

The Azores Archipelago, 1997

Sylvie Guénette and Telmo Morato²

¹*Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver BC, V6T 1Z4, Canada email: s.guenette@fisheries.ubc.ca*

²*Departamento de Oceanografia e Pescas, Universidade dos Açores, Horta, Portugal (present address: Fisheries Centre, UBC).*

ABSTRACT

The Azores Archipelago consists of a small shelf surrounded by a large component of deep oceanic waters dotted with seamounts. The present model is structured by depth and constitutes a first step in applying the Ecopath modeling approach to Atlantic seamounts. It is the result of a collaborative effort with several researchers of the University of the Azores. The model is composed of 43 functional groups including 26 groups of fish classified according to their size and their preferred depth range. Suggestions for future developments are presented.

INTRODUCTION

The Azores archipelago is a group of nine volcanic islands that are parts of the Mid-Atlantic ridge (Figure 1). The islands and the contiguous shallower waters (< 500 m depth) have an estimated area of 412 km², only 0.4% of the EEZ area of about one million km², while seamounts (< 500 m depth) account for another 0.3% (Isidro, 1996). The present model considers only the area that is being exploited by Azorean fishers, 584,000 km², i.e., slightly more than half the EEZ. We assumed an annual average water temperature of 19EC (range: 16-22EC). The present model is the product of a collaboration with many scientists of the University of the Azores who shared their knowledge of the ecosystem with the two researchers in charge of constructing the model. (The collaborating researchers are mentioned under the title of the functional group they helped with.)

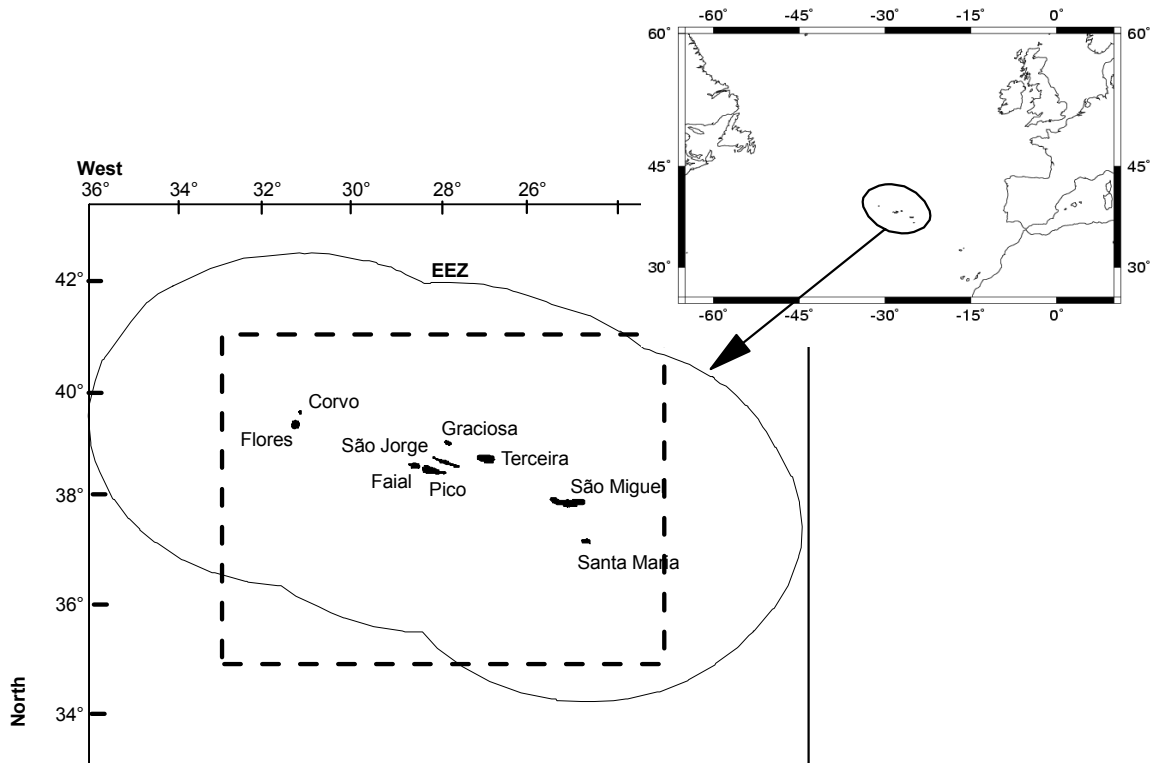


Figure 1. Location of the Azores Archipelago, its EEZ, and the area covered by the model (broken line).

Fisheries

Fishing grounds are limited to the narrow belt of shallow water, around the islands and to nearby seamounts. The fishery is characterized by small-scale vessels using gillnets, traps and various forms of hook and lines (Morato *et al.*, 2001). Trawlers have never been used around the Azores. Landing data were obtained from the Secretary of Agriculture and Fisheries of the Azores and described in Morato *et al.* (2001). The Azorean fisheries have been divided in 13 fleets: sharks (*Dalatias*), demersals (bottom longline), deep water longline (black scabbardfish), handline, lobsters, squids (*Loligo*), nets and hook and line (*Balistes*), octopus, other benthos, algae, small pelagics, swordfish, and tuna (Table 1). The fish species presented as a group in the fisheries statistics (i.e., 'various species') were redistributed into groups exploited by the demersal (or bottom longline) fishery. All other groups were easily attributed to a given fleet.

Parameters

The model parameters, production per biomass (P/B), consumption per biomass (Q/B) are calculated on a yearly basis. Biomass and catch are expressed in tonnes wet weight per square kilometer. When no biomass estimate was available, this parameter was left to be estimated by Ecopath using a value of 0.95 for the ecological efficiency (EE). It was assumed that, under steady-state conditions, production per biomass per year (P/B) equals total mortality, the sum of natural (M) and fishing mortality (F).

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-scaled to 100% to exclude these groups.

Phytoplankton, group 1

The biomass of phytoplankton is based on the samples taken at the Azores front (south of Azores), in early October (Li, 1994). This author measured Chlorophyll *a* in the first 200 m, which sums up to 22.4 mg Chl m^{-2} . Using a ratio of 1 g Chl *a* for 32 g of carbon for the Eastern Atlantic Water (Fasham *et al.*, 1985) and a ratio of 10 g wet weight for each gram of carbon (Pauly and Christensen, 1995), we obtained a biomass of 7.16 $\text{g} \cdot \text{m}^{-2}$. Fasham *et al.* (1985) obtained 3.52 $\text{g} \cdot \text{m}^{-2}$ WW in April-May in the same area for the upper 30 m. Assuming that the general pattern of plankton biomass (one peak in April and a lesser one in October) described for the North Atlantic by Lalli and Parsons (1993), applies for the Azores region we took the value found in October by Li (1994) as a proxy for the annual average. The primary productivity of phytoplankton (SeaWiFS data set, www.me.sai.jrc.it) was estimated at 203 $\text{gC} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ or 2,030 $\text{g WW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ using the same conversion factors. The production divided by the biomass yielded a P/B value of 290 year^{-1} .

Macrophytes, group 2

(with the collaboration of Fernando Tempera)

Macrophytes are present in rocky habitats around the islands which generally have a narrow shelf area. Using bathymetric maps, we estimated the percentage of rocky habitats around the islands from the shore to a depth of about 25 m (Table 2). The surface of macrophytes beds were estimated with two methods: (1) by using the surface of the islands as a proxy for the area available; (2) calculating the surface by using the perimeter of the island (S_i), and, assuming that macrophytes bed would extend 100 m from the shore, a radius of 100 m (S_{i+100}) was added to the island radius so that the resulting area has the shape of a doughnut $S_{i+100} - S_i$. The mean of the two estimates, 827 km^2 , was kept.

Table 2. Calculation of the surface of rocky bottom around the Azores Islands. See explanation of surface method in text; areas are in km^2 and perimeter in km.

Islands	Island area km^2	% of rocky habitat	Surface method 1	Island perimeter	Area of the donut	Surface method 2
Santa Maria	97.18	80	77.74	50.00	106.80	85.44
São Miguel	746.76	15	112.01	175.45	1720.43	258.06
Terceira	402.17	25	100.54	95.00	325.55	81.39
Graciosa	61.17	80	48.94	36.25	47.06	37.64
São Jorge	245.76	30	73.73	124.00	990.25	297.08
Pico	447.74	10	44.77	109.50	517.40	51.74
Faial	173.11	70	121.18	61.15	130.60	91.42
Flores	141.70	65	92.11	57.00	122.58	79.68
Corvo	17.12			17.75		
Sum	-	-	671.02	-	-	982.45

Table 1. Reported landings by fleet as allocated for the model (not incl. 570 t of algae; see text). The demersal fleet catch is the sum of the species known to be caught by the demersal fishery and the unidentified demersal fish. The catch of the other benthos fishery already includes unreported catch.

Fishery:	Demersal		DW Longline	Handline	Lobsters	Loligo	Nets + Balistes	Octopus	Other Benthos	Small pelagic	Swordfish	Tuna	Sum
	Dalatias	original											
5 <i>Loligo</i>						302.9							302.9
6 <i>Octopus</i>								47.2					47.2
9 Lobsters					5.90 ^a								5.9
10 Shrimps and crabs									22.16 ^b				22.16
11 Other Benthos									100.16 ^c				100.16
14 Coastal S Inv							8.1						8.1
16 Coastal M Herb							53.2						53.2
17 Coastal M Inv		15.8	0.5		25.4		75.7						117.5
18 Coastal M Pred		54.4	1.7		108.6								164.7
19 Coastal L Pred					70.3								70.3
21 <i>P. bogaraveo</i>		1012.0	31.0										1043.3
22 Demersal M Inv		459.4	14.0										473.5
23 Demersal M Pred		95.3	2.9										98.3
24 <i>H. dactylopterus</i>		410.3	13.0										422.9
25 Demersal L Pred		1738.8	53.0		177.2								1969.4
26 <i>Phycis phycis</i>		363.5	11.0										374.6
27 Pelagic S Inv										1.3			1.3
28 Pelagic S Pred		709.8	22.0				17.6			1921.8			2671.0
29 Pelagic M Pred					7.7		60.1						67.8
30 Pelagic L Pred											147.5		147.5
34 Deep Water L											0.3		0.3
35 Rays Pred		99.0											102.0
36 Sharks M Pred	30												30.1
37 Sharks L Pred		103.8									96.1		203.1
38 Tunas Pred												6513	6513.3

^aIncludes reported (2.95t.) and unreported (2.95t.) catches;

^bIncludes reported (13.36t.) and unreported (8.8t.) catches;

^cIncludes reported (6.66t.) and unreported (98.82t.) catches.

A study of the algae density on the shore of São Vicente showed an average dry weight of 500-600 $\text{g}\cdot\text{m}^{-2}$ (Neto, 1997). Assuming that dry weight equals 21% of wet weight (Mackinson, 1996), we obtained a density of 2,619 $\text{t}\cdot\text{km}^{-2}$ for 827 km^2 of potential algae beds. Reported on the total area of study, the biomass of macroalgae was: 3.71 $\text{t}\cdot\text{km}^{-2}$. In absence of other data, we used the P/B ratio for benthic plants of 4.34 year^{-1} used in the Strait of Georgia model (Canada) (Mackinson, 1996). Algae landings amount to 570 t or 0.00098 $\text{t}\cdot\text{km}^{-2}$ (Azorean Regional Statistical Services at www.ine.pt/srea/).

Zooplankton

Some recent descriptive studies focusing on the zooplanktonic community around Faial Island found that abundance estimates for the Azores were similar to that of the Canary Islands and Iberian Peninsula continental shelf (Sobrinho-Gonçalves and Isidro, 2001). They also reported that abundances were not significantly correlated to distance from the coast or depth. However, one should keep in mind that sampling did not occur on seamounts, which have peculiar current patterns. Sobrinho-Gonçalves and Isidro (2001) considered a group of 'Partial Zooplankton' that included individuals with a displacement volume smaller than 5 ml. This group includes organisms we have classified both as small and large zooplankton. Silva (2000) reported the small zooplankton around Faial island to be composed of copepods (68.9% by number), chaetognaths (5.2%), euphausiids (4.7%), ostracods (3.9%), thaliacea (3.0%), and appendicularia (2.5%), with other groups remaining undefined.

