spawning (Clarke *et al.*, 1996). They are often long-lived (some species to over 100 years), slow growing, late maturing (at about 30 years), and have low reproductive potential (Koslow, 1997). When they have been fished out it is estimated that it will take decades for these localised stocks to recover, as they are thought to have limited exchange with other seamounts (Koslow, 1997). This makes these fish communities very vulnerable to overfishing and the problem is even more pronounced in seamounts located in international waters where management strategies and agreements are absent.

However, information on seamounts fisheries is very sparse, and it is difficult to make a distinction between deep-water fishing activities in general and those occurring on seamounts (Koslow *et al.*, 2000). Moreover, fish species living on seamounts are also known to occur on other habitats, such as the continental slope, and landings statistics are not spatially allocated,

making it difficult to make an estimate of the total fisheries occurring on seamounts worldwide.

Depletion of fish stocks is not the only concern. Extensive trawling activities on seamounts are damaging benthic (bottom living) communities, particularly for dominant communities of corals and other suspension feeders (Koslow *et al.*, 2001). The impact of trawling on complex seamount reefs appears to be dramatic, with the coral substrate and associated community largely removed from the most heavily fished seamounts (Koslow *et al.*, 2001). Such massive removal of natural and structural components to the ecosystem has negative consequences on seamount biodiversity (Probert, 1999).

There is a rising concern about the threats to seamount ecosystems in the Economic Exclusive Zones of coastal states and on the High Seas. Overfishing, even depletion, of the often slow-growing and late-reproducing fish populations, and the destructive impact of trawling activities on the benthic communities of seamounts, poses an immediate risk to these isolated ecosystems.

Consequently, Canada, Australia, Portugal and New Zealand have begun to take the first steps towards protecting seamounts. In the Atlantic, no such protective measures have been established, but the Oslo and Paris Commission (OSPAR) is considering this issue at the moment within the framework of Annex V of the Convention on the Protection of the Marine Environment in the North-East Atlantic (OSPAR Convention). Seamounts are on an initial draft list of habitats and species that require conservation action, and the developing OSPAR Marine Protected Areas programme may provide one of the possible mechanisms. In addition, seamounts dominated by hard substrata in the waters of the European Community qualify for site protection under the European Habitats Directive (1992, Natura 2000 code 1170 "reefs" in the Interpretation Manual of European Union Habitats EUR 15/2).

## 1.8 THESIS THEME AND OBJECTIVES

The presence of numerous seamounts in the world's oceans has only become known to the scientific community during the last 50 years (Rogers, 1994). The potential importance of these steep-sided undersea mountains to biogeography and diversity was only recognized after Hubbs (1959) work, but this environment has remained very poorly investigated (Forges *et al.*, 2000). Hence, the most fundamental questions remain incompletely answered (see Table 1.1).

The general objective of this PhD was to explore some fundamental questions about seamount ecology and fisheries:

1) Estimate seamount numbers and locations around the Azores islands;

The main goal of Chapter 2 is to infer potential seamount locations and thus to generate estimates of the actual number of seamounts in the Azores. I will also describe seamount population according to location, depth of the summit, height, basal area, height to radius ratio, the average slope, and distance to nearest seamount. The output of this chapter will be used later (Chapter 4) to test some hypothesis related to seamount ecosystem functioning.

2) Examine the impact of a potential increase of local primary production on higher trophic levels;

In an effort to better understand seamount ecosystem functioning, Chapter 3 will address how complex seamount food web structures are sustained. A generic seamount ecosystem model from the Northeast Atlantic will be used to test the impact of a potential increase of local primary production on higher trophic levels.

3) Quantify the amount of advected prey necessary to sustain a "typical" seamount fish community and to explore if the necessary prey can be supported with food provided by local oceanographic conditions (also in Chapter 3);

- 4) Test if the reported high abundances of seamount “visitors” on top and around seamounts are true;

Some previous studies have focused on analysing the auto-ecology of some organisms in relation to seamounts. In Chapter 4, I will use data from a fishery observer program to explicitly test if the abundances of tuna, marine mammals, sea turtles and seabirds observed at Azores seamounts are higher than expected by chance. This chapter will also use the seamount dataset produced in chapter 2.

- 5) Test if a reported historical expansion into deeper-waters can be detected in global landings datasets;

Whereas previous studies on global trends of fisheries have focused on catch or biomass changes over time, in Chapter 5 I will analyse changes in the mean depth of fishing to test if the predicted expansion into deeper-waters can be detected in global landings datasets. I will also test for the predicted higher vulnerability of deep-water fisheries resources, using longevity as the main proxy for vulnerability.

- 6) Test the hypothesis that “seamount fishes” generally have a higher than average vulnerability to fishing exploitation;

Previous studies have found that vulnerability of fishes to exploitation is correlated with their life history characteristics. However, no attempt has been made to review, summarize and compare the life-history of seamount species with species typical from other habitats. Therefore, Chapter 6 will test the generalization that “seamount fishes” possess specific life history characteristics that render them more vulnerable than other species. Vulnerability was estimated quantitatively by analysis of life-history characteristics using a fuzzy-logic algorithm.

- 7) investigate if whole-ecosystem simulations can help in understanding the impact of fishing on pristine seamounts and provide guidelines for sustainable fisheries.

Using ecosystem modeling loosely structured on North Atlantic case studies, data gathered from elsewhere, and optimization methods for policy search, in this Chapter I

will explore the types of fisheries that might be sustainable on seamount ecosystems. I will also investigate if ecosystem simulations can help in understanding the impact of fishing on pristine seamounts.

Additionally, and in collaboration with the "Sea Around Us Project" I was involved in small *ad-hoc* projects that helped:

- a) estimating of the number of seamounts in the world's oceans by inferring potential seamount locations;
- b) detecting primary production enhancement by world's oceanic seamounts using remotely sensed data on primary production
- c) estimating potential yield from seamounts and determining how catches have changed in recent years.

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## CHAPTER 2

### ABUNDANCE AND DISTRIBUTION OF SEAMOUNTS IN THE AZORES<sup>1</sup>

#### 2.1 INTRODUCTION

Seamounts have been recently recognized as highly important habitats for fisheries and biodiversity, and a target for conservation as they support often isolated but rich underwater ecosystems (Morato and Pauly, 2004). However, only a few seamount datasets containing information on positions are available (e.g., Fornari *et al.*, 1987; Smith and Jordan, 1988; Epp and Smoot, 1989; Smith and Cann, 1990; Wessel and Lyons, 1997; Wessel, 2001). In fact only a small fraction of seamounts have actually been mapped (Wessel and Lyons, 1997). Recently, Kitchingman and Lai (2004) have conducted a global analysis with the goal of generating a spatial dataset of points across the world's oceans that indicate large peaked bathymetric anomalies with a high probability of being seamounts. In that study 14,287 potential large seamounts were identified in the world's oceans.

Seamounts are thought to be common topographic features in the Azorean archipelago sub-area of the Portuguese Economic Exclusive Zone (EEZ), hereafter named Azores EEZ. However, their numbers and locations are poorly known. The Azores archipelago is a group of nine volcanic islands and many small islets that are parts of the Mid-Atlantic Ridge in the Northeast Atlantic Ocean (an irregular area within 33.5-43° N, 21-35.5° W). Relatively shallow seabed less than 600 m deep cover less than 1 % of the 953,633 km<sup>2</sup> of the Azorean EEZ. This reflects the narrowness of the island shelves and means that most fishing grounds are scattered (Santos *et al.*, 1995; Menezes, 2003). The only easily accessible seamount datasets that include the Azores are those of Wessel (2001) and Kitchingman and Lai (2004), with the later describing 58 seamounts in the Azores EEZ. Few other studies have been conducted in the Mid Atlantic Ridge, where estimates vary from 58 (Jaroslow *et al.*, 2000) to

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<sup>1</sup> A version of this chapter has been submitted for publication. Morato, T.; M. Machete; A. Kitchingman; F. Tempera; S. Lai; G. Menezes; R.S. Santos; and T.J. Pitcher (submitted). Abundance and distribution of seamounts in the Azores. Marine Ecology Progress Series.

80 (Smith and Cann, 1990) seamounts per 1000 km<sup>2</sup>. These estimates are about 1000 times higher than the numbers presented by Kitchingman and Lai (2004) because their study accounts only for those topographic features with a relief larger than 1000m.

Seamounts are important areas for conservation and fisheries in the Azores (Santos *et al.*, 1995) and the knowledge of their locations are highly important for choosing and implementing management measures. In this study, seamounts are defined as any topographically distinct seafloor feature that is at least 200 meters high but which does not break the sea surface. The 200 meters threshold was chosen for being the smallest peak size that fit the negative exponential model (see Results). I classify seamounts as being large or small, depending on whether the height exceeds 1000 meters (regardless of depth). For standard cone like seamounts height and width are highly correlated (Smith, 1988). Thus, this height separation is useful in isolating large seamounts, whose global distribution is well resolved by satellite altimetry, from small seamounts the distribution of which must be inferred from local acoustic mapping and therefore remain poorly sampled.

The main goal of this paper is to infer potential seamount locations and thus to generate estimates of the actual number of seamounts in the Azores. I will also describe seamount population according to location, depth of the summit, height, basal area, height to radius ratio, the average slope, and distance to nearest seamount.

## 2.2 METHODS

I used an automated methodology adapted from Kitchingman and Lai (2004) to identified topographic structures with high probability of being seamounts. For this I used two bathymetric datasets with different resolutions.

The MOMAR (Monitoring the Mid Atlantic Ridge) mid-resolution bathymetric map (Lourenço *et al.*, 1998; <http://www.momar.org>) was the finest available bathymetrical grid

for the Azores region at the date of the analysis (February 2006) and was used for the area comprised by the parallels 36°N and 41°N and the meridians 24°W and 32°W. The dataset is supplied at a 1 minute cell resolution (approx. 1.8 km in length), thus allowing a reasonable scale at which to perform an analysis for large seamount like features. The “Global seafloor topography from satellite altimetry and ship depth soundings” database (Smith and Sandwell, 1997; <http://topex.ucsd.edu/sandwell/sandwell.html>; also called S&S dataset) was used as the bathymetry dataset for the remaining area. This dataset is at a 2 minute cell resolution (approx. 3.7 km in length). This dataset contains some artefacts such as a spurious deep trough in the NE region of the study area.

The methodology followed three succeeding steps: 1) identifying all detectable peaks in the bathymetry dataset; 2) isolating peaks with heights greater than 200m and displaying an approximately circular or elliptical shape; and 3) isolating large seamount-like features. The datasets produced after step 1 will be called the peaks dataset, while the dataset produced after step 3 will be used as the Azores seamount dataset. The dataset produced after step 2 minus those produced after step 3 will be called the small seamounts dataset.

The initial process of determining the locations of all detectable peaks (local maxima) in the elevation data was performed with the ESRI ArcGIS (ESRI, 1999-2004) software flow direction and sink algorithms. Both bathymetry datasets were used in an ESRI grid format for the cell-by-cell analysis. The ESRI flow direction algorithm was first used on the bathymetry data. This algorithm produces a grid in which each cell is allocated a flow direction value determined by the steepest descent from the immediate surrounding cells. There are eight valid flow direction values. Cells determined to have an undefined flow direction are given a value equal to the sum of the possible flow direction values. Undefined flow directions occur when all surrounding cells are higher than the focus cell or when two adjacent cells flow into each other. The ESRI sink algorithm is used on the resulting flow direction grid to identify all flow direction cells that have undefined flow directions. The resulting sink (seafloor peak) grid can then be overlaid with the depth grid to indicate all identifiable peaks on the seafloor.

The bathymetry data was prepared by first eliminating all land cells (any elevation above 0) and then converting negative values (known as depths) to absolute numbers. This allowed the ESRI hydrology algorithms, designed to detect downhill flow direction and sinks, to identify the uphill flow directions and peaks. The next step of the analysis will isolate those the detected peaks that have a significant rise from the ocean floor and that have an approximate circular or elliptical base in an effort to eliminate small peaks found along the ridges or island slopes.

The raw peak grid dataset was compared with the bathymetry data. An algorithm was developed that scanned depths around each peak, along 8 radii of 20 km each at 45° intervals. The lowest and highest depths over the radii and the cells where those values were obtained were then recorded. Subsequently, I isolated a dataset of potential seamounts and then extracted the large seamounts. A peak was considered to be a potential seamount when the following conditions were met:

- 1 Each and all of the 8 radii included depths differing by at least 200 m. This helped eliminate all peaks of insignificant rises.
- 2 No more than one of the 8 radii has the highest depth shallower than the depth of the peak and if the distance between these two cells is greater than 10 km. This helped eliminate peaks that were part of a larger structure and peaks close to island slopes.
- 3 If 2 radii included depths between 200 and 1000 m with the shallowest point being closer to the peak than to the deepest point, and if the radii formed an angle of less than 135°. This condition was created to help separate ridges from seamounts.
- 4 At least 5 of the 8 radii around a peak included depths with a difference of at least 1000 m, with the shallowest point being closer to the peak than to the deepest point.
- 5 The average height of the peak is greater than 1000 m.

Peaks that met all five conditions were considered large seamounts while those that met the first three conditions but failed to meet the fourth and fifth were considered small seamounts. For the detected small and large seamounts several characteristics were recorded: 1) location;

2) depth of the summit (m); 3) seamount height ( $h$  in m); 4) basal area ( $a_b$  in  $\text{km}^2$ ); 5) height to radius ratio ( $\xi_r$ ); 6) the average slope ( $\phi$  in degrees); and 7) distance to nearest seamount (km).

The location of the seamounts was recorded as the latitude and longitude of the centroid of the detected peak or seamount. The depth of the summit was recorded as the depth of the cell where the peak was located and must be interpreted as the average depth of the cell, not the absolute minimum depth of the seamount. The seamount height was estimated as the average height of the 8 radii of the seamount, where each radius height was estimated as the difference between the summit and the deepest record. The area of the base of the seamount was approximated by the area of the octagon formed by the location of the deepest cell in each radius. The slope of the seamount was estimated as the average steepness of the 8 radii of the seamount calculated by the slope algorithm of ArcGIS software. The ArcGIS 'Slope' function calculates the maximum rate of change between each cell and its neighbours using the average maximum technique. Finally, the distance to the nearest seamount was calculated by identifying the closest feature and then estimating its distance.

Seamount size distribution is well characterized by a negative exponential model that considers the cumulative numbers of seamounts having heights greater than a certain value (Jordan *et al.*, 1983; Smith and Jordan, 1988). This distribution is expressed as  $v(H) = v_o \cdot \exp(-\beta \cdot H)$ , where  $v(H)$  is the number of peaks per unit area with height greater than  $H$ ,  $v_o$  is the total number of peaks per unit area and  $\beta$  is the negative of the slope of a line fitting  $\ln(v(H))$  and  $H$ .

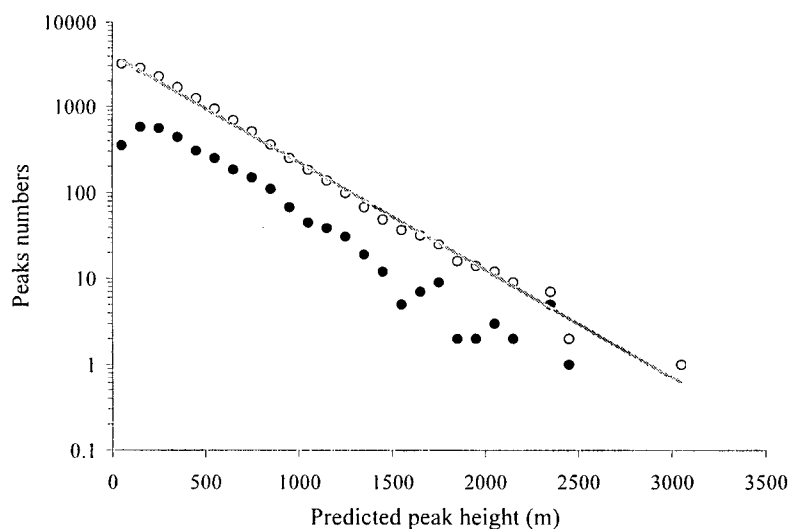


## 2.3 RESULTS

### 2.3.1 Peaks dataset

A total of 3177 peaks were identified by the ArcGIS flow direction and sink algorithms, yielding an average density of 3.3 peaks per 1000 km<sup>2</sup>. Of these peaks, 1104 were found with the MOMAR Azores dataset (24°W 36°N to 32°W 41°N), whereas 2073 were found with the S&S dataset used to cover the rest of the EEZ.

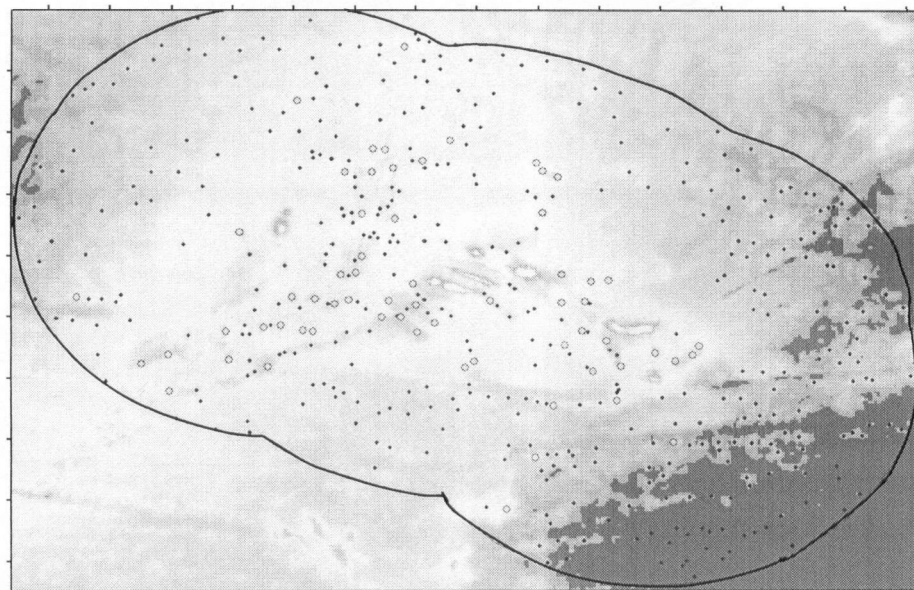
The peaks dataset adequately identified topographic structures with heights larger than 100m (Figure 2.1). The resolution of the bathymetry data seems to be inadequate for peaks smaller than 100m, leading to an underestimation of the counts. Thus, this data point was excluded from the fit. The exponential model adequately fits the Azores peaks counts with  $v_o = 4.31$  peaks per 1000 km<sup>2</sup> and  $\beta = 2.89$  km<sup>-1</sup>, yielding a characteristic height ( $\beta^{-1}$ ) of ~350 m. According to this exponential model there are about 4100 potential peaks in the Azores where 1000 km<sup>2</sup> contain an average of ~4 peaks of all sizes.



**Figure 2.1** – Height ( $h$ ) frequency distribution of all identified peaks. Solid circles are actual counts while open circles are the cumulative counts. The grey circle data point was excluded from the exponential model fit. The relationship can be expressed as  $N = 4107.6 \cdot e^{-2.89 \cdot h}$ , with  $h$  in km;  $r^2 = 0.99$ . If expressed by unit area (km<sup>-2</sup>),  $v(H) = 4.31 \cdot e^{-2.89 \cdot h}$ .

### 2.3.2 Small and large seamounts dataset

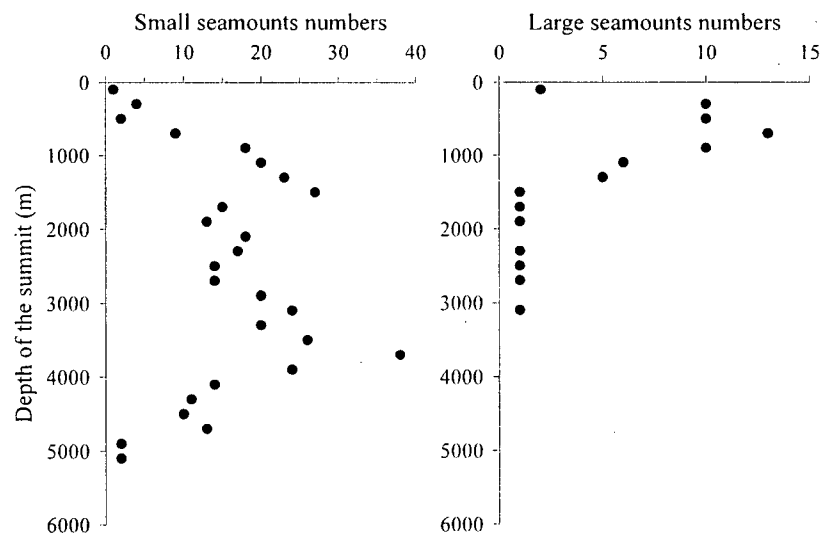
Figure 2.2 shows the location of 461 potential small and large seamount-like features in the Azores EEZ. Detailed tables of results for each seamount with location, depth of the summit, base area and average slope are shown in Appendix 2<sup>2</sup>. Our methodology identified a total of 398 small features, which represents only 12% of the 3177 identified peaks. This discrepancy shows that our methodology successfully eliminated peaks of insignificant rises as well those that were part of larger structures or were in ridges or island slopes. Of the 398 potential small seamounts, 151 were identified around the islands with the Lourenço *et al.* (1999) bathymetrical dataset while 247 were identified offshore with the Smith and Sandwell (1997) dataset. I have also detected 63 large potential seamounts, which is only 2% of the identified peaks. Of these, 52 were identified with the Lourenço *et al.* (1999) dataset while 11 were identified with S&S dataset. The mean abundance of small and large seamounts in the Azores EEZ is 0.42 and 0.07 per 1000 km<sup>2</sup>, respectively.



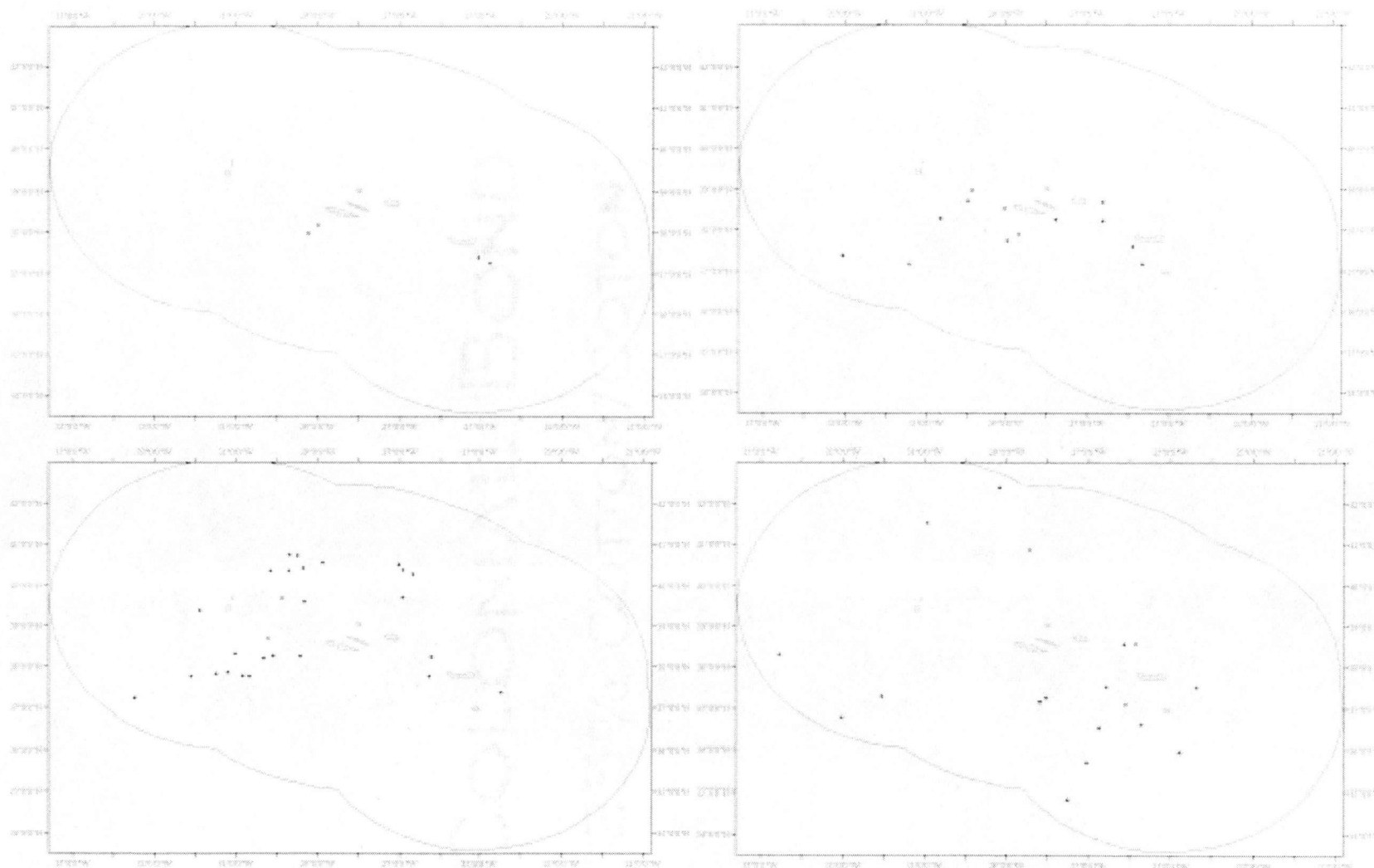
**Figure 2.2** – Distribution of seamounts in the Azores Exclusive Economic Zone (black line). Circles show large seamounts while black dots show small seamount-like features. Scale goes from dark grey (deep water; about 5000m) to light grey (shallow water).

<sup>2</sup> A digital version of this table is provided in the webaddress  
[http://www.horta.uac.pt/ppl/tmorato/pdf/Appendix2\\_Morato\\_PhD.pdf](http://www.horta.uac.pt/ppl/tmorato/pdf/Appendix2_Morato_PhD.pdf)

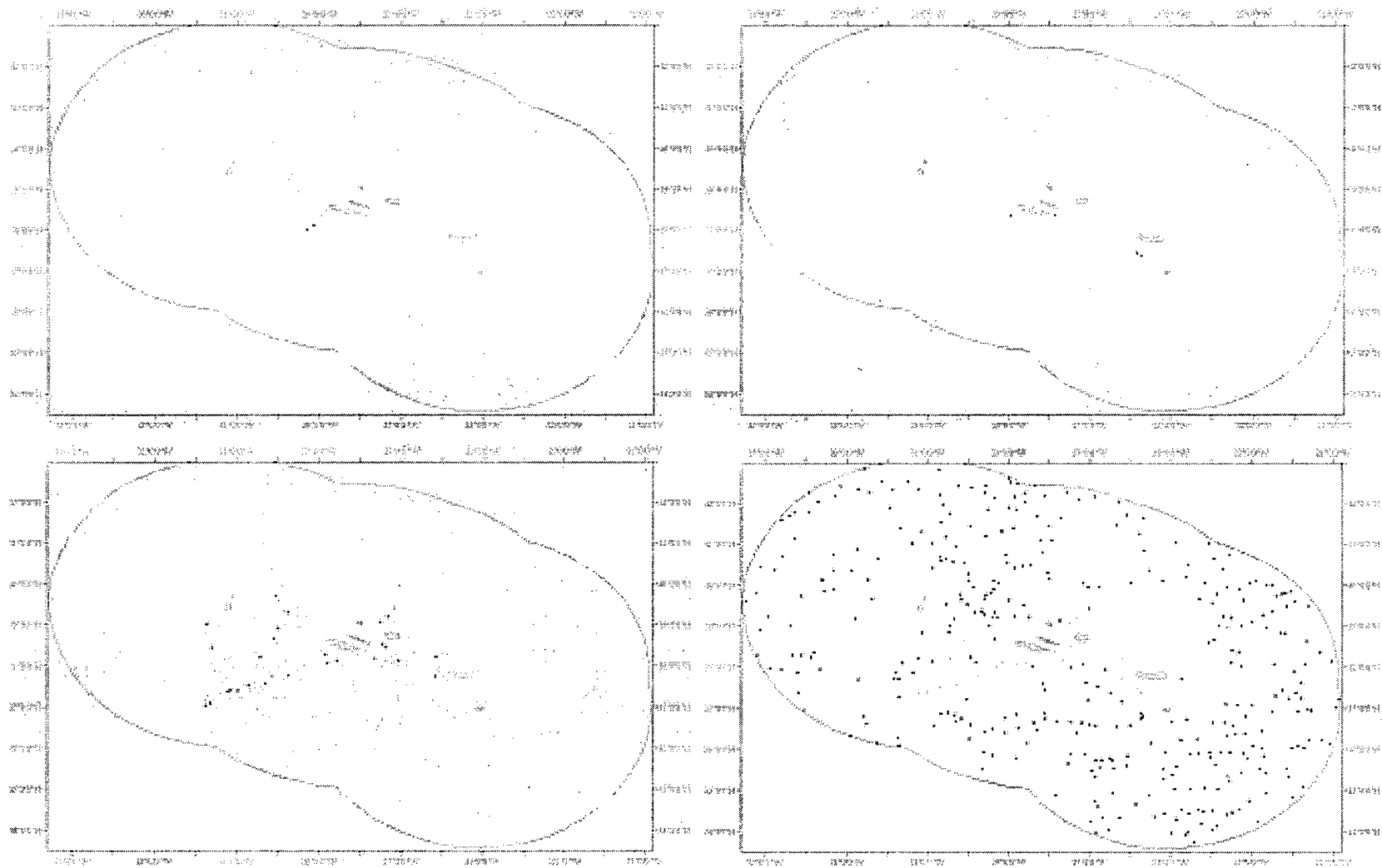
Most of the seamounts in the Azores have deep summits (Figure 2.3) with a strong predominance of summit depths of 800-1500m. Only 4 large seamounts have a mean depth of the peak shallower than 250m while 14 lay in the depth range 250-500m. The other 45 large seamounts have their summits deeper than 500m. Small seamount-like features show a similar pattern with only 6 shallower than 500 m. Location of large and small seamounts by depth of the summit is presented in Figures 2.4 and 2.5.



**Figure 2.3** – Depth of the summit frequency distribution of small (left) and large (right) seamounts-like features.

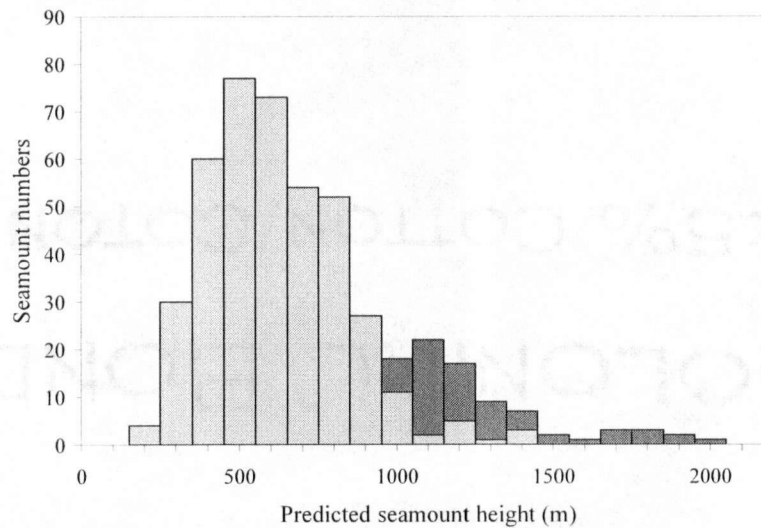


**Figure 2.4** – Distribution of large seamounts in the Azores EEZ by mean depth of summit: a) <250m; b) 250-500; c) 501-1000; d) >1000m. Black dots indicate seamounts of the referred category.



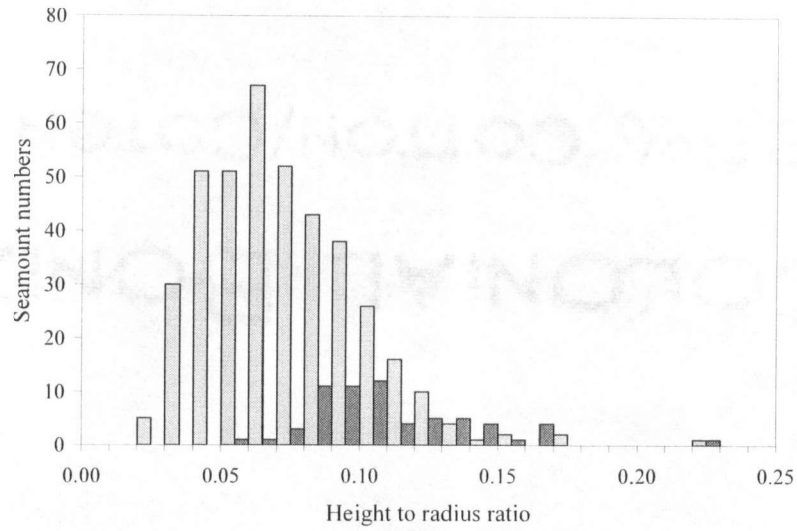
**Figure 2.5** – Distribution of small seamount-like features in the Azores EEZ by mean depth of summit: a) <250m; b) 250-500; c) 501-1000; d) >1000m. Black dots indicate seamounts of the referred category.

The distribution of small and large seamounts heights ( $h$ ) distribution is shown in Figure 2.6. Small seamounts had a mean height of 612 m (S.D. = 210) while the mean height for large seamounts was 1267 m (S.D. = 272). Seamounts with small heights are much more abundant than larger seamounts.

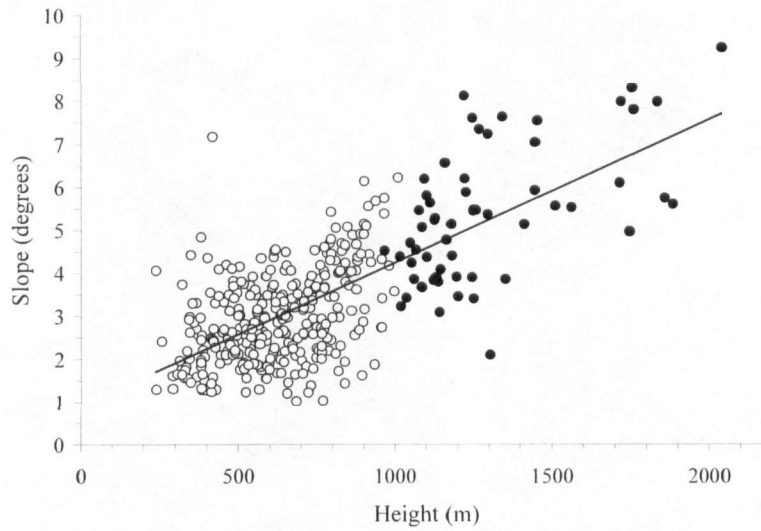


**Figure 2.6** – Histogram of the predicted height distribution of small (light grey bars) and large (black bars) seamounts-like features. Bin size is 100m.

Shapes of seamounts as characterized by basal radius ( $r_b$ ), by the height to radius ratio ( $\xi_r$ ) and by the slope ( $\phi$ ) show marked differences between small and large seamount like features. Small seamount-like features showed a mean basal radius of  $r_b = 9.4$  km (SD=2.0) while large seamounts showed a mean basal radius of  $r_b = 11.2$  km (SD= 1.8). Accordingly, basal area is smaller on small seamounts ( $a_b = 742$  km<sup>2</sup>; SD= 213) than on large seamounts ( $a_b = 961$  km<sup>2</sup>; SD= 171). The mean height to radius ratio increase from  $\xi_r = 0.07$  (SD= 0.027) on small seamounts to  $\xi_r = 0.12$  (SD= 0.030) on large seamounts (Figure 2.7). Average slope angles ranged from  $\phi = 0.73$  to  $\phi = 9.27$ . The sample mean slope angle was  $\phi = 2.90$  for small seamounts and  $\phi = 5.23$  for large seamounts. Slope angle and summit height relationship is presented in Figure 2.8.



**Figure 2.7** – Histogram of the seamounts height to radius ratio  $\xi_r$  for small (grey bars) and large (black bars) seamount-like features. Bin size is 0.010.



**Figure 2.8** – Slope angle ( $\phi$ ) and seamount height ( $h$ ) linear relationship for small (open circles) and large (filled circles) seamount-like features. For all seamounts the relationship can be expressed as  $\phi = 0.003 \cdot h + 0.86$ ;  $r^2 = 0.53$ .

## 2.4 DISCUSSION

This work is the first attempt to identify the seamounts in the Azorean EEZ. It must be emphasized that there are some potential sources of uncertainty in this study. First, the bathymetry of the Azores EEZ is not perfectly known and has not been, to our knowledge, extensively surveyed. Both bathymetry datasets used (Smith and Sandwell, 1997; Lourenço *et al.*, 1999) may lack resolution and thus preclude the identification of some small seamount-like features. For this reason, our references to seamounts should be interpreted as potential seamounts. A better but very costly solution would be to perform extensive multi-beam surveys that would provide not only excellent bathymetric data for mapping seamounts and estimating depths, areas and slopes but also backscatter data for mapping the nature of the seafloor.

Our methodology of identification shows that peaks and seamounts are common features in the Azorean EEZ. The average density of 3.3 peaks of all sizes per 1000 km<sup>2</sup> is in the same order of magnitude of that obtained in some studies in the Mid Atlantic Ridge (Batiza *et al.*, 1989) but is an order of magnitude lower than obtained by Smith and Cann (1990) and by Jaroslow *et al.* (2000). The observed discrepancies are due to the facts that the later studies focused only on the MAR region, an area with a higher abundance of topographic structures (Smith and Cann, 1990), and that the resolution of our datasets is inadequate to detect peaks smaller than 100m height. The difference of about 1000 peaks between the real counts and the exponential model estimates ( $n \approx 4100$ ) are due to underestimation of the counts for peaks smaller than 100m, suggesting that our methodology successfully identified small and large seamount-like features ( $h > 200$ m height).

In this study, I was able to map and describe 63 large and 398 small seamount-like features in the whole EEZ of the Azores. The total area where seamounts are found is much larger than previous thought. However, most of the summits are in waters deeper than 1000m. Etnoyer (2005) presented some evidences that small features with deep peaks predicted by some bathymetry datasets can actually be large seamounts with shallower summits. Therefore, our



estimates of seamount abundance may perhaps be biased by underestimating seamounts heights and overestimating depth of summits. For that reason, the large seamount abundance in the Azores may be even higher than presented here. Also, the depth of the summits may be shallower than I have estimated.

The distribution suggests that a large proportion of the seamounts occur in chains along the Mid Atlantic Ridge. However, isolated seamounts are also present in the Azores. Seamounts showed a wide range of sizes (heights), depth of summits, slopes, and areas being difficult to make generalization about the seamounts in the Azores. Our data suggests that seamounts provide a large diversity of habitats that can be suitable for different type of faunal associations. Similar findings and suggestion were made by Rowden *et al.* (2004) for New Zealand seamounts.

The fact that most of the seamounts have small heights and deep summits has strong implications for fisheries exploitation in the region where most of the bottom longlining occurs at depths of up to 600 m (Morato *et al.*, 2001). Our data suggests that only 29 of the 461 seamounts (small and large) are available for this type of fisheries. Thus, our work supports the idea that fishing grounds for existing fisheries are limited in the Azores. It should be noticed that deep-water trawl operates at deeper waters and thus the potential fishing grounds for this fishery could be slightly larger.

Recently, the EU regulation 1568/2005 (European Commission, 2005) banned deep water trawling in a large area of the Azorean EEZ. According to our distribution of seamounts, this regulation protects 58 large and 207 small seamounts. Thus, 57% of the potential Azores seamounts are protected against deep-water trawling.

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# CHAPTER 3

## MODELLED EFFECTS OF PRIMARY AND SECONDARY PRODUCTION ENHANCEMENT BY SEAMOUNTS ON LOCAL FISH STOCKS<sup>1</sup>

### 3.1 INTRODUCTION

It has long been recognized that many seamounts may harbour large aggregations of demersal or benthopelagic fish (Rogers, 1994; Boehlert and Sasaki, 1988; Koslow, 1996, 1997; Koslow *et al.*, 2000) such as orange roughy, *Hoplostethus atlanticus*, pelagic armorhead, *Pseudopentaceros wheeleri*, and alfonsoinos, *Beryx* spp. (Morato *et al.*, 2006). However, the mechanisms under which these aggregations are sustained are still under debate. Three hypotheses have been presented to explain how large aggregations of fish found on seamounts are energetically supported (see Genin, 2004 for a review).

The first hypothesis (*I*) proposes that the high biomass of fish results, at least in part, from locally enhanced primary production (PP) and the subsequent bottom-up transfer of this energy to higher trophic levels in seamount food chains (Uda and Ishino, 1958; Hubbs, 1959; Uchida and Tagami, 1984). It is unlikely, however, that water could be retained around a seamount for the several months needed for production to work its way through the food-web to the higher trophic level fish residing on the seamount itself. Thus, it is not surprising that evidence for enhanced primary production leading to concentrations of fish over seamounts is sparse (Rogers, 1994). Moreover, evidence of increased primary production over conical seamounts located in the path of marine currents is still contradictory. While upwelling that drives patches of high primary production has been detected using field sampling over certain well-studied seamounts (Genin and Boehlert, 1985; Dower *et al.*, 1992; Comeau *et al.*, 1995; Odate and Furuya, 1998; Mouriño *et al.*, 2001, 2005), many studies have failed to demonstrate persistent high chlorophyll *a* patches over seamounts (e.g., Peláez and

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<sup>1</sup> A version of this chapter has been submitted for publication. T. Morato, C. Bulman and T.J. Pitcher (submitted) Impact of primary production enhancement by seamounts on local fish stocks. Deep-Sea Research II.

McGowan, 1986). In general, seamounts reaching close to the surface enhance local primary production, but its contribution to primary production enhancement is generally low (Mouriño *et al.*, 2005).

The second hypothesis (2) proposes that fish aggregations are sustained by the enhanced horizontal flux of prey organisms past the seamount (Tseytlin, 1985; Dower and Mackas, 1996; Koslow, 1997), named as the “feed-rest” hypothesis by Genin (2004). Enhanced fluxes of prey in regions of amplified currents augment feeding by site-attached fish but at the same time may have extremely high energetic costs. The “feed-rest” hypothesis suggests that the fish rest motionless in quiescent shelters during non-feeding intervals and, when conditions are right, the fish emerge from shelter, feed quickly, and then retreat back to rest.

Another possible mechanism (hypothesis 3) is the interception and trapping of vertical migrators – both descending and ascending (Isaacs and Schwartzlose, 1965; Genin *et al.*, 1988, 1994; Williams and Koslow, 1997; Fock *et al.*, 2002), named as the “topographic blockage” hypothesis by Genin (2004). Most of the studies supporting hypotheses 2 and 3 are based on observations of potential prey (micronekton) rather than on the predatory fish themselves. Only two studies have examined fish energetic requirements and food availability on seamounts (Tseytlin, 1985; Koslow, 1997).

On seamounts off southern Tasmania, Australia, Koslow (1997) assumed an orange roughy biomass of  $100 \text{ t} \cdot \text{km}^{-2}$ , with a consumption of 1% of its body weight, a trophic level of four, a trophic efficiency of 10%. Net primary production in the region was  $200 \text{ gC} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ ; enough to sustain only about one-tenth of the estimated biomass, or about  $11 \text{ t} \cdot \text{km}^{-2}$  of orange roughy, assuming a conversion of carbon as 5% of wet weight. Using a different approach, Koslow (1997) took into account the annual contribution to the fourth trophic level of the particle flux from the surface (sinking of ungrazed phytoplankton) and vertical migrators. He estimated that local production available to the fourth trophic level was about  $1.25 \text{ gC} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  which I estimate could only sustain about  $7 \text{ t} \cdot \text{km}^{-2}$  of orange roughy. Moreover, after an extensive field sampling program off southern Tasmania, Williams and Koslow (1997)

estimated a biomass of micronekton migrating to about 900m depth between 0.94 to 3.36  $\text{gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ . Using the conversion ratios presented by Koslow (1997) this micronekton could sustain only between 5 to 18  $\text{t}\cdot\text{km}^{-2}$  of orange roughy. All of these values are much less than orange roughy biomass estimates for Tasmania seamounts (50-125  $\text{t}\cdot\text{km}^{-2}$ ; Koslow, 1997). From these calculations Koslow (1997) concluded that local productivity (hypothesis 1) and vertical migrators (hypothesis 3) are not sufficient to sustain known aggregations of seamount fishes on seamounts. Alternatively, they could be supported by advected sources (hypothesis 2).

On the other hand, Tseytlin (1985) modelled the biomass of predatory fish that could be sustained at a seamount by food sources explained in hypothesis 2 and 3. With several assumptions, including a summit depth of 500m, a known mesozooplankton biomass of 50  $\text{mg}\cdot\text{m}^{-3}$ , a mean current velocity of 0.1  $\text{m}\cdot\text{s}^{-1}$ , and an average fish wet weight of 200g, he concluded that a maximum of 40  $\text{t}\cdot\text{km}^{-2}$  of fish could be supported by the horizontal flow of prey, while an extra 75  $\text{t}\cdot\text{km}^{-2}$  of fish could be supported by vertical migrators, leading to a total of about 115  $\text{t}\cdot\text{km}^{-2}$ , in the range of known orange roughy biomasses.

All of these studies strengthen hypothesis that imported food supplies support large fish aggregations on seamounts. However, these estimates account only for a single species and do not take into account the multispecies complexity of seamount ecosystems in which there may be more predators as well as additional sources of carbon and nutrients entering the food web from mesopelagic fish, visiting fish, squid and crustaceans, and, in some cases, detritus (Pitcher and Bulman, in press). On the south-eastern Australian and New Zealand seamounts, for instance, several species of oreo dories (e.g., *Pseudocyttus maculatus* and *Allocyttus niger*) are also aggregating in high densities (Koslow, 1997; Bulman, 2002) and other members of these communities such as the squalids and macrourids are also abundant (Koslow *et al.*, 1994; Bulman, 2002). Many of these species consume similar prey as orange roughy and are therefore adding to the predation pressure on these prey (Bulman *et al.*, 2001; Bulman *et al.*, 2002a).

Ecosystem-based modelling approaches can help in understanding the complex nature of ecosystem function. In seamount ecosystems, in particular, the complexity of the ecosystem is heightened by the apparent trophic inequities. However, there have been few attempts to fully model seamount ecosystems. Trophic models of the Tasmanian seamounts and large aggregations of orange roughy and oreos living on them were constructed using Ecopath with Ecosim to explore the hypothesis of Koslow (1997) that these large fish aggregations were supported by advection of prey past the seamounts (Bulman, 2002; Bulman *et al.*, 2002b).

Among the many tools for modelling marine ecosystems, the Ecopath with Ecosim (EwE) modelling approach and software has proved to be one of the most successful. It has seen widespread use and has generated helpful insights (Whipple *et al.*, 2000; Robinson and Frid, 2003). The development of Ecopath in the early 1980s (Polovina, 1984) and its evolution in the following years into a dynamic modelling tool (Walters *et al.*, 1997, 1999, 2000; Christensen and Walters, 2004a, b), has allowed us to address ecological questions, evaluate ecosystem effects of fishing, explore management policy options, analyse impact and placement of marine protected areas, and model the effect of environmental changes (e.g., Christensen and Pauly, 1993; Jarre-Teichmann, 1998; Pitcher *et al.*, 2000; Shannon *et al.*, 2000; Watson *et al.*, 2000; Gu  nette *et al.*, 2001; Watson and Pauly, 2001; Walter *et al.*, 2002; Christensen and Maclean, 2004; Morato and Pitcher, 2005; Pitcher *et al.*, 2005).

