

Challenges and problems in modelling seamount ecosystems and their fisheries

Telmo Morato and Tony Pitcher

Abstract

The ecological and oceanographic importance of seamounts for the status of marine food webs and biodiversity has recently been recognized. Seamounts have been intensively exploited in all world oceans, and serious stock depletion has been detected in every case. Resident seamount fish are mostly slow-growing and late-reproducing while transient migratory fish also rely on seamount food webs, so that the impact of overfishing raises serious concerns. Moreover, trawling threatens the integrity of benthic habitats. The prevention of further negative impacts on these sensitive ecosystems is now an important policy objective. Because of the extensive trophic links on seamounts, ecosystem-based modelling approaches are essential to understand the ecosystem functioning and to ensure an effective management. However, there have been few attempts to model seamount communities. This talk will discuss the problems associated with modelling seamount ecosystems using the Ecopath-with-Ecosim framework. We propose modelling approaches to seamount processes such as the influences of peculiar current patterns on the seamount system and complex food web structure depending on advective food supplies. The hypothesis that the aggregating fish stocks on seamounts are supported from external sources was supported by the Ecopath models.

Keywords: Seamounts, trophic models, Ecopath, Ecosim, ecosystem-based management

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INTRODUCTION

World's fisheries resources have been characterized as seriously depleted or in danger of depletion (e.g. Pauly and Christensen 1995; Pauly et al. 1998; Pitcher 2001; Pauly et al., 2002), with global catches declining since late 1980's (Watson and Pauly, 2001). Although not unexpectedly there is a debate about the causes for this. Poor management practices and increased fishing pressure are among them. Unsustainable fishing practices along with an excessive level of investment in fishing capacity have resulted in serious stock depletion on continental shelves, creating new pressures on alternative fishing grounds (Pauly et al., 2002). In particular, seamounts are among those "newly" targeted ecosystems that have been intensively fished since the second half of the XX century (Rogers, 1994; Koslow et al., 2000). Targeted seamount fish communities are highly susceptible to overfishing because they are characterised by extremely low productivity (long-lived, slow growing, late maturity, and with low recruitment) and by being dependent for food on meso- and bathypelagic organisms that drift past seamounts (Koslow, 1997). Moreover, these fish species tend to form highly localized aggregations, which make them highly susceptible to overfishing (Clarke et al., 1996). Additionally, many seamounts are located in international waters, where there is no management, making these species even more susceptible to overfishing. Even for seamount fisheries within areas of national jurisdiction, the experience of the past few decades has been that they are typically depleted within 5 to 10 years. Once depleted, seamount populations will likely require decades to recover (Koslow, 1997). In addition, side effects caused by overfishing or the use of extensive trawling activities on seamounts are raising serious concerns: for example, damage to benthic communities typically dominated by corals and other suspension feeders (Koslow et al., 2001), and impacts on transient migratory species whose life history relies on seamount food webs. The prevention of further negative impacts on these sensitive ecosystems is now an important policy objective.

Because of the complex trophic links of seamounts, ecosystem-based modelling approaches can help in understanding ecosystem functioning and in planning effective management. However, there have been only a few attempts to model seamount ecosystems. The development of ECOPATH in the early 1980s (Polovina, 1984; Christensen and Pauly, 1992, 1993) and its evolution in the following years into a dynamic modelling tool (ECOPATH/ECOSIM/ECOSPACE: Walters et al., 1997, 1999, 2000a; Christensen et al., 2000), has allowed quantification of ecosystem parameters and the study of the effects of fisheries on several ecosystems (e.g., Christensen and Pauly, 1993; Jarre-Teichmann, 1998; Pitcher et al., 2000; Shannon et al., 2000; Walter et al., 2000b; Guénette et al., 2001; Watson and Pauly, 2001). A detailed description of the ECOPATH with ECOSIM (EwE) modelling tool in Christensen et al. (2000) and <http://www.ecopath.org>. Limitations and problems associated to the use of this approach has been a point of dispute since the early versions. The uncertainty associated to the input parameters as well as to some of the routines has been pointed out. Recently, Christensen and Walters (2000) discuss the capabilities and limitations of Ecopath with Ecosim. They pointed out that this approach did not intend to replace traditional single-species assessment methods; on the contrary it was developed mainly to conduct fisheries policy analyses that cannot be addressed with traditional assessment methods. Within this context some routines (e.g. policy exploration routines) has been recently developed and

included in the software (Walters et al., 2002). This routine has been considered a “powerful and sophisticated tool” that requires to be used carefully because without cautions, thoughtful and active use of the software, the probability of dangerously misleading results and conclusion is far greater than that of obtaining sensible and meaningful information (Cochrane, 2002).

Within the framework of ecosystem-based management, this paper will discuss problems associated with modelling seamount ecosystems using the Ecopath-with-Ecosim software and presents a preliminary generic seamount model. In an effort to understand seamount ecosystem functioning, we propose a range of modelling approaches, such as the influence of peculiar current patterns on the seamount system, complex food web structure depending on advective food supplies, predation by transient visitors like tuna and whales, and the integration of different environmental compartments stratified by depth. We use the preliminary model to examine which types of fisheries might be sustainable on seamounts.

METHODS

MODELLING APPROACH

The modelling approach used in this study was the Ecopath with Ecosim system version 5.0 Beta (Christensen et al., 2000). Two models (non-migrating and migrating) of a theoretical isolated seamount, somewhere in the North Atlantic were built. The depth of the summit was set to be at around 300 m and the base at around 2000m (or more – 4000). 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 km².

A total of 37 functional groups were included in the seamount model, stratified by depth of habitat (see **Appendix** for details). 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 (see **Appendix** for a complete description of the groups). Fish groups were divided based on environment use (depth and habitat – e.g. benthonic, pelagic or benthopelagic), size, energetic and life-history (Childress et al., 1980; Koslow, 1996; Melo and Menezes, 2002). 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 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. At this stage the deep scattering layer (DSL; 50-200 m thick, sound-reflecting layer in ocean waters, consisting of a stratified, dense concentration of zooplankton and fish and causing scattering of sound. DSL tends to raise at night and

descend during daytime) 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 (shrimps), small mesopelagic migrating fishes].

The model parameters, production to biomass ratios (P/B), consumption to biomass ratios (Q/B) are calculated on a yearly basis. Biomass and catch are expressed in tonnes of wet weight per square kilometre. The Q/B ratios for fish groups were estimated using an empirical equation (Palomares and Pauly, 1998). Temperature values 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 (Christensen, 1996). Following Shannon and Jarre-Teichmann (1999), the proportion of food consumed and not assimilated was taken as 0.2. When no biomass estimate was available, this parameter was left to estimate by Ecopath using a value of 0.95 for Ecological Efficiency (EE). A preliminary diet matrix was assembled using published data, unpublished local information, or empirical knowledge. When unidentified categories were found in the literature, data were re-expressed out of 100% to exclude these groups.