Small zooplankton, group 3

We defined this group as small herbivores, such as copepods. The most common copepod species in the Azores are *Clausocalanus arcuicornis*, *Pleuromamma gracilis*, *Calanus minor*, and *Acartia danae* (Silva, 2000). The production estimates for *Pseudocalanus* are highly variable for different regions (Table 3); we used an average value of 60 year^{-1} . The ratio between production and consumption (P/Q), 0.3, was taken from Christensen (1996). Zooplankton was sampled over the first 100 meters at night (Sobrinho-Gonçalves and Isidro, 2001). As plankton migrates towards the surface at night, the value probably represents the bulk of the zooplankton in the upper 300 m. Thus we assumed that this value could be used as a first estimate of depth-integrated biomass. The resulting average yearly abundance of 15.2 $\text{ml}\cdot 100\text{m}^{-2}$ (Table 4) for the first 100 meters depth was converted to 12.7 $\text{g}\cdot\text{m}^{-2}$, using the conversion factor found in Cushing *et al.* (1958). Because we were not sure of these values, and it was difficult to balance the model, we left the biomass to be estimated by the model, and obtained a value of 3.84 $\text{g}\cdot\text{m}^{-2}$.

Table 3. P/B for *Pseudocalanus* by area according to Corkett and McLaren (1978)

Location	P/B (year^{-1})
Black Sea	32
Sea of Japan	66
Baltic Sea	38
North Sea	73
<i>Average</i>	52

Table 4. Estimative of biomass for small and large zooplankton for the first 100 meters depth in the Azores.

Group	Months Sampled	Plankton Biomass ^a ($\text{ml}\cdot 100\text{m}^{-3}$)	N months with similar biomass	Weight average ^b ($\text{ml}\cdot 100\text{m}^{-3}$)	Weight average ($\text{g}\cdot\text{m}^{-2}$)
<i>Small</i>	February	11.5	5	4.79	3.99
	March	14.2	2	2.37	1.97
	May	48.7	1	4.06	3.38
	June	12.0	4	4.00	3.33
	Weighted mean^c			15.22	12.68
<i>Large</i>	March	3.4	4	1.13	0.94
	May	51.0	1	4.25	3.54
	June	0.4	7	0.23	0.19
	Weighted mean^c			5.62	4.68

^afrom Sobrinho-Gonçalves and Isidro (2001);

^busing the conversion factor found in Cushing *et al.* (1958), i.e. 1 ml of displacement volume represents 0.0012 mg;

^cif we consider two months with bloom phenomena; i.e., the value of march representing one month and the value of May representing 2 months (April and May), we obtain a biomass of 15.08 $\text{g}\cdot\text{m}^{-2}$ and 7.99 $\text{g}\cdot\text{m}^{-2}$ for small and large zooplankton, respectively.

Large zooplankton, group 4

A first estimate of large zooplankton was derived from integrated profiles (0-1900 m) of zooplankton for the Azores Front (Angel, 1989). A very general relationship between volume and biomass (Wiebe *et al.*, 1975) was used to obtain a first estimate of biomass of the species considered: chaetognaths, amphipods, decapods, mysids, euphausiids, and salps, and it added up to 29 g·m⁻². The jellies were probably underestimated as they are easily destroyed in nets; however they still constituted 50% of the volume of the samples. Assuming a conversion factor for jellies similar to zooplankton, 15 ml of displacement volume would equal 12.3 g·m⁻². The total biomass is then close to 30 g·m⁻².

Using the same study as for the small zooplankton (Sobrinho-Gonçalves and Isidro, 2001), large zooplankton was evaluated at 4.68 g·m⁻² (Table 4), a value much smaller than that derived from Angel (1989), i.g., ~ 30 g·m⁻² (Table 5). However, because of the discrepancy between the two estimates, we let the model estimate the biomass using an EE value of 0.8, which resulted in a biomass of 7.31 g·m⁻². We used a P/B of 5 year⁻¹ and a Q/B of 32 year⁻¹ based on average estimates for euphausiids, carnivorous jellies, salps, and chaetognaths (Table 6).

Table 5. Biomass estimates for large zooplankton in the Front of the Azores derived from Angel (1989).

	Integration 0-1900m ^a		Weight ^b (g·m ⁻²)
	Volume (ml·m ⁻²)	Numbers (n·m ⁻²)	
Chaetognatha	14.2	54.22	5.41
Amphipoda	8.5	1.66	3.90
Mysidacea	3.6	2.93	2.26
Euphausiacea	3.8	15.28	2.34
Salpa	4.6	9.25	2.64
Siphonophora ^c	15.4		12.32
Total/mean			28.88
Decapoda ^d	1.1	3.31	1.06

^aaccording to Angel (1989);

^bweight according to the general equation from Wiebe *et al.* (1975);

^cjellyfishes: weight based on a conversion factor of 1 ml = 0.8 g;

^dDecapods were not kept in this group as they were already included in the Shrimps and crabs group.

Table 6. P/B and Q/B (per year) estimates for Large zooplankton in the Front of the Azores.

	P/B	Q/B
Chaetognatha	3 ^a	19.5 ^c
Amphipoda	-	-
Mysidacea	-	-
Euphausiacea	6 ^b	48 ^b
Salpa	2 - 4 ^a	30 ^a
Mean	5	32

^aAlaska Gyre, (Arai, 1996);

^bAlaska Gyre, (Jarre-Teichmann and Guénette, 1996);

^cBundy *et al.* (2000), Newfoundland shelf.

Mysids are omnivorous, preying on dead and live animals and plants. Salps eat mainly phytoplankton, plus other particles (Raymont, 1983). Adult amphipods are free-living carnivores feeding on copepods, chaetognaths, euphausiids, and fish larvae (Lalli and Parsons, 1993). Chaetognaths eat mainly copepods but also fish larvae, other chaetognaths, medusae, siphonophores, salps, etc. (Raymont, 1983). The average diet derived from these qualitative descriptions is: 30% phytoplankton, 44% small zooplankton, 15% detritus and 11% cannibalism. The diet has been slightly modified while balancing the model, by increasing the proportion of small zooplankton to 73% and decreasing cannibalism to 2% (see Table 18).

Cephalopods, groups 5-8

Squid, *Loligo forbesi* (group 5), and the common octopus, *Octopus vulgaris* (group 6), were separated from the other cephalopods because of their commercial exploitation. All other cephalopods were separated in two size class, smaller and larger than 30 cm (small cephalopods, group 7; large cephalopods, group 8). Squids are fished at depths of 135-270 m close to the islands using manual jigs. Male squids can reach a dorsal mantle length of 95 cm and a weight of 9 kg while females reach 46 cm and 2 kg (Porteiro, 1994). Squid landings amounted to 302.9 t·year⁻¹ or 0.000519 t·m⁻²·year⁻¹. Octopus landings were estimated at 47.1 t·year⁻¹ or 0.000081 t·m⁻²·year⁻¹.

Daily food consumption has been estimated at 14% of body weight for *Loligo* (Segawa 1990 in Pierce *et al.*, 1994), which amounts to an annual Q/B of 51 year⁻¹. However, taking into account that most cephalopods are carnivorous, this estimate was considered too high. A more conservative value of Q/B of 10 year⁻¹ was used (Christensen, 1996).

Gonçalves (1993), using various methods, estimated the total mortality of the Azores octopus to be between 0.22 to 2.89 year⁻¹ ($M=0.62$ year⁻¹ using Pauly's empirical equation). We chose the higher value for the model. As they have about the same life expectancy, we used the same P/B value for squids. We assumed that the P/B of small squids would be higher than that of *Loligo* (P/B= 4 year⁻¹) based on their size. Large squids were assumed to live longer and have less predators than the small ones and *Loligo*, so their P/B = 2.5 year⁻¹.

Fish consumption represented 71-85% in weight for *Loligo vulgaris* and 9-19% of cephalopods depending on the location (Morocco or Algarve Coelho *et al.*, 1997). Occurrence of preys in *Loligo forbesi* stomachs showed that fish contributed 82%, among which *Trachurus picturatus*, *Boops boops*, *Lepidopus caudatus*, *Phycis phycis*, and *Capros aper* were dominant. Juvenile octopus and other cephalopods accounted for 12.7%, crustaceans (mainly planktonic) 12.1%, and other invertebrates (polychaetes and others) for 2.6% (Martins, 1985). Although the range of fish species was similar, Pierce *et al.* (1994) found that fish occur in 60% of the stomach, while other cephalopods amounted to 16%. In absence of average sizes for their preys and to account for the larger weight of fish, we used the percentage occurrence as a proxy for the percentage in weight, assuming that each stomach contains only one type of prey most of the time (Martins, 1985). This added up to 77%, and the remaining 27% were redistributed among the categories of fish already listed.

Small pelagics constituted 67% of *Loligo* prey; this was considered excessive, so this figure was split between small pelagics (31%), small pelagic invertebrates eaters (32%), *Pagellus bogaraveo* (0.2%), and deepwater small (Group 32) (5%). Invertebrate preys were 1.3% other benthos, 3.9% shrimps/crabs, and 6% cephalopods, separated equally between *Loligo* (cannibalism) and small cephalopods. The proportion of large and medium fish in the diet was difficult to maintain in the present model structure, as this does not separate the juveniles (high production) from the adults (low production). Thus, all large and medium fish were removed from the diet composition while predation on small fish was increased (Table 19).

Octopus continue to feed on crustaceans even as adults (Akimushkin, 1965). The frequency of prey occurrence in octopus stomach found in Gonçalves (1991) were: 14% worms, 14% gastropods, 21% cephalopods, 92% shrimps. In

absence of weight information, we assumed that octopus ate 40% each of shrimps/crabs, and other benthos, 3% of small cephalopods, while the remaining 17% were distributed equally between lobsters and octopus (cannibalism). The diet had to be modified to balance the model by increasing the proportion of other benthos to 44.2%, decrease lobster to 0.1% and add sea stars (0.1%) (see Table 19).

Small cephalopods (2-20 cm) feed on planktonic organisms (crustaceans, pteropods, mollusks) (Akimushkin, 1965). We assumed their diet to be 71% large zooplankton, 5% each of small pelagics (invertebrate and fish feeders, groups 27-28) and small deepwater fishes, 10% mesopelagics, 1% *Loligo* and 3% cannibalism.

Large squids feed on pelagic fish and smaller cephalopods (Akimushkin, 1965). Their diet was assumed to be composed of 20% small cephalopods, 10% pelagics, 20% mesopelagics, and 40% deepwater fish. For the same reason as for *Loligo*, all medium and large fish were removed from the diet while large zooplankton were added (41%) (Table 19).

Lobsters, group 9

This groups includes the common spiny lobster (*Palinurus elephas*) and the Spanish lobster (*Scyllarides latus*). The mean weight of lobsters caught by fishers was estimated from Martins (1985) at 714 and 818 g for males and females respectively. Using a temperature of 19EC and an empirical equation (Brey, 1999), natural mortality was estimated at 0.3 year⁻¹. Assuming that fishing mortality is equal to M resulted in a P/B of 0.6 year⁻¹. In absence of data on their consumption we used a gross efficiency of 0.06 from the crab and lobster group of the French Frigate shoals (Pauly *et al.*, 1993). Reported landings were estimated at 2.95 t·year⁻¹, which we doubled to account for the large unreported catch, yielding a relative landing value of 0.00001 t·km⁻²·year⁻¹ (Table 6). This value is probably still an underestimate.

In absence of better data, we used the relative abundance from the Newfoundland shelf based on the assumption that lobster habitat constitutes a small proportion of the area considered in both models. The relative biomass from the Newfoundland model, 0.0045 t·km⁻² (Bundy *et al.*, 2000), seemed credible when compared with the other biomasses in the model.

Spanish lobster was found to eat mainly limpets in the summer in the Azores (Martins, 1985).

