

ANALYSES

MASS-BALANCE MODELS OF OCEANIC SYSTEMS IN THE ATLANTIC¹

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ABSTRACT

This report describes the methods and data sources used to estimate ecological parameters and to construct mass-balance models of oceanic ecosystem of the Atlantic using the Ecopath with Ecosim (EwE) software. Six models were constructed representing oceanic ecosystems of the North, Central and South Atlantic for the 1950s and the late 1990s (1997-1998). The first section of this report characterizes some of the fundamental characteristics of oceanic ecosystems which were captured in a model template for oceanic areas. The subsequent sections are devoted to individual functional groups, composed of species or group of species that share similar ecological functions, habitats and demographic characteristics, or represent important fisheries resources, such as tunas and swordfish. The last sections describe the approach used to balance the models in EwE and the adjustments made to the late 1990s model so that it could represent the ecosystem state in 1950.

A MODEL TEMPLATE FOR OCEANIC ECOSYSTEMS

What would be the essential characteristics of oceanic ecosystems that one needs to capture in an ecological model? Oceanic ecosystems present low overall productivity, and are dominated by pelagic (plankton-nekton) species communities. Approximately half of the total area of the open ocean is between the latitudes 25°N and 25°S, and 75% is between 45°N and 45°S, meaning that most oceanic ecosystems are within the tropical and subtropical zones (Mann 1984). Of importance to fisheries management is the fact that a large proportion of oceanic areas are beyond the margins of the continental shelves and mostly beyond the EEZs of countries, meaning that resources in these high seas areas are accessible to fleets of all countries (although some form of access control may apply, such as the quota allocations for tunas and billfishes).

The open ocean is characterized by horizontal and vertical physical-biological discontinuities which are useful for defining system boundaries and model structure. Based on geographical discontinuities in the physical processes affecting the stability of the mixed layer, Longhurst (1998) defined four major biomes in the world's oceans: Westerlies, Trades, Polar and Coastal biomes. According to the author the large oceanic areas of the Atlantic fall mostly within the Westerlies and Trades biomes. While in the first the main physical processes affecting the depth of the mixed layer are winds and irradiance, in the Trades biome it is the geostrophic adjustment to the trade wind regimes that conditions the dynamics of the mixed layer (Longhurst, 1998). Within each biome Longhurst (1998) defines biogeochemical provinces

¹ Cite as: Vasconcellos, M., Watson, R. 2004. Mass balance of Atlantic oceanic systems, p. 171-214. *In*: Palomares, M.L.D., Pauly, D. (eds.) West African marine ecosystems: models and fisheries impacts. Fisheries Centre Research Reports 12(7). Fisheries Centre, UBC, Vancouver.

distinguished by their unique patterns of surface chlorophyll fields, primary productivity, mixed layer topography and related physical forcing (climatic and oceanographic), photic depth and surface nutrient fields. Figure 1 present a map with the location of the biomes and provinces that are used here to characterize the oceanic ecosystem of the Atlantic. The names of the biogeochemical provinces are provided in Table 1. Models were constructed to represent three oceanic areas over 200 m depths: A North Atlantic model, composed of provinces of the North Atlantic Westerly Winds biome (NADR, GFST, NASW, NASE); a Central Atlantic model, composed of the provinces of the Trade Wind biome (NATR, WTRA and ETRA); and a South Atlantic model, composed of the only province of the Westerly Wind biome in the southern ocean (SATL). The total area of the oceanic provinces represented in the models is ca. 50×10^6 km², which is roughly equally divided among the three modeled areas (Table 1).

Table 1. Area of models and biogeochemical provinces of the oceanic ecosystems of the Atlantic.

Model	Province	Code	Area (km ²)
North Atlantic	North Atlantic Drift	NADR	3,477,925
	Gulf Stream	GFST	1,086,696
	Northwest Atlantic Sub-tropical Gyral	NASW	5,784,896
	Northeast Atlantic Sub-tropical Gyral	NASE	4,379,757
			14,729,274
Central Atlantic	North Atlantic Tropical Gyral	NATR	7,895,149
	Western Tropical Atlantic	WTRA	5,199,487
	Eastern Tropical Atlantic	ETRA	5,324,555
			18,419,191
South Atlantic	South Atlantic Gyral	SATL	17,618,486
Total	–	–	50,766,952

Vertical discontinuities in the open ocean are determined by vertical gradients of light, temperature and abundance of organisms (Longhurst and Pauly 1987). Legand *et al.* (1972) and Longhurst and Pauly (1987) distinguished two vertical systems in the open ocean: a superficial one occupying the 0- 450 m layer of the ocean and consisted of phytoplankton, mesoplankton, micronektonic and nektonic species; and a deeper system, below 450 m depth, which has no phytoplankton, low mesoplankton biomass, and had mesopelagic and intrusive bathypelagic micronekton and nekton. The authors structured the biota into five main components (top predatory fish, cephalopods, micronektonic fish, euphausiids and other large crustaceans) which are further divided according to their vertical distribution. Vertically migrating species (such as mesopelagic fish) are in the deeper system during the day and in the superficial system at night. For this reason mesopelagic fish are often considered important vertical transporters of organic matter (Gjøsaeter and Kawaguchi, 1980).

Mann (1984) proposed a vertical structure for the open ocean fish communities according to 4 zones. An epipelagic zone (correspondent to the euphotic zone) extending down to a depth of 200 m. In this zone the main predators are sharks, tunas, billfish and swordfish, although some tuna may feed to a depth of about 400 m. The mesopelagic zone extends from 200 m to about 1000 m.

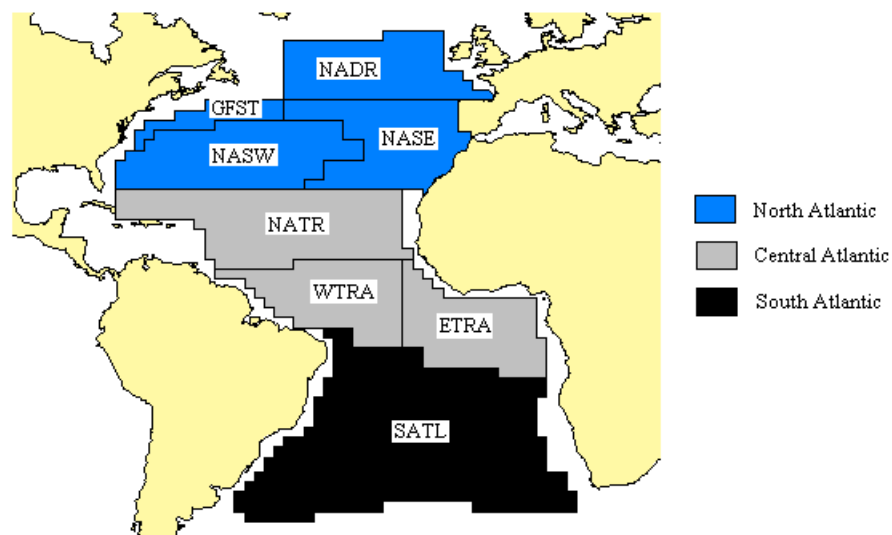


Figure 1. Map of the biogeochemical provinces (Longhurst, 1998) that compose each oceanic ecosystem of the Atlantic as defined in this contribution.

Characteristics of this zone is the constant presence of a “deep scattering layer” which is normally dominated by myctophids, gonostomatids and sternoptychids (Mann, 1982). At night a large proportion of the mesopelagic fauna migrates to the epipelagic zone. The bathypelagic zone starts below 1000 m. Bathypelagic fish fauna are characterized by dark colour, small eyes, weak musculature and large mouths, and are best represented by the angler fish (ceratioids) and species of the genus *Cyclothone* (Mann, 1984). These species are adapted to the low food availability of the environment, i.e., they decreased the amount of energy expenditure associated with feeding and reproduction (e.g., angler fishes have developed elaborate lures to attract prey close to their mouth). Close to the bottom of the ocean, Mann (1984) recognizes two distinct groups of bottom dwelling fish. The “sit and wait” predators (e.g. *Bathysaurus* and chlorophthalmids), which lack swimbladders and are negatively buoyant, and the benthopelagic fishes including a wide ranging species with swimbladders such as rat-tails (Macrouridae), deep-sea cods (Moridae) and brotulids that live close to the bottom. These organisms are largely supported by the carcasses of dead animals sinking from above. Mann (1984) also cites the existence of a community of large amphipods of the family Lysianassidae, shrimps and other decapods which may serve as food for the benthic fish community.

Many authors have contributed to the conceptualization of the trophic relationships and the transfer of organic matter between the vertical layers of the open ocean. Longhurst and Pauly (1987) described three pathways by which organic material is produced and transformed by consumption by larger organisms in the pelagic ecosystem: the first is the microbial loop, in which dissolved organic material, originated mostly from plant cells, is utilized by bacterial and fungal cells of small size, which are consumed by a variety of heterotrophic protists, which are then consumed by larger zooplankton. The second pathway is based on the growth of picoplankton (e.g. cyanobacteria) which is consumed mostly by protists, but also by salps and tunicates. Because copepods cannot graze on cyanobacteria, the authors presumed that these cells are grazed initially by heterotrophic nanoplankton. The third pathway is the classical food chain, based on the consumption by zooplankton of phytoplankton cells such flagellates, coccolithophores, dinoflagellates and diatoms (Longhurst and Pauly, 1987).

Diel vertical migrations are ubiquitous for all organisms in the oceanic ecosystem. In these areas a large fraction of the zooplankton and nekton perform extensive vertical migrations, rising to the surface after dusk and descending to 200-500 meters at dawn. A two layered trophic model has been suggested by Longhurst and Pauly (1987) to represent this pattern in the tropical oceanic ecosystem. Associated with the epiplankton are tunas feeding on smaller fish (Gempylidae and Bramidae) and small euphausiids which feed on smaller components of the epiplankton. Lying deeper, in the daytime below 250 m depth, are interzonal fish (Myctophidae and Gonostomatidae) and large euphausiids. These organisms rise at dusk to feed nocturnally on smaller species of the epiplankton, but are not fed upon by tunas and fish of the surface layer which cease feeding at night. In this two-layered ecosystem energy is mostly transported downward below the euphotic zone, where it is utilized by large bathypelagic, nonmigrating predators and by omnivorous and carnivorous deep zooplankton. As noted by Longhurst and Pauly (1987), only in special cases there is an active transport of energy upward, by feeding excursions of larger surface biota (bigeye tuna, sperm whales) toward deeper zones.

The two layered model of Longhurst and Pauly (1987) mirrors the description of pelagic food webs described by (Roger and Grandperrin (1976). Analyzing the stomach content of tunas caught in longlines the authors showed that the micronektonic fishes ingested by albacore and yellowfin tunas are mostly epipelagic fish, and that the contribution of the abundant migratory mesopelagic fish is rather small. Analysing the stomach content of the epipelagic fish found in the stomach of tunas, (Roger and Grandperrin 1976) showed that the euphasiids found in the stomachs of the epipelagic fishes were mainly nonmigrating *Stylocheiron* species which stays in the upper layer during the day. The authors therefore concluded that the epipelagic fish eaten by tunas are also day-feeders, preying upon zooplankton organisms that stay in the upper layer during the day. This study has demonstrated that each link in the food chain leading to tunas has food sources restricted only to the biomass which stays between the upper layers of the ocean (0 to 450 m) during daytime. Roger and Grandperrin (1976) proposed that the day-night pattern of feeding in the epipelagic zone is responsible for a large downward flow of energy that supports the large biomass of organisms in the deeper layer of the ocean (the “energy valve” concept).

Vinogradov (1970) proposed yet another mechanism by which organic matter is actively transferred from the surface to the deeper layers of the ocean. Studying the pattern of vertical migrations (both diurnal and seasonal) adopted by organisms at different depth layers of tropical and temperate oceans, this author

proposed that the animals descending from the more productive surface layers must serve as food for the population of the depths. These species in turn can descend to even greater depths and serve as food for the more deep-sea animals. Thus according to the author organic material is actively transferred downward through a “ladder of migrations” of planktonic and micronektonic animals.

At the bottom of the deep oceans life is supported by four main sources of organic matter (Rowen, 1981): the rain of particles from the pelagic environment, dead carcasses, the “ladder of migration” of micronektonic organisms, and turbidity currents that carry organic matter from the continental shelves towards the slope and abyssal zones. The contribution of the latter tends to be small. (Rowe, Smith *et al.* (1986) showed, for instance, that only a small proportion of the phytodetritus in continental shelves of the Northwest Atlantic is exported to deeper zones. Once in the system, the organic matter is consumed by bathypelagic organisms, by demersal fishes and crustaceans that migrate off the bottom to scavenge, or sink to the bottom into the benthic layer. In the benthic layer the organic matter can be consumed by benthic invertebrates or heterotrophic bacteria. The remaining detritus is buried into the ground (Rowen, 1981).

Table 2. Input parameters of the North Atlantic model for the late 1990s.

Functional group	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	24.634	0.020	4.394		0.000
Toothed whales	51.144	0.020	6.689		0.000
Beaked whales	0.536	0.020	8.806		0.000
Seabirds	0.204	0.078	72.779		0.000
Pelagic sharks		0.390	10.000	0.9	1.731
Yellowfin	0.015	1.050	15.530		0.005
Bluefin	2.030	0.500	4.000		0.731
Skipjack	0.463	1.350	19.610		0.162
Albacore	0.000	0.800	9.600		0.000
Bigeye	26.944	0.750	17.160		9.430
Swordfish	0.059	0.700	4.000		0.030
Billfishes	0.051	0.404	4.690		0.010
Large planktivorous fish		0.112	1.800	0.1	0.006
Large epipelagic fish	2.204	0.690	8.938		0.661
Medium epipelagic fish		1.080	7.671	0.9	15.909
Small epipelagic fish		2.053	12.549	0.9	0.017
Large mesopelagic fish		0.150	3.550	0.9	0.000
Small mesopelagic fish	1724.369	1.983	18.250		0.000
Small bathypelagic fish		1.040	3.650	0.9	0.000
Medium bathypelagic fish		0.190	0.290	0.9	0.000
Large bathypelagic fish		0.270	0.490	0.9	0.662
Small bathydemersal fish slope	45.054	0.345	0.628		21.619
Large bathydemersal slope	53.246	0.175	0.318		10.519
Small bathydemersal abyss	121.430	0.378	0.687		0.000
Large bathydemersal abyss	189.631	0.209	0.380		0.000
Small squids		4.600	36.500	0.9	0.163
Large squids		4.600	36.500	0.9	0.000
Benthic cephalopods		1.150	2.300	0.9	0.000
Meiobenthos	1234.000	2.250	22.650		0.000
Macro-benthos	545.000	1.000	9.850		0.000
Megabenthos	493.000	1.100	6.700		0.000
Heterotrophic bacteria	28167.000	18.450	25.000		0.000
Small zooplankton shallow	118184.639	17.300	57.700		0.000
Large zooplankton shallow	7377.317	8.700	29.000		0.000
Small zooplankton deep	46164.009	17.300	57.700		0.000
Large zooplankton deep	1392.264	8.700	29.000		0.000
Phytoplankton	13500.000	259.274			0.000
Detritus					

Based on the background information presented above, a model template was developed to serve as tool to both evaluate hypotheses about fluxes of biomass in the oceanic food web and to evaluate the ecosystem

impacts of fisheries in oceanic ecosystem of the Atlantic. Characteristics of the model template developed here are: 1) a multilayered structure that represents the plankton and nekton of the epipelagic, mesopelagic, bathypelagic and bathydemersal zones; 2) the detailed representation of benthic fauna and microbial loop; and 3) the detailed representation of swordfish and tuna species, notably the main fisheries resources in oceanic areas. Tables 2-4 present the functional groups and the input parameters for each oceanic ecosystems of the Atlantic. Sources and methods used to estimate each parameter are described in the following sections.

Table 3. Input parameters of the Central Atlantic model for the late 1990s.