The theoretical seamount was assumed to have a low initial level of exploitation. The seamount fisheries were loosely based on those apparently in 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); Deepwater Longline (targeting bathypelagic and bathybenthic); Small Pelagics fishery (for small pelagic fishes); tuna fishery; swordfish fishery; deepwater trawl (targeting seamount associated species, including orange roughy and alfonsinos). Landings (Table 1) were assumed to be small and varied from 218 t/y for shallow benthic fishes to 2.7 t/y for billfishes.

MODELLING CURRENT PATTERNS, UPWELLING, AND INCREASED PRIMARY PRODUCTIVITY

The influences of peculiar current patterns on the seamount system

In order to explore whether the increased primary production generated by upwelling events would be amplified and positively affect higher trophic levels, we spatially simulated the non-migrating model using ECOSPACE (Walters et al., 1999). This was done mainly to test if increased primary production would generate higher biomasses of Seamount Associated Fish.

In detail, six habitats were established: Open water (0.725 of total habitat), Coastal (0.035), 300-500m depth (0.054), 500-1000m (0.097), 1000-2000m (0.079), and Seamount summit (0.009). In addition, ECOPATH groups were assigned to their preferred habitat. No modifications were made to the default ECOSPACE movement rates. To simulate the effects of these particular features, fishing was eliminated (F=0). Several scenarios were then explored: A) no fishing but no current patterns simulated (control); B) no fishing and MDL (Mixed Depth Layer); C) no fishing, MDL, and eddies; D) no fishing, MDL, eddies, and a 2x increase of PP on the seamount summit; E) no fishing,

MDL, eddies, and a 4x increase of PP on the seamount summit. ECOSPACE was run to simulate the effect of the different scenarios during a 50-year-period.

THE “IMMIGRATION” SEAMOUNT MODEL

Modelling complex food web structure depending on advective food supplies

In spite of evidence of localized upwelling and eddies around seamounts, which may enhance primary productivity near the surface, it is unlikely that water could be retained around a seamount sufficiently long enough to work its way through the food-web to the higher trophic level fish residing on the seamount itself (Koslow, 1997). Several studies have shown that large seamount fish communities are supported mainly by the flow of organisms that pass the seamounts and by trapped migrating prey species (Genin et al., 1988). For example, Koslow (1997) estimated that the orange roughy food requirements are ten times higher than what is available or produced at the seamounts.

Using the EwE software, food web structure depending on advective food supplies can be modelled in two different ways. In particular, the first approach, which is used only when there is a real, permanent addition of organisms from other areas outside the system, assumed treatment of migratory flows as dispersal (immigration / emigration) rates across the system boundaries (Christensen et al., 2000). It must be noted that dispersal rates allow quantification of the amount of imported resources needed to maintain the system and simulation of the impact of different levels of migration, due to inter-annual changes in climate, primary production, and currents. The second approach involves the assignment of a high diet proportion as “import” in the Ecopath diet composition matrix (Christensen et al., 2000), and was not used at this stage.

We tried to simulate the immigration of prey organisms and quantify the levels of immigration of prey that would be required to maintain a “typical” seamount fish community. We assumed that the standing biomasses estimated by the non-migrating model, would roughly represent the biomasses of most of the groups, except for seamount aggregating fishes, *Hoplostethus atlanticus*, *Beryx* spp, and some pelagic fish groups that are attracted to seamounts. P/B, Q/B, EE (Ecotrophic Efficiency), 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 accessible and so data presented by Bulman (2002) were used. Biomasses were re-scaled to the total area, assuming that part of it is open water where seamount associated species unlikely occur; 2) biomass of groups attracted to seamounts was slightly increased and thus considered greater than in the open ocean (i.e., seabirds, tunas, billfishes, and pelagic sharks). No changes were made to the benthic filter feeding group.

RESULTS AND DISCUSSION

THE “NON-MIGRATION” SEAMOUNT MODEL

The initial model was built with no special features in the seamount ecosystem, in order to estimate base standing biomasses for the different groups (Table 2). In comparison

with a general “open ocean” model built for the North Atlantic (Vasconcellos and Watson, in press), the biomasses estimated for the pelagic groups were very similar. Such a result was expected because we did not take into account any ecological processes, such as high densities of fish aggregations around seamounts, trapping of small organisms, increased primary production. In contrast, estimated biomasses for benthic and demersal groups of the present study were higher, due to greater habitat availability for these groups. Our biomass estimates were very close to the estimates for a flat deepwater model (Bulman, 2002). With respect to seamount associated species, the estimated biomasses were very low (i.e., 0.45 t/km² of orange roughy, 0.34 t/km² of alfonsinos, and 0.89 t/km² of other seamount associated fish species). Biomass of orange roughy off Tasmania has been estimated as being 50-125 t/km² (Koslow, 1997), while for the same region Bulman (2002) estimated biomasses on seamounts of 106.7 t/km² of orange roughy, 4.11 t/km² of oreos and 8.21 t/km² of warty dory. Thus, our results may indicate lack of resources in the system to support such amounts of seamount aggregating fish.

MODELLING CURRENT PATTERNS, UPWELLING, AND INCREASED PRIMARY PRODUCTIVITY

The influences of peculiar current patterns on the seamount system

The final biomass estimated by the scenario (A) was used to compare with the final results of the other scenarios. Inter-comparisons between all the other spatial scenarios are also presented. The observed results on the non-migrating model were similar to those generated by the migrating one.

The final biomass of the scenario with MDL (scenarios B) was 1.027 times greater than in the control, representing an increase in biomass of 2.679 t/km²/y. This increase was mainly attributed to the increased biomass of detritus (0.750 t/km²/y), shallow zooplankton (0.580 t/km²/y), gelatinous zooplankton (0.563 t/km²/y), deepwater zooplankton (0.294 t/km²/y), phytoplankton (0.152 t/km²/y), pelagic crustaceans (0.089 t/km²/y), and small migrating mesopelagic fish (0.063 t/km²/y). However, the increase of the biomass of lower trophic levels was not amplified in the food web.

When we simulated eddies around the seamounts, only a small additional increase of the biomass was observed (0.114 t/km²/y; 1.001 times the biomass of scenario B). Eddies promoted a slight increase on the biomass of lower trophic levels (e.g. 0.043 t/km²/y of gelatinous zooplankton), as well as a decrease in some groups, such as benthic crustacean (-0.006 t/km²/y), pelagic crustaceans (-0.005 t/km²/y), and benthic scavengers invertebrates (-0.004 t/km²/y).

The water column above seamounts can be stabilized, maintaining phytoplankton cells in a suitable light regime, promoting the growth of diatoms, and increasing growth rates and primary production (PP; Comeau et al., 1995). To simulate such an increase in PP, we increased twice and four times the relative primary production over the seamount summit. In both cases, an unexpected decrease in total biomass was observed (0.999 and 0.956 x times the biomass of scenario C). In the 4x increased relative primary production spatial scenario, the decrease in the total biomass was noticeable even when compared with the control scenario (0.981 times the biomass of control). These values represented a loss of biomass of 1.872 t/km²/y to control and of 4.665 t/km²/y to the previous scenario. The main decrease in biomass was observed on the lower trophic level groups, but also

on shallow demersal fishes (-0.040 t/km²/y), resident cephalopods (-0.009 t/km²/y), and small drifting cephalopods (-0.006 t/km²/y).