In an effort to better understand seamount ecosystem functioning, this paper will address how complex seamount food web structures are sustained. I used a generic seamount ecosystem model from the Northeast Atlantic to examine 1) the impact of a potential increase of local primary production on higher trophic levels, 2) to quantify the immigration of micronekton that would be required to maintain a “typical” seamount community, and 3) to quantify if the necessary immigration ratios could be supported by local oceanographic conditions.

## 3.2 METHODS

### 3.2.1 Modelling approach

The modelling approach used in this study was Ecopath with Ecosim (EwE), including Ecospace (Christensen and Walters, 2004a). The parameterisation of an Ecopath model is based on satisfying two ‘master’ equations. The first describes how production for each group can be divided up, and the second is based on the principle of conservation of matter. As a trophic mass-balanced model Ecopath assumes that, for each functional group  $i$  in an ecosystem, mass balance should occur over a given time period. In the first ‘master’ equation biomass production of a compartment ( $P_i$ ) is balanced by catches ( $Y_i$ ), predation mortality ( $B_i \cdot M2_i$ , where  $B_i$  is the biomass of the group and  $M2_i$  is the total predation rate for the group), biomass accumulation ( $BA_i$ ), net migration ( $E_i$  = emigration-immigration) and other mortality ( $MO_i$ ), such that:

$$(1) \quad P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + MO_i$$

Production is usually estimated from the production/biomass ratio ( $P/B$ ) and the average annual biomass ( $B$ ) and can be expressed as ( $P_i = B_i \cdot (P/B)_i$ ). Predation mortality can be expressed as the sum of consumption by all predators ( $j$ ) preying upon group ( $i$ ), *i.e.*:

$$(2) \quad B_i \cdot M2_i = \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji}$$

where  $(Q/B)_j$  is the consumption/biomass ratio of the predator ( $j$ ) and  $DC_{ji}$  is the fraction of the prey ( $i$ ) in the average diet of the predator ( $j$ ). The other mortality can also be expressed as:

$$(3) \quad MO_i = P_i \cdot (1 - EE_i)$$

where  $EE$  is the ecotrophic efficiency, or the proportion of the production that is utilized in the system.

Substituting (2) and (3) into the equation (1) means it can be re-expressed as:

$$(4) \quad B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} + E_i + BA_i$$



The second 'master' equation is:

$$(5) \quad Q_i = P_i + R_i + U_i$$

where  $R_i$  is respiration and  $U_i$  is unassimilated food.

Ecosim uses the Ecopath model to estimate its initial parameters. It then uses a system of differential equations of the form given in (6) to calculate the biomass fluxes between pools through time:

$$(6) \quad \frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i$$

where  $dB_i/dt$  represents the growth rate of  $i$  during the time interval  $dt$ ,  $g_i$  is the net growth efficiency,  $M_i$  the natural mortality rate,  $F_i$  is fishing mortality rate,  $e_i$  is emigration rate,  $I_i$  is immigration rate. The  $Q$  terms refer to consumption by group  $i$  ( $Q_{ji}$ ) and predation on  $i$  ( $Q_{ij}$ ), and are calculated using the 'forage arena' concept. For further details regarding the equations and their solutions see Walters *et al.* (1997, 2000) and Christensen and Walters (2004a).

Ecospace represents biomass dynamics (as in eq. 6) over a two-dimensional rectangular grid space ( $x$ ,  $y$ ) and time ( $t$ ). Such representations involve very complex sets of partial differential equations. For each cell the immigration rate  $I_i$  of eq. (6) is assumed to consist of up to four immigration flows from the neighbouring cells in the grid. Similarly, the emigration flows  $e_i$  in eq. (6) are represented as instantaneous movement rates to nearby cells. For further details see Walters *et al.* (1999).

### 3.2.2 Generic model for seamounts in the North-Atlantic

A model of a hypothetical isolated seamount in the North Atlantic was built. The depth of the summit below the surface was set to be at around 300 m and the base at around 2000m. The area of the model was assumed to be 30 km radius from the summit, in order to include the theoretical area of its influence (see Chapter 4). As a result the total area under consideration was equal to 2827 km<sup>2</sup>.

A total of 37 functional groups were included in the seamount EwE model, stratified by depth of habitat (see Appendix 3 for details). The models included three marine mammal groups (toothed whales, baleen whales and dolphins), seabirds, turtles, seven invertebrate groups (benthic filter feeders such as corals or gorgonians, benthic scavengers, benthic crustaceans, pelagic crustaceans, seamount resident cephalopods, small and large drifting cephalopods), three zooplankton groups (gelatinous, shallow and deepwater zooplankton), primary producers (phytoplankton), detritus and twenty fish groups.

Fish groups were divided based on environment use (depth and habitat – e.g., benthic, pelagic or benthopelagic), size, energetics (Childress *et al.*, 1980; Koslow, 1996) and life-history. A general stratification by depth was used: epipelagic, between of 0-200 m depth; mesopelagic, the region of the oceanic zone from 200 m to 1000 m; and bathypelagic, between 1000 m to 4000 m depth. Seamount associated fishes were divided into three different groups. Two groups contained species that are targeted by the north Atlantic fishery (*Hoplostethus atlanticus* and *Beryx* spp.), and a third group had the other seamount associated species. The deep scattering layer (DSL; a 50-200 m thick, sound-reflecting layer in ocean waters, consisting of a stratified, dense concentration of zooplankton and fish) was not considered as a single group, but as several groups that take part in its formation (i.e. shallow and gelatinous zooplankton, pelagic crustaceans, and small mesopelagic migrating fishes).

The model parameters (Table 3.1) production to biomass ratios (P/B), consumption to biomass ratios (Q/B) were calculated on a yearly basis ( $\text{year}^{-1}$ ). Biomass ( $\text{t}\cdot\text{km}^{-2}$ ) and catch ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ) were expressed in wet weight. The Q/B ratios for fish groups were estimated using an empirical equation (Palomares and Pauly, 1998). Temperature values (Celsius degrees) were established as being 18°C for the epipelagic region (0-200m), 8°C for the mesopelagic region (200-1000m), and 6°C for the bathypelagic region (1000-4000m). For some groups Q/B values were taken from other models. For most groups P/B ratios were extracted from previously constructed models or were estimated assuming production and consumption ratio equal to 0.3. The proportion of food consumed and not assimilated was

taken as 0.2. When no biomass estimate was available, this parameter was estimated by Ecopath using a value of 0.95 for Ecological Efficiency (EE). A preliminary diet matrix was assembled using published data, unpublished local information, and empirical knowledge (Table 3.2). Unidentified diet categories were excluded from the diet matrix and data were re-scaled to 100%.

The theoretical seamount was assumed to have a low initial level of exploitation. Modelled seamount fisheries were loosely based on those operating at the Azores / North Atlantic ridge, and thus divided in 6 fleets (Morato *et al.*, 2001): demersal longline (targeting shallow water demersal and benthic fish species; operating mainly up to 600m depth); deepwater longline (targeting bathypelagic and bathybenthic; operating mainly at 800-1200m); small pelagics fishery (for small pelagic fishes); tuna fishery; swordfish fishery; deepwater trawl (targeting seamount associated species, including orange roughy and alfonsinos; operating mainly at 800-1200). Landings (Table 3.3) were assumed to be small and varied from 218 t·year<sup>-1</sup> for shallow benthic fishes to 2.7 t·year<sup>-1</sup> for billfishes.

Initially, I assumed the seamount to be a closed system with no advection of micronekton from outside the system or biomass accumulation. Thus, this model was named “closed seamount model”. Another model was built which estimated rates of advection of micronekton into the system required to sustain various levels of fish biomass. This later model was named “advection seamount model” (described in section 3.2.4).

**Table 3.1** – Input parameters and estimates (in parentheses) from the theoretical “closed seamount” (closed) and “advection” (adv.) models of a seamount. P/B is production to biomass ratio, Q/B is consumption to biomass ratio, EE is ecotrophic efficiency, and TL is trophic level of the groups. P/B, Q/B, TL and catch were the same in the immigration and no-migration models. Bold numbers show those groups with increased biomass as a result some type of seamount effect.

Group name	Biomass (t·km <sup>-2</sup> ) closed	Biomass (t·km <sup>-2</sup> ) adv.	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	EE closed	EE adv.	TL	Catch (t·km <sup>-2</sup> ·year <sup>-1</sup> )
Toothed whales	0.0001	0.0001	0.020	10.270	(0.514)	0.514	5.03	
Baleen whales	0.123	0.123	0.060	5.563	(0.024)	0.024	3.45	
Dolphins	0.040	<b>0.100</b>	0.070	11.410	(0.049)	0.020	4.31	
Sea turtles	0.001	0.001	0.150	3.500	(0.900)	0.900	3.83	
Seabirds	0.0001	<b>0.00025</b>	0.040	84.390	(0.257)	0.103	4.25	
Tunas	0.032	<b>0.191</b>	0.742	16.291	(0.706)	0.118	4.34	0.011
Billfishes	0.020	0.020	0.500	4.200	(0.101)	0.101	4.53	0.001
Pelagic sharks	0.011	0.011	0.300	3.100	(0.916)	0.914	4.57	0.002
Benthopelagic sharks	0.030	0.030	0.510	6.900	(0.154)	0.154	4.33	0.002
Rays and skates	0.020	0.020	0.170	1.500	(0.678)	0.678	3.84	0.002
Large oceanic planktivores	(0.003)	0.003	0.112	2.066	0.100	(0.100)	3.50	
Small epipelagic fish	0.859	0.859	2.053	19.867	(0.734)	0.734	3.07	0.050
Medium epipelagic fish	0.113	0.113	1.080	10.750	(0.982)	0.983	3.53	0.010
Large epipelagic fish	0.014	0.014	0.690	5.095	(0.870)	0.870	4.10	
Small mig. mesopelagic fish	2.000	2.000	1.980	8.000	(0.974)	0.974	3.30	
Large mig. mesopelagic fish	(0.970)	0.970	0.600	3.550	0.950	(0.950)	3.98	
Non-mig. mesopelagic fish	(3.974)	3.974	0.500	1.570	0.950	(0.950)	3.17	
Shallow benthic fish	(0.723)	(0.723)	0.590	4.700	0.950	0.950	3.64	0.080
Shallow demersal fish	(0.215)	(0.215)	0.660	5.200	0.950	0.950	3.98	0.020
Seamounts-associated fish	(0.592)	0.592	0.060	2.200	0.950	(0.945)	4.08	0.011
<i>Hoplostethus atlanticus</i>	(0.780)	<b>41.930</b>	0.048	2.000	0.850	(0.040)	4.19	0.010
<i>Beryx</i> spp.	(0.531)	<b>5.313</b>	0.060	2.000	0.950	(0.095)	3.87	0.010
Bathypelagic fishes	(0.796)	0.796	0.500	1.477	0.950	(0.950)	3.82	0.006
Bathybenthic fishes	(1.264)	(1.265)	0.200	0.500	0.950	(0.950)	3.27	0.003
Bathydemersal Fishes	(1.009)	(1.010)	0.200	0.600	0.950	0.950	3.86	0.002
Benthic invert. filter feeders	(0.755)	0.755	0.800	9.000	0.950	(0.950)	2.00	
Benthic invert. scavengers	(2.869)	(2.870)	1.830	13.567	0.950	0.950	2.37	
Benthic crustaceans	(3.425)	(3.426)	1.600	10.000	0.950	0.950	2.22	
Pelagic crustaceans	(6.094)	6.094	1.450	9.667	0.950	(0.950)	2.69	
Cephalopods resident	(0.120)	(0.119)	2.890	10.000	0.950	0.950	3.39	
Cephalopods drifting small	(0.349)	0.349	4.450	16.863	0.950	(0.950)	3.60	
Cephalopods drifting large	(0.006)	0.006	2.500	10.000	0.950	(0.951)	4.15	
Gelatinous zooplankton	(9.428)	9.428	0.850	2.000	0.800	(0.800)	2.84	
Shallow zooplankton	16.684	16.684	(11.214)	37.379	(0.710)	0.710	2.11	
Deep zooplankton	6.849	6.849	(8.700)	29.000	(0.718)	0.718	2.11	
Phytoplankton	7.160	7.160	283.500	-	(0.261)	0.267	1.00	
Detritus	100.000	100.000	-	-	(0.160)	0.162	1.00	

**Table 3.2** – Diet matrix in weight proportions for a generic seamount model in the Northeast Atlantic. Columns stand for predators while rows stand for prey. Numbers in columns headings represent the predator groups as defined in different rows of the first two columns.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1 Toothed whales	0.001																		
2 Baleen whales	0.001							0.005											
3 Dolphins	0.10							0.001											
4 Sea turtles								0.001											
5 Seabirds	0.001																		
6 Tunas	0.10							0.140					0.01						
7 Billfishes	0.007																		
8 Pelagic sharks	0.08						0.01	0.005											
9 Benthopelagic sharks								0.01											
10 Rays and skates								0.007		0.002									
11 Large oceanic planktivores								0.001											
12 Small epipelagic fish	0.01	0.10	0.30		0.25	0.42	0.30	0.20		0.08	0.10		0.20	0.40				0.03	0.05
13 Medium epipelagic fish			0.05			0.08	0.35	0.05						0.20					
14 Large epipelagic fish							0.10												
15 Small mig. mesopelagic fish		0.10	0.10	0.05	0.05	0.04		0.05	0.01		0.09		0.05	0.01		0.167		0.20	0.15
16 Large mig. mesopelagic fish								0.05						0.01					
17 Non-mig. mesopelagic fish			0.06		0.05	0.05			0.10	0.03				0.02		0.156	0.01		
18 Shallow benthic fishes			0.10		0.25	0.05		0.05	0.10	0.07									0.15
19 Shallow demersal fishes	0.10		0.10			0.10	0.01	0.15	0.05	0.015									
20 Seamouths-associated fishes	0.05								0.05	0.005						0.001			
21 <i>Hoplostethus atlanticus</i>	0.10								0.05										
22 <i>Beryx</i> spp.	0.05								0.05							0.001			
23 Bathypelagic fishes							0.08		0.05							0.056			
24 Bathybenthic fishes									0.10	0.03									
25 Bathydemersal Fishes								0.10	0.05	0.08						0.009			
26 Benthic invert. filter feeders									0.05	0.08								0.07	0.05
27 Benthic invert. scavengers			0.02						0.05	0.18								0.15	0.15
28 Benthic crustaceans			0.01						0.01	0.05	0.07							0.25	0.05
29 Pelagic crustaceans			0.06		0.05				0.01	0.10	0.18	0.09		0.10	0.05	0.20	0.11	0.09	0.10
30 Cephalopods resident	0.20	0.05	0.10		0.10	0.08		0.05	0.10	0.01									0.05
31 Cephalopods drifting small		0.05	0.10	0.01	0.15	0.15	0.10			0.01	0.09		0.05	0.10		0.167			0.10
32 Cephalopods drifting large	0.20						0.05	0.06	0.04										
33 Gelatinous zooplankton		0.05		0.89	0.03	0.03				0.158		0.100	0.05	0.10	0.10	0.111		0.20	0.10
34 Shallow zooplankton		0.25		0.05	0.07							0.35	0.800	0.55	0.10	0.35		0.90	
35 Deep zooplankton		0.35										0.28				0.35	0.222		
36 Phytoplankton		0.05											0.100						
37 Detritus								0.05											
38 Import																			

**Table 3.2 – cont.**

Prey \ Predator	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1 Toothed whales																
2 Baleen whales																
3 Dolphins																
4 Sea turtles																
5 Seabirds																
6 Tunas																
7 Billfishes																
8 Pelagic sharks																
9 Benthopelagic sharks																
10 Rays and skates																
11 Large oceanic planktivores																
12 Small epipelagic fish											0.05	0.05				
13 Medium epipelagic fish																
14 Large epipelagic fish																
15 Small mig. mesopelagic fish	0.35	0.35	0.10	0.10		0.10					0.05	0.15	0.10			
16 Large mig. mesopelagic fish		0.05		0.10		0.10						0.05				
17 Non-mig. mesopelagic fish		0.15	0.05	0.10	0.10	0.05					0.10	0.10	0.10			
18 Shallow benthic fishes											0.05					
19 Shallow demersal fishes																
20 Seamouth-associated fishes			0.005			0.005										
21 <i>Hoplostethus atlanticus</i>			0.005			0.01										
22 <i>Beryx</i> spp.						0.01										
23 Bathypelagic fishes	0.10				0.005	0.05										
24 Bathybenthic fishes	0.045		0.05			0.15							0.20			
25 Bathydemersal Fishes	0.05		0.05			0.01							0.30			
26 Benthic invert. filter feeders				0.20	0.05											
27 Benthic invert. scavengers	0.10		0.10		0.20	0.05		0.10								
28 Benthic crustaceans			0.05		0.25	0.10		0.10			0.10					
29 Pelagic crustaceans	0.05	0.25	0.50	0.10	0.10	0.05					0.15	0.05	0.10	0.10		
30 Cephalopods resident	0.05				0.05	0.05										
31 Cephalopods drifting small	0.05	0.15	0.04	0.15	0.01	0.05										
32 Cephalopods drifting large																
33 Gelatinous zooplankton	0.15	0.05	0.05	0.05	0.05	0.05					0.15	0.20				
34 Shallow zooplankton								0.05	0.10	0.375	0.15	0.10		0.35	0.10	0.05
35 Deep zooplankton				0.20		0.015		0.05	0.10	0.25		0.20	0.20	0.25		0.05
36 Phytoplankton							0.25		0.10	0.25				0.10	0.80	0.10
37 Detritus	0.055				0.185	0.15	0.75	0.70	0.70	0.125	0.20	0.10		0.20	0.10	0.80
38 Import																

**Table 3.3**— Catch ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ) and total catch ( $\text{t}\cdot\text{year}^{-1}$ ) estimated for the different fisheries considered in the theoretical seamount. DL is demersal longline; DWL is deep-water longline; SP is small pelagics fishery; T is tuna pole-and-line fishery; SW is swordfish longline fishery; and DWT is deep-water trawl.

Group name	Landings by fleet ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ )						$\text{t}\cdot\text{year}^{-1}$
	DL	DWL	SP	T	SW	DWT	Total
Tunas				0.011			30.0
Billfishes					0.001		2.7
Sharks Pelagic	0.001				0.001		5.5
Sharks Benthopelagic	0.001					0.001	5.5
Rays and Skates	0.002						5.5
Epipelagic S			0.050				136.4
Epipelagic M			0.010				27.3
Shallow Benthic Fishes	0.080						218.2
Shallow Demersal fishes	0.020						54.6
Seamounts-associated Fishes		0.001				0.010	30.0
<i>Hoplostethus atlanticus</i>						0.010	27.3
<i>Beryx</i> spp.	0.005					0.005	27.3
Bathypelagic		0.005				0.001	16.4
Bathybenthic fishes		0.002				0.001	8.2
Bathydemersal Fishes	0.001					0.001	5.5
Total ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ )	0.110	0.008	0.060	0.011	0.002	0.029	

### **3.2.3 Impact of primary production enhancement**

I explored the potential impact of heightened levels of primary production on higher trophic levels, using the “closed model”. The estimated primary productivity for the Northeast Atlantic region was  $2030 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  (SeaWIFS data set). Pauly *et al.* (pers. comm.) found that seamounts whose peak reaches to within 100 m of the surface would generate an increase in local primary production of between 50 to 70% of the surrounding areas, while those with summits at 300m depth would generate an increase of only between 2 and 5%. I used these values to estimate the biomasses of orange roughy that could be sustained under these conditions. Also, I quantified the amount of primary production required (PPR) to sustain different levels of orange roughy biomasses, as reported for several geographical areas.

The “closed” seamount model was balanced by providing the biomasses of ten top predators: toothed whales, baleen whales, dolphins, sea-turtles, seabirds, tunas, billfishes, pelagic sharks, benthopelagic sharks, rays and skates. The Ecopath model was then run with different biomasses of orange roughy and the primary production required to sustain the new system was calculated. The linear relationship between PPR and orange roughy biomass was then computed and the levels of orange roughy sustained by different levels of local PP estimated.

### **3.2.4 The “advection model”**

Using the EwE approach, advection of prey can be modelled in two ways. The first approach, which is used only when there is a permanent addition of organisms from other areas outside the system, assumes treatment of migratory flows as dispersal (immigration / emigration) rates across the system boundaries (Christensen *et al.*, 2005). Dispersal rates allow quantification of the amount of imported resources needed to maintain the system and simulation of the impact of different levels of immigration, due to inter-annual changes in climate, primary production, and currents. The second approach, which I did not use, involves the assignment of a high diet proportion as “import” in the Ecopath diet composition matrix (Christensen *et al.*, 2005).



I simulated and quantified the immigration of prey organisms that would be required to maintain a “hypothetical” seamount community. Total immigration rates required were estimated as a function of potential biomass of predators as:

$$(7) \quad I = a \cdot B_j + b$$

where the slope  $a$  is the Q/B ratio of predator  $j$  and the intercept  $b$  is roughly the consumption of the predator in the balanced “closed seamount model”.

To estimate the total immigration required to sustain a “typical” seamount community in the northeast Atlantic, I assumed that the standing biomasses estimated by the “closed seamount model” would roughly represent the biomasses of most of the groups, except for seamount aggregating fish, orange roughy, *Beryx* spp., and some pelagic fish groups that are attracted to seamounts (i.e., seabirds, tunas, billfishes, and pelagic sharks). P/B, Q/B, EE, and the estimated standing biomasses were re-entered in the new model and the following assumptions were made: 1) biomass estimates for orange roughy in the North Atlantic are not available and so southern hemisphere data from Bulman (2002) were used. Biomass was re-scaled to the total area, assuming that part of it is open water where seamount associated species are unlikely to occur ( $41.9 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ); 2) biomasses alfonsinos were estimated to be 10 times higher than in the “closed seamount model” ( $5.3 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ); 3) biomass of groups attracted to seamounts was increased based on data from Chapter 4, and thus considered greater than in the open ocean, i.e. abundances of marine mammals, seabirds and tuna were assumed to be 2.5, 2.5 and 6 times higher than in the “closed seamount model”. No changes were made to the benthic filter feeding group.

In order to check if the necessary immigration ratios could be supported by local oceanographic conditions I estimated the available micronekton in  $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$  that could be advected to the system. Ocean current velocity ( $V_c$ ) was derived from local measurements at the Sedlo seamount North of the Azores island of Graciosa while the standing biomass ( $B$ ) of migrating groups ( $j$ ) were assumed to be those of the “closed seamount model”. The immigration ( $I$ ) of micronekton can thus be estimated as:

$$(8) \quad I_j = V_c \cdot B_j \cdot W^l$$

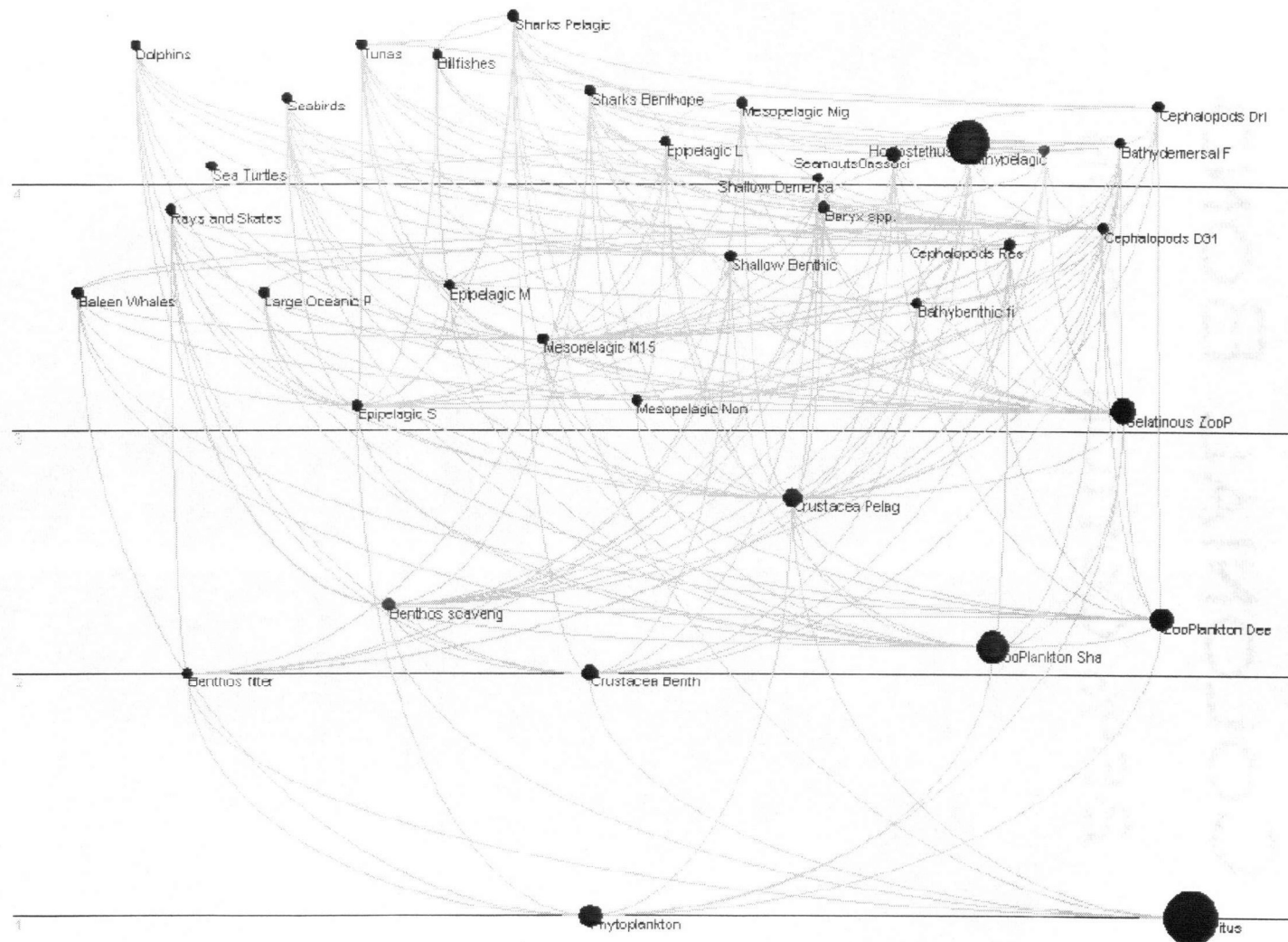
where  $W$  is the average width of the area covered by the model.

Sedlo seamount (40° 20'N, 26° 54'W) current patterns have been described by White *et al.* (2006). Sedlo is an elongated, multi-peaked seamount located within the sub tropical north Atlantic gyre. Current residual flow at Sedlo seamount may average 5 cm·s<sup>-1</sup> in the upper 800m while in deeper waters (>800m) may average 1 cm·s<sup>-1</sup>. Tidal currents appeared to be amplified by about 2-4x the surrounding ocean values. Since most of the orange roughy aggregations are found at 800m or deeper, and in order to have conservative estimates of immigration rates, I assumed  $V_c$  of 1 cm·s<sup>-1</sup>.

### 3.3 RESULTS

#### 3.3.1 The “closed seamount model”

The initial model was built with no special features in the seamount ecosystem, in order to estimate baseline standing biomasses for the different groups. This “closed model” was balanced after small changes in the diet matrix and the resulting parameter set is given in Tables 3.1 and 3.2; trophic structure is shown in Figure 3.1. The total biomass of the modeled ecosystem, excluding detritus, was estimated as 68 t·km<sup>-2</sup>. Primary producers account for 10.5% of the total biomass of our “closed model”, whereas the highest trophic levels ( $TL > 4.30$ ), i.e., toothed whales, pelagic sharks, billfishes, tunas, benthopelagic sharks and dolphins, account for 0.14% of the total biomass. Aggregating fishes account for only 2.8% of the total biomass of the system. The estimated biomasses were 0.78 t·km<sup>-2</sup> of orange roughy, 0.53 t·km<sup>-2</sup> of alfonsoinos, and 0.59 t·km<sup>-2</sup> of other seamount-associated fish species.



**Figure 3.1** - Flow diagram of a seamount ecosystem. The area of the nodes is proportional to the biomass of each group.

### 3.3.2 Impact of primary production enhancement

In our system the biomass of orange roughy ( $B_{\text{orh}}$ ) can be expressed as a function of the primary production (PP) as:  $B_{\text{orh}} \text{ (t}\cdot\text{km}^{-2}) = 0.0018\cdot\text{PPR}-2.965$  (or  $\text{PPR (t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}) = 542.1\cdot B_{\text{orh}}+1607.6$ ). The average primary productivity for the Northeast Atlantic ( $\text{PP}_{\text{NEA}}$ ) could sustain only about  $0.78 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  of orange roughy for our generic seamount model. This analysis is based on the assumption of a linear relationship between PP and biomass of higher trophic levels, which may not always be the case, thus warranting further examination mainly through dynamic simulations modelling.

The effect of primary production (PP) enhancement on orange roughy biomass at the “closed seamount model” in the Northeast Atlantic is presented in Table 3.4. A 50-70% increase in local PP, typical for seamounts reaching to about 100 m of the surface (Pauly *et al.*, pers. comm.), could sustain about  $3.0\text{-}7.3 \text{ t}\cdot\text{km}^{-2}$  of orange roughy biomass, which represents a four to nine fold increase in biomass when compared to the non PP enhancement scenario. Our results suggested that seamounts with summits at about 300m depth (depth of the summit in the generic seamount model), and which generate an increase in PP between 2 and 5%, could sustain only  $0.8\text{-}1.0 \text{ t}\cdot\text{km}^{-2}$  of orange roughy. As previously suggested, the values of PP required to sustain the levels of orange roughy biomass reported from different seamounts around the world are much higher than the observed values. For example, to sustain  $100 \text{ t}\cdot\text{km}^{-2}$  of orange roughy (similar to that observed off Tasmania; Koslow, 1997; Bulman, 2002) the PPR is about  $55800 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , 28 times higher than the observed values for the Northeast Atlantic.

### 3.3.3 The “advection model”

Total immigration biomass was estimated as a function of the potential biomass of different predatory groups that are somehow attracted to seamounts (Table 3.5). Taking as an example the orange roughy, the total immigration rate required ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ) was estimated as:  $I = 2.00\cdot B_{\text{orh}}-1.560$ . Thus, a potential biomass of orange roughy of  $100 \text{ t}\cdot\text{km}^{-2}$  will require a total immigration rate of  $198.4 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , which represents an import of 119% the total

standing biomass of the system (excluding detritus). Prey groups with higher immigration rates were: small (vertical) migrating mesopelagic fish ( $69.5 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), pelagic crustaceans ( $49.6 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), mesopelagic non-migrating fish ( $29.8 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), small drifting cephalopods ( $29.8 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), gelatinous zooplankton ( $9.9 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ) and large (vertical) migrating mesopelagic fish ( $9.9 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ).

**Table 3.4** –Effect of primary production (PP) enhancement on orange roughy biomass at a generic seamount in the Northeast Atlantic. Estimated primary productivity for the Northeast Atlantic ( $\text{PP}_{\text{NEA}}$ ) region was  $2030 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  (SeaWIFS data set).

PP Enhancement	PP ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ )	Biomass (orange roughy) ( $\text{t}\cdot\text{km}^{-2}$ )
1.00	2030	0.780
1.02	2071	0.855
1.05	2171	1.046
1.50	3261	3.052
1.70	5544	7.263

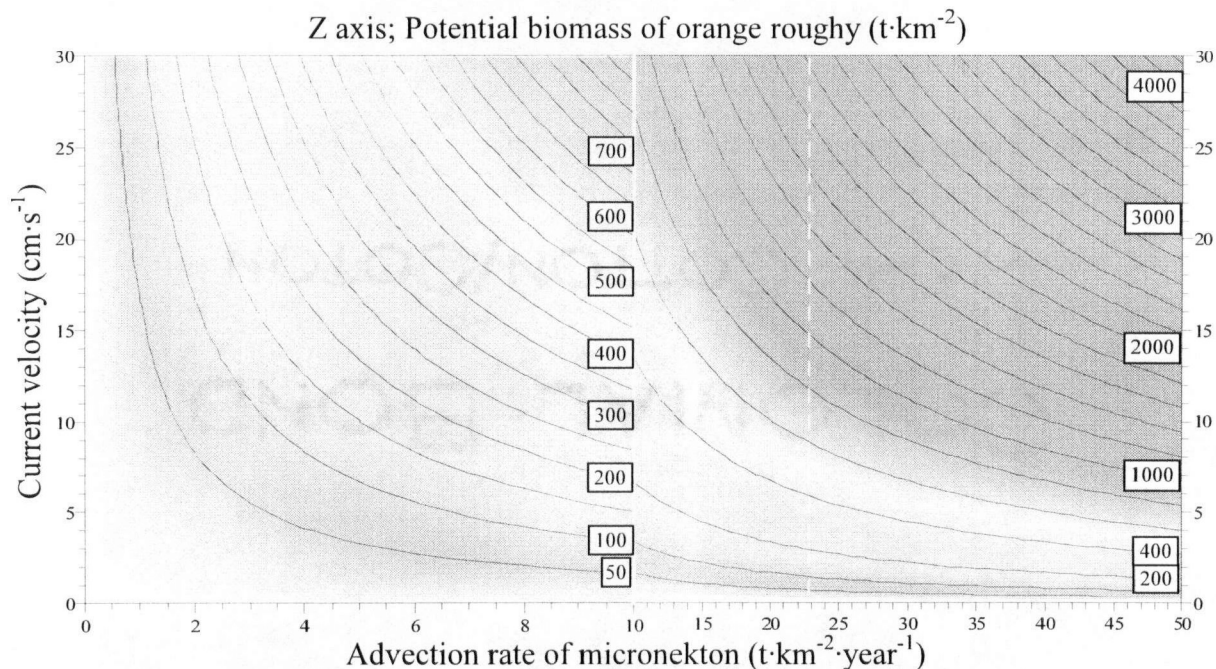
**Table 3.5** - Total immigration rate required ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), estimated as a function of potential biomass of predators as:  $I = a\cdot B_j + b$ ; where  $B_j$  is the biomass of the predator  $j$ , the slope  $a$  is the Q/B ratio of  $i$  and the intercept  $b$  is roughly the consumption of  $i$  in the balanced “closed seamount model”.

Predator Group	$a$	$b$
Orange roughy	2.000	-1.560
Alfonsinos	2.000	-1.062
Dolphins	11.410	-0.456
Seabirds	84.390	-0.008
Tuna	16.291	-0.519

To enable the model to estimate the total immigration required to sustain a “typical” seamount community in the northeast Atlantic, abundances of dolphins, seabirds and tuna were assumed to be 0.1, 0.00025 and 0.191  $\text{t}\cdot\text{km}^{-2}$ , respectively. Using these abundances to estimate the prey immigration rates required to sustain these predatory groups, I calculated that marine mammals (dolphins only) require 0.7  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , seabirds 0.01  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , and tuna 2.6  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ . Additionally, I assumed biomasses of orange roughy of 41.9  $\text{t}\cdot\text{km}^{-2}$  and of alfonsoinos of 5.3  $\text{t}\cdot\text{km}^{-2}$  requiring immigration rates of 82.3  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  and 9.6  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , respectively. In this case, the total immigration rate required to sustain this “typical” seamount community would be 95.2  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ .

If I assumed an average current velocity ( $V_c$ ) of 1  $\text{cm}\cdot\text{s}^{-1}$  (or 315  $\text{km}\cdot\text{year}^{-1}$ ), a model width ( $W$ ) of 53 km and a standing biomass ( $B$ ) of migrating groups of 23.787  $\text{t}\cdot\text{km}^{-2}$  (i.e. small epipelagic fish, medium epipelagic fish, small migrating mesopelagic fish, large migrating mesopelagic fish, non-migrating mesopelagic fish, pelagic crustaceans, drifting small cephalopods, and gelatinous zooplankton), the total immigration rates available to the system was about 141.5  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , about 50% more than what may be needed by the “typical” seamount ecosystem (95.2  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ). Higher current velocities, typical from seamount summits, generated even higher biomasses of advected organisms.

I also tested the extent to which current velocities and advected rates of organisms may influence the potential standing biomass of orange roughy. For most current velocities there was enough food to sustain high standing biomasses of orange roughy (Figure 3.2). Only when the biomass of advected micronekton and current velocity were both very low (below 10  $\text{t}\cdot\text{km}^{-2}$  and 5  $\text{cm}\cdot\text{s}^{-1}$ , respectively), may food be a limiting factor for orange roughy. Otherwise, it seems that food is not the limiting factor for orange roughy abundance.



**Figure 3.2** – Potential biomass of orange roughy ( $\text{t}\cdot\text{km}^{-2}$ ) that could be sustained by different rates of advected micronekton ( $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ) and oceanic current velocities ( $\text{cm}\cdot\text{s}^{-1}$ ). Scale goes from white and light blue (low rates of advection) to dark red (high rates of advection).

### 3.4 DISCUSSION

The “closed seamount model” was built to estimate baseline standing biomasses for the different groups. Compared to a general “open ocean” model built for the North Atlantic (Vasconcellos and Watson, 2004) the biomasses estimated for the pelagic groups were very similar. Such a result was expected because I did not take into account any ecological processes such as dense fish aggregations around seamounts, the hydrological trapping of small organisms or horizontal flux of micronekton. In contrast, estimated biomasses for benthic and demersal groups of the present study were higher than in the open ocean model. For example, Vasconcellos and Watson (2004) estimated biomass of small and large bathydemersal fish in the slope and abyss zones of the North Atlantic as being  $0.45 \text{ t}\cdot\text{km}^{-2}$  while in the seamount models the biomass of bathydemersal and bathybenthic fishes summed to almost five times as much,  $2.06 \text{ t}\cdot\text{km}^{-2}$ . These differences are due to greater habitat

availability at suitable depths for these groups on seamounts. On the other hand, our biomass estimates of benthic organisms were very similar to the estimates for a deepwater flat bottom model off Tasmania (Bulman, 2002).

The estimated biomasses of seamount associated species (orange roughy, alfonsinos, and other seamount associated fishes) in the "closed model" were very low ( $<2 \text{ t}\cdot\text{km}^{-2}$ ) when compared to reported abundances found in the literature (Koslow, 1997; Bulman, 2002). For example, off Tasmania Bulman (2002) estimated biomasses of different seamount aggregating fish as  $106.7 \text{ t}\cdot\text{km}^{-2}$  of orange roughy,  $4.11 \text{ t}\cdot\text{km}^{-2}$  of oreos (*Pseudocyttus maculatus*, *Neocyttus rhomboidalis* and *Alloctytus niger*) and  $8.21 \text{ t}\cdot\text{km}^{-2}$  of warty dory (*Alloctytus verrucosus*). These estimates were based on many assumptions and were later found to be conservative. Using commercial catch data from Tasmania seamounts Bulman *et al.* (2002b) found the biomass of oreos to be  $300 \text{ t}\cdot\text{km}^{-2}$ . Thus, these results suggest lack of resources in the system to support such amounts of seamount aggregating fish. In other words, local seamount production may be responsible for sustaining only a small amount of its total biomass. The question of whether increased primary production could explain the occurrence of large aggregations of seamount fishes was thus tested.

The second part of this work was to obtain more accurate estimates of the primary production required (PPR) to sustain large aggregations of fish around seamount ecosystems. Our study supports the idea that local primary productivity enhancement cannot sustain large aggregations of seamount fishes. However, our results differ markedly from those of the previous study based on a simpler approach. Koslow (1997), estimated that the PPR to sustain  $100 \text{ t}\cdot\text{km}^{-2}$  of orange roughy was about  $18000 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ , while in our study the PPR to sustain the same biomass would be about  $56500 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ . The difference is due to our use of an ecosystem approach instead of single species perspective, i.e., not all PP will be available to orange roughy as in Koslow (1997) assumptions. Instead, there will be many other predators feeding on same prey as roughy that will also require some PP. From these calculations, I can conclude that aggregations of seamount fishes on seamounts cannot likely



be sustained by local biological productivity. This finding refutes the first hypothesis and supports Koslow (1997).

Therefore, how are large aggregations of fish sustained around seamounts? Both local production and enhanced primary production (Uda and Ishino, 1958; Hubbs, 1959; Uchida and Tagami, 1984) are clearly not sufficient sources of energy to these aggregations. Our simulations using the “advection” model clearly show that these aggregations might be sustained by the horizontal flux of prey organisms that pass seamounts, thus supporting the “feed-rest” hypothesis (term used by Genin, 2004) originally proposed by Tseytlin (1985). I suggest that the required flux of micronekton to an intermediate seamount can be measured as  $I = 2.00 \cdot B_{orh} - 1.560$  (where  $I$  is the immigration to the system and  $B_{orh}$  is the biomass of orange roughy).

This seamount model, which took into account high abundances of fish, marine mammals, seabirds and tuna, required a total immigration of micronekton of  $95.2 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ , which is less than the potential available biomass after considering currents ( $141.5 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ). Therefore, I suggest that the horizontal flux of prey may be sufficient to sustain the rich communities living on seamounts. Problems with these calculations may arise from over-estimation of standing biomasses of micronekton ( $23.8 \text{ t} \cdot \text{km}^{-2}$  in our example); or from over-estimation of current velocities ( $0.1 \text{ cm} \cdot \text{s}^{-1}$  in our example). However, using acoustic and trawling methods, the standing biomasses of mesopelagic fishes and pelagic crustaceans off southern Tasmania were estimated to be about  $100 \text{ t} \cdot \text{km}^{-2}$  and  $5 \text{ t} \cdot \text{km}^{-2}$  respectively (Koslow *et al.*, 1997; Williams and Koslow, 1997). These values are four times higher than the values I used in our model. Furthermore, the current velocity I used is a very conservative value. Current velocities measured in different intermediate or shallow seamounts in northeast Pacific Ocean range from about  $12 \text{ cm} \cdot \text{s}^{-1}$  at Cobb seamount (Freeland, 1994) to  $20\text{--}40 \text{ cm} \cdot \text{s}^{-1}$  at Fieberling seamount (Eriksen, 1991) or  $15\text{--}35 \text{ cm} \cdot \text{s}^{-1}$  at Emperor Seamount (Roden, 1987). In the north Atlantic current velocities at Great Meteor Seamount measured  $12\text{--}15 \text{ cm} \cdot \text{s}^{-1}$  (Mohn and Beckmann, 2002) and at Gorrington seamount measured  $15\text{--}20 \text{ cm} \cdot \text{s}^{-1}$  (Serra and Ambar, 2002).

These results suggest that food may not be a limiting factor for orange roughy at some seamounts. Only when the biomass of advected micronekton and current velocity are both extremely low (below  $10 \text{ t}\cdot\text{km}^{-2}$  and  $5 \text{ cm}\cdot\text{s}^{-1}$ , respectively) will the flux of prey be insufficient to sustain large aggregations of orange roughy (Figure 3.2).

The question now is what can influence seamount fish abundance and explain the high variability of abundances from one seamount to the other (e.g., Clark *et al.*, 2001; McClatchie and Coombs, 2005; Rowden *et al.*, 2005). There is a considerable literature dealing with the composition of fish assemblages and their association with various environmental factors. Aspects of bottom depth, latitude, longitude, sediment type, bottom temperature, and oceanographic water masses are frequently recorded as important in determining fish species composition and abundance (e.g., Haedrich and Merrett, 1990; Koslow, 1993; Koslow *et al.*, 1994; Francis *et al.*, 2002). Clark *et al.* (2001) examined relationships between physical variables of seamounts around New Zealand, and the estimated size of orange roughy populations from those seamounts. They used multiple regression procedures to model the effects of the physical variables. Seamount location, depth of the peak, slope of the seamount flanks, and geological association (continental or oceanic) were significant factors in determining stock size in various analyses.

Since I have shown that food may not be a limiting factor, other factors may explain the high variability of abundances between seamounts (Melo and Menezes, 2002). For large aggregations of seamount fish the availability of sheltered or resting areas may be a determinant factor in explaining intra-seamount differences in abundance. This is probably the reason why Clark *et al.* (2001) found the slope of the seamount flanks a significant factor. For example, orange roughy and some oreos have a relatively high metabolic rate compared to many other deep-sea fishes as they in order to maintain position in highly dynamic current regimes require strong locomotory performance (Koslow, 1996; Bulman, 2002). However, they will also need quiescent areas for resting between feeding events. Some observational studies support this hypothesis (Lorance *et al.*, 2002), showing that perhaps the fish has

evolved to efficiently utilize enhanced horizontal fluxes in strong currents and to effectively reduce their metabolic expenditure by resting motionless in topographic shelters (Genin, 2004).

Another key element that can explain the high variability in abundance from one seamount to the other is recruitment. Different seamounts will have different probabilities of hosting large aggregations of fish due to different probabilities of receiving those fish from elsewhere, as juveniles or adults. Clark's *et al.* (2001) factors, seamount location and geological association may play an important role in explaining recruitment variability.

### 3.5 REFERENCES

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## CHAPTER 4

### TESTING A SEAMOUNT EFFECT ON AGGREGATING VISITORS<sup>1</sup>

#### 4.1 INTRODUCTION

Seamounts have been recently recognized as highly important for fisheries, biodiversity and conservation as they often support isolated but rich underwater ecosystems (Morato and Pauly, 2004). One important characteristic of seamounts is that they tend to enhance water currents (Genin *et al.*, 1986; Boehlert, 1988) thus enhancing the flux of prey organisms that pass the seamounts (Chapter 3; Tseitin, 1985; Genin *et al.*, 1986; Koslow, 1997). This characteristic has been used to explain the occurrence of large aggregations of bottom fishes around seamounts.

While the importance of seamounts for bottom fishes is very well documented (Boehlert and Sasaki, 1988; Koslow, 1996; Koslow, 1997; Koslow *et al.*, 2000), the importance for large pelagic or visiting organisms has been poorly examined. However, it has been hypothesised that there are higher abundances of some “visiting” animals, such as tuna, sharks, billfishes, marine mammals, sea-turtles and even seabirds, over seamounts but this has been based on sparse records, warranting further examination.

It is known from tagging studies that some seamounts host transient populations of bigeye tuna *Thunnus obesus* and yellowfin tuna *T. albacares* (Holland *et al.*, 1999; Itano and Holland, 2000; Sibert *et al.*, 2000; Klimley *et al.*, 2003; Musyl *et al.*, 2003; Sibert *et al.*, 2003), consequently some fisheries have taken advantage of these and other tuna aggregations (like albacore *T. alalunga* and skipjack *Katsuwonus pelamis*) to increase their yields (Yasui, 1986; Fonteneau, 1991; Adam *et al.*, 2003). Other pelagic fishes such as billfishes (Ward *et al.*, 2000; Sedberry and Loefer, 2001) and pelagic sharks (Hazin *et al.*,

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<sup>1</sup> A version of this chapter has been submitted for publication. Morato, T.; M. Machete; A. Kitchingman; F. Tempera; S. Lai; G. Menezes; R.S. Santos; and T.J. Pitcher (submitted). Abundance and distribution of seamounts in the Azores. Marine Ecology Progress Series.