Functional group	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	20.642	0.020	4.394		0.000
Toothed whales	42.856	0.020	6.689		0.000
Beaked whales	0.449	0.020	8.806		0.000
Seabirds	0.125	0.078	73.562		0.000
Pelagic sharks	0.000	0.390	10.000	0.9	0.372
Yellowfin	0.078	1.050	15.530		0.027
Bluefin	0.008	0.500	4.000		0.003
Skipjack	2.605	1.350	19.610		0.912
Albacore	0.155	0.800	9.600		0.078
Bigeye	8.942	0.750	17.160		3.130
Swordfish	0.302	0.700	4.000		0.151
Billfishes	1.657	0.416	4.137		0.331
Large planktivorous fish		0.112	1.800	0.1	0.000
Large epipelagic fish	6.753	0.693	8.938		2.026
Medium epipelagic fish		1.080	7.671	0.9	0.800
Small epipelagic fish		2.053	12.549	0.9	0.000
Large mesopelagic fish		0.150	3.550	0.9	0.000
Small mesopelagic fish	3253.854	3.757	18.250		0.000
Small bathypelagic fish		1.040	3.650	0.9	0.000
Medium bathypelagic fish		0.190	0.290	0.9	0.000
Large bathypelagic fish		0.270	0.490	0.9	0.000
Small bathydemersal fish slope	15.938	0.355	0.645		0.576
Large bathydemersal slope	18.835	0.160	0.291		1.075
Small bathydemersal abyss	93.452	0.343	0.623		0.000
Large bathydemersal abyss	145.938	0.202	0.368		0.000
Small squids		4.600	36.500	0.9	0.276
Large squids		4.600	36.500	0.9	0.000
Benthic cephalopods		1.150	2.300	0.9	0.000
Meiobenthos	984.000	2.250	22.650		0.000
Macrobenthos	369.000	1.000	9.850		0.000
Megabenthos	394.000	1.100	6.700		0.000
Heterotrophic bacteria	22542.999	18.450	25.000		0.000
Small zooplankton shalow	76767.265	17.300	57.700		0.000
Large zooplankton shalow	17567.677	8.700	29.000		0.000
Small zooplankton deep	18858.584	17.300	57.700		0.000
Large zooplankton deep	5931.747	8.700	29.000		0.000
Phytoplankton	20250.000	146.382			0.000
Detritus					

FISHERIES LANDINGS

Fisheries landing statistics for each biogeochemical province of the Atlantic were obtained from the *Sea Around Us Project* database. In this database FAO fisheries landing statistics were disaggregated spatially in cells ½ degree of latitude x ½ degree longitude applying a rule based procedure that account for the known distribution limits of each taxa, oceanographic features and the fishing access rights of each reporting country. Details on the procedure are provided by (Watson *et al.* 2004). For the purpose of the models here described the spatially disaggregated catches were reaggregated by biogeochemical provinces within each of the oceanic ecosystems of the Atlantic, as defined in section 2. Table 5 shows the average landings of each taxon in each functional group and area for the period 1997-1998 and for 1950.

Table 4. Input parameters of the South Atlantic model for the late 1990s.

Functional group	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	21.580	0.020	4.394		0.000
Toothed whales	44.804	0.020	6.689		0.000
Beaked whales	0.470	0.020	8.806		0.000
Seabirds	0.137	0.081	73.757		0.000
Pelagic sharks	0.000	0.390	10.000	0.9	0.094
Yellowfin	0.066	1.050	15.530		0.023
Bluefin	0.003	0.500	4.000		0.001
Skipjack	3.988	1.350	19.610		1.396
Albacore	0.446	0.800	9.600		0.223
Bigeye	0.100	0.750	17.160		0.035
Swordfish	0.291	0.700	4.000		0.145
Billfishes	0.586	0.409	4.212		0.117
Large planktivorous fish		0.113	1.800	0.1	0.000
Large epipelagic fish	0.208	0.690	8.938		0.062
Medium epipelagic fish		1.080	7.671	0.9	0.043
Small epipelagic fish		2.053	12.549	0.9	0.000
Large mesopelagic fish		0.150	3.550	0.9	0.000
Small mesopelagic fish	1164.093	2.445	18.250		0.141
Small bathypelagic fish		1.040	3.650	0.9	0.000
Medium bathypelagic fish		0.190	0.290	0.9	0.000
Large bathypelagic fish		0.270	0.490	0.9	0.000
Small bathydemersal fish slope	7.509	0.412	0.748		0.965
Large bathydemersal slope	8.874	0.207	0.376		0.571
Small bathydemersal abyss	109.387	0.378	0.687		0.000
Large bathydemersal abyss	170.823	0.209	0.380		0.000
Small squids		4.600	36.500	0.9	0.000
Large squids		4.600	36.500	0.9	0.000
Benthic cephalopods		1.150	2.300	0.9	0.000
Meiobenthos	1073.000	2.250	22.650		0.000
Macrobenthos	414.000	1.000	9.850		0.000
Megabenthos	429.000	1.100	6.700		0.000
Heterotrophic bacteria	24562.000	18.450	25.000		0.000
Small zooplankton shallow	107402.947	17.300	57.700		0.000
Large zooplankton shallow	3537.318	8.700	29.000		0.000
Small zooplankton deep	27809.732	17.300	57.700		0.000
Large zooplankton deep	986.818	8.700	29.000		0.000
Phytoplankton	13500.000	192.982			0.000

DAILY RATION AND Q/B OF DEEP WATER ORGANISMS

Deep sea organisms have life history strategies adapted to live in a cold, dark, and very unproductive environment with low oxygen concentrations. These life history strategies are translated into morphological, behavioral and metabolic adaptations that preclude the use of some widely accepted rules for estimating consumption rates. Mahaut *et al.* (1995) showed that the respiration rate of benthic megafauna organisms in shallower water tend to be between 4 and 10 times that of deep sea organisms. Likewise, Childress *et al.* (1980) estimated high food conversion efficiencies for bathypelagic fishes. According to these authors this decrease in metabolism appears to be more an adaptation to life in the deep sea than to the effect of temperature alone. This appendix explains the procedure used to calculate the daily ration, and consequently the Q/B, of bathypelagic, bathydemersal and deep sea benthic organisms based on a published relationship between respiration rate and weight of deep sea organisms (Mahaut *et al.*, 1995).

Assuming that the energy devoted to growth and metabolism total approximately 73% of the total ingested energy of an average carnivore (Brett and Groves, 1979; Childress *et al.*, 1980), the total energy consumed by an individual (C, in Kcal) of weight *i* is:

Table 5. Landings in kg·km⁻² by taxa and functional groups for each oceanic area of the Atlantic.

Groups/taxa	1997-98			1950		
	North	Central	South	North	Central	South
Yellowfin, <i>T.albacares</i>	81.80	502.98	405.85	0.00	0.00	0.00
Bluefin, <i>T. thynnus</i>	11277.18	51.81	20.14	15228.61	16.53	0.00
Skipjack, <i>K. pelamis</i>	2503.05	16790.29	24593.89	705.00	0.00	0.00
Albacore, <i>T.alalunga</i>	1.37	1431.12	3931.41	28578.94	0.00	0.00
Bigeye, <i>T. obesus</i>	145550.35	57643.36	615.62	809.00	0.00	0.00
Swordfish, <i>X. gladius</i>	456.36	2784.30	2560.23	1679.15	0.00	0.00
Billfishes	156.14	6102.15	2063.84	0.00	0.00	0.00
<i>M. nigricans</i>	48.35	5266.26	1625.71			
<i>Tetrapturus</i> spp.	6.89	160.01	322.99			
<i>I. platypterus</i>	13.02	80.40	46.19			
<i>Tetrapturus</i> spp.	0.00	0.79	0.98			
Billfishes	87.88	594.69	67.97			
Pelagic sharks	26714.28	6848.07	1648.59	4087.11	0.00	0.00
Blue shark	173.68	374.66	1374.55			
Greenland shark	5.17	0.00	0.00			
<i>Isurus</i>	7.30	56.63	0.00			
Longfin mako	0.21	0.59	0.00			
Porbeagle	203.17	0.00	0.00	252.11		
Requiem sharks	3107.03	6331.31	0.00	390.56	839.66	
Shortfin mako	0.00	81.34	258.87			
Silky shark	0.00	0.31	0.00			
Various sharks nei	23217.73	3.23	15.16	3444.43		
Large Plank. fish	96.16	0.00	0.00	584.55	0.00	0.00
Basking shark	96.16	0.00	0.00	584.55		
Large epipelagic fish	10203.10	37315.65	1098.52	6085.76	5326.43	0.00
Atlantic bonito	371.96	0.43	0.00			
Blackfin tuna	598.56	2130.22	65.40	96.82	323.03	
<i>Cobia</i>	0.34	171.55	1.65	0.10	6.45	
Mackerels, snoeks, cutlassfishes	6438.07	19195.03	98.33			
Mackerels, tunas, bonitos	340.56	0.00	0.00	4368.89	45.53	
Serra Spanish mackerel	0.00	5126.12	773.27		219.54	
<i>Scomberomorus</i>				48.95	154.33	
King mackerel				1053.36	2770.82	
<i>Sphyræna</i>	2453.61	10692.30	159.88	517.65	1806.74	
Medium epipelagic fish	245546.35	14736.09	763.88	27152.15	2295.56	2120.69
Atlantic mackerel				293.69		
Atlantic horse mackerel	33204.07	6.21	0.00	2727.35		
<i>Caranx</i>	17.96	50.43	6.11		77.14	
Chub mackerel	83220.38	0.00	588.82	1198.35	1.06	
Frigate tuna	1586.62	6956.97	0.00	559.59	2152.57	2079.90
Jacks and pompanos	1514.22	7256.06	75.58			
Jacks, mullets, sauries	223.59	466.42	93.36	27.06	51.28	40.79
Pelagic fishes nei	9680.49	0.00	0.00	11957.09		
Trachurus	116099.01	0.00	0.00	10389.02		
Creville jack					13.52	
Small epipelagic fish	266.00	0.00	0.00	0.00	0.00	0.00
Longspine spinefish	266.00					
Flyingfishes				487.57	720.16	
Small mesopelagic fish	0.00	0.00	2483.43	0.00	0.00	0.00
Hector's lanternfish			2483.43			
Large bathypelagic fish	10212.18	0.00	0.00	0.00	0.00	0.00

Table 5. Continued.

Groups/taxa	1997-98			1950		
	North	Central	South	North	Central	South
Atlantic pomfret	2997.85			1676.24		
Black scabbardfish	7214.33					
Small bathydemersal fish (slope)	247324.60	10601.93	16994.22	17272.43	3465.55	81.58
Argentina	24212.70	0.00	0.00			
Axillary seabream	1047.80	0.00	0.00			
<i>Beryx</i>	192.56	0.32	1727.63			
Black seabream	15.87	0.00	0.00			
Blackbelly rosefish	0.00	388.73	1589.44			
Blackspot seabream	2234.23	0.00	0.00	885.84		
Blue whiting	162336.48	0.00	0.00	5787.88		
Bogue				314.23		
Bramble, sleeper and dogfish sharks	556.70	232.65	0.00			
Bulls-eye	92.90	0.00	0.00			
Cods, hakes, haddocks	0.00	2476.90	8544.16			
Common pandora	93.50	0.00	0.00	483.90		
Conger and garden eels	142.16	747.79	1.44			
Cuckoo ray	833.21	0.00	0.00			
Cutlassfishes	578.78	790.07	44.08			
Dogfish sharks	3144.70	0.00	0.00	1989.98		
East Atlantic red gurnard	30.87	0.00	0.00			
European conger				1552.27		
Forkbeard	267.00	0.00	0.00			
Large-eye dentex	1030.37	0.00	0.00	2090.36		
Lefteye flounders	0.16	0.71	0.00			
Megrim	6492.29	0.00	0.00	428.35		
<i>Pagellus</i>	25.12	0.00	0.00			
Redfishes, basses, congers	6657.38	5964.76	4807.83	2334.06	3465.55	81.58
Sand sole	70.57	0.00	0.00			
Scorpionfishes or rockfishes	1230.98	0.00	0.00			
<i>Sebastes</i>	27266.60	0.00	0.00			
Senegalese hake	3616.82	0.00	0.00			
Silvery John dory	0.21	0.00	0.00			
Slimeheads	530.40	0.00	0.00			
Torpedo	3.43	0.00	0.00			
Tub gurnard	0.14	0.00	0.00			
Wedge sole	233.76	0.00	0.00	444.34		
White snake mackerel	0.00	0.00	279.64			
Witch	4386.89	0.00	0.00	155.07		
Large bathydemersal fish (slope)	86151.90	19802.15	10057.49	24652.52	1178.07	287.75
American conger	0.00	0.00	0.00			
<i>Anarhichas</i>	1926.88	0.00	0.00	539.34		
Angler	3925.41	0.00	0.00	396.59		
Argentine hake						35.50
Atlantic halibut	585.29	0.00	0.00	3490.83		
Black-bellied angler	201.18	0.00	0.00			
Blue ling	3595.14	0.00	0.00	129.30		
Cusk-eels	1.79	124.05	176.47			
Dusky grouper	7.84	0.00	0.00			
European conger	2794.91	0.00	0.00			
European hake	8621.80	0.00	0.00	16326.45		
Great northern tilefish				28.60		

Table 5. Continued.

Groups/taxa	1997-98			1950		
	North	Central	South	North	Central	South
Greater forkbeard	2564.73	0.00	0.00	116.96		
John dory	906.64	0.00	0.00			
Largehead hairtail	26912.06	66.22	15.53		78.99	
Leafscale gulper shark	66.02	0.00	0.00			
Ling	3900.34	0.00	0.00	910.96		
Longnosed skate	84.97	0.00	0.00			
<i>Molva</i>	2305.59	0.00	0.00			
Onion-eye grenadier	84.23	0.00	0.00			
Orange roughy	1233.72	0.00	493.74			
Patagonian toothfish	0.00	0.00	560.52			
Piked dogfish	585.61	0.00	0.00			
Pink cusk-eel	0.00	0.00	1509.75			4.28
Portuguese dogfish	176.85	0.00	0.00			
Rabbit fish	9.13	0.00	0.00			
Red grouper	0.00	6.30	0.00			
Roundnose grenadier	14621.16	0.00	0.00			
Sea lamprey	5.12	0.00	0.00			
<i>Seriola</i>	909.61	1462.93	199.47			
Shagreen ray	12.90	0.00	0.00			
Shallow-water Cape hake	0.00	0.00	3.60			5.82
Silver scabbardfish	2762.18	0.00	0.00	2215.59		
Skates and rays	5557.55	18142.66	7097.40	383.73	1099.08	242.14
Spotted wolffish	188.11	0.00	0.00			
Thornback ray	116.79	0.00	0.00			
Thorny skate	214.96	0.00	0.00			
Tope shark	20.69	0.00	1.01			
Wolf-fish	776.28	0.00	0.00	114.16		
Wreckfish	476.42	0.00	0.00			
Small squids	2508.26	5087.40	0.00	799.55	0.00	0.00
European flying squid	1423.33	0.00	0.00			
Squids, cuttlefishes, octopuses	1084.92	5087.40	0.00			
Northern shortfin squid				799.55		

$$C_i = (\Delta W + Resp) / 0.73 \dots\dots\dots 5)$$

where ΔW is the caloric growth and $Resp$ the energy expired. ΔW is estimated by the first derivative of von Bertalanffy growth equation (as in (Pauly 1994))

$$dW/dt = 3 \cdot K \cdot W \cdot ((W_\infty/W)^{1/b} - 1) \dots\dots\dots 6)$$

To convert from growth in wet weight to calorific growth, we assume that the energy density of deep water fish averages 0.6 Kcal·g⁻¹ (Childress *et al.*, 1980).

$Resp$ is estimated based on the relationship between respiration rate (day⁻¹; expired weight of carbon per individual weight of carbon) and total weight (W ; mgC) of deep sea organisms proposed by Mahaut *et al.* (1995):

$$R = 7.4 \cdot 10^{-3} \cdot W^{-0.24} \dots\dots\dots 7)$$

Assuming an organic carbon content in dry organic matter of 51.8 % (Mahaut *et al.*, 1995), an average of 70 % content of water in fish wet weight (Christensen and Pauly 1993), and the calorific value of fish wet weight of 0.6 Kcal·g⁻¹, the conversion factor between mgC into Kcal is estimated at 0.003861.

Using the daily ration and the daily growth the food conversion efficiency, K_i , was computed as follows

$$K_i = (dW/dt) / C_i \dots\dots\dots 8)$$

Q/B (year) was then computed, according to Palomares and Pauly (1998) as

$$Q/B = \sum_{(t,t_{max})} N_t \cdot (\Delta W / K_t) / \sum_{(t,t_{max})} W_t \cdot N_t \dots\dots\dots 9)$$

In this equation the value of W_t is obtained from published length-weight relationships ($W = a \cdot L^b$), or when these were available, by assuming isometric growth in weight, i.e. $W = a \cdot L^3$ (Palomares and Pauly 1998). N_t is estimated from exponential decrease in numbers with age and a total mortality rate (Z) calculated using Pauly (1980) equation. Table 6 presents the Q/B values computed for bathydemersal (*Lepidopus caudatus*) and bathypelagic fish (*Alepocephalus rostratus* and *Aphanopus carbo*). The mean of the gross efficiencies (0.55) was used to estimate Q/B from P/B estimates for the other bathydemersal and bathypelagic fish groups in the model.

Table 6. Estimated Q/B and gross ecological efficiency (P/Q) for key bathydemersal and bathypelagic fish species. P/B estimated using Pauly (1980) relationship between natural mortality rate, growth parameters, and mean temperature (8 °C).

Species	K (year ⁻¹)	L _∞ (cm)	P/B (year ⁻¹)	Q/B (year ⁻¹)	P/Q
<i>Lepidopus caudatus</i> ^a	0.238	200	0.26	0.52	0.50
<i>Alepocephalus rostratus</i> ^a	0.090	45	0.19	0.29	0.65
<i>Aphanopus carbo</i> ^b	0.251	139	0.27	0.49	0.55

Growth parameters from (a) Morales-Nin (2001) and (b) Morales-Nin and Sena-Carvalho (1996).