In general, we found that the hydrographical peculiarities and the resulting biological conditions observed on seamounts were difficult to simulate. In addition, the simulated increase in biomass was not amplified in the food chain, which is in accordance with the literature (Koslow, 1997), thus supporting the advection theory that resources to sustain seamounts' fish communities are generally imported.

THE “IMMIGRATION” SEAMOUNT MODEL

Modelling complex food web structure depending on advective food supplies

Total immigration was estimated to be 84.1 t/km²/year (Table 3), which represents an import of 0.79 times of the total standing biomass of the system (excluding detritus). Groups with higher immigration rates were: small (vertical) migrating mesopelagic fish, mesopelagic non-migrating fish, pelagic crustaceans, and gelatinous zooplankton. Immigration to the system by small (vertical) migrating mesopelagic fish was estimated to be 14.8 times the standing biomass of this group. According to Bulman (2002), total immigration was found to be approximately 565 t/km²/year, representing 2.1 times the total standing biomass of the system. These values were much higher than ours and were partly due to extremely high immigration (i.e., 370 t/km²/year) of pelagic crustaceans.

COMPARING THE TWO MODELS

Several ecosystem indices that indicate resilience, resistance to perturbations, and flow between ecosystem elements are shown for the non-migrating and migrating models. These indices (Table 4) allow the comparison of the ecological characteristics of ecosystems (Christensen et al., 2000). The ratio primary production/total respiration reflects the maturity and development of the system. This ratio was greater than 1.0 in both models (3.8 and 3.4) suggesting non-mature early developed systems. The ratio total primary production/total biomass also pointed out the immaturity of the systems (33.2 and 19.3). The values for these two ratios in the migrating model were slightly lower than in the non-migrating, indicating a more developed system. Large values of net system production are expected in immature systems, and values close to zero in mature ones. Again, the estimated values pointed towards immature system, whereas the migrating system being more mature than the non-migrating.

The biomass supported by the non-migrating model for all the seamount aggregating fish was 1.685 t/km², while for the migrating model was 47.78 t/km². The net primary production required to sustain the systems were the same for the two models (2076.4 t/km²/year) and similar to the estimated primary production in the North Atlantic (2030 t/km²/year, Guénette and Morato, 2001). The hypothesis that the aggregating fish stocks on seamounts (assuming that the biomasses estimates from other places were correct) are supported from external sources was supported by the ECOPATH models.

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Bibliography

- Bulman, C.M. 2002. Trophic ecology and food web modelling of mid-slope demersal fishes off southern Tasmania, Australia. PhD thesis, University of Tasmania, Hobart, Australia.
- Childress, J.J., S.M. Taylor; G.M. Cailliet and M.H. Price. 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. *Marine Biology* 61: 27-40.
- Christensen, V. and D. Pauly. 1992. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61: 169-185.
- Christensen, V. and D. Pauly. 1993. Trophic Models of Aquatic Ecosystems. ICLARM, Manila Philippines. 390 pp.
- Christensen, V. 1996. Balancing the Alaska gyre model. Pp: 32-36 *in* D. Pauly and V. Christensen (eds). Mass-balance models of North-eastern Pacific ecosystems. Fisheries Centre Research Report 4(1), University of British Columbia, Vancouver, Canada. 129pp.
- Christensen, V. and C. Walters. 2002. Ecopath with Ecosim: methods, capabilities and limitations. Pp 75-105 *in* D. Pauly and T.J. Pitcher (eds). Methods for Evaluating the Impacts of Fisheries on North Atlantic Ecosystems. Fisheries Centre Research Report 8(2), University of British Columbia, Vancouver, Canada. 195pp.
- Cochrane, K. 2002. Using of ecosystem models to investigate ecosystem-based management strategies for capture fisheries: Introduction. Pp: 5-10 *in* T. Pitcher and K. Cochrane (eds). The use of ecosystem models to investigate multispecies management strategies for capture fisheries. Fisheries Centre Research Report 10(2), University of British Columbia, Vancouver, Canada. 156pp.
- Comeau, L.A.; A.F. Vezina; M. Bourgeois and S.K. Juniper. 1995. Relationship between phytoplankton production and the physical structure of the water column near Cobb Seamount, northeast Pacific. *Deep-Sea Research I* 42(6): 993-1005.
- Christensen, V.; C.J. Walters and D. Pauly. 2000. Ecopath with Ecosim: A user's guide. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia. 131 pp.
- Clark, M.R. 1996. Biomass estimation of orange roughy: a summary and evaluation of techniques for measuring stock size of a deep-water fish species in New Zealand. *J. Fish Biol.* 49(Supplement A): 114-131.
- Genin, A.; L. Hauray and P. Greenblatt 1988. Interactions of migrating zooplankton with shallow topography: Predation by rockfishes and intensification of patchiness. *Deep-Sea Research* 35(2): 151-175.

- Gu nette, S.; V. Christensen and D. Pauly (eds). 2001. Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4), 334pp.
- Gu nette, S. and T. Morato. 2001. The Azores archipelago, 1997: and Ecopath approach. Pp: 241-270 in S. Gu nette; V. Christensen and D. Pauly (eds). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4), University of British Columbia, Vancouver, Canada.
- Jarre-Teichmann, A. 1998. The potential role of mass balance models for the management of upwelling ecosystems. Ecological Applications 8 (suppl.), 93-103.
- Koslow, J.A. 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. Journal of Fish Biology 49(Supplement A): 54-74.
- Koslow, J.A. 1997. Seamounts and the ecology of deep-sea fisheries. American Scientist 85: 168-176.
- Koslow, J.A.; G.W. Boehlert; J.D.M. Gordon; R.L. Haedrich; P. Lorange and N. Parin. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57: 548-557.
- Koslow, J.A.; K. Gowlett-Holmes; J.K. Lowry; T. O'Hara; G.C.B. Poore and A. Williams. 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Marine Ecology Progress Series 213: 111-125.
- Melo, O. and G. Menezes 2002. Projecto de acompanhamento da experi ncia de pesca dirigida ao peixe-rel gio (*Hoplostethus atlanticus*) - FISHOR: relat rio final. Arquivos do DOP. S rie Estudos 4/2002, 38 pp.
- Morato, T.; S. Gu nette and T. Pitcher. 2001. Fisheries of the Azores, 1982-1999. Pp: 214-220 in D. Zeller; R. Watson; T. Pitcher, and D. Pauly (eds). Fisheries impacts on North Atlantic Ecosystems: Catch, effort and national/regional data sets. Fisheries Centre Research Reports 9(3), University of British Columbia, Vancouver, Canada.
- Odate, T. and K. Furuya. 1998. Well-developed subsurface Chlorophyll maximum near Komahashi No. 2 Seamount in the Summer of 1991. Deep-Sea Research Part I 45(10): 1595-1607.
- Palomares, M.L.D. and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Marine and Freshwater Research 49: 447-453.
- Pauly, D. and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature 374: 255-257.
- Pauly, D.; V. Christensen; J. Dalsgaard; R. Froese and F. Torres Jr. 1998. Fishing down marine food webs. Science 279: 860-863.
- Pauly, D., V. Christensen; S. Gu nette; T.J. Pitcher; U.R. Sumaila and C.J. Walters. 2002. Towards sustainability in world fisheries. Nature 418(8): 689-695.
- Pitcher, T.J.; R. Watson; N. Haggan; S. Gu nette; R. Kennish and R. Sumaila. 2000. Marine reserves and the restoration of fisheries and marine ecosystems in the South China Sea. Bulletin of Marine Science 66(3): 527-534.
- Pitcher, T.J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. Ecological Applications 11(2): 601-617.
- Polovina, J.J. 1984. Models of a coral reef ecosystem I: the ECOPATH model and its application to French frigate shoals. Coral Reefs 3: 1-11.
- Rogers, A.D. 1994. The biology of seamounts. Advances in Marine Biology 30: 305-350.