1998; Klimley *et al.*, 1988) appear also to be attracted to complex high-relief bottom structures where they may be subject to local depletion. The reasons for these aggregations are still under debate but most seamounts act both as feeding stations and as orientation points in the larger-scale movement patterns of these visitors (e.g., Fréon and Dagorn, 2000).

Although several works have correlated cetacean occurrence with complex and steep topographies (e. g. Schoenherr, 1991; Balcomb, 1989; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; Hastie *et al.*, 2004; Yen *et al.*, 2004) the literature addressing their association with seamounts is scarce. Santos *et al.* (in press) concluded that seamounts are “hotspots” for sea-turtles because they found that tracked loggerhead *Caretta caretta* move toward seamounts where they have increased residence time. As to seabirds, Cory’s shearwater *Calonectris diomedea*, yellow-legged gull *Larus cachinnans atlantis*, Madeiran storm petrel *Oceanodroma castro* (Monteiro *et al.* 1996), Cassin’s auklet *Ptychoramphus aleuticus* (Yen *et al.*, 2004, 2005), and black-footed albatross *Diomedea nigripes* (Haney *et al.*, 1995) have also been observed aggregating above seamounts summits where they feed on zooplankton, small fish and small cephalopods.

Whereas previous studies have focused on analysing the auto-ecology of some organisms, in this paper, using data from a fishery observer program, I explicitly test if the abundances of tuna, marine mammals, sea turtles and seabirds observed at Azores seamounts are higher than expected by chance.

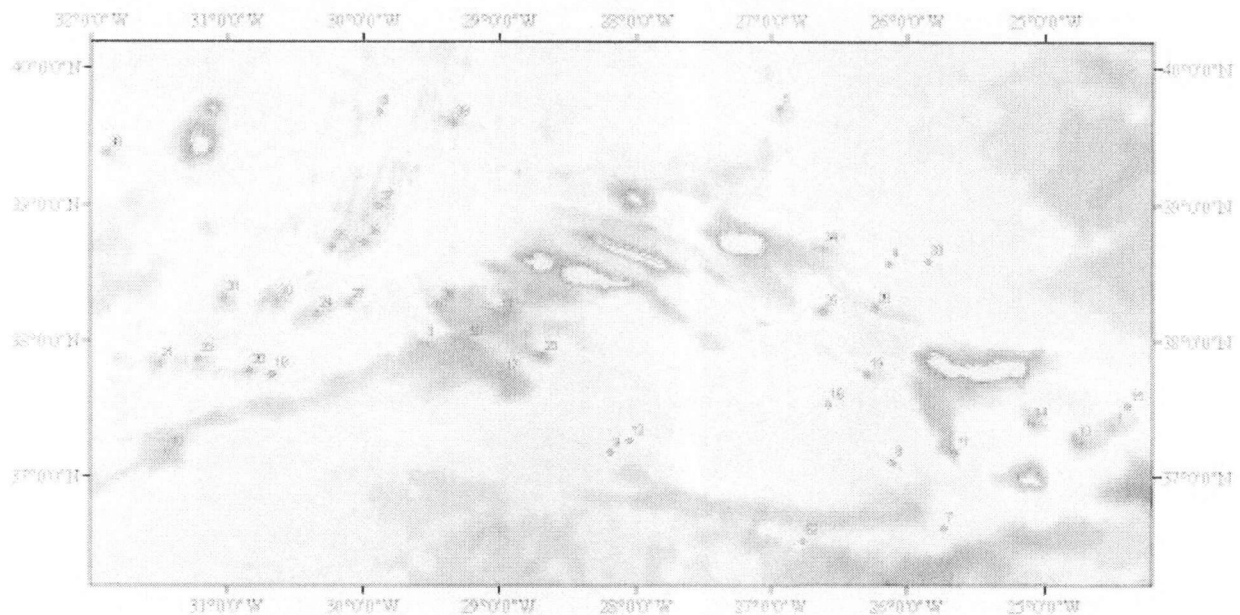
## 4.2 METHODS

### 4.2.1 Study area

The Azores archipelago is a group of nine volcanic islands and many small islets that are parts of the Mid-Atlantic Ridge in the Northeast Atlantic Ocean (an irregular area within 33.5-43° N, 21-35.5° W). Shallow seabed less than 600 m deep cover less than 1% of the 953,633 km<sup>2</sup> of the Azorean EEZ. This reflects the narrowness of the island shelves and

supports scattered fishing grounds. This study was conducted in a small rectangular area of the Azores EEZ (36.20-40.20° N, 24.20-32.00° W) chosen because it includes most of the seamounts, has better bathymetry data, and because all the tuna fishing effort and thus the fishery observer program was conducted within this area.

In this study, I used seamounts mapped (using an automated technique –Chapter 2) in the designated area of the Azores EEZ as described above which contains 39 large and 151 small seamount-like features (Figure 4.1) with different shapes, heights and depth of summits. The seamounts included in this study are those with numbers 1, 3-28, 30, 31, 33-39, and 50-52 in Appendix 2. Data from island shores (<30 km) were excluded from the analyses because they may be biased by the Island Mass Effect and because I wanted to test the effect of offshore seamounts.



**Figure 4.1** – Map of the Azores archipelago and its seamounts.

#### 4.2.2 Data collection: POPA Observer program

The observer program for fisheries in the Azores (POPA, <http://www.horta.uac.pt/projectos/popa>) was launched in 1998 with the main goal of gathering data on the pole-and-line tuna fisheries in order to certify the fisheries as 'dolphin safe'. The program covers about 50% of the fleet of around 20 vessels and often covers over 50% of the tuna catches. The program operates with observers onboard tuna fishing vessels recording data on fishing activities and gathering other scientifically-relevant information.

Geo-referenced data collected onboard includes: fishing effort, tuna catch, sighting effort for different species, and sighting of named species of marine mammals, sea turtles, and seabirds. Fishing effort is estimated as the amount of time fishermen spent looking for tuna schools. Sighting effort is defined as the time the observer spent looking at the sea searching for species other than tuna. Marine mammals, sea-turtles and seabirds were quantified by counting individuals (or estimation when in large groups) that were up to 300 meters from the vessel. The average speed of the boats when searching was 8 knots ( $\sim 15 \text{ km}\cdot\text{h}^{-1}$ ).

#### 4.2.3 Species

The present study focused on different species of tuna, marine mammals, sea turtles and seabirds (Table 4.1). Tuna are present in the Azores EEZ only during summer months: our study focuses on adult bigeye and skipjack, the most common tuna species caught in the Azores. The first species is present during April to June, while the second is usually caught from June to October. Albacore, yellowfin and bluefin tuna (*Thunnus thynnus*) are also caught in the Azores in small quantities. Tunas are caught with pole-and-line, usually with water spray and live bait. Only about 20 medium-sized Azorean boats (28-32 m long) fish within the EEZ. In fact, tuna fishery catches are relatively small and can be around 5000 tons in a good year.

**Table 4.1** – Species included in the present study, the number of observations by species and summary of the data on distance from observed data points to closest seamount (km).

Species	observations n	Dist. to seamount (km)	
		Min - max	Mean $\pm$ SD
Tuna			
Skipjack, <i>Katsuwonus pelamis</i>	1675	0.4->100	50.7 $\pm$ 49.2
Bigeye tuna, <i>Thunnus obesus</i>	1497	2.0->100	28.4 $\pm$ 36.3
Marine mammals			
Common dolphin, <i>Delphinus delphis</i>	2008	0.2->100	30.1 $\pm$ 33.0
Spotted dolphin, <i>Stenella frontalis</i>	528	0.7->100	44.3 $\pm$ 53.9
Bottlenose dolphins, <i>Tursiops truncatus</i>	303	0.3->100	29.7 $\pm$ 33.1
Sperm whale, <i>Physeter macrocephalus</i>	233	1.6->100	44.1 $\pm$ 35.8
Sea Turtles			
Loggerhead turtle, <i>Caretta caretta</i>	566	0.6->100	52.5 $\pm$ 65.6
Seabirds			
Cory's shearwater, <i>Calonectris diomedea borealis</i>	1681	0.4->100	37.0 $\pm$ 46.8
Yellow-legged gull, <i>Larus cachinnans atlantis</i>	329	1.7->100	43.2 $\pm$ 52.5
Terns, <i>Sterna hirundo</i> and <i>S. dougalli</i>	134	3.2->100	54.2 $\pm$ 58.9

Over twenty-three species of cetaceans have been reported for the Azores (Gonçalves *et al.*, 1992, 1996; Silva *et al.*, 2003). From these only a part is recorded yearly and from those the most common species are the spotted dolphin *Stenella frontalis*, common dolphin *Delphinus delphis*, bottlenose dolphin *Tursiops truncatus*, sperm whale *Physeter macrocephalus*, Risso's dolphin *Grampus griseus*, striped dolphin *Stenella coeruleoalba*, short-finned pilot whale *Globicephala macrorhynchus* (Silva *et al.*, 2003). Our study will focus on only the first four species because of the lack of data for the others.

The sea-turtles occurring in the Azores are loggerhead, leatherback *Dermochelys coriacea*, and green turtles *Chelonia mydas*, the first being the most commonly sighted species. Juvenile loggerhead turtles are transported by the North Atlantic Gyre current and live a pelagic life for about 8 years in the Eastern Atlantic, including around the Azores (Bjorndal *et al.*, 2000). This study will focus only on the loggerhead turtle.

Several seabird species are found in the Azores. However, the most commonly-sighted species are Cory's shearwater, yellow-legged gull, terns *Sterna hirundo* and *S. dougalli*, Madeiran storm petrel *Oceanodroma castro*, greater shearwater *Puffinus gravis*, and the little shearwater *Puffinus assimilis*. The petrels feed on vertical migrating fish while Cory's shearwater feeds often in association with marine predators such as dolphins and tuna (Monteiro *et al.*, 1996). This study will focus only on Cory's shearwater, the yellow-legged gull and the terns.

#### **4.2.4 Data analyses**

I used spatial data from the POPA program to test if tuna catches and sightings of sea-turtles, marine mammals and seabirds were higher closer to seamount summits. Data was available for the period 1998 to 2004 for tuna and marine mammals and for the period 2000-2004 for seabirds and sea turtles. A preliminary analyses showed no inter annual differences in the tuna catch or sighting effort. Thus, data for all years was pooled.

I built grids of tuna catch, sighting effort, and sightings of different species by allocating each data point to a 0.05 x 0.05 degree cell (~5.5 x 5.5 km). This procedure produced two grids of tuna catch per 30.9 km<sup>2</sup>, one grid of sighting effort in hours per 30.9 km<sup>2</sup>, and several grids of numbers of individuals per 30.9 km<sup>2</sup>. The latter grids were then divided by the effort grid to produce grids of numbers of individuals per 30.9 km<sup>2</sup> per hour of search. These grids included cells with zero values, i.e., those cells with fishing or sighting effort but zero catch or observations. Null data cells were those with no fishing or sighting effort.

Distances of observation cell to nearest seamount summit were separated into 10 classes of 10 km intervals from 0 to 100 km. Each cell with data was then allocated to one of the distance classes and the average catch and sightings were calculated for each class. The estimated averages were transformed in catches or sightings per km<sup>2</sup>.

I test if fishing locations were randomly selected by comparing the frequency distribution of the distances to seamount summit of the dataset of tuna fishing events and of a set of an equal



number of randomly selected locations using the G statistic for the log-likelihood ratio goodness of fit.

One-way analysis of variance (ANOVA) was used to test for significant differences between Log (x+1) transformed mean abundances (catch or sightings) at different distances from seamount summits. When significant *F* tests from the ANOVA were found, I looked for those means contributing to the effect using a post-hoc comparison. In this case, I used Dunnett's multiple comparison test to determine the significant differences between a control group mean and the treatment group means in the analysis of variance setting (Zar, 1999). The overall mean value was used as the control group mean, since I wanted to compare each distance to seamount to the overall mean (C.W. Dunnett, pers. comm.).

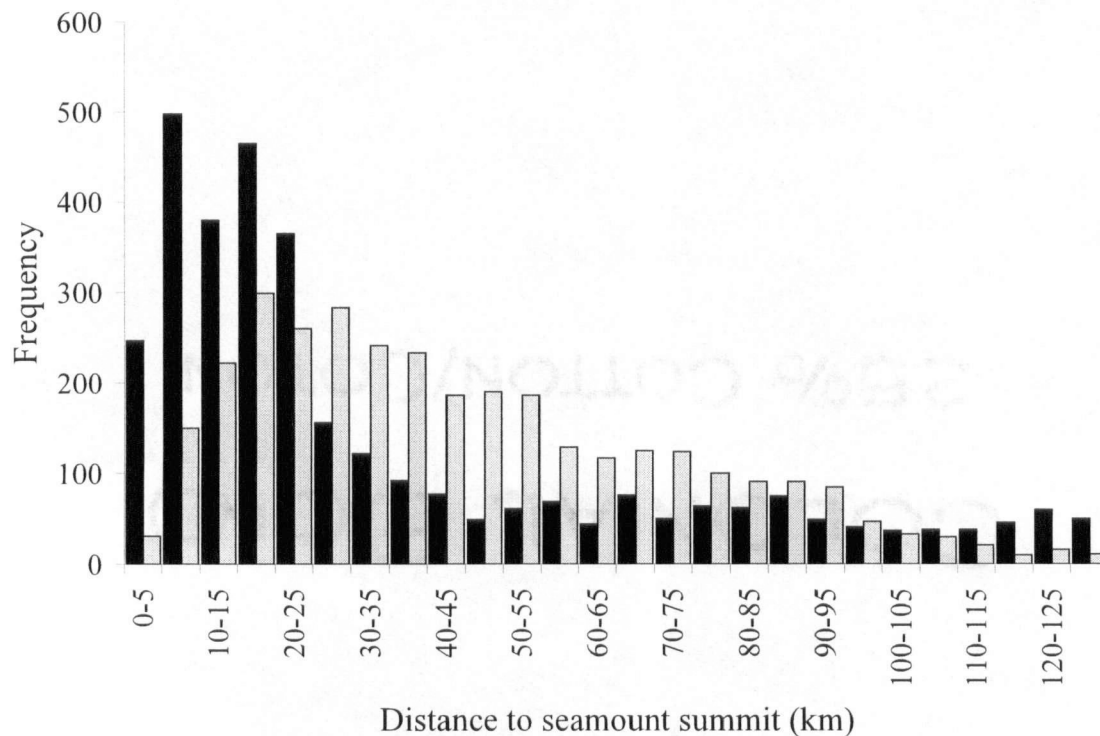
Additionally, I have tested for seamounts that produced a significant effect on species association. Firstly, for those species that showed significant associations with seamounts I have estimated its abundance in the first 10 km for each seamount and compared these values with the overall mean for the 10 km bin. These analyses were performed with a common Z test on log (x+1) transformed data. Finally, I have estimated species abundance in relation to seamount summits depth. Mean values of abundance for each seamount depth interval were then compared with the overall mean abundance to test if seamounts depth could be an important factor on explaining species abundances. These analyses were also performed with a common Z test (Zar, 1999).

## **4.3 RESULTS**

### **4.3.1 Tuna**

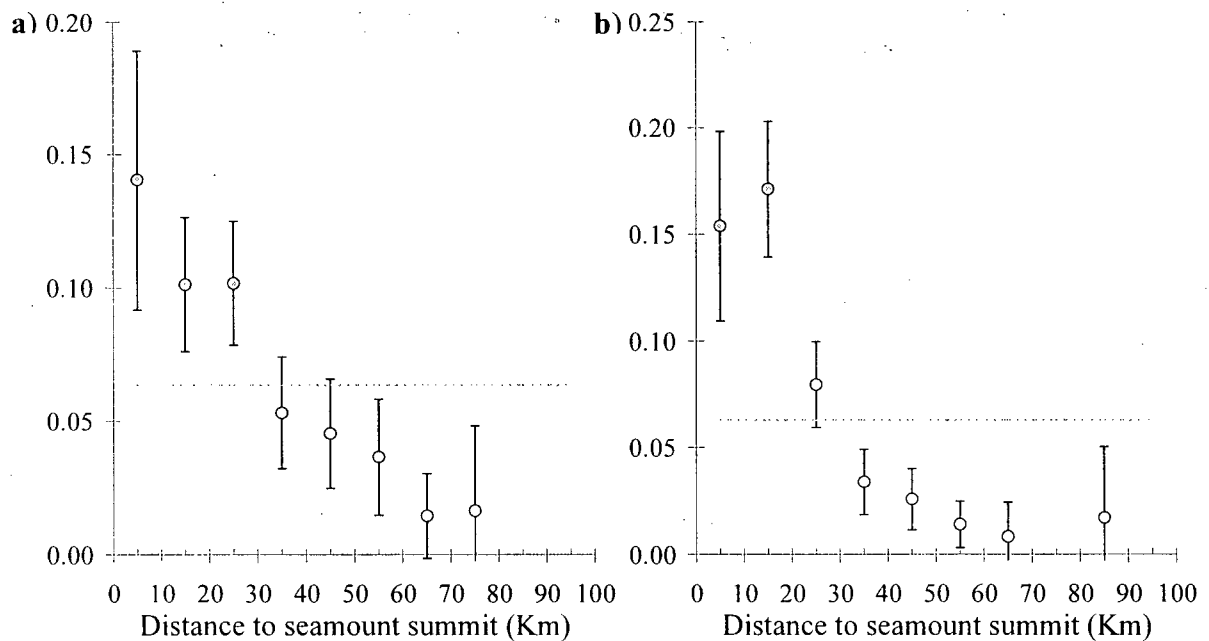
Observers recorded over four thousand tuna fishing events during the period from 1998 to 2004. The most common species caught with observers onboard during this period were skipjack and bigeye tuna with about 1500 and 962 tons, respectively. The frequency distribution of the distances to seamount summit of the dataset of tuna fishing events and of a

set of an equal number of randomly selected locations is shown in Figure 4.2. Calculation of the G statistic for the log-likelihood ratio goodness of fit test show significant differences ( $G = 2344$ ,  $df = 25$ ,  $p < 0.001$ ) between both distributions. This test allows us to assume that fishing locations were not randomly selected and thus to explore the influence of seamounts on tuna catches.



**Figure 4.2** - Frequency distribution of the distances to seamount summit of the dataset of tuna fishing events and of a set of an equal number of randomly selected locations. Black bars indicate observed data while light grey bars indicate randomly selected locations.

Tuna catches per square kilometre per year were significantly different (ANOVA  $p < 0.001$  for skipjack and bigeye tuna) at different distances from seamount summits (Figure 4.3). For skipjack (Figure 4.3a), catches occurring within 30 km from seamount summits were significant higher than the overall mean (Dunnett tests for 10km, 20km and 30km  $p < 0.01$ ) with all other catches being smaller. Bigeye tuna catches per square kilometre per year (Figure 4.3b) were significant higher within 20 km from the summits (Dunnett tests for 10km and 20km  $p < 0.01$ ; Dunnett tests for 30km  $p > 0.05$ ).

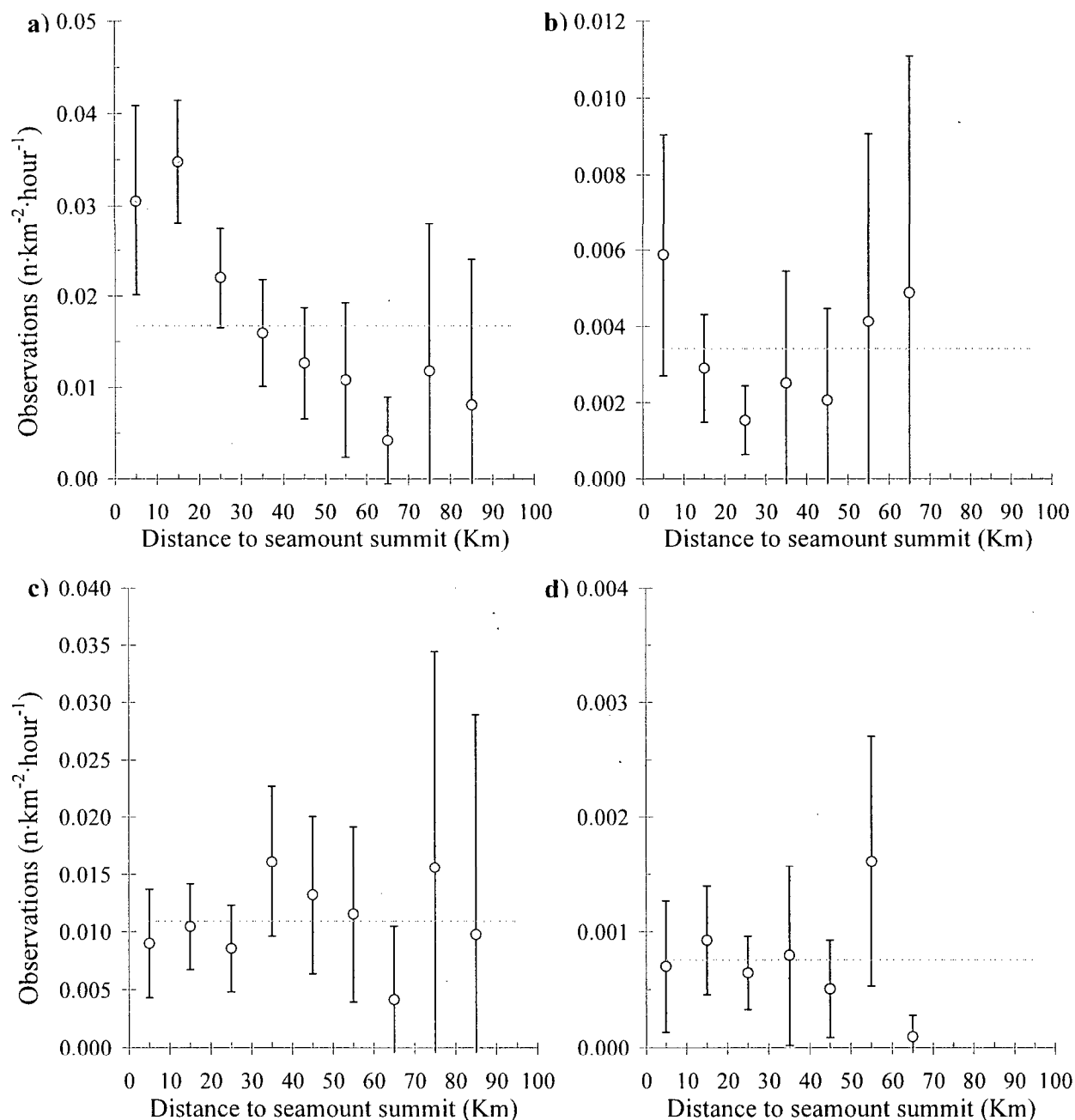


**Figure 4.3** – Tuna catch per square kilometre per year ( $\pm 95\%CL$ ) in relation to the distance to the nearest seamount summit in the Azores. a) skipjack, b) bigeye tuna. Bin size is 10 km. Light grey circles are those significantly higher (Dunnett test) than the overall mean (light grey line).

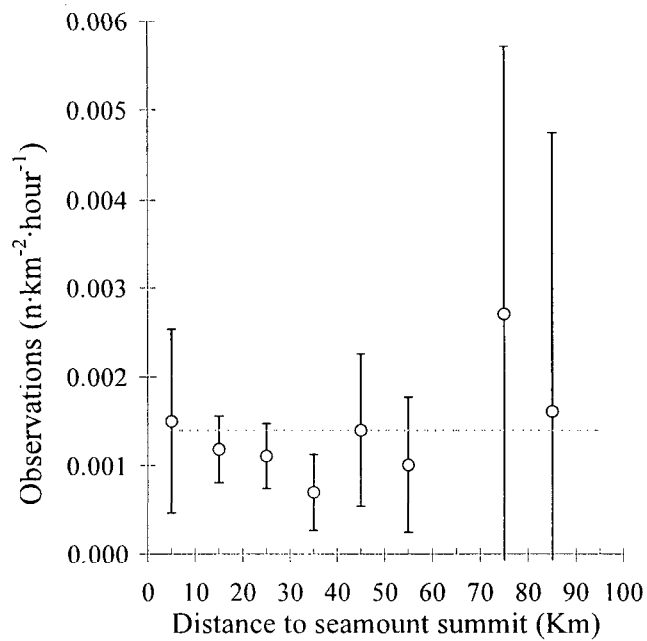
#### 4.3.2 Other visitors

A total of 3910 sightings of marine mammals were recorded from 1998 to 2004. The most commonly sighted species were common dolphin, spotted dolphin, bottlenose dolphin and sperm whale. Common dolphins showed significant different sightings at different distances from seamounts (ANOVA  $p < 0.001$ ) whereas all other species showed no significant differences (ANOVAs bottlenose dolphin,  $p = 0.278$ ; spotted dolphin,  $p = 0.392$ ; sperm whale,  $p = 0.233$ ). The common dolphin (Figure 4.4a) showed some association with seamounts where the highest observations per square kilometre per hour being recorded close to their summits (Dunnett (10km)  $p < 0.02$ ; Dunnett (20km)  $p < 0.01$ ; Dunnett (30km)  $p > 0.05$ ). On the other hand, bottlenose dolphins (Figure 4.4b), spotted dolphins (Figure 4.4c), and sperm whales (Figure 4.4d) showed no association with seamount and were not more abundant in the vicinity of the features.

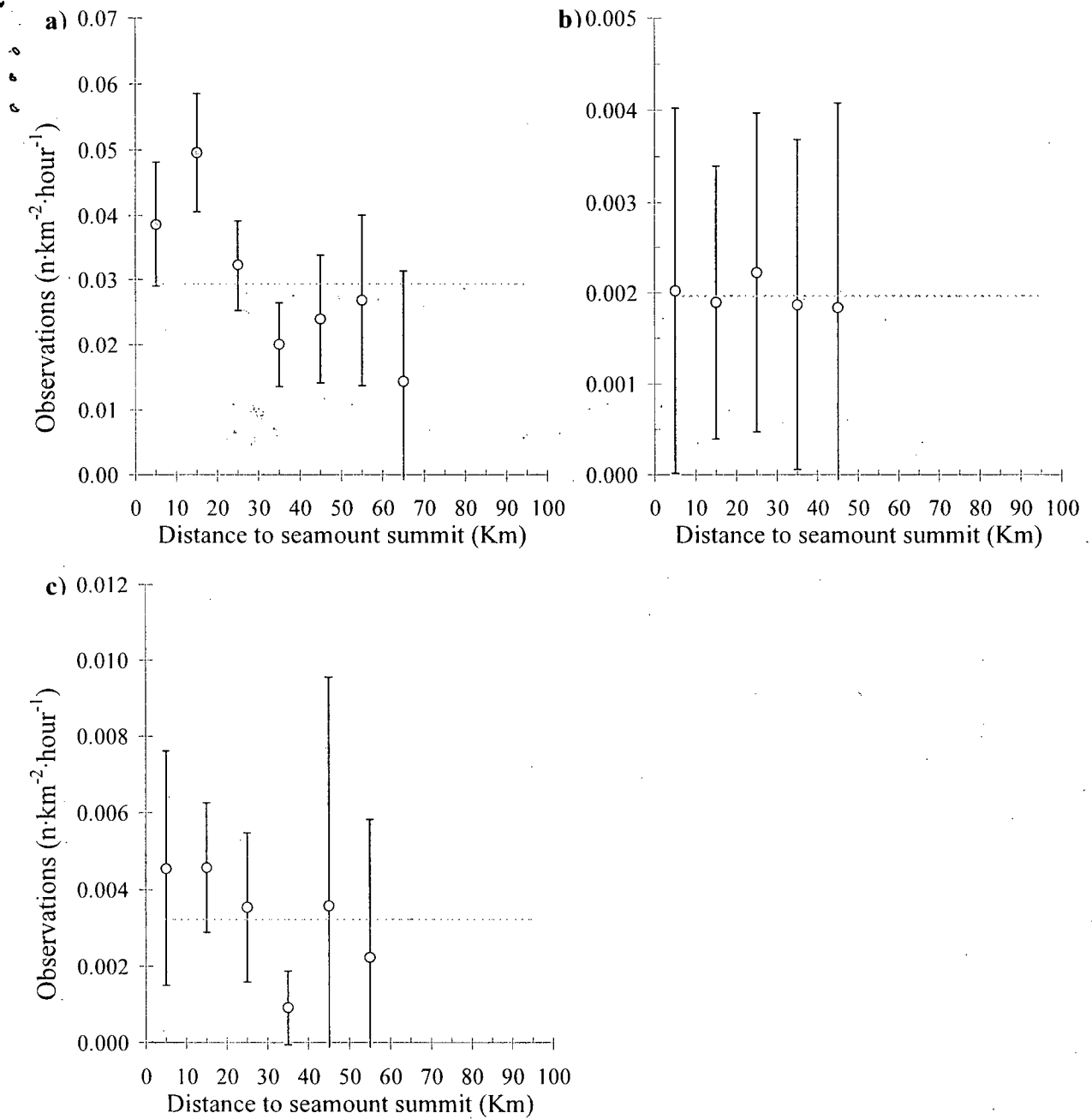
From 2000 to 2004 there were 566 valid observer sighting records of loggerhead turtle. The analyses of the number of loggerheads per square kilometre per hour (Figure 4.5) show no differences with distance to seamount summits (ANOVA sea turtles,  $p = 0.403$ ). On the other hand, the distance to seamount summit influenced the abundance of Cory's shearwater (ANOVA  $p < 0.001$ ). The abundance of Cory's shearwater (Figure 4.6a) was higher in the first 20 km from the seamount summit. However, only the second distance bin (10-20km) was significant higher than the overall mean (Dunnett 10km  $p > 0.05$ ; Dunnett (20km)  $p < 0.01$ ; Dunnett (30km)  $p > 0.05$ ). Terns (Figure 4.6b) and yellow-legged gull (Figure 4.6c) abundances were not different at different distances from seamounts (ANOVA yellow-legged gull,  $p = 0.364$ ; terns,  $p = 0.998$ ).



**Figure 4.4** – Marine mammals sightings per square kilometre per hour ( $\pm 95\%CL$ ) in relation to the distance to the nearest seamount summit in the Azores. a) common dolphin, b) bottlenose dolphins, c) spotted dolphin and d) sperm whale. Bin size is 10 km. Light grey circles are those significantly higher (Dunnnett test) than the overall mean (light grey line).



**Figure 4.5** – Loggerhead turtles sightings per square kilometre per hour ( $\pm 95\%CL$ ) in relation to the distance to the nearest seamount summit in the Azores. Bin size is 10 km.



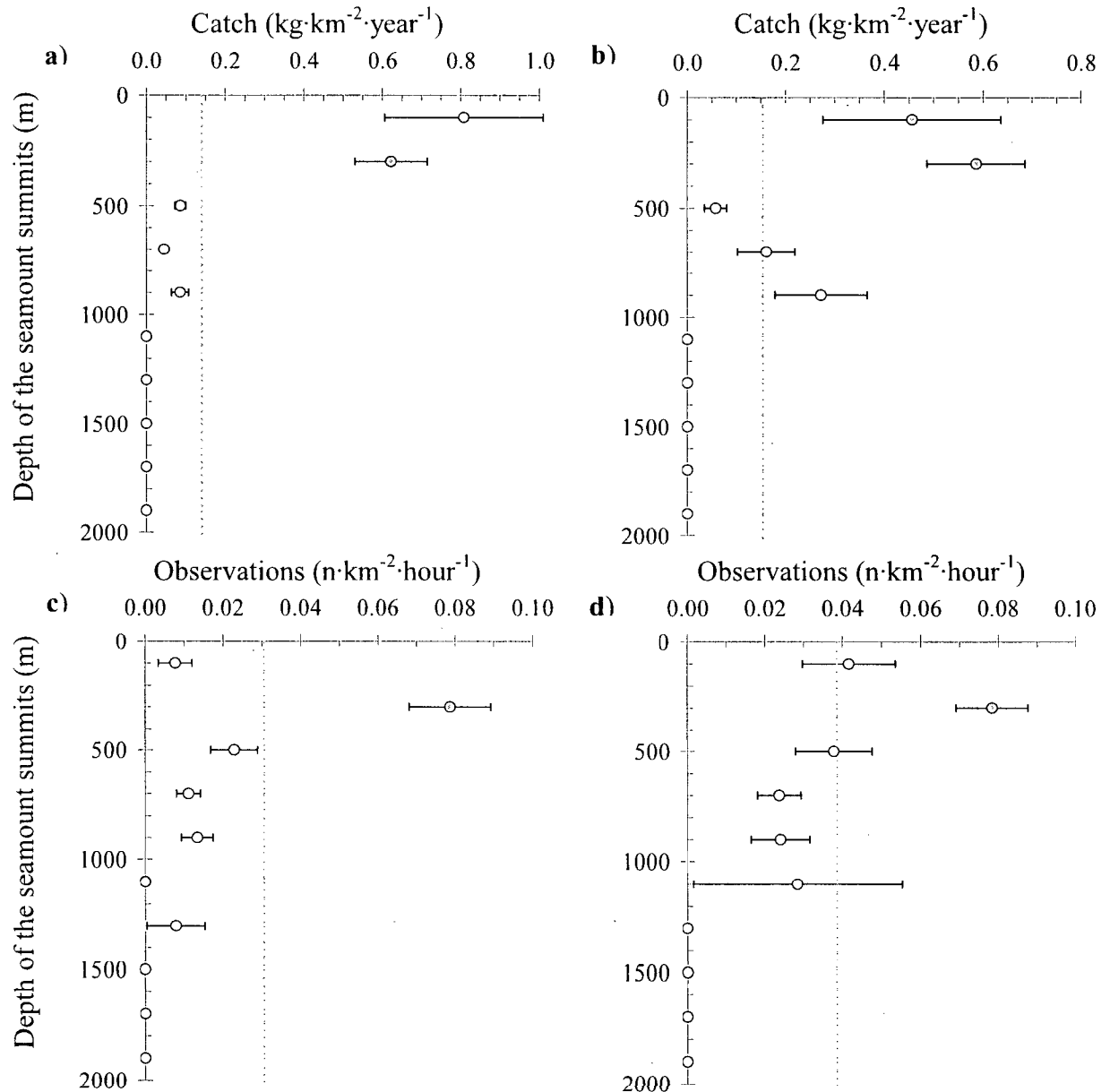
**Figure 4.6** – Seabirds sightings per square kilometre per hour ( $\pm 95\%CL$ ) in relation to the distance to the nearest seamount summit in the Azores. a) Cory's shearwater, b) terns, c) yellow-legged gull. Bin size is 10 km. Light grey circles are those significantly higher (Dunnett test) than the overall mean (light grey line).

#### 4.3.3 Seamounts

Catches and sightings above seamounts of various depths are showed in Figure 4.7, for those species with a significant association with seamounts. Skipjack and bigeye tuna showed significantly higher catches on seamounts shallower than 400 m depth (Figure 4.7a,b), whereas common dolphin (Figure 4.7c) and Cory's shearwater (Figure 4.7d) showed significantly higher sightings on seamounts with depths between 200 and 400 meters. In all cases, seamounts with deep summits had relatively low catches and sightings.

I have also tested which seamounts produced a significant effect on species association. For skipjack, "*Formigas and Dollabarã*" (seamount # 13;  $P=0.012$ ), "*Princesa Alice*" (# 50,  $P=0.014$ ), "*D. João de Castro*" (# 25,  $P=0.026$ ), "*Açores*" (# 51;  $P=0.030$ ) and "*Pico Leste*" of the Princesa Alice (# 23,  $P=0.031$ ), all showed significant higher catches than the overall mean. For bigeye, only "*Açores*" (# 51,  $P=0.004$ ), "*Princesa Alice*" (# 50,  $P=0.009$ ), and "*D. João de Castro*" (# 25,  $P=0.044$ ), showed significant higher catches than the overall mean. Common dolphin showed higher abundances on top of "*Açores*" (# 51,  $P=0.002$ ), "*Princesa Alice*" (# 50,  $P=0.014$ ), "*Agulhas do Sul do Gigante*" (# 36,  $P=0.044$ ), whereas Cory's shearwater showed higher sightings on top of "*Princesa Alice*" (# 50,  $P=0.003$ ) and "*Açores*" (# 51,  $P=0.006$ ).





**Figure 4.7** – Catches and sightings ( $\pm 95\% \text{CL}$ ) above seamounts of various depths for those species with a significant association with seamounts. a) skipjack, b) bigeye tuna, c) common dolphin, d) Cory's shearwater. Bin size is 10 km. Light grey circles are those significantly higher (Z test) than the overall mean (light grey line).

#### 4.4 DISCUSSION

This study has demonstrated that some marine predators are associated with seamounts with shallow summits. This was the case of tuna species skipjack and bigeye, common dolphin and Cory's shearwater. These species were significantly more abundant in the vicinity of some seamount summits than far from these features. Our methodology, however, failed to demonstrate seamounts' association for bottlenose dolphins, spotted dolphin, sperm whale, terns, yellow-legged gull, and loggerhead sea turtles.

Seamounts play a major role in localizing pelagic prey and thus attracting some pelagic fish, seabirds and marine mammals. Therefore, some seamounts in the Azores may act as feeding stations for some of these visitors. Tuna species such as skipjack and bigeye have previously been acknowledged to occur on seamounts. However, this study was the first to quantitatively demonstrate these associations. Common dolphins are known to feed mostly on small pelagic fish and squids (Silva, 1999) and may, therefore, take advantage of the localized abundance of prey on seamounts. These species are also known to be comparatively more characteristic of offshore habitats than the bottlenose or spotted dolphins. Thus, the common dolphins may use seamounts as important feeding areas (Lopez *et al.*, 2004). Similarly, Monteiro *et al.* (1996) inferred from stomach contents data that Cory's shearwaters feed often in association with seamounts, therefore, supporting our results.

Not all seamounts, however, seemed to be equally important for these associations. For all species only seamounts shallower than 400m depth showed significant aggregation effects. The important seamounts in the Azores for these visitors are "Princesa Alice" and "Açores" for all four species, also "D. João de Castro" for both tuna species, "Formigas and Dollabarat" and "Pico Leste" of the Princesa Alice for skipjack, and "Agulhas do Sul do Gigante" for common dolphin. These seamounts should be considered hotspots of marine life in the Azores and a special effort should be made in order to ensure a sustainable management of these habitats. These seamounts are also known to be heavily exploited by local fishermen, with the exception of "Formigas and Dollabarat" which are a marine reserve. Reconciling fisheries with conservation on these seamounts should be a priority for the local

management authorities. On the other hand, the area of influence of the seamounts seemed to be about 20 to 30 km, since only the observations at these distances were significant higher than the average.

The lack of association of sperm whales with seamounts summit is not surprisingly since these animals prey mostly in deep waters on large squid (Clarke *et al.*, 1993) by echolocating deep prey patches in the mesopelagic environment (Watwood *et al.*, 2006). However, the lack of association with seamounts for bottlenose and spotted dolphins is more difficult to explain. Stomach contents data for these two species in the Azores are not available. Bottlenose dolphins have a high degree of foraging plasticity (Spitz *et al.*, 2006) but in coastal waters seem to prefer benthic species. For instance, around Scotland (UK) this species feeds mostly on benthic fish such as cod (*Gadus morhua*), saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*), and also cephalopods (Santos *et al.*, 2001). Similar patterns were observed for bottlenose dolphins from the U.S. mid-Atlantic coast (Gannon and Waples, 2004). On the other hand, bottlenose dolphins off Galicia (Lopez *et al.*, 2004) and off Gulf of Mexico (Jefferson and Schiro, 1997) have been considered to be more common in coastal areas when compared to common dolphin. This pattern may also be true in the Azores since depth was found to be a significant but negative factor explaining bottlenose dolphins' distribution (Seabra *et al.*, 2005), and therefore this species has been considered to be more associated with coastal habitats than common dolphin. Pelagic and mesopelagic prey may thus have less importance in bottlenose dolphins' diet as compared to common dolphin, meaning that the seamount effect on enhancing secondary and tertiary production may not be important for bottlenose dolphins. Spotted dolphins are known to associate with relatively low seafloor relief gradients (Davis *et al.*, 1998; Mignucci-Giannoni, 1998; Perrin, 2002) and thus may display a stronger association with coastal habitats than with seamounts.

Yellow-legged gulls feed opportunistically on several prey such as fish, barnacles and rats (Monteiro *et al.*, 1996), therefore there is no reason to expect an association of this species with seamounts. However, the lack of association with seamounts of terns was somehow unexpected because in the Azores these species feed mainly on small pelagic and

mesopelagic fish (Monteiro *et al.*, 1996), which are expected to have higher abundances close to seamounts. Probably, the number of observation available for these species was not sufficient to detect such associations.

The presence of large concentrations of forage fish during the summer in the Azores originates mixed-species feeding aggregations (Clua and Grosvalet, 2001). Tuna fish may help prey rising to the surface before being concentrated by common dolphins, resulting in the formation of a compact 'ball' of forage fish close to the surface. Tuna, common dolphins and Cory's shearwater collectively feed on this concentration of prey. Therefore, an alternative explanation for the association with seamounts of common dolphins and Cory's shearwater and the lack of association for bottlenose and spotted dolphin is the interaction with tuna: I cannot exclude the hypothesis that the seamount association of these species is an indirect effect of the seamount. The rationale for this would be seamounts attracting tuna species and, in turn, tuna species attracting common dolphins and Cory's shearwater but not bottlenose and spotted dolphins. Silva *et al.* (2002) have demonstrated that common dolphin is significantly associated with tuna in the Azores and that bottlenose and spotted dolphins show lower degree of interaction.

Loggerhead sea turtle is widely distributed in the North Atlantic where it feeds mainly on jellyfish. The lack of association of loggerhead with seamounts may be simply explained by the lack of reasons to believe that jellyfish abundance should be higher on top of seamounts than elsewhere. This species may be significantly associated with large oceanographic anomalies, such as fronts and currents (Polovina *et al.*, 2004, 2006), where food for loggerheads may be more abundant. Etnoyer *et al.* (2006) also found topographic features like the shelf break and seamounts not important factors in explaining the distribution of these turtles. Loggerheads, however, may use seamounts for large-scale navigation proposes (Lohmann and Lohmann, 2003).

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## CHAPTER 5

### FISHING DOWN THE DEEP<sup>1</sup>

#### 5.1 INTRODUCTION

A global crisis in marine fisheries was regarded with scepticism by many fisheries scientists as recently as ten years ago. Today, however, few dispute worrying trends (Pitcher and Pauly, 1998; Pitcher, 2001; Pauly *et al.*, 2002; Christensen *et al.*, 2003; Hilborn *et al.*, 2003; Pauly and Maclean, 2003; FAO, 2004). Historical data from marine ecosystems clearly suggest that overfishing has had, for thousands of years, a major impact on target species and have fundamentally altered marine ecosystems (Jackson *et al.*, 2001; Pitcher, 2001), including coral reefs (Pandolfi *et al.*, 2003). A dramatic depletion of large predators (Baum *et al.*, 2003; Christensen *et al.*, 2003; Myers and Worm, 2003) has triggered fisheries to target species of lower trophic levels in a process called “fishing down marine food webs” (Pauly *et al.*, 1998a). More recently, fisheries exploitation has spread from coastal areas to the open ocean and a general decline in fish biomass has been reported (Baum *et al.*, 2003; Christensen *et al.*, 2003; Myers and Worm, 2003): as a consequence, many marine species are of serious conservation concern (Casey and Myers, 1998; Spotila *et al.*, 2000; Baum *et al.*, 2003; Sadovy and Cheung, 2003). Not surprisingly, there has been a decline in global fisheries catches since the late 1980s (Watson and Pauly, 2001; Zeller and Pauly, 2005) at an approximate rate of 0.36 million tonnes per year. Nevertheless, a global increase of fishing effort and catching power has continued (Gréboval, 2003).

With the decline of shallow coastal waters resources, increasing demand, and new technology, fisheries are evidently expanding offshore (e.g., Christensen *et al.*, 2003; Myers and Worm, 2003; Pauly *et al.*, 2003) and into deeper waters (Koslow *et al.*, 2000; Garibaldi and Limongelli, 2003; FAO, 2004; Gianni, 2004). The expansion into offshore areas has been well documented (for example, fisheries targeting oceanic tuna, billfishes and their relatives covered the world ocean by the early 1980s; Myers and Worm, 2003), but the extension into

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<sup>1</sup> A version of this chapter has been published. Morato, T., R. Watson, T.J. Pitcher and D. Pauly. 2006. Fishing down the deep. *Fish and Fisheries* 7:24-34.

deeper waters is less well analysed. While many local examples of fisheries expansion into deeper waters have been reported (e.g., some European, Soviet, U.S.A., Canada, New Zealand and Australian fishing fleets: see references in Hopper, 1995; Moore, 1999; Koslow *et al.*, 2000; Roberts, 2002), we lack a global quantitative analysis.

Deep-water fish resources are generally considered to have high longevity, slow growth, late maturity, and low fecundity. Thus, they have been considered more vulnerable to fishing than most species exploited on the continental shelf, upper continental slope or in open ocean pelagic ecosystems (Merrett and Haedrich, 1997; Koslow *et al.*, 2000). Deep-water stocks can be rapidly depleted and recovery can be very slow, although this will not apply to a few deep-water species with life history traits comparable to shallow water species (Large *et al.*, 2003).

Whereas previous studies on global trends of fisheries have focused on catch or biomass changes over time (e.g., Christensen *et al.*, 2003; Myers and Worm, 2003), in this paper I have analysed changes in the mean depth of fishing to test if the predicted expansion into deeper-waters can be detected in global landings datasets. I also tested for the predicted higher vulnerability of deep-water fisheries resources, using longevity as the main proxy for vulnerability.

## 5.2 METHODS

I used three publicly-available databases; official landings statistics from the Food and Agriculture Organization (FAO) from 1950 to 2001, which are based on reports submitted annually by FAO member states; FishBase (<http://www.fishbase.org>), an information system with key data on the biology of fishes (Froese and Pauly, 2003); and the Sea Around Us Project database (SAUP: <http://www.seaaroundus.org>), which contains estimated maps of global fisheries catches from 1950 to the present. The SAUP database includes data from the Food and Agriculture Organization (FAO), International Council for the Exploration of the Seas (ICES), Northwest Atlantic Fisheries Organization (NAFO), and other sources (Watson *et al.*, 2004) and was used to compile catch data for high seas areas.

In this study, depth range is defined as the extremes of the depths reported for juveniles and adults (but not larvae), while common depth is the range where adults are most often found, and is more precisely defined as the range within which approximately 95% of the biomass of a species occurs (Froese and Pauly, 2003). For those taxa not reported to species level, the average for the genus or family was calculated using the species most likely to be present at that locality.

FishBase was used to estimate the average depth of occurrence for most of the 775 different species or groups of marine fishes included in the FAO landings statistics, and to gather data on their longevity. Average depth of occurrence for taxa identified at species level in the landings statistics was estimated as the mean of the common depth range or as 1/3 of the total depth range. In the latter case, I assume fish to have a lognormal distribution with depth, whose peak in abundance is at 1/3 of their range (Alverson *et al.*, 1964; Pauly and Chua, 1988). I have tested this assumption using FishBase data on full depth ranges and common depth ranges for 136 fish species; the only species with both ranges in the database. The average peak abundance was 0.302 of the full depth range (95% confidence interval; 0.28-0.33): this value is not significantly different from a 1/3 assumption (t-test:  $P > 0.01$ ).