MARINE MAMMALS

Following (Kaschner *et al.* 2001) and Trites and Heise (1996), marine mammals were divided in three functional groups: **Ballen whales** (Mysticetes), **Toothed whales** (Odontocetes) and **Beaked whales** (family Ziphiidae). Species specific abundance estimates, mean body weights, standardized diet compositions and feeding rates, obtained from the marine mammal database for the North Atlantic (Kaschner *et al.* 2001), were used to compute biomass (only for North Atlantic provinces), Q/B and diets of each functional group. P/B estimates were obtained from other published ecosystem models (Trites and Heise 1996; Trites *et al.* 1999). Parameter values for marine mammals in the provinces of the Central and South Atlantic were tentatively assumed to be similar to the North Atlantic provinces. Table 7 shows parameter values for individual species of marine mammals included in the model of the North Atlantic.

SEA BIRDS

The sea birds group is composed of species that inhabit mid-oceanic islands and pelagic migratory species that spend their lives at sea far from land, except when nesting. Typical of this group are the species of the order Procellariiformes, which are divided in four families: Diomedidae (albatrosses), Procellariidae (petrels and shearwaters), Hydrobathidae (storm petrels) and Pelecanoididae (diving petrels); the order Pelecaniformes (gannets, frigatebirds and tropicbirds), and the order Lariformes (terns and noddy; Croxall *et al.* 1984; Prince and Morgan 1987). For most of the species in this group the only available abundance and biomass data come from censuses of breeding populations. However, given the fact that many of them are also highly migratory (such as most Procellariiformes), the estimation of abundance and biomass in each modeled areas had to take into consideration the amount of time each species spend in the oceanic region.

Table 7. Biomasses (kg·km⁻²) and consumption/biomass ratios (year⁻¹) of marine mammal species included in the North Atlantic Oceanic ecosystem (from Kaschner *et al.*, 2001).

	Scientific name	Common name	Q/B	Biomass
Ballen whales	<i>Balaenoptera acutorostrata</i>	Minke	6.290	293670.3
	<i>Balaenoptera borealis</i>	Sei	5.214	54809.0
	<i>Balaenoptera edeni</i>	Bryde's	5.256	72687.5
	<i>Balaenoptera musculus</i>	Blue	3.629	25754.3
	<i>Balaenoptera physalus</i>	Fin	4.103	844768.5
	<i>Eubalaena glacialis</i>	Northern right	4.879	4798.7
	<i>Megaptera novaeangliae</i>	Humpback	4.629	94455.2
Toothed whales	<i>Delphinapterus leucas</i>	Beluga or white	11.560	689.8
	<i>Delphinus delphis</i>	Common dolphin	15.162	6525.5
	<i>Feresa attenuata</i>	Pygmy killer	14.559	41.8
	<i>Globicephala macrorhynchus</i>	Short-finned pilot	9.954	9945.6
	<i>Globicephala melas</i>	Long-finned pilot	9.437	457648.6
	<i>Grampus griseus</i>	Risso's dolphin	12.368	7260.9
	<i>Kogia breviceps</i>	Pygmy sperm	12.969	113.0
	<i>Kogia simus</i>	Dwarf sperm	14.508	58.8
	<i>Lagenodelphis hosei</i>	Fraser's dolphin	14.668	723.3
	<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin	14.758	1921.2
	<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	13.561	4430.0
	<i>Orcinus orca</i>	Killer	7.763	9553.7
	<i>Peponocephala electra</i>	Melon-headed	14.403	186.6
	<i>Phocoena phocoena</i>	Harbour porpoise	18.357	4276.3
	<i>Physeter macrocephalus</i>	Sperm	5.025	749131.3
	<i>Pseudorca crassidens</i>	False killer	10.199	3144.3
	<i>Sousa teuszii</i>	Atlantic hump-backed dolphin	15.307	15.4
	<i>Stenella attenuata</i>	Pantropical spotted dolphin	15.807	4415.4
	<i>Stenella clymene</i>	Clymene dolphin	16.914	106.9
	<i>Stenella coeruleoalba</i>	Striped dolphin	14.116	24795.4
<i>Stenella frontalis</i>	Atlantic spotted dolphin	15.768	158.8	
<i>Stenella longirostris</i>	Spinner dolphin	17.340	1943.0	
<i>Steno bredanensis</i>	Rough-toothed dolphin	14.773	593.2	
<i>Tursiops truncatus</i>	Bottlenose dolphin	12.806	4012.5	
Beaked whales	<i>Hyperoodon ampullatus</i>	Northern bottlenose	8.255	23147.8
	<i>Mesoplodon bidens</i>	Sowerby's beaked	10.731	425.5
	<i>Mesoplodon densirostris</i>	Blainville's beaked	10.747	628.2
	<i>Mesoplodon europaeus</i>	Gervais' beaked	10.991	596.2
	<i>Mesoplodon mirus</i>	True's beaked	10.777	610.9
	<i>Ziphius cavirostris</i>	Cuvier's beaked	9.516	1125.5

The first type of information used to estimate seabird biomass was the size of breeding colonies in oceanic islands. Three main sources of data were used: Williams (1984) for the South and Central Atlantic, Le Grand *et al.* (1984) for the tropical northeastern Atlantic, and van Halewyn and Norton (1984) for the islands of the eastern Caribbean and Bahamas. Parallel to the estimates of breeding populations in oceanic islands, data were also compiled for all breeding population of Procellariiformes in the Atlantic. Given their life history adaptation to life in the sea, the species in this order are perhaps the most representative pelagic sea birds. According to Prince and Morgan (1987), Procellariiformes breeding in high latitudes generally migrate towards more temperate regions during the winter, while species breeding in the tropics are relatively sedentary. It is also common for some species to migrate between hemispheres (Prince and Morgan, 1987). For instance, as much as 5 million Greater shearwater, *Puffinus gravis* that breed in the South Atlantic migrate during the austral winter to the North Atlantic, especially to Newfoundland and New England waters (Brown and Nettleship, 1984). Estimates of breeding populations sizes of Procellariiformes were obtained from Evans (1984), Brown and Nettleship (1984), Evans (1984), Croxall (1984), Barret and Vader (1984), Barcena (1984), Williams (1984), Croxall (1984), Cooper (1984) and Brown and Nettleship (1984).

Based on the above information, the total biomass of seabirds in the Atlantic was distributed as follows. For the Procellariiformes it was assumed that all breeding populations in the tropical and sub-tropical regions remain in their respective areas throughout the year. For the species that breed in the Arctic and Antarctic regions, it was assumed that they spend 1/2 year feeding in the northern, central and southern oceanic regions of the Atlantic (as defined in the models). As shown by Furness (1994), the breeding populations of shearwater and petrels of Northeast Atlantic spend between 60 days and 1 year feeding in their respective breeding areas. An equal proportion of the total number of seasonal migratory birds was allocated to each of the three regions. Moreover, in order to account for the fact that the migrant species also feed actively on the more productive shelf waters of both hemispheres (e.g., Neves, 2000 for the Southwest Atlantic), their biomass in the oceanic areas was assumed to be 50 % of the total. A more accurate distribution of seabird biomasses will be possible with more detailed information about the migratory patterns and habit preferences of each individual species. Finally, the breeding populations of Pelicaniformes and Lariformes found in oceanic islands were assumed to remain all year in their respective areas.

Species mean weights reported in the literature (Croxall, 1987; Prince and Morgan, 1987; Vooren and Fernandes, 1989; Mackinson, *in press*) were used to estimate seabird biomasses from total numbers. P/B ratios were estimated from adult annual survival rates (Croxall, 1987). Q/B ratios were estimated using the relationship between seabirds daily ration and body weight proposed by (Nilsson and Nilsson, 1976):

$$\log_{10}R = -0.293 + 0.85 \cdot \log_{10}W \dots\dots\dots 10)$$

where R is the food consumption per day, in grams, and W is the body weight, in grams. P/B and Q/B values for the group were calculated as the weighted average parameters of the species using the biomass contribution of each species in the group. Table 8 shows the parameters used to calculate biomass, P/B and Q/B ratios for each species. Diet information for Procellariiformes was obtained from Prince and Morgan (1987), for Pelecaniformes from (Schreiber and Clapp, 1987), and the diet of Lariformes were derived from the model of the Eastern Gulf of Mexico (Mackinson et al, *in press*).

LARGE OCEANIC PISCIVORES

This group includes highly migratory fish species which were subdivided in 8 functional groups: Yellowfin tuna, Bluefin tuna, Skipjack tuna, Albacore, Bigeye tuna, Swordfish, Billfishes and Pelagic sharks. Although these species inhabit mostly oceanic and outer shelf areas, they often migrate into shallower shelf areas for feeding. A general approach was used to calculate the proportion of the biomass of the individual populations in each oceanic basin: assuming that the stocks are under the same fishing pressure (F) throughout their distribution range, the catches taken in each basin were considered proportional to the biomasses present in the area, i.e. Catches = F · Biomass. Biomasses were then calculated as the ratio of catches and fishing mortality. These estimates should be considered only preliminary since fishing effort, stock biomass and catchability are not spatially homogeneous, and fishing mortality ought to vary between fishing areas. However, these biases are probably smaller for the large oceanic areas covered by the models. Additional parameters for the groups were drawn from the literature cited within each individual section.

Table 8. Parameters of seabirds species in each oceanic area of the Atlantic. See below for sources and estimation procedures.

Species	Mean weight (kg)	Survival rates (% year ⁻¹)	P/B (year ⁻¹)	Daily ration (%bw)	Q/B (year ⁻¹)	Resident in low latitudes			Migrants from high latitudes			
						South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	
Procellariiformes												
Diomedidae												
<i>Diomedea exulans</i>	8.00	95	0.051	0.132	48.287						16,242	
<i>Diomedea melanophrys</i>	3.00	95	0.051	0.153	55.940						910,000	
<i>Diomedea chlororhynchus</i>	3.00	95	0.051	0.153	55.940						74,000	
<i>Diomedea chrysostoma</i>	3.00	95	0.051	0.153	55.940						129,740	
<i>Phoebastria fusca</i>	3.00	95	0.051	0.153	55.940						29,835	
<i>Phoebastria palpebrata</i>	3.00	95	0.051	0.153	55.940						16,000	
Procellariidae												
<i>Pterodroma aminjoniana</i>	1.20	93	0.073	0.176	64.182							
<i>Pterodroma mollis</i>	0.20	93	0.073	0.230	83.973			100			4,800	
<i>Pterodroma cahow</i>	1.20	93	0.073	0.176	64.182			64				
<i>Pterodroma nivea</i>	0.30	93	0.073	0.216	79.018							
<i>Pterodroma macroptera</i>	0.40	93	0.073	0.207	75.680						24,000	
<i>Pterodroma lessonii</i>	0.50	93	0.073	0.201	73.189							
<i>Pterodroma hasitata</i>	1.20	93	0.073	0.176	64.182							
<i>Pterodroma incerta</i>	0.42	93	0.073	0.206	75.129						300	
<i>Pterodroma brevirostris</i>	0.30	93	0.073	0.216	79.018						20,000	
<i>Bulweria bulwerii</i>	0.10	93	0.073	0.255	93.174				400			
<i>Calonectris diomedea</i>	0.72	93	0.073	0.190	69.294			1,030,425				1,690
<i>Puffinus gravis</i>	0.55	93	0.073	0.198	72.150						10,000,000	
<i>Puffinus griseus</i>	0.55	93	0.073	0.198	72.150							
<i>Puffinus puffinus</i>	0.55	93	0.073	0.198	72.150			100				548,520
<i>Puffinus assimilis</i>	0.55	93	0.073	0.198	72.150			30,027			2,200	
<i>Puffinus lherminieri</i>	0.55	93	0.073	0.198	72.150			1,784				
<i>Macronectes halli</i>	5.00	93	0.073	0.142	51.814						6,620	
<i>Macronectes giganteus</i>	5.00	93	0.073	0.142	51.814						47,324	
<i>Fulmarus glacialis</i>	0.80	93	0.073	0.187	68.207						3,162,000	
<i>Fulmarus glacialis</i>	0.80	93	0.073	0.187	68.207							4,231,542
<i>Thalassoica antarctica</i>	0.70	93	0.073	0.191	69.587							
<i>Daption capense</i>	0.40	93	0.073	0.207	75.680						20,000	
<i>Pagodroma nivea</i>	0.30	93	0.073	0.216	79.018						1,100,000	
<i>Habobaena caerulea</i>	0.20	93	0.073	0.230	83.973						200,000	
											160,000	

Table 8. Continued.

Species	Mean weight (kg)	Survival rates (% year ⁻¹)	P/B (year ⁻¹)	Daily ration (%bw)	Q/B (year ⁻¹)	Resident in low latitudes			Migrants from high latitudes			
						South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	
Procellariidae												
<i>Pachyptila vittata</i>	0.15	93	0.073	0.240	87.676				2,000			
<i>Pachyptila valvini</i>	0.15	93	0.073	0.240	87.676				200,000			
<i>Pachyptila desolata</i>	0.15	93	0.073	0.240	87.676				44,000,000			
<i>Pachyptila belcheri</i>	0.09	93	0.073	0.259	94.658							
<i>Pachyptila turtur</i>	0.15	93	0.073	0.240	87.676				2,200			
<i>Pachyptila crassirostris</i>	0.15	93	0.073	0.240	87.676							
<i>Procellaria cinerea</i>	1.00	93	0.073	0.181	65.962				2,150			
<i>Procellaria aequinoctialis</i>	0.79	93	0.073	0.187	68.336				4,020,200			
Hydrobatidae												
<i>Oceanites oceanicus</i>	0.04	90	0.105	0.293	106.902				6,638,000			
<i>Garrodia nereis</i>	0.03	90	0.105	0.306	111.616				310			
<i>Fregata tropica</i>	0.05	90	0.105	0.283	103.383				104,200			
<i>Pelagodroma marina</i>	0.05	90	0.105	0.283	103.383			530,000	10,000			
<i>Hydrobates pelagicus</i>	0.03	90	0.105	0.306	111.616			8				486,425
<i>Oceanodroma castro</i>	0.05	90	0.105	0.283	103.383	3,046		3,000				100
<i>Oceanodroma leucorhoa</i>	0.05	90	0.105	0.283	103.383							121,710
Pelecanoididae												
<i>Plecanoides georgicus</i>	0.10	77	0.261	0.255	93.174				4,002,000			
<i>Plecanoides urinatrix</i>	0.10	77	0.261	0.255	93.174				7,604,000			
Pelecaniformes												
<i>Pelecanus occidentalis</i>	3.50	85	0.163	0.150	54.662			2,500				
<i>Fregata ariel</i>	1.10	85	0.163	0.178	65.026		75					
<i>Fregata aquila</i>	1.10	85	0.163	0.178	65.026		9,000					
<i>Fregata magnificens</i>	1.50	85	0.163	0.170	62.070			4,310				
<i>Sula dactylatra</i>	2.20	93	0.073	0.161	58.604		2,500	3,000	100			
<i>Sula sula</i>	2.20	93	0.073	0.161	58.604		200	2,000	2,000			
<i>Sula leucogaster</i>	1.50	93	0.073	0.170	62.070		1,400	1,139	4,000			
<i>Phaeton aethereus</i>	0.70	85	0.163	0.191	69.587		1,372	4,200	4,200			
<i>Phaeton lepturus</i>	0.70	85	0.163	0.191	69.587		2,100	4,110	4,110			

Table 8. Continued.

Species	Mean weight (kg)	Survival rates (% year ⁻¹)	P/B (year ⁻¹)	Daily ration (%bw)	Q/B (year ⁻¹)	Resident in low latitudes			Migrants from high latitudes			
						South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	South Atlantic (nos)	Central Atlantic (nos)	North Atlantic (nos)	
Lariformes												
<i>Gelochelidon nilotica</i>	0.30	87	0.139	0.216	79.018						10	
<i>Sterna maxima</i>	0.30	87	0.139	0.216	79.018						210	
<i>Sterna sandvicensis</i>	0.30	87	0.139	0.216	79.018						1,200	
<i>Sterna anaethetus</i>	0.30	87	0.139	0.216	79.018						2,000	
<i>Sterna fuscata</i>	0.30	87	0.139	0.216	79.018	210,000	30,000	146,202				
<i>Sterna dougallii</i>	0.30	87	0.139	0.216	79.018						3,910	
<i>Sterna hirundo</i>	0.30	87	0.139	0.216	79.018						4,100	
<i>Sterna albifrons</i>	0.30	87	0.139	0.216	79.018						100	
<i>Anous stolidus</i>	0.30	87	0.139	0.216	79.018	3,400	2,613	3,800				
<i>Anous minutus</i>	0.30	87	0.139	0.216	79.018	156,200	481					
<i>Gygis alba</i>	0.30	87	0.139	0.216	79.018	2,960						

Yellowfin tuna, Thunnus albacares

The species is found worldwide in tropical and subtropical waters. The most acceptable hypothesis today is that all individuals in the Atlantic comprise a single stock (ICCAT 2001). The adults usually occur above the thermocline, while the juveniles are found in schools at the surface mixed with skipjack and bigeye tunas. Large and adult fish are found in deeper water and also extend their range into higher latitudes than smaller fish. Natural mortality rates between 0.8 year⁻¹ (ages 0 and 1) and 0.6 year⁻¹ (ages 2+) are normally used in stock assessments (ICCAT, 1999e). Hampton (2000) estimated M for midsized yellowfin tuna between 0.44 and 0.69 year⁻¹. Fishing mortality is estimated to be close to an F_{MSY} of 0.379 year⁻¹ (ICCAT, 2001). A fishing mortality of 0.35 year⁻¹ and a natural mortality of 0.7 year⁻¹ were used to estimate yellowfin biomass and P/B ratio.