- Shannon, L.J., P.M. Cury; and A. Jarre. 2000. Modelling effects of fishing in the southern Benguela ecosystem. *ICES Journal of Marine Science* 57: 720–722.
- Vasconcellos, M. and R. Watson. *In press*. Mass-balance models of oceanic ecosystems of the Atlantic. Fisheries Centre Research Reports, University of British Columbia, Vancouver, Canada.
- Walters, C.; V. Christensen and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7: 139-172.
- Walters, C.; D. Pauly and V. Christensen. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2: 539-554.
- Walters, C.; V. Christensen and D. Pauly. 2002. Searching for optimum fishing strategies for fishery development, recovery and sustainability. Pp: 11-15 *in* T. Pitcher and K. Cochrane (eds). The use of ecosystem models to investigate multispecies management strategies for capture fisheries. Fisheries Centre Research Report 10(2), University of British Columbia, Vancouver, Canada. 156pp.
- Walters, C.; D. Pauly; V. Chistensen, and J.F. Kitchell. 2000a. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3: 70-83.
- Watson, R.; J. Alder and C. Walters. 2000b. A dynamic mass-balance model for marine protected areas. *Fish and Fisheries* 1: 94-98.
- Watson, R. and D. Pauly. 2001. Systematic distortions in the world fisheries catch trends. *Nature* 424: 534-536.

Table 1 – Average landings (t/km²/year) estimated for the different fisheries considered in the theoretical seamount. DL= Demersal longline; DWL= DeepWater Longline; SP= Small Pelagics fishery; T= Tuna; SW= Swordfish; DWT= DeepWater Trawl

Group name	Landings by Fleet (t/km ² /y)						Total
	DL	DWL	SP	T	SW	DWT	
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			0.05				136.4
Epipelagic M			0.01				27.3
Shallow Benthic Fishes	0.08						218.2
Shallow Demersal fishes	0.02						54.6
Seamounts-associated Fishes		0.001				0.01	30.0
Hoplostethus atlanticus						0.01	27.3
Beryx 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				0.001	5.5
Total t/km²/y	0.11	0.008	0.06	0.011	0.002	0.029	

Table 2 – Input parameters and estimates (in parentheses) from the theoretical non-migratory model 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.

Group name	Biomass (t/km ²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	TL	Landings (t/km ²)
Toothed Whales	0.000	0.020	10.270	(0.513)	5.17	
Baleen Whales	0.123	0.060	5.563	(0.024)	3.56	
Dolphins	0.040	0.070	11.410	(0.050)	4.58	
Sea Turtles	0.001	0.150	3.500	(0.899)	4.08	
Seabirds	0.000	0.040	84.390	(0.000)	4.36	
Tunas	0.032	0.742	16.291	(0.686)	4.58	0.011
Billfishes	0.020	0.500	4.200	(0.101)	4.54	0.001
Sharks Pelagic	0.011	0.300	3.100	(0.868)	4.70	0.002
Sharks Benthopelagic	0.030	0.510	6.900	(0.160)	4.40	0.002
Rays and Skates	0.020	0.170	1.500	(0.678)	3.91	0.002
Large Oceanic Planktivores	(0.003)	0.112	2.066	0.100	3.56	
Epipelagic S	0.859	2.053	19.867	(0.567)	3.10	0.050
Epipelagic M	0.113	1.080	10.750	(0.902)	3.59	0.010
Epipelagic L	0.014	0.690	5.095	(0.487)	4.18	
Mesopelagic Mig S	2.000	1.980	8.000	(0.981)	3.37	
Mesopelagic Mig L	(0.003)	0.600	3.550	0.950	4.34	
Mesopelagic NonMigrating	(1.421)	0.500	1.570	0.950	3.12	
Shallow Benthic Fishes	(0.820)	0.590	4.700	0.950	3.70	0.080
Shallow Demersal fishes	(0.193)	0.660	5.200	0.950	4.04	0.020
Seamounts-associated Fishes	(0.890)	0.060	2.200	0.950	4.14	0.011
Hoplostethus atlanticus	(0.452)	0.048	2.000	0.900	4.39	0.010
Beryx spp.	(0.343)	0.060	2.000	0.950	3.90	0.010
Bathypelagic	(0.029)	0.500	1.477	0.950	4.12	0.006
Bathybenthic fishes	(1.143)	0.200	0.500	0.950	3.54	0.003
Bathydemersal Fishes	(1.283)	0.200	0.600	0.950	4.19	0.002
Benthos filter feeders	(0.595)	0.800	9.000	0.950	2.00	
Benthos scavengers	(3.089)	1.830	13.567	0.950	2.35	
Crustacea Benthic	(3.858)	1.600	10.000	0.950	2.00	
Crustacea Pelagic	(5.161)	1.450	9.667	0.950	2.72	
Cephalopods Resident	(0.189)	2.890	10.000	0.950	3.78	
Cephalopods Drifting S	(0.175)	4.450	16.863	0.950	3.83	
Cephalopods Drifting L	(0.001)	2.500	10.000	(0.726)	4.33	
Gelatinous ZooPlankton	(8.895)	0.850	2.000	0.800	3.08	
ZooPlankton Shallow	16.684	(11.214)	37.379	(0.774)	2.11	
ZooPlankton Deep	6.849	(8.700)	29.000	(0.595)	2.23	
Phytoplankton	7.160	290.000	-	(0.358)	1.00	
Detritus	-	-	-	(0.045)	1.00	

Table 3 – Estimated immigration rates and its proportion of the initial standing biomass for the migrating Ecopath model.