Spiny lobster feed preferentially on echinoderms (ophiuroids and crinoids) and mollusks, although macroalgae, polychaetes, bryozoans, shrimp larvae and fish are also found in their stomachs (Hunter, 1999). Lobsters were assumed to feed on other benthos (66%), detritus (14%), coastal small fishes (5%), large zooplankton (10%) and shrimps (5%). During the balancing process, a number of lobster predators had to have their diets modified to decrease the quantity of lobsters consumed (see Tables 18 and 19).

Shrimps and crabs, group 10

This group includes pelagic and benthic shrimps such as the pandalids *Plesionika narval*, *P. edwardsii*, *P. martia*, *P. gigliolii*, and the hippolytids *Ligur ensiferus* (Martins and Hargreaves, 1991). There are several species of crabs in the area, among which some species are assumed to be moderately fished (*Maja squinado*, *Grapsus grapsus* and *Cancer bellianus*).

Crabs catches were estimated at 24.16 tonnes per year or $0.00004 \text{ t km}^{-2}\text{-year}^{-1}$ (See Table 7). In absence of local estimates, we used $P/B=1.4 \text{ year}^{-1}$ for shrimps based on the Newfoundland shelf model (Bundy *et al.*, 2000). P/B for crabs was based on the value used for the Prince Williams Sound (Dean, 1999); P/Q for shrimps and crabs was assumed equal to 0.15 (Jarre-Teichmann and

Guénette, 1996), which gives a Q/B of 10 year^{-1} . P/B was increased to 1.6 year^{-1} to balance the model and account for the smaller pelagic shrimps.

Pelagic shrimps were assumed to eat detritus, euphausiids and chaetognaths. Benthic shrimps and crabs diet were taken from Jarre-Teichmann and Guénette (1996). The resulting diet is: 10% each of small and large zooplankton, 10% of shrimps and crabs, 30% of other benthos, 40% detritus.

Other benthos, group 11

This group includes mollusks such as *Patella*, small crustaceans such as *Gammarus*, brittle stars, worms, and sponges, urchins (*Arbacia lixula*, *Arbaciella elegans*, *Centrostephanus longispinus*, *Paracentrotus lividus*). A small fishery targeted mainly *Patella* and *Megabalanus*. In the 1980s, the abundance of *Patella* decreased dramatically, possibly because of an epidemic (Ferraz *et al.*, 2001), and thus the catch is now very low (around 1 tonne per year). Annual landings of other benthos were very small (1.4 t) and composed of a variety of organisms. However, including estimates of unreported catch leads to landings of $100.16 \text{ t-year}^{-1}$, or $0.00017 \text{ t km}^{-2}\text{-year}^{-1}$ (see Table 7).

Table 7. Estimated annual landings (tonnes) for some commercially important crustaceans and mollusks.

Group	Species	Commercial landings		Non-commercial	Total
		Reported	Unreported	Unreported ^a	
Lobsters	<i>Palinurus elephas</i>	2.60	2.60 ^a	-	5.20
Lobsters	<i>Scyllarus latus</i>	0.35	0.35 ^a	-	0.70
Subtotal	-	-	-	-	5.90
Shrimps and crabs	<i>Grapsus grapsus</i>	0.57	8.80 ^b	2	11.37
	<i>Maja squinado</i>	0.22	-	-	0.22
	<i>Cancer bellianus</i>	12.57	-	-	12.57
Subtotal	-	-	-	-	24.16
Other benthos	<i>Patella</i> spp.	5.30	60 ^c	30 ^d	90.00
Other benthos	<i>Megabalanus tintinabulum</i>	0.12	8.80 ^b	0	8.92
Other benthos	<i>Thaio haemastoma</i>	1.24	-	-	1.24
Subtotal	-	-	-	-	100.16

^aValues similar to the reported landings were empirically assigned. It is probably still very low and will be refined in the next versions of the model;

^bEstimated by T. Morato based on an average consumption during the summer festivals;

^cEstimated by R. Ferraz including the reported landings;

^dEstimated by T. Morato based on an average annual consumption per family.

Table 8. P/B (year⁻¹), gross efficiency (GE), and Q/P (year⁻¹) from various sources for the Other benthos group.

Group	Common name	P/B	GE ^a	Q/B
Crustaceans	<i>Gammarus</i>	2.44 ^b	0.25	-
Echinoderms	Urchins, sea cucumbers	0.54	0.095	-
Mollusks	<i>Littorina</i> , bivalves	2.24 ^b	0.095	62 ^d
Annelida	Polychaetes	2.54 ^b	0.095	-
Cnidaria	Sponges	0.68 ^c	-	36.5 ^d
Tunicata	Ascidians	-	-	36.5 ^d
Hydrozoa	Hydroids	-	-	60 ^d
Mean		2	0.12	-

^aJarre-Teichmann and Guénette (1996); ^bBrey's data base (Brey, 1995); ^cFlorida Bay (Banse and Mosher, 1980); ^dComa *et al.* (1995).

In absence of local data, we based our estimates on T. Brey's data base (Brey, 1995), by first looking for similar organisms and most importantly, choosing groups of animals with a range of temperature of 15 to 26 (average = 20.8EC). Only three genera present in the Azores were directly represented in Brey's data base: *Tellina* and *Patella* (Mollusks), *Holothuria* (Echinoderms) (Table 8). GE for these groups was calculated as the average GE (=0.12) used in the southern British Columbia shelf model (Jarre-Teichmann and Guénette, 1996) (Table 8).

Bivalves were assumed to feed on 70% detritus, 20% zooplankton, 10% phytoplankton; polychaetes feed on 100% detritus; small crustaceans (amphipods, isopods) feed on 90% detritus and 10% zooplankton. Hydroids eat 40% zooplankton, 60% detritus, based on a study on *Campanularia* (Coma *et al.*, 1995). The diet of sea anemones is composed of zooplankton, polychaetes, detritus and small crustaceans (Van-Praët, 1985) which was allocated as: 30% zooplankton 10% small benthos, and 60% detritus. Thus the global diet for this group is 10% zooplankton, 1.4 phytoplankton, 6.6% benthic plants, 10% cannibalism, and 72% detritus. This diet was then modified to release pressure on macrophytes (to 1%) and decrease cannibalism (2%) which had the effect of inflating the biomass of the group (see Table 19).

Carnivorous sea stars, group 12

In absence of any detailed information, we took the P/B (=0.4 year⁻¹) and P/Q (=0.09 year⁻¹) values used in the British Columbia shelf model (Jarre-Teichmann and Guénette, 1996). Sea stars were assumed to feed upon 70% benthos and 30% detritus (Jarre-Teichmann and Guénette, 1996).

Fish

One hundred sixty five fish species were considered, based on a checklist of marine fishes of the Azores (Santos *et al.*, 1997). These species were separated in 26 functional groups based on their habitat, size and diet. In addition, some species were separated out into their own groups because they are the target of fisheries. Coastal fishes are defined as sedentary species that live mainly around the islands and have their maximum abundance distribution situated at depth less than 200 meters. Demersal species live both around the islands and at offshore banks and at depths between 200 and 800 meters. Deepwater species are most abundant below 800 meters depth and can occur at depth of 3,000 meters or more. Pelagic species are defined as fish living both around the islands and at offshore banks. However, this category excludes tunas and sharks.

Coastal demersal and deepwater fishes are divided into 3 group sizes based on their maximum length: small (<35 cm), medium (35-80 cm) and large (>80 cm). Small pelagics are smaller than 80 cm, medium pelagics between 80 and 150 cm, while large pelagics are larger than 150 cm. *Phycis phycis* was separated for use as a case study of a highly caught coastal medium predator. *Pagellus bogaraveo* was separated for use as a case study of a highly fished demersal medium invertebrate feeder. *Helicolenus dactylopterus* was distinguished to serve as an example of a highly fished demersal medium predator. The source and region of each diet used in the model is listed in Table 9.

Fish natural mortality was derived from the empirical model of Pauly (1980):

$$M = K^{0.65} L4^{-0.279} T^{0.463} \dots 1)$$

where K and L4 (cm) refer to the curvature and asymptotic length parameters, respectively, of the von Bertalanffy growth function, and T is the mean annual water temperature in degrees Celsius. When no published growth data was available, K was estimated through the equation of Pauly and Munro (1984): $\log_{10} K = \Phi - 2\log_{10} L4$ where Φ was estimated from the growth parameters of similar species, generally of the same genus, i.e., with similar shape and habits (in FishBase).

Table 9: Source and region of the study for the diets used in the model.

N°	Group Species	Location	Source
13	Coastal Small Herbivorous		
	<i>Ophioblennius atlanticus</i> <i>atlanticus</i>	Azores	Adapted from (Azevedo, 1997)
	<i>Parablennius sanguinolentus</i>	Azores	Adapted from (Santos and Barreiros, 1993)
14	Coastal Small Invertebrate feeders		
	<i>Abudefduf luridus</i>	Azores	(Ribeiro, 1998)
	<i>Chromis limbata</i>	Mediterranea and Black Seas	Adapted from (Duka and Shevenko, 1988)
	<i>Coris julis</i>	Mediterranean	(Khoury, 1987)
	<i>Coryphoblennius galerita</i>	Azores	(Azevedo, 1995)
	<i>Diplecogaster bimaculata</i>	Scotland	Adapted from (Gibson and Ezzi, 1987)
	<i>Echiichtys vipera</i>	Azores	Adapted from (Azevedo, 1995; Gibson and Robb, 1996)
	<i>Gobius paganellus</i>	Azores	Adapted from (Azevedo, 1997)
	<i>Lipophrys pholis</i>	Azores	Adapted from (Azevedo, 1995; Gibson and Robb, 1996)
	<i>Parablennius ruber</i>	Azores	Adapted from (Azevedo, 1997)
	<i>Thalassoma pavo</i>	Azores	Adapted from (Azevedo, 1997)
	<i>Tripterygion delaisi</i>	Azores	(Oliveira, 1997)
	<i>Xyrichtys novacula</i>	West Indies	Adapted from (Randall, 1967)
15	Coastal Small Predators		
	<i>Apogon imberbis</i>	Medit	(Garnaud, 1962)
	<i>Atherina presbiter</i>	Canaries	Adapted from (Moreno and Castro, 1995)
	<i>Bothus podas, maderensis</i>	Azores	Adapted from (Nash <i>et al.</i> , 1991)
	<i>Scorpaena maderensis</i>	Azores	Adapted from (Azevedo, 1997)
	<i>Scorpaena notata</i>	Medit	Adapted from (Harmelin-Vivien <i>et al.</i> , 1989)
16	Coastal Medium Herbivorous (and small invertebrates)		
	<i>Chelon labrosus</i>	general	Fishbase
	<i>Kyphosus spp.</i>	West Indies	Adapted from (Randall, 1967)
	<i>Sarpa salpa</i>	Mediterranean	Adapted from (Verlarque, 1990)
	<i>Sparisoma cretense</i>	Mediterranean + NE Atl.	(Quignard and Pras, 1986)
17	Coastal Medium Invertebrate feeders		
	<i>Aspitrigla cuculus</i>	Cantabrian shelf, Spain	(Velasco <i>et al.</i> , 1996)
	<i>Boops boops</i>	Canaries	Adapted from (Moreno and Castro, 1995)
	<i>Diplodus sargus cadenati</i>	Azores	(Figuerido, 1999)
	<i>Labrus bergylta</i>	Azores	(Figuerido, 1999)
	<i>Mullus surmuletus</i>	Azores	(Vieira, unpublished data)
	<i>Pseudocaranx dentex</i>	general	Fishbase
18	Coastal Medium Predators		
	<i>Pagrus pagrus</i>	Mediterranean	(Papaconstantinou and Caragitsou, 1989)
	<i>Scorpaena scrofa</i>	Mediterranean	(Harmelin-Vivien <i>et al.</i> , 1989)
	<i>Serranus atricauda</i> <i>Synodus saurus</i>	Azores	(Morato <i>et al.</i> , 2000)
19	Coastal Large Predators		
	<i>Enchelycore anatina</i>	general	FishBase
	<i>Epinephelus marginatus</i>	Azores	(Barreiros and Santos, 1998)
	<i>Gymnothorax unicolor</i>	FishBase	Fishbase
	<i>Muraena augusti</i> <i>Muraena helena</i>	Azores Azores	(Azevedo, 1995) (Azevedo, 1995)
20	Demersal Small Invertebrate feeder		
<i>Callyonimus reticulatus</i>	FishBase	Adapted from (Gibson and Ezzi, 1987) and information in Fishbase	
21	<i>Pagellus bogaraveo</i>	Azores	(Morato <i>et al.</i> , in press)
22	Demersal Medium Invertebrate and predators		
	<i>Beryx decadactylus</i>	Azores	(Morato-Gomes <i>et al.</i> , 1998)
	<i>Beryx splendens</i>	Azores	(Morato-Gomes <i>et al.</i> , 1998)
	<i>Pagellus acarne</i>	Azores	(Morato <i>et al.</i> , in press)