By combining mean depths and catch series, time series of the mean depth of the catch of marine bottom fishes (excluding pelagic) and for all marine fishes were estimated for the world and for different groupings of FAO statistical areas (ocean basis). The mean depth of the fisheries catch by year and ocean basis was estimated as the average depth of occurrence of the species (or group caught) weighted by the logarithm of their catch.

Visual inspection of different datasets suggested an inflection point such that a single regression line would not suffice. I therefore fitted simple linear biphasic regression models, using the algorithm described in Hintze (1998). I then compared biphasic regression models to other simpler and more complex models. For this, I have fitted simple linear regression models as well as quadratic, cubic and fourth order models to the data. If the simpler model fits better (has a smaller sum-of-squares) than the more complex model (more parameters),

then no statistical analysis was performed and the simpler model was accepted. Since this rarely occurred, I used the likelihood ratio test (Hilborn and Mangel, 1997) to compare the goodness-of-fit of two models, where the more complex equation fits better than the simple equation. For most of the cases (8 out of 10) biphasic regression models fitted the data significantly better than any other tested model (Table 5.1). Thus, biphasic regression models were preferred. The only cases where biphasic regression models were not preferred were for the time series data of mean depth of the fisheries catch for the whole world, where quadratic models fitted the data significantly better.

Additionally, I estimated a time series of the mean longevity of fish in the world catch by combining data on fish longevity from FishBase with fish landings from FAO. The mean longevity of landings for each year and FAO area were estimated as the mean of the longevity of each species or group, weighted by the logarithm of their catch. The mean fish longevity of the catch was also estimated as a function of depth of fish occurrence. Since this has to be done in a yearly basis, I used year 2001 in FAO dataset.

**Table 5.1** - Summary of the likelihood ratio test (Hilborn and Mangel, 1997) used to compare the goodness-of-fit of different models where the more complex equation fits better than the simple equation. Where  $n$  is the number of parameters estimated in each model; d.f. the degrees of freedom; SS the sum-of-squares. L stands for Linear models, Q for quadratic, LL for the biphasic linear-linear models, C for cubic models and F for fourth order models.

Ocean basis	Model	$n$	d.f.	SS	Comparisons	Ratio (F)	P	Best Fit
N. Atlantic	Linear	2	50	2378.2				
	Quadratic	3	49	777.6	L/Q	100.86	>0.001	Quadratic
	Linear-Linear	4	48	351.7	Q/LL	58.12	>0.001	Linear-Linear
	Cubic	4	48	429.5	LL/C			
	Fourth	5	47	334.1	LL/F	2.48	0.122	Linear-Linear
C. Atlantic	Linear	2	50	184.5				
	Quadratic	3	49	148.8	L/Q	11.76	0.001	Quadratic
	Linear-Linear	4	48	129.0	Q/LL	7.35	0.009	Linear-Linear
	Cubic	4	48	130.1	LL/C			
	Fourth	5	47	126.1	LL/F	1.10	0.300	Linear-Linear
S. Atlantic	Linear	2	50	2928.9				
	Quadratic	3	49	2002.3	L/Q	22.67	>0.001	Quadratic
	Linear-Linear	4	48	1270.6	Q/LL	27.64	>0.001	Linear-Linear
	Cubic	4	48	1125.9	LL/C			
	Fourth	5	47	1105.1	LL/F	7.04	0.011	Linear-Linear
N. Pacific	Linear	2	50	1501.5				
	Quadratic	3	49	1258.0	L/Q	9.48	0.003	Quadratic
	Linear-Linear	4	48	876.9	Q/LL	20.86	>0.001	Linear-Linear
	Cubic	4	48	800.1	LL/C			Cubic
	Fourth	5	47	791.6	LL/F	5.07	0.029	Linear-Linear
C. Pacific	Linear	2	50	1287.7				
	Quadratic	3	49	672.6	L/Q	44.81	>0.001	Quadratic
	Linear-Linear	4	48	426.7	Q/LL	27.67	>0.001	Linear-Linear
	Cubic	4	48	476.7	LL/C			
	Fourth	5	47	381.3	LL/F	5.59	0.022	Linear-Linear
S. Pacific	Linear	2	50	13764.4				
	Quadratic	3	49	6441.9	L/Q	37.51	>0.001	Quadratic
	Linear-Linear	4	48	3645.6	Q/LL	24.54	>0.001	Linear-Linear
	Cubic	4	48	4576.5	LL/C			
	Fourth	5	47	4568.7	LL/F			
Indian Ocean	Linear	2	50	3135.4				
	Quadratic	3	49	1124.9	L/Q	87.57	>0.001	Quadratic
	Linear-Linear	4	48	946.8	Q/LL	9.03	0.006	Linear-Linear
	Cubic	4	48	921.2	LL/C			
	Fourth	5	47	823.0	C/F	7.07	0.011	Linear-Linear
Antarctic	Linear	2	50	48560.6				
	Quadratic	3	49	37051.8	L/Q	15.22	>0.001	Quadratic
	Linear-Linear	4	48	32769.0	Q/LL	6.27	0.016	Linear-Linear
	Cubic	4	48	36762.0	LL/C			
	Fourth	5	47	36415.9	LL/F			

## 5.3 RESULTS

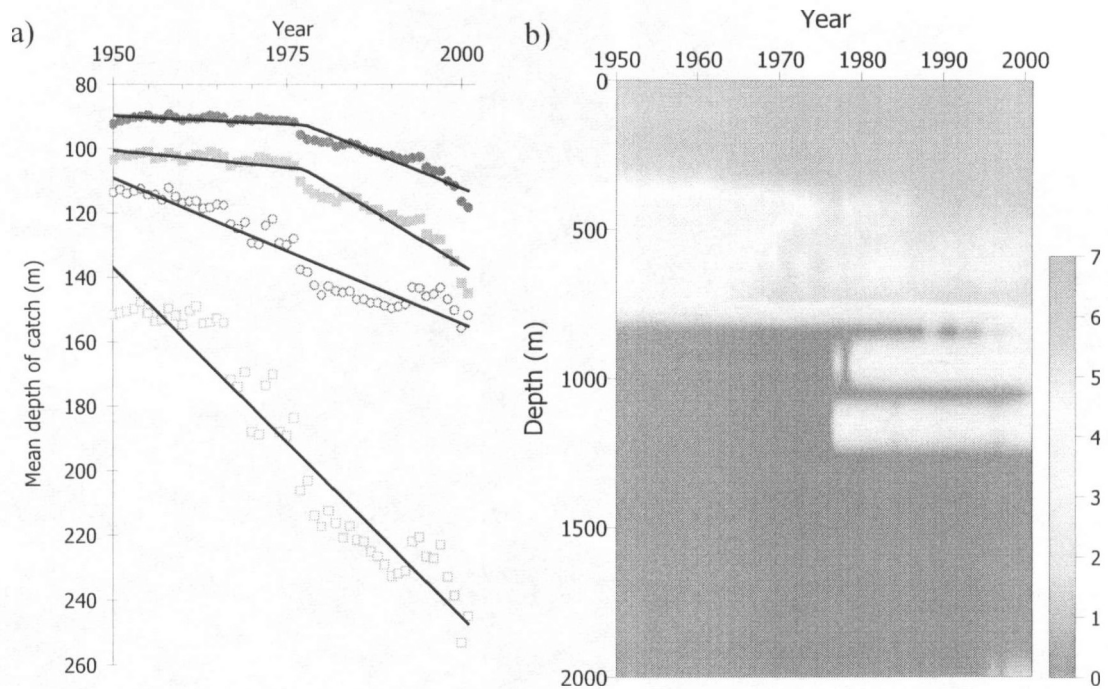
### 5.3.1 Global trends

Our results (Figure 5.1a) show that, for bottom marine fishes, the overall trend over the past 50 years has been a 42 m increase in the mean depth of the catch, from around 103 m in the early 1950's to 145 m in 2001. The biphasic linear regression fitting the data (overall  $r^2 = 0.94$ ) suggests two periods with different trends: a period of slow increase in the mean depth of fishing from 1950 to 1978 with a slope of about 2 m·decade<sup>-1</sup>, followed by a period of marked increase in the mean depth of fishing at a rate of about 13 m·decade<sup>-1</sup> (Table 5.2). If I include pelagic fishes in the analysis (Figure 5.1a), the increase in mean depth of the catch is lower but still considerable, with two distinguishable periods (overall  $r^2 = 0.93$ ). In both cases, the early plateau and the estimated break point can be attributed to either a real increase in the fishing deeper trend, or to a lack of taxonomic resolution in the FAO landing statistics before the 1970's. Application of our method to catches from high seas areas only (i.e., beyond countries' EEZ) showed a more dramatic decline in the mean depth of fishing, at a rate of 22 m·decade<sup>-1</sup> for bottom fishes only and 9.0 m·decade<sup>-1</sup> when considering pelagic fishes.

In general, fishing began to operate deeper from the late 1960's. Since the taxonomic resolution in the FAO landing statistics improved after the 1970's, this increase in depth could be caused by, 1) a proportional decrease in the catches of shallow water species (resulting from collapse of coastal resources); 2) a proportional increase in the landings of deep-water species (from the expansion of fisheries into deep water); or 3) both. Figure 5.1b helps elucidate this by showing that, at a global level, the increase in the mean depth of fishing has been caused by an increase in landings of deep-water species such as the orange roughy (*Hoplostethus atlanticus*, Trachichthyidae), grenadiers (Macrouridae), alfonsoinos (*Beryx* spp., Berycidae) and several deepwater sharks. The steepest rates of depth increase match the development of most of the deepwater fisheries around the world (Hopper, 1995; Merrett and Haedrich, 1997; Moore, 1999; Koslow *et al.*, 2000; Roberts, 2002; Garibaldi and Limongelli, 2003).



Similar trends of increased mean depth of fishing were observed for all oceans, with rates ranging from 1 m·decade<sup>-1</sup> deeper for the North Pacific to 180 m·decade<sup>-1</sup> for Antarctic fisheries (Table 5.1).



**Figure 5.1 - (a)** Global trend of mean depth of world marine fisheries catches from 1950 to 2001 for all marine fishes including pelagics (dark grey dots) and for bottom marine fishes only (light grey squares). Open symbols are estimates for high seas areas only (beyond countries EEZs). Trend lines are fitted using the piecewise-polynomial model linear-linear (Hintze, 1998) or simple linear regression. **(b)** Time series of world marine bottom fisheries catches by depth strata. Catch in tonnes are log<sub>10</sub> transformed.

**Table 5.2** - Rate of increasing depth of fishing per decade before and after the breaking point (BP) estimated using a two phase model (linear-linear) as described in Hintze (1998). Coefficient of determination ( $r^2$ ) for regressions also presented.

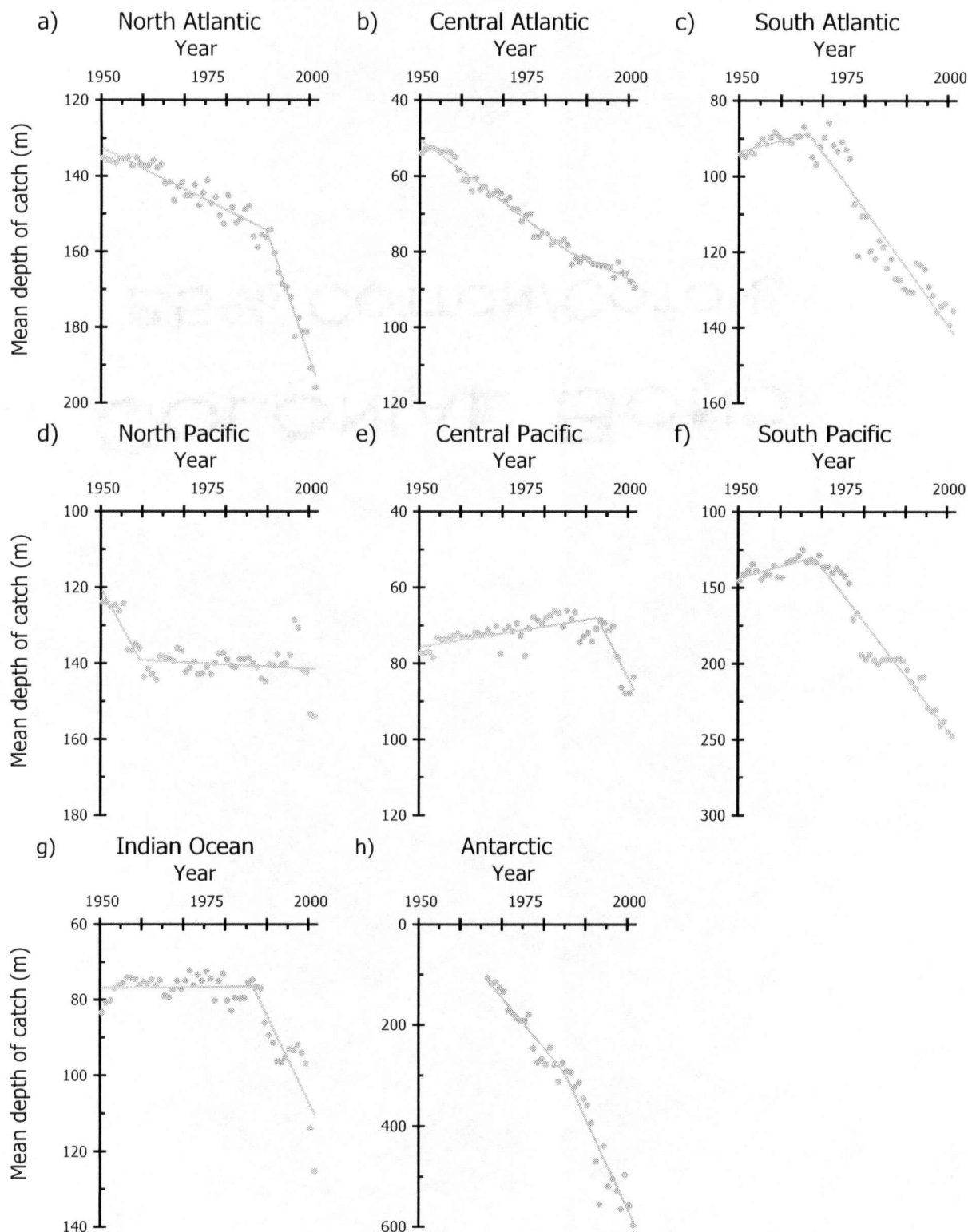
	Linear-linear two model				
	Slope (m·decade <sup>-1</sup> )	BP		Slope (m·decade <sup>-1</sup> )	$r^2$
	1950 - B.P	Year	SE	B.P.-2001	
All fish	1.06	1978	2.0	8.80	0.93
Demersal fish	2.13	1978	2.0	13.17	0.94
Atlantic, North	5.49	1989	1.8	32.05	0.97
Central	8.36	1985	5.6	5.05	0.98
South	-3.05	1966	1.9	15.17	0.92
Pacific, North	20.03	1959	1.4	0.58	0.59
Central	-1.80	1992	6.0	21.76	0.67
South	-7.64	1968	1.3	35.55	0.95
Indian Ocean	-0.09	1986	2.4	22.54	0.83
Antarctica	99.84	1985	4.6	180.13	0.96

### 5.3.2 Atlantic Ocean

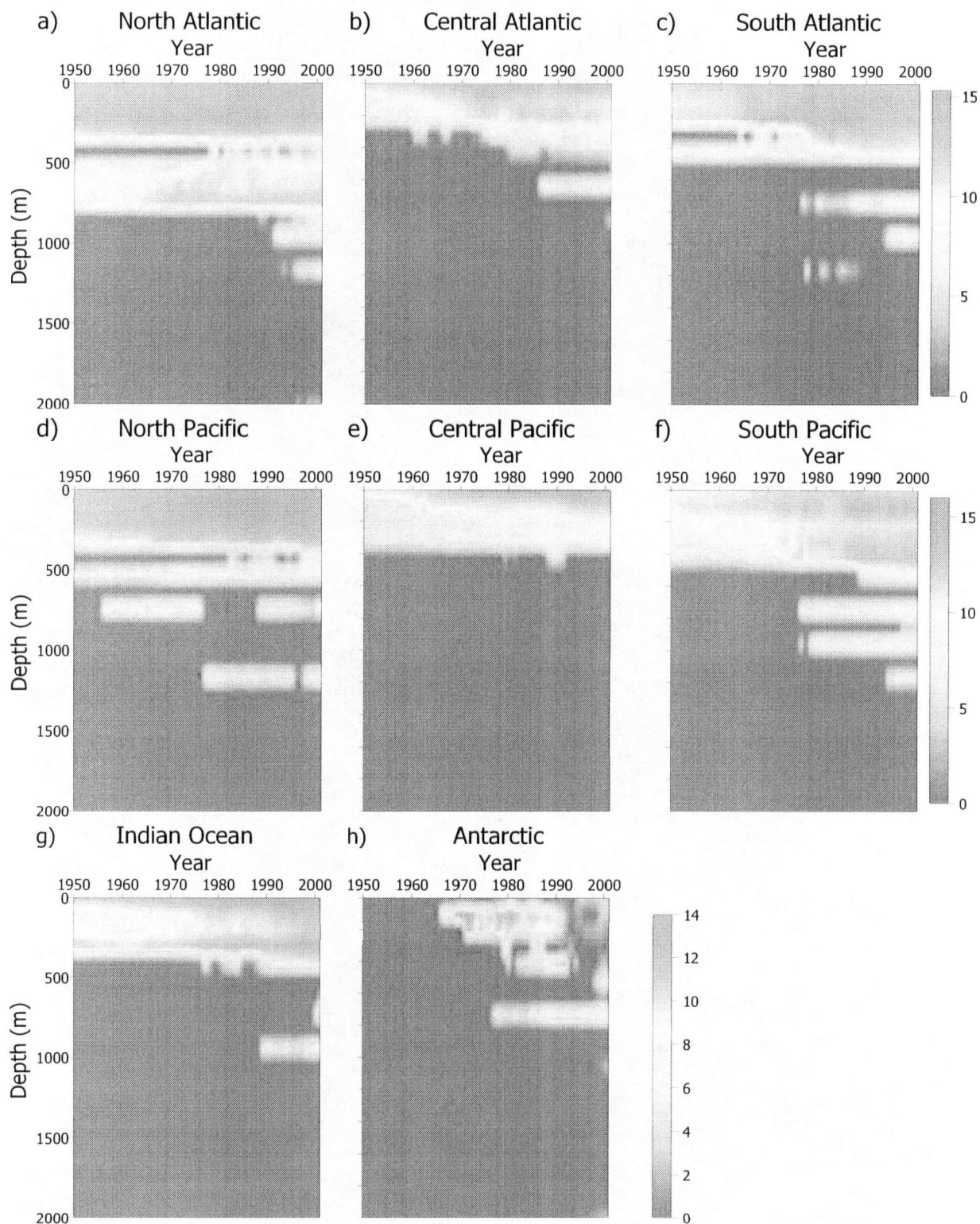
In the Atlantic Ocean, the mean depth of the catch has increased steadily over the last decades at a rate of 32, 5 and 15 metres per decade for the North, Central and South Atlantic, respectively. In the North Atlantic (Figure 5.2a), the simplest biphasic linear regression that fit the data suggests two periods with different trends: a period with a small rate of fishing deeper from 1950 to 1989 ( $\pm 1.8$  S.E.), with a slope of 5.5 m·decade<sup>-1</sup>, followed by a period of marked increase in fishing deeper at a rate of 32.1 m·decade<sup>-1</sup>.

The first period corresponds to the relative increase in the reported landings of some deep-water species (Figure 5.3a) such as the roundnose grenadier (*Coryphaenoides rupestris*, Macrouridae), alfonsinos, ling (*Molva molva*, Lotidae), blue ling (*M. dypterygia*, Lotidae), and tusk (*Brosme brosme*, Lotidae). The steepest increase observed for the second period, after 1989, matches the development of most of the deepwater fisheries in the North Atlantic (Hopper, 1995; Merrett and Haedrich, 1997; Moore, 1999; Koslow *et al.*, 2000; Gianni, 2004). In Figure 5.3a one can clearly see some new deepwater species, with an average depth of about 1000m, being reported for the first time after 1989. These were orange roughy, bulls-eye (*Epigonus telescopus*, Epigonidae), and deepwater sharks (*Centroscymnus coelolepis*, Dalatiidae; *Dalatias licha*, Dalatiidae; *Centrophorus squamosus*, Centrophoridae; *Deania calcea*, Centrophoridae).

Similar trends are apparent throughout the time series for the Central (Figure 5.2b) and South Atlantic (Figure 5.2c), although in the Central Atlantic fishing operates in more shallow waters (Figure 5.3b). In the South Atlantic (Figure 5.2c), the mean depth of fishing time series suggests two periods with different depth of fishing trends: a period of fluctuating mean depth of fishing from 1950 to 1966 ( $\pm 1.9$  S.E), with a slope of  $-3.0 \text{ m-decade}^{-1}$ , followed by a period of marked increase in the mean depth of fishing at a rate of  $15.2 \text{ m-decade}^{-1}$ . In the South Atlantic basin, some deepwater fisheries have developed since the 1970's on the Patagonian shelf, Western South Atlantic (Catarci, 2004), and on the deeper continental shelf and slope of the Eastern South Atlantic (Boyer *et al.*, 2001). The highest rate of fishing deeper corresponds with increased landings of species with average depths at about four, seven and eleven hundred meters (Figure 5.3c).



**Figure 5.2** - Trend of mean depth of marine bottom fisheries catches for: **(a)** North Atlantic; **(b)** Central Atlantic; **(c)** South Atlantic; **(d)** North Pacific; **(e)** Central Pacific; **(f)** South Pacific; **(g)** the Indian Ocean; and **(h)** Antarctic. Trend lines are fitted using the piecewise-polynomial model linear-linear (Hintze, 1998) or simple linear regression.



**Figure 5.3** - Time series of marine bottom fisheries catches by depth strata for: (a) North Atlantic; (b) Central Atlantic; (c) South Atlantic; (d) North Pacific; (e) Central Pacific; (f) South Pacific; (g) the Indian Ocean; and (h) Antarctic. Catch in tonnes are  $\log_e$  transformed.

### 5.3.3 Pacific Ocean

The Pacific Ocean shows somewhat contrasting trends. The North Pacific (Figure 5.2d) has a steep increase in the mean depth of fishing ( $20 \text{ m} \cdot \text{decade}^{-1}$ ) for the period from 1950 to 1959 ( $\pm 1.4 \text{ S.E.}$ ), but no significant change after that. Large-scale deepwater fisheries have a long history in the North Pacific Ocean with some of the targeted species been fished since the early 1900s (Moore, 1999). There are also established deepwater fisheries for dover sole (*Microstomus pacificus*, Pleuronectidae), thornyheads (*Sebastolobus* spp., Sebastidae), other rockfishes (*Sebastes* spp., Sebastidae), pelagic armorhead (*Pseudopentaceros wheeleri*, Pentacerotidae) and alfonsinos. The lack of a clear trend in the mean depth of fishing in the North Pacific may be attributed to the time scale used in the analysis, because most of the deepwater fisheries started before 1950s or early 1960s (Moore, 1999; Koslow *et al.*, 2000). Nevertheless, Figure 5.3d clearly shows the start of fisheries of some deep-water species, observed in the early 1960s and the late 1970s.

The overall trend for Central Pacific Ocean (Figure 5.2e) is not clear. Until early 1990's the mean depth of the catch got shallower. This trend may be explained by three alternative hypotheses: 1) a problem with the official landings statistics mainly by assigning catches to broad categories; 2) a proportional increase in shallow water fish landings greater than for deeper water species; and 3) a real lack of fisheries expansion into deeper waters. The last is not likely to be true, because it is clear from Figure 5.3b that in early 1970's some deeper water fish species like sablefish were being reported in the official landing statistics. After 1992 ( $\pm 6.0 \text{ S.E.}$ ) the mean depth of fishing in the central Pacific increased at a rate of  $21.8 \text{ m} \cdot \text{decade}^{-1}$ , with the increase in importance of some deeper water fish species (Figure 5.3e), such as the dover sole.

In the South Pacific (Figure 5.2f) the mean depth of fishing has increased rapidly since 1968, at a rate of  $36 \text{ m} \cdot \text{decade}^{-1}$ , coinciding with the start of orange roughy and other deepwater fisheries around New Zealand and Australia (Koslow *et al.*, 2000). Figure 5.3f clearly shows that some deepwater species with average depths of fishing at about four, seven and nine hundred meters start being reported during the 1970s.

#### **5.3.4 Indian Ocean**

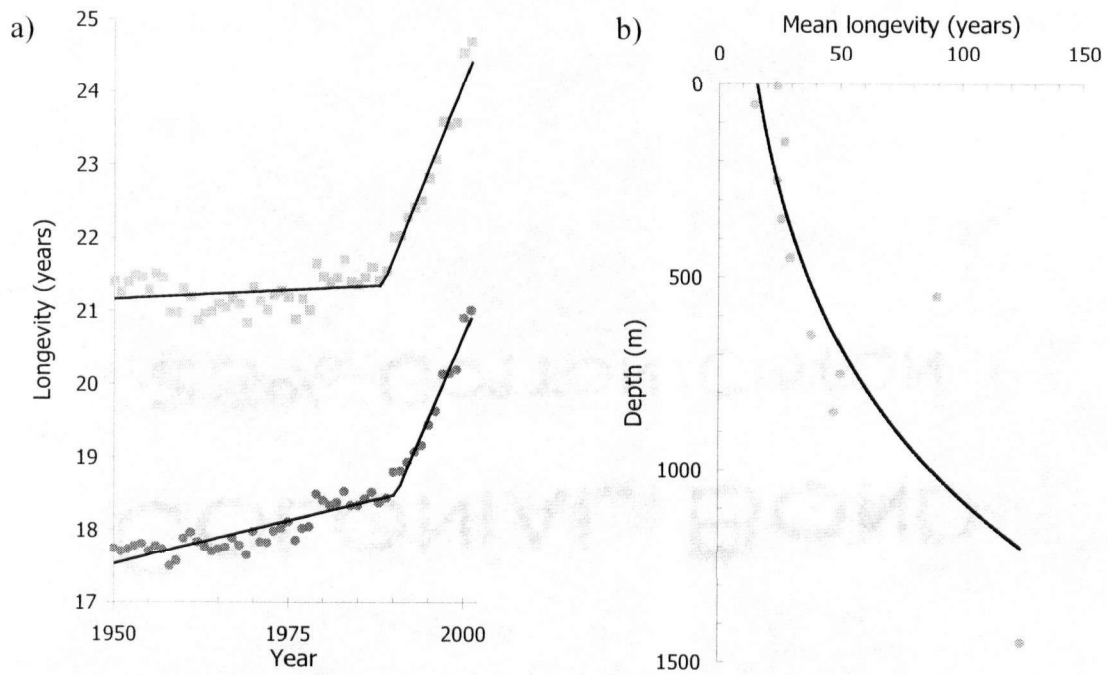
The Indian Ocean (Figure 5.2g) shows no clear trend until 1986, but a steep increase in depth afterwards, at a rate of 22m per decade. The second period matches the appearance of deepwater species, such as the silver gemfish, *Rexea solandri*, orange roughy and Patagonian toothfish in landing statistics (Figure 5.3g).

#### **5.3.5 Antarctic**

Finfish fisheries in Antarctica began only during the mid 1960s (Koch, 1992). This region (Figure 5.2h) exhibits the most dramatic increase in mean depth of the catch, from about 100m in the mid 1960's to 600m in 2001, a rate of more than 100 metres per decade. The observed trend in Antarctica clearly reflects the collapse and the implementation of fisheries restrictions for some shallower water fishes (Figure 5.3h) such as marble rockcod (*Notothenia rossii*, Nototheniidae) and other Nototheniidae species in the late 1980s (CCAMLR, 2004). It also reflects the increase landings of the deepwater Patagonian toothfish (*Dissostichus eleginoides*, Nototheniidae) during late 1980s (Koch, 1992; Constable *et al.*, 2000).

#### **5.3.6 Mean longevity of the catch**

The mean longevity of the catch (Figure 5.4a) has increased during the past 50 years, but most dramatically since the early 1990's. Mean longevity of the catch by depth (Figure 5.4b) in landings from shallow waters has a lower mean longevity (about 15 years) when compared to intermediate (about 40 years) or deeper waters (over 100 years). Hence, fishing deeper means fishing for increasingly longer-lived and thus more vulnerable species.



**Figure 5.4 - (a)** Global trend of mean fish longevity of the catches for all marine fishes including pelagics (dark grey dots), and for bottom marine fishes only (light grey squares). **(b)** Global trend of mean longevity of the 2001 world bottom marine fisheries catch by depth. Line is the least squares fit through points by using the logarithmic equation ( $r^2 = 0.75$ ). Mean age at maturity shows a similar pattern.



## 5.4 DISCUSSION

I have shown that global landings of fishes have shifted in the last 50 years from shallow to deeper water species, and also that, as a likely consequence, the mean longevity of the fish species caught has increased dramatically. This trend is a serious concern because species with larger body size, longer life span, later sexual maturity, and slow growth are more vulnerable to overfishing and pseudo-extinction (Jennings *et al.*, 1998; Dulvy *et al.*, 2003; Dulvy *et al.*, 2004; Chueng *et al.*, 2005). Deep-water fishes are thus highly vulnerable to overfishing and potentially have little resilience to overexploitation (Koslow *et al.*, 2000; Clark, 2001; Morato *et al.*, 2006). Moreover, deep waters act as the last refuge for some coastal stocks with an extensive vertical distribution where no fishing was occurring some decades ago (Caddy, 1993). With a fisheries expansion to deeper waters those refuges will no longer operate.

There is a recent tendency in fisheries development to argue for a diversification of target fish species, mainly through the exploitation of 'under-utilised' deepwater species (see Moore, 1999). In fact we are already seeing the well-documented declines observed for shallow water fish stocks repeated in deepwater stocks (see Roberts, 2002 for some examples). Because of their life-history characteristics (Merrett and Haedrich, 1997; Morato *et al.*, 2006) this phenomenon will be much faster with a smaller likelihood of recovery after collapse. Hence, deep-sea fisheries cannot be seen as a replacement for declining shallow-water resources; instead, deep-water habitats should be considered as the new candidates for conservation.

This work is based on the FAO catch statistics and on the reported average depth range of fish from FishBase. The reliability of the FAO catch statistics is of some concern (for more details see FAO, 2002; Pauly *et al.*, 2002; Watson *et al.*, 2004) and the lack of taxonomic resolution can be a problem when drawing general conclusions at a global scale (Watson *et al.*, 2004). However, I have demonstrated global and regional trends towards fishing deeper in the oceans in spite of a large portion of the world's landings being assigned to broad categories. This is especially true for newly-developed or undocumented fisheries as is the case of many deep-water demersal fisheries. As an example, the dropline fishery around the

Madeira Islands for the deepwater black scabbardfish (*Aphanopus carbo*, Trichiuridae) is known to have operated since the early 19<sup>th</sup> century (Martins and Ferreira, 1995), but the first official record of landings of this species is in 1986. As in this case, landing statistics may include a great proportion of deepwater species in broader categories, and because many deep-sea fishes are not very well known, the likelihood of having them aggregated in broader categories is higher when compared to well-known shallow coastal bottom fishes. Assigning catches to broad categories is often the case in tropical developing countries with strongly multispecies fisheries (Pauly *et al.*, 1998b) and I did, in fact, find trends in the tropics less evident. In both cases I believe that, if better taxonomic resolution were to be available, the effect would be stronger because more deepwater fish species would be taken into account.

I used the average depth range of fish distribution as an indicator of fishing depths because fisheries will mainly operate at depths where higher abundances of target species occur. Although this is probably not true for non-target species and by-catch, I do not think it unduly affected the analysis because a), the proportion of non-target landings is smaller and thus will not have a significant effect on the general trends; or, b), by-catch species are not generally reported in FAO statistics.

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## CHAPTER 6

### VULNERABILITY OF SEAMOUNT FISH TO FISHING: FUZZY ANALYSIS OF LIFE HISTORY ATTRIBUTES<sup>1</sup>

#### 6.1 INTRODUCTION

Seamounts are biologically distinctive habitats of the open ocean exhibiting a number of unique features (see Rogers, 1994). Seamounts have received much attention mainly because of the presence of substantial aggregations of forage fishes in mid- and deep-water (Boehlert and Sasaki, 1988; Rogers, 1994; Koslow, 1996, 1997; Koslow *et al.*, 2000), which became the prime target of a highly technological fishery. Based on life history and ecological characteristics, several authors have placed “seamount fishes” at the extreme end of the vulnerability spectrum (Koslow, 1997; Branch, 2001; Boyer *et al.*, 2001; Clark, 2001). However, with the exception of works by Koslow (1996) and Froese and Sampang (2004), few attempts have been made to review, summarize and compare the life-history of seamount species. Therefore, this paper tests the generalization that “seamount fishes” possess specific life history characteristics that render them more vulnerable than other species. A detailed description of what are seamount fishes is given in Chapter 1.5.

Responses of a fish species to exploitation may be partly determined by life history and ecological characteristics (Adams, 1980; Roff, 1984; Stokes *et al.*, 1993; Kirkwood *et al.*, 1994). Fish that are large in size, mature late, have slow growth and low mortality rates, are likely to have higher vulnerability to fishing (Jennings *et al.*, 1998, 1999; Russ and Alcala, 1998; Musick, 1999; Denney *et al.*, 2002). In addition, species that display social aggregation behaviours such as shoaling, schooling (Pitcher and Parrish, 1993) or shoal spawning may have higher vulnerability because of increased catchability when their abundance declines, often referred to as hyperstability of catch rates (Hilborn and Walters, 1992; Pitcher, 1995,

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<sup>1</sup> A version of this chapter has been published. Morato, T., W.W.L. Cheung and T.J. Pitcher. (2006) Vulnerability of seamount fish to fishing: fuzzy analysis of life history attributes. *Journal of Fish Biology* 68(1): 209-221.

1997; Walters, 2003), and their spawning behaviour may also be disrupted by fishing (Johannes, 1998; Sala *et al.*, 2001; Sadovy and Domeier, 2005).

This paper attempts to test the hypothesis that “seamount fishes” generally have a high vulnerability to fishing exploitation. Previous studies have found that vulnerability of fishes to exploitation is correlated with their life history characteristics. Vulnerability was estimated quantitatively by analysis of life-history characteristics using a fuzzy-logic algorithm (Cheung *et al.*, 2005).

## **6.2 METHODS**

### ***6.2.1 Compilation of species list***

Based on the best available information, I collated species lists for fishes that occur or aggregate in and around seamounts. “Seamount fishes” are defined as fish that have been reported as occurring on seamounts, even if rare. A total of 798 species of marine fishes were classified as “seamount fishes” and 23 as “seamount-aggregating” fishes (Appendix 1).

### ***6.2.2 Comparisons of biological characteristics and vulnerabilities***

I compiled estimates of life history and ecological attributes for over 14,000 marine fish species based on information available on Fishbase (Froese and Pauly, 2004). These attributes include longevity ( $T_{\text{Max}}$ ), age at maturity ( $T_{\text{m}}$ ), asymptotic length ( $L_{\infty}$ ), total fecundity ( $F_{\text{T}}$ ), von-Bertalanffy growth parameter ( $K$ ), natural mortality rate ( $M$ ), together with information on spatial behaviour and preferred habitat (pelagic, demersal, reef-associated, bethopelagic, bathypelagic and bathydemersal). Only those parameters directly estimated from empirical studies were used, while those that were calculated from empirical relationships between life history parameters were excluded. If more than one estimate was available for a particular life history parameter of a particular species, the arithmetic mean was used.



I used a fuzzy expert system developed by Cheung *et al.* (2005) to predict intrinsic vulnerability to fishing. This index was demonstrated to provide vulnerability estimates that correlate better with observed data than existing alternatives (Musick, 1999; Hilton-Taylor 2000; ICES, 2001; Froese and Pauly, 2004). Cheung *et al.* (2005) defined intrinsic vulnerability as inherent capacity to respond to fishing that relates to the fish's maximum rate of population growth and strength of density dependence. The fuzzy expert system classifies fishes into different levels of vulnerability based on basic life history and ecological characteristics. The input variables include maximum length, age at first maturity, longevity, von Bertalanffy growth parameter K, natural mortality rate, fecundity, strength of spatial behaviour, and geographic range. Heuristic rules were incorporated to describe the relationships between these biological traits and fish's intrinsic vulnerability, through which the latter can be predicted. Intrinsic vulnerability was expressed on an arbitrary scale from 1 to 100, with 100 being the most vulnerable. Comparisons with empirical data showed that the fuzzy expert system successfully predicted the intrinsic vulnerability of fishes to fishing (Cheung *et al.*, 2005).

Here, I have predicted the intrinsic vulnerability for 1,600 species of fish for comparison between seamount and non-seamount associated fishes (Table 6.1). To increase robustness, I excluded species for which total length was the only available life-history parameter.

Biological characteristics and the estimated fuzzy intrinsic vulnerabilities were compared between "non-seamount fishes", "seamount fishes" and "seamount-aggregating" fishes. To test if commercially-targeted seamount fish species were also more vulnerable than other target fish species, intrinsic vulnerability was also estimated for those species reported in the Food and Agriculture Organization (FAO) official landing statistics. Additionally, to correct for the confounding factor that deep-sea and bathydemersal fish may have higher vulnerability in general, multiple regression analysis was used to explore the relationship between depth (log transformed median of depth range), habitats (seamount fishes, seamount-aggregating), and environmental preferences (pelagic, demersal or bathypelagic) with vulnerability. Differences between the biological characteristics estimates were tested by one-

way ANOVA, while multiple comparisons were performed by Tukey test with unequal sample sizes. Differences between intrinsic vulnerability estimates were tested with Mann-Whitney ( $U$ ) non-parametric statistics (see Zar, 1999).

**Table 6.1** - Number of fish species considered as “non-seamount fishes”, “seamount fishes” and “seamount-aggregating” fishes, and number of available estimates of life history attributes and intrinsic vulnerability. Sample sizes for fish species grouped by preferred habitat is also shown. NS are “non-seamount” fish species while S are fish occurring on seamounts.

	Number of Species	$T_{Max}$	$T_m$	$M$	$K$	$L_{\infty}$	$F_T$	$V_I^*$
“Non-Seamount”	14924	430	460	176	1087	11900	482	1407
“Seamount”	798	92	85	38	150	726	77	193
“Seamount-aggregating”	23	19	16	10	18	22	11	18
Pelagic NS	1013	76	84	45	165	871	74	193
Pelagic S	40	11	13	7	18	36	9	18
Demersal NS	6047	200	201	66	417	4538	220	596
Demersal S	118	23	23	9	31	96	21	39
Reef-associated NS	4159	99	109	45	365	3828	111	421
Reef-associated S	94	11	13	8	29	92	10	35
Benthopelagic NS	831	39	54	18	92	646	39	114
Benthopelagic S	67	15	12	6	20	60	7	23
Bathypelagic NS	1051	7	4	1	26	736	5	31
Bathypelagic S	223	11	9	3	25	214	9	33
Bathydemersal NS	1827	11	10	2	24	1284	34	54
Bathydemersal S	252	19	13	4	25	225	20	43

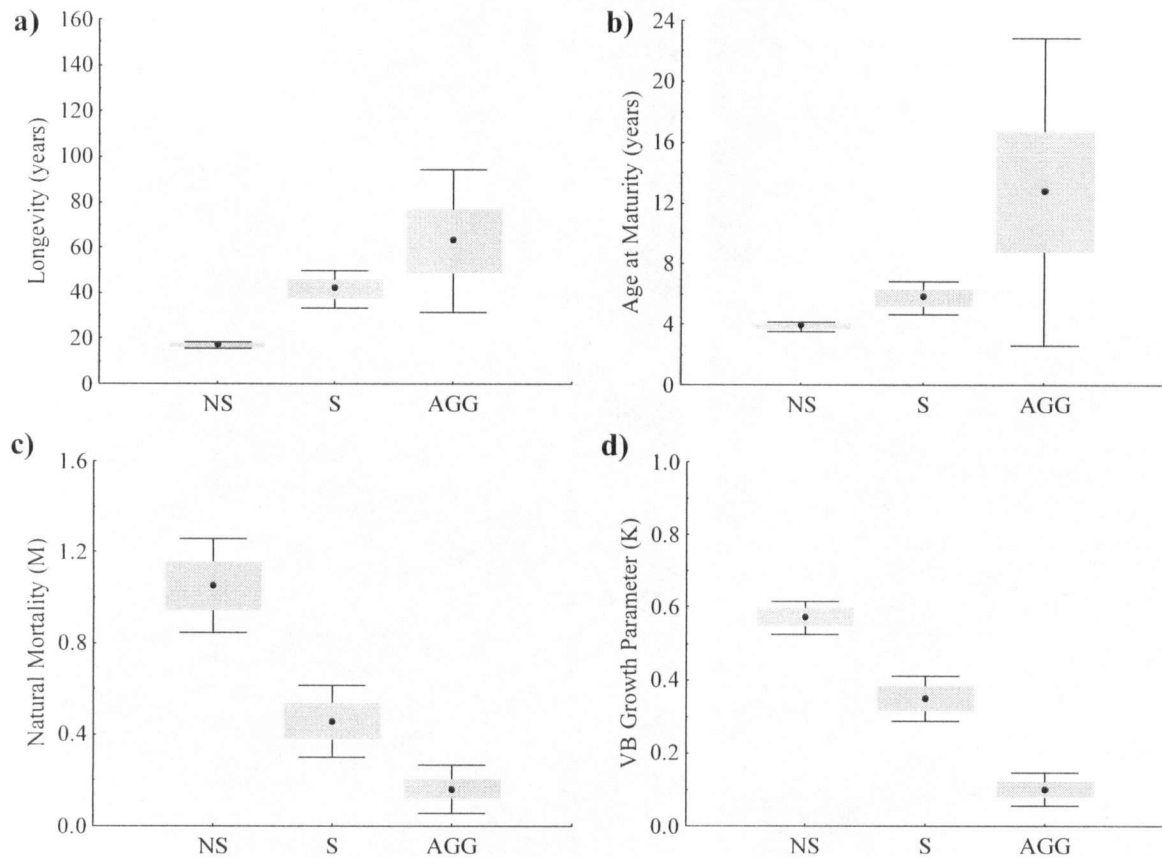
Where:  $T_{Max}$  is the longevity,  $T_m$  the age at maturity,  $M$  is the natural mortality,  $K$  is the Von-Bertalanffy Growth function  $K$ ,  $L_{\infty}$  is the Total Length infinity,  $F_T$  is total fecundity, and  $V_I$  is the intrinsic vulnerability. \* Even though vulnerability was estimated for almost all fish species ( $n=14148$ ), this table only shows the number of species included in further analysis, i.e. excluding those species from which total length was the only available life-history parameter.

### 6.2.3 Responses to fishing

The relationship between vulnerability estimates and biomass change over time caused by fishing was evaluated using a simulation model. A mass-balanced ecosystem model (Ecopath with Ecosim, see Christensen and Walters, 2004 for details) developed for a theoretical isolated North Atlantic seamount (Morato and Pitcher, 2002) was used. This model included 37 functional groups, of which twenty were fish groups assembled according to environmental preference (i.e., depth and habitat: e.g., benthic, pelagic or benthopelagic), body size, energetics and life-history characteristics (see Morato and Pitcher, 2002 for a complete description of the model). The seamount fisheries were loosely based on those operating at the Azores / Mid Atlantic Ridge, and thus divided into six fleets (see Morato and Pitcher, 2002). Biomass changes over 20 years were simulated by assuming a fishing mortality rate of 0.3 for one fish group at a time.

### 6.3 RESULTS

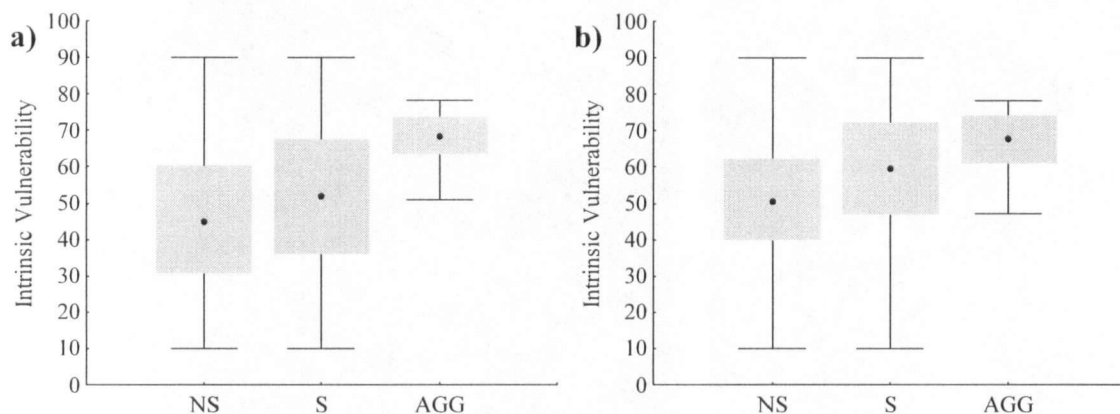
Significant differences in longevity (ANOVA, d.f.= 2;  $p < 0.001$ ) and age at maturity (ANOVA, d.f.= 2;  $p < 0.001$ ) were found among “seamount”, “non-seamount” and “seamount-aggregating” fishes (Figure 6.1). The longevity (Figure 6.1a) of seamount fishes was significantly higher than “non-seamount” fishes (mean  $T_{\text{Max}}$  = 41.6 years and 16.9 years respectively; Tukey test; d.f.= 519;  $p < 0.001$ ). “Seamount-aggregating” fishes have the highest longevity among the three categories (mean  $T_{\text{Max}}$  = 62.7 years), although the difference is significant only when comparing with “non-seamount” fishes (Tukey test; d.f.= 519;  $p < 0.001$ ). Accordingly, age at maturity (Figure 6.1b) of both seamount and “seamount-aggregation” fishes were significantly higher (mean  $T_m$  = 6.5 years and 15.6 years respectively) than the “non-seamount fishes” (mean  $T_m$  = 3.9 y) (all Tukey test; d.f.= 542;  $p < 0.001$ ). “Seamount-aggregating” fishes also have a significantly higher age at maturity than “seamount fishes” (Tukey test;  $p < 0.001$ ).



**Figure 6.1** - Comparison of some life-history characteristics of “non-seamount” fish species (NS), fish occurring on seamounts (S), and “seamount-aggregating” species (AGG). **a)** longevity ( $T_{Max}$ ); **b)** age at maturity ( $T_m$ ); **c)** natural mortality ( $M$ ); **d)** Von-Bertalanffy growth parameter ( $K$ ). In the graphs the middle point is the mean, the box is the Mean  $\pm$  S.E., and the whisker is the Mean  $\pm$  95% CL.

Comparisons of natural mortality rate (Figure 6.1c) and the von Bertalanffy growth parameter  $K$  (Figure 6.1d) among the three categories of fishes show similar, but reciprocal, trends as longevity and age at maturity. “Seamount-aggregating” fishes have the lowest natural mortality and von Bertalanffy growth parameter (mean  $M= 0.16$  and mean  $K= 0.10$ ) while “non-seamount fishes” have highest among the three fish categories (mean  $M= 1.05$  and mean  $K= 0.57$ ). Although, paired comparisons (Tukey test) were only significantly different at the 5% confidence level for “seamount fishes” and “non-seamount fishes”.