	Immigration (t/km ² /year)	Proportion of standing Biomass
Epipelagic S	0.093	0.11
Epipelagic M	0.018	0.16
Epipelagic L	0.001	0.07
Mesopelagic Mig S	29.616	14.81
Mesopelagic Mig L	0.001	0.33
Mesopelagic NonMigrating	10.148	7.14
Shallow Demersal fishes	0.015	0.08
Bathypelagic	0.419	14.45
Bathybenthic fishes	0.404	0.35
Bathydemersal Fishes	8.242	6.42
Crustacea Pelagic	18.37	3.56
Cephalopods Drifting S	2.012	11.50
Cephalopods Drifting L	0.008	8.00
Gelatinous ZooPlankton	14.796	1.66
TOTAL	84.143	0.79*

*excluding detritus

Table 4 – System statistics for the Ecopath non-migrating and migrating models.

Parameter	Non-migrating Model	Migrating model	Units
Sum of all consumption	1029.7	1119.9	t/km ² /year
Sum of consumption from PP	872.0	955.1	t/km ² /year
Sum of all exports	1536.0	1465.8	t/km ² /year
Sum of exports from PP	0.171	-76.899	t/km ² /year
Sum of all respiratory flows	540.4	610.6	t/km ² /year
Sum of all flows into detritus	1608.8	1623.7	t/km ² /year
Total system throughput	4715.0	4820.0	t/km ² /year
Sum of all production	2359.0	2361.0	t/km ² /year
Mean trophic level of the catch	3.73	4.08	
Gross efficiency (catch/net p.p.)	0.00011	0.00052	
Calculated total net primary production	2076.4	2076.4	t/km ² /year
Total primary production/total respiration	3.842	3.401	
Net system production	1536.0	1465.8	t/km ² /year
Total primary production/total biomass	33.2	19.3	
Total biomass/total throughput	0.013	0.022	
Total biomass (excluding detritus)	62.6	107.6	t/km ²
Total catches	0.221	1.088	t/km ² /year
Connectance Index	0.200	0.204	
System Omnivory Index	0.237	0.232	

APPENDIX

ECOLOGICAL GROUPS

Primary Producers:

An increase in PP has been observed over seamounts due to either uplifting of isotherms into the euphotic zone that can introduce biogenes into nutrient-poor water (Genin and Boehlert, 1985; Dower et al., 1992; Odate and Furuya, 1998; Mouriño, 2001) or due 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). However, some investigations failed to demonstrate persistent high chlorophyll *a* patches over seamounts (Pelaez and McGowan, 1986). Mouriño, et al. (2001) concluded that local increase in chlorophyll *a*, enhanced carbon incorporation rates and changes in phytoplankton species composition were associated with the seamount. However, they demonstrated that these effects were subjected to a large degree of temporal and spatial 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 several studies.

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⁻². Based on the SeaWIFS data set (www.me.sai.jrc.it), Guénette and Morato (2001) estimated a primary productivity of phytoplankton at 2,030 g WW*m⁻²*year⁻¹. The P/B was estimated at 290 y⁻¹, based on the primary production and phytoplankton biomass.

Zooplankton

Effects of seamounts on biological processes have been described in many occasions (e.g. Boehlert and Genin, 1987; Rogers, 1994), but evidence concerning zooplankton features over seamounts is conflicting (Huskin et al., 2001). 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. Gaps of zooplankton above seamounts due to grazing or other effects were detected in several studies (Genin et al., 1994; Haurry et al., 2000), while other studies reported no differences in zooplankton biomass on- versus off-seamounts (Voronina and Timonin, 1986; Dower and Mackas, 1996). Sime-Ngado et al. (1992) reported an increase of ciliate biomass over seamounts probably related to seamount induced physical forcing which likely generates microhabitats favourable to the growth of opportunistic or physiologically adapted populations. Other example of high abundance of zooplankton over seamounts was found in Dower and Perry (2001). They reported high abundance of larval rockfish over Cobb Seamount and suggested that a persistent clockwise eddy, consistent with a stratified Taylor cone, plays a critical role in

retaining larval rockfish over Cobb Seamount and may contribute to the process of self-recruitment. Huskin et al. (2001) concluded that mesoscale structures (seamounts) influence zooplankton distribution and abundance, although more detailed temporal and spatial studies are required to determine the real influence of them.

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).

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 t/km² and a Q/B of 43.285 y⁻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 t/km². Q/B estimate (i.e., 34 y⁻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 (Q/B= 37.379 y⁻¹). Finally, production over consumption (P/Q) ratio was considered equal to 0.3 (Christensen, 1996).

Deep-water Zooplankton

Biomass estimated for deep large zooplankton from 0 to 1100 meters was 4.357 t/km² (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 t/km². In addition, total biomass of deepwater zooplankton was 6.849 t/km². Finally, Q/B value was equal to 29.0 y⁻¹, while P/Q of 0.3 (Christensen, 1996) was also used to estimate P/B.

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 t/km². This value was extremely high when compared to other models, such as the Eastern Bering Sea (0.048 t/km²; Trites et al., 1999) and the Barents Sea (6.47 t/km²; 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 y⁻¹) and Q/B (2.0 y⁻¹) values were adopted from Trites et al. (1999).

Cephalopods:

The only work focusing on cephalopods at seamounts was done by Nesis (1986). The author concluded that cephalopod fauna of seamounts consists of four main components: 1) bottom and near-bottom species that reside there permanently; 2) pelagic species that descend to or near the bottom to spawn, and include either those that maintain themselves constantly in midwater above or near seamounts or those that migrate actively to seamounts for sexual maturation; 3) mesopelagic species that may migrate vertically and

descend to the bottom during the daytime; and 4) nonmigrating pelagic species that permanently inhabit the water column. Individuals of the last 2 groups drift passively through seamounts and are subject to predation by seamount predators. Nesis (1986) suggests that this link may be one of the reasons for the high abundance of benthic and demersal fish species on certain seamounts.

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.

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*, *Ornitorhynchus*, *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 (Guénette and Morato, 2001) and were equal to 2.89 y^{-1} and 10.0 y^{-1} respectively. Biomass was estimated by the model assuming an EE of 0.95.

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 y^{-1} . P/B ratio was inferred from daily growth rate for the same species and was equal to 4.45 y^{-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 y^{-1} and 10.0 y^{-1} respectively. Biomass was set at a very small value of 0.001 t/km^2 .

Crustacea:

Crustaceans were considered separately from the other 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). However, some authors have showed that the near bottom layer in shelf regions (e.g. Oug, 1977) as well as in seamounts (e.g. Boehlert, 1988; Vereshchaka, 1995) supports at least two

different ecological groups: 1) those living in the water column and accidentally brought to the vicinity of the sea floor, and 2) those constantly living near the sea floor. The second groups (i.e, the benthopelagics) can be then sub-divided into three sub-groups with finer ecological differences: hypo-, epi-, and amphi-benthopelagic (see Vereshchaka, 1995). At this stage we considered only two groups of crustaceans (pelagic and benthic). 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.