23 Demersal Medium Predator		
<i>Lepidorhombus whiffiagonis</i>	Thyrrenes Sea, Medit	Adapted from (Mannini <i>et al.</i> , 1990)
<i>Phycis blennoides</i>	FishBase	Fishbase
<i>Serranus cabrilla</i>	Canary islands + Medit	Adapted from (Tuset <i>et al.</i> , 1996; Labropoulou and Eleftheriou, 1997)
<i>Zeus faber</i>	Atlantic Portuguses	(Silva, 1999)
24 <i>Helicolenus d. dactylopterus</i>		(Meyer and Smale, 1991a)
	South Africa	
25 Demersal Large Predator		
<i>Conger conger</i>	Azores	(Morato <i>et al.</i> , 1999)
<i>Lepidopus caudatus</i>	Azores	(Morato-Gomes <i>et al.</i> , 1998)
<i>Lophius Piscatorius</i>	Spain VIIIc	Adapted from (Velasco <i>et al.</i> , 1996) and information in Fishabse
<i>Molva Dyterygia macrophthalmia</i>	FishBase	Fishbase
26 <i>Phycis phycis</i>	Azores	(Morato <i>et al.</i> , 1999)
27 Pelagic Small Invertebrate and plankton feeder		
<i>Sardina pilchardus</i>	general	Fishbase
<i>Scomberesox saurus saurus</i>	general	Fishbase
28 Pelagic Small Predator		
<i>Balistes carolinensis</i>	West Indies	Adapted from (Randall, 1967)
<i>Scomber japonicus</i>	general	Fishbase
<i>Trachurus picturatus</i>	general	Fishbase
29 Pelagic Medium Predator		
<i>Cubiceps gracilis</i>	general	(Gorelova <i>et al.</i> , 1994)
<i>Sphyræna viridensis</i>	Azores	J.P. Barreiros, University of the Azores, unpublished data
30 Pelagic Large Predator		
<i>Xiphia gladius</i>	Azores	(Clarke <i>et al.</i> , 1995)
31 Mesopelagic		
<i>Ceratoscopelus maderensis</i>	general	(Tsarin, 1997)
33 Deep-water Medium		
<i>Epigonus telescopus</i>	Mediterranean and Rockall Through	(Macpherson, 1981)
<i>Hoplostethus atlanticus</i>	Rockall through	(Mauchline and Gordon, 1984)
<i>Nezumia aequalis</i>	Mediterranean	(Macpherson, 1981)
34 Deep-water Large		
<i>Aphanopus carbo</i>	Rockall through	(Mauchline and Gordon, 1984)
<i>Synaphobranchus kaupi</i>	Rockall through	(Gordon and Mauchline, 1996)
35 Rays		
<i>Raja brachyura</i>	NE Atlantic	(Ellis <i>et al.</i> , 1996)
<i>Raja clavata</i>	Azores	(Morato <i>et al.</i> , unpublished data)
36 Sharks Medium		
<i>Dalatias licha</i>	Catalan waters	(Matallanas, 1982)
<i>Galeus melastomus</i>	W Mediterranean	(MacPherson, 1980)
37 Sharks Large		
<i>Galeorhinus galeus</i>	Azores	(Morato <i>et al.</i> , unpublished data)
<i>Lamna nasus</i>	Bristol Channel	(Ellis and Shackley, 1995; Cortés, 1999)
<i>Prionace glauca</i>	Azores	(Clarke <i>et al.</i> , 1996)
38 Tunas		
<i>Thunnus thynnus</i>	Bay of Biscay	(Clarke <i>et al.</i> , 1996)

Fish consumption per biomass (Q/B) per year was calculated according to the empirical regression of Palomares and Pauly (1988).

$$Q/B = 10^{6.37} @ 0.0313^T @ W_4^{-0.168} @ 1.38^P @ 1.89^H \dots 2)$$

where W_4 is the asymptotic body weight in grams, T is the mean annual temperature expressed as $1000/(TEC + 273.1)$, P equals one for predators and zooplankton feeders and zero for all others, and H equals one for herbivores and zero for carnivores. W_4 is generally calculated from L_4 using published length-weight relationships or, in absence of data, L_4 was assumed to be equal to $L_{max} @ 0.95$ (Pauly, 1984).

Coastal small herbivorous, group 13

This group included redlip blenny (*Ophioblennius atlanticus*) and herbivorous blenny (*Parablennius sanguinolentus*), which are not fished. The growth data came from the Mediterranean and Florida. The values of Q/B and P/B were 13 year⁻¹ and 0.53 year⁻¹ respectively, based on Azores growth data on herbivorous blenny (Santos *et al.*, 1995). However the value of P/B was considered too low for such a small fish and increased to 1.07 year⁻¹. The diet, adapted from studies done in the Azores, show that benthic algae constituted 88% of their diet, which was too high. The proportion of macrophytes was reduced to 46% and the remaining redistributed into phytoplankton, small zooplankton and other benthos.

Coastal small invertebrate feeders, group 14

This group included species such as the Canary damsel (*Abudefduf luridus*), Atlantic wrasse (*Centrolabrus trutta*), Azores chromis (*Chromis limbata*), Mediterranean rainbow wrasse (*Coris julis*), ornate wrasse (*Thalassoma pavo*). The value of Q/B was estimated at 10.5 year⁻¹. In absence of a value for P/B we assumed a ratio production/consumption of 0.25. Most of the feeding studies were from the Azores. The diet composition is dominated by small benthic invertebrates (64%) such as amphipods, isopods, copepods, small gastropods, small bivalves, and small decapods. The diet was then modified to decrease the proportion of other benthos and shrimps and crabs consumed (Table 19). In 1997, landings of *Coris julis*, the only species fished in this group, amounted to 8 t or 0.000014 t@m⁻². Unreported catch (including subsistence fishery) was estimated at 10% of the reported landings, which brings the total landings to 8.8 t.

Coastal small predators, group 15

This group included several species such as swallowtail seaperch (*Anthias anthias*), wide-eyed flounder (*Bothus podas maderensis*), Madeira rockfish (*Scorpaena maderensis*), small red scorpionfish (*Scorpaena notata*) and cardinal fish (*Apogon imberbis*). Natural mortality for the latter was first estimated at 1.7 year⁻¹ but lowered to 0.8 year⁻¹ based on a maximum age of around 6-7 years. Q/B was estimated at 8.4 year⁻¹. None of these species are fished. The diet composition, taken from studies made in the Azores, the Canaries and the Mediterranean, is dominated by coastal small invertebrate feeders (18%), shrimps and crabs (36%) and other benthos (22%). The proportion of shrimps and crabs was reduced by a factor of 10 to reduce the inflation of the biomass estimated by Ecopath (Table 19).

Coastal medium herbivorous, group 16

This group includes species such as thicklip grey mullet (*Chelon labrosus*), salema (*Sarpa salpa*) and parrotfish (*Sparisoma cretense*). Natural mortality was estimated at 0.25 year⁻¹ and fishing mortality assumed to amount to about two thirds of M for a P/B value of 0.4 year⁻¹. Q/B was estimated at 6 year⁻¹. Growth data originated from various location on the coasts of Northeast Atlantic, the Mediterranean and the Azores. Data on diet is derived from general information found in FishBase. Fish of this group were assumed to feed mainly on benthic algae (78%), but could also feed in a small proportion upon small crustaceans such as copepods and amphipods. Reported landings for the three species amount to 53 t, to which can be added 20% of unreported catch (including the spearfishing and subsistence fisheries) or 0.000109 t@m⁻².

Coastal medium invertebrate feeders, group 17

This group is composed of bogue (*Boops boops*), white seabream (*Diplodus sargus cadenati*), ballan wrasse (*Labrus bergylta*), striped red mullet (*Mullus surmuletus*), gully jack (*Pseudocaranx dentex*) and various Labridae. Most of the growth information for this group came from the French coast and the Azores. Values of P/B and Q/B were estimated at 0.89 year⁻¹ and 6.9 year⁻¹ respectively. Data on feeding habits were mainly taken from studies of the Azores and the Canaries. Fish of this group feed mainly on shrimps and crabs (20%), and other benthos (32%) such as gastropods, bivalves, polychaetes. Also these species could occasionally feed upon fish, amounting to a small proportion

of the diet (2%). Landings for the three species amounted to 117.4 t·year⁻¹. We assumed that unreported catches amounted to at least 20% resulting from spearfishing (for *Diplodus* and *Labrus*), subsistence fishing (*Diplodus*) and commercial fishing, for a total of 0.00024 t·km⁻²·year⁻¹.

Coastal medium predators, group 18

This group is composed of common seabream (*Pagrus pagrus*), great rockfish (*Scorpaena scrofa*), blacktail comber (*Serranus atricauda*) and Atlantic lizardfish (*Synodus saurus*). The growth data came from the Azores and the Canaries. P/B and Q/B were estimated at 0.45 year⁻¹ and 6.6 year⁻¹ respectively. P/B was calculated as the sum of F (=0.1 year⁻¹) estimated for seabream (Menezes *et al.*, 1998) and M (=0.35). Only one of the 3 diet compositions available was for the Azores, the remaining being taken from Mediterranean studies. The diet is dominated by small coastal (27%) and demersal fish (21%), shrimps and crabs (23%) and other benthos (12%). The presence of medium and large fish in the diet albeit in small proportions, inflated their respective biomass. Thus, their proportion were reduced or eliminated, and mesopelagics were added to the list (Table 19). Landings for this group amounted to 164.6 t. We assumed that unreported catches amounted to at least 20% resulting from spearfishing (*Serranus*), subsistence fishing (*Serranus*, *Pagrus*) and other commercial sources (*Pagrus*) for a total landing of 0.0003 t·km⁻².

Coastal large predators, group 19

This group included dusky grouper (*Epinephelus marginatus*), brown moray (*Gymnothorax unicolor*), Duke Augustus moray (*Muraena augusti*), and Mediterranean moray (*Muraena helena*). For 3 species out 5, the diet information was taken from Azorean studies while the two others were adapted from general diet information from FishBase (Table 9). Fish of this group feed mainly on fish (51%), octopus (17%), shrimps and crabs (23%), cephalopods (2%) and lobster (1%). As in the precedent group, predation on large fish was reduced (Table 19). P/B (based on dusky grouper only) and Q/B were estimated at 0.25 year⁻¹ and 4.1 year⁻¹ respectively. P/B was estimated from the addition of M (=0.15 year⁻¹) and an assumed value of F roughly equal to two thirds of M (i.e., F =0.1 year⁻¹).

Landings amounted to 70.3 t·year⁻¹. We assumed unreported catches of at least 10% resulting from spearfishing, subsistence fishing and other

sources for total landings of 0.00013 t·km⁻²·year⁻¹. A first guess of biomass (0.02t·km⁻²) was required to run the model.