Significant differences in the estimated intrinsic vulnerabilities were observed between “seamount”, “non-seamount” and “seamount-aggregating” fishes. Median intrinsic vulnerabilities (Figure 6.2a) for “non-seamount fishes”, “seamount” and “seamount-aggregating” fishes were estimated to be 45.0, 51.8 and 68.2 respectively. The differences in intrinsic vulnerabilities are significant when comparing both “non-seamount” and “seamounts fishes” ( $U; p < 0.001$ ), and comparing “seamount fishes” and “seamount-aggregating” fishes ( $U; p < 0.007$ ).



**Figure 6.2** - Intrinsic vulnerability ( $V_I$ ) index for fish species no-occurring on seamounts (NS), occurring on seamounts (S), and “seamount-aggregating” species (AGG). **a)** including all fish species; **b)** for species reported in FAO official landing statistics. In the graphs the middle point is the median, the box the 25%-75% percentiles, and the whisker is the range.

Vulnerabilities of fish reported as catches in the FAO landings statistics were also higher for “seamount fishes”, and significantly different from the median for “non-seamount fishes” ( $U$ ;  $p < 0.001$ ). However, there were no significant differences between the vulnerabilities of “seamount fishes” and “seamount-aggregating” species ( $U$ ;  $p < 0.111$ ), even though the median was higher for the later. Additionally, the mean of vulnerability weighted by volume of catch (log-transformed) (Table 6.2) was estimated. Similarly, vulnerability was higher for “seamount-aggregation” species and lower for “non-seamount fishes”.

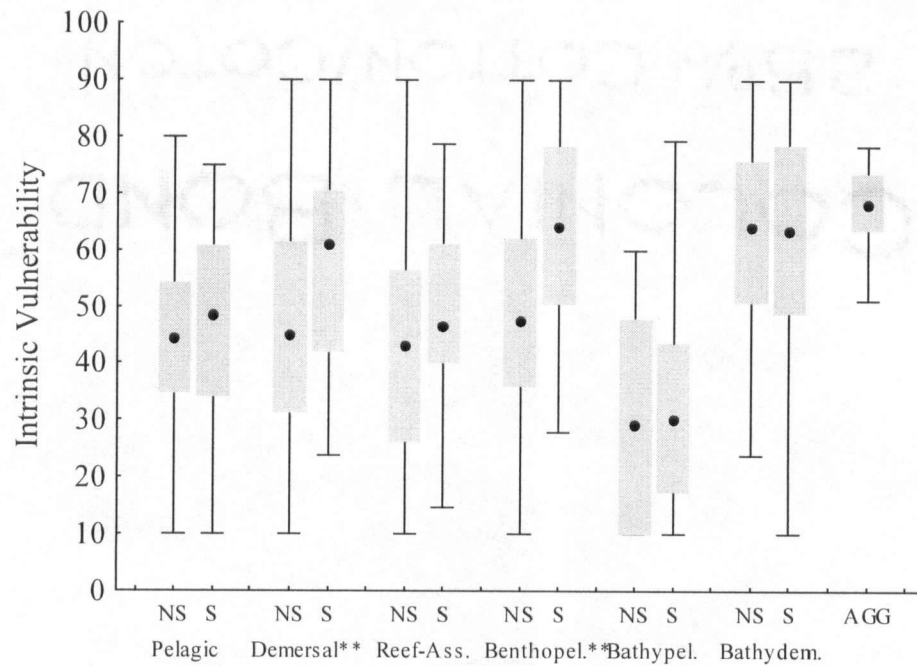
The differences in vulnerability between “seamount” and “non-seamount fishes” were mainly due to benthopelagic and demersal fishes (Figure 6.3), which were found to have significantly different medians of intrinsic vulnerability ( $U$ ; Demersal  $p = 0.003$ ; Benthopelagic  $p = 0.001$ ). For all other fish groups paired comparisons of medians were not significantly different. Bathydemersal fishes, benthopelagic and demersal fishes were among the most vulnerable fish groups, with “seamount-aggregating” fishes having the highest intrinsic vulnerability.

Vulnerabilities of the “deep-sea fish” group (bathydemersal fishes not occurring on seamounts) (median  $V_I = 64.0$ ) were not significantly different from seamount demersal fishes (median  $V_I = 61.0$ ;  $U$ ,  $p = 0.194$ ), seamount benthopelagic fishes (median  $V_I = 64.0$ ;  $U$ ,  $p = 0.819$ ) and seamount bathydemersal fishes (median  $V_I = 63.5$ ;  $U$ ,  $p = 0.833$ ). “Seamount-aggregating” fishes (median  $V_I = 68.2$ ) were the only group having higher vulnerability estimates than the “deep-sea fish” group, but this difference was not statistically significant ( $U$ ,  $p = 0.335$ ).

Multiple regression analysis showed that “seamount-aggregating” was a significant factor ( $p = 0.011$ ) in explaining the variance in vulnerability between species, when differences in depth range (log-transformed) were accounted for in the regression model. However, the “seamount-aggregating” factor was significant only when the lower vulnerability of bathypelagic fishes was accounted for in the regression model.

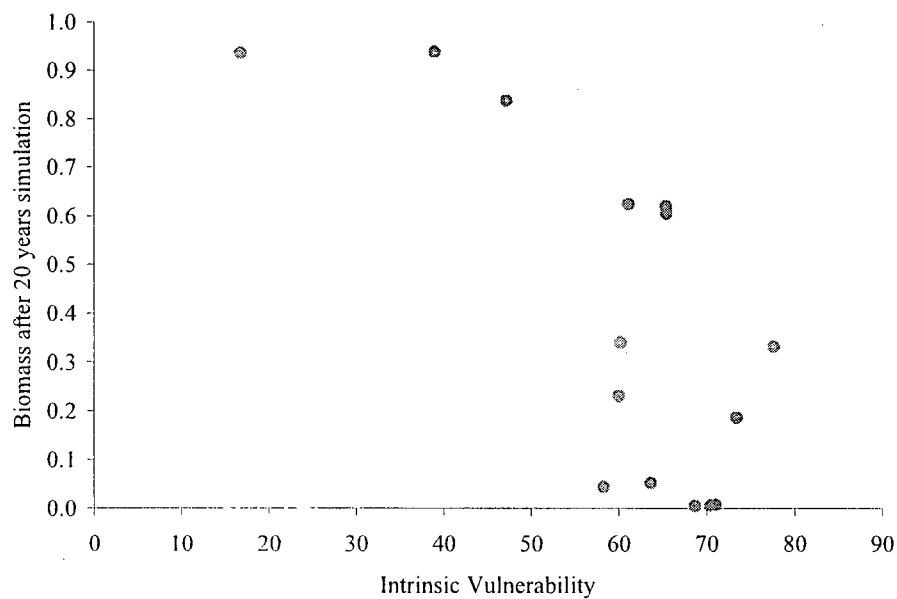
**Table 6.2** - Intrinsic vulnerability weighted by the Log(catch) for “seamount” and “seamount-aggregating” species reported explicitly in FAO catches.

	“Non-seamount”	“Seamounts”	“Seamount-aggregating”
Number of Species	508	102	13
Vulnerability	39.9	47.9	64.5



**Figure 6.3** - Intrinsic vulnerability ( $V_1$ ) index for fish species of different habitats no-occurring on seamounts (NS), occurring on seamounts (S). Vulnerability for “seamount-aggregating” species (AGG) also presented. In the graphs the middle point is the Median, the box the 25%-75% percentiles, and the whisker is the range. \*\* indicates significant differences between medians (Mann-Whitney test; Pelagic:  $p= 0.471$ ; Demersal:  $p= 0.003$ ; Reef-Associated:  $p= 0.076$ ; Benthopelagic:  $p= 0.001$ ; Bathypelagic:  $p= 0.806$ ; Bathydemersal:  $p= 0.833$ ).

The intrinsic vulnerabilities estimated from the fuzzy system were significantly related ( $R^2=0.738$ ,  $p=0.007$ ) to the simulated population declines of marine fish groups (Figure 6.4) caused by fishing. Groups of species with higher vulnerabilities had larger biomass declines than species with lower vulnerabilities. Simulations showed that even at modest levels of fishing, seamount species were depleted, not sustained.



**Figure 6.4** - Proportion of biomass change over time for fish groups with different intrinsic vulnerabilities ( $V_I$ ). Biomass change was estimated by a generic seamount ecosystem model (Morato and Pitcher, 2002) and simulating the effect of a 0.3 fishing mortality rate for each group over a 20 years period.



## 6.4 DISCUSSION

Despite rather broad definitions, this global analysis of over 1,600 species shows that “seamount fishes”, particularly “seamount-aggregating” fishes, have higher intrinsic vulnerability than other groups of fishes. Similar patterns were found when considering commercially exploited species only. Biological characteristics leading to greater vulnerability include a longer lifespan, later sexual maturation, slower growth and lower natural mortality. However, as fish vulnerability was strongly related to depth range, seamount-association (as in “seamount fishes” group) may not be the proximal factor; higher vulnerability of fish found at seamounts may be confounded because they include more deep-water species. These findings are in agreement with life-history qualities for “seamount fishes” proposed by Koslow (1996, 1997), although very few complete case studies are available. In any case, seamounts provide physical and biological conditions for aggregation of vulnerable deep-water fishes and thus unsustainable exploitation in such habitats should be a concern.

Deep-water species were considered sensitive to exploitation because of their vulnerable biological characteristics (Merrett and Haedrich, 1997; Roberts, 2002). The analysis presented here supports this theory. Particularly, bathydemersal fishes were more vulnerable than any other “non-seamount” group of fish; only “seamount aggregating” fish had higher vulnerabilities. As these species are often targeted by deep-sea fishing (trawling in particular), proper monitoring and management of their exploitation should be a priority.

Conservation concerns about the exploitation of “seamount fishes” were supported by results from our simulation modelling. The simulation model confirmed that the biomass of fish with higher vulnerabilities declined more rapidly under exploitation. Although data limitations prevent prevents us from validating the modelling results using empirical data, evidence from other species assemblages suggests a significant positive correlation between vulnerability and population decline (Cheung *et al.*, 2005). Considering that seamount fishes are increasingly being targeted by fishing (Watson and Morato, 2004), populations of highly

vulnerable seamount species such as orange roughy, alfonsinos and other “seamount-aggregating” fishes may be under considerable risk of local extinction (extirpation) under only moderate fishing intensity ( $F=0.3$  in simulation model).

In the light of this analysis, one may ask whether seamount fisheries may be sustainable in the long term (Clark, 2001). Examples from all over the world have showed the “boom and bust” characteristic of seamount trawling fisheries, with rapid stock reduction and serial depletion of successively-exploited new seamounts. The case of the orange roughy, a “seamount-aggregating” fish, is well known. In Namibian waters, orange roughy has been fished down to 10% of its virgin biomass in six years (Branch, 2001), while in Australia biomass levels dropped to 7-13% in about 15 years (Lack, 2003). The orange roughy stock in New Zealand was fished down to 15-20% of virgin biomass in less than 15 years (Clark, 2001) while annual sustainable levels of fishing have been estimated to be less than 2% of virgin biomass (Francis *et al.*, 1995), which may not be economically viable. Another example is Russian fishing on seamounts at the Mid Atlantic Ridge. Vinnichenko (2002) showed that the total catch (mainly of alfonsino and scabbardfish *Lepidopus caudatus* Euphrasen 1788) at 9 seamounts in the South Azores area and in three seamounts at the Corner Rising area declined, in each area, from 12000t to below 2000t in just two years. In a larger area of the ridge that included 34 seamounts, catches declined from 30000t to below 2000t in about 15 years (mainly roundnose grenadier and orange roughy).

The high vulnerability of “seamount fishes” should encourage more precaution in managing seamount resources. Collapse of seamount fisheries have been partially attributed to the lack of management. However, even in places where detailed research programmes were in place when exploitation by trawl fisheries commenced, and where scientific recommendations for management were followed and the fisheries controlled, catches declined unexpectedly fast and stocks have been depressed well below  $B_{MSY}$  (Boyer *et al.*, 2001). Our research supports the conclusion that fishing on seamounts is not sustainable, at current levels and with current methods. A number of seamount populations have already been depleted. More will be

depleted and some will be extirpated if fishing on seamounts continues at current or even more moderate levels.

The fuzzy-logic life-history attributes method of estimating intrinsic vulnerability to depletion by fishing, followed by evaluation of sensitivity and local extinction risk using simulation, is a relatively new technique, but it has proved more robust than previous methods (Cheung *et al.*, 2005). It provides a quantitative basis for more precautionary management of fisheries for “seamount” and “seamount-aggregating” fish in the future.

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## CHAPTER 7

### ECOSYSTEM SIMULATIONS OF MANAGEMENT STRATEGIES FOR DATA-LIMITED SEAMOUNT FISHERIES<sup>1</sup>

#### 7.1 INTRODUCTION

With global catches declining since the late 1980's (Watson and Pauly, 2001), the world's fisheries resources have been characterized as seriously depleted or in danger of depletion (e.g. Jackson *et al.*, 2001; Pauly *et al.*, 2002; Baum *et al.*, 2003; Christensen *et al.*, 2003; Myers and Worm, 2003), with very little evidence for any recovery (Hutchings, 2000). What has caused this phenomenon has been the subject of serious debate (Pitcher, 2001). Indeed, poor management practices and increased fishing pressure (Ludwig *et al.*, 1993), along with an excessive level of investment in fishing capacity, have resulted in serious stock depletion on continental shelves and have created serial depletion from new pressures on alternative fishing grounds (Pauly *et al.*, 2002). Seamounts are among those "newly" targeted ecosystems that have been intensively fished since the second half of the 20<sup>th</sup> century (Rogers, 1994; Koslow *et al.*, 2000).

Deep-water fisheries in general, and seamounts fisheries in particular, are usually characterized by a boom and bust sequence (Koslow *et al.*, 2000; Watson and Morato, 2004), with the targeted fish stocks showing signs of overexploitation within a short period after the beginning of the fishery. For example, this has been the case with the orange roughy (*Hoplostethus atlanticus*) fishery off the waters of New Zealand (Clark, 1999; Clark *et al.*, 2000), Australia (Koslow, 1997), Namibia (Boyer *et al.*, 2001), and the North Atlantic (Branch, 2001); the pelagic armourhead (*Pseudopentaceros wheeleri*) fishery over seamounts

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in international waters off Hawaii (Sasaki, 1986); and the blue ling (*Molva dipterygia*) fishery in the North Atlantic (Bergstad *et al.*, 2003). Seamount aggregating fish stocks are long-lived, slow growing species, with late maturity and low recruitment rates (Koslow, 1997; Rico *et al.*, 2001; Morato *et al.*, 2004), often forming highly localized aggregations (Clark, 1996). Thus, seamount fish stocks are rapidly depleted and maintenance of seamount fisheries depends on the discovery of unexploited seamounts. Moreover, many seamounts are located in international waters where no management is applied. Once depleted, seamount populations likely require decades to recover (Koslow, 1997). Side effects caused by overfishing or extensive trawling on seamounts raise serious concerns: for example, damage to benthic communities dominated by corals and other fragile suspension feeders is common (Richer de Forges, 2000; Koslow *et al.*, 2001) and impacts on transient migratory species whose life histories rely on seamount food webs (Haney, 1995; Holland *et al.*, 1999; Weimerskirch *et al.*, 2002). The prevention of further negative impacts on these sensitive ecosystems is now an important policy objective (Probert, 1999; Roberts, 2002).

There is rising concern about threats to seamount ecosystems in the Exclusive Economic Zones of coastal states and the high seas; several countries, such as Canada, Australia, New Zealand and Portugal have begun to take action for the protection of such 'fragile' ecosystems. However, seamount ecosystems remain one of the worst cases of data-limited situations, comprising a true challenge for fishery scientists and managers who are urged to develop new fisheries under the precautionary approach of the Code of Conduct for Responsible Fisheries (FAO, 1995). Little is known about seamount ecosystems in the NE Atlantic and elsewhere, or the impact of human activities upon them. A recent attempt to tackle this global lack of information has been made by the European Commission, which has funded the first European Seamount Project to integrate physical, biogeochemical and biological research - the 'OASIS project' (OceAnic Seamounts: an Integrated Study).

In this paper I investigate if ecosystem simulations can help in understanding the impact of fishing on pristine seamounts. By using ecosystem modeling loosely structured on North

Atlantic case studies, data gathered from elsewhere, and optimization methods for policy search, I explore the types of fisheries that might be sustainable on seamount ecosystems.

## 7.2 METHODS

### 7.2.1 *Trophic model of seamount ecosystems*

In this study, I used a general ecosystem model developed for North Atlantic seamounts (Morato and Pitcher, 2002) based on the 'Ecopath with Ecosim' approach (EwE; <http://www.ecopath.org>), a software for ecosystem trophic mass-balance analysis (Ecopath), with a dynamic modeling capability (Ecosim) (for details see Christensen and Walters, 2004). This model was developed for a theoretical isolated seamount. Habitat covered by the model was defined by the summit, set at around 300 m, down to the base of the seamount at around 2000 m. The model covered a small area of about 3000 km<sup>2</sup> and included 37 functional groups: three marine mammal groups (i.e., toothed whales, baleen whales and dolphins), seabirds, turtles, seven invertebrate groups (i.e., benthic filter feeders, such as corals or gorgonians, benthic scavengers, benthic crustaceans, pelagic crustaceans, seamount resident cephalopods, small and large drifting cephalopods), three zooplankton groups (i.e., gelatinous, shallow and deepwater zooplankton), primary producers (i.e., phytoplankton), detritus and twenty fish groups assembled according to their environmental preferences (i.e., depth and habitat: e.g. benthic, pelagic or benthopelagic), body size, energetics and life-history characteristics (see Appendix 3 and Morato and Pitcher, 2002 for a complete description of the model).

The theoretical seamount was assumed to have a low initial level of exploitation and its fisheries were loosely based on those operating at the Azores / Mid Atlantic Ridge comprising 6 fleets (see Appendix 3 and Morato *et al.*, 2001): (a) demersal longline (targeting shallow water demersal and benthic fishes); (b) deepwater longline (targeting bathypelagic and bathybenthic fishes); (c) small pelagics fishery (for small pelagic fishes); (d) tuna fishery; (e) swordfish fishery; and (f) deepwater trawl (targeting seamount associated

fishes, including orange roughy and alfonsinos, *Beryx splendens* and *B. decadactylus*). Landings, prices, and job estimates were loosely based on the Azores case study (Morato *et al.*, 2001; Morato and Pitcher, 2002).

Ecopath outputs are known to be very sensitive to the vulnerability parameters (see Walters *et al.*, 1997; Pitcher and Cochrane, 2002). In this study a standard value of 0.3 representing mixed predator/prey control was used. A brief sensitivity analysis of the policy simulations to different vulnerability settings was conducted by repeating simulations with vulnerabilities of 0.2, 0.3 and 0.5. Results from simulations were generally consistent between different vulnerabilities.

### **7.2.2 Model analyses**

The impacts of alternative time patterns of fishing mortalities were explored using an optimization method (Walters *et al.*, 2002; Christensen and Walters, 2004) to search for patterns of relative fishing effort by fishing fleets which would maximize one or more of the considered objectives:

- 1) 'Economy', or net present economic value (i.e., total present value of the catch);
- 2) 'Jobs', or employment (i.e., a social indicator, assumed proportional to gross landed value of catch for each fleet with a different jobs/landed value ratio for each fleet);
- 3) 'Ecology', or ecological 'stability' (i.e., measured by assigning a weighting factor to each group based on their longevity, and optimizing for the weighted sum).

Net present economic value of landed catches was calculated as the discounted sum over all fleets and times of catches multiplied by the prices of landed fish species. A discount rate of 0.04 was used. The ecological criterion component is based on Odum's (1971) definition of 'maturity', with mature ecosystems being dominated by large, long-lived organisms. Thus, it is intended to identify the fleet structure that maximizes biomass of long-lived organisms, defined by the inverse of their production/ biomass ratios (P/B).

The objective function can be thought of as a ‘multi-criterion objective function’, represented as a weighted sum for the three above-mentioned criteria indicators:

$$OBJ = W_V \cdot \sum NPV_{ijt} + W_J \cdot \sum J_{ijt} + W_E \cdot \sum \left( \frac{B}{P} \right)_{ijt} + \varepsilon$$

where  $W$ = weighting factors;  $V$ = value;  $J$ = jobs;  $E$ = ecology;  $i$ = fleets;  $j$ =species caught;  $t$ = time in years; NPV= net present value; and  $B/P$ = biomass production ratio, assumed to be proportional to species longevity and thus ecological stability, with  $\varepsilon$  a normally distributed error term.

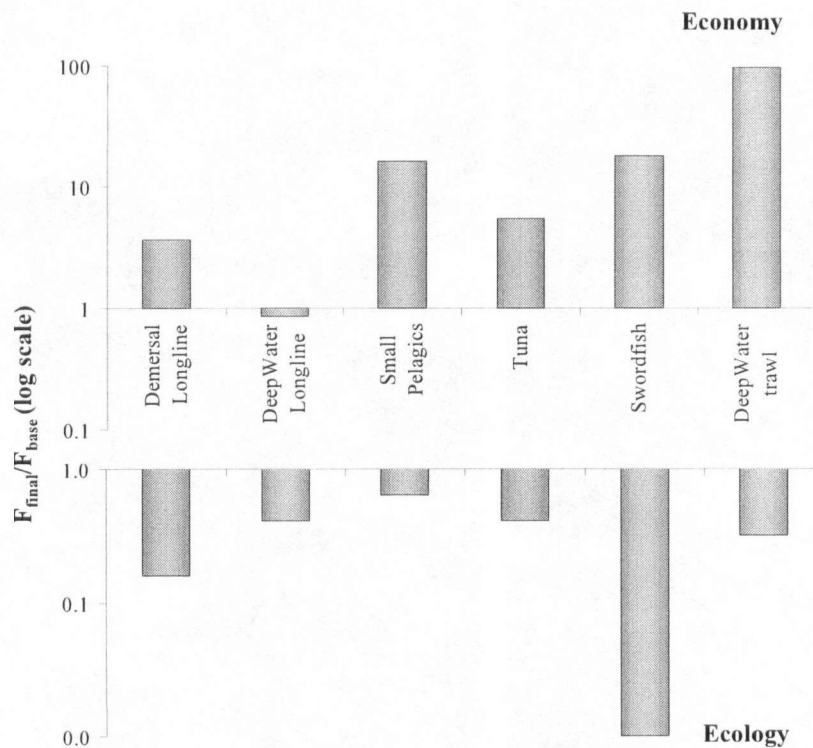
The Davidon-Fletcher-Powell (DFP) non-linear optimization procedure was used to iteratively optimize the three above-mentioned objectives by changing relative fishing rates ( $F$ ) (Walters *et al.*, 2002). This search procedure results in what control systems analysts call an ‘open loop policy’; a recommendation for what to do at different future times without reference to what the system actually ends up doing along the way (Christensen and Walters, 2004). The resulting ‘optimum’ fishing rates by year/fleet served as input for the dynamic simulation, ‘Ecosim’, where they replaced the baseline relative efforts by fleet/gear type. Ecosim, was then run for a 50-year-period to simulate the effect of the optimized fishing rates and to estimate the biomass, catch and value variation. These two scenarios were compared with a ‘no fishing’ scenario where all the fishing rates were set to 0.

Non-linear optimization methods, such as DFP, can be difficult to use and can be misleading. In particular, the method can ‘hang up’ on a local maximum and can give extreme answers due to an inappropriate objective function (Walters *et al.*, 2002). To check for false convergence to local maxima, random starting  $F$ ’s were used. To search for trade-offs among objective functions, optimal scenario solutions for a range of weightings of ecological and economic objectives were accessed. Additionally, at the end of each run, ecosystem indicators such as the mean trophic level of the catch (see equation in Pauly *et al.*, 1998) and biodiversity index (modified from Kempton and Taylor, 1976, Q75; Ainsworth and Pitcher, 2006) which resulted from the suggested fishing effort in each range of weighting, were estimated.

## 7.3 RESULTS

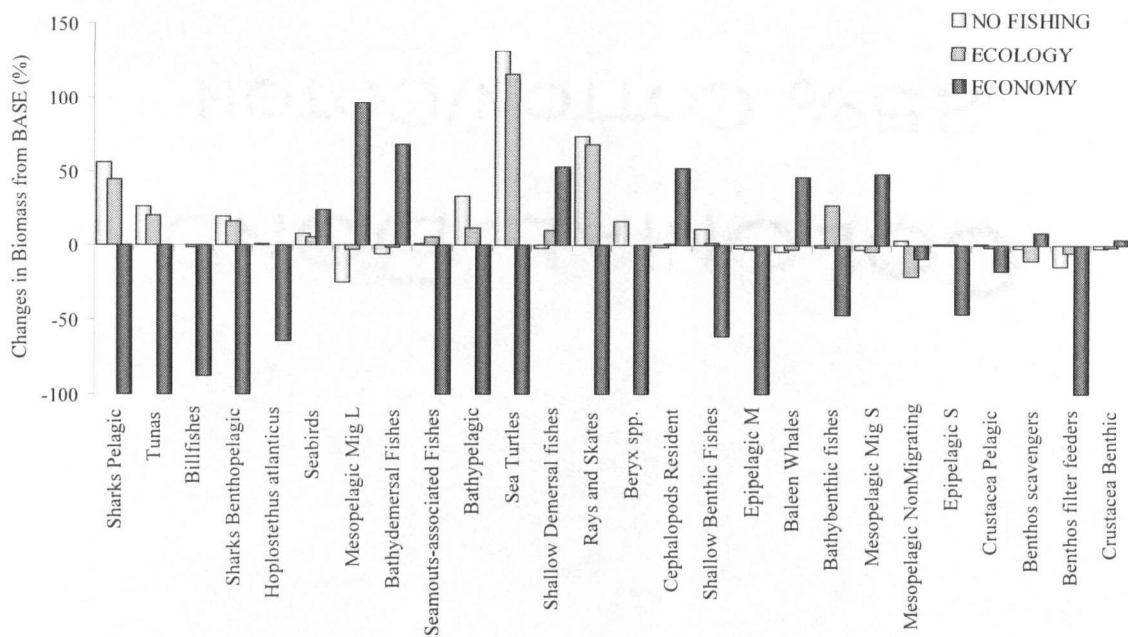
### 7.3.1 Optimal fishing scenarios

The optimized fishing rates ( $F$ ) for the 'economy' and 'ecology' objectives, expressed as proportions of the base model fishing rates are summarized in Figure 7.1. Maximizing net economic value led to an increase in fishing rate in all fisheries (deepwater trawl,  $F_{\text{final}}/F_{\text{base}} = 97.6$ ; swordfish fisheries ( $F_{\text{final}}/F_{\text{base}} = 18.1$ ); small pelagic fisheries,  $F_{\text{final}}/F_{\text{base}} = 16.2$ ), except for the deepwater longline, where the fishing rate was reduced to 0.86 of the base model value. In contrast, maximizing 'ecosystem' stability led to a large decrease in all fishing rates (swordfish fisheries, ( $F_{\text{final}}/F_{\text{base}} = 0.01$ ; demersal longline,  $F_{\text{final}}/F_{\text{base}} = 0.16$ ; deepwater trawl,  $F_{\text{final}}/F_{\text{base}} = 0.32$ ).



**Figure 7.1** - Optimized fishing rates ( $F$ ), expressed as proportions of the base model, obtained by maximizing 'economy' and 'ecology' objectives. Note differences in scale.

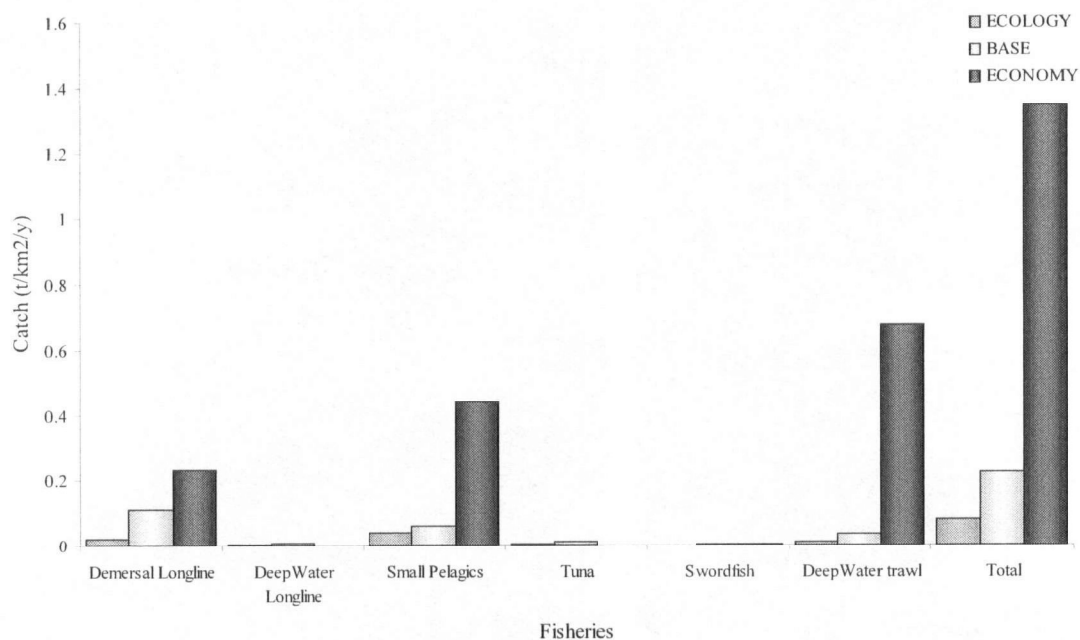
The effects of the optimized fishing rates on biomass (i.e., percentage of biomass change from base model) after a 50-year simulation are presented, together with a ‘no fishing’ scenario, in Figure 7.2. Not surprisingly, the ‘no fishing’ scenario produced a general increase in biomass for most of the groups, but particularly for sea turtles, rays and skates, and pelagic sharks. However, this was not the case for the most important prey groups of the system: mesopelagic fish and benthic invertebrates. The optimized fishing rates for the ‘ecology’ objective function produced very similar results when compared with the ‘no fishing’ scenario, producing a large increase in groups that have slow turnover and higher trophic levels. When economic value was maximized, a general decrease in biomass was observed associated with collapse of ten functional groups (pelagic sharks, tunas, bathypelagic sharks, seamount-associated fishes, bathypelagic fishes, sea-turtles, rays and skates, alfonsonos, medium-sized epipelagic fish, and benthic invertebrate filter feeders, e.g. deep-sea corals).



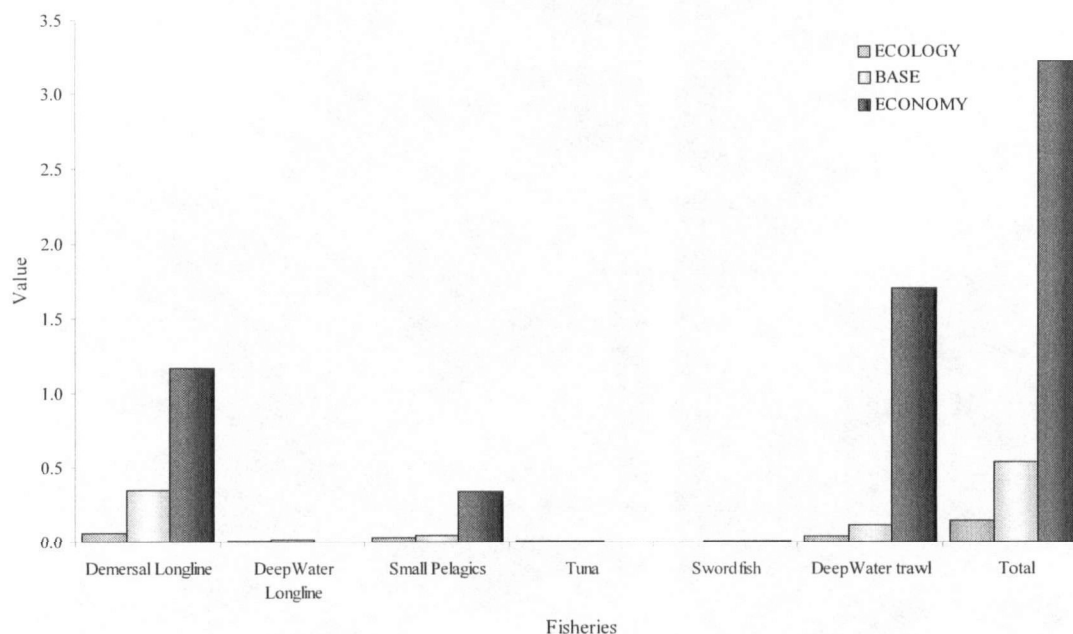
**Figure 7.2** - Changes in group biomasses (percent change of biomass from base model) under the three different fishing scenarios: no fishing, maximizing the ‘ecology’ objective, and maximizing the ‘economy’ objective.

The effects of the different fishing policies on the total landed catches are shown in Figure 7.3. Maximizing the ‘economy’ objective led to an increase in landings when compared to the base model. In this scenario, the deepwater trawl fishery was favoured and had the highest contribution to the total catch. In contrast, maximizing the ‘ecology’ objective required an overall decrease in catches and fishery operations conducted mostly by small pelagic and bottom longline fishing fleets.

Comparing the total value of the catches for the three scenarios (i.e., base model, maximizing ‘economy’, and maximizing ‘ecology’; Figure 7.4), maximizing ‘economy’ generated more money than the base model and the ‘ecology’ scenario. In all cases, deepwater trawl and bottom longline fishing fleets contributed the most to the total value.



**Figure 7.3** - Catches ( $\text{t} \cdot \text{km}^{-2} \cdot \text{y}^{-1}$ ) for the different fishing fleets under the base model and two fishing scenarios: maximizing the ‘ecology’ objective function, and maximizing the ‘economy’ objective function.



**Figure 7.4** - Value of the catches (relative value) for the different fishing fleets under the base model and two fishing scenarios: maximizing the ‘ecology’ objective, and maximizing the ‘economy’ objective.

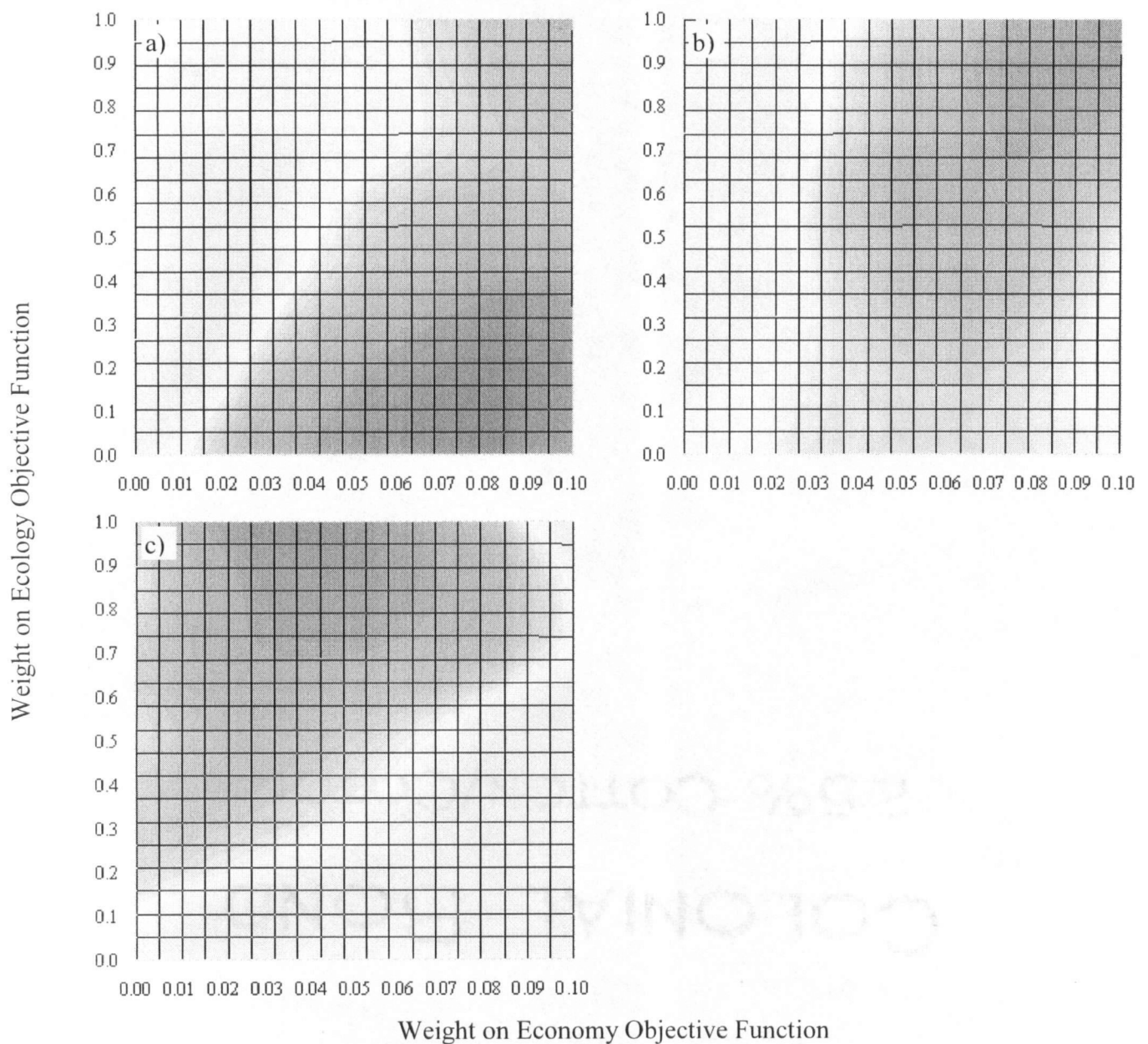
### 7.3.2 Trade-offs

Surface plots of optimal scenario solutions for a range of weightings of ecological and economic objective functions are shown in Figures 7.5 to 7.7. They show that it was not possible to maximize the performance of all three objectives (i.e., net economic value, number of jobs, and ecological ‘stability’) simultaneously. This is true because net economic value (Figure 7.5a) and number of jobs (Figure 7.5b) reach a maximum with a high weighting factor on the economy objective and a small weight on ecology. This results in a decrease in the stability of the system. On the contrary, to maximize ‘ecosystem stability’ a high weighting was assigned to the ‘ecology’ objective (Figure 7.5c). Assigning a low weighting factor to ‘economy’ and a high weighting factor to ‘ecology’ resulted in a decrease of net economic value and number of jobs, with a corresponding increase in the system’s stability. Intermediate weightings produced, in general, intermediate performances for the three objective functions.

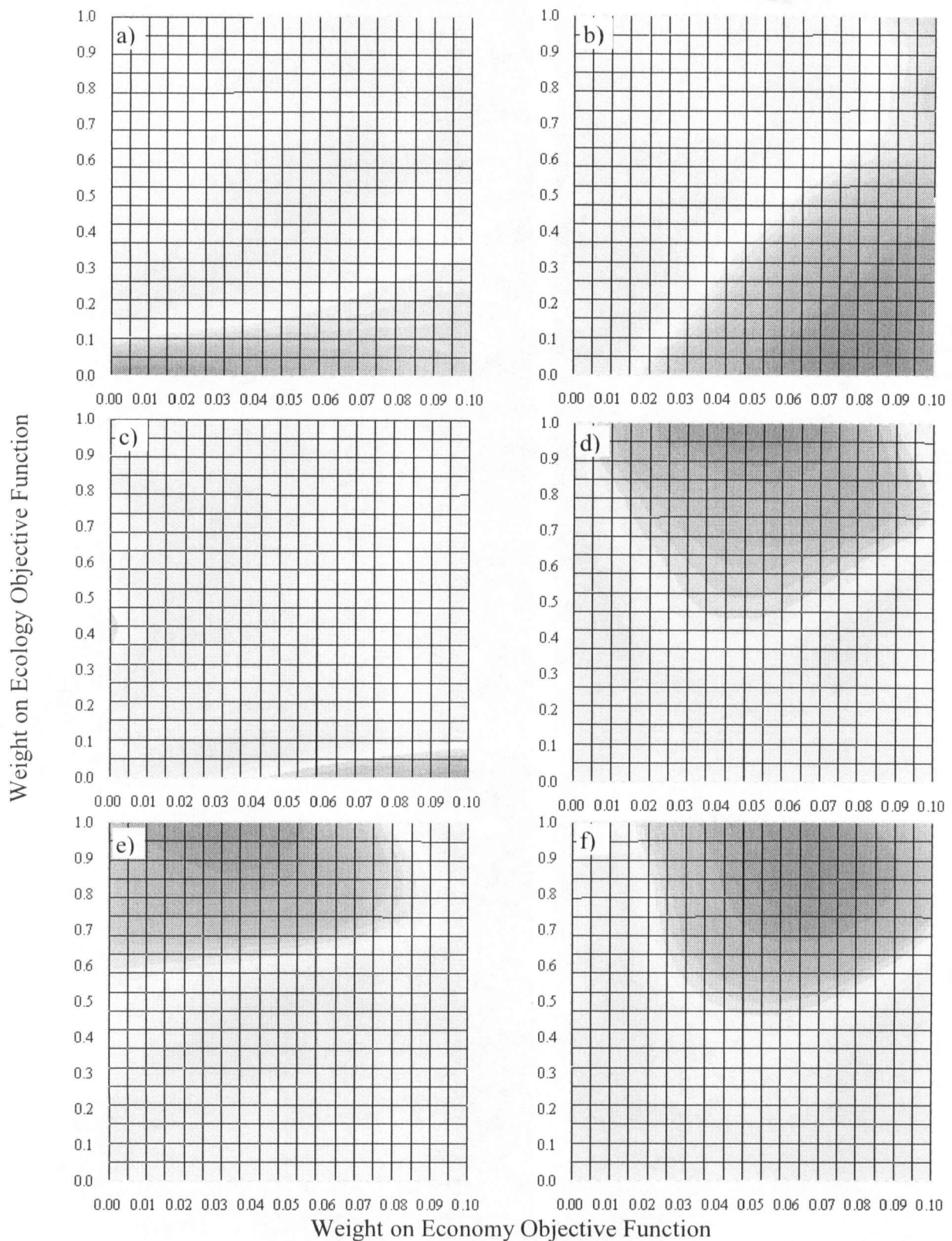


The fishing rates required to achieve different performances of the objective functions (i.e., fishing policies) are presented in Figure 7.6. In order to maximize the net economic value of the system all fisheries, except deepwater longline (Figure 7.6a), required an increase in their fishing rates. These increases were of approximately: 50 times the base model rate for the deepwater trawl fishery (Figure 7.6b); 16 times for the swordfish fishery (Figure 7.6c); 15 times for the small pelagic fish fishery (Figure 7.6d); 3.5 times for the tuna fishery (Figure 7.6e); and 2.5 times for the bottom longline fishery (Figure 7.6f). To achieve ecological stability in the system, however, a decrease in the fishing rates of most of the fisheries was required with the exception of the tuna, swordfish and, to a lesser extent, the bottom longline fisheries. The latter, along with the small pelagic fisheries, reached their highest fishing rates when a high weighting factor was assigned to the 'ecology' objective and an intermediate weight to 'economy'.

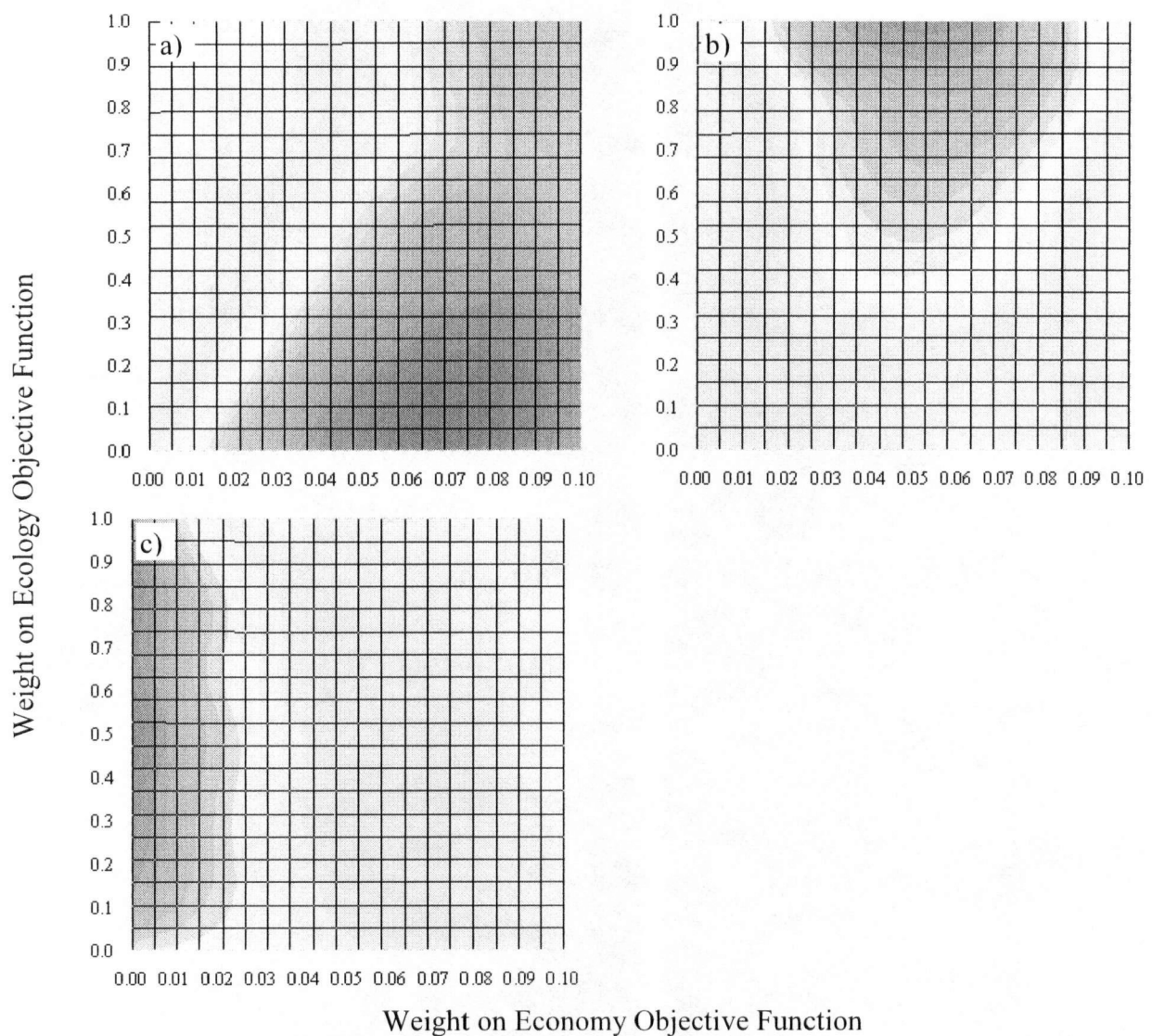
Ecosystem indicators (i.e., mean trophic level of the catch and biodiversity) and total catches derived from the optimal fishing strategies for the overall range of weighting factors for 'ecology' and 'economy' are presented in Figure 7.7. Total catches were maximized when weighting was high for 'economy' and low for 'ecology' objective functions (Figure 7.7a). In contrast, the biodiversity index (Figure 7.7b) was high only when a very small weight was assigned to 'economy'. The mean trophic level of the catch (Figure 7.7c), in general, decreased with a corresponding increase in the weighting of 'economy' and a decrease in the weighting of 'ecology' objective functions. However, maximum trophic level was achieved with a high weighting of 'ecology' and an intermediate weighting of 'economy'.