Yellowfin tuna are opportunistic feeders, feeding on a variety of fish and invertebrates (Roger, 1993). Stomachs of fish caught in the Caribbean contained squid, larvae of stomatopods, crabs and squirrelfish (Dragovich, 1969). In the equatorial Atlantic a large proportion of the diet of small yellowfin is made of *Vinciguerria nimbaria* (Menard *et al.*, 2000), a small mesopelagic fish that seems to remain at the surface layers of the ocean during the day and thus becomes available as food for tropical tunas (Lebourges-Dhaussy *et al.*, 2000). Menard *et al.* (2000) estimated the daily rations of yellowfin tuna smaller than 90 cm and larger than 90 cm at 6.12 and 2.59 %, respectively. That corresponds to a Q/B ratio for the species between 9.2 and 21.7 year⁻¹. Cox *et al.* (*in press*) applied Q/B of 14 and 17.6 year⁻¹ for large and small yellowfin tuna for the model of the Central Pacific ocean. In the present models Q/B was set to 15.53 year⁻¹ to represent an expected average metabolic rate during the life span of the species.

Atlantic bluefin tuna, Thunnus thynnus

For assessment purposes, two stocks of bluefin tuna are currently recognized in the north Atlantic, although some level of mixing is known to occur (Clay, 1991; ICCAT, 2001b). The western stock extends from Labrador to northern South America and has the Gulf of Mexico as the main spawning area. The eastern Atlantic stock spawns mainly in the Mediterranean Sea. Both stocks are currently considered depleted and the current population biomass is well below the level of B_{MSY} (ICCAT, 2001b). In the West Atlantic bluefin tuna move seasonally from spring (May to June) spawning grounds in the Gulf of Mexico, through the Straits of Florida, to feeding grounds off the northeastern US coast. Juvenile BFT are often found in mixed schools with skipjack tuna. The species is caught with many gears including longlines, purse seines, and various handgears, and is also incidentally caught in longline fisheries for yellowfin and swordfish. Fishing mortality is estimated at 0.36 year⁻¹ (ICCAT, 2001b). ICCAT (2001b) adopts an M of 0.14 year⁻¹ in stock assessment of western BFT, which was used here to calculate the total mortality rate and P/B ratio of 0.50 year⁻¹.

Although BFT are epipelagic and usually oceanic, they often occur over the continental shelf and in embayments, especially during summer months, to feed on herring, mackerel and squids. Adults consume squids, pelagic crustaceans, and schooling fishes such as anchovies, sauries and hakes (Dragovich, 1969). The diet composition of bluefins were complemented by data reported by Orsi Relini *et al.* (1994) and Ortiz de Zarate and Cort (1986), the latter based on BFT caught in the Bay of Biscay. The average gross food conversion efficiency of fish between 0.4 and 7 kg was estimated at 0.1247 (Palomares, 1987). For a population with P/B of 0.5 year⁻¹, this represents a Q/B of ca. 4 year⁻¹. This value, adopted here, is close to the Q/B of 3.93 year⁻¹ estimated for the species using the equation proposed by Palomares and Pauly (1998).

Atlantic skipjack, Katsuwonus pelamis

There are two stocks of skipjack tuna in the Atlantic, to the east and west of 30°W (Fonteneau and Marcille, 1993). Aggregations of skipjack are associated with convergences and other hydrographic discontinuities, especially with floating objects. Skipjacks spawn in equatorial waters throughout the year, and in subtropical waters from spring to early fall. Most spawning takes place during summer months in the Caribbean, off Brazil, in the Gulf of Mexico, and in the Gulf of Guinea (Fonteneau and Marcille, 1993). Abundance indices from the Brazilian baitboat fishery and the Venezuelan purse seine fishery indicates a stable stock status in western Atlantic (ICCAT, 1999a-c), while the eastern stock is considered overfished (ICCAT, 1999a-c). Natural mortality rate was estimated at 0.94 year⁻¹ using (Pauly, 1980) empirical equation. Hampton (2000) estimated M of the exploitable size range of skipjack in the tropical Pacific at 1.9 year⁻¹ and F between 0.3 and 0.5 year⁻¹. In the Atlantic, M has been estimated between 0.6 and

0.8 year⁻¹ and F between 0.3 and 0.35 year⁻¹ (ICCAT, 1999a-c). Brown *et al.* (1991) estimated a fishing mortality of skipjack of 0.2 year⁻¹ for the Gulf of Mexico. A mid-range M of 1 year⁻¹ was used in the present models, while F was set to 0.35 year⁻¹. Diet information for skipjack was obtained from Dragovich (1969). The proportions between fish and crustacean prey was maintained the same as with other tunas species for which detailed quantitative diets were available. The daily rations of skipjack tuna in the equatorial Atlantic was estimated at 5.51 % (Menard *et al.*, 2000), corresponding to a Q/B of 19.61 year⁻¹. This value is consistent with the Q/B of 20 year⁻¹ used by Cox *et al.* (*in press*) for skipjacks in the Central Pacific.

Albacore, Thunnus alalunga

Albacore is a temperate species widely distributed throughout the Atlantic Ocean and Mediterranean Sea (Fonteneau and Marcille, 1993). For assessment purposes, the population is divided in a northern and southern Atlantic stock, separated at 5°N (ICCAT, 2001). Until the age of maturity (5 years) albacore is mainly found in surface waters, where they are targeted by surface gears. Some adult albacore are also caught using surface gears but, as a result of their deeper distribution, they are mainly caught using longlines (Fonteneau and Marcille, 1993). Young albacore are also caught by longline in temperate waters. The natural mortality rate is estimated at 0.28 year⁻¹ using Pauly's (1980) empirical equation. ICCAT (2001) uses an M of 0.3 year⁻¹, which is assumed constant for all ages. Equilibrium yield analyses for albacore indicated that current fishing mortality may be about 25 % higher than F_{MSY}, but F values as high as 140 % of F_{MSY} are also possible due to current uncertainties in stock assessment methods (ICCAT, 2001). The current estimated F values for the northern and southern Atlantic albacore stocks are 0.57 and 0.41 year⁻¹, respectively (ICCAT, 2001). In the present models an average F of 0.5 year⁻¹ was used for the three areas of the Atlantic, while M was set to 0.3 year⁻¹. (Cox *et al.*, *in press*) estimated Q/B ratios between 7.3 and 9.6 year⁻¹ for large and small albacore in the model of the Central Pacific. In the present model Q/B was set to 9.6 year⁻¹. Diet information was obtained from Dragovich (1969), Mackinson *et al.* (*in press*) and Cox *et al.* (*in press*).

Bigeye tuna, Thunnus obesus

The geographical distribution of bigeye tuna is very wide and covers almost the entire Atlantic Ocean between 50° N and 45° S (Fonteneau and Marcille, 1993). A single Atlantic-wide stock is currently accepted by ICCAT (1999). Adult bigeye dwells in deeper water than other tuna species and performs extensive vertical movements. Young fish form schools mostly mixed with other tunas such as yellowfin and skipjack tunas. Spawning takes place in tropical waters and after spawning fish tend to migrate into temperate waters. Catch information from the surface gears indicates that the Gulf of Guinea is a major nursery ground for this species (Fonteneau and Marcille 1993). Assessments of bigeye tuna indicate that the stock is overfished, and that the current biomass is only 16 % of the unexploited stock biomass (ICCAT, 1999). All stock assessment methods confirm that F has been increasing steadily since the early 1990s, but the current average F values for ages 0 to 7 varies, among methods, from 0.26 to 1.06 year⁻¹ (ICCAT, 1999). Although there is no agreement on the current F value, it is very likely that it is higher than the F_{max} of 0.35 year⁻¹ estimated by yield-per-recruit analysis. Natural mortality rate was estimated at 0.29 year⁻¹ based on Pauly (1980). ICCAT (1999) uses an M of 0.8 year⁻¹ for the juveniles and 0.4 year⁻¹ for adult bigeye. For the tropical Pacific, Hampton (2000) estimated that M varies between 0.15 and 0.9 year⁻¹ for fish larger than 40 cm. In the present model, M was set to 0.4 year⁻¹ and F to 0.35 year⁻¹. Diet information was obtained from Dragovich (1969), Fuentes *et al.* (1988) and Menard *et al.* (2000). To account for the diel feeding migrations, the proportion of zooplankton in the diet of bigeye was split between shallow water (90 %) and deep water (10 %) zooplankton groups. The daily ration of bigeye in the equatorial Atlantic was estimated at 4.82 % (Menard *et al.*, 2000), which corresponds to a Q/B of 17.16 year⁻¹.

Swordfish, Xiphias gladius

Two stocks of swordfish are currently recognized to the north and south of 5°N (NMFS, 2002). Swordfish is overfished (ICCAT, 1999; NMFS, 2002). Biomass of the north Atlantic stock was estimated at 58 % of B_{MSY}, and the current fishing mortality is estimated to be ca. 2 times F_{MSY} (ICCAT, 1999). The current status of the southern stock is more uncertain, and the biomass is estimated to be close to the level that would support MSY (ICCAT, 1999). Natural mortality rate is estimated to be between 0.21 to 0.43 year⁻¹ (Palko *et al.*, 1981), and fishing mortality rate for the northern Atlantic stock between 0.39 (males) to 0.61 year⁻¹ (females) (ICCAT, 1999). In the present models, M was set to 0.2 year⁻¹ (adopted by ICCAT), and an average F of 0.5 year⁻¹ was used for the Atlantic stocks. Adult swordfish are opportunistic feeders, having no specific prey requirements and feeding at the bottom as well as at the surface, in both shallow

and deep waters. The diet of adult swordfish is normally dominated by fish and cephalopods (Ribeiro-Simões and Andrade, 2000), while decapod crustaceans (shrimps) can also be important for smaller individuals (Velasco and Quintans, 2000). In deeper waters, the species feed primarily on pelagic fishes including small tunas, dolphinfishes, lancetfish (*Alepisaurus*), snake mackerel (*Gempylus*), flyingfishes, barracudas and squids such as *Ommastrephes* sp., *Loligo* sp. and *Illex* spp, but also take occasionally demersal fishes such as hakes, pomfrets (Bromidae), snake mackerels, cutlass fish, lightfishes (Gonostomidae), hatchet fishes (Sternoptychidae), redfish, lanternfishes, and cuttlefishes (Nakamura, 1985). Important families of teleosts in the stomach contents of swordfish captured in the Caribbean were Bramidae, Dactylopteridae and Clupeidae (Barreto *et al.*, 1996). The diet of swordfish in the model was assigned as follows: 70 % on fishes, divided equally between the families and genus listed above, and 30 % on squids - assuming that the diet composition mirrors that of tunas (see previous sections). Estimates of Q/B ratio for swordfish vary between 2.93 and 5 year⁻¹ (Brown *et al.*, 1991; Cox *et al.*, *in press*). In the present models, Q/B was set at 4 year⁻¹.

Billfishes

Four species of Atlantic billfishes are recognized: blue marlin, *Makaira nigricans*, white marlin, *Tetrapturus albidus*, sailfish, *Istiophorus platypterus*, and the long spearfish, *Tetrapturus pfluegeri*. For management purposes, the species are divided in stocks for different regions of the Atlantic, with the exception of blue marlin which is recognized as a single Atlantic stock (NMFS, 2002). White marlin is currently divided in two stocks, one in the north Atlantic, the other in the south Atlantic. Sailfishes are divided between west and east Atlantic stocks.

Blue and white Marlins are considered overfished. Biomasses in 1996 were estimated to be ca. 24 % and 23 % of B_{MSY} , respectively (NMFS, 1998). Both species are caught in recreational fisheries and as bycatch in tropical tuna longline fisheries. Natural mortality rates are estimated to be in the range of 0.15 to 0.30 year⁻¹ for blue marlin and 0.1 to 0.2 year⁻¹ for white marlin (ICCAT, 2001). Mid-range values were used in the present models. Sailfish is also considered overfished. The biomass of the western Atlantic stock in 1996 was ca. 60 % of B_{MSY} (NMFS, 1998). Catches are mainly taken from recreational fisheries and as bycatch in longline fisheries for tunas and swordfish. Natural mortality rate of sailfish is estimated in the range from 0.2 to 0.3 year⁻¹ (ICCAT, 2001). The status of the longbill spearfish stock is unknown, but as for others billfishes catches are taken by sportfisheries and also as bycatch in longlines. Until recently, spearfish and sailfish were treated as a same species in the catch statistics and assessment reports (ICCAT, 2001). The same parameters were assumed for spearfish and white marlin. In lack of other estimates of fishing mortality rates for billfishes, in the present model F was set to 0.2 year⁻¹, as proposed by (Brown *et al.*, 1991) for the model of the Gulf of Mexico.

Blue marlin feed primarily on tuna-like fishes (*Auxis* sp.; *Euthynnus* sp.), squids, dolphinfishes and scombrids (NMFS, 2002). The most important prey items of white marlin in the Gulf of Mexico are squids, dolphinfishes, hardtail jack (*Caranx* sp.), followed by mackerels, flyingfishes and bonitos (Davies and Bortone, 1976). Other less common prey items are cutlassfish, puffers, herrings, barracudas, moonfishes, triggerfish, remoras, hammerhead sharks, and crabs. Teleosts are the most common prey items of sailfish, and Scombridae, primarily little tunny *Euthynnus alletteratus*, is the single most common food (Jolley, 1977). Cephalopods are the most common invertebrates, second only to scombrids. Other common fish groups are Exocoetidae, mostly halfbeaks, Carangidae, Belonidae and Clupeidae (Jolley, 1977). Predators include killer whales, bottlenose dolphin (*Tursiops truncatus*) and sharks (NMFS, 2002). Following Cox *et al.* (*in press*) Q/B ratio for blue marlin was set to 4 year⁻¹ and to 5 year⁻¹ for all other billfishes. Final P/B and Q/B ratios for billfishes were estimated as the weighted average ratios estimated for the individual species.

Pelagic sharks

The group represents the highly migratory shark species common in tropical and temperate oceanic areas of the Atlantic. Parameters were estimated for the most important species of oceanic sharks included in the management plans of institutions such as NMFS (2002) and ICCAT (2001). The species are the Atlantic blue shark, *Prionace glauca*, the porbeagle *Lamna nasus*, the longfin mako, *Isurus paucus*, the shortfin mako, *Isurus oxyrinchus*, the threshers, *Alopias vulpinus* and *Alopias superciliosus*, and the hammerhead sharks, *Sphyrna* spp. Although largely oceanic, most species may also be found on the shelf and shallow coastal areas for feeding and reproduction. For some species there is growing evidence of multiple stocks in the Atlantic (ICCAT, 2001). Tagging studies have showed, for instance, that blue sharks

on the north Atlantic constitute a single stock, and that there are two distinct stocks of porbeagles in the eastern and western regions of both North and South Atlantic (ICCAT, 2001). Pelagic sharks are mainly caught in recreational, hook-and-line, and longline fisheries, and also as bycatch in longline fisheries for swordfish and tunas. (Buencuerpo *et al.*, 1998) showed for instance that five species of large sharks seem to dominate the bycatch in swordfish longline fisheries in the northeast Atlantic: *Isurus oxyrinchus*, *Prionace glauca*, *Alopias superciliosus*, *Alopias vulpinus* and *Sphyrna zygaena*. Likewise, the blue shark is one of the most frequent species in the shark bycatches from Venezuelan tuna and swordfish fisheries (ICCAT, 2001). The rate of discards of some species may be high. NMFS (2002) estimated that 75 % of the discarded sharks in U.S. fisheries are blue sharks. The population dynamics of the species in the group are poorly known, and few attempts have been made to make detailed stock assessments in the Atlantic (ICCAT, 2001). Natural mortality rates between 0.09 and 0.24 year⁻¹ were estimated based on Pauly (1980). Cox *et al.* (*in press*) estimated P/B ratios for blue and other large sharks at 0.32 and 0.39 year⁻¹, respectively. In lack of independent estimates of fishing mortality rates, in the present model P/B was set to 0.39 year⁻¹. Q/B ratios were estimated at about 10 year⁻¹ for large pelagic sharks (Stillwell and Kohler, 1992) and between 2.5 and 3.5 year⁻¹ for large sharks of the tropical Pacific (Cox *et al.*, *in press*). The former was adopted in the present models since it is closer to values reported for other large piscivores sharks in other tropical systems, e.g., 7 year⁻¹ for *Negaprion brevirostris* (Cortes, 1997); 10.5 year⁻¹ for large oceanic piscivores (Mackinson *et al.*, *in press*). Diets were obtained from Cortes (1999); ICCAT (2001); Henderson *et al.* (2001); and Vaske-Junior and Rincon-Filho (1998). Biomass was estimated by the model assuming an ecotrophic efficiency of 0.9. The high EE value is justified by the high fishing pressure on the species of the group, some of them showing signs of overfishing and collapse in different parts of the Atlantic, e.g., porbeagle shark in the northwest Atlantic (ICCAT, 2001).