Demersal small invertebrate feeders, group 20

This group is composed of boarfish (*Capros aper*), longspine spinefish (*Macroramphosus scolopax*), reticulated dragonet (*Callyonimus reticulatus*), gadella (*Gadella maraldi*), blackfin wartyfish (*Scopelosaurus lepidus*), *Scopelosaurus argenteus*, and *Synchiropus phaeton*. Few data were available for species of this group. Estimation of natural mortality was only possible for spinefish (P/B=1.02 year⁻¹). This was considered too low for such a small fish and increased to 2. Q/B (=11.5 year⁻¹) was based on boarfish and spinefish. Based on a general description of the diet for the reticulated dragonet only (in FishBase), we assumed that this group fed upon other benthos (86%) and shrimps and crabs (14%). The consumption of shrimps was reduced to 1.1%, the remaining redistributed among the other groups and a new prey item, *Loligo*.

Pagellus bogaraveo, group 21

Blackspot seabream *Pagellus bogaraveo* was singled out as a case study of a highly fished demersal medium invertebrate feeder. Both growth data and diet information came from Azorean studies. Fishing mortality was estimated at 0.34 year⁻¹ (Menezes *et al.*, 1998) which, added to natural mortality (M=0.33 year⁻¹), yielded a P/B value of 0.66 year⁻¹. Q/B was estimated at 5.2 year⁻¹. Seabreams' diet is dominated by large zooplankton (23%), mesopelagics (33%) and small demersal invertebrates (33%). Landings amounted to 1,043 t·year⁻¹ or 0.001786 t·km⁻²·year⁻¹. The biomass was calculated from the ratio catch/F and equal 0.006 t·km⁻².

Demersal medium invertebrate and predators, group 22

Species of this group are of high commercial value and included alfonsinos (*Beryx decadactylus* and *B. splendens*) and axillary seabream (*Pagellus acarne*). Growth and diet data both came from the Azores. Landings amounted to 473.5 t (459.4 t as in Table 10 plus 14.1 t of unidentified fish, see Table 1). Unreported landings were estimated to amount to 5% of the landings of *Pagellus acarne* (4 t), for total landings of 0.000811 t·km⁻²·year⁻¹.

The average fishing mortality for the two species of alfonsinos was estimated at 0.29 year⁻¹

Table 10. Calculation of biomass for species of group 22 using the estimation of F provided in Menezes (1998). A value in parenthesis indicates that the biomass was obtained by using the relative abundance index.

Species	Landing (t year ⁻¹)	F (year ⁻¹)	Relative abundance (%) ^a	Biomass (t)	Relative biomass (t·km ⁻²)
<i>Beryx decadactylus</i>	110.694	0.38	20	291.3	0.0005
<i>Beryx splendens</i>	267.677	0.19	50	1408.826	0.0024
<i>Pagellus acarne</i>	81.029	-	30	(728.63)	0.0012
Sum	459.4	-	-	2428.752	0.0042

^afrom T. Morato, personal observation.

(Menezes *et al.*, 1998) (see Table 10). Natural mortality being estimated to 0.544, P/B amounted to 0.83 year⁻¹. P/B was considered too low and increased to 1.2 year⁻¹, which is close to the value used in the Hong Kong model for a similar functional group (Buchary *et al.*, 2001). The total biomass of this group (0.0042 t·km⁻²) was based on the ratio catch/F and the use of relative abundance index for seabream (T. Morato, pers. obs.). Alfonsinos' biomasses were estimated by dividing the landing by the estimate of F for each species.

Q/B (=8.149 year⁻¹) was based on data from *P. acarne* only. Fish of this group feed upon large zooplankton (19%), shrimps and crabs (25%), other benthos (8%) and small fish (demersal small inv. 39%, deep-water medium inv. 1%).

Demersal medium predators, group 23

The group is composed of John dory (*Zeus faber*), megrim (*Lepidorhombus whiffiagonis*), greater forkbeard (*Phycis blennoides*), yellow-orange scorpionfish (*Pontinus kuhlii*), comber (*Serranus cabrilla*). Natural mortality based on growth data from the North-East Atlantic, varied largely among species of this group with an average of 0.426 year⁻¹ (Table 11). Fishing mortality (F=0.13 year⁻¹) was taken from Menezes (1998) based on *P. kuhlii*, for a P/B ratio of 0.556 year⁻¹. This value was believed to low and increased to 0.8 year⁻¹. Landings amounted to 98 t or 0.000168 t·km⁻²·year⁻¹. Q/B was estimated at 6.82 year⁻¹. Diet information came from various studies in the Mediterranean and North-East Atlantic. These fish feed upon small demersal and small pelagic fishes (55%), shrimps and crabs (22%) and other benthos (12%). During the balancing process, cannibalism was reduced from 11 to 4.1% and the consumption of group 20 reduced to a fourth of its original value.

Table 11. Calculation of natural mortality (year⁻¹) by species of group 23.

Species	M
<i>Phycis blennoides</i>	0.519
<i>Lepidorhombus whiffiagonis</i>	0.332
<i>Pontinus kuhlii</i>	0.237
<i>Zeus faber</i>	0.617
Mean	0.426

Helicolenus dactylopterus, group 24

Blackbelly rosefish *Helicolenus dactylopterus* was distinguished to serve as an example of a highly fished species. The problem is related with the multispecies characteristic of the bottom longline fishery which is catching 11 fish groups. There are concerns that the target fishing mortality based on *Pagellus bogaraveo* is being overfished. Fishing mortality has been estimated at 0.23 year⁻¹ (Menezes *et al.*, 1998) which, added to natural mortality (M=0.27 year⁻¹), yielded a P/B value of 0.5 year⁻¹. This value was increased to 0.8 year⁻¹ while balancing the model. Q/B was estimated at 7.3 year⁻¹. Growth data came from the Azores (Isidro, 1996) while the diet was adapted from a South African study (Meyer and Smale, 1991b). The biomass was estimated at 0.003 t·km⁻² from the ratio Catch/F.

Rosefish feed on small demersal, deepwater, pelagic and mesopelagic fish (50%), other benthos (42%), shrimps and crabs (6%) and cephalopods (2%). Diet was adjusted by decreasing the consumption of group 22 (medium demersal) to a twentieth of the value assumed originally (see Table 19). Landings amounted to 422.9 t·year⁻¹. We assumed a small level of discards of 1-2%, contributed by small individuals of no commercial value.

Demersal large predator, group 25

This group includes high-value commercial species such as European conger (*Conger conger*), silver scabbardfish (*Lepidopus caudatus*), wreckfish (*Polyprion americanus*), anglerfish (*Lophius piscatorius*), and blue ling (*Molva macrophthalma*).

Menezes (1998) estimated fishing mortality of *L. caudatus* at 0.31 year⁻¹; adding a natural mortality of 0.28 year⁻¹, P/B equals 0.59 year⁻¹. Annual landings amounted to 1916 t (Table 12) plus 53 t from unidentified fish that is 1,969 t or 0.0034 t·km⁻²·year⁻¹. The biomass of *L. caudatus* was estimated by dividing landings by F (Menezes, 1998). The abundance of other species was estimated using relative abundance (T. Morato, pers. obs.). The resulting biomass amounted to 0.0239 t·km⁻².

The average Q/B was equal to 4.7 year⁻¹. Most diet information came from the Azores. Fish of this group feed almost exclusively upon demersal and pelagic fishes (80%), cephalopods (7%), sea stars (6%), shrimps (1%) and sharks medium (1%). Cannibalism was estimated at 5%. The consumption of medium and large fish (groups 21-25) was decreased in order to diminish the inflated biomass.

Phycis phycis, group 26

The forkbeard *Phycis phycis* was singled out as an example of a highly fished member of the coastal large predator functional group. Based on growth data from the Azores, natural mortality was estimated as 0.25. Menezes (1998) estimated a fishing mortality of 0.24 year⁻¹, which led to a P/B value of 0.49 year⁻¹. Q/B was estimated at 5.5 year⁻¹. Diet information came from an Azorean study. Landings amounted to 374.6 t·year⁻¹ or 0.000641 t·km⁻²·year⁻¹. The biomass was estimated at 0.003 t·km⁻² from the ratio catch/F. Forkbeard feed mainly on fish (80%) and shrimps and crabs (19%).

Pelagic small invertebrate and plankton feeders, group 27

This group is composed of European sardine (*Sardina pilchardus*), European anchovy (*Engraulis encrasicolus*), Atlantic saury (*Scorpaenopsis scorpaenoides*) and silvery cod (*Gadiculus argenteus*). M was estimated at 1.06 year⁻¹ based on growth data from various locations in NE Atlantic and the Mediterranean, while F was originally given a low value of 0.2 year⁻¹ to account for a small fishery for bait amounting to 1.3 t·year⁻¹ or 0.000002 t·km⁻²·year⁻¹. Upon balancing the model, F was assumed to be equal to M. Q/B was equal to 11.3. Diet information came from general information in FishBase for sardine and saury. These fish feed on phytoplankton (50%) and small zooplankton (50%).

Pelagic small predators, group 28

This group includes garpike *Belone belone*, chub mackerel (*Scorpaenopsis scorpaenoides*), derbio (*Trachinotus ovatus*), blue jack mackerel (*Trachurus picturatus*), grey triggerfish (*Balistes carolinensis*). They feed mainly upon small pelagic and demersal fishes. Based on growth data for chub mackerel, natural mortality was estimated at 0.58 year⁻¹. In absence of data we first assumed that fishing mortality equaled natural mortality (P/B =1.2 year⁻¹). Landings amounted to 2671 t·year⁻¹ or 0.00457 t·km⁻²·year⁻¹.

Q/B was estimated at 6.58 year⁻¹ based on chub mackerel and derbio. Diet information was based on general information found in FishBase and one study from the West Indies, and was available for three species out of five. Fish of this group were assumed to eat mainly benthos (35%), shrimps (20%) and plankton (13%), the remaining of the diet is composed of small pelagic fish (11%) and cannibalism (7%). In order to deflate the biomass of fish (including cannibalism), other benthos and shrimps, their importance in the diet was decreased (Table 19).

Table 12. Calculation of biomass for species of group 25, using the estimation of F (per year) provided in Menezes (1998). A value in parenthesis indicates that the biomass was obtained by using the relative abundance index.

Species	Landings (t year ⁻¹)	F	Relative abundance (%) ^a	Biomass (t)	Biomass (t·km ⁻²)
<i>Conger conger</i>	596.456	-	25	-	(0.006)
<i>Lepidopus caudatus</i>	1114.667	0.31	30	4182	0.0072
<i>Lophius piscatorius</i>	6.635	-	10	-	(0.0024)
<i>Polyprion americanus</i>	177.153	-	20	-	(0.0048)
<i>Molva macrophthalma</i>	21.054	-	15	-	(0.0036)
Sum	1915.965	-	-	-	0.0239

^afrom T. Morato personal observation.

Pelagic medium predators, group 29

This group is composed of bluefish (*Pomatomus saltator*), Atlantic bonito (*Sarda sarda*), almaco jack (*Seriola dumerili*), barracuda (*Sphyraena viridensis*), driftfish (*Cubiceps gracilis*), longnose lancetfish (*Alepisaurus ferox*), and blue runner (*Caranx crysos*). M was estimated at 0.246 year⁻¹ based on bluefish and Atlantic bonito. F was assumed to be equal to half the M value, for a total P/B of 0.36 year⁻¹. Landings amounted to 67.8 t·year⁻¹. We assumed unreported catches of at least 5% from spearfishing, subsistence fishing and other commercial sources, resulting in total landings of 0.00011 t·km⁻²·year⁻¹.

Q/B was estimated at 5.2 year⁻¹. Diet information was based on driftfish (Gorelova *et al.*, 1994, Atlantic Ocean) and barracuda (Azores, J.P. Barreiros, unpublished data). The resulting diet was dominated by large zooplankton (jellyfish, salpida; 46%) and small pelagic fish (50%). The large proportion of large zooplankton in the diet of driftfish may have skewed the resulting diet. A revised version of the model would include better information on feeding habits of bonitos and jacks. In order to deflate the biomass of fish that were estimated by Ecopath, it was necessary to decrease the consumption of most fish. The remaining was redistributed to large zooplankton and *Loligo*, a new item, was added (Table 20).