**Figure 7.5** - Surface plots showing optimal scenario solutions for a range of weightings of ecological and economic objective functions: a) performance of 'economy' objective, maximizing net economic value; b) performance of 'social' objective, maximizing number of jobs; c) performance of 'ecology' objective, maximizing ecological 'stability' of the ecosystem. Scale goes from light blue (low performance) to dark red (high performance). Smooth surface is interpolated.



**Figure 7.6** - Surface plots from EwE model showing the resulting fishing rates, as proportion of base model rates, of the optimal scenario solutions for a range of weightings of ecological and economic objective functions: a) deepwater longline; b) deepwater trawl; c) pelagic longline; d) small pelagic fishery; e) tuna fishery; f) demersal (bottom) longline. Scale goes from light blue (low proportion of base model rates) to dark red (high proportion of base model rates).



**Figure 7.7** - Surface plots showing the resulting ecosystem indicators and total fisheries catch for the optimal scenario solutions for a range of weightings of ecological and economic objective functions: a) total catch; b) biodiversity index (Q75), please note that this figures is shown from a different viewpoint; c) mean trophic level of the catch. Scale goes from light blue (low) to dark red (high).

#### 7.4 DISCUSSION

The analyses in this paper are not meant to describe actual fisheries for seamounts, but rather as an exercise to explore the overall responses of seamount ecosystems to various multi-species management strategies.

The use of 'open loop policy' search procedures can be unrealistic because it can entrust a fishery to fishing rates calculated at some time in the past and from data available from that time (Walters *et al.*, 2002; Christensen and Walters, 2004). Fisheries management needs to be implemented using 'feedback policies' in which harvest goals are adjusted over time as new information becomes available and in response to unpredicted ecological changes (Christensen and Walters, 2004). However, 'open loop policy' calculations can give insights and directional guidance to where the system might be heading. In this study, this method appeared to be appropriate due to both the exploratory characteristic of the study and the data-limited situation of the N. Atlantic seamounts.

Different extreme policy objectives for seamount fisheries may require different fleet configurations. Simulations that maximize economic performance favour deepwater trawling and require an increase in the fishing rates of all other fishing fleets, the only exception being the deepwater longline. On the other hand, maximization of ecological performance is achieved by favouring the operation of small pelagic and bottom longline fisheries. At the same time, a decrease in the fishing rates of all other fishing fleets is necessary.

Different fishing rates and fleet configurations produced different impacts on catches and consequently in the whole ecosystem. Optimizing for economics yielded six times the amount of landed catch and money than the base model scenario and, 17 and 23 times the amount of landed catches and money yielded by the scenario where ecology was maximized. This would, however, have implications to the whole ecosystem. While maximizing ecology produces an overall increase in biomass of most functional groups in the model, maximizing economics leads to a decrease and further collapse of some groups such as tuna, seamount associated fishes, alfonosinos, as well as some charismatic

species such as sea turtles and sharks. This point was well illustrated some time ago by Clark (1973) who pointed out that for populations that are economically valuable but possess low reproductive capacities (such as seamount associated fishes, alfonosinos and sharks), common property competitive exploitation and private property maximization of profits may lead to overexploitation and even to extinction of the population.

It is interesting to note that major collapses in deepwater fisheries, for example off New Zealand (Clark, 1999; Clark *et al.*, 2000), Tasmania (Koslow, 1997) and Namibia (Boyer *et al.*, 2001), and habitat degradation (Probert *et al.*, 1997; Koslow *et al.*, 2001) were attributed to extensive deepwater trawling. In the Azores where no deepwater trawling is known to occur, seamount fisheries are mainly longline, handline and pole-and-line, and are believed to be more sustainable. However, signs of stock decline are becoming apparent even in these systems (Santos *et al.*, 1995; Menezes, 2003). Thus, the question of whether deepwater (mainly trawl) fisheries are sustainable in the long term remains open (Clark, 2001). Some authors (e.g. Probert, 1999; Roberts, 2002), agencies (WWF; IUCN), and governments strongly advocate an urgent need for fishing regulations and/or the establishment of marine reserves in such areas.

It is apparent that major conflicts among stakeholders might emerge when different optimization scenarios result in completely different fishing policies (Figure 7.5, 7.6). In addition, our results illustrate that maximizing 'economy' affects biodiversity in the ecosystem and probably the trophic level of the catch, while maximizing the total landed catches (see Figure 7.7). The opposite is true when 'ecology' is favoured; the total catch and the number of jobs are decreased in order to achieve high biomass of long-lived species and increased biodiversity in the ecosystem.

In conclusion, sustainable seamount fisheries with minimal ecosystem effects appear to be achieved when the 'ecology' objective is maximized. However, more information for these fragile ecosystems and the long-term impacts of fishing and other human activities needs to be acquired. Meanwhile, the precautionary principle ought to be applied to seamount ecosystems, in order to ensure protection and sustainable management.

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# CHAPTER 8

## CONCLUSIONS: ECOLOGY AND FISHERIES OF SEAMOUNT ECOSYSTEMS

### 8.1 INTRODUCTION

The general objectives of this PhD were to explore some fundamental questions about seamount ecology and fisheries, namely to:

- a) examine the impact of a potential increase of local primary production on higher trophic levels;
- b) quantify the amount of advected prey necessary to sustain a “typical” seamount fish community and to explore if the necessary prey can be supported with food provided by local oceanographic conditions;
- c) test if the reported high abundances of seamount “visitors” such as tuna, marine mammals, sea turtles and seabirds on top and around seamounts are true;
- d) analyse changes in the mean depth of fishing to test if reported historical expansion into deeper-waters can be detected in global landings datasets. Also to test the hypothesis that deep-water fisheries resources are vulnerable;
- e) test the hypothesis that “seamount fishes” generally have a higher than average vulnerability to fishing exploitation;
- f) investigate if whole-ecosystem simulations can help in understanding the impact of fishing on pristine seamounts and provide guidelines for sustainable fisheries.

Additionally, and in collaboration with the “Sea Around Us Project” I participated in small *ad-hoc* projects that helped:

- a) estimating of the number of seamounts in the world’s oceans by inferring potential seamount locations;
- b) estimating seamount numbers and locations around the Azores islands;

- c) detecting primary production enhancement by world's oceanic seamounts using remotely sensed data on primary production
- d) estimating potential yield from seamounts and determining how catches have changed in recent years.

## **8.2 MAIN RESULTS**

### ***# 1 Introduction: Seamounts as hotspots of marine life***

Seamounts are underwater volcanoes occurring throughout the world's oceans. In Chapter # 1 I introduced the topic highlighting the main characteristics of seamount ecosystems. Additionally, I have tried to compile a list of fish species living on seamounts. This is because the designation of "seamount" species has been widely employed, but rigorous criteria used in identifying these taxa have not been defined. The definition of "seamount fishes" may involve a redundancy as we try to define a functional type of label that applies only in part to the ecology of the species: seamount fishes are those individual fishes that live on seamounts. Species that aggregate in association with seamounts and other topographic features have been called "seamount-aggregating" fishes. I compiled a total of 798 species of marine fishes that fall under the classification of seamount fishes and a total of 23 potential seamount-aggregating species. This list is preliminary and its accuracy will improve as we gain more knowledge about the ecology of seamount and deepwater fish species.

### ***#2 Abundances and distribution of seamounts in the Azores***

Seamounts are important areas for conservation and fisheries in the Azores and the knowledge of its location is highly important for implementing management options and for testing hypothesis about ecosystem functioning. In Chapter #2, I characterized the seamount distribution on the Azores Economic Exclusive Zone using two bathymetry datasets. I identified seamount locations from local *maxima* in the bathymetry grid. The algorithm developed showed that peaks and seamounts are common features in the Azores EEZ. The real count average density of 3.3 peaks of all sizes per 1000 km<sup>2</sup> is in the same order of magnitude than obtained in some studies in the Mid Atlantic Ridge. Nevertheless, I was able

to map and describe 63 large and 332 small seamount-like features in the EEZ of the Azores. The distribution suggests that large proportions of seamounts occur in chains along the Mid Atlantic Ridge, however, few isolated seamounts are also present in the Azores. Our distribution of seamounts predicts that about 63% of the potential Azores seamounts are protected against deep water trawling by the European Commission Council Regulation No. 1568/2005.

### ***#3 Modelled effects of primary and secondary production enhancement by seamounts on local fish stocks***

Chapter #3 addresses how large aggregations of fish found on many seamounts are sustained. I used a generic seamount ecosystem model from the Northeast Atlantic to examine the impact of a potential increase of local primary production on higher trophic levels, to quantify the immigration of micronekton that would be required to maintain a “typical” seamount community, and to quantify if the necessary immigration ratios could be supported by local oceanographic conditions. The results indicate lack of resources in the system to support large amounts of seamount aggregating fish. In other words, local seamount production may be responsible for sustaining only a small amount of its total biomass. Additionally, our study supports the idea that enhancement of primary productivity can also not sustain large aggregations of seamount fishes. The seamount model, which took into account high abundances of fish, marine mammals, seabirds and tuna, required a total immigration of micronekton of  $95.2 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$  less than the potential available biomass after considering currents of  $141.5 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ . Therefore, I suggest that the horizontal flux of prey is sufficient to sustain the rich communities living on seamounts. Additionally, the simulation results suggest that food may not be a limiting factor for fish aggregations at intermediate seamounts. I discussed what could influence seamount fish abundance and explain the high variability of abundances from one seamount to the other.

### ***# 4 Testing a seamount effect on aggregating visitors***

The importance of seamounts for large pelagic or visiting organisms has been poorly tested. However, it has been hypothesised higher abundances of some “visiting” animals, such as

tuna, sharks, billfishes, marine mammals, sea-turtles and even seabirds, over seamounts. Surprisingly, this has been based on some sparse records, warranting further examination. In Chapter #4 I tested if the predicted high abundances of tuna, marine mammals, sea turtles and seabirds on top and around the Azores seamounts are true. This study has demonstrated that some marine predators are associated with shallow waters seamounts. This was the case of tuna species skipjack and bigeye, common dolphin and Cory's shearwater. These species were significantly more abundant in the vicinity of some seamount summits than far from these features. The methodology developed, however, failed to demonstrate seamounts' association for bottlenose dolphins, spotted dolphin, sperm whale, terns, yellow-legged gull, and loggerhead sea turtles. Seamounts play a major role in localizing pelagic prey and thus attracting some pelagic fish, seabirds and marine mammals. Therefore, some seamounts in the Azores may act as feeding stations for some of these visitors. Not all seamounts, however, seemed to be equally important for these associations. Only seamounts shallower than 400m depth showed significant aggregation effects. The important seamounts in the Azores for these visitors are "Princesa Alice" and "Açores" for all four species, also "D. João de Castro" for both tuna species, "Formigas and Dollabarat" and "Pico Leste" of the Princesa Alice for skipjack, and "Agulhas do Sul do Gigante" for common dolphin. These seamounts should be considered hotspots of marine life in the Azores and a special effort should be made in order to ensure a sustainable management of these habitats.

#### ***# 5 Fishing down the deep***

With the decline of shallow coastal waters resources, increasing demand, and new technology, fisheries are evidently expanding offshore and into deeper waters. In particular, seamounts are among those "newly" targeted ecosystems. However, information on seamounts fisheries is very sparse, and it is difficult to make a distinction between deep-water fishing activities in general and those occurring on seamounts. Moreover, fish species living on seamounts are also known to occur on other habitats, such as continental slope, and landings statistics are not spatially allocated, making it difficult to make an estimate of the total fisheries occurring on seamounts worldwide. The expansion into offshore areas has been well documented, but the extension into deeper waters is less well analysed. Whereas

previous studies on global trends of fisheries have focused on catch or biomass changes over time, in Chapter #5 I have analysed changes in the mean depth of fishing to test if the predicted expansion into deeper-waters can be detected in global landings datasets. I also tested for the predicted higher vulnerability of deep-water fisheries resources, using longevity as the main proxy for vulnerability. Global landings of demersal marine fishes are demonstrated to have shifted to deeper water species over the last 50 years. Our analysis suggests deep-water fish stocks may be at serious risk of depletion, since their life histories render them highly vulnerable to overfishing with little resilience to overexploitation. Deep-sea fisheries are exploiting the last refuges for commercial fish species and should not be seen as a replacement for declining resources in shallower waters. Instead, deep-water habitats are new candidates for conservation.

#### ***# 6 Vulnerability of seamount fish to fishing: fuzzy analysis of life history attributes***

Chapter #6 attempts to test the hypothesis that “seamount fishes” generally have a high vulnerability to exploitation and that this is correlated with their life history characteristics. Despite rather broad definitions, global analysis shows that “seamount fishes”, particularly “seamount-aggregating” fishes, have higher intrinsic vulnerability than other groups of fishes. The pattern is similar when considering only commercially exploited species. Biological characteristics leading to greater vulnerability include a longer lifespan, later sexual maturation, slower growth and lower natural mortality. This research supports the contention that “seamount fishes”, especially those that aggregate on seamounts, are highly vulnerable to exploitation and that fishing on seamounts may not be sustainable at current levels and with current methods. A number of seamount populations have already been depleted; more depletion, extirpations, and even species extinctions may follow if fishing on seamounts is not reduced.

#### ***# 7 Ecosystem simulations of management strategies for data-limited seamount fisheries***

Traditional fisheries stock assessment requires large amounts of information, mainly from long-term data series, a requirement that is hard to apply to new or poorly-documented fishing grounds. In Chapter #7 I investigate if ecosystem simulations can help to understand

the impact of fishing on pristine seamounts. Using ecosystem modelling tools, data gathered from elsewhere, and methods that search for optimal fishing policies, I explored what types of fisheries might be sustainable on seamounts. Although the analyses in this paper are not meant to describe actual fisheries for seamounts, some generalizations can be made. Simulations with policy objectives that maximize economic performance favour fleet configurations based on deepwater trawling, but entail a cost to biodiversity. Maximizing ecological performance favours fleets on based on small pelagic and bottom longline fisheries, and maximizes biomass of long-lived species and biodiversity, but sacrifices total catches and jobs. The overall study suggested that sustainable seamount fisheries with tolerable ecosystem impacts appear to be closer to those found by maximizing an 'ecological' objective function.

### **8.3 CONCLUSIONS**

In conclusion, this PhD have shown that the primary production enhancement by seamounts is not sufficient to support the well-documented large aggregations of fish; my work supports the alternative hypothesis that the horizontal flux of prey is the key factor sustaining the rich communities living on seamounts. This PhD has also demonstrated the importance of seamounts to some large pelagic fish, marine mammals and seabirds. Fisheries exploitation is a major threat to seamount ecosystems, however I was not able to quantify the amount of catches taken from the seamounts around the world. Instead, I was able to demonstrate that global landings of demersal marine fishes have shifted to deeper water species over the last 50 years. This result is an indirect indication that seamounts have also increased in commercial importance over the last years. I have also demonstrated that "deep-water", "seamount" and "seamount-aggregating" fish stocks may be at serious risk of depletion, since their life histories render them highly vulnerable to overfishing, and provide with little resilience to overexploitation. Finally, ecosystem modelling analyses showed that sustainable seamount fisheries with tolerable ecosystem impacts appear to be closer to those found by maximizing an 'ecological' objective function. This suggested that industrial-scale fishery



cannot be supported by seamount. However, some regulated small-scale artisanal like fleet could be supported by seamounts ecosystems.

#### **8.4 FUTURE RESEARCH**

Despite considerable recent research effort, including that presented in this thesis, our knowledge on seamounts ecosystems is still limited when compared to coastal / shallow ecosystems. A landmark on seamounts research was the launch in 2005 of a Global Census of Marine Life on Seamounts (CenSeam). This program was build towards “a global understanding of seamount ecosystems, and the roles they have in biogeography, biodiversity, productivity, and evolution of marine organisms.” The CenSeam project along with SeamountsOnline (an online information system for seamount biology) will hopefully help in the development of new understandings on seamount ecosystems.

In my view, three goals should guide the future work on seamounts:

##### **1 – Assess and monitor biodiversity both at global and local scales**

A detailed catalogue of species occurring on seamounts should be the top priority when assessing these habitats. This should 1) produce exhaustive lists of species living seamounts; 2) help findings new species to science; 3) identify the fraction of endemic species living on seamounts. This task could involve 1) the synthesis of seamount studies that have been conducted and 2) promote field efforts to improve our knowledge on the species inhabiting worldwide seamounts.

##### **2- Increase understanding of seamount ecosystem functioning in terms of productivity and the underlying biological characteristics**

Extensive experimental fieldwork should be carried in different seamounts around the world to examine particular aspects of seamount ecosystem functioning that are not yet well understood. Topics to be addressed should include 1) examine zooplankton biomass over and around seamounts, with emphasis to fish larvae biomass; 2) using tagging techniques to better examine tuna, swordfish, sharks, aggregations on seamounts; 3)

understand how cephalopods interact with seamounts; 4) better examine the importance of seamounts for marine mammals, seabirds and sea-turtles; 5) better understanding the importance of corals and other epibenthic megafauna to the seamount biota; 6) to validate the assumption that seamount fish biomass are supported by bottom trapping of migrating zooplankton and by the horizontal flux of non-migrating zooplankton.

## 2 – Assess the human impacts on seamount communities both at global and local scales

Describing the catch of fishes from worldwide seamounts presents a major challenge, because information on seamounts fisheries is very sparse, and it is difficult to make a distinction between deep-water fishing activities in general and those occurring on seamounts. We should be able 1) to quantify total catches from world's seamounts and 2) to quantify catches from selected individual seamounts. The first goal could be achieved by automated mapping techniques as the ones developed by the Sea Around Us Project at the University of British Columbia. This algorithm could then be run to analyses the development of fishing catches from seamounts. The second goal could only be achieved with information from fishing vessels, i.e., where individual fishing vessels were operating. This could be accomplished by analyzing satellite tracking of fishing vessels along with data from landings. This could produce the first dataset with real information of catches from individual seamounts and would help identifying those seamounts that are under most threats.

## 3 - Long term monitoring of seamount communities

There is also an urgent need for the establishment of long-term programmes to assess population trends of selected species in seamounts as a whole or in reference sites subject to different ecological and exploitation regimes. For the later, focus could be on seamounts where exploitation is more intense. Selected species should be those more vulnerable and those that are likely to be heavily damaged by fishing activities. The methodologies involved in assessing the status of the communities and species should be standardized and involve *in situ* observations using advanced technology such as ROV's and submersibles.

## APPENDIX 1

### COMPILATION OF FISH SPECIES RECORDED ON SEAMOUNTS

**Table 1** - List of species considered as *S* "seamount fishes" and *AGG* "seamount-aggregating" fishes. Intrinsic Vulnerability ( $V_i$ ) index and \*  $V_i$  excluding species from only Total length infinity is available, are also presented.

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Acanthocybium solandri</i>	S	Pelagic	50.22	50.22
<i>Acantholabrus palloni</i>	S	Reef-associated	16.29	
<i>Acanthurus olivaceus</i>	S	Reef-associated	32.23	
<i>Acromycter perturbator</i>	S	Bathydemersal	76.17	
<i>Adelosebastes latens</i>	S	Bathydemersal	21.45	
<i>Ahliesaurus berryi</i>	S	Bathypelagic	18.25	
<i>Albatrossia pectoralis</i>	S	Bathydemersal	90	90
<i>Aldrovandia affinis</i>	S	Bathydemersal	40	
<i>Aldrovandia oleosa</i>	S	Bathypelagic	40	
<i>Aldrovandia phalacra</i>	S	Bathydemersal	40	
<i>Aldrovandia rostrata</i>	S	Bathypelagic	64.7	
<i>Alepisaurus brevirostris</i>	S	Pelagic	60	
<i>Alepocephalus agassizii</i>	S	Bathydemersal	52.62	
<i>Alepocephalus australis</i>	S	Bathydemersal	44.89	
<i>Alepocephalus bairdii</i>	AGG	Bathydemersal	71.14	76.97
<i>Alepocephalus productus</i>	S	Bathydemersal	32.77	
<i>Alepocephalus rostratus</i>	S	Bathydemersal	10	10
<i>Alepocephalus tenebrosus</i>	S	Bathydemersal	49.55	49.55
<i>Allocyttus niger</i>	AGG	Bathypelagic	40	62.35
<i>Allocyttus verrucosus</i>	AGG	Bathypelagic	40	65.75
<i>Amphichaetodon howensis</i>	S	Reef-associated	10	
<i>Anarhichas denticulatus</i>	S	Benthopelagic	82.43	82.43
<i>Anarrhichthys ocellatus</i>	S	Demersal	90	90
<i>Anatolanthias apiomycter</i>	S	Pelagic		
<i>Anoplogaster cornuta</i>	S	Bathypelagic	42	42
<i>Anoplopoma fimbria</i>	S	Bathydemersal	62.24	62.24
<i>Anthias anthias</i>	S	Reef-associated	18.35	
<i>Antigonia aurorosea</i>	S	Bathydemersal		

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Antigonia capros</i>	S	Demersal	21.97	
<i>Antigonia eos</i>	S	Bathydemersal		
<i>Antigonia malayana</i>	S	Demersal		
<i>Antigonia rubescens</i>	S	Bathydemersal	10	
<i>Antimora microlepis</i>	S	Bathypelagic	51	
<i>Antimora rostrata</i>	S	Bathypelagic	49.89	49.89
<i>Aphanopus capricornis</i>	S	Bathypelagic	52.13	
<i>Aphanopus carbo</i>	AGG	Benthopelagic	74.48	54.09
<i>Aphanopus intermedius</i>	S	Bathypelagic	73.91	
<i>Aphareus furca</i>	S	Reef-associated	29.48	
<i>Aprion virescens</i>	S	Reef-associated	40.73	40.73
<i>Apristurus brunneus</i>	S	Demersal	48.15	
<i>Apristurus laurussonii</i>	S	Bathydemersal	48.15	
<i>Apristurus manis</i>	S	Bathydemersal	55.06	
<i>Apristurus profundorum</i>	S	Bathydemersal		
<i>Aptocyclus ventricosus</i>	S	Benthopelagic	32.26	
<i>Arctozenus rissø</i>	S	Bathypelagic	34.41	
<i>Argentina sphyraena</i>	S	Bathydemersal	37.09	37.09
<i>Argyripnus atlanticus</i>	S	Benthopelagic	50	
<i>Argyripnus electronus</i>	S	Bathydemersal		
<i>Argyripnus iridescent</i>	S	Bathypelagic	10	
<i>Argyropelecus aculeatus</i>	S	Bathypelagic	10	
<i>Argyropelecus affinis</i>	S	Bathypelagic	17.57	17.57
<i>Argyropelecus gigas</i>	S	Bathypelagic	10	
<i>Argyropelecus hemigymnus</i>	S	Bathypelagic	10	10
<i>Argyropelecus lychnus</i>	S	Bathypelagic	10	
<i>Ariomma bondi</i>	S	Demersal	55.73	
<i>Ariomma lurida</i>	S	Bathypelagic	26.6	
<i>Ariomma melanum</i>	S	Bathydemersal	21.45	
<i>Ariosoma balearicum</i>	S	Reef-associated	26.6	
<i>Ariosoma marginatum</i>	S	Demersal	29.69	
<i>Aristostomias tittmanni</i>	S	Pelagic	10	
<i>Arnoglossus imperialis</i>	S	Demersal	16.29	
<i>Arnoglossus multirastris</i>	S	Demersal	76.67	
<i>Arnoglossus rueppelii</i>	S	Demersal	10	
<i>Arnoglossus septemventralis</i>	S	Bathydemersal	80.42	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Arothron firmamentum</i>	S	Demersal	26.6	
<i>Aspitrigla cuculus</i>	S	Demersal	32.41	32.41
<i>Assurger anzac</i>	S	Benthopelagic	90	
<i>Astronesthes gemmifer</i>	S	Bathypelagic	10	
<i>Astronesthes ijimai</i>	S	Bathypelagic	10	
<i>Astronesthes macropogon</i>	S	Bathypelagic	10	
<i>Atheresthes stomias</i>	S	Demersal	54.65	54.65
<i>Aulopus filamentosus</i>	S	Demersal	40	
<i>Aulopus japonicus</i>	S	Demersal	90	
<i>Aulostomus chinensis</i>	S	Reef-associated	53.03	
<i>Avocettina bowersii</i>	S	Bathypelagic		
<i>Avocettina infans</i>	S	Bathypelagic	50.79	
<i>Bajacalifornia megalops</i>	S	Bathypelagic	31.74	
<i>Balistes capriscus</i>	S	Reef-associated	27.73	27.73
<i>Banjós banjos</i>	S	Demersal	10	
<i>Barbantus curvifrons</i>	S	Bathypelagic	10	
<i>Bassogigas gillii</i>	S	Bathydemersal	55.06	
<i>Bathophilus flemingi</i>	S	Bathypelagic	29.17	29.17
<i>Bathophilus longipinnis</i>	S	Bathypelagic	10	
<i>Bathophilus pawneeii</i>	S	Bathypelagic	10	
<i>Bathygadus favosus</i>	S	Bathydemersal	40	
<i>Bathygadus melanobranchus</i>	S	Bathydemersal	40	
<i>Bathylagus euryops</i>	S	Bathypelagic	40	
<i>Bathylagus pacificus</i>	S	Bathypelagic	43.12	43.12
<i>Bathymicrops regis</i>	S	Bathydemersal	10	
<i>Bathypterois atricolor</i>	S	Bathydemersal	10	
<i>Bathypterois dubius</i>	S	Bathydemersal	32.77	32.77
<i>Bathypterois longipes</i>	S	Bathydemersal	16.18	
<i>Bathypterois phenax</i>	S	Bathydemersal	10	
<i>Bathypterois quadrifilis</i>	S	Bathydemersal	10	
<i>Bathyraja shuntovi</i>	S	Bathydemersal	81.35	
<i>Bathysaurus ferox</i>	S	Bathydemersal	46.52	
<i>Bathytroctes oligolepis</i>	S	Bathypelagic	23.82	
<i>Bathytyphlops marionae</i>	S	Bathydemersal	29.69	
<i>Bellottia apoda</i>	S	Bathydemersal	34.18	
<i>Bembradium furici</i>	S	Bathydemersal		

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Bembradium roseum</i>	S	Bathydemersal	10	
<i>Bembrops filifera</i>	S	Bathydemersal	10	
<i>Benthalbella dentata</i>	S	Bathypelagic	10	
<i>Benthodesmus elongatus</i>	S	Bathydemersal	64.72	64.72
<i>Benthodesmus tenuis</i>	S	Bathydemersal	90	
<i>Benthoosema glaciale</i>	S	Pelagic	28.72	28.72
<i>Beryx decadactylus</i>	AGG	Bathydemersal	60	74.07
<i>Beryx splendens</i>	AGG	Bathydemersal	59.53	66.84
<i>Bodianus bilunulatus</i>	S	Reef-associated	40	
<i>Bodianus cylindriatus</i>	S	Reef-associated	10	
<i>Bolinichthys photothorax</i>	S	Bathypelagic	10	
<i>Bonapartia pedaliota</i>	S	Bathypelagic	10	
<i>Borostomias antarcticus</i>	S	Bathydemersal	21.45	
<i>Bothrocara brunneum</i>	S	Bathydemersal	47.33	
<i>Bothrocara molle</i>	S	Bathydemersal	40	
<i>Brama brama</i>	S	Bathypelagic	53.16	53.16
<i>Brosme brosme</i>	S	Demersal	54.22	54.22
<i>Brotulotaenia brevicauda</i>	S	Bathypelagic	52.74	
<i>Brotulotaenia crassa</i>	S	Bathypelagic	55.46	
<i>Caelorinchus bollonsi</i>	S	Benthopelagic	60	
<i>Caelorinchus caelorhincus caelorhincus</i>	S	Benthopelagic	50.49	50.49
<i>Caelorinchus celaenostomus</i>	S	Bathydemersal	51.76	
<i>Caelorinchus fasciatus</i>	S	Bathydemersal	40	
<i>Caelorinchus immaculatus</i>	S	Bathydemersal	50.09	
<i>Caelorinchus innotabilis</i>	S	Bathydemersal	23.51	
<i>Caelorinchus kaiyomaru</i>	S	Bathydemersal	40	
<i>Caelorinchus labiatus</i>	S	Bathydemersal	40	
<i>Caelorinchus matamua</i>	S	Bathydemersal	46.92	
<i>Caelorinchus multifasciatus</i>	S	Bathydemersal	10	
<i>Caelorinchus nazcaensis</i>	S	Bathypelagic	31.74	
<i>Caelorinchus spilonotus</i>	S	Bathydemersal	10	
<i>Caelorinchus trachycarus</i>	S	Bathydemersal	40	
<i>Callanthias parini</i>	S	Reef-associated	43.33	
<i>Callanthias ruber</i>	S	Demersal	44.89	
<i>Callionymus maculatus</i>	S	Demersal	10	
<i>Canthigaster callisterna</i>	S	Demersal	10	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Canthigaster coronata</i>	S	Reef-associated	10	
<i>Canthigaster epilampra</i>	S	Reef-associated	10	
<i>Canthigaster rivulata</i>	S	Reef-associated	10	
<i>Caprodon longimanus</i>	S	Reef-associated	40	
<i>Caprodon schlegelii</i>	S	Benthopelagic	26.6	
<i>Capros aper</i>	S	Demersal	55.73	
<i>Carangoides orthogrammus</i>	S	Reef-associated	30.5	
<i>Caranx ignobilis</i>	S	Reef-associated	61.4	61.4
<i>Caranx lugubris</i>	S	Reef-associated	53.38	53.38
<i>Caranx melampygus</i>	S	Reef-associated	45.28	45.28
<i>Careproctus melanurus</i>	S	Bathydemersal	29.26	29.26
<i>Caristius maderensis</i>	S	Pelagic	56.76	
<i>Cataetyx laticeps</i>	S	Bathydemersal	26.6	
<i>Centracanthus cirrus</i>	S	Demersal	25.57	
<i>Centroberyx affinis</i>	S	Benthopelagic	61.77	61.77
<i>Centrodraco acanthopoma</i>	S	Bathydemersal	10	
<i>Centrodraco nakaboi</i>	S	Bathydemersal		
<i>Centrodraco otohime</i>	S	Bathydemersal	10	
<i>Centrodraco striatus</i>	S	Bathydemersal	43.33	
<i>Centrolophus niger</i>	S	Bathypelagic	50	
<i>Centrophorus granulosus</i>	S	Bathydemersal	90	
<i>Centrophorus squamosus</i>	S	Benthopelagic	90	90
<i>Centroscyllium fabricii</i>	S	Bathydemersal	79.32	79.32
<i>Centroscyllium ritteri</i>	S	Demersal	49.37	
<i>Centroscymnus coelolepis</i>	S	Bathydemersal	80.4	80.4
<i>Centroscymnus crepidater</i>	S	Bathydemersal	83.94	83.94
<i>Centroscymnus cryptacanthus</i>	S	Bathydemersal	71.92	
<i>Centroscymnus owstoni</i>	S	Bathydemersal	74.44	
<i>Centroscymnus plunketi</i>	S	Bathydemersal	78.83	78.83
<i>Ceratoscopelus maderensis</i>	S	Bathypelagic	50	
<i>Ceratoscopelus warmingii</i>	S	Bathypelagic	10	
<i>Cetonus crassiceps</i>	S	Bathydemersal	40	
<i>Cetorhinus maximus</i>	S	Pelagic	60.53	60.53
<i>Cetostoma regani</i>	S	Bathypelagic	18.02	18.02
<i>Chaetodon fremblii</i>	S	Reef-associated	10	
<i>Chaetodon kleinii</i>	S	Reef-associated	10	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Chaetodon miliaris</i>	S	Reef-associated	51.89	51.89
<i>Chascanopsetta megagnatha</i>	S	Bathymersal	10	
<i>Chascanopsetta prorigera</i>	S	Bathymersal	10	
<i>Chauliodus macouni</i>	S	Bathypelagic	31.05	31.05
<i>Chauliodus sloani</i>	S	Bathypelagic	26.6	
<i>Chaunax fimbriatus</i>	S	Bathymersal	10	
<i>Chaunax latipunctatus</i>	S	Bathymersal		
<i>Chaunax pictus</i>	S	Bathymersal	31.74	
<i>Chaunax umbrinus</i>	S	Demersal		
<i>Chelidonichthys gurnardus</i>	S	Demersal	37.07	37.07
<i>Chelidoperca lecromi</i>	S	Demersal	10	
<i>Chiasmodon niger</i>	S	Bathypelagic	16.29	
<i>Chimaera lignaria</i>	S	Bathymersal	90	
<i>Chimaera monstrosa</i>	S	Bathymersal	50	
<i>Chimaera owstoni</i>	S	Bathymersal	60	
<i>Chirostomias pliopterus</i>	S	Bathypelagic	10	
<i>Chlamydoselachus anguineus</i>	S	Bathymersal	90	90
<i>Chlopsis bicolor</i>	S	Demersal	33.8	
<i>Chlorophthalmus agassizi</i>	S	Bathymersal	60.87	
<i>Chlorophthalmus albatrossis</i>	S	Demersal	10	
<i>Chlorophthalmus ichthyandri</i>	S	Demersal	76.67	
<i>Chlorophthalmus zvezdae</i>	S	Demersal	76.67	
<i>Chrionema pallidum</i>	S	Bathymersal	10	
<i>Chromis verater</i>	S	Reef-associated	32.22	
<i>Coccorella atlantica</i>	S	Bathypelagic	10	
<i>Conger conger</i>	S	Demersal	81.18	81.18
<i>Conger oligoporus</i>	S	Reef-associated		
<i>Conocara macropterus</i>	S	Bathypelagic	25.57	
<i>Cookeolus japonicus</i>	S	Reef-associated	48.15	48.15
<i>Coris ballieui</i>	S	Reef-associated	21.45	
<i>Coryphaena hippurus</i>	S	Pelagic	50	50
<i>Coryphaenoides acrolepis</i>	S	Bathymersal	79.66	79.66
<i>Coryphaenoides alatalis</i>	S	Bathymersal	17.84	
<i>Coryphaenoides armatus</i>	S	Bathymersal	60	
<i>Coryphaenoides carapinus</i>	S	Bathymersal	40	
<i>Coryphaenoides cinereus</i>	S	Bathymersal	40	



Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Coryphaenoides guentheri</i>	S	Bathydemersal	36.18	36.18
<i>Coryphaenoides longifilis</i>	S	Bathydemersal	48.96	
<i>Coryphaenoides murrayi</i>	S	Bathydemersal	28.66	
<i>Coryphaenoides rudis</i>	S	Bathypelagic	68.38	
<i>Coryphaenoides rupestris</i>	AGG	Bathypelagic	75.4	76.25
<i>Coryphaenoides serrulatus</i>	S	Bathydemersal	40	
<i>Coryphaenoides subserrulatus</i>	S	Bathydemersal	28.66	
<i>Cottunculus thomsonii</i>	S	Bathydemersal	26.6	
<i>Cryptopsaras couesii</i>	S	Bathypelagic	35	35
<i>Cubiceps pauciradiatus</i>	S	Bathypelagic	10	
<i>Cyclothone braueri</i>	S	Bathypelagic	10	10
<i>Cyclothone microdon</i>	S	Bathypelagic	10	10
<i>Cyclothone pallida</i>	S	Bathypelagic	27.5	27.5
<i>Cyttomimus stelgis</i>	S	Bathydemersal	76.67	
<i>Cyrtopsis rosea</i>	S	Bathypelagic	56.24	
<i>Dactylopsaron dimorphicum</i>	S	Bathydemersal	43.33	
<i>Dalatias licha</i>	S	Bathydemersal	72.94	72.94
<i>Dasyatis pastinaca</i>	S	Demersal	67.52	67.52
<i>Deania calcea</i>	S	Bathydemersal	78.24	78.24
<i>Deania profundorum</i>	S	Bathydemersal	71.31	71.31
<i>Decapterus macarellus</i>	S	Pelagic	43.85	43.85
<i>Decapterus maruadsi</i>	S	Reef-associated	29.34	29.34
<i>Decapterus muroadsi</i>	S	Pelagic	65.51	
<i>Decapterus russelli</i>	S	Reef-associated	14.75	14.75
<i>Dendrochirus barberi</i>	S	Reef-associated	10	
<i>Derichthys serpentinus</i>	S	Bathypelagic	31.74	
<i>Diaphus adenomus</i>	S	Bathypelagic	10	
<i>Diaphus brachycephalus</i>	S	Bathypelagic	10	
<i>Diaphus confusus</i>	S	Bathydemersal		
<i>Diaphus dumerilii</i>	S	Pelagic	10	10
<i>Diaphus lucidus</i>	S	Bathypelagic	10	
<i>Diaphus parini</i>	S	Benthopelagic		
<i>Diaphus perspicillatus</i>	S	Bathypelagic	10	
<i>Diaphus rafinesquii</i>	S	Bathypelagic	10	
<i>Diaphus splendidus</i>	S	Bathypelagic	10	
<i>Diaphus theta</i>	S	Bathypelagic	10	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Diastobranchus capensis</i>	S	Bathydemersal	76.86	
<i>Dibranchius tremendus</i>	S	Bathydemersal	10	
<i>Dicrolene introniger</i>	S	Bathydemersal	26.6	
<i>Dicrolene nigra</i>	S	Bathydemersal	45.22	
<i>Diodon holocanthus</i>	S	Reef-associated	24.69	
<i>Diplospinus multistriatus</i>	S	Bathypelagic	35.98	35.98
<i>Dipturus batis</i>	S	Demersal	79.58	79.58
<i>Dipturus oxyrinchus</i>	S	Bathydemersal	90	
<i>Dirtmichthys parini</i>	S	Bathypelagic	31.74	
<i>Dirtmus argenteus</i>	S	Bathypelagic	17.58	
<i>Dissostichus eleginoides</i>	AGG	Pelagic	78.84	68.94
<i>Dolicholagus longirostris</i>	S	Bathypelagic	10	
<i>Dolichopteryx longipes</i>	S	Bathypelagic	25	25
<i>Echinorhinus cookei</i>	S	Demersal	90	
<i>Echiodon dentatus</i>	S	Demersal	10	
<i>Echiostoma barbatum</i>	S	Bathypelagic	28.45	
<i>Ectreposebastes imus</i>	S	Bathypelagic	10	
<i>Einara macrolepis</i>	S	Bathypelagic	34.74	
<i>Emmelichthys elongatus</i>	S	Demersal		
<i>Emmelichthys nitidus cyanescens</i>	S	Bathydemersal	51.22	
<i>Emmelichthys nitidus nitidus</i>	S	Bathydemersal	65.51	
<i>Emmelichthys struhsakeri</i>	S	Demersal	21.45	
<i>Engyprosope regani</i>	S	Demersal	76.67	
<i>Enigmapercis acutirostris</i>	S	Bathydemersal	76.67	
<i>Eopsetta jordani</i>	S	Demersal	64.92	64.92
<i>Epigonus atherinoides</i>	S	Bathydemersal	10	
<i>Epigonus denticulatus</i>	S	Bathydemersal	10	
<i>Epigonus elegans</i>	S	Bathydemersal		
<i>Epigonus notacanthus</i>	S	Bathydemersal	10	
<i>Epigonus robustus</i>	S	Bathydemersal	10	
<i>Epigonus telescopus</i>	AGG	Bathydemersal	51	51
<i>Epinephelus quernus</i>	S	Demersal	75.05	
<i>Epinephelus septemfasciatus</i>	S	Reef-associated	90	
<i>Erilepis zonifer</i>	S	Bathydemersal	90	
<i>Etelis carbunculus</i>	S	Reef-associated	70.9	70.9
<i>Etelis coruscans</i>	S	Reef-associated	63.22	63.22

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Etmopterus baxteri</i>	S	Bathydemersal	51	
<i>Etmopterus gracilispinis</i>	S	Benthopelagic	26.6	
<i>Etmopterus litvinovi</i>	S	Bathydemersal		
<i>Etmopterus lucifer</i>	S	Bathydemersal	65.46	
<i>Etmopterus princeps</i>	S	Bathydemersal	51	
<i>Etmopterus pusillus</i>	S	Bathydemersal	40	
<i>Etmopterus pycnolepis</i>	S	Bathydemersal		
<i>Etmopterus spinax</i>	S	Bathydemersal	66.56	66.56
<i>Eurypharynx pelecانoides</i>	S	Bathypelagic	60	
<i>Eurypleuron owasianum</i>	S	Bathydemersal	10	
<i>Eustomias obscurus</i>	S	Bathypelagic	10	
<i>Eustomias schmidtii</i>	S	Bathypelagic	10	
<i>Euthynnus affinis</i>	S	Reef-associated	59.78	59.78
<i>Evistias acutirostris</i>	S	Reef-associated	33.04	
<i>Facciolella castlei</i>	S	Demersal	76.67	
<i>Fistularia commersonii</i>	S	Reef-associated	90	
<i>Fistularia petimba</i>	S	Reef-associated	90	
<i>Flagellostomias boureei</i>	S	Bathypelagic	23.72	
<i>Foetorepus kanmuensis</i>	S	Bathydemersal	10	
<i>Foetorepus kinmeiensis</i>	S	Bathydemersal	10	
<i>Gadella maraldi</i>	S	Benthopelagic	21.45	
<i>Gadella norops</i>	S	Benthopelagic	18.15	
<i>Gadella obscurus</i>	S	Benthopelagic	10	
<i>Gadiculus argenteus thori</i>	S	Pelagic	16.38	16.38
<i>Gadomus aoteanus</i>	S	Benthopelagic	60	
<i>Gadomus arcuatus</i>	S	Bathypelagic	44.07	
<i>Gadomus dispar</i>	S	Bathydemersal	77.28	
<i>Gadomus melanopterus</i>	S	Bathydemersal		
<i>Gadus macrocephalus</i>	S	Demersal	54.58	54.58
<i>Gaidropsarus argentatus</i>	S	Bathydemersal	26.6	
<i>Gaidropsarus ensis</i>	S	Benthopelagic	31.74	
<i>Gaidropsarus granti</i>	S	Demersal	27.63	
<i>Gaidropsarus macrophthalmus</i>	S	Demersal	16.29	
<i>Gaidropsarus mediterraneus</i>	S	Demersal	23.75	23.75
<i>Gaidropsarus parini</i>	S	Demersal		
<i>Galeorhinus galeus</i>	S	Benthopelagic	72.2	72.2

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Galeus melastomus</i>	S	Bathydemersal	51	
<i>Galeus murinus</i>	S	Bathydemersal	68.05	
<i>Gephyroberyx darwinii</i>	S	Benthopelagic	44.89	
<i>Gephyroberyx japonicus</i>	S	Benthopelagic	10	
<i>Gigantura indica</i>	S	Bathypelagic	15.1	15.1
<i>Glossanodon danieli</i>	S	Bathydemersal	10	
<i>Glossanodon leioglossus</i>	S	Bathydemersal	10	
<i>Glossanodon nazca</i>	S	Bathydemersal		
<i>Glyptocephalus cynoglossus</i>	S	Demersal	60.18	60.18
<i>Gnathophis andriashevi</i>	S	Bathydemersal	76.67	
<i>Gnathophis cinctus</i>	S	Demersal	33.8	
<i>Gnathophis codoniphorus</i>	S	Demersal		
<i>Gnathophis mystax</i>	S	Demersal	44.89	
<i>Gnathophis parini</i>	S	Bathydemersal	43.33	
<i>Gnathophis smithi</i>	S	Demersal	54.77	
<i>Gonichthys cocco</i>	S	Bathypelagic	10	
<i>Goniistius vittatus</i>	S	Reef-associated	32.77	
<i>Gonostoma bathyphilum</i>	S	Bathypelagic	10	
<i>Gonostoma denudatum</i>	S	Bathypelagic	10	
<i>Gonostoma elongatum</i>	S	Bathypelagic	18.87	
<i>Grammatonotus laysanus</i>	S	Demersal	75.18	
<i>Grammatostomias dentatus</i>	S	Bathypelagic	50	
<i>Grammicolepis brachiusculus</i>	S	Bathypelagic	46.52	
<i>Gymnothorax flavimarginatus</i>	S	Reef-associated	90	
<i>Gymnothorax hepaticus</i>	S	Reef-associated	60	
<i>Gymnothorax maderensis</i>	S	Demersal	60	
<i>Gymnothorax punctatofasciatus</i>	S	Reef-associated	40	
<i>Gymnothorax steindachneri</i>	S	Reef-associated	60	
<i>Halargyreus johnsonii</i>	S	Bathypelagic	40	
<i>Halosauropsis macrochir</i>	S	Bathydemersal	60	
<i>Haplomacrourus nudirostris</i>	S	Bathypelagic	40	
<i>Harriotta raleighana</i>	S	Bathydemersal	73.84	
<i>Helicolenus avius</i>	S	Bathydemersal		
<i>Helicolenus dactylopterus dactylopterus</i>	S	Bathydemersal	59.44	59.44
<i>Helicolenus fedorovi</i>	S	Bathydemersal	18.35	
<i>Helicolenus lengerichi</i>	S	Bathydemersal	34.58	34.58