Pelagic Crustacea

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

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 (Gu nette and Morato, 2001) and were equal to 1.6 y^{-1} , 10.0 y^{-1} and 0.95 respectively.

Benthic invertebrates

The seamount benthic environment is generally considered to be distinct from the surrounding seafloor (Richer de Forges et al., 2000; Koslow et al., 2001; Ohkushi and Natori, 2001), and may be particularly susceptible and sensitive to disturbance by trawling (Probert et al., 1997; Koslow et al., 2001). Because of enhanced currents, the benthic communities around seamounts are typically dominated by corals and other suspension feeders (Genin et al., 1986; Wilson and Kaufmann, 1987; Rogers, 1994; Grigg et al., 1997), rather than the deposit feeders that are typical of most of the deep-sea benthos. The diversity and exceptionally localized distribution of species from these unique deep-sea communities have recently been recognized (Richer de Forges et al., 2000). However, the biology and life history of seamount benthic species remain very poorly known, but some species appear to be extremely long-lived (Grigg, 1993). The abundance and biomass of benthic organisms on some seamounts was observed to be very low when compared to other hard bottom habitats at similar depths (Grigg et al., 1987; Gillet and Dauvin, 2000). A bycatch of coral and other invertebrates characteristic of seamount benthic communities have been reported from the New Zealand orange

roughly trawl fishery (Probert et al., 1997), but the overall community impacts are poorly known. 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). However, no secondary ecological impacts to the deepwater fisheries deriving from the loss of coral habitat have been reported. Even so, the removal of some benthic communities may affect several fishes and invertebrate species associated with the coral substrate (Koslow et al., 2001).

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 y^{-1} and 9.0 y^{-1} respectively. These values were estimated based on sponges and corals. An EE of 0.95 was adopted.

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 y^{-1} and 13.57 y^{-1} respectively. An EE of 0.95 was adopted.

Bony Fish groups

Seamounts are characterized by the presence of substantial aggregations of deep-bodied fishes in the water column (Boehlert and Sasaki, 1988; Koslow, 1996, 1997; Koslow et al., 2000). These 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). Discovery of these aggregations led to seamounts being increasingly targeted by trawlers throughout the world's oceans: i.e. the massive but short-lived fishery for pelagic armourhead in the North Pacific in the 1960s and the development of orange roughy and oreosomatid fisheries in the waters around New Zealand and southeastern Australia in the 1980s and subsequently in the North Atlantic and elsewhere (Clark, 1999; Koslow et al., 2000).

Epipelagic

Epipelagic Small (25 cm)

This group included species small (< 25 cm) Clupeidae (e.g. *Sardina pilchardus*), Atherinidae (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.

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.

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*), Sphyraenidae (e.g. *Sphyraena* 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 y^{-1} for small epipelagic fish, 10.750 y^{-1} for medium, and 5.095 y^{-1} for large. P/B values were taken from the model of the Oceanic ecosystems of the Atlantic (Vansconcellos and Watson, in press), 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 Vansconcellos and Watson (in press). The values were 0.859 t/km^2 for small epipelagic, 0.112 t/km^2 for medium, and 0.014 t/km^2 for the large group.

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).

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., *Mauroliticus 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 y^{-1} and 8.0 y^{-1} (Koslow, 1996; Williams, et al., 2001) respectively. A biomass of 2.0 t/km^2 was taken from the Azores model (Gu nette and Morato, 2001), which was similar to the biomass estimated (i.e., 1.720 t/km^2) by Vasconcellos and Watson (in press).

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*, *Photonectes dinema*), Paralepididae (e.g. *Macroparalepis affinis*, *Paralepis coregonoides borealis*), Melanonidae (e.g. *Melanomus zugmayeri*), Macrouridae (e.g. *Odontomacrurus 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 y^{-1} and 3.550 y^{-1} respectively. An EE value of 0.95 was used to let the model estimate the biomass of this group.

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.

Bathypelagic Fishes (Q/B lower than meso mig)

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*), Melamphidae (e.g. *Melamphaes microps*), Trichiuridae (*Aphanopus carbo*). For this group, P/B and Q/B values were assumed to be 0.5 y^{-1} and 1.477 y^{-1} respectively.

Bathybenthic fishes (Deep-sea Benthic)

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 y^{-1} and 0.5 y^{-1} respectively.

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. *Halosaurus* sp.), Notacanthidae (e.g. *Polyacanthonotus rissoanus*), Synphobranchidae (e.g. *Synphobranchus kaupii*), Bythitidae (e.g. *Cataetx 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 y^{-1} and 0.6 y^{-1} respectively.

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 y^{-1} and Q/B= 2.0 y^{-1} 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 *Allocyttus 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 y^{-1} and Q/B= 2.2 y^{-1}).

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 y^{-1} and 4.70 y^{-1} respectively (based on the group of demersal large predators) for benthic fishes and 0.66 y^{-1} and 5.20 y^{-1} respectively for benthopelagic fishes (based on *P. bogaraveo*).

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 y^{-1} . The other parameters for this group were taken from Vasconcellos and Watson (in press; P/B= 0.112 y^{-1} and EE= 0.1). Biomass was estimated by the model assuming no fishing mortality but allowing Pelagic Sharks to feed upon this group (0.001% of PS diet).

Tunas

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 closer to land seamounts are apparently always poor in tuna, even when they are located in regular fishing areas (Fonteneau, 1991). It is possible that, rather than acting as feeding stations, seamounts act as orientation points in the larger-scale movement patterns of these fish (Holland et al., 1999). Thus, this navigation role might explain why remote seamounts aggregate more tuna than seamounts located closer to land masses, as noticed by Fonteneau (1991). Three species are usually caught in similar proportions 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 (in press) estimated the biomass for these five species in the North Atlantic as being 0.029 t/km^2 , similar to that estimated by Gu nette and Morato (2001) for the Azores area (0.032 t/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 (in press), as the weighted mean of P/B and Q/B values for the five tuna species (i.e., $P/B = 0.742 \text{ y}^{-1}$ and $Q/B = 16.291 \text{ y}^{-1}$). 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 (in press) estimated their Q/B values based on daily rations while Gu nette and Morato (2001) used the empirical equation from Palomares and Pauly (1998).

Billfishes

Swordfish and other billfishes appear 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 et al., 2001). It is not clear why billfishes move to these areas, which may probably act as feeding areas. This group consisted of swordfish (*Xiphias gladius*) and several billfishes: blue marlin, (*Makaira nigriscans*), white marlin (*Tetrapturus albidus*), and longbill spearfish (*T. pfluegeri*). P/B value was equal to 0.5 y^{-1} based on an average F value of 0.3 y^{-1} and an average M of 0.2 y^{-1} . The biomass for this group was taken from Gu nette and Morato (2001; 0.02 t/km^2), while an average Q/B was estimated from the empirical equation from Palomares and Pauly (1998; 4.2 y^{-1}).