LARGE OCEANIC PLANKTIVORES

The group includes large oceanic planktivorous fish, such as the giant manta ray (Mobulidae), whale shark, *Rhincondon typus*, basking shark, *Cetorhinus maximus*, and the sunfish *Mola mola*, which occur in tropical and temperate waters of all oceans. Although mostly planktivorous, practically all of the above species may also feed on small fishes and squids (Clemens and Wilby, 1961; Compagno, 1984; Cortes, 1999), and when close to shore may also feed upon benthic organisms. P/B ratio of the group was estimated as the average natural mortality rate of the individual species, assuming that fishing mortality is minor for the group (less than 100 tons of basking shark were landed annually in the North Atlantic between 1997 and 1998). Natural mortality rates and Q/B ratios were estimated with Pauly (1980) and Palomares and Pauly (1998) using growth parameters and a mean water temperature of 25°C, provided in FishBase (www.fishbase.org). Diets were derived from qualitative and quantitative information provided in FishBase, and in the references herein, and also from quantitative information available in Cortes (1999). Biomass was estimated by the model assuming an ecotrophic efficiency of 0.1, i.e., only 10 % of the production is utilized in or exported from the system.

EPIPELAGIC FISH

Epipelagic fish were divided in three functional groups according to their maximum size. **Large epipelagic fish** are species that reach a maximum size of more than 90 cm. **Medium epipelagic fish** were species with maximum length between 30 and 90 cm, and **Small epipelagic fish** represented species with less than 30 cm. Epipelagic fish occupy the warmer superficial layer of the ocean. For the estimation of production and consumption rates, it was assumed that the species inhabit waters with a mean temperature of 25°C. The representative species of each group were selected based on their occurrence in the FAO landing statistics and in the diets of other species/functional groups in the model.

Data for the following species were used to characterize the ecological parameters of **Large epipelagic fish**: *Thunnus atlanticus*, *Euthynnus* spp., *Coryphaena hippurus*, *C. equiselis*, *Sphyrna barracuda*, *Scomberomorus* spp., *Sarda sarda*, and *Rachycentron canadum*. Parameters and diets were obtained from the models of the eastern Gulf of Mexico (for mackerels and pelagic oceanic piscivores; see Mackinson *et al.*, *in press*) and the central Pacific ocean (for *C. hippurus*; see Cox *et al.*, *in press*). Complementary information was obtained from FishBase (www.fishbase.org). Although these species are targeted by commercial and recreational fisheries in many regions of the Atlantic, there are few detailed stock assessments studies available for the group. In the models on the Atlantic ocean we tentatively adopted a mean F value of 0.3 year⁻¹ reported by (Brown *et al.*, 1991) for pelagic predators in the Gulf of Mexico. P/B for the group (0.69 year⁻¹) was calculated as the sum of F and the mean natural mortality rate

of the species. As for tunas and billfishes, biomass was estimated as the ratio between landings and fishing mortality.

Data for the following species were used to characterize the ecological parameters of **Medium epipelagic fish**: *Trachurus trachurus*, *T. lathami*, *Caranx rhoncus*, *Scomber japonicus*, *Auxis thazard*, *Scomberesox saurus*, *Vomer setapinnis*, *Tetragonurus atlanticus*, *Lagocephalus lagocephalus*, *Balistes* spp., and *Remora remora*. Parameters and diets were obtained from the models of the eastern Gulf of Mexico (for *Caranx* sp., *Scomber japonicus* and *Trachurus* sp.; see Mackinson *et al.*, *in press*) and the central Pacific ocean (for small scombrids; see Cox *et al.*, *in press*). Complementary information was obtained from FishBase. A P/B of 1.08 year⁻¹, estimated by Cox *et al.* (*in press*) for small scombrids of the tropical Pacific, was considered appropriate for medium epipelagic fish (M of individual species varies between 0.26 and 1.51 year⁻¹) and was therefore used in the models of the Atlantic. Q/B was set to the average Q/B ratios estimated using Palomares and Pauly (1998) for each representative species. Biomass was left to be estimated by the model assuming an ecotrophic efficiency of 0.9.

Data for the following species were used to characterize the ecological parameters of **Small epipelagic fish**: Clupeidae (*Engraulis encrasicolus*), Exocoetidae (*Exocoetus* spp., *Hirundichthys speculiger*), *Gadiculus argenteus*, and *Macroramphosus scolopax*. Parameters and diets were obtained from the models of the eastern Gulf of Mexico (for surface pelagics and sardine-herring complex; see Mackinson *et al.*, *in press*) and the central Pacific ocean (for flying fish; see Cox *et al.*, *in press*). Complementary information was obtained from FishBase. P/B was set to 2.0 year⁻¹, the average value for small pelagics in the tropical Pacific (Cox *et al.*, *in press*) and eastern Gulf of Mexico (Mackinson *et al.*, *in press*) models. Biomass was left to be estimated by the model assuming an ecotrophic efficiency of 0.9. Childress *et al.* (1980) estimated the daily ration of small epipelagic fish at 3.6 %·day⁻¹ (Q/B of 13.14 year⁻¹). The Q/B ratio for the group (12.549 year⁻¹) was computed as the average Q/B of the representative species estimated using Palomares and Pauly (1998).

MESOPELAGIC FISH

Information on the ecology, growth, distribution and biomass of mesopelagic fish was obtained mainly from (Gjøsaeter and Kawaguchi, 1980). Mesopelagic fish are the species that perform large vertical migrations, spending the day in the the mesopelagic zone (200 to 1000 m) and rising to the upper 200 m of the ocean during the night. The most common species of **Small mesopelagic fish** are in the families Myctophidae and Gonostomatidae. The following paragraphs describe the dominant species in each of the oceanic areas of the Atlantic according to (Gjøsaeter and Kawaguchi, 1980).

In the Northeast Atlantic oceanic area the dominant species are *Benthoosema glaciale*, *Mauroliticus muelleri*, *Notoscopelus kroeyeri*, *Lobianchia dofleini*, *Lampanyctus pusillus*, *Ceratoscopelus maderensis*, *Argyropeleceus olfersi* and the genus *Cyclothone* spp. In the Northwest Atlantic (excluding the Labrador area) the important species are *B. glaciale*, *Ceratoscopelus maderensis*, *C. warmingi*, *Diogenichthys atlanticus*, *Lepidophanes guentheri*, *Lobianchia dofleini*, *Notolychnus valdiviae* and *Stomia boa*. There are no commercial fisheries for **Small mesopelagic fish** in the Northern Atlantic

The mesopelagic fish fauna in the Eastern Central Atlantic is very rich, including 37 families, 66 genera, and 98 species. Among them, the most abundant were *Cyclothone braueri*, *C. microdon*, *Vinciguerrria tripunctulatus*, *Agyropeleceus himigymus*, *Sternoptyx diaphana*, *Benthoosema suborbitale*, *Lobianchia dofleini*, *Lampanyctus pusillus*. In the Sargasso Sea area the dominant species are *Diogenichthys atlanticus*, *Ceratoscopelus warmingi*, *Notolychnus valdiviae*, *Pollochthys maui*, *Lepidophanes gaussi*, and *Lampanyctus pusillus*. **Small mesopelagic fish** are not commercially harvested in the Central Atlantic.

Three species are important in the Southeast Atlantic: *Lampanyctodes hectoris*, *Mauroliticus muelleri* and *Diaphus dumerili*. *L. hectoris* sustains a commercial purse seine fishery off South Africa. In the Southwest Atlantic the most important species are *Cyclothone microdon*, *Bathylagus antarcticus*, *Gymnoscopelus braueri*, *Diaphus theta* and *Vinciguerrria nimbaria*.

Biomass of **Small mesopelagic fish** in each oceanic area of the Atlantic was obtained from maps of mesopelagic fish biomass (Gjøsaeter and Kawaguchi, 1980) which were digitized into a spatial database developed by one of us (R. Watson). Figure 2 shows the biomass distribution of mesopelagic fish

generated by applying a rule to the Gjøsæter and Kawaguchi (1980) maps that limits the distribution of mesopelagic fish to a minimum depth of 200 m. P/B was calculated as the mean natural mortality rate estimated for the dominant species in each area (Gjøsæter and Kawaguchi, 1980). Mann (1984) suggested that, for species with an annual life history (e.g. *Valenciennellus* spp.), P/B ratio is in the range of 3 to 5 year⁻¹. For species of the genus *Triphoturus* and *Lympanyctus*, which may live up to 5 years, P/B ratio is in the order of 0.56 year⁻¹. Childress *et al.* (1980) estimated the daily ration of small mesopelagic fish at 0.87 % day⁻¹ (Q/B of 3.175 year⁻¹), and the P/B ratio at 0.987 year⁻¹. Mann (1984) reported estimates of daily feeding ration of adult myctophiids in the order of 4 % of the body weight per day. Likewise, Gorelova (1986) estimates the daily ration of migratory bathylagid fish at 5 %, which corresponds to a Q/B of 18.25 year⁻¹. The difference between Q/B estimated by Gorelova (1986) and Childress *et al.* (1980) are according to the fact that Childress *et al.* (1980) did not account for the time migrating mesopelagic species spend in warmer surface layers of the ocean, where metabolic rates ought to be higher than in colder, deeper waters. In the present models Q/B was set to 18.25 year⁻¹, but both Childress *et al.* (1980) and Gorelova (1986) estimates were used during the model balancing as extremes in the possible range of values for the group. The species feed mainly on copepods and euphausiids. Diet compositions of oceanic mesopelagic fish were obtained from Hopkins and Baird (1977) and from Kinzer (1977). To account for the diel feeding migrations, the proportion of zooplankton in the diet of mesopelagic fish was split between shallow water (90 %) and deep water (10 %) zooplankton groups.

Due to their larger size and differences in life history, the mesopelagic fish *Gempylus serpens* and *Alepsaurus ferox* (found in stomach contents of *T. alalunga*) were grouped into a **Large Mesopelagic fish** group. Both species feed actively on mesopelagic fauna and perform marked diel migrations between the surface and 1000 m (Post 1984). To account for the diel feeding migrations, the proportion of zooplankton in the diet of Large mesopelagic fish was split between shallow water (90%) and deep water (10%) zooplankton groups. The P/B, Q/B and diet of Large Mesopelagic fish were obtained from FishBase assuming a mean temperature of 15 °C. Biomass was left to be estimated by the model, assuming an ectotrophic efficiency of 0.9.

BATHYPELAGIC FISH

To characterize the ecological parameters of bathypelagic fish, biological data were obtained for representative species in distinct size categories. **Large bathypelagic fish** were considered species that reach a maximum length of more than 90 cm. **Medium bathypelagic fish** were species with maximum length between 30 and 90 cm, and **Small bathypelagic fish** represented species reading less than 30 cm. These species were selected based on their occurrence in fisheries landings, the presence in the stomach contents of other species in the model, and data from the literature. The main sources used in this characterization were Marshall (1971), Miya and Nishida (1997), Gorelova (1986), Cowles and Childress (1995), Morales-Nin and Sena-Carvalho (1996), Carrasson and Matallanas (1990), Gartner and Zwerner (1989) and FishBase (www.fishbase.org).

The **Small Bathypelagic fish** are mainly represented by the gonostomatid fish of the genus *Cyclothone* spp. The genus (2 to 7 cm total length) tend to be one of the most abundant components of the bathypelagic fish fauna down to 2500 m (Marshall, 1971; Miya and Nishida, 1997)). Other representative

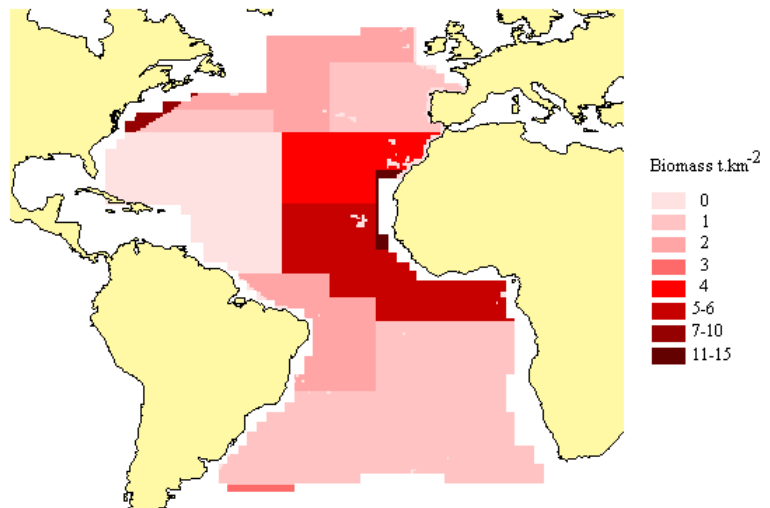


Figure 2. Distribution of small mesopelagic fish biomass, based on Gjøsæter and Kawaguchi (1980) and a rule that limits the distribution to depths > 200 m.

small bathypelagic fish species are *Gonostoma bathyphilum*, *Lampanyctus macdonaldi*, *Scopelogadus beanii*, *Bathylagus nigrubenys*, *Sternoptyx diaphana*, *Argyropelecus olfersi* and *Melanocetus spp.* (the angler fish). Q/B of small bathypelagic fish was estimated at 3.65 year⁻¹, based on a daily ration of 1% estimated by Gorelova (1986) for bathypelagic bathylagids. (Childress *et al.*, 1980) estimated the daily ration of small bathypelagic fish at 0.68 % day⁻¹ (Q/B of 2.48 year⁻¹), and a P/B ratio of 1.042 year⁻¹. The high food conversion efficiency of small bathypelagics (0.42), compared to small epi and mesopelagic fishes, is according to the authors attained with a life history strategy that gives high priority to growth.

The **Medium Bathypelagic fish** were represented by the species *Macroparalepis sp.*, *Serrivomer beanii*, *S. brevidentatus*, *Alepocephalus rostratus*, *Halargyreus johnsonii* and *Psenes pellicidus*. Parameters for the **Large Bathypelagic fish** fauna were based on data for *Eurypharynx pelecoides*, *Aphanopus carbo* and *Brama brama*. P/B and Q/B ratios for medium and large bathypelagic fish were estimated using growth and metabolic rates for *Alepocephalus rostratus* and *Aphanopus carbo*, respectively.

It has been suggested that the biomass of bathypelagic fish is probably 2 orders of magnitude lower than that of mesopelagic fish (Marshall, 1971; Mann, 1984). In the present models the biomass of all three size classes of bathypelagic fish was left to be estimated by the model assuming an ecotrophic efficiency of 0.9. The diet of bathypelagic fish remains unclear, and two possible routes have been suggested (Mann, 1984): the first that bathypelagic fish prey upon migrant bathypelagic organisms that obtain food in the mesopelagic-epipelagic zone (Vinogradov's "ladder of migration"); the other that bathypelagic fish feed mainly upon sinking detritus and carcasses. Both pathways are represented in the present models based on qualitative and quantitative diet information available in FishBase about the dominant species in each size class.

BATHYDEMERSAL FISH

The bathydemersal fish fauna is characteristically more diverse and abundant than that of the bathypelagic zone. By the early 1990s Haedrich and Merret (1992) reported that there were at least 308 species of deep demersal fish known in the Atlantic. The group includes important fishery resources, such as the orange roughy *Hoplostethus atlanticus*, the patagonian toothfish *Dissostichus eleginoides*, grenadiers and raitails (Macrouridae), hagfish *Eptatretus spp.*, and many other shelf demersal resources that extend their distribution range towards the continental slope (Table 5). One of the reasons for the larger biomass at the bottom of the ocean seems to be the higher availability of food from the epipelagic and mesopelagic zone that sinks and accumulates in the deep ocean (Mann, 1984).

The most comprehensive studies on bathydemersal fish fauna are in the North Atlantic. Based on biomass and size composition data on deep demersal fishes from the Porcupine Seabight and the Madeira Abyssal plain in the eastern North Atlantic (40°-30°N), Haedrich and Merret (1992) drew a number of conclusions relevant to the present models of the Atlantic oceanic ecosystems. The authors recognized five depth zones with relative integrity in topography and species diversity: the upper slope (200–600 m, which correspond to the upper mesopelagic zone), the middle slope (600–1000 m, lower mesopelagic), lower slope (1000–2000 m, upper bathypelagic), upper rise (2000–3000 m, deep bathypelagic), lower rise/abyss (3000–4600 m, deeper bathypelagic). The dominant families across the different zones and sampling gears were Macrouridae, Alepocephalidae, Moridae, and Synphobranchidae. For each bathymetric zone, Haedrich and Merret (1992) provide estimates of the mean biomass, fish size spectrum, and production/biomass ratios. Based on this information the author suggested different feeding strategies of deep demersal fish communities. Smaller fish predominate in the upper slopes, where they feed mainly on vertically migrating animals from the upper mesopelagic. The largest fish occur between the lower slope and upper rise, where foraging/scavenging is the most common feeding mode. Deeper, the authors found a more fixed size composition reflecting two feeding modes, foraging/scavenging performed by larger fish, and the smaller species which depend on small particles within the benthic layer. Re-expressing the size spectra data as biomass spectra allowed Haedrich and Merret (1992) to differentiate two zones based on the relative contribution of different sizes of fish to the total energy flow in the deep sea: the continental slope depths (200-2000 m) and the continental rise/abyss depths (2000-5400 m). Bathydemersal fish biomass in the slope ranges from 0.64 to 3.10 t·km⁻² and in the abyss zone from 0.05 to 1.81 t·km⁻² (Haedrich and Merret, 1992).