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Hemilepidotus hemilepidotus</i>	S	Demersal	40	
<i>Hemilepidotus spinosus</i>	S	Demersal	20.42	
<i>Heniochus diphreutes</i>	S	Reef-associated	51.48	
<i>Heptanchias perlo</i>	S	Bathydemersal	90	90
<i>Heterophotus ophistoma</i>	S	Bathypelagic	27.22	
<i>Heteropriacanthus cruentatus</i>	S	Reef-associated	24.58	
<i>Hexanchus griseus</i>	S	Reef-associated	77.65	77.65
<i>Himantolophus albinareus</i>	S	Bathypelagic	50.04	
<i>Hippoglossoides platessoides</i>	S	Demersal	65.86	65.86
<i>Hippoglossus hippoglossus</i>	S	Demersal	76.46	76.46
<i>Hippoglossus stenolepis</i>	S	Demersal	79.18	79.18
<i>Hollardia goslinei</i>	S	Demersal		
<i>Holtbyrnia anomala</i>	S	Bathypelagic	52.87	
<i>Holtbyrnia macrops</i>	S	Benthopelagic	10	
<i>Hoplichthys citrinus</i>	S	Demersal	60	
<i>Hoplichthys gilberti</i>	S	Demersal	10	
<i>Hoplostethus atlanticus</i>	AGG	Bathypelagic	63.79	68.65
<i>Hoplostethus crassispinus</i>	S	Bathypelagic	34.97	
<i>Hoplostethus mediterraneus mediterraneus</i>	AGG	Benthopelagic	45.11	66.22
<i>Howella brodiei</i>	S	Bathypelagic	10	10
<i>Hozukius guyotensis</i>	S	Bathydemersal	40	
<i>Hydrolagus affinis</i>	S	Bathydemersal	79.89	
<i>Hydrolagus bemisi</i>	S	Bathydemersal	67.09	
<i>Hydrolagus mirabilis</i>	S	Bathydemersal	29.69	
<i>Hydrolagus pallidus</i>	S	Bathydemersal	83.27	
<i>Hydrolagus trolli</i>	S	Bathydemersal	68.69	
<i>Hygophum hygomii</i>	S	Bathypelagic	10	
<i>Hygophum taaningi</i>	S	Bathypelagic	10	
<i>Hymenocephalus aterrimus</i>	S	Bathypelagic	10	
<i>Hymenocephalus gracilis</i>	S	Bathypelagic	10	
<i>Hymenocephalus italicus</i>	S	Benthopelagic	36.96	36.96
<i>Hymenocephalus longibarbis</i>	S	Benthopelagic	60	
<i>Hymenocephalus longiceps</i>	S	Benthopelagic		
<i>Hymenocephalus neglectissimus</i>	S	Bathydemersal	10	
<i>Hymenocephalus semipellucidus</i>	S	Bathydemersal	10	
<i>Hymenocephalus striatulus</i>	S	Bathypelagic	10	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Hyperoglyphe japonica</i>	S	Benthopelagic	60	
<i>Hyperoglyphe perciformis</i>	S	Pelagic	36.11	
<i>Icichthys australis</i>	S	Pelagic	53.43	
<i>Icosteus aenigmaticus</i>	S	Bathypelagic	79.44	79.44
<i>Idiacanthus fasciola</i>	S	Bathypelagic	40	
<i>Idiolychnus urolampus</i>	S	Pelagic	19.2	
<i>Ilyophis brunneus</i>	S	Bathypelagic	44.07	
<i>Kali indica</i>	S	Bathypelagic	17.47	
<i>Katsuwonus pelamis</i>	S	Pelagic	48.31	48.31
<i>Kentrocapros flavofasciatus</i>	S	Demersal	10	
<i>Kuronezumia pallida</i>	S	Bathydemersal	40	
<i>Lactoria fornasini</i>	S	Reef-associated	10	
<i>Laemonema longipes</i>	S	Bathydemersal	50.79	
<i>Laemonema rhodochir</i>	S	Benthopelagic	10	
<i>Laemonema yarrellii</i>	S	Bathydemersal	50	
<i>Laemonema yuvto</i>	S	Bathydemersal		
<i>Lampadena luminosa</i>	S	Bathypelagic	10	
<i>Lampadena speculigera</i>	S	Bathypelagic	10	
<i>Lampadena urophaos atlantica</i>	S	Bathypelagic	10	
<i>Lampadena urophaos urophaos</i>	S	Pelagic	10	
<i>Lampanyctus photonotus</i>	S	Bathypelagic	10	
<i>Lappanella fasciata</i>	S	Reef-associated	50	
<i>Lepidion eques</i>	AGG	Benthopelagic	40	
<i>Lepidion guentheri</i>	S	Benthopelagic	55.87	
<i>Lepidion inosimae</i>	S	Bathydemersal	45.09	
<i>Lepidion microcephalus</i>	S	Bathydemersal	40	
<i>Lepidion schmidtii</i>	S	Bathydemersal	55.06	
<i>Lepidocybium flavobrunneum</i>	S	Bathypelagic	90	
<i>Lepidophanes guentheri</i>	S	Pelagic	10	10
<i>Lepidopsetta bilineata</i>	S	Demersal	66.75	66.75
<i>Lepidopus calcar</i>	S	Bathydemersal	52.62	
<i>Lepidopus caudatus</i>	S	Bathydemersal	78.61	78.61
<i>Lepidorhombus boschii</i>	S	Demersal	41.98	41.98
<i>Lepidorhombus whiffiagonis</i>	S	Bathydemersal	58.43	58.43
<i>Lepidorhynchus denticulatus</i>	S	Bathypelagic	40	
<i>Leptostomias haplocaulus</i>	S	Pelagic	36.18	

Species	S vs AGG.	Habitat	$V_i$	$V_i^*$
<i>Leptostomias longibarba</i>	S	Bathypelagic	45.64	
<i>Lestrolepis intermedia</i>	S	Bathypelagic	16.29	
<i>Leucoraja circularis</i>	S	Demersal	73.84	
<i>Leucoraja fullonica</i>	S	Bathydemersal	73.84	
<i>Leuroglossus schmidtii</i>	S	Bathypelagic	10	
<i>Lobianchia dofleini</i>	S	Bathypelagic	10	10
<i>Lobianchia gemellarii</i>	S	Bathypelagic	10	
<i>Lophiodes miacanthus</i>	S	Bathydemersal	31.09	
<i>Lophius piscatorius</i>	S	Bathydemersal	68.48	68.48
<i>Lucigadus microlepis</i>	S	Bathydemersal	10	
<i>Lutjanus kasmira</i>	S	Reef-associated	43.94	43.94
<i>Lycodes esmarkii</i>	S	Bathydemersal	51	
<i>Lycodes terraenovae</i>	S	Bathydemersal	40	
<i>Lyconus brachycolus</i>	S	Bathydemersal	36.49	
<i>Macropinna microstoma</i>	S	Bathypelagic	10	
<i>Macroramphosus gracilis</i>	S	Pelagic	42	42
<i>Macroramphosus scolopax</i>	S	Demersal	27.97	27.97
<i>Macrorhamphosodes uradoi</i>	S	Demersal	10	
<i>Macrouroides inflaticeps</i>	S	Bathypelagic	53.06	
<i>Macrourus berglax</i>	S	Benthopelagic	78.08	78.08
<i>Macrourus carinatus</i>	S	Bathydemersal	60	60
<i>Macruronus magellanicus</i>	S	Benthopelagic	71.19	71.19
<i>Macruronus novaezelandiae</i>	S	Benthopelagic	69.18	69.18
<i>Magnisudis atlantica</i>	S	Pelagic	40	
<i>Malacocephalus laevis</i>	S	Bathydemersal	44.89	
<i>Malacosteus niger</i>	S	Bathypelagic	10	
<i>Malthopsis annulifera</i>	S	Bathydemersal	10	
<i>Malthopsis lutea</i>	S	Bathydemersal	10	
<i>Malthopsis tiarella</i>	S	Demersal	10	
<i>Manducus maderensis</i>	S	Bathypelagic	19.28	
<i>Marukawichthys ambulator</i>	S	Bathydemersal	31.55	
<i>Marukawichthys pacificus</i>	S	Bathydemersal	10	
<i>Mataeocephalus acipenserinus</i>	S	Bathypelagic	10	
<i>Maulisia argipalla</i>	S	Bathypelagic	33.08	
<i>Maulisia mauili</i>	S	Bathypelagic	10	
<i>Maulisia microlepis</i>	S	Bathypelagic	44.55	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Maurolicus muelleri</i>	S	Bathypelagic	10	10
<i>Maurolicus rudjakovi</i>	S	Bathypelagic	10	
<i>Maurolicus weitzmani</i>	S	Bathypelagic	10	
<i>Melamphaes lugubris</i>	S	Bathypelagic	10	
<i>Melamphaes microps</i>	S	Bathypelagic	10	
<i>Melamphaes suborbitalis</i>	S	Bathypelagic	10	
<i>Melanocetus murrayi</i>	S	Bathypelagic	10	
<i>Melanogrammus aeglefinus</i>	S	Demersal	43.31	43.31
<i>Melanolagus bericoides</i>	S	Bathypelagic	10	
<i>Melanonus zugmayeri</i>	S	Bathypelagic	19.39	
<i>Melanostigma atlanticum</i>	S	Bathypelagic	10	
<i>Melanostomias bartonbeani</i>	S	Bathypelagic	17.53	
<i>Merluccius australis</i>	S	Benthopelagic	72.28	72.28
<i>Mesobius antipodum</i>	S	Bathypelagic	47.33	
<i>Metavelifer multiradiatus</i>	S	Benthopelagic	19.39	
<i>Microcanthus strigatus</i>	S	Reef-associated	32.22	
<i>Micromesistius poutassou</i>	S	Pelagic	34.1	34.1
<i>Microstomus bathybius</i>	S	Bathydemersal	40	
<i>Microstomus kitt</i>	S	Demersal	40.41	40.41
<i>Microstomus pacificus</i>	S	Demersal	64.75	64.75
<i>Microstomus shuntovi</i>	S	Bathydemersal		
<i>Mirognathus normani</i>	S	Bathypelagic	31.13	
<i>Mitsukurina owstoni</i>	S	Bathydemersal	90	
<i>Mola mola</i>	S	Pelagic	71.33	71.33
<i>Molva dypterygia</i>	S	Demersal	78.39	64.99
<i>Molva macrophthalma</i>	S	Demersal	66.56	
<i>Molva molva</i>	S	Demersal	75.34	75.34
<i>Monocentris reedi</i>	S	Demersal	49.47	49.47
<i>Mora moro</i>	AGG	Bathypelagic	53.03	47.36
<i>Muraena helena</i>	S	Reef-associated	90	
<i>Myctophum affine</i>	S	Bathypelagic	10	
<i>Myctophum selenops</i>	S	Bathypelagic	10	
<i>Myripristis murdjan</i>	S	Reef-associated	19.86	19.86
<i>Nannobranchium atrum</i>	S	Bathypelagic	10	
<i>Nannobranchium cuprarium</i>	S	Bathypelagic	50.82	
<i>Nannobranchium lineatum</i>	S	Bathypelagic	10	



Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Nannobranchium regale</i>	S	Bathypelagic	10	
<i>Nannobranchium ritteri</i>	S	Bathypelagic	10	
<i>Nansenia ardesiaca</i>	S	Benthopelagic	10	
<i>Nansenia candida</i>	S	Bathypelagic	10	
<i>Narcetes stomias</i>	S	Bathypelagic	40	
<i>Naso brevirostris</i>	S	Reef-associated	44.89	
<i>Naso hexacanthus</i>	S	Reef-associated	51	
<i>Naso maculatus</i>	S	Reef-associated	44.89	
<i>Naso unicornis</i>	S	Reef-associated	41.21	41.21
<i>Nealotus tripes</i>	S	Bathypelagic	16.29	
<i>Nemadactylus gayi</i>	S	Demersal	76.67	
<i>Nemichthys scolopaceus</i>	S	Bathypelagic	56	56
<i>Neobythites zonatus</i>	S	Bathydemersal	50.13	
<i>Neocyttus helgae</i>	S	Bathypelagic	55.98	
<i>Neocyttus rhomboidalis</i>	AGG	Bathypelagic	31.74	31.74
<i>Neomerinthe procurva</i>	S	Demersal		
<i>Neoscopelus macrolepidotus</i>	S	Bathypelagic	16.29	
<i>Neoscopelus microchir</i>	S	Bathypelagic	21.97	
<i>Nesiarchus nasutus</i>	S	Bathydemersal	79.89	
<i>Nessorhamphus ingolfianus</i>	S	Bathypelagic	44.8	
<i>Nettastoma falcinaris</i>	S	Bathydemersal	76.67	
<i>Nettastoma parviceps</i>	S	Bathydemersal	53.84	
<i>Nezumia aequalis</i>	S	Benthopelagic	27.63	
<i>Nezumia convergens</i>	S	Bathydemersal	21.45	
<i>Nezumia longebarbata</i>	S	Bathypelagic	32.26	
<i>Nezumia propinqua</i>	S	Bathydemersal	18.35	
<i>Nezumia sclerorhynchus</i>	S	Bathypelagic	44.02	44.02
<i>Normichthys operosus</i>	S	Bathypelagic	10	
<i>Notacanthus bonaparte</i>	S	Bathypelagic	60	
<i>Notacanthus chemnitzii</i>	S	Benthopelagic	73.84	
<i>Notacanthus sexspinis</i>	S	Bathydemersal	44.89	
<i>Notopogon fernandezianus</i>	S	Bathydemersal	10	
<i>Notopogon lilliei</i>	S	Demersal	18.35	
<i>Notopogon xenosoma</i>	S	Bathydemersal	10	
<i>Notoscopelus caudispinosus</i>	S	Bathypelagic	10	
<i>Notoscopelus resplendens</i>	S	Bathypelagic	10	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Odontaspis ferox</i>	S	Bathydemersal	90	
<i>Odontomacrurus murrayi</i>	S	Bathypelagic	46.52	
<i>Omosudis lowii</i>	S	Bathypelagic	10	
<i>Oneirodes macrosteus</i>	S	Bathypelagic	83.27	
<i>Oneirodes thompsoni</i>	S	Bathypelagic	10	
<i>Osopsaron karlik</i>	S	Bathydemersal	43.33	
<i>Ostichthys kaianus</i>	S	Bathydemersal	27.63	
<i>Ostracion cubicus</i>	S	Reef-associated	40	
<i>Oxycheilinus unifasciatus</i>	S	Reef-associated	40	
<i>Oxynotus bruniensis</i>	S	Bathydemersal	67.44	67.44
<i>Pagellus bogaraveo</i>	S	Benthopelagic	54.73	54.73
<i>Pagrus pagrus</i>	S	Reef-associated	38.85	38.85
<i>Parabothus amaokai</i>	S	Demersal	76.67	
<i>Parabothus coarctatus</i>	S	Bathydemersal	10	
<i>Parabrotula plagiophthalmus</i>	S	Bathypelagic	10	
<i>Paraconger macrops</i>	S	Demersal	40	
<i>Paralepis coregonoides</i>	S	Pelagic	40	
<i>Parapercis dockinsi</i>	S	Demersal	43.33	
<i>Parapercis roseoviridis</i>	S	Demersal	31.09	
<i>Parapristipomoides squamimaxillaris</i>	S	Reef-associated	39.4	
<i>Paraulopus filamentosus</i>	S	Bathydemersal	31.09	
<i>Parupeneus chrysonemus</i>	S	Demersal		
<i>Parupeneus multifasciatus</i>	S	Reef-associated	37.06	
<i>Parupeneus pleurostigma</i>	S	Reef-associated	24.54	
<i>Parupeneus porphyreus</i>	S	Reef-associated	47.85	
<i>Penopus microphthalmus</i>	S	Bathydemersal	26.6	
<i>Pentaceros decacanthus</i>	S	Bathydemersal	10	
<i>Pentaceros japonicus</i>	S	Benthopelagic	16.29	
<i>Pentaceros quinquespinis</i>	S	Pelagic	76.67	
<i>Phenacoscorpius eschmeyeri</i>	S	Demersal	10	
<i>Photoneustes dinema</i>	S	Pelagic	16.29	
<i>Photostomias guernei</i>	S	Bathypelagic	10	
<i>Photostylus pycnopterus</i>	S	Bathypelagic	10	
<i>Phycis blennoides</i>	S	Benthopelagic	48.86	48.86
<i>Phycis phycis</i>	S	Benthopelagic	52.3	52.3
<i>Physiculus dalwigki</i>	S	Benthopelagic	21.45	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Physiculus hexacytus</i>	S	Bathydemersal	43.33	
<i>Physiculus japonicus</i>	S	Bathydemersal	40.69	
<i>Physiculus longicavis</i>	S	Benthopelagic	10	
<i>Physiculus luminosus</i>	S	Bathydemersal	21.45	
<i>Physiculus parini</i>	S	Bathypelagic	43.33	
<i>Physiculus sazónovi</i>	S	Bathypelagic	43.33	
<i>Physiculus therosideros</i>	S	Bathypelagic	10	
<i>Plagiogeneion geminatum</i>	S	Demersal	19.39	
<i>Plagiogeneion unispina</i>	S	Bathydemersal	10	
<i>Plagiopsetta glossa</i>	S	Demersal	10	
<i>Platyberyx opalescens</i>	S	Pelagic	69.99	
<i>Plectranthias exsul</i>	S	Demersal	43.33	
<i>Plectranthias kelloggi</i>	S	Demersal	10	
<i>Plectranthias parini</i>	S	Bathypelagic	76.67	
<i>Plectrogenium barsukovi</i>	S	Bathydemersal		
<i>Plectrogenium nanum</i>	S	Bathydemersal	10	
<i>Pollachius virens</i>	S	Demersal	63.3	63.3
<i>Polyacanthonotus challengerii</i>	S	Bathypelagic	44.89	
<i>Polyipnus clarus</i>	S	Bathydemersal	10	
<i>Polyipnus inermis</i>	S	Bathypelagic	43.33	
<i>Polyipnus kiwiensis</i>	S	Benthopelagic	10	
<i>Polyipnus matsubarae</i>	S	Benthopelagic	31.09	
<i>Polymetme andriashevi</i>	S	Bathydemersal	10	
<i>Polymetme corythaeola</i>	S	Benthopelagic	17.32	
<i>Polymixia berndti</i>	S	Reef-associated	40	
<i>Polymixia japonica</i>	S	Bathypelagic	21.45	
<i>Polymixia lowei</i>	S	Bathydemersal	10	
<i>Polymixia nobilis</i>	S	Bathydemersal	44.76	
<i>Polymixia salagomeziensis</i>	S	Bathydemersal	10	
<i>Polymixia yuri</i>	S	Bathydemersal	34.81	34.81
<i>Polyprion americanus</i>	S	Bathydemersal	90	
<i>Pontinus kuhlii</i>	S	Bathydemersal	40	
<i>Pontinus macrocephalus</i>	S	Demersal	28.15	
<i>Pontinus tentacularis</i>	S	Demersal	60	
<i>Porogadus miles</i>	S	Bathydemersal	21.45	
<i>Poromitra capito</i>	S	Bathypelagic	22.97	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Poromitra crassiceps</i>	S	Bathypelagic	10	
<i>Poromitra megalops</i>	S	Bathypelagic	10	
<i>Priacanthus macracanthus</i>	S	Reef-associated	26.71	26.71
<i>Priacanthus meeki</i>	S	Reef-associated	24.54	
<i>Prionace glauca</i>	S	Pelagic	75.01	75.01
<i>Pristipomoides argyrogrammicus</i>	S	Reef-associated	31.74	
<i>Pristipomoides auricilla</i>	S	Reef-associated	31.21	31.21
<i>Pristipomoides filamentosus</i>	S	Reef-associated	45.39	45.39
<i>Pristipomoides multidentis</i>	S	Demersal	66.85	66.85
<i>Pristipomoides sieboldii</i>	S	Reef-associated	45.69	45.69
<i>Pristipomoides zonatus</i>	S	Reef-associated	27.39	27.39
<i>Promethichthys prometheus</i>	S	Benthopelagic	55.06	55.06
<i>Protogrammus sousai</i>	S	Bathydemersal	10	
<i>Protomyctophum thompsoni</i>	S	Bathypelagic	10	
<i>Psenes cyanophrys</i>	S	Bathypelagic	10	
<i>Psenes maculatus</i>	S	Pelagic	19.75	
<i>Psenopsis anomala</i>	S	Benthopelagic	37.71	
<i>Pseudanthias thompsoni</i>	S	Reef-associated	32.47	
<i>Pseudobathylagus milleri</i>	S	Bathypelagic	10	
<i>Pseudocaranx dentex</i>	S	Reef-associated	47.2	47.2
<i>Pseudocetonus septifer</i>	S	Bathydemersal	30.72	
<i>Pseudocyttus maculatus</i>	AGG	Bathydemersal	57.31	72.9
<i>Pseudopentaceros pectoralis</i>	S	Pelagic	44.91	
<i>Pseudopentaceros richardsoni</i>	AGG	Pelagic	40	78.25
<i>Pseudopentaceros wheeleri</i>	AGG	Benthopelagic	60	
<i>Pseudotriakis microdon</i>	S	Bathydemersal	79.18	79.18
<i>Pteroplatytrygon violacea</i>	S	Reef-associated	78.77	78.77
<i>Pterycombus brama</i>	S	Pelagic	40	
<i>Pterygotrigla picta</i>	S	Bathydemersal	25.99	
<i>Pycnocrasedum armatum</i>	S	Benthopelagic		
<i>Pyramodon parini</i>	S	Benthopelagic	21.97	
<i>Pyramodon ventralis</i>	S	Benthopelagic	10	
<i>Raja brachyura</i>	S	Demersal	70.35	70.35
<i>Raja clavata</i>	S	Demersal	75.51	75.51
<i>Raja maderensis</i>	S	Bathydemersal	70.94	
<i>Raja rhina</i>	S	Bathydemersal	60	60

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Rajella bigelowi</i>	S	Bathydemersal	40	
<i>Regalecus glesne</i>	S	Pelagic	90	
<i>Rexea antefurcata</i>	S	Benthopelagic	49.13	
<i>Rexea brevilineata</i>	S	Benthopelagic	60.07	60.07
<i>Rhadinesthes decimus</i>	S	Bathypelagic	32.77	
<i>Rhinochimaera atlantica</i>	S	Bathydemersal	47.09	
<i>Rhinochimaera pacifica</i>	S	Bathydemersal	79.89	
<i>Rondeletia loricata</i>	S	Bathypelagic	28.33	28.33
<i>Rostroraja alba</i>	S	Demersal	90	90
<i>Rouleina attrita</i>	S	Bathypelagic	40	
<i>Rouleina maderensis</i>	S	Bathypelagic	23.51	
<i>Ruvettus pretiosus</i>	S	Benthopelagic	90	
<i>Saccopharynx ampullaceus</i>	S	Bathypelagic	77.15	
<i>Sagamichthys abei</i>	S	Bathypelagic	18.57	18.57
<i>Sagamichthys schnakenbecki</i>	S	Bathypelagic	18.35	
<i>Sarda sarda</i>	S	Pelagic	48.46	48.46
<i>Satyrichthys engyceros</i>	S	Demersal	38.91	
<i>Satyrichthys quadratorostratus</i>	S	Bathydemersal	50.21	
<i>Schedophilus medusophagus</i>	S	Pelagic	40	
<i>Schedophilus ovalis</i>	S	Benthopelagic	60	
<i>Schindleria praematura</i>	S	Reef-associated	10	
<i>Scomber japonicus</i>	S	Pelagic	46.46	46.46
<i>Scombrobrax heterolepis</i>	S	Benthopelagic	21.45	
<i>Scopelarchus guentheri</i>	S	Bathypelagic	10	
<i>Scopeloberyx opisthopterus</i>	S	Bathypelagic	10	
<i>Scopelogadus beanii</i>	S	Bathypelagic		
<i>Scopelosaurus harryi</i>	S	Bathypelagic	17.9	17.9
<i>Scopelosaurus maui</i>	S	Bathypelagic	10	
<i>Scorpaena azorica</i>	S	Demersal	10	
<i>Scorpaena loppei</i>	S	Demersal	29.61	
<i>Scorpaena neglecta</i>	S	Demersal	29.17	
<i>Scorpaena notata</i>	S	Demersal	10	
<i>Scorpaena scrofa</i>	S	Demersal	60.76	60.76
<i>Scorpaena uncinata</i>	S	Demersal	76.67	
<i>Scorpaenopsis oxycephala</i>	S	Reef-associated	27.63	
<i>Scymnodalatias garricki</i>	S	Bathypelagic		

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Scymnodon obscurus</i>	S	Benthopelagic	48.96	
<i>Scymnodon ringens</i>	S	Bathypelagic	67.78	
<i>Searsia koefoedi</i>	S	Bathypelagic	10	
<i>Sebastes aleutianus</i>	S	Bathydemersal	60	
<i>Sebastes alutus</i>	S	Bathydemersal	70.24	70.24
<i>Sebastes aurora</i>	S	Bathydemersal	32.77	
<i>Sebastes babcocki</i>	S	Demersal	46.52	46.52
<i>Sebastes borealis</i>	S	Bathydemersal	66.56	66.56
<i>Sebastes brevispinis</i>	S	Demersal	61.17	61.17
<i>Sebastes crameri</i>	S	Demersal	61.99	61.99
<i>Sebastes diploproa</i>	S	Bathydemersal	50.36	50.36
<i>Sebastes elongatus</i>	S	Demersal	30.72	30.72
<i>Sebastes entomelas</i>	AGG	Pelagic	63.15	63.15
<i>Sebastes flammeus</i>	S	Bathydemersal	48.64	
<i>Sebastes flavidus</i>	S	Reef-associated	67.15	67.15
<i>Sebastes helvomaculatus</i>	AGG	Demersal	32.77	32.77
<i>Sebastes iracundus</i>	S	Bathydemersal	50.79	
<i>Sebastes maliger</i>	S	Demersal	45.29	45.29
<i>Sebastes marinus</i>	AGG	Pelagic	68.01	68.01
<i>Sebastes mentella</i>	AGG	Bathypelagic	67.81	67.74
<i>Sebastes miniatus</i>	S	Reef-associated	60	60
<i>Sebastes nebulosus</i>	S	Reef-associated	40	40
<i>Sebastes nigrocinctus</i>	S	Reef-associated	45.29	45.29
<i>Sebastes paucispinis</i>	AGG	Reef-associated	55.24	60.87
<i>Sebastes pinniger</i>	S	Reef-associated	46.3	46.3
<i>Sebastes proriger</i>	S	Bathydemersal	42.54	42.54
<i>Sebastes reedi</i>	S	Bathydemersal	56.28	56.28
<i>Sebastes ruberrimus</i>	AGG	Reef-associated	70.9	65.31
<i>Sebastes variegatus</i>	S	Demersal	29.69	29.69
<i>Sebastolobus alascanus</i>	S	Bathydemersal	53.03	53.03
<i>Sebastolobus altivelis</i>	S	Bathydemersal	30.72	30.72
<i>Seriola dumerili</i>	S	Reef-associated	54.2	54.2
<i>Seriola lalandi</i>	S	Reef-associated	43.62	43.62
<i>Serranus atricauda</i>	S	Demersal	58.57	
<i>Serranus cabrilla</i>	S	Demersal	33.64	33.64
<i>Serrivomer beanii</i>	S	Bathypelagic	52.22	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Setarches guentheri</i>	S	Bathydemersal	16.29	
<i>Sladenia remiger</i>	S	Bathydemersal	31.74	
<i>Sladenia shaeferi</i>	S	Bathydemersal		
<i>Somniosus microcephalus</i>	S	Benthopelagic	90	90
<i>Somniosus pacificus</i>	S	Benthopelagic	90	90
<i>Somniosus rostratus</i>	S	Bathydemersal	90	
<i>Spectrunculus grandis</i>	S	Bathydemersal	78.07	
<i>Sphagemacrurus grenadae</i>	S	Bathypelagic	16.29	
<i>Sphagemacrurus hirundo</i>	S	Bathydemersal	53.92	
<i>Sphoeroides pachygaster</i>	S	Demersal	32.26	
<i>Sphyraenops bairdianus</i>	S	Pelagic	60	
<i>Spiniphryne gladisfenae</i>	S	Bathypelagic		
<i>Squaliolus laticaudus</i>	S	Bathypelagic	10	
<i>Squalogadus modificatus</i>	S	Bathypelagic	26.6	
<i>Squalus acanthias</i>	S	Benthopelagic	79.42	79.42
<i>Squalus blainville</i>	S	Demersal	77.21	77.21
<i>Stenobranchius leucopsarus</i>	S	Bathypelagic	36.51	36.51
<i>Sternoptyx diaphana</i>	S	Bathypelagic	10	
<i>Sternoptyx pseudobscura</i>	S	Bathypelagic	10	
<i>Stethopristes eos</i>	S	Bathypelagic	76.67	
<i>Stomias affinis</i>	S	Bathypelagic	10	
<i>Stomias boa ferox</i>	S	Bathypelagic	21.45	
<i>Stylephorus chordatus</i>	S	Bathypelagic	19.39	
<i>Sudis atrox</i>	S	Bathypelagic	10	
<i>Sudis hyalina</i>	S	Bathypelagic	60	
<i>Sufflamen fraenatum</i>	S	Reef-associated	29.69	
<i>Symbolophorus veranyi</i>	S	Bathypelagic	10	
<i>Symphysanodon maunaloae</i>	S	Demersal	10	
<i>Synagrops japonicus</i>	S	Bathydemersal	26.6	
<i>Synagrops philippinensis</i>	S	Bathydemersal	10	
<i>Synaphobranchus affinis</i>	S	Bathydemersal	90	
<i>Synaphobranchus brevidorsalis</i>	S	Bathydemersal	68.38	
<i>Synaphobranchus kaupii</i>	S	Bathydemersal	60	
<i>Synchiropus phaeton</i>	S	Demersal	10	
<i>Synodus doaki</i>	S	Reef-associated	19.39	
<i>Synodus synodus</i>	S	Reef-associated	24.54	

Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Taaningichthys bathyphilus</i>	S	Bathypelagic	10	
<i>Tactostoma macropus</i>	S	Bathypelagic	38.52	38.52
<i>Talismania antillarum</i>	S	Bathypelagic	10	
<i>Talismania longifilis</i>	S	Bathypelagic	40	
<i>Taractichthys longipinnis</i>	S	Pelagic	60	
<i>Thalassobathia pelagica</i>	S	Bathypelagic	52.31	
<i>Thamnaconus analis</i>	S	Reef-associated		
<i>Thamnaconus tessellatus</i>	S	Bathydemersal	10	
<i>Theragra chalcogramma</i>	S	Benthopelagic	42.36	42.36
<i>Thunnus albacares</i>	S	Reef-associated	51.79	51.79
<i>Torpedo fairchildi</i>	S	Bathydemersal	60	
<i>Torpedo microdiscus</i>	S	Demersal	76.67	
<i>Torpedo nobiliana</i>	S	Reef-associated	76.67	76.67
<i>Torpedo semipelagica</i>	S	Demersal	76.67	
<i>Trachipterus trachipterus</i>	S	Bathypelagic	90	
<i>Trachonurus sulcatus</i>	S	Bathypelagic	40	
<i>Trachonurus villosus</i>	S	Bathypelagic	44.89	
<i>Trachurus picturatus</i>	S	Benthopelagic	67.44	
<i>Trachurus symmetricus</i>	S	Pelagic	60.41	60.41
<i>Trachyrincus longirostris</i>	S	Bathydemersal	44.89	
<i>Trachyrincus murrayi</i>	S	Benthopelagic	90	
<i>Trachyrincus scabrus</i>	S	Bathydemersal	48.04	48.04
<i>Trachyscorpia capensis</i>	S	Bathydemersal	26.6	
<i>Trachyscorpia cristulata echinata</i>	S	Bathydemersal	40	
<i>Triodon macropterus</i>	S	Reef-associated	40	
<i>Tripterophycis svetovidovi</i>	S	Bathypelagic	10	
<i>Trisopterus minutus</i>	S	Benthopelagic	27.89	27.89
<i>Tubbia tasmanica</i>	S	Bathypelagic	47.74	
<i>Valenciennellus tripunctulatus</i>	S	Bathypelagic	10	
<i>Venefica procera</i>	S	Bathydemersal	67.05	
<i>Ventrifossa johnborum</i>	S	Bathydemersal	57.76	
<i>Ventrifossa macrodon</i>	S	Bathydemersal	31.74	
<i>Ventrifossa macropogon</i>	S	Bathydemersal	40	
<i>Ventrifossa obtusirostris</i>	S	Bathydemersal	21.45	
<i>Ventrifossa teres</i>	S	Bathydemersal	10	
<i>Vinciguerrria nimbaria</i>	S	Bathypelagic	10	



Species	S vs AGG	Habitat	$V_i$	$V_i^*$
<i>Xanthichthys mento</i>	S	Reef-associated	55.21	
<i>Xenodermichthys copei</i>	S	Bathypelagic	10	
<i>Xenolepidichthys dalgleishi</i>	S	Benthopelagic	10	
<i>Xiphias gladius</i>	S	Pelagic	73.5	73.5
<i>Yarrella blackfordi</i>	S	Bathypelagic	35.98	
<i>Zanclus cornutus</i>	S	Reef-associated	10	
<i>Zaprora silenus</i>	S	Demersal	60	
<i>Zenion hololepis</i>	S	Bathydemersal	10	
<i>Zenion leptolepis</i>	S	Bathypelagic	10	
<i>Zenopsis conchifera</i>	S	Benthopelagic	50.44	
<i>Zenopsis nebulosa</i>	S	Bathydemersal	49.79	49.79
<i>Zenopsis oblongus</i>	S	Demersal		
<i>Zeus faber</i>	S	Benthopelagic	46.85	46.85
<i>Zu cristatus</i>	S	Bathypelagic	72.63	

## APPENDIX 2

### LIST OF LARGE AND SMALL SEAMOUNTS IDENTIFIED IN THE AZORES ECONOMIC EXCLUSIVE ZONE

**Table 1** – Seamounts characteristics: number; category (large and small); location; depth of the summit (m); seamount height ( $h$  in m); basal area ( $a_b$  in  $\text{km}^2$ ); height to radius ratio ( $\xi_r$ ); the average slope ( $\phi$  in degrees); distance to nearest large seamount ( $d_L$  in km, for large seamounts only); and distance to nearest seamount ( $d$  in km).

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
1	Large	-24.4850	37.3610	821	1252	1291	0.10	3.41	21.4	15	21.4	15
2	Large	-25.8794	37.6032	265	1050	974	0.09	4.71	48.4	19	18.2	100
3	Large	-29.5534	37.9873	364	1161	895	0.11	6.57	33.3	28	27.9	111
4	Large	-26.1300	38.5718	1154	1038	964	0.08	3.43	31.6	33	31.6	33
5	Large	-29.8791	39.6824	886	1020	796	0.10	3.23	60.9	39	19.7	142
6	Large	-26.9316	39.7074	756	1125	1159	0.09	3.84	69.4	40	29.5	146
7	Large	-25.7292	36.6179	1957	1144	1180	0.11	3.09	62.7	11	13.9	84
8	Large	-26.1049	37.1022	1048	1721	1004	0.15	8.00	50.8	11	12.6	93
9	Large	-28.1840	37.1690	1646	1141	654	0.10	3.80	18.0	12	18.0	12
10	Large	-31.4322	37.1774	413	1305	1295	0.09	2.10	71.1	57	25.0	174
11	Large	-25.6540	37.1773	270	2040	916	0.16	9.27	50.8	8	21.7	95
12	Large	-28.0504	37.2609	1478	1148	1114	0.08	4.09	18.0	9	18.0	9
13	Large	-24.7605	37.2609	65	1754	1054	0.12	8.32	32.6	1	32.6	1
14	Large	-25.0945	37.3945	195	1835	1022	0.13	7.99	40.0	13	40.0	13
15	Large	-24.3764	37.5197	1063	1086	1114	0.09	3.68	21.4	1	21.4	1
16	Large	-26.5725	37.5281	1265	1079	947	0.10	5.47	40.3	19	19.1	97
17	Large	-28.9689	37.7368	309	956	1062	0.08	2.74	35.7	23	35.7	23
18	Large	-30.6723	37.7535	735	1088	596	0.11	5.07	18.8	20	18.8	20
19	Large	-26.2886	37.7535	816	1448	1264	0.13	7.05	40.3	16	12.2	107
20	Large	-30.8394	37.7786	679	1096	568	0.10	6.20	18.8	18	18.8	18

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
21	Large	-31.4990	37.8287	824	1129	1009	0.11	3.88	31.8	22	13.5	181
22	Large	-31.2151	37.8621	707	1454	903	0.14	7.55	31.8	21	18.6	181
23	Large	-28.6851	37.8871	408	1297	557	0.12	7.24	35.7	17	23.4	182
24	Large	-30.3384	38.2044	592	1354	1150	0.11	3.86	27.0	27	9.3	118
25	Large	-26.6143	38.2211	390	1760	964	0.14	7.81	42.8	26	30.6	110
26	Large	-26.2301	38.2462	650	1747	1156	0.14	4.97	37.9	4	10.4	119
27	Large	-30.1046	38.2712	730	1166	1013	0.11	4.78	27.0	24	17.1	188
28	Large	-29.4366	38.2629	549	1134	1144	0.10	3.91	33.3	3	32.4	111
29	Large	-27.7832	38.2629	473	1103	1075	0.10	5.81	108.6	23	16.4	190
30	Large	-30.6389	38.2963	485	1414	1009	0.15	5.14	34.9	24	26.2	118
31	Large	-31.0231	38.3213	712	1197	1106	0.09	3.91	42.8	30	25.2	185
32	Large	-29.0357	38.5468	261	1269	718	0.11	7.35	39.2	51	23.3	189
33	Large	-25.8460	38.5885	1264	1260	1015	0.09	5.47	31.6	4	31.6	4
34	Large	-26.6143	38.6887	468	968	1065	0.09	4.53	52.0	25	52.0	25
35	Large	-30.2298	38.6971	671	1055	798	0.11	4.24	27.2	36	15.0	191
36	Large	-29.9876	38.7305	380	1251	945	0.11	5.48	27.2	35	13.3	191
37	Large	-29.8875	38.9893	438	1069	1079	0.10	4.55	30.8	36	14.7	192
38	Large	-31.8831	39.3818	556	1223	906	0.09	6.21	151.7	31	43.6	128
39	Large	-29.3363	39.6072	603	1128	1144	0.09	5.24	60.9	5	25.8	144
40	Large	-26.6894	40.2835	705	1716	1095	0.12	6.11	29.1	43	29.1	43
41	Large	-30.1714	40.3587	661	1183	799	0.17	4.41	51.0	42	20.8	209
42	Large	-29.7121	40.3671	958	1447	839	0.13	5.93	38.6	44	34.0	209
43	Large	-26.9315	40.3838	804	1297	994	0.09	5.37	18.0	45	18.0	45
44	Large	-29.3698	40.4255	570	1884	790	0.23	5.61	36.6	47	35.3	207
45	Large	-27.0234	40.5174	985	1227	991	0.11	5.89	18.0	43	18.0	43
46	Large	-28.8938	40.5424	896	1247	891	0.13	7.61	54.5	44	12.6	211
47	Large	-29.5034	40.7261	888	1511	921	0.17	5.57	22.3	48	22.3	48
48	Large	-29.7038	40.7428	751	1562	990	0.15	5.54	22.3	47	22.3	47
49	Large	-28.4346	40.8764	1230	1250	766	0.09	5.46	63.1	46	29.5	163

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
50	Large	-29.2361	37.9873	206	625	796	0.06	2.86	35.3	3	7.7	111
51	Large	-28.9940	38.1961	204	876	961	0.07	4.06	35.5	50	17.8	116
52	Large	-26.7562	36.5260	2226	1344	940	0.10	7.64	96.6	8	12.6	75
53	Large	-27.5112	34.8413	1241	1858	1048	0.17	5.75	107.8	54	37.1	239
54	Large	-27.0457	35.6925	2668	1220	832	0.14	8.13	98.0	52	24.5	266
55	Large	-24.7980	35.9452	3176	1130	515	0.15	5.28	127.6	7	30.1	267
56	Large	-33.0307	36.7831	1146	1247	883	0.17	3.91	66.5	62	51.6	282
57	Large	-32.0598	37.3018	1057	1088	1040	0.12	3.67	51.9	58	37.4	176
58	Large	-32.0997	37.7673	989	1202	921	0.14	3.46	51.9	57	29.6	105
59	Large	-34.5469	38.3259	2402	1062	1059	0.10	3.86	169.3	62	22.4	311
60	Large	-30.9426	41.5312	1080	1181	1045	0.11	5.14	155.9	41	29.7	365
61	Large	-29.1870	42.4090	1306	1103	758	0.13	4.37	189.7	49	29.1	390
62	Large	-33.4829	37.2353	606	1017	1083	0.10	4.39	51.4	63	51.4	63
63	Large	-33.0440	37.3816	377	1114	959	0.11	5.64	51.4	62	50.2	299
64	Small	-31.7161	36.1085	2377	466	606	0.04	1.99			20.0	68
65	Small	-28.5515	36.1503	2927	446	672	0.04	2.09			44.9	71
66	Small	-29.9877	36.2505	2798	414	535	0.04	1.47			39.1	76
67	Small	-24.3681	36.2505	3135	751	1004	0.06	2.25			38.6	269
68	Small	-31.7578	36.2839	2459	443	258	0.06	1.90			20.0	64
69	Small	-29.1193	36.4008	2949	578	487	0.06	2.46			34.9	72
70	Small	-29.6036	36.4175	3023	330	633	0.04	1.57			22.1	72
71	Small	-28.3010	36.4676	2777	506	917	0.04	1.76			22.4	78
72	Small	-29.4198	36.4927	3019	383	518	0.07	1.82			22.1	70
73	Small	-26.3137	36.5511	2249	1214	1001	0.09	5.57			36.3	169
74	Small	-30.8393	36.5678	2337	495	1264	0.04	2.15			39.4	89
75	Small	-26.8647	36.5595	2530	1012	1054	0.09	5.08			12.6	52
76	Small	-29.9543	36.6012	2666	540	1096	0.04	2.24			30.1	172
77	Small	-27.0151	36.6012	2621	967	567	0.09	5.75			17.3	75
78	Small	-28.3845	36.6513	2828	476	689	0.05	2.33			22.4	71

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
79	Small	-27.1987	36.6513	3080	544	455	0.06	2.51			21.2	77
80	Small	-27.4826	36.6597	2918	659	576	0.06	3.19			31.6	79
81	Small	-30.3133	36.6763	2683	320	820	0.03	1.76			17.0	172
82	Small	-27.8167	36.6847	2749	655	912	0.06	3.25			32.2	83
83	Small	-28.1005	36.7432	2595	648	602	0.06	4.07			15.9	173
84	Small	-25.7208	36.7432	1991	918	1174	0.09	4.44			7.1	86
85	Small	-29.1026	36.7682	3155	332	345	0.04	1.62			32.9	88
86	Small	-25.6958	36.8016	1881	982	839	0.12	4.17			7.1	84
87	Small	-30.3551	36.8350	2574	452	500	0.04	2.62			16.2	91
88	Small	-28.8187	36.8517	2659	547	676	0.07	2.51			32.9	85
89	Small	-30.6807	36.8851	2364	414	382	0.05	2.49			21.4	91
90	Small	-25.7292	36.8851	2088	866	472	0.11	4.89			10.0	86
91	Small	-30.4887	36.8935	2492	373	611	0.04	2.57			16.2	87
92	Small	-31.7579	37.0271	915	902	747	0.08	6.14			15.0	174
93	Small	-26.1968	37.1690	1209	1406	1019	0.13	6.27			12.6	8
94	Small	-30.0545	37.2191	1900	688	771	0.06	2.48			50.5	102
95	Small	-25.7208	37.3610	393	1203	1114	0.11	6.03			16.0	100
96	Small	-31.2235	37.3861	678	1142	883	0.09	6.42			10.0	99
97	Small	-26.4890	37.3778	1618	842	1000	0.07	4.62			19.1	16
98	Small	-30.9730	37.4028	816	1047	995	0.09	4.52			18.6	99
99	Small	-31.1400	37.4195	710	1132	797	0.11	6.46			10.0	96
100	Small	-25.8377	37.4445	393	1288	1175	0.12	5.02			16.0	95
101	Small	-26.7979	37.5364	1577	857	711	0.08	4.02			25.1	16
102	Small	-30.3217	37.5865	994	790	1298	0.07	2.20			26.4	106
103	Small	-28.1507	37.6032	1986	463	504	0.08	2.64			18.2	177
104	Small	-27.0986	37.6199	1729	707	600	0.08	3.15			34.7	101
105	Small	-31.8414	37.7034	1205	915	621	0.10	5.56			13.9	179
106	Small	-30.1380	37.7368	881	730	1020	0.09	3.80			26.4	102
107	Small	-26.1800	37.7368	919	1377	993	0.15	4.63			12.2	19

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
108	Small	-29.7539	37.7535	804	639	640	0.09	2.60			34.2	3
109	Small	-31.8079	37.8537	1014	959	1067	0.09	4.33			17.1	105
110	Small	-26.6226	37.9456	1303	818	1230	0.06	3.20			30.6	25
111	Small	-29.3030	38.0040	131	756	837	0.08	3.86			7.7	50
112	Small	-27.4576	37.9957	1047	767	1174	0.06	2.60			29.6	117
113	Small	-28.4262	38.0124	1203	751	993	0.07	2.75			19.9	184
114	Small	-27.1653	38.0708	1068	812	905	0.07	4.29			13.7	186
115	Small	-31.6326	38.1126	1182	843	449	0.10	4.24			34.7	109
116	Small	-29.1360	38.1209	234	727	639	0.07	3.76			17.8	51
117	Small	-27.6580	38.1710	644	902	1012	0.09	5.15			17.3	29
118	Small	-30.4219	38.2044	866	1208	1060	0.10	4.36			9.3	24
119	Small	-26.1466	38.2044	960	1374	1082	0.13	6.12			10.4	26
120	Small	-28.8520	38.2796	502	613	344	0.09	4.37			13.9	189
121	Small	-31.5992	38.4382	962	635	1084	0.05	1.99			36.4	115
122	Small	-27.3741	38.4633	607	850	631	0.07	5.08			12.6	123
123	Small	-27.4659	38.5301	674	820	646	0.09	4.01			12.6	122
124	Small	-24.0759	38.5885	3302	389	521	0.04	2.21			15.8	316
125	Small	-29.3531	38.6971	1427	485	764	0.04	2.45			38.6	129
126	Small	-31.1483	38.8307	1149	740	1129	0.05	2.94			58.3	31
127	Small	-30.4803	38.8474	1140	735	738	0.11	3.50			19.7	193
128	Small	-31.7245	39.0227	965	502	1234	0.04	2.13			43.6	38
129	Small	-29.4950	39.0144	1514	489	510	0.06	2.40			24.7	196
130	Small	-27.5161	39.0561	753	831	688	0.08	4.70			26.5	131
131	Small	-27.3240	39.1981	882	527	1166	0.04	1.56			26.5	130
132	Small	-29.2862	39.2231	1437	568	544	0.06	2.37			14.9	196
133	Small	-28.5013	39.2231	1064	966	837	0.07	5.39			34.4	137
134	Small	-29.6119	39.2816	1067	909	684	0.12	5.10			13.2	199
135	Small	-29.7538	39.3066	967	881	690	0.14	4.29			10.5	199
136	Small	-29.3698	39.3316	1552	468	660	0.07	2.46			13.3	196

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
137	Small	-28.6433	39.4987	1217	777	706	0.06	3.67			34.4	133
138	Small	-30.5471	39.5320	1403	526	911	0.04	2.38			42.8	202
139	Small	-29.0023	39.6323	1226	730	611	0.08	3.19			37.2	39
140	Small	-29.6203	39.6657	1200	784	779	0.08	4.47			12.1	203
141	Small	-24.3180	39.6657	3195	537	1204	0.04	2.16			46.9	149
142	Small	-30.0545	39.7074	985	734	643	0.09	3.94			15.4	202
143	Small	-30.2131	39.7659	1210	636	720	0.07	2.63			13.5	202
144	Small	-29.4533	39.8076	1177	718	551	0.12	2.82			13.4	145
145	Small	-29.3865	39.9078	1242	615	253	0.09	3.45			13.4	144
146	Small	-27.0401	39.9496	1122	825	974	0.06	4.03			18.8	206
147	Small	-29.2612	40.0414	1245	503	632	0.06	3.17			15.8	207
148	Small	-25.9630	40.0581	2809	293	560	0.03	1.31			60.0	154
149	Small	-24.1844	40.0665	3260	420	985	0.03	1.58			46.9	141
150	Small	-30.0043	40.1082	1257	472	529	0.07	2.20			18.6	209
151	Small	-25.2115	40.1082	2893	391	1013	0.03	1.52			44.8	154
152	Small	-24.6270	40.1917	3249	370	1015	0.03	1.59			36.5	157
153	Small	-28.0504	40.3086	1574	579	755	0.06	2.64			16.4	208
154	Small	-25.5204	40.3671	2730	385	1100	0.04	1.29			44.8	151
155	Small	-28.6600	40.4840	1554	793	488	0.08	4.70			21.4	156
156	Small	-28.4679	40.4923	1943	505	531	0.05	2.72			21.4	155
157	Small	-24.5852	40.5174	3217	387	1055	0.03	1.65			36.5	152
158	Small	-30.1046	40.5424	1497	641	739	0.07	2.93			21.7	41
159	Small	-29.0524	40.5424	1062	1153	512	0.10	7.60			17.6	46
160	Small	-30.3884	40.5758	1455	784	880	0.07	2.48			20.0	212
161	Small	-30.6724	40.5925	1792	590	517	0.06	2.43			12.4	162
162	Small	-30.6974	40.7010	1918	561	415	0.06	2.66			12.4	161
163	Small	-28.1757	40.8180	1926	798	921	0.06	4.45			29.5	49
164	Small	-30.3217	40.9432	1607	891	387	0.11	4.92			38.6	359
165	Small	-25.4870	36.1586	3286	574	1073	0.04	1.75			49.0	268