Pelagic large predators, group 30

This group includes dolphinfish (*Coryphaena equiselis* and *C. hippurus*), billfish (*Makaira nigricans*), white marlin (*Tetrapturus albidus*), longbill spearfish (*Tetrapterus pfluegeri*), and swordfish (*Xiphias gladius*). However, the group is really represented by swordfish, if only because of lack of data for the other species.

In FishBase, natural mortality and maximum age of swordfish were estimated at 0.09 (0.06-0.14) year⁻¹ and 73 years, respectively (based on estimations of growth parameters). However, measurements of radiocarbon in vertebrae, suggest that this species rarely live past 25 years (Ward and Elscot, 2000). This would lead to a natural mortality of about 0.2 year⁻¹. Fishing mortality was estimated at 0.25 year⁻¹ for males (5+) and 0.57 year⁻¹ for females (9+), which was over F_{msy} in the late 1990s (Anon., 1999b). We used an F of 0.3 year⁻¹ and M of 0.2 year⁻¹ for a total P/B value of 0.5 year⁻¹. Landings, composed of swordfish (147 t) and dolphinfish (mainly *C. hippurus*), were estimated at 147.4 t·year⁻¹ or 0.00025 t·km⁻²·year⁻¹. Biomass of swordfish alone would be of 0.0008 t·km⁻² (catch/F). The biomass

for the whole group was assumed to amount to 0.02 t·km⁻².

Q/B was based on growth data for swordfish only and equaled 2.8 year⁻¹. Diet information was based on a study of swordfish in Azorean waters, which shows that this species feed on small cephalopods (52%) as well as pelagic and demersal fish (48%) (Clarke *et al.*, 1995). The proportion of demersal large and medium (groups 23 and 25) in the diet had to be reduced to balance the model (Table 19).

Mesopelagics, group 31

Although they represent an important part of the pelagic environment, little is known about this group which includes all species of the families Myctophidae, Stomiidae, and Gonostomatidae. P/B (=2.39 year⁻¹) was based on two species only and quite variable (*Maurolicus muelleri*, 2.19 year⁻¹; *Myctophum punctatum*, 0.96 year⁻¹). This value was increased to 3 to account for very small species in this group. Q/B was estimated at 14.4 year⁻¹. Based on a trawl survey done in 1970-71 (Babcock and Merret, 1976; in Gjøsaeter and Kawaguchi, 1980), the biomass was estimated at 2 t·km⁻². None of these species are fished. In absence of field data, this group was assumed to prey on small (33%) and large zooplankton (67%).

Small deepwater, group 32

Small deepwater are composed of Dana viperfish (*Chauliodus danae*), and Sloane's viperfish (*Chauliodus sloani*). In the absence of field data, P/B and Q/B were assumed to be similar to other deepwater fish and given values of 0.35 year⁻¹ and 5 year⁻¹ respectively. It became evident that this was too low and the P/B should rather be similar to small demersal fish (P/B = 0.8 year⁻¹). There is no landings for this group. We assumed that this group fed on mesopelagics (60%), small demersal invertebrate (10%), shrimps (20%) and other benthos (10%). The diet was modified by adding small zooplankton (10%) to the prey list and decreasing the proportion of mesopelagics, shrimps and other benthos.

Medium deepwater, group 33

Fish of the medium deepwater group include orange roughy (*Hoplostethus atlanticus*), Mediterranean slimehead (*Hoplostethus mediterraneus*), common mora (*Mora moro*), common Atlantic grenadier (*Nezumia aequalis*), roundhead grenadier (*Odontomacrus murrayi*), Valiant's grenadier (*Bathygadus melanobranchus*), hollowsnout grenadier

(*Coelorhynchus coelorhynchus*), and bulls-eye (*Epigonus telescopus*).

Growth information was taken from studies done in New Zealand (Mace *et al.*, 1990) and the Mediterranean (D'Onghia *et al.*, 1998) for the two *Hoplostethus* species only, and P/B and Q/B were estimated at 0.3 year⁻¹ and 8 year⁻¹ respectively. Although none of these species are fished, a small proportion of the catch of common mora is commonly misidentified as *Phycis blennoides* at fish auctions. Assuming that proportion to be 10% of the catch of *Phycis*, the resulting by-catch of common mora would be 2.9 t·year⁻¹. Diet information was taken from studies made in the Mediterranean and the Rockall Through (NE Atlantic). Their diet is dominated by shrimps (30%), other benthos (23%), small (8%), large (12%) zooplankton, and various small fish. To deflate their biomass, the consumption of shrimps and some fish (groups 20, 31, 32) was decreased.

Large deepwater, group 34

The group includes black scabbardfish (*Aphanopus carbo*) and roundnose grenadier (*Coryphaenoides rupestris*). Natural mortality for the scabbardfish was estimated to 0.17 year⁻¹ based on growth data from the Azores. Using data from Madeira islands (scabbardfish, M=0.4 year⁻¹) and Rockall Trough (grenadier, M= 0.31 year⁻¹), M would amount to 0.35 year⁻¹. We chose to keep the estimate for the Azores and add F of 0.13 year⁻¹ to obtain a P/B of 0.3 year⁻¹. Q/B was estimated at 6.5 year⁻¹. Diet data were taken from the Rockall Through (NE Atlantic). The fish of this group prey on various fish of small and medium sizes (67%), 9% on small cephalopods, and the rest on small invertebrates. Their landings amounted to 256 kg·year⁻¹.

Rays, group 35

Although this group includes all rays occurring around the Azores (Table 13), the lack of data obliged us to use thornback ray (*Raja clavata*) as a representative. Natural mortality (0.409 year⁻¹) was based on the median value found in FishBase for *R. clavata*. We assumed a fishing mortality equals to half the M value, which leads to a P/B value of 0.61 year⁻¹. Q/B was estimated at 5.8 year⁻¹. Rays are assumed to eat various fish living at the bottom (48%) and shrimps and crabs and other benthos (17% each), and large zooplankton (14%). Diets were derived from *R. clavata* (Azores, Morato-Gomes *et al.*, 1998) and *R. brachyura* (North-east Atlantic, Ellis *et al.*, 1996). Landings were estimated at 102 t·year⁻¹ or

0.000175 t·km⁻²·year⁻¹. In absence of other information, a tentative value of 0.02 t·km⁻², equivalent to the biomass of large pelagic predators, was entered in Ecopath.

Table 13. Species of rays occurring in the Azores

Scientific name	Common name
<i>Torpedo nobiliana</i>	Atlantic torpedo
<i>Raja fullonica</i>	Shagreen ray
<i>Raja brachyura</i>	Broadnose ray
<i>Raja cf. clavata</i>	Thornback ray
<i>Raja cf. maderensis</i>	Maderian ray
<i>Raja bigelowi</i>	Bigelow's ray
<i>Raja batis</i>	Blue skate
<i>Raja oxyrinchus</i>	Longnosed skate
<i>Dasyatis pastinaca</i>	Common stingray
<i>Dasyatis violacea</i>	Pelagic stingray
<i>Taeniura grabata</i>	Round stingray
<i>Manta birostris</i>	Manta
<i>Mobula tarapacana</i>	Devil ray
<i>Myliobatis aquila</i>	Eagle ray

Sharks medium, group 36

This group is composed of kitefin (*Dalatias licha*), smooth lanternshark (*Etmopterus pusillus*), velvet belly (*Etmopterus spinax*), smallspotted catshark (*Scyliorhinus canicula*), blackmouth catshark (*Galeus melastomus*), and *Deania* spp.

Natural mortality and Q/B were estimated at 0.394 year⁻¹ and 6.9 year⁻¹. We assumed a fishing mortality equals to a third the M value, which leads to a P/B value of 0.51. Landings were estimated at 30 t·year⁻¹ or 0.00005 t·km⁻²·year⁻¹. We assumed discards of 10%. A tentative biomass value of 0.03 t·km⁻² was entered in Ecopath.

Diets were derived from information for kitefin (Catalan waters, Matallanas, 1982) and catshark (West Mediterranean, MacPherson, 1980). Sharks were assumed to eat various fish in the water column (69%), small cephalopods (14%), shrimps and crabs (13%).

Sharks large, group 37

This group is composed of tope shark (*Galeorhinus galeus*), bluntnose sixgill shark (*Hexanchus griseus*), short fin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*), and porbeagle (*Lamna nasus*). Growth data came from various locations, but mainly from the North-East Atlantic. Natural mortality and Q/B were estimated to 0.2 year⁻¹ and 3.1 year⁻¹

respectively. We assumed a fishing mortality equals to half the M value, which leads to a P/B value of 0.3. Landings were estimated at 203 t·year⁻¹ or 0.000348 t·km⁻²·year⁻¹. A tentative biomass value of 0.01 t·km⁻² was entered in Ecopath.

Diets were taken after descriptions of tope shark (Azores, Morato-Gomes *et al.*, 1998), porbeagle (Bristol Channel, Ellis and Shackley, 1995) and blue shark (Azores, Clarke *et al.*, 1996). Large sharks eat fish of various habitats (57%) and small cephalopods (30%).

Tunas, group 38

This group includes all species of tunas (Scombridae), except *Sarda sarda*, that occur and are fished around the Azores: skipjack (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), yellowfin (*T. albacares*), bigeye (*T. obesus*) and northern bluefin (*T. thynnus*). Natural mortality was estimated at 0.33 year⁻¹. Fishing mortality (=0.57 year⁻¹) for the whole group was obtained by using the average fishing mortality weighted by the 1997 catch (Table 14). However, this seems overestimated due to the large catch and high F estimate for skipjack. P/B was considered too high for a fish that lives so long and its value was reduced to 0.7 year⁻¹. Biomass (=0.031 t·km⁻²) was estimated from the ratio catch/F.

Q/B was estimated as 3.5 year⁻¹. Total landings were estimated at 6,513 t·year⁻¹ or 0.011 t·km⁻²·year⁻¹. Diet information was scarce, and thus this group is represented by bluefin tuna only (Bay of Biscay, Ortiz de Zarate, 1987). Tuna were assumed to feed mainly on small pelagic inv. (68%), medium pelagic (14%) and planktonic invertebrates (8%).

Turtles, group 39

with the collaboration of Helen R. Martins

The turtles occurring in the Azores are loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and green turtles (*Chelonia mydas*), whereas *Eretmochelys imbricata* and *Lepidochelys kempfi* were observed only few times during the last twenty years. Adult loggerhead turtles, *Caretta caretta*, live a benthic life along the Florida coast (Carr, 1986). Juvenile 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) where they appear to feed mainly on jellyfish. Turtles have been found in sharks stomach (H.R. Martins, unpublished data). Their abundance is unknown but the by-catch by the pelagic longline swordfish fishery was estimated to be about 4,910 for the entire fleet fishing in the Exclusive Economic Zone of the Azores during the swordfish season, i.e., May to December (estimates of 0.04-0.79 per 1000 hooks) (Ferreira *et al.*, 2001).

Leatherback turtles, *Dermochelys coriacea*, are also caught by the swordfish fishery. Their abundance ratio with loggerhead is thought to be 1:100. We concentrated on the loggerhead turtle at this stage.

P/B and Q/B were based on data used for green turtles in Polovina's Frigate Shoal model (Pauly *et al.*, 1993). Opitz (1996) used a Q/B of 2.8 year⁻¹ based on studies on two species of turtles feeding respectively on benthic invertebrates and algae. As juvenile loggerheads are likely feeding on jellyfish and perhaps other large planktonic organisms, a value of 3.5 year⁻¹ would be conservative. As a preliminary estimate, the biomass was assumed to 10% of the biomass used in a Caribbean reef model (Opitz, 1996), that is 0.001 t·km⁻², and the discards assumed to be 2% of the population size.

Table 14. Calculation of fishing mortality (per year) for tunas.