Information about the biomass and depth distribution of bathydemersal fish fauna for other regions of the Atlantic is scarce. A similar pattern of zonation of megabenthic fauna (invertebrates and fish) was found by Haedrich *et al.* (1980) for the Northwest Atlantic. In this area, species abundance and diversity tend to be greatest at the transition from lower continental slope to upper rise, with the lowest values at greatest depths. Haedrich and Rowe (1977) estimated that the biomass of demersal fish at depths 500-2500 m in the Western Atlantic ranged from 5.78 t·km⁻² to less than 1.0 t·km⁻². Martini (1998) reports hagfish *Myxine glutinosa* densities of up to 500,000 ind·km⁻² for the Gulf of Maine (600-800 m). Based on photographs and trawling samples, Christiansen and Thiel (1992) showed that macrourids and synphobranchids (deep-sea eels) dominated the biomass of benthic megafauna in the mid-northeastern Atlantic ocean, with a mean biomass of 4.68 t·km⁻².

Merret and Marshall (1981) analyzed the composition and relative abundance of demersal fish off northwest Africa (8–27°N) at depths between 200-6000 m. In this area, the authors found that density of fish declines exponentially to about 2000 m, where the density is two orders of magnitude lower than at 200 m. From 2000 m to the deepest parts of the ocean, density declines more slowly. Comparing abundance indexes from other areas, Merret and Marshall (1981) concluded that the biomass of slope fish off west Africa is higher than that observed in more temperate areas of the North Atlantic. The authors noticed other important differences between west Africa and North Atlantic oceanic areas (e.g., higher diversity and smaller mean size of fish off Africa) which were attributed to the greater productivity caused by the upwelling along the African coast. This environmental setting supports a more abundant and diverse fish fauna, while favouring species of small mean size with less need for nutrient storage.

Information on bathydemersal fish fauna in the southern Atlantic ocean is based on the paper by Pakhorukov (2001). The author reports the list of dominant species and an estimate of the mean fish density at 2015 m over the Rio Grande Plateau, Southwest Atlantic. The most abundant species were *Bathygadus* sp., *Coelorinchus* sp., *Coryphaenoides* sp., *Hymenocephalus* sp., *Aldrovandia* spp., *Chaunax suttkusi*, *Epigonus denticulatus*, *Etmopterus* spp., and *Trachyscorpia capensis*. The average fish density in the area was 3.91 specimens/1000 m⁻². Assuming an average individual weight of 1000 g, this represents ca. 3.91 t·km⁻².

Summarizing the available data on bathydemersal fauna, Mann (1984) concluded that the fish biomass near the floor of the ocean is close to 1 t·km⁻² on the abyssal plains and to about 5 t·km⁻² on the continental slopes. The brief review presented above corroborates Mann's conclusion. The lack of more detailed assessments of the abundance of demersal fish fauna in the central and southern Atlantic precludes, however, a more accurate representation of the differences among these systems.

In the present models of the Atlantic oceanic ecosystems, four groups of bathydemersal fish were defined, based on size and depth zonation proposed by Haedrich and Merret (1992) for the North Atlantic: the **Large and Small (<1000 g) Bathydemersal fish of the continental slope (200-2000 m) and of the continental rise/abyss zone (>2000 m)**. A list of dominant species in each functional group and each oceanic area were obtained from Merret and Marshall (1981), Haedrich *et al.* (1980), Pakhorukov (2001) and Haedrich and Merrett (1988).

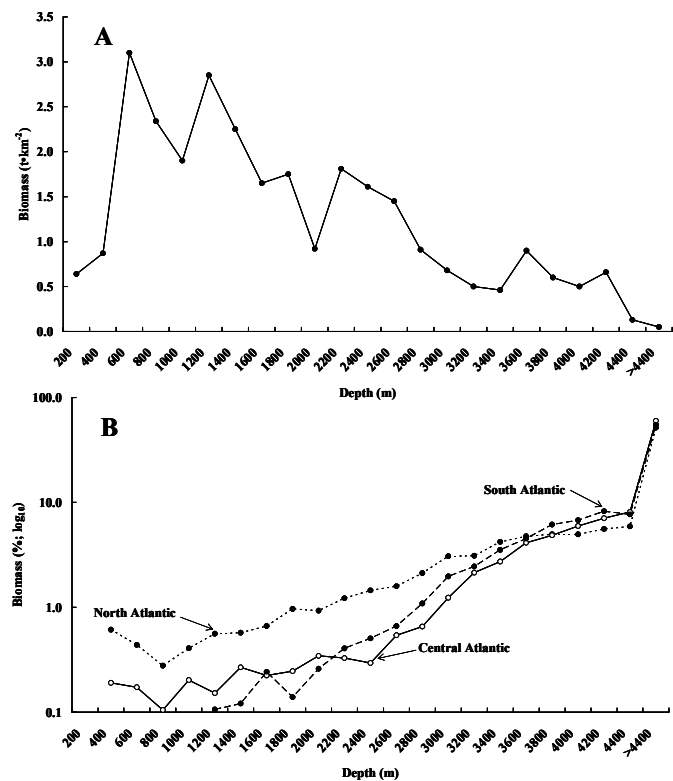


Figure 3. A. Biomass distribution by depth based on Haedrich and Merret (1992); B. Biomass as percentage of the total area of bathymetric zones in each basin.

Biomass and size spectrum data by bathymetric zone for the North Atlantic (Haedrich and Merret, 1992) were used to estimate the biomass of each functional group in each oceanic basin. The first step was to calculate, based on Haedrich's (1992) data, the percentage of the total biomass by depth zone composed of small and large bathydemersal fish (Table 9). Second, the total biomass in each oceanic area was computed by multiplying the biomass depth profile proposed by Haedrich (1992) by the total area of each bathymetric zone in each oceanic basin (Figure 3). Then, for each oceanic area, the biomass of small and large bathydemersal fish was calculated by applying the percentages computed in the first step. Results are shown in Table 9.

Table 9. Estimated biomass of small and large bathydemersal fish in the slope (200-2000 m) and abyss (>2000 m) zones of the Atlantic oceanic ecosystems.

Depth zone Group	Percent total biomass		North Atlantic		Central Atlantic		South Atlantic	
	Small (<1000g)	Large (>1000 g)	Small (t·km ⁻²)	Large (t·km ⁻²)	Small (t·km ⁻²)	Large (t·km ⁻²)	Small (t·km ⁻²)	Large (t·km ⁻²)
Slope	45.83	54.17	0.045	0.053	0.016	0.019	0.008	0.009
Rise/Abyss	39.04	60.96	0.121	0.190	0.093	0.146	0.109	0.171

As for bathypelagic fish, lower metabolic rates are expected for bathydemersal fish as a consequence of biological adaptations to life in the deep sea. The oxygen consumption of a rattail (*Coryphoenoides* sp.) at 1230 m is, for instance, two orders of magnitude lower than that of a cod of similar weight and measured at a similar temperature (Mann, 1984). Macpherson (1985) estimated the daily ration of fish in the upper continental shelf and slope off west Africa between 0.5 and 2 % of the wet body weight per day (Q/B between 1.82 and 7.3 year⁻¹). In the present models we used the average gross efficiency of 0.55 estimated for bathydemersal and bathypelagic fish to calculate Q/B from P/Bs. P/B ratios were estimated applying Pauly's (1980) empirical equation for the dominant species in each functional group, with mean temperatures between 4 and 11°C.

The diet of bathydemersal fish seems to be made of three main sources (Mann, 1984): large particles on which they scavenge, benthic epifauna and infauna. Mann (1984) suggested that benthic infauna is probably the least important among the food sources. Pelagic prey, especially vertically migrating fish and zooplankton, can be important in bathydemersal fish diets. Haedrich and Merret (1992) showed that, in the Porcupine Seabight in the North Atlantic, 35 % of the demersal fish species fed on pelagic prey, 52 % fed on a mixed diet, and that only 13 % of depend on benthos for food. Diet for slope species were obtained from Santos and Borges (2001), Drazen et al. (2001), Jakobsdóttir (2001), Martin and Christiansen (1997) and Gordon and Gordon (1984). Complementary information was obtained from FishBase (www.fishbase.org). Distinctions between the diet of small and large bathydemersal fish were based on species-specific diets (when available) or on size specific diets of the same species. For instance, it has been noted for many macrourid species that the smaller, juveniles tend to feed predominantly on benthic organisms, while larger individuals consume increasingly larger, more pelagic prey such as fish, squid and large crustaceans (Merrett and Haedrich, 1997). This ontogenetic shift in diet is explained by both an increase in scavenging for large food particles falling from the epipelagic and mesopelagic zones (Drazen et al., 2001) and by the increase in vertical migration with size (Haedrich and Henderson, 1974). For instance, Percy (1991) reported the capture of bathydemersal macrourid fish in the water column ca. 900 m off the bottom. Complementary diet information was obtained from the description of the diet of dominant bathydemersal fish fauna off west Africa (Merret and Marshall, 1981).

CEPHALOPODS

Cephalopods were divided in three functional groups, representing distinct ecological niches. The species of octopus (Octopoda) and cuttlefish (Sepioidea) were grouped in a **Benthic cephalopods** group. Although some species of Octopoda are also bathypelagic (Voss, 1988), few species have been caught between 1500 m from the surface and 100 from the bottom (Clarke, 1996). The benthic deep-sea octopuses live just above the bottom of the ocean and have a limited ability to swim. They are classified in the suborders Cirrata and Incirrata and include species of the families Cirroteuthidae, Stauroteuthidae, Opisthoteuthidae, Bathypolypodinae, Pareledoninae, and Granelledoninae (Voss, 1988). Of the 77 species of deep-water octopods, 43% occur in the tropical and warm temperate regions of the ocean (Voss, 1988). This author suggested that there is a high correlation between species richness and primary productivity, with few species in less productive areas.

The squids (Teuthoidea) were split in two functional groups: **Small** and **Large squids**. The representation of two groups of squids is supported by differences in feeding habits, since smaller/juvenile squids feed preferentially on zooplankton and macrocrustaceans while larger/adult squids feed mainly on fish (Nixon, 1987). Cannibalism is common for both small and large squids (Nixon, 1987). Also, as suggested by Pauly *et al.* (1998), the split between small and large squids would separate families such as Gonatidae (ML<50 cm), Onychoteuthidae and Architeuthidae (ML>50 cm), the latter two important food sources of toothed whales. According to Arnold (1979) almost all oegopsid families (Ommastrephidae, Onychoteuthidae, Gonatidae, Architeuthidae and Enoploteuthidae) occur in oceanic waters and occupy epipelagic, mesopelagic and bathypelagic zones. The species of Ommastrephidae and Onychoteuthidae are known to seasonally migrate horizontally between feeding and spawning areas on the shelf and off-shore deeper waters (Clarke, 1996). Some species are adapted to live in the surface waters (e.g. *Onychia* spp. and *Cranchia* spp), while other spend their entire life at depths greater than 500 m (Clarke, 1996). The pelagic cephalopod assemblage in the epi-mesopelagic zone (0-1000 m) of the Eastern Gulf of Mexico has been shown to be very diverse (47 species were identified), with a biomass estimated between 10.1 and 42.0 kg·km⁻² (Passarella and Hopkins, 1991). The most abundant species were from the families Enoploteuthidae and Cranchiidae. Most of the species sampled in this area showed a diel vertical migration pattern occurring in the upper 200 m at night and staying 100 and 400 m during the day (Passarella and Hopkins, 1991). In the Gulf stream system, *Illex* sp. is the most abundant species of pelagic cephalopod, followed by species of the Enoploteuthidae and Cranchiidae families (Dawe and Stephen, 1988). These species also have a strong vertical migratory behavior, becoming concentrated in the surface layers during the nights and diving deeper during the day (Dawe and Stephen, 1988). The ommastrephid squids represent important fisheries resources. In the Atlantic ocean five species are particularly abundant and some of them support important fisheries since the 1970s (Arnold, 1979): *Illex illecebrosus* in the slope waters of Northwest Atlantic, *I. coindeti* in the Gulf of Guinea, *I. argentinus* in the Southwest Atlantic, *Ommastrephes calori* in the Northeastern coast of the Atlantic, *O. pteropus* in the South Atlantic, and *Todarodes sagittatus* in the whole eastern Atlantic. These oceanic squids approach the surface at night when they are susceptible to jigging fisheries.

Characteristic of squid stocks is the large variations in abundance caused by the combined effect of fluctuations in year-class strength and a short life cycle. Direct estimates of population biomasses exists for only a few commercially exploited species, most of them occurring on the shelf waters (Boyle and Boletzky, 1996). For instance, Lange and Sissenwine (1983) estimated that the minimum stock biomass of the exploitable population of *I. illecebrosus* in the Northwest Atlantic during the 1970s ranged from 3,400 t to 264,000 t, illustrating the marked variability of the stock. Biomass assessment of oceanic species is normally hampered by their difficult sampling and complicated life cycles and distribution patterns (Clarke, 1987; Piatkowski *et al.*, 2001). The few available estimates of oceanic squid abundance were made indirectly, based on the estimated consumption by top predators, such as sperm whales, seals and birds. Arnold (1979), for instance, reports results from studies in which the biomass of oceanic squid resources is estimated at between 8 and 60 times greater than that of shelf resources. (Clarke, 1987) estimated the amount of squids consumed by top predators in the Antarctic Sea at ca. 35 Mt·year⁻¹. Using the same rationale on a global scale, the author estimated that biomass of squids required to sustain the world population of sperm whales annually is about 100 million t. Similar studies in the North Atlantic estimated that over 2.4 Mt of cephalopods are consumed by sperm whales (Santos *et al.*, 2001) and ca. 103,000 t are consumed by seabirds in the Eastern North Atlantic (Furness, 1994). Following the same logic, in the models of the Atlantic oceanic ecosystem we opted to leave the biomass of cephalopods to be estimated by the model based on consumption requirements of their predators and on an ecotrophic efficiency of 0.9.

Most squids have a fast growth and short life cycles, dying after spawning normally when they are between 1 and 3 year olds (Arnold 1979). Species of small (*I. illecebrosus* and *Todarodes* sp.) and large (*Dosidicus gigas*) squids have an estimated life span of 1 year (Mangold, 1987; Arguelles *et al.*, 2002). On the other hand, species of deep sea octopods grow at slower rates. For instance, *Bathypolypus arcticus* have a life span of at least 4 years (Mangold, 1987). Caddy (1983) reports estimated natural mortality rates for *Illex* spp. in the range between 1 and 1.5 year⁻¹. Considering that the average life span of small and large squids is 1 year, and assuming that 99 % of squids in a population die after 1 year with an exponential decrease in numbers, the natural mortality rate is estimated at 4.6 year⁻¹. This value was therefore accepted as an estimate of the P/B ratio for small and large squids. Applying the same reasoning for benthic cephalopods (life span of 4 years), the P/B ratio for the group is estimated at 1.15 year⁻¹.

O'Dor and Wells (1987) reported gross efficiency and daily feeding rates for benthic and pelagic cephalopods. For the benthic cephalopods (*Octopus* spp., *Eledone* sp. and *Sepia* sp.) the daily feeding rates vary among species and temperatures between 1.3 and 8.8 % of the body weight, and the gross conversion efficiency between 43 and 69 %. For pelagic cephalopods the daily feeding rate is estimated between 3.5 and 10 % (depending on the temperature) and the gross efficiency at 29 % (Amaratunga, 1983; O'Dor and Wells, 1987). The high food conversion efficiency of cephalopods is in part explained by the ability most species have of avoiding metabolic waste by not ingesting, for instance, the hard crustacean exoskeleton (Boucher-Rodoni *et al.*, 1987), and also by a highly efficient (up to 70 %) incorporation of food into the body tissues (Nixon, 1987). The Q/B of benthic cephalopods was estimated by the model from P/B and a gross conversion efficiency of 0.5 (50 %). The Q/B of small and large squids was estimated at 36.5 year⁻¹, based on a daily ration of 10 % of body weight.

According to Arnold (1979) squids are active predators and occupy the same trophic level as mackerel. As a general rule, squids feed on macrozooplankton when young and shift the diet to small fish when adult. For instance the diet of *I. illecebrosus* on the Grand Banks shift with as the species grow, the small individuals feeding mostly on inshore crustaceans and the larger ones on capelin, redfish, cod and haddock (Squires, 1957; Arnold, 1979). Some level of cannibalism is also evident among ommastrephid squids (Arnold, 1979). Information about cephalopods diets was extracted from Nixon (1987). The author provides diet information (mostly qualitative data) for species representative of each cephalopod family, which were turned into diet matrix for the three functional groups. As a general rule it was considered that fish and squids increase in importance for Large squids, and Benthic cephalopods have a diet dominated by macrobenthic and meiobenthic organisms.