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
166	Small	-24.7522	36.2422	3063	681	1264	0.05	1.64			33.4	55
167	Small	-27.3324	36.4008	2960	430	1114	0.05	1.30			31.5	79
168	Small	-28.7519	36.5177	3174	294	612	0.03	1.61			37.8	88
169	Small	-25.9880	36.5761	2591	843	867	0.06	3.80			29.1	7
170	Small	-24.9777	36.6680	2352	939	500	0.09	5.68			40.4	171
171	Small	-24.6186	36.7264	2903	584	669	0.05	2.99			40.4	170
172	Small	-30.1797	36.7515	2788	341	574	0.04	1.55			17.0	81
173	Small	-28.1172	36.8851	2774	626	303	0.08	3.24			15.9	83
174	Small	-31.6410	37.0939	935	774	592	0.10	4.05			15.0	92
175	Small	-27.0401	37.1940	2225	336	593	0.03	1.82			46.6	101
176	Small	-31.7245	37.2776	1140	832	490	0.09	4.52			22.4	174
177	Small	-28.1089	37.4445	2105	315	734	0.04	1.96			18.2	103
178	Small	-30.7141	37.5281	923	811	1045	0.07	2.13			25.5	18
179	Small	-31.7161	37.7118	1265	776	593	0.10	4.61			13.9	105
180	Small	-24.7355	37.7118	1564	826	701	0.10	4.06			45.2	15
181	Small	-31.3821	37.8621	1090	862	900	0.10	4.04			13.5	21
182	Small	-28.8020	38.0625	623	670	670	0.07	3.41			23.4	23
183	Small	-29.8206	38.1209	1570	542	590	0.06	2.51			19.7	188
184	Small	-28.5682	38.1209	930	641	479	0.06	3.49			19.9	113
185	Small	-30.8895	38.1376	1350	842	351	0.11	4.66			25.2	31
186	Small	-27.0568	38.1293	941	901	701	0.08	4.91			13.7	114
187	Small	-31.2402	38.2044	1434	682	933	0.09	3.75			27.4	31
188	Small	-29.9542	38.2378	1261	777	656	0.10	3.95			17.1	27
189	Small	-28.9523	38.3547	488	797	451	0.10	4.79			13.9	120
190	Small	-27.8834	38.3714	376	1011	774	0.11	6.22			16.4	29
191	Small	-30.0962	38.6804	819	855	1155	0.07	3.71			13.3	36
192	Small	-29.9960	38.9141	787	644	805	0.08	3.21			14.7	37
193	Small	-30.4553	39.0227	1520	346	151	0.07	2.01			19.7	127
194	Small	-27.7498	39.1396	1052	566	584	0.06	3.00			27.6	130



N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
195	Small	-30.3634	39.1814	1330	608	725	0.06	3.67			20.4	193
196	Small	-29.4199	39.2231	1472	572	915	0.06	1.83			13.3	136
197	Small	-28.8604	39.2315	1358	566	868	0.04	2.80			38.3	137
198	Small	-29.8457	39.3316	1218	672	569	0.07	3.71			10.6	135
199	Small	-29.6870	39.3734	1136	812	724	0.11	5.06			10.5	135
200	Small	-27.0234	39.4319	1001	689	889	0.05	3.52			32.3	6
201	Small	-30.0377	39.5320	1154	797	297	0.10	5.43			19.6	142
202	Small	-30.1797	39.6489	1309	561	537	0.10	3.10			13.5	143
203	Small	-29.5785	39.7659	1245	654	992	0.09	4.18			12.1	140
204	Small	-26.7645	39.9579	1807	555	614	0.05	1.88			30.6	146
205	Small	-29.8791	39.9663	1381	623	822	0.13	1.68			21.0	150
206	Small	-27.1821	40.0414	1420	548	746	0.05	2.83			18.8	146
207	Small	-29.3865	40.1082	1227	682	747	0.09	2.09			15.8	147
208	Small	-28.0087	40.1667	1852	242	795	0.02	1.30			16.4	153
209	Small	-30.0043	40.2752	1089	585	580	0.06	2.96			18.6	150
210	Small	-30.8978	40.4255	1874	350	773	0.03	1.46			31.2	161
211	Small	-28.8604	40.4338	1392	824	976	0.08	2.97			12.6	46
212	Small	-30.5555	40.6426	2009	394	742	0.05	2.05			14.1	161
213	Small	-29.0942	40.7511	1552	797	794	0.08	2.44			23.7	159
214	Small	-25.6540	40.8513	3009	382	679	0.03	1.98			46.3	361
215	Small	-24.4522	33.7374	4727	660	664	0.07	2.82			28.2	216
216	Small	-24.6384	33.9103	4722	522	834	0.07	2.04			11.9	218
217	Small	-26.8462	33.9635	3775	749	393	0.10	3.92			36.2	219
218	Small	-24.5852	34.0034	4683	547	871	0.07	2.19			11.9	216
219	Small	-26.5270	34.0300	4266	467	313	0.07	1.91			36.2	217
220	Small	-24.0000	34.0300	4624	551	948	0.06	2.18			34.5	221
221	Small	-24.2660	34.1896	4688	611	803	0.06	2.57			33.0	230
222	Small	-22.8562	34.2428	4713	591	800	0.09	3.71			58.0	237
223	Small	-24.8512	34.2960	4843	539	528	0.08	3.64			29.1	232

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
224	Small	-26.2477	34.3359	3959	742	708	0.08	4.30			46.0	219
225	Small	-25.3965	34.3625	4501	794	966	0.07	4.19			28.0	228
226	Small	-24.5586	34.4290	4596	762	498	0.11	4.06			23.8	232
227	Small	-23.6276	34.4157	5005	241	541	0.03	1.29			18.3	229
228	Small	-25.1571	34.4423	4953	398	555	0.05	3.02			28.0	225
229	Small	-23.4680	34.4556	4722	507	606	0.06	2.49			18.3	227
230	Small	-24.2128	34.4822	4428	785	926	0.08	3.12			14.0	233
231	Small	-24.0000	34.5088	4751	474	781	0.07	3.19			23.8	230
232	Small	-24.7448	34.5354	4664	618	644	0.08	3.49			23.8	226
233	Small	-24.3325	34.5221	4714	558	618	0.07	3.30			14.0	230
234	Small	-23.2818	34.5487	4502	702	736	0.09	3.51			23.1	229
235	Small	-26.7930	34.6152	3760	541	512	0.06	2.60			68.1	224
236	Small	-25.8620	34.6684	4313	651	449	0.09	3.58			44.7	240
237	Small	-23.0291	34.7349	4203	999	539	0.12	4.35			34.9	234
238	Small	-22.0050	34.8280	4587	573	1002	0.09	3.62			39.8	244
239	Small	-27.8437	34.8679	1945	878	905	0.08	2.50			37.1	53
240	Small	-25.5295	34.8945	4125	574	1002	0.06	1.92			44.7	236
241	Small	-22.6434	34.9344	4528	519	836	0.05	1.94			48.3	237
242	Small	-24.5320	35.0408	4036	841	1014	0.07	3.37			60.9	232
243	Small	-23.8670	35.0275	4146	737	697	0.11	4.15			47.3	248
244	Small	-21.7656	35.0940	4604	505	948	0.06	3.28			39.8	238
245	Small	-25.1970	35.2802	4021	576	831	0.05	2.44			29.1	249
246	Small	-26.8595	35.3201	3664	501	747	0.05	2.70			19.3	251
247	Small	-22.1114	35.3334	4620	368	919	0.03	1.62			23.8	254
248	Small	-23.6010	35.3600	3971	895	1038	0.08	4.53			47.3	243
249	Small	-24.9576	35.3866	3838	745	755	0.08	4.06			24.5	257
250	Small	-22.6567	35.4265	4218	668	514	0.08	3.02			44.4	263
251	Small	-26.9526	35.4664	3440	635	665	0.07	2.79			19.3	246
252	Small	-29.6658	35.5196	2912	564	385	0.08	3.20			46.0	272

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
253	Small	-26.4073	35.5329	3290	709	729	0.08	3.30			20.9	259
254	Small	-22.1380	35.5462	4541	427	591	0.05	2.21			23.8	247
255	Small	-26.7531	35.5595	3255	757	603	0.09	4.36			21.5	260
256	Small	-26.0748	35.5994	3688	403	943	0.04	1.68			37.7	253
257	Small	-24.8645	35.5861	3710	636	964	0.06	2.40			24.5	249
258	Small	-27.5378	35.6526	3075	484	810	0.07	2.17			27.3	265
259	Small	-26.4339	35.7191	3333	767	657	0.12	3.66			10.5	261
260	Small	-26.6999	35.7457	3136	749	522	0.10	4.38			21.5	255
261	Small	-26.5004	35.7856	3105	883	653	0.12	4.26			10.5	259
262	Small	-23.0823	35.7723	3686	924	546	0.10	4.84			19.9	271
263	Small	-22.6833	35.8255	4258	383	406	0.06	1.88			23.4	275
264	Small	-29.4131	35.8521	2779	515	924	0.05	2.31			25.3	272
265	Small	-27.4846	35.8920	3004	672	520	0.07	2.73			27.3	258
266	Small	-27.1388	35.8920	3156	765	499	0.11	3.61			24.5	54
267	Small	-24.5320	35.8920	3810	555	599	0.09	2.26			22.2	269
268	Small	-25.1172	35.9186	3561	615	910	0.06	2.69			35.6	55
269	Small	-24.3325	35.9053	3963	527	703	0.07	2.35			22.2	267
270	Small	-23.5212	35.9186	4037	487	916	0.06	2.11			31.1	274
271	Small	-23.2020	35.9053	3976	549	802	0.08	2.56			19.9	262
272	Small	-29.6259	35.9319	2800	497	884	0.05	1.92			25.3	264
273	Small	-24.0665	35.9319	3950	599	1018	0.06	2.66			29.6	274
274	Small	-23.8005	35.9319	3955	644	644	0.08	3.16			29.6	273
275	Small	-22.7498	36.0250	3782	903	921	0.08	3.54			23.4	263
276	Small	-22.9626	36.0782	4088	498	639	0.06	2.30			24.4	275
277	Small	-21.8720	36.0782	4026	767	762	0.08	3.45			33.7	281
278	Small	-21.1006	36.1314	4137	791	878	0.11	3.32			22.5	280
279	Small	-32.2726	36.1580	2179	455	596	0.07	2.55			58.9	68
280	Small	-21.2868	36.2112	4422	386	1010	0.04	2.10			22.5	278
281	Small	-21.6060	36.2245	4296	461	406	0.06	2.45			33.7	277

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
282	Small	-32.9243	36.3309	1823	383	646	0.06	1.39			51.6	56
283	Small	-23.6276	36.3309	3682	732	568	0.09	3.82			27.0	284
284	Small	-23.3882	36.3708	3866	486	671	0.11	1.97			23.4	287
285	Small	-23.1488	36.3841	3750	703	843	0.07	2.97			26.6	284
286	Small	-22.7498	36.4506	3841	657	897	0.07	2.98			44.9	285
287	Small	-23.4547	36.5703	3840	347	494	0.06	1.84			23.4	284
288	Small	-23.6941	36.6501	3454	717	900	0.07	2.61			28.0	287
289	Small	-23.1488	36.7964	3691	627	632	0.07	3.20			37.3	294
290	Small	-22.4971	36.9161	3742	679	563	0.11	3.69			56.8	296
291	Small	-21.8720	36.9294	3448	748	730	0.09	4.49			24.4	292
292	Small	-21.6592	36.9826	3443	651	805	0.08	2.57			24.4	291
293	Small	-20.9410	37.0092	3595	708	932	0.08	2.87			25.8	297
294	Small	-23.3350	37.0757	2898	898	788	0.09	3.42			37.1	295
295	Small	-23.6675	37.1023	2956	959	890	0.17	1.23			37.1	294
296	Small	-22.0981	37.2353	3627	525	851	0.05	1.88			29.6	298
297	Small	-20.8878	37.2353	3086	935	671	0.11	4.20			25.8	293
298	Small	-22.2577	37.4481	3890	463	698	0.07	2.49			29.6	296
299	Small	-32.7115	37.6875	1196	689	702	0.10	3.12			50.2	63
300	Small	-34.2144	37.8604	2202	862	1158	0.07	2.70			45.2	302
301	Small	-21.9784	37.8870	3641	775	548	0.09	4.45			36.1	306
302	Small	-34.6134	37.9402	2451	892	821	0.09	4.11			28.4	304
303	Small	-33.6558	37.9402	2098	481	636	0.06	2.74			50.5	312
304	Small	-34.8661	37.9801	2756	959	392	0.17	7.17			28.4	302
305	Small	-23.2552	38.0200	3551	419	756	0.06	1.83			27.2	307
306	Small	-21.7124	38.0732	3866	592	720	0.06	2.86			36.1	301
307	Small	-23.4813	38.1131	3423	360	507	0.05	1.46			27.2	305
308	Small	-21.0607	38.1397	3973	658	588	0.07	3.44			39.9	313
309	Small	-35.1986	38.2860	3420	635	730	0.09	2.56			50.2	304
310	Small	-34.1346	38.2860	2294	873	878	0.09	3.45			23.7	311

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
311	Small	-34.3474	38.2993	2551	807	980	0.08	2.10			22.4	59
312	Small	-33.8154	38.3658	2260	484	859	0.06	1.78			36.6	310
313	Small	-21.3400	38.3658	3900	739	791	0.08	3.31			39.9	308
314	Small	-23.4680	38.4190	3480	368	697	0.05	1.67			34.0	307
315	Small	-21.6725	38.6451	3757	706	951	0.09	2.92			48.3	313
316	Small	-23.9601	38.6717	3437	344	503	0.05	1.25			15.8	124
317	Small	-22.2976	38.8313	3846	415	960	0.05	1.65			40.4	320
318	Small	-35.1321	38.9111	3605	307	910	0.03	1.02			43.1	326
319	Small	-23.6010	38.9643	3175	684	632	0.08	3.34			28.7	322
320	Small	-22.6301	38.9776	3575	710	1158	0.08	3.16			34.1	328
321	Small	-34.3873	39.0175	2935	562	699	0.07	2.63			65.6	326
322	Small	-23.8537	39.0175	3311	481	714	0.07	2.16			28.4	327
323	Small	-22.9892	39.1106	3399	697	741	0.07	2.70			34.5	328
324	Small	-32.8046	39.1904	1617	422	458	0.05	2.19			71.2	332
325	Small	-23.4813	39.2037	3314	648	686	0.08	3.70			28.4	327
326	Small	-34.9326	39.2436	3456	486	828	0.09	2.02			43.1	318
327	Small	-23.7340	39.2436	3305	601	797	0.06	2.94			28.4	322
328	Small	-22.7232	39.2702	3393	766	750	0.07	3.34			34.1	320
329	Small	-22.1646	39.4830	3832	645	795	0.08	3.30			25.9	331
330	Small	-35.4646	39.6160	3890	355	831	0.03	1.44			33.7	335
331	Small	-21.9651	39.6027	4009	415	476	0.06	2.47			25.9	329
332	Small	-32.3790	39.6692	1523	419	1078	0.04	1.92			63.7	38
333	Small	-34.1213	39.7357	3314	383	700	0.04	1.72			63.2	338
334	Small	-22.4040	39.7357	3591	821	681	0.12	3.32			15.9	336
335	Small	-35.2252	39.8022	3682	618	738	0.07	2.97			33.7	330
336	Small	-22.2710	39.7889	3627	801	483	0.10	4.67			9.0	337
337	Small	-22.1912	39.8022	3647	878	169	0.22	4.52			9.0	336
338	Small	-33.5627	39.8421	2909	615	572	0.07	2.60			27.3	340
339	Small	-22.0582	39.8554	3791	708	718	0.10	4.42			15.9	337

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
340	Small	-33.3233	39.8953	3071	351	448	0.05	1.55			27.3	338
341	Small	-23.6409	39.9485	3237	590	916	0.07	3.48			51.6	350
342	Small	-22.6301	40.0150	3747	539	959	0.06	2.33			13.4	343
343	Small	-22.5104	40.0017	3770	476	843	0.05	1.87			13.4	342
344	Small	-23.0424	40.0549	3646	563	977	0.11	2.81			19.2	345
345	Small	-22.8828	40.1214	3468	780	625	0.10	3.93			19.2	344
346	Small	-33.6159	40.1347	3070	589	621	0.07	3.48			33.0	338
347	Small	-33.3366	40.3608	2831	592	781	0.07	2.35			39.9	346
348	Small	-32.8844	40.3608	2514	569	943	0.05	2.44			50.2	347
349	Small	-34.7730	40.3874	3779	423	968	0.04	1.78			38.9	351
350	Small	-23.7473	40.4007	3665	521	832	0.05	2.25			51.6	341
351	Small	-35.1188	40.4406	3690	674	589	0.07	3.50			38.9	349
352	Small	-34.5868	40.7066	3533	471	844	0.05	2.15			41.1	349
353	Small	-33.3366	40.7598	3055	491	608	0.05	2.70			44.3	347
354	Small	-31.3948	41.0258	2031	456	614	0.05	2.18			42.3	363
355	Small	-24.0798	41.0258	3472	338	905	0.04	1.32			78.7	350
356	Small	-24.8911	41.0657	3200	384	840	0.04	1.21			69.8	157
357	Small	-28.2294	41.1056	2096	655	670	0.08	3.06			31.1	358
358	Small	-27.9501	41.0923	2029	639	1034	0.06	2.21			31.1	357
359	Small	-30.5702	41.1854	2109	491	457	0.07	1.76			38.6	164
360	Small	-29.5860	41.2120	1429	599	905	0.08	1.90			45.9	362
361	Small	-25.7689	41.2519	2937	551	905	0.05	1.94			46.3	214
362	Small	-29.1870	41.3184	1414	645	859	0.08	3.56			45.9	360
363	Small	-31.1687	41.3317	1612	723	832	0.07	3.47			33.5	60
364	Small	-26.3408	41.4780	2598	439	456	0.05	2.01			41.9	370
365	Small	-30.6766	41.5578	1506	766	894	0.08	3.55			29.7	60
366	Small	-34.6134	41.6110	3667	412	789	0.04	2.41			24.5	369
367	Small	-25.6758	41.6642	3055	422	802	0.05	2.85			43.5	370
368	Small	-28.3092	41.6908	2046	553	849	0.06	2.62			50.3	375

N	Category	Location		Depth	$h$	$a_b$	$\xi_r$	$\phi$	$d_L$	N	$d$	N
		Longitude	Latitude	(m)	(m)	Km2		degrees	km		km	
369	Small	-34.4139	41.7041	3612	347	723	0.04	1.44			24.5	366
370	Small	-26.0615	41.7307	2316	841	925	0.08	3.75			40.6	376
371	Small	-30.4638	41.7573	2004	519	565	0.06	2.70			30.5	374
372	Small	-28.8279	41.8371	1699	545	202	0.12	3.01			20.6	373
373	Small	-29.0008	41.9036	1602	501	953	0.06	1.87			20.6	372
374	Small	-30.6367	41.9701	2072	534	627	0.06	2.58			30.5	371
375	Small	-28.6018	42.0366	1670	739	591	0.10	3.66			23.6	379
376	Small	-26.2610	42.0366	2303	776	438	0.10	3.01			40.6	370
377	Small	-28.8678	42.1696	1645	650	500	0.12	3.80			30.9	379
378	Small	-26.8595	42.1696	2514	511	792	0.05	2.59			68.1	376
379	Small	-28.6018	42.2494	1713	768	607	0.10	3.42			23.6	375
380	Small	-33.9218	42.2760	3582	488	769	0.05	2.41			83.8	369
381	Small	-32.4455	42.2627	3088	260	836	0.02	1.04			32.7	384
382	Small	-29.5993	42.2627	1520	771	679	0.09	4.09			19.3	387
383	Small	-27.5777	42.2627	2347	439	887	0.05	2.27			80.5	378
384	Small	-32.7248	42.3558	3153	428	706	0.05	1.75			32.7	381
385	Small	-31.2352	42.3558	2680	332	932	0.03	1.30			36.1	392
386	Small	-30.2510	42.4356	2049	567	937	0.06	2.31			67.2	374
387	Small	-29.5860	42.4356	1461	827	912	0.09	2.68			19.3	382
388	Small	-28.3624	42.4356	1791	886	688	0.10	4.56			33.7	379
389	Small	-28.7880	42.4888	1705	619	380	0.10	4.08			18.0	390
390	Small	-28.9476	42.5154	1531	602	457	0.15	3.74			13.2	393
391	Small	-32.1529	42.5287	2957	323	700	0.03	1.64			43.9	381
392	Small	-31.5012	42.5420	2833	322	999	0.03	1.22			36.1	385
393	Small	-29.0008	42.6218	1414	723	401	0.13	3.73			13.2	390
394	Small	-30.7298	42.8346	2502	612	403	0.09	2.96			69.3	386
395	Small	-32.5652	42.8612	3010	381	898	0.03	1.42			58.9	391

## APPENDIX 3

### DETAILS OF THE GENERIC SEAMOUNT MODEL

#### ECOLOGICAL GROUPS OF THE GENERIC SEAMOUNT MODEL

A model of a theoretical isolated seamount in the North Atlantic was built. The depth of the summit was set to be at around 300 m and the base at around 2000m. The area of the model is assumed as 30 km radius from the summit, in order to include the theoretical area of its influence. As a result the total area under consideration was equal to 2827 km<sup>2</sup>.

A total of 37 functional groups were included in the seamount model, stratified by depth of habitat. The models included three marine mammals groups (toothed whales, baleen whales and dolphins), seabirds, turtles, seven invertebrate groups (benthic filter feeders such as corals or gorgonians, benthic scavengers, benthic crustaceans, pelagic crustaceans, seamount resident cephalopods, small and large drifting cephalopods), three zooplankton groups (gelatinous, shallow and deepwater zooplankton), primary producers (phytoplankton), detritus and twenty fish groups.

#### 1 Primary Producers

In this model we assumed that the primary production was the same as in the surrounded areas, expecting that the upwelling generated by the model increased phytoplankton biomass over the seamount. Phytoplankton biomass was estimated based on the Azores model (Guénette and Morato, 2001). The authors used information taken at the Azores front (south of Azores), in early October (Li, 1994) and obtained a biomass of 7.16 g·m<sup>-2</sup>. Based on the SeaWiFS data set ([www.me.sai.jrc.it](http://www.me.sai.jrc.it)), Guénette and Morato (2001) estimated a primary productivity of phytoplankton at 2030 g·m<sup>-2</sup>·year<sup>-1</sup>. The P/B was estimated at 283.5 year<sup>-1</sup>, based on the primary production and phytoplankton biomass.



## **2 Zooplankton**

The shallow and deep-water zooplankton groups included both small and large size organisms. The small zooplankton was defined as small herbivores, while the large zooplankton included, among others, mysids, euphausiids, chaetognaths, decapods' larvae. The gelatinous zooplankton consisted mainly of Thaliacea (salps, pyrosomes), Hydrozoa (siphonophores, hydroids) and Scyphozoa (jellyfish).

### **2.1 Shallow Zooplankton**

Huskin et al. (2001) found that about 90% of the small zooplankton of the Subtropical Atlantic near the Azores was composed by copepods, mainly small calanoids. Using the data presented by Huskin et al. (2001), we estimated small zooplankton biomass (until 200 m) of  $6.071 \text{ t}\cdot\text{km}^{-2}$  and a Q/B of  $43.285 \text{ year}^{-1}$ . Large shallow water zooplankton biomass was estimated from profiles of the zooplankton of the Azores front (Angel, 1989) from 0 to 1100 meters to be equal to  $10.613 \text{ t}\cdot\text{km}^{-2}$ . Q/B estimate (i.e.,  $34 \text{ year}^{-1}$ ) was taken from the Azores model (Guénette and Morato, 2001; salps were not considered). Total biomass was then equal to the sum of small and large shallow water zooplankton, while for the final Q/B a weighted average was calculated ( $\text{Q/B} = 37.379 \text{ year}^{-1}$ ). Finally, production over consumption (P/Q) ratio was considered equal to 0.3 (Christensen, 1996).

### **2.2 Deep-water Zooplankton**

Biomass estimated for deep large zooplankton from 0 to 1100 meters was  $4.357 \text{ t}\cdot\text{km}^{-2}$  (based on Angel, 1989). Assuming the same ratio large/small zooplankton as in shallow water, the estimate of deep small zooplankton biomass was equal to  $2.492 \text{ t}\cdot\text{km}^{-2}$ . In addition, total biomass of deepwater zooplankton was  $6.849 \text{ t}\cdot\text{km}^{-2}$ . Finally, Q/B value was equal to  $29.0 \text{ year}^{-1}$ , while P/Q of 0.3 (Christensen, 1996) was also used to estimate P/B.

### **2.3 Gelatinous Zooplankton**

Biomass estimation of gelatinous zooplankton was derived from data presented by Angel (1989). Using a conversion factor of 1 ml of displacement volume to 0.8 g of jellyfish we obtained a total biomass of  $14.960 \text{ t}\cdot\text{km}^{-2}$ . This value was extremely high when compared to

other models, such as the Eastern Bering Sea ( $0.048 \text{ t} \cdot \text{km}^{-2}$ ; Trites et al., 1999) and the Barents Sea ( $6.47 \text{ t} \cdot \text{km}^{-2}$ ; Dommasnes et al., 2001). We decided to enter an EE of 0.8 and let the model estimate the biomass for this group. P/B ( $0.85 \text{ year}^{-1}$ ) and Q/B ( $2.0 \text{ year}^{-1}$ ) values were adopted from Trites et al. (1999).

### 3 Cephalopods

We used Nesis (1986) faunal components to originate two cephalopod groups. The Resident (benthic) Cephalopods includes groups 1 and 2 from Nesis (1986), while the group Drifting (pelagic) Cephalopods includes groups 3 and 4.

#### 3.1 Resident (benthic) Cephalopods

This group included mainly deep-sea octopus (Order Octopoda) and some species of squids that maintain themselves constantly above seamounts (e.g. *Todarodes*, *Ornroteuthis*, *Lycoteuthis*, etc.). The occurrence of cuttlefish (Order Sepiida) and little cuttlefish like (Order Sepiolida) species over or around seamounts was not confirmed. At this stage these Orders were excluded from the model. P/B and Q/B values for this group were taken from the Azores model (Gu  nette and Morato, 2001) and were equal to  $2.89 \text{ year}^{-1}$  and  $10.0 \text{ year}^{-1}$  respectively. Biomass was estimated by the model assuming an EE of 0.95.

#### 3.2 Drifting (pelagic) Cephalopods

This group included mainly squids (Order Teuthida) and vampire squid (Order Vampyromorphida) and was divided in two sub-groups depending on the size of the species. The small drifting cephalopods (mantle length < 50 cm) included species of the families Loliginidae, Histioteuthidae, as well as some small members of the families Onychoteuthidae and Ommastrephidae. Daily feeding rates were estimated at 4.09% of body weight for *Loligo forbesi* (Porteiro et al., 1995) and from 3.6% to 6.7% for *Illex* sp. (O'Dor, 1980). An average feeding rate of 4.62% was used to estimate the Q/B for small drifting cephalopods and was found equal to  $16.863 \text{ year}^{-1}$ . P/B ratio was inferred from daily growth rate for the same species and was equal to  $4.45 \text{ year}^{-1}$ . Biomass was estimated by the model assuming an EE of 0.95.

The large drifting cephalopods (mantle length > 50 cm) included species of the families Architeuthidae and Lepidoteuthidae as well as the large members of the families Onychoteuthidae and Ommastrephidae. P/B and Q/B values for this group were also taken from the Azores model (Guénette and Morato, 2001) and were equal to  $2.5 \text{ year}^{-1}$  and  $10.0 \text{ year}^{-1}$  respectively. Biomass was set at a very small value of  $0.001 \text{ t}\cdot\text{km}^{-2}$ .

#### **4 Crustacea**

Crustaceans were considered separately from the other benthic or pelagic groups because of their importance in the seamount food web. The easiest way of sub-dividing crustaceans is to split them in two groups: pelagic (mainly shrimps) and benthic (mainly crabs). Two main features have been observed for pelagic crustaceans over and around seamounts (Vereshchaka, 1994): 1) the rise of lines of equal size, abundances and biomass of the pelagic animals, and 2) the decrease in abundance, biomass and sizes of pelagic animals near the bottom water layer. One of the possible important causes of the decrease in abundance and biomass of pelagic shrimps near the bottom is that they are consumed by benthic and benthopelagic predators. Many fish and invertebrates dwelling over seamounts are known to live mainly on pelagic macroplankton brought there by the ocean currents. Vereshchaka (1996) concluded that the abundance of pelagic animals decreases while the concentration of benthopelagic predators increases near the seafloor and the role of the former in planktonic communities falls in the near-bottom layer.

##### **4.1 Pelagic Crustacea**

This group included mainly pelagic shrimps, such as Sergestidae, Penaeidae, Oplophoridae, Pandalidae, etc. P/B and Q/B values were taken from Bundy et al. (2000) and were equal to  $1.45 \text{ year}^{-1}$  and  $9.667 \text{ year}^{-1}$ , respectively. An EE of 0.95 was used and the biomass was estimate by the model.

#### **4.2 Benthic Crustacea**

This group included the benthic crab species (including deep-water species such as *Chaceon affinis*) as well as some benthic shrimps. P/B, Q/B and EE parameters were taken from the Azores model (Guénette and Morato, 2001) and were equal to  $1.6 \text{ year}^{-1}$ ,  $10.0 \text{ year}^{-1}$  and 0.95 respectively.

### **5 Benthic invertebrates**

The seamount benthic environment is typically dominated by corals and other suspension feeders, rather than the deposit feeders that are typical of most of the deep-sea benthos.

#### **5.1 Benthos filter feeders**

This group consisted of benthic filter feeders, such as hard corals, gorgonian and anthipatharian corals, suspension feeding ophiuroids and polychaetes, etc. P/B and Q/B values were taken from Optiz (1993) and were equal to  $0.8 \text{ year}^{-1}$  and  $9.0 \text{ year}^{-1}$  respectively. These values were estimated based on sponges and corals. An EE of 0.95 was adopted.

#### **5.2 Benthos scavengers**

This group consisted mainly of echinoderms (such as brittle stars Ophiuroidea, seastars Asteroidea, sea cucumbers Holothuroidea, and sea urchins Echinoidea), worms (Annelida), bivalves (Bivalvia), etc. P/B and Q/B values were estimated as the average of the groups “worms”, “mollusks”, “echinoderms” from Okey et al. (2001) and Ainsworth et al. (2001), and were equal to  $1.83 \text{ year}^{-1}$  and  $13.57 \text{ year}^{-1}$  respectively. An EE of 0.95 was adopted.

### **6 Epipelagic fishes**

#### **6.1 Epipelagic Small**

This group included species small ( $< 25 \text{ cm}$ ) Clupeidae (e.g. *Sardina pilchardus*), Atherinindae (e.g. *Atherina presbyter*), Scomberesocidae (e.g. *Nanycthyus simulans*), Exocoetidae (e.g. *Exocoetus volitans*), Macroramphosidae (e.g. *Macroramphosus scolopax*), Caproidae (*Capros aper*), etc. These last two species are known as benthopelagic, but since

they are preyed in the water column up to 200 m depth we opted to include them in the epipelagic group.

### **6.2 Epipelagic Medium**

This group included epipelagic fishes with more than 25 cm and less than 100 cm of total length (TL), such as the Scomberesocidae (e.g. *Scomberesox saurus*), Carangidae (e.g. *Caranx* sp., *Trachurus* sp., *Trachinotus* sp.), Scombridae (e.g. *Scomber* sp.), Centrolophidae (e.g. *Schedophilus* sp.), Balistidae (e.g. *Balistes* sp.), etc.

### **6.3 Epipelagic Large**

This group included epipelagic fish greater than 100 cm TL, such as Coryphaenidae (e.g. *Coryphaena* sp.), Carangidae (e.g. *Seriola* sp., *Acanthocybium solandri*), Sphyrinae (e.g. *Sphyrna* sp.), etc.

The average Q/B values for each group were estimated using the empirical equation of Palomares and Pauly (1998) and were equal to 19.867 year<sup>-1</sup> for small epipelagic fish, 10.750 year<sup>-1</sup> for medium, and 5.095 year<sup>-1</sup> for large. P/B values were taken from the model of the Oceanic ecosystems of the Atlantic (Vasconcellos and Watson, 2004), and were equal to 2.053, 1.080, 0.690 for small, medium and large epipelagic groups, respectively. The Biomasses for the epipelagic groups were assumed to be same as those estimated for the North Atlantic by Vasconcellos and Watson (2004). The values were 0.859 t·km<sup>-2</sup> for small epipelagic, 0.112 t·km<sup>-2</sup> for medium, and 0.014 t·km<sup>-2</sup> for the large group.

## **7 Mesopelagic and Deep-water fish groups**

Childress et al. (1980) showed that the estimated food intake of migratory fishes was greater than that of non-migratory ones. This food was channelled into activity, development of energy stores, and earlier reproduction. As a result, the growth rate of migratory fish was significantly greater than in non-migratory species. Thus, the Q/B and P/B values of migratory species were greater than in non-migratory species. Demersal deep water species are generally classified as either benthic (Bathybenthic) or benthopelagic (bathydemersal).

Benthic fishes include those that sit and wait for prey or forage slowly over the bottom, while benthopelagic fishes move to the water column to feed (Childress and Somero, 1990). It has been suggested that benthic fishes have lower metabolic rates than benthopelagic fishes. Those fishes found in association with seamounts and other topographic features form another distinct group (Koslow, 1996). These fishes are typically robust-bodied and capable of strong swimming performances (Koslow et al., 1995). These species are known to have high metabolic rates (Koslow, 1996). Since it is required to maintain position in highly dynamic current regimes, such as at seamounts, with frequent movements and strong locomotory performance, these species require greater metabolic expenditure than benthic or benthopelagic ones. These fishes usually exhibit delayed age of first maturity, low growth, and low mortality (Roff, 1984).

## 7 Mesopelagic migrating fishes

This group contained mesopelagic (200-1000 m depth) species that migrate diurnally into near-surface, and was sub-divided into two groups based upon body size. The **small** group (< 25 cm TL) consisted of Gonostomatidae (e.g. *Bonapartia pedaliota*, *Cyclothone* sp., *Gonostoma* sp.), Sternoptychidae (e.g. *Argyropelecus* sp., *Maurolicus muelleri*), Melanostomiidae (e.g. *Bathophilus* sp.), Myctophidae (e.g. *Electrona rissoi*, *Hygophum hygomii*, *Lampanyctus* sp., *Lobianchia dofleini*, *Myctophum* sp.), Diretmidae (*Diretmus argenteus*). P/B and Q/B values were assumed to be 2.053 year<sup>-1</sup> and 8.0 year<sup>-1</sup> (Koslow, 1996; Williams, et al., 2001) respectively. A biomass of 2.0 t·km<sup>-2</sup> was taken from the Azores model (Guénette and Morato, 2001), which was similar to the biomass estimated (i.e., 1.720 t/km<sup>2</sup>) by Vasconcellos and Watson (2004).

The **large** (> 25 cm TL) **mesopelagic migrating** fish group included a large range of sizes (25 up to 250 cm TL) and consists of Melanostomiidae (e.g. *Echiostoma barbatum*, *Eustomias Obscurus*, *Leptostomias haplocaulus*, *Photonektes dinema*), Paralepididae (e.g. *Macroparalepis affinis*, *Paralepis coregonoides borealis*), Melanonidae (e.g. *Melanomus zugmayeri*), Macrouridae (e.g. *Odontomacrus murrayi*), Regalecidae (e.g. *Regalecus glesne*), Gempylidae (e.g. *Gempylus serpens*), Alepisauridae (*Alepisaurus brevirostris*),

Centrolophidae (*Centrolophus niger*). P/B and Q/B values were assumed to be 0.600 year<sup>-1</sup> and 3.550 year<sup>-1</sup> respectively. An EE value of 0.95 was used to let the model estimate the biomass of this group.

## **8 Mesopelagic non-migrating fishes**

The mesopelagic non-migrating fishes group consisted of species that remain at depth (until 1000 m), including some Gonostomatidae, Myctophidae species. For this group, P/B, Q/B and EE values were assumed to be 0.500, 1.507 (from Williams et al., 2001), and 0.95 respectively.

## **9 Bathypelagic fishes**

This group included non-migratory deepwater (>1000m) pelagic species that remain at depth and have a reduced metabolic rate and “poor” condition (Koslow, 1996). This group includes some species of Saccopharyngidae (e.g. *Saccopharynx ampullaceus*), Alepocephalidae (e.g. *Herwigia krefftii*, *Photostylus pycnopterus*), Gonostomatidae (e.g. *Gonostoma bathyphilum*), Melamphaidae (e.g. *Melamphaes microps*), Trichiuridae (*Aphanopus carbo*). For this group, P/B and Q/B values were assumed to be 0.5 year<sup>-1</sup> and 1.477 year<sup>-1</sup> respectively.

## **10 Bathybenthic fishes**

This group included non-aggregating deep-water (>1000m) benthic species that do not feed in the water column. Some examples are: Apogonidae (e.g. *Epigonus telescopus*), Chlorophthalmidae (e.g. *Bathypterois* sp.), Synodontidae (e.g. *Bathysaurus ferox*), Aphyonidae (e.g. *Aphyonus gelatinosus*), Scorpaenidae (e.g. *Trachyscorpia cristulata echinata*). For this group, P/B and Q/B values were assumed to be 0.2 year<sup>-1</sup> and 0.5 year<sup>-1</sup> respectively.

## **11 Bathydemersal (Deep-sea Benthopelagic)**

This group included non-aggregating deep-water (>1000m) benthopelagic species that feed in the water column, thus having higher metabolic rates. Some of these species are: Alepocephalidae (e.g. *Alepocephalus rostratus*, *A. bardii*), Halosauridae (e.g. *Halosauropsis*

sp.), Notacanthidae (e.g. *Polyacanthonotus rissoanus*), Synphobranchidae (e.g. *Synphobranchius kaupii*), Bythitidae (e.g. *Cataetys laticeps*), Moridae (e.g. *Mora moro*, *Lepidion guentheri*), Macrouridae (e.g. *Bathygadus melanobranchus*, *Cetonurus globiceps*, *Chalinura* sp., *Nezumia* sp., *Trachonurus villosus*, *Coelorhynchus labiatus*), Gempylidae (e.g. *Nesiarchus nasutus*). For this group, P/B and Q/B values were assumed to be 0.2 year<sup>-1</sup> and 0.6 year<sup>-1</sup> respectively.

## 12 Seamount-associated fishes

Seamount associated fishes were divided into three different groups. Two groups containing species that are targeted by the north Atlantic fishery (*Hoplostethus atlanticus* and *Beryx* spp.), and a third one with the other seamount associated species. Parameters for these three groups were taken from Bulman (2002; P/B=0.048 year<sup>-1</sup> and Q/B=2.0year<sup>-1</sup> for *Hoplostethus atlanticus*). For the other two groups, “*Beryx* spp.” (*B. splendens* and *B. decadactylus*) and “**Other Seamount-associated fishes**” (including some Oreosomatidae species inhabiting the North Atlantic waters, such as *Alloctytus verrucosus*, *Neocyttus helgae*, and some aggregating Macrouridae such as *Coryphaenoides rupestris*), we used the values estimated by Bulman (2002) for oreos (i.e., P/B= 0.06 year<sup>-1</sup> and Q/B= 2.2 year<sup>-1</sup>).

## 13 Shallower Fish groups

Shallower water fish groups included those fishes with benthic or benthopelagic affinities occurring between 200 and 1000m depth. This group was divided further into “**Shallow Benthic fishes**”, and “**Shallow Benthopelagic fishes**”. The first group included benthic fishes, such as *Helicolenus dactylopterus*, *Ponthinus kuhlii*, *Molva macrophthalma*, *Conger conger* *Phycis phycis*, *Lophius piscatorius*, etc. The second group included species such as *Pagellus bogaraveo*. P/B and Q/B values were taken from the Azores model (Guénette and Morato, 2001) and were equal to 0.59 year<sup>-1</sup> and 4.70 year<sup>-1</sup> respectively (based on the group of demersal large predators) for benthic fishes and 0.66 year<sup>-1</sup> and 5.20 year<sup>-1</sup> respectively for benthopelagic fishes (based on *P. bogaraveo*).



#### 14 Large Oceanic Planktivores

This group consisted of large oceanic planktivorous fish, such as the whale shark (*Rhincondon typus*), basking shark (*Cetorhinus maximus*), manta rays (*Mobula* spp., *Manta* spp.), and sunfish (*Mola mola*, *Masturus* spp.). There is some anecdotic information (e.g. fishermen and observers onboard of tuna vessels) suggesting that these species may stop over and around seamount to feed during their migrations routes. An average Q/B was estimated from the empirical equation of Palomares and Pauly (1998) and was equal to  $2.06 \text{ year}^{-1}$ . The other parameters for this group were taken from Vasconcellos and Watson (2004;  $P/B = 0.112 \text{ year}^{-1}$  and  $EE = 0.1$ ). Biomass was estimated by the model assuming no fishing mortality but allowing Pelagic Sharks to feed upon this group.

#### 15 Tunas

Three species are usually caught on the seamounts (Fonteneau, 1991; Holland et al., 1999): yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*) and bigeye tuna (*T. obesus*). The Tuna group also includes other species, such as bluefin tuna (*T. thynnus*) and albacore (*T. alalunga*). Vasconcellos and Watson (2004) estimated the biomass for these five species in the North Atlantic as being  $0.029 \text{ t}\cdot\text{km}^{-2}$ , similar to that estimated by Gu  nette and Morato (2001) for the Azores area ( $0.032 \text{ t}\cdot\text{km}^{-2}$ ). We used the first value as a general estimation for the North Atlantic. For the same reason P/B and Q/B values were taken from Vasconcellos and Watson (2004), as the weighted mean of P/B and Q/B values for the five tuna species (i.e.,  $P/B = 0.742 \text{ year}^{-1}$  and  $Q/B = 16.291 \text{ year}^{-1}$ ). Comparing these values with the ones used by Gu  nette and Morato (2001) in the Azores model we found that the estimated P/B were very similar, while Q/B was much greater. This is probably due to that Vasconcellos and Watson (2004) estimated their Q/B values based on daily rations while Gu  nette and Morato (2001) used the empirical equation from Palomares and Pauly (1998).

#### 16 Billfishes

This group consisted of swordfish (*Xiphias gladius*) and several billfishes: blue marlin, (*Makaira nigricans*), white marlin (*Tetrapturus albidus*), and longbill spearfish (*T. pfluegeri*). P/B value was equal to  $0.5 \text{ year}^{-1}$  based on an average F value of  $0.3 \text{ year}^{-1}$  and an

average  $M$  of  $0.2 \text{ year}^{-1}$ . The biomass for this group was taken from Guénette and Morato (2001;  $0.02 \text{ t}\cdot\text{km}^{-2}$ ), while an average  $Q/B$  was estimated from the empirical equation from Palomares and Pauly (1998;  $4.2 \text{ year}^{-1}$ ).

### 17 Rays and Skates

This group consisted of all Rajiformes species (except Manta rays) such as *Torpedo* spp., *Raja* spp., *Dasyatis* spp., *Myliobatis* spp.

### 18 Pelagic Sharks

Pelagic shark consisted of *Carcharodon carcharias*, *Prionace glauca*, *Isurus oxyrinchus*, *Sphyrna* spp., *Alopias* spp., *Lamna nasus*.  $P/B$ ,  $Q/B$  and biomass for this group were taken from the Azores model (Guénette and Morato, 2001), based on *P. glauca*, *L. nasus* and *Galeorhinus galeus*.

### 19 Benthopelagic Sharks

Benthopelagic sharks consisted mainly of deep-water species such as Squaliformes (*Centroscymnus* spp., *Etmopterus* spp., *Daenia* spp., *Dalathia* spp., *Oxynotus* spp., etc.) or Hexanchiformes. The Ecopath parameters came from the Azores model (Guénette and Morato, 2001), based on *D. licha* and *Galeus melastomus*.

### 20 Sea-Turtles

Turtles occurring in the North Atlantic included the loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and green turtles (*Chelonia mydas*), whereas other species have been considered rare. Juvenile loggerhead turtles are transported by the North Atlantic Gyre current and live a pelagic life for about 8.2 years in the Eastern Atlantic (Bjorndal et al., 2000) where they seem to feed mainly on jellyfish (Bjorndal, 1997).  $P/B$ ,  $Q/B$  and biomass values were taken from the Azores model (Guénette and Morato, 2001) and were equal to  $0.15 \text{ year}^{-1}$ ,  $3.50 \text{ year}^{-1}$ , and  $0.001 \text{ t}\cdot\text{km}^{-2}$  respectively. Turtles have been found in sharks stomach (H. Rost Martins, unpublished data) and a considerable by-catch by the pelagic longline swordfish fishery has been reported (Ferreira et al., 2001).

## 21 Seabirds

Seabirds occurring around this theoretical seamount were assumed to be the same occurring around the Azores (Guénette and Morato, 2001). This is not totally true because we assumed to simulate an isolated seamount without islands nearby. However, the values presented for the Azores were very similar to those presented for the North Atlantic (Vasconcellos and Watson, 2004). P/B, Q/B and biomass were assumed to be  $0.04 \text{ year}^{-1}$ ,  $84.39 \text{ year}^{-1}$ , and  $0.0002 \text{ t/km}^2$  respectively.

## 22 Marine Mammals

Marine mammals were separated in three groups based on their diets. **Baleen whales** that feed mainly on zooplankton and small fish included minke whale (*Balenoptera acutorostrata*), sei whale (*Balaenoptera borealis*), blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), and humpback whales (*Megaptera novaeangliae*). **Toothed whales** included killer whale (*Orcinus orca*), false killer (*Pseudorca crassidens*), pilot whale (*Globicephala* sp.), northern bottlenose whale (*Hyperoodon ampullatus*), Gervais' beaked whale (*Mesoplodon europaeus*), Sowerby's beaked whale (*Mesoplodon bidens*), and the sperm whale (*Physeter macrocephalus*). **Dolphins** included the common dolphin (*Delphinus delphis*), striped dolphins (*Stenella coeruleoalba*), spotted dolphins (*Stenella frontalis*), Risso's dolphins (*Grampus griseus*), bottlenose dolphins (*Tursiops truncatus*). Ecopath parameters were taken from the Azores model (Guénette and Morato, 2001).

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