Sharks, rays and skates

As billfishes and tunas, sharks appear to be attracted to seamounts. For example, Klimley et al. (1988) 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, and mainly in those that had relatively deep summits (300m) and low-sloping depth profiles. As with billfishes, the reasons for these aggregations are not clear, but Hazin et al. (1998) assumed that seamounts were used by some sharks as feeding stations.

Rays and Skates

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

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*.

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*.

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. P/B, Q/B and biomass values were taken from the Azores model (Guénette and Morato, 2001) and were equal to 0.15 y^{-1} , 3.50 y^{-1} , and 0.001 t/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).

Seabirds

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. (1996) showed that within a 30-km radius centered on a seamount summit seabirds' biomass was eight times higher. The authors attributed seabird aggregation observed at the seamount to be related to an increase of food availability in those areas. 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, in press). P/B, Q/B and biomass were assumed to be 0.04 y^{-1} , 84.39 y^{-1} , and 0.0002 t/km^2 respectively.

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 (Gu nette and Morato, 2001). It must be noted that biomass value for marine mammal groups are provisional and subject to revision.

Appendix Bibliography

- Ainsworth, C.; B. Ferris; E. Leblond and S. Gu nette. 2001. Pp: 271-313 in S. Gu nette; V. Christensen and D. Pauly (eds). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4), University of British Columbia, Vancouver, Canada.
- Angel, M.V. 1989. Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean biology. Progress in Oceanography 22: 1-46.
- Boehlert, G.W. and A. Genin. 1987. A review of the effects of seamounts on biological processes. Pp: 319-334 in B.H. Keating; P. Fryer; R. Batiza and G.W. Boehlert (eds). Seamounts, Islands, and Atolls. Geophysical Monograph 43. Washington, D.C.
- Boehlert, G.W. 1988. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems. GeoJournal 16: 45-52.
- Boehlert, G.W. and T. Sasaki. 1988. Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. Fishery Bulletin 86(3): 453-466.
- Bulman, C.M. 2002. Trophic ecology and food web modelling of mid-slope demersal fishes off southern Tasmania, Australia. PhD thesis, University of Tasmania, Hobart, Australia.
- Bundy, A.; G.R. Lilly and P.A. Shelton. 2000. A mass balance model of the Newfoundland-Labrador shelf. Canadian Technical Report of Fisheries and Aquatic Sciences 2310, 157 pp.
- Childress, J.J.; S.M. Taylor; G.M. Cailliet and M.H. Price. 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. Marine Biology 61: 27-40.
- Childress, J.J.; G.N. Somero. 1990. Metabolic scaling: A new perspective based on scaling of glycolytic enzyme activities. American Zoologist 30(1): 161-173.

- Christensen, V. 1996. Balancing the Alaska gyre model. Pp: 32-36 *in* D. Pauly and V. Christensen (eds). Mass-balance models of North-eastern Pacific ecosystems. Fisheries Centre Research Report 4(1), University of British Columbia, Vancouver, Canada.
- Clark, M. 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. *Oceanologica Acta* 22: 593-602.
- Comeau, L.A.; A.F. Vezina; M. Bourgeois and S.K. Juniper. 1995. Relationship between phytoplankton production and the physical structure of the water column near Cobb Seamount, northeast Pacific. *Deep-Sea Research I* 42(6): 993-1005.
- Dommasnes, A.; V. Christensen; B. Ellertsen; C. Kvamme; W. Melle; L. Nøttestad; T. Pedersen; S. Tjelmeland and D. Zeller. 2001. Pp: 213-240 *in* S. Guénette; V. Christensen and D. Pauly (eds). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4), University of British Columbia, Vancouver, Canada.
- Dower, J.; H. Freeland and K. Juniper 1992. A strong biological response to oceanic flow past Cobb Seamount. *Deep-Sea Research* 39(7/8): 1139-1145.
- Dower, J.F and R.I. Perry. 2001. High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific. *Fisheries Oceanography* 10(3): 268-274.
- Dower, J.F. and D.L. Mackas. 1996. "Seamount effects" in the zooplankton community near Cobb Seamount. *Deep-Sea Research I* 43: 837-858.
- Fedosova, R.A. 1974. Distribution of some copepods species in the vicinity of an underwater Hawaiian Ridge. *Oceanology* 14: 724-727.
- Fonteneau, A. 1991. Monts sous-marins et thons dans l'Atlantique tropical Est. *Aquatic Living Resources* 4(1): 13-25.
- Genin, A. and G.W. Boehlert. 1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. *Journal of Marine Research* 43(4): 907-924.
- Genin, A.; P.K. Dayton; P.F. Lonsdale and F.N. Spiess. 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* 322 (6074): 59-61.
- Genin, A.; L. Haury and P. Greenblatt. 1988. Interactions of migrating zooplankton with shallow topography: Predation by rockfishes and intensification of patchiness. *Deep-Sea Research* 35(2): 151-175.
- Genin, A.; C. Greene; L. Haury; P. Wiebe; G. Gal; S. Kaartvedt; E. Meir; C. Fey and J. Dawson. 1994. Zooplankton patch dynamics: Daily gap formation over abrupt topography. *Deep-Sea Research I*. 41(5/6): 941-951.
- Gillet, P. and J.-C. Dauvin. 2000. Polychaetes from the Atlantic seamounts of the southern Azores: biogeographical distribution and reproductive patterns. *Journal of the Marine Biological Association of the U.K.* 80: 1019-1029.
- Grigg, R.W.; A. Malahoff; E.H. Chave and J. Landahl. 1987. Seamount benthic ecology and potential environmental impact from manganese crust mining in Hawaii. Pp: 379-390 *in* B.H. Keating; P. Fryer; R. Batiza and G.W. Boehlert (eds). Seamounts, Islands, and Atolls. Geophysical Monograph 43. Washington, D.C.
- Grigg, R.W. 1993. Precious coral fisheries of Hawaii and US Pacific islands. *Marine Fisheries Review*. 55: 50-60.