BENTHIC INVERTEBRATES

Four benthic functional groups are represented in the models: **Megabenthos**, **Macrobenthos**, metazoan **Meiobenthos** and **Heterotrophic bacteria**. The megabenthos has as important components the mobile epifauna, which is dominated by amphipods (e.g. *Lysianassidae*), shrimps and other decapods, coelenterates and echinoderms (Hessler *et al.*, 1978; Dahl, 1979). Meiobenthos are normally organisms with less than 0.5 mm in length that live interstitially in the sediment ((Mackinson *et al.*, *in press*). The distinction between macrofauna and meiofauna is made based on the mesh sieves used by benthic ecologists. For instance, benthic meiofauna is refereed to as the animals that pass through 500 um mesh sieves and are retained in 37 to 44 um mesh openings. The meiofauna is normally dominated by nematods, harpacticoids, ostracods, turbellarians, kinorhynch, and gastrotrichs (Rowe, 1981), although foraminifers may become important with depth (Gooday *et al.*, 1992). Bivalves are the dominant organisms in the deep-sea benthic macrofauna in the northeastern Atlantic (Gage, 1992), which may also include polychaetes, small (> 0.5 mm but < 20 mm) crustaceans and small echinoderms. Most of the biomass of the benthic macrofauna is found along the margins of the continental shelves. The biomass in the abyssal plains under the central open gyres is about 1 % of the biomass of the continental shelves and slopes (Rowe, 1981).

Rowe (1971) demonstrated that the biomass of the benthic macrofauna follows a negative exponential relationship with depth of the type

$$\text{Biomass} = a \cdot e^{-b \cdot \text{Depth}} \dots\dots\dots 11)$$

where *a* is a constant directly related to surface primary productivity. According to the author, each oceanic basin has a characteristic regression influenced by the magnitude of primary production and the magnitude of change of primary production from shallow to deep offshore waters. Using the available data from Pacific and Atlantic oceanic basins, Rowen (1981) re-expressed the above relationship in the form of a linear regression

$$\text{Biomass (log}_{10} \text{ mg wet weight} \cdot \text{m}^{-2}) = 3.86 - 0.0003 \cdot \text{Depth (m)} \dots\dots\dots 12)$$

This equation was used here to map the predicted macrobenthic biomass by depth and to calculate the mean biomass in each oceanic province of the Atlantic. The same approach was used to compute meiobenthos biomass based on an equation proposed by (Tietjen, 1992). Tietjen (1992) demonstrated similar relationship between metazoan meiobenthos and depth for the Atlantic Ocean, where biomass decreases by 56 % from 500-2000 m and reaches, at 5000 m, 10 % of the value measured at 500 m.

According to the author the decline in meiobenthos biomass with depth is expressed by a logarithmic relationship of the type

$$\text{Biomass (mgC}\cdot\text{m}^{-2}) = 1268 - 143.8 \cdot \log_e \text{Depth (m)} \dots\dots\dots 13)$$

To convert biomass from carbon to wet weight a conversion factor of 0.06 gC = 1 g wet weight was used (Walsh, 1981). Figures 4 and 5 show the predicted biomass distribution of macrobenthos and meiobenthos in the oceanic provinces of the Atlantic. As depth was the only dependent variable for both cases, the maps mirror the bathymetric profiles of each basin. More accurate distribution maps of benthos biomass will need other set of dependent variables, mainly surface primary productivity, which has been proposed as the main factor controlling the biomass of benthos in the deep sea (Rowe, 1971).

Tietjen (1992) also suggested that the biomass ratios between the different benthic size groups vary little across oceanic basins (depths between 450 and 5000 m). Bacterial biomass is normally one to two orders of magnitude greater than meiofaunal biomass (biomass ratio bacteria/meiobenthos = 22.9), which tends to be within an order of magnitude of

Table 10. Biomass (t·km⁻²) of benthic functional groups in the oceanic ecosystem of the Atlantic.

	North Atlantic	Central Atlantic	South Atlantic
Megabenthos ^c	0.493	0.394	0.429
Macrobenthos ^a	0.545	0.369	0.414
Meiobenthos ^b	1.234	0.984	1.073
Bacteria ^c	28.167	22.543	24.562

^a, based on Rowe (1981); ^b, based on Tietjen (1992); ^c, calculated using meiobenthos biomass and the biomass ratios proposed by Tietjen (1992).

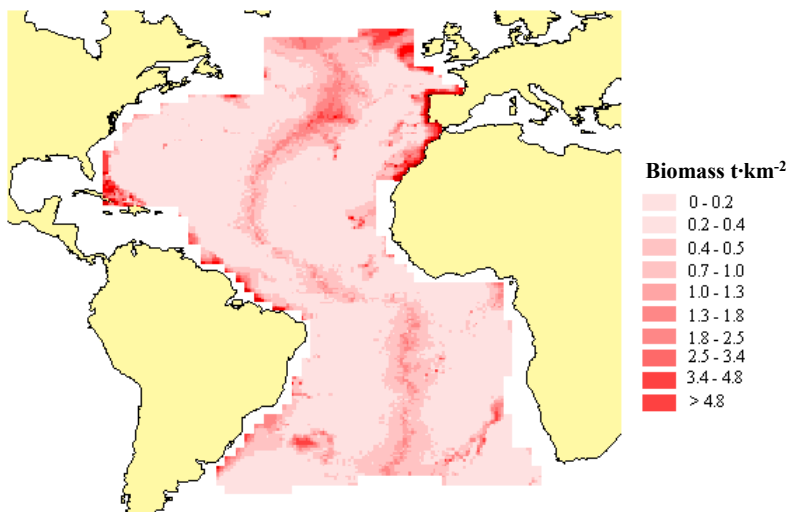


Figure 4. Biomass distribution of Macrobenthos as predicted by the relationship between biomass and depth of Rowen (1981).

macrofaunal and invertebrate megabenthic biomass (biomass ratio megabenthos/meiobenthos = 0.4). Applying these ratios to the average biomass of meiobenthos (estimated using the procedure explained above), it was then possible to calculate the biomass of other benthic functional groups for each oceanic area of the Atlantic (Table 10). These values are within the same order of magnitude of other direct estimates of benthic biomass for the Atlantic reported in the literature. For instance, the estimated biomass of benthic macrofauna in the northeastern Atlantic (depths between 2,100 and 2,500 m) ranged from 1.3 to 2.67 t·km⁻² (Gage, 1992; Mahaut *et al.*, 1995). Mahaut *et al.* (1995) estimated the biomass of

megabenthos and meiobenthos in the Northeast Atlantic at 1.65 and 0.3 t·km⁻², respectively. (Christiansen and Thiel, 1992) estimated a mean biomass of benthic megafauna of 6.5 t·km⁻² in the mid-Northeast Atlantic (depth 2837 to 5806 m). As for bacteria, Deming and Yager (1992) demonstrated that their biomass decreases logarithmically with depth, from values as high as 6000 mgC·m⁻² (ca. 100 t·km⁻²) in the shallow seas to ca. 10 mgC·m⁻² (0.166 t·km⁻²) in the deep sea. According to Lochte (1991) the bulk (75 %) of the deep sea bacterial biomass occur in the sediment, compared to 15 % in the surface water down to 100 m, and 10 % in the meso-bathypelagic zone.

The metabolic rates of benthic communities in the deep sea tend towards the same level as the ones measured at the same temperature in shallow environments (Mahault *et al.*, 1995). Likewise, bacterial mineralization and growth rates in the deep sea tend to be similar to those measured in shallow water environments (Deming, 1992; Mahault *et al.*, 1995). Therefore, in the present models P/B and Q/B ratios of bacteria and benthic communities were considered similar to the ones reported for other cold water environments. Longhurst and Pauly (1987) report P/B estimates for

benthic communities in the Bristol Channel and Celtic Sea ranging from 0.56 year⁻¹ for communities dominated by bivalves to 1.28 year⁻¹ for communities with many fast-growing polychaetes and small bivalves. P/B ratio of benthic macrofauna in the northeastern Atlantic (2500 m) was estimated at 0.98 year⁻¹ (Gage, 1992). The P/B of benthic communities estimated for the Eastern Bering Sea (Trites *et al.*, 1999) and Southern B.C shelf (Jarre-Teichmann and Guenette 1996) ranged from 0.4 to 1.8 year⁻¹ for megabenthos, from 0.7 to 1.3 year⁻¹ for macrobenthos, and from 1.5 to 3 year⁻¹ for meiobenthos. In the same models, the estimated Q/B ratios ranged from 4.4 to 9 year⁻¹ for megabenthos, from 7.7 to 12 year⁻¹ for macrobenthos, and from 12 to 33.3 year⁻¹ for meiobenthos. Mid-range values for both parameters were used in the oceanic model of the Atlantic (Tables 2-4). The P/B ratio of bacteria (18.45 year⁻¹) was assumed the same as the value estimated by (Polovina, 1996) for the Alaska Gyre model. Q/B was estimated from P/B assuming a gross food conversion efficiency of approximately 60 %. Diets of benthic functional groups were also considered similar to the ones estimated for the ecosystem models referred to above.

ZOOPLANKTON

To represent differences in size and in the vertical distribution of zooplankton biomass, four zooplankton functional groups were defined, representing **Small and Large zooplankton of shallow waters** (0-1000 m) **and deep waters** (>1000 m). As such, the model provides better ecological constraints to the predicted biomass of other functional groups in each bathymetric zone. Following (Vinogradov, 1970), the **Small Zooplankton** group included organisms of the micro-mesoplankton, of sizes up to 3-4 cm. Included in the **Large Zooplankton** groups are organisms of the macroplankton, of sizes larger than 3-4 cm, consisting mainly of decapods, large euphasiids, mysids and gelatinous plankton.

Zooplankton biomass was obtained from the world atlas of surface (0-100 m) zooplankton biomass (FAO, 1981) and from depth profiles of zooplankton abundance for the Atlantic ocean (Vinogradov, 1970; Longhurst and Williams, 1979; Koppelman and Weikert, 1992; Vinogradov *et al.*, 1998; Dadou *et al.*, 2001). Vinogradov (1970) showed that the biomass of zooplankton decrease exponentially with depth, and that each area of the ocean can be characterized by a regression equation with different constants for initial abundance at the surface and the rate of decrease with depth. Zooplankton profiles in most low latitude tropical regions follows a pattern in which a near surface layer of high abundance is separated by a stratum of rapidly decreasing abundance (planktocline) from the deeper zone of relatively uniform low abundance (Longhurst and Williams, 1979). In contrast, in some higher latitude regions, particularly in the periphery of the central waters close to the slope zone, many authors have found a pattern of marked enrichment of zooplankton at depths of 400 to 1000 m (Vinogradov, 1970; Longhurst and Williams, 1979; Koppelman and Weikert, 1992; Vinogradov *et al.*, 1998). The processes behind these patterns in the vertical distribution of zooplankton varies, and have been associated to the advection of plankton-rich, subarctic intermediate waters (Vinogradov, 1970) and to mechanism of diapausing and zooplankton feeding strategies in latitudes with deep winter mixing (Longhurst, 1998). Vinogradov *et al.* (1998)

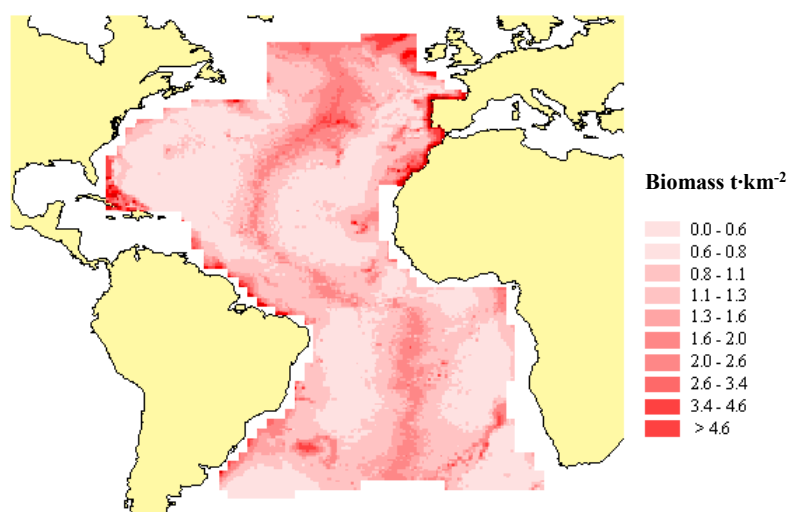


Figure 5. Biomass distribution of Meiobenthos as predicted by the relationship between biomass and depth of Tietjen (1992).

showed, for instance, that the deep concentrations of zooplankton in the frontal zone between the Labrador and Gulf Stream currents consist almost exclusively of macroplankton carnivores and scavengers, mostly shrimps, which rely on the plankton dying off within the frontal zone as source of food. In the North Atlantic drift region, the deep zooplankton layer is a typical winter feature; as summer progresses, the zooplankton profiles approach the vertical patterns found in tropical regions (Longhurst, 1998). As a general rule, zooplankton biomass below 1000 m follows a pattern of exponential decrease with depth (Koppelman, 1992).

To integrate zooplankton biomass over depth in the oceanic regions of the Atlantic, the following procedure was used. Each ½ degree square in the Atlantic was assigned a value for the surface zooplankton biomass based on the atlas of zooplankton biomass distribution redraw from FAO (1981). The map produced by FAO (1981) categorizes zooplankton biomass in four classes, and in order to obtain absolute biomass values for each spatial cell, representative biomass values within each class had to be selected. Thus an average biomass of 25 mg·m⁻³ was elected for the <50 mg·m⁻³ class; for the 51–200 mg·m⁻³ class a value of 125 mg·m⁻³; for the 201–500 mg·m⁻³ class a value of 350 mg·m⁻³, and for the >500 mg·m⁻³ class a value of 500 mg·m⁻³. The latter was chosen based on published estimates of zooplankton biomass in highly productive regions of the Atlantic. Three studies support the choice for the minimum limit in the higher biomass class proposed by FAO (1981). For the Benguela system, Armstrong (1987) estimated zooplankton biomass for the upper 100 m between 0.54 and 3.76 g dry weight·m⁻². Taking the maximum value reported by Armstrong *et al.* (1987), and converting it to wet weight (or displacement volume) using the equation proposed by Bode *et al.* (1998), the wet weight biomass is estimated at 403 mg·m⁻³. Also, Bode *et al.* (1998) reports zooplankton biomass values in a coastal upwelling system off Spain between 33.6 and 1,169 mg wet weight·m⁻³. Finally, Vinogradov *et al.* (1998) estimated an average depth (0–200 m) integrated zooplankton biomass of 64.7 g wet weight·m⁻² in a productive boreal region of the Northwest Atlantic. That is equivalent to an average zooplankton biomass of 323 mg·m⁻³. A biomass of 500 mg·m⁻³ was therefore considered a reasonably good reference value for the expected zooplankton biomass in the highly productive zones of the ocean.

Each biogeochemical provinces was assigned a vertical profile of zooplankton biomass distribution obtained by fitting an exponential function (Biomass = a·Depth^{-b}) to data drawn from the literature (Figure 6; Table 11). For the North Atlantic Drift province a profile was constructed to represent the occurrence of below surface maximum in zooplankton biomass. In this case the exponential mode was fitted only to data below 600 m. Table 11 presents the best fit parameters for each province. The profiles present the predicted change in zooplankton biomass relative to the average biomass in the 0–100 m layer. The depth integrated zooplankton biomass (t·km⁻²) for each biogeochemical province and for each depth strata (0–1000 m, and >1000 m) was then calculated using a spatial database (FishMap; R. Watson, *the Sea Around Us Project*, Fisheries Centre, UBC) that integrates surface biomass values and the vertical profiles. Figures 7 and 8 show the predicted biomass

Table 11. Parameters of exponential function ($B_{rel.} = a \cdot \text{Depth}^{-b}$) fitted to data on zooplankton biomass with depth for different biogeochemical provinces of the Atlantic: GFST, Gulf Stream (Vinogradov, 1970); NADR, North Atlantic Drift (Koppleman and Wiekert, 1992); NAS (E and W), North Atlantic Subtropical Gyral (Vinogradov, 1970); CNRY, Eastern Canary Coastal (Vinogradov, 1970); Trade Wind Biome (Vinogradov, 1970; Dadou *et al.*, 2001), applied to provinces NATR, WTRA, ETRA and also the south Atlantic Westerly province (SATL).