Species	1997 catch (t)	F (year⁻¹)	Source
<i>Thunnus obesus</i>	2789	0.35 ^a	(Anon., 1999a)
<i>Thunnus thynnus</i>	108.2	0.25 ^b	(Anon., 1998b)
<i>Katsuwonus pelamis</i>	3610.3	0.75	(Anon., 1999b)
<i>Thunnus alalunga</i>	179.4	0.44	(Anon., 1998a)
Weighted mean	-	0.57	-

^aprobably larger than 0.35 (Fmax) and considered overexploited;

^bF is 0.1 for ages 6-7; 0.25-0.4 for ages 8+.

Birds, group 40

with the collaboration of Veronica Neves

Breeding birds in the Azores are Bulwer's petrel (*Bulweria bulwerii*), Cory's shearwater (*Calonectris diomedea borealis*), Manx shearwater (*Puffinus puffinus*), Madeiran storm petrel (*Oceanodroma castro*), common tern (*Sterna hirundo*) and Roseate tern (*Sterna dougalli*). There are only two resident birds, the little shearwater (*Puffinus assimilis*) and yellow-legged gull (*Larus cachinnans*). The Greater shearwater (*Puffinus gravis*) appear only on its migration path.

Natural mortality is thought to be very low (0.04 year⁻¹) for most birds. The daily ration of birds in grams per day was derived using an empirical equation: $\log R = 0.293 + 0.85 \cdot \log W$ (Nilsson and Nilsson, 1976 in Wada, 1996) where W is the body weight in grams and R the ration in grams per day. Biomass was calculated from the numbers of pairs reported in Monteiro *et al.* (1996b; 1999) multiplied by the body weight (Monteiro *et al.*, 1996a) and the number of days they are present in the Azores (Monteiro *et al.*, 1996a) (Table 15).

Diets came from analysis prey occurrences of the pellets contents (Monteiro *et al.*, 1996b; Granadeiro *et al.*, 1998) that we transformed into weight assuming one prey per pellet and calculating the mean prey of identified preys.

Marine mammals, groups 41-43,

with the collaboration of Rui Pietro and Mónica Silva

Marine mammals were separated in three groups based on their diets. Baleen whales (group 41) eat mainly zooplankton and squids and include sperm whales (*Physeter macrocephalus*), minke whales (*Balaenoptera acutorostrata*), sei whales (*Balaenoptera borealis*), blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), and humpback whales (*Megaptera novaeangliae*). Dolphins and toothed whales (group 42) include long-finned pilot whales (*Globicephala melas*), short-finned pilot whales (*Globicephala macrorhynchus*), northern bottlenose whales (*Hyperoodon ampullatus*), Gervais' beaked whales (*Mesoplodon europaeus*), Sowerby's beaked whales (*Mesoplodon bidens*), Cuvier's beaked whales (*Ziphius cavirostris*), common dolphins (*Delphinus delphis*), striped dolphins (*Stenella coeruleoalba*), spotted dolphins (*Stenella frontalis*), Risso's dolphins (*Grampus griseus*), and bottlenose dolphins (*Tursiops truncatus*). The false killer whale (*Pseudorca crassidens*) has been kept in a separate group (43) because they eat other marine mammals.

The diet of sperm whale was taken after Clarke (1993). For all other species, diets were derived from general diet description given in (Pauly *et al.*, 1998) (Table 16). Diet composition attributed to general groups in Pauly *et al.* (1998) were reallocated into the model functional groups according to their most probable preys (Table 17).

Table 15. Number, biomass and residence times for aquatic birds present in the Azores.

Species	N pairs	Population abundance	Body weight (g)	N days present	Biomass (kg·km ⁻²)
Bulwer's petrel	500-1,000 ^a	1,500	97.7	240	0.00016
Cory's shearwater	49,500-89,000 ^a	138,500	839	270	0.147
Manx shearwater	235 ^b	470	345	181	0.00033
Madeiran storm petrel	740 ^b	1,600	49.2	150	0.000005
Common tern	4,015 ^a	8,030	135.7	168	0.001
Roseate tern	379-1051 ^a	1,984	118.9	168	0.00019
Little shearwater	1,530 ^b	3,060	171	365	0.001
Yellow-legged gull	6,415 ^a	6,415	888	365	0.0195
Sum	63,314 - 194,961	303,629	-	-	0.169

^aMonteiro *et al.* (1999);^bMonteiro *et al.* (1996b).

Table 16. Marine mammals diet composition in % of wet weight consumed (from Pauly *et al.*, 1998).

Predator	Prey							Mammals
	Small squids	Large squids	Small pelagic	Large plankton	Mesopelagic	Other fish	Benthic invertebrates	
Sperm whale	0.318	0.632			0.05			
Minke whale			0.3	0.65		0.05		
Sei whale	0.05		0.05	0.8	0.05	0.05		
Blue whale				1				
Fin whale	0.05		0.05	0.8	0.05	0.05		
Humpback whale			0.15	0.55		0.3		
Subtotal baleen whales	0.07	0.105	0.092	0.633	0	0.075	0	0
Common dolphin	0.15	0.15	0.1		0.4	0.2		
Striped dolphin	0.2	0.15	0.05		0.3	0.25	0.05	
Northern bottlenose whale	0.35	0.35			0.05	0.1	0.15	
Sowerby's beaked whale	0.25	0.3	0.05		0.2	0.2		
Cuvier's beaked whale	0.3	0.3			0.15	0.15	0.1	
Risso's dolphin	0.5	0.35	0.05			0.05	0.05	
Bottlenose dolphin	0.2	0.05	0.15			0.6		
Subtotal toothed whales	0.279	0.236	0.057	0	0.157	0.221	0.05	0
False killer whale	0.2	0.3				0.3		0.2

Table 17. Redistribution of prey items of marine mammals

Original prey group Pauly <i>et al.</i> (1998)	New groups	Predator		
		Baleen whales	Toothed whales	Killer whales
Small squids	Small squids	0.07	0.277	0.2
Large squids	Large squids	0.1	0.236	0.3
	<i>Loligo</i>		0.01	
L. plankton		0.63		
Mesopelagics		0.03	0.157	
Small pelagics	Pelagic S inv.	0.045	0.057	
	Pelagic S pred.	0.046		0.1
Other fish	Pelagic M pred.	0.045		0.1
	Coastal S pred.		0.07	
	Coastal M inv.		0.07	
	Coastal L pred.		0.01	
	Demersal S inv.		0.07	
	Demersal M pred.			0.1
	Deepwater S	0.03		
Benthic invertebrates	Lobster		0.01	
	Shrimps and crabs		0.02	
	Other benthos		0.02	
Mammals	Toothed whales			0.2

The P/B of 0.06 year⁻¹ for baleen whales (average maximum age for this group is 79 years) was based on the natural mortality of sperm whales (Rice, 1989), which agrees with a maximum age of 69 years found for that species (Trites and Pauly, 1998). The natural mortality for dolphins and toothed whales, was based on an estimate for long-finned pilot whales (M=0.07 year⁻¹, maximum age = 55 years), but was increased to 0.1 year⁻¹ to account for shorter life expectancy of dolphin species. Based on maximum age of the false killer whale, its natural mortality was estimated at 0.07 year⁻¹.

Sperm whale's daily consumption was assumed to be of 2.5% of their body weight (Clarke *et al.*, 1998). Q/B values of all other species were calculated using an empirical equation for daily ration $R=0.1*W^{0.8}$, modified from Innes *et al.* (1987), where W is body weight in kg and R the daily ration in kg•day⁻¹. The mean weight was obtained from Trites and Pauly (1998).

Biomass

The biomass was taken from the *Sea Around Us* project (SAUP) data base (Kaschner *et al.*, 2001) and adjusted according to their occurrence in the Azores and the number of months they are thought to be present around the Azores, and the size of the model area, about 2% of the North Atlantic (Table 18).

Table 18. Abundance and biomass estimates for three groups of whales.

Species	Population	N days in the area	Biomass (t•km ⁻²)
Baleen whales			
Sperm whale	3234	182	0.0897
Minke whale	1441 ^a	30 ^b	0.0011
Sei whale	120	90	0.00085
Blue whale	9	90	0.0004
Fin whale	1318	90	0.0309
Sum			0.123
Toothed whales			
Long-finned pilot whale	11,302	20	0.0009
Short-finned pilot whale	1,591	90	0.0004
Common dolphin	13,075	182	0.0009
Striped dolphin	37,845	45	0.0009
Spotted dolphin	1,480	90	0.00006
Northern bottlenose whale	88	182	0.0001
Sowerby's beaked whale	246	182	0.0001
Cuvier's beaked whale	282	182	0.0002
Risso's dolphin	662	365	0.0002
Bottlenose dolphin	1,634 ^a	365	0.0005
Sum			0.0044
False killer whale			
False killer whale	256	90	0.00006

^aTaken from Trites *et al.* (1997).

^bMinke whale are not commonly seen in the Azores.

Baleen whales

Sperm whales are thought to be present all year round in the Azores but are most common in summer. In whaling days, females were absent from the catch in January and February (Clarke, 1956). It is believed that only a small fraction of the population, males only, stays around the Azores while the rest spends the winter southward, in the Canary and Cape Verde Islands and come back in May. Clarke (1998) estimated that about 5600 sperm whales had to be present to sustain the catch during whaling times. Current observations yielded the identification of 400 individuals and it is believed that their population could reach over 900. We used the estimate of the database, that is 3234 individuals. Sperm whales were assumed to stay half the year.

The world population of minke whale is estimated at 800,000 (Trites *et al.*, 1997; Trites and Pauly, 1998; Kaschner *et al.*, 2001) divided in 3 populations: North Atlantic, Pacific, Southern hemisphere and 1,441 in the Azores alone. They are uncommon around the Azores and they prefer cold waters. As they make only brief appearances, we assumed that they stay only 30 days per year in the region.

Sei, blue and fin whales are observed for 3 months around the Azores. Their biomass was taken from the SAUP database. They are mostly seen during the spring (February to May), possibly feeding during their passage (days-weeks) in the Azores. Although there is no data for autumn, they might pass again on their way south. We ignored the humpback whales as they are assumed to migrate the same way through the region and are quite uncommon.

Toothed cetaceans

Although uncommon, members of the Ziphiidae family are generally considered more common in the Azores than elsewhere. Thus, the present estimate of biomass taken from the data base could be underestimated.

Long-finned whales stay only for a very short time as there are rarely observed around in the Azores. The short-finned pilot whale is observed in the summer with their calves in the region which is at the northern limit of their range distribution (Cawardine, 1995). False killer whales are not frequent around the Azores although are seen every year.

DISCUSSION

We balanced the model by modifying diets that were implying that a fast growing and abundant species would eat large amounts of a scarce, slow growing group. For example, the proportion of lobster in the diet of octopus had to be decreased from 8.5 to 0.1% (Tables 19 to 21). Decreasing cannibalism was also crucial for some groups such as lobster, other benthos and birds.

The use of growth data originating from other region led to inconsistencies in the estimation of P/B and Q/B values and to low P/Q ratios for several fish species. For future versions of this model, this problem will have to be addressed. The construction of this model highlighted the lack of information in some groups, such as benthos density and composition, which would be required to validate the model later on. The islands and seamounts are believed to act as an aggregating device for nutrients and thus several species of fish (Koslow, 1997). Thus the structure of the study area, small islands/shelves surrounded by deep oceanic waters, would warrant the construction of a space-structured model (Ecospace).

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Table 19. Final diet matrix for fish groups. Numbers in italics at the second line of a cell indicate the values in the original matrix; for clarity differences of 0.001 or less have been ignored. L is large, M is medium, and S is small.