- Guénette, S. and T. Morato. 2001. The Azores archipelago, 1997: and Ecopath approach. Pp: 241-270 in S. Guénette; V. Christensen and D. Pauly (eds). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4), University of British Columbia, Vancouver, Canada.
- Ferreira, R.L.; H.R. Martins; A.A. Silva and A.B. Bolten. 2001. Impact of swordfish fisheries on sea turtles in the Azores. *Arquipélago. Life and Marine Sciences* 18A: 75-79.
- Haney, J.C.; L.R. Haury; L.S. Mullineaux and C.L. Fey. 1995. Sea-bird aggregation at a deep North Pacific seamount. *Marine Biology* 123(1): 1-9.
- Haury, L.; C. Fey; C. Newland and A. Genin. 2000. Zooplankton distribution around four eastern North Pacific seamounts. *Progress in Oceanography* 45: 69-105.
- Hazin, F.H.V.; J.R. Zagaglia; M.K. Broadhurst; P.E.P. Travassos and T.R.Q. Bezerra. 1998. Review of a small-scale pelagic longline fishery off northeastern Brazil. *Marine Fisheries Review* 60(3): 1-8.
- Holland, K.N.; P. Kleiber and S.M. Kajiura. 1999. Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. *Fishery Bulletin*. 97: 392-395.
- Huskin, I.; R. Anadon; G. Medina; R.N. Head and R.P. Harris. 2001. Mesozooplankton distribution and copepod grazing in the subtropical Atlantic near the Azores: influence of mesoscale structures. *Journal of Plankton Research* 23(7): 671-691.
- Itano, D.G. and K.N. Holland. 2000. Movement and vulnerability of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) in relation to FADs and natural aggregation points. *Aquatic Living Resources* 13(4): 213-223.
- Klimley, A.P.; S.B. Butler; D.R. Nelson and A.T. Stull. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California (Mexico). *Journal of Fish Biology* 33(5): 751-762.
- Koslow, J.A.; J. Bell; P. Virtue and D.C. Smith. 1995. Fecundity and its variability in orange roughy: effects of population density, condition, egg size, and senescence. *Journal Fish Biology* 47: 1063-1080.
- Koslow, J.A. 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *Journal of Fish Biology* 49(Supplement A): 54-74.
- Koslow, J.A. 1997. Seamounts and the ecology of deep-sea fisheries. *American Scientist* 85: 168-176.
- Koslow, J.A.; G.W. Boehlert; J.D.M. Gordon; R.L. Haedrich; P. Lorange and N. Parin. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science*. 57: 548-557.
- Koslow, J.A.; K. Gowlett-Holmes; J.K. Lowry; T. O'Hara; G.C.B. Poore and A. Williams. 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology Progress Series* 213: 111-125.
- Monteiro, L.R.; J.A. Ramos; F.W. Furness and A.J. del Nevo. 1996. Movements, morphology, breeding, molt, diet and feeding of seabirds in the Azores. *Colonial Waterbirds*, 19:82-97.
- Mouriño, B.; E. Fernández; P. Serret; D. Harbour; B. Sinha and R. Pingree. 2001. Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). *Oceanologica Acta* 24(2): 167-185.

- Nesis, K. N. Cephalopods of seamounts in the western Indian Ocean. *Oceanology*. 26(1): 91-96.
- O'Dor, R.K.; R.D. Durward; E. Vessey and T. Amaratunga. 1980. Feeding and growth in captive squid, *Illex illecebrosus*, and the influence of food availability on growth in the natural population. *Sel. Pap. ICNAF* 6: 15-21.
- Odate, T. and K. Furuya. 1998. Well-developed subsurface Chlorophyll maximum near Komahashi No. 2 Seamount in the Summer of 1991. *Deep-Sea Research Part I* 45(10): 1595-1607.
- Ohkushi, K. and H. Natori. 2001. Living benthic foraminifera of the Hess Rise and Suiko Seamount, central North Pacific. 48: 1309-1324.
- Oug, E. 1977. Faunal distribution close to the sediment of a shallow marine environment. *Sarsia* 63: 115-121.
- Okey, T.A. and R. Pugliese. 2001. A preliminary Ecopath model of the Atlantic continental shelf adjacent to the southeastern United States. Pp: 167-181 in S. Guénette; V. Christensen and D. Pauly (eds). *Fisheries impacts on North Atlantic ecosystems: models and analyses*. Fisheries Centre Research Reports 9(4), University of British Columbia, Vancouver, Canada.
- Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. Pp: 259-267 in V. Christensen and D. Pauly (eds.) *Trophic models of aquatic ecosystems*. ICLARM Conf. 26, 390 p.
- Palomares, M.L.D. and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and sanility. *Marine and Freshwater Research* 49: 447-453.
- Pelaez, J. and J.A. McGowan. 1986. Phytoplankton pigment patterns in the California current determined by satellite. *Limnology and Oceanography* 31: 927-950.
- Porteiro, F.M.; J.M. Gonçalves; F. Cardigos; P. Martins and H.R. Martins. 1995. The Azorean squid *Loligo forbesi* (Cephalopoda: Loliginidae) in captivity: Feeding and growth. *ICES Council Meeting Papers*. 12 pp.
- Probert, P.K.; D.G. McKnight and S.L. Grove. 1997. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7(1): 27-40.
- Richer-de-Forges, B.R.; J.A. Koslow and G.C.B Poore. 2000. Diversity and endemism of the benthic fauna in the Southwest Pacific. *Nature* 405: 944-947.
- Roff, D.A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 989-1000.
- Sedberry, G.R. and J.K. Loefer. 2001. Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Marine Biology* 139(2): 355-360.
- Rogers, A.D. 1994. The biology of seamounts. *Advances in Marine Biology* 30: 305-350.
- Sibert, J., K. Holland, and D. Itano. 2000. Exchange rates of yellowfin and bigeye tunas and fishery interaction between Cross seamount and near-shore fads in Hawaii. *Aquatic Living Resources* 13(4): 225-232.
- Sime-Ngando, T.; K. Juniper and A. Vezina. 1992. Ciliated protozoan communities over Cobb Seamount: Increase in biomass and spatial patchiness. *Marine Ecology Progress Series* 89(1): 37-51.
- Trites, A.W.; P.A. Livingston; S. Mackinson; M.C. Vasconcellos; A.M. Springer and D. Pauly. 1999. Ecosystem change and the decline of marine mammals in the Eastern

- Bering Sea. Fisheries Centre Research Report 7(1), University of British Columbia, Vancouver, Canada. 106pp.
- Tseytlin, V.B. 1985. Energetics of fish populations inhabiting seamounts. *Oceanology* 25(2): 237-239.
- Vasconcellos, M. and R. Watson. *In press*. Mass-balance models of oceanic ecosystems of the Atlantic. Fisheries Centre Research Reports, University of British Columbia, Vancouver, Canada.
- Vereshchaka, A.L. 1994. Distribution of pelagic macroplankton (mysids, euphausiids, decapods) over the continental slope and submarine elevations of the West Indian Ocean. *Okeanologiya* 34(1): 88-94.
- Vereshchaka, A.L. 1995a. Macroplankton in the Near-Bottom Layer of Continental Slopes and Seamounts. *Deep-Sea Research Part I: Oceanographic Research Papers* 42(9): 1639-1668.
- Vereshchaka A.L. 1995b. Distribution of benthopelagic shrimps over continental slopes and seamounts of the Western Indian Ocean. *Okeanologiya* 35(4) 574-578.
- Voronina, N.M. and A.G. Timonin. 1986. Zooplankton of the region of seamounts in the western Indian Ocean. *Oceanology* 26(6): 745-748.
- Williams, A.; J.A. Koslow; A. Terauds and K. Haskard. 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. *Marine Biology* 139: 1177-1192.
- Wilson, R.R. and R.S. Kaufmann. 1987. Seamount biota and biogeography. Pp: 355-377 *in* B.H. Keating; P. Fryer; R. Batiza and G.W. Boehlert (eds). *Seamounts, Islands, and Atolls*. Geophysical Monograph 43. Washington, D.C.