Parameters	GFST	NADR	NAS (E and W)	CNRY	Trade Wind Biome
a	29.203	37.916	204.336	71.545	349.513
b	0.729	0.814	1.149	0.932	1.278

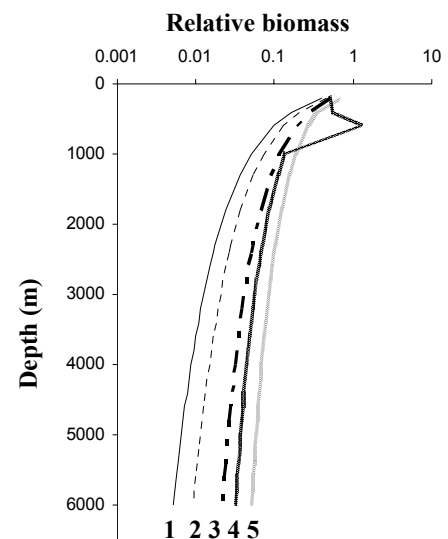


Figure 6. Vertical profiles of zooplankton biomass relative to the biomass in the surface layer (0–100 m) in each biogeochemical provinces: 1 (Trade Wind Provinces); 2 (CNRY); 3 (NASE and NASW); 4 (NADR); and 5 (GFST). See text and Table 11 for details about data sources and parameters.

Table 12. Percentage of macrozooplankton in the total zooplankton biomass at depth in the equatorial and tropical zones of the Pacific ocean (source Vinogradov, 1970).

Depth range (m)	Equatorial zone 12°N-12°S	Tropical zone 40°N-12°N; 12°S-40°S
0 – 50	0.0	0.0
50 – 100	22.5	0.0
100 – 200	1.6	0.0
200 – 500	22.3	10.5
500 – 1000	34.2	25.0
1000 – 2000	74.0	14.2
2000 – 4000	8.0	0.0

distribution of shallow and deep zooplankton groups.

Vinogradov (1970) noted that, contrary to mesozooplankton, the macrozooplankton organisms occupy comparatively narrower vertical ranges in the deep waters, have an irregular distribution, and do not show a steady decrease in biomass with depth. The author suggests a pattern of vertical distribution in which macrozooplankton is mostly concentrated in middepth layers of the ocean, and occur in very low numbers below 2000 m. (Blackburn 1977) showed similar results for the tropical Pacific. The author estimates that macrozooplankton is less than 4 % of the mesoplankton biomass in the upper 200 m, and becomes more important in deeper layers of the ocean. Table 12 shows the proportion of the total zooplankton biomass by depth made of macrozooplankton in the tropical and equatorial zones of the Pacific according to Vinogradov (1970). These proportions are used here to divide the total zooplankton biomass between small and large zooplankton by depth.

Average proportions of large and small zooplankton in each depth stratum in each area of the Atlantic were calculated based on the proportions shown in Table 12 and on the vertical profiles of zooplankton biomass of each province (Table 11, Figure 6). That is, the proportions of macrozooplankton in the layers of 0-1000 m and >1000 m in each oceanic province were calculated as the average proportions reported by Vinogradov (1970), weighted by the expected biomass at depth estimated with the vertical profiles of each province. Vinogradov's equatorial data was applied to the Central Atlantic provinces, while the tropical data were applied to the Southern and Northern Atlantic provinces. Finally, to obtain average proportions for the modelled areas, the proportion of macrozooplankton by depth and province was weighted by the total area of the provinces in each area of the Atlantic. Results for each oceanic area of the Atlantic are shown in Table 13. The

Table 13. Proportion of large zooplankton (macrozooplankton) by depth in the Atlantic.

Depth range (m)	North Atlantic	Central Atlantic	South Atlantic
0-1000	0.059	0.186	0.032
>1000	0.029	0.239	0.034

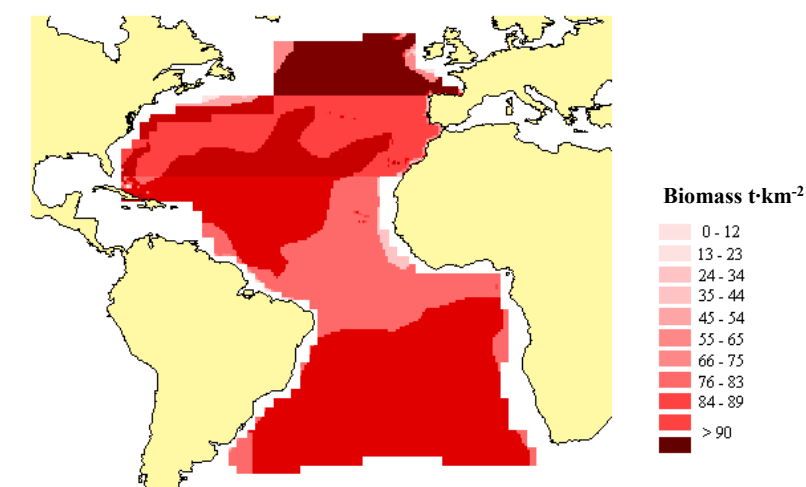


Figure 7. Distribution of zooplankton biomass between 0 and 1000 m depth.

estimated biomass of each zooplankton functional group is shown in Tables 2 to 4.

Longhurst and Pauly (1987) report daily turnover rates of mesozooplankton in tropical Atlantic between 0.15 and 0.62. Assuming a daily turnover rate of 0.3, P/B of Small zooplankton is estimated at 109 year⁻¹, which is considerably higher than the values used in other ecosystem models (Browder, 1993; Venier and Pauly, 1997; Trites *et al.*, 1999; Cox *et al.*, 2002; Mackinson *et al.*, *in press*). Alternatively, in the present models the P/B and Q/B ratios for small and large zooplankton were assumed the same as the values estimated for mesozooplankton and carnivorous zooplankton, respectively, in the Gulf of Mexico (Mackinson *et al.*, *in press*). For small zooplankton P/B was set to 17.3 year⁻¹ and Q/B to 57 year⁻¹. For large zooplankton P/B was set to 8.7 year⁻¹ and Q/B to 29 year⁻¹.

Most species of macrozooplankton are carnivorous, feeding on mesozooplankton organisms (Vinogradov, 1970), whereas a mix of predators, herbivores and detritivores is characteristic of the mesoplankton groups (Longhurst, 1998). Longhurst (1998) estimated the contribution of each mesozooplankton trophic mode in the Trade and Westerlies biomes (Table 14), which are used here to define the diet of Small zooplankton. To represent Vinogradov's "ladder of migration" the diet of deepwater zooplankton was split between shallow (30 %) and deep water (70 %) small zooplankton. The diet of deep water small zooplankton was divided between detritus and shallow and deep water small zooplankton.

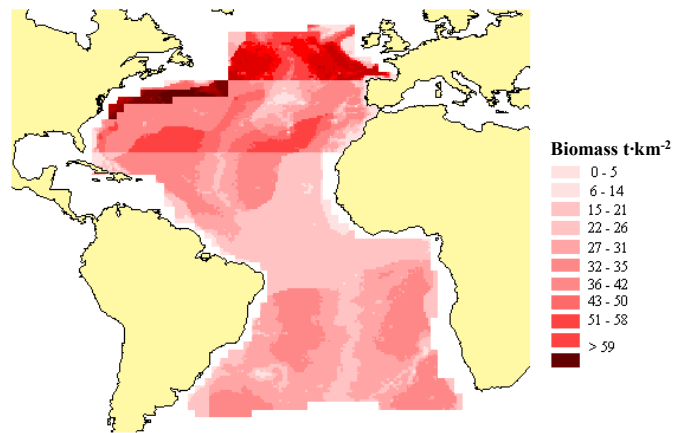


Figure 8. Distribution of zooplankton biomass below 1000 m depth.

PHYTOPLANKTON

Primary production data for each oceanic region of the Atlantic was obtained from the GoMor database (Marine Environment Unit, Joint Research Centre, European Commission) (Figure 9). Blackburn (1981) suggested that phytoplankton biomass within the equatorial divergence is normally between 15 and 30 mgChl·m⁻², while values between 5 and 25 mgChl·m⁻² are expected for areas under the Subtropical gyres. Therefore, phytoplankton biomass for the central Atlantic was considered the average value for equatorial areas (22.5 mgChl·m⁻² or 20.25 t·km⁻²) and for the Northern and Southern Atlantic the average of Subtropical gyres (15 mgChl·m⁻² or 13.5 t·km⁻²). A Carbon:Chlorophyll ratio of 54 (Fasham *et al.*, 1985) was used to convert biomass from mgChl to mgC. To convert phytoplankton biomass and primary productivity from gC to wet weight, a conversion ratio of 0.06:1 was used (Walsh, 1981). The P/B ratios for each area were then computed based on the average primary productivity and phytoplankton biomass (Tables 2 to 4).

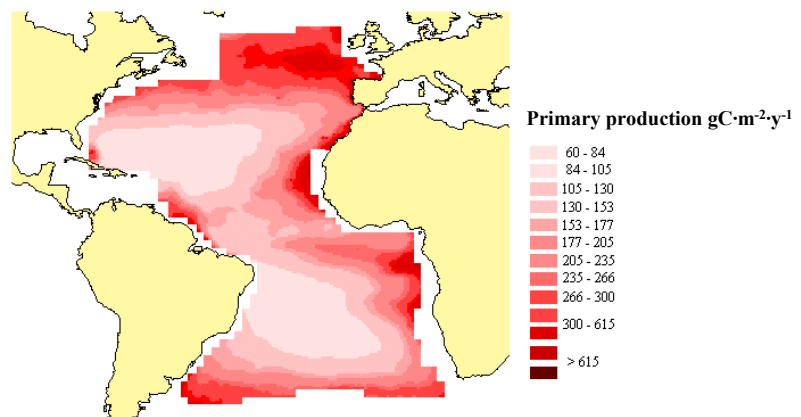


Figure 9. Primary production for 1999 (source: GoMor database).

Table 14. Percentage contribution of zooplankton trophic groups to the total carbon biomass in the Westerlies and Trades biomes of the Atlantic (source Longhurst, 1998).

Biomes	Trophic mode			
	Predators	Herbivores	Omnivores	Detritivores
Westerlies	33.43	21.85	43.79	0.93
Trades	42.96	30.94	25.27	0.84

DETRITUS

The sources of organic matter to the deep sea are phytoplankton, other pelagic phytodetritus, carcasses and feces from pelagic animals, and materials from the continents carried to the deep seas by oceans or downslope transport. Detritus was estimated by the model assuming that organic material from other sources of mortality and non-assimilated food (20 %) of each group are exported to the detritus group.

MODEL BALANCING: LATE 1990S

The approach used to balance the models was to leave unchanged as much as possible the biomasses; P/B and Q/B ratios for the groups for which these parameters were estimated independently. Thus, model balancing was carried mostly by adjusting the diet matrix so that the system could support the estimated biomasses and fluxes between groups. The only exceptions in which biomasses had to be changed were: Small Bathydemersal fish of slope regions in the North Atlantic; Large epipelagic fish; and Small zooplankton groups (see below). Diet adjustments were done in a way as to avoid changing the essential trophic linkages that characterize the functional groups.

In the North Atlantic model, the most important causes of imbalances and the approach used to adjust the model are described below:

1. The high EEs of whales and seabirds were lowered by adjusting their proportions in the diets of pelagic sharks and toothed whales. The remaining proportions were allocated to epipelagic groups and large squids (in the case of toothed whales);
2. The biomasses estimated by Ecopath for groups 15, 16, 17, 18, 19, 20, 21, 26 and 27 were all unrealistically high, and were causing imbalances to other groups in the system. Diets for these groups were adjusted by decreasing the level of cannibalism and eliminating dubious or unimportant trophic linkages (such as the predation of Large mesopelagic fish on Epipelagic fish and the predation of Small squids on Medium epipelagic fish). As a general rule, cannibalism was limited to values between 1 and 5 % of the diet (the representation of different size classes for each functional group was the mechanism adopted to avoid having high cannibalism rates in the model in the first place). The adjustments made were sufficient to release the predation pressure on all groups and to bring the model close to balance. The final biomass of Small and Large squids estimated by Ecopath (0.37 t·km⁻² or ca. 6 Mt) is in the same order of magnitude of the total consumption of cephalopods by top predators in the North Atlantic (Santos *et al.*, 2001), which was estimated at 2.4 Mt based on sperm whale consumption alone;
3. The proportion of tunas in the diet of Pelagic sharks and Large epipelagic fish had to be adjusted in order to account for differences in biomass of each tuna species. For instance, in the North Atlantic albacores are much less abundant than bigeye, while the proportions of these species in the diet of sharks was initially assumed the same. Diets were therefore adjusted to reflect the relative abundance of each tuna species, allowing more predation to the most abundant groups;
4. The biomass of Large epipelagic fish (initially estimated based on landings and an F of 0.3 year⁻¹) was not enough to support the predation. Therefore, this biomass was left to be estimated by Ecopath using EE of 0.9.
5. The fishing mortality of Small bathydemersal fish (slope), estimated by Ecopath from input catch and biomass values, was too high for the group. That showed potential problems in either catch data or biomass values estimated from the literature. The catch of blue whiting in the NADR province was adjusted to reflect the fact that ca. 40 % of the species' catch in the Northeast Atlantic comes from ICES area VIa (Gordon, 2001), which is outside of the model area. EE however remained unchanged. The approach used was therefore to set EE for the group to 0.9. Biomass estimated by Ecopath (0.08110 t·km⁻²) was almost twice the value estimated from the literature (0.045505 t·km⁻²). The possibility that catches are too high due to errors in the procedure used to allocate catches by provinces cannot be ruled out and need to be addressed in a later stage;
6. Imbalances at the bottom of the food web were corrected by adjusting the proportions of diets among small and large zooplankton and between bacteria and detritus. Cannibalism was decreased to 1 % for all zooplankton groups and the remaining diet proportions allocated to phytoplankton (in the case of shallow zooplankton) and to detritus in the case of deep zooplankton groups. The model remained unbalanced because more detritus was being consumed than accumulated. The main cause of imbalance was the consumption of detritus by small zooplankton groups. At this point in the balancing the EE of small zooplankton was relatively small (between 0.1 and 0.2), meaning that the demand for small zooplankton in the system was much lower than the

zooplankton production. Therefore, in order to balance the model, the biomass of small zooplankton was decreased from 118 to 90 t·km⁻² (ca. 20 % decrease) for the shallow water group, and from 46 to 20 t·km⁻² (56 %) for the deep water group. The decision to lower the small zooplankton biomass was consistent with the lower biomass estimates reported in other models of open oceanic systems (Polovina, 1996; Cox *et al.*, 2002).

The final diet matrix obtained after balancing the North Atlantic model was used as starting point to balance the models of the Central and South Atlantic. Only three groups were not balanced (EE>1) in the Central Atlantic model: Bluefin tuna, Large epipelagic fish and Detritus. As for the North Atlantic model, the proportion of tuna species in the diet of Pelagic sharks and Large epipelagic fish were adjusted to represent the relative biomass of the tuna species. In the Central Atlantic predation was assumed higher on bigeye and skipjack than on yellowfin and bluefin tunas. The biomass of Large epipelagic fish was left to be estimated by the model assuming an EE of 0.9. Finally to balance the Detritus group the biomass of Small zooplankton was decreased from 76.7 to 66 t·km⁻² (ca. 13 % decrease).

In the South Atlantic model, the unbalanced groups were Bluefin, Bigeye tuna, Large epipelagic fish, Phytoplankton and Detritus. As in the other two models, the proportion of tunas in the diets of predators were adjusted to reflect the abundance of each species (Skipjack>Albacore>Bigeye>Yellowfin>Bluefin). The EE of Large epipelagic fish was set to 0.9. Finally to lower the consumption of phytoplankton and detritus, the biomass of Small zooplankton was decreased from 107.4 to 65 t·km⁻² (39 % decrease) for shallow zooplankton and from 27.8 to 16 t·km⁻² (42 % decrease) for deep water zooplankton.

Final parameters values of the balanced models are presented in Tables 15, 16 and 17.

PARAMETERS ADJUSTMENTS FOR THE 1950S MODEL

To construct models of the Atlantic oceanic ecosystem in 1950 the following adjustments were made to the balanced models of the recent period (1997-1998):

1. Input landing values of each functional group for the year 1950. Landing statistics for the year 1950 and for each biogeochemical province were obtained from SAU database applying the same procedure as outlined in section 3;
2. Input biomass values for tunas and swordfish based on reported unexploited stock biomass, fishing mortality rates and landing values for the year 1950. Time series of stock biomass and fishing mortality rates for tunas and swordfish were obtained from ICCAT stock assessment reports (references for each species were presented in section 6). Unfortunately, not all stock assessment reports had the same temporal coverage, and assumptions had to be made to set biomass for some of the species. Estimated F values for yellowfin, bigeye and swordfish for the mid-1950s were 0.01, 0.016 and 0.028 year⁻¹, respectively. For the other species the earliest estimates of F was 0.03 year⁻¹ for skipjack in 1969, 0.223 year⁻¹ for bluefin in 1970 and 0.175 year⁻¹ for albacore in 1975. A first attempt was made to estimate biomasses by assuming that fishing mortality rates for tunas in the early 1950s were probably in the same order of magnitude as the earliest F estimates for yellowfin, bigeye and swordfish. Therefore, F for tunas, swordfish and billfishes was set to 0.01 year⁻¹. Results obtained were generally unrealistic. For instance, the estimated biomass of albacore from F and catch data was 3 orders of magnitude higher than the present time biomass, and less bigeye was estimated for the 1950s than for the present time model. In the case of yellowfin tuna, no catches were reported for 1950 which precluded the