Prey \ Predator	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
1 Phytoplankton	0.364 <i>0.08</i>			0.067												0.5	0.146 <i>0.104</i>									0.041
2 Macrophytes	0.455 <i>0.88</i>	0.162 <i>0.14</i>	0.011 <i>0.008</i>	0.783	0.139	0.008								0.004		0.023 <i>0.016</i>										0.002
3 Small zooplankton	0.114 <i>0.025</i>	0.119 <i>0.104</i>	0.204 <i>0.147</i>	0.1	0.070				0.027							0.5	0.088 <i>0.063</i>		0.333		0.133 <i>0.076</i>					0.081
4 Large zooplankton		0.032 <i>0.028</i>	0.056 <i>0.04</i>		0.174	0.006			0.23	0.189		0.019 <i>0.015</i>		0.002		0.088 <i>0.063</i>	0.707 <i>0.46</i>		0.667	0.094	0.215 <i>0.123</i>	0.042	0.137	0.033		0.065
5 <i>Loligo</i>								0.02								0.001	0.076									
6 <i>Octopus</i>					0.018 <i>0.014</i>	0.174 <i>0.171</i>								0.001		0.001										0.001
7 Cephalopods S		0.005 <i>0.004</i>				0.021 <i>0.020</i>		0.036	0.003	0.002	0.025 <i>0.02</i>	0.087 <i>0.067</i>				0.012 <i>0.009</i>	0.607 <i>0.055</i>			0.038 <i>0.022</i>	0.119 <i>0.094</i>	0.007	0.143 <i>0.140</i>	0.0309 <i>0.306</i>	0.015	
8 Cephalopods L																					0.02					
9 Lobsters						0.006 <i>0.012</i>																				
10 Shrimps and crabs		0.004 <i>0.034</i>	0.038 <i>0.356</i>		0.198	0.26 <i>0.241</i>	0.239 <i>0.233</i>	0.011 <i>0.14</i>	0.005	0.248	0.218	0.073 <i>0.059</i>	0.012 <i>0.01</i>	0.190		-	0.199			0.069 <i>0.2</i>	0.059 <i>0.3</i>	0.185 <i>0.178</i>	0.171 <i>0.169</i>	0.132	0.002	
11 Other benthos	0.068 <i>0.015</i>	0.624 <i>0.642</i>	0.305 <i>0.218</i>	0.017	0.324	0.13	0.051 <i>0.050</i>	0.963 <i>0.856</i>	0.032	0.075	0.124	0.507 <i>0.416</i>	0.005	0.001		0.557 <i>0.354</i>				0.708 <i>0.1</i>	0.405 <i>0.231</i>	0.018	0.171		0.002	0.011
12 Sea stars		0.001	0.025		0.021			0.004					0.081 <i>0.062</i>			0.002 <i>0.012</i>										
13 Coastal S herb		0.053 <i>0.01</i>			0.019 <i>0.035</i>	0.001					0.017 <i>0</i>															
14 Coastal S inv		0.034 <i>0.03</i>	0.25 <i>0.178</i>		0.012	0.182 <i>0.14</i>	0.172 <i>0.168</i>				0.077		0.006 <i>0.004</i>	0.163			0.024 <i>0.016</i>						0.046			
15 Coastal S predator		0.009 <i>0.036</i>	0.051		0.003	0.165 <i>0.127</i>	0.82 <i>0.080</i>						0.014 <i>0.010</i>	0.165												
16 Coastal M herbivorous						-	0.015 <i>0.045</i>																			
17 Coastal M Invertebrate feeder					0.036 <i>0.027</i>	0.07 <i>0.068</i>				0.03		0.018 <i>0.015</i>					0.024 <i>0.016</i>						0.029			
18 Coastal M predator					0.018 <i>0.014</i>	0.065 <i>0.063</i>		0	0.005				0.002										0.01		0.028	
19 Coastal L predator																										0.02 <i>0.012</i>
20 Demersal S Invertebrate feeder	0.009			0.018	0.084	0.103 <i>0.206</i>		0.331 <i>0.326</i>	0.388 <i>0.392</i>	0.3 <i>0.28</i>		0.422 <i>0.327</i>	0.388				0.179 <i>0.149</i>		0.047 <i>0.1</i>	0.057 <i>0.074</i>	0.104	0.395 <i>0.392</i>	0.191 <i>0.188</i>	0.087 <i>0.085</i>		

Prey \ Predator	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
21 <i>Pagellus bogaraveo</i>													0.001 0.023										0.007 0.013	0.01 0.059		
Demersal M					0.001						0.01	0.005				-	0.01					0.006	0.013	0.013		
22 Invertebrate feeder					0.005						0.2	0.089				0.008	0.056									
23 Demersal M predator									0.001	0.05		0.052					0.051				0.073	0.07	-	0.087		
<i>Helicolenus dactylopterus</i>										0.108		0.88					0.044				0		0.02			
24 demersal L predator												-	0.034													
25 <i>Phycis phycis</i>						-	-					0.021					0.02							0.059		
Pelagic S					0.001	0.02																				
27 Invertebrate feeder										0.109	0.122	0.043				0.058	0.015	0.041			0.053		0.319	0.160	0.681	
28 Pelagic S predator										0.1	0.047					0.112	0.027	-			0.03		0.314	0.157		
29 Pelagic M predator					0.002					0.02		0.143				0.023	0.152	0.041				0.104	0.021	0.088		
30 Pelagic L predator												0.114				0.067	0.473	-						0.085		
31 Mesopelagics									0.029		0.023	0.005									0.052		0.069	0.141		
32 Deepwater S												0.018												0.02		
33 Deepwater M					0.074			0.338	0.087		0.122	0.041	0.045			0.036	0.031			0.082	0.036	0.022	0.107	0.002		
34 Deepwater L						-		0.333			0.099	0.031				-	0.03			0.6	0.097		0.105			
35 Rays										0.02	0.122										0.01	0.130	0.005	-		
36 Sharks M									0.006		0.099										0.047	0.125		0.005		
37 Sharks L												0.002				0.014	0.012					0.130		0.007		
38 Tunas									0.003							-						0.125				
39 Turtles													0.017													
40 Birds													0.013													
41 Baleen whales																										
42 Dolphins																										
43 Killer whales																										
44 Detritus		0.006	0.002	0.033	0.038																					
45 Import																										

Table 20. Final diet matrix for non-fish groups. Numbers in italics at the second row of a cell indicate the values in the original matrix. L is large, M is medium, and S is small.

Prey \ Predator	3	4	5	6	7	8	9	10	11	12	39	40	41	42	43
1 Phytoplankton	0.9 <i>1</i>	0.1 <i>0.3</i>							0.017 <i>0.014</i>						
2 Macrophytes									0.002 <i>0.066</i>						
3 Small zooplankton		0.73 <i>0.44</i>						0.1 <i>0.15</i>	0.15 <i>0.1</i>						
4 Large zooplankton		0.02 <i>0.11</i>	0.004 <i>0.003</i>		0.71	0.41	0.1	0.1			1	0.036	0.63		
5 <i>Loligo</i>			0.05 <i>0.03</i>		0.01							0.054		0.01	
6 <i>Octopus</i>				0.094 <i>0.085</i>											
7 Cephalopods S			0.03	0.011 <i>0.03</i>	0.03	0.22 <i>0.2</i>						0.141 <i>0.194</i>	0.07	0.299 <i>0.277</i>	0.222 <i>0.2</i>
8 Cephalopods L													0.1	0.253 <i>0.236</i>	0.333 <i>0.3</i>
9 Lobsters				0.001 <i>0.085</i>										0.005 <i>0.01</i>	
10 Shrimps and crabs			0.04	0.442			0.05	0.1				0.083		0.022 <i>0.02</i>	
11 Other benthos			0.013	0.442 <i>0.4</i>			0.66	0.3	0.02 <i>0.1</i>	0.7		0.006		0.016 <i>0.02</i>	
12 Sea stars				0.001 <i>0</i>											
13 Coastal S herb.			0.018 <i>0</i>				0.05								
14 Coastal S Inv.			0.018 <i>0</i>									- <i>0</i>			
15 Coastal S predator												0.001		0.075 <i>0.07</i>	
16 Coastal M herbiv.															
17 Coastal M Inv.			0.004											0.011 <i>0.07</i>	
18 Coastal M pred.															
19 Coastal L predator														0.003 <i>0.01</i>	
20 Demersal S Inv.			0.13									0.26 <i>0.22</i>		0.075 <i>0.07</i>	
21 <i>Pagellus bogaraveo</i>			- <i>0.002</i>												
22 Demersal M inv.															
23 Demersal M pred.															- <i>0.1</i>
24 <i>H. dactylopterus</i>															
25 Demersal L pred.			- <i>0.05</i>												
26 <i>Phycis phycis</i>			- <i>0.02</i>												
27 Pelagic S Inv.			0.32 <i>0.31</i>		0.05							0.083	0.045	0.061 <i>0.057</i>	
28 Pelagic S predator			0.32 <i>0.31</i>		0.05	0.11 <i>0.1</i>						0.103	0.046		

Table 21. Parameters matrix after balancing. Parameters estimated by the model are in bold.

	Group name	Trophic level	Biomass (t·km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	P/Q
1	Phytoplankton	1.0	7	290	-	0.32	-
2	Macrophytes	1.0	3.71	4.34	-	0.18	-
3	Small zooplankton	2.0	3.429	60	200	0.95	0.3
4	Large zooplankton	2.5	6.918	5	32	0.8	0.16
5	<i>Loligo</i>	4.0	0.066	2.89	10	0.95	0.29
6	<i>Octopus</i>	3.5	0.013	2.89	10	0.95	0.29
7	Cephalopods S	3.8	0.088	4	10	0.95	0.4
8	Cephalopods L	4.7	0.034	2.5	10	0.95	0.25
9	Lobsters	3.1	0.0045	0.6	10	0.35	0.06
10	Shrimps and crabs	2.6	1.306	1.6	10	0.95	0.16
11	Other benthos	2.2	7.932	2	16.70	0.95	0.12
12	Sea stars	2.8	0.271	0.4	4.44	0.95	0.09
13	Coastal S herbivorous	2.0	0.133	1.07	13	0.95	0.08
14	Coastal S inv.	3.0	0.330	2.625	10.50	0.95	0.25
15	Coastal S predator	3.5	0.259	0.8	8.40	0.95	0.1
16	Coastal M herbivorous	2.1	0.004	0.4	6	0.95	0.07
17	Coastal M inv.	3.2	0.083	0.89	6.90	0.95	0.13
18	Coastal M predator	3.9	0.035	0.45	6.60	0.95	0.07
19	Coastal L predator	4.3	0.02	0.25	4.10	0.18	0.06
20	Demersal S inv.	3.2	0.221	2	11.60	0.95	0.17
21	<i>Pagellus bogaraveo</i>	4.0	0.006	0.66	5.20	0.77	0.13
22	Demersal M inv.	3.9	0.0042	1.2	8.10	0.72	0.15
23	Demersal M predator	3.9	0.068	0.8	6.80	0.95	0.12
24	<i>H. dactylopterus</i>	3.7	0.003	0.8	7.30	0.54	0.11
25	Demersal L predator	4.4	0.024	0.59	4.70	0.62	0.13
26	<i>Phycis phycis</i>	4.1	0.003	0.49	5.50	0.52	0.09
27	Pelagic S inv.	2.5	0.303	2.6	11.30	0.95	0.23
28	Pelagic S predator	3.3	0.543	1.2	6.58	0.95	0.18
29	Pelagic M predator	3.9	0.207	0.36	5.20	0.95	0.07
30	Pelagic L predator	4.6	0.02	0.5	2.80	0.09	0.18
31	Mesopelagics	3.2	2	3	14.40	0.06	0.21
32	Deepwater S	4.0	0.184	0.8	5	0.95	0.16
33	Deepwater M	3.7	0.006	0.3	8	0.95	0.04
34	Deepwater L	4.4	0.0003	0.3	6.50	0.95	0.05
35	Rays	3.9	0.02	0.61	5.80	0.01	0.1
36	Sharks M	4.0	0.03	0.51	6.90	0.13	0.07
37	Sharks L	4.3	0.01	0.3	3.10	0.12	0.1
38	Tunas	3.8	0.03	0.7	3.50	0.5	0.2
39	Turtles	3.5	0.001	0.15	3.50	0	0.04
40	Birds	4.2	0.0002	0.04	84.39	0.21	0.0005
41	Baleen whales	4.0	0.165	0.06	5.56	0	0.01
42	Dolphins	4.8	0.027	0.1	11.41	0.46	0.01
43	Killer whales	5.4	0.0002	0.07	10.27	0	0.01
44	Detritus	1.0	1	-	-	0.12	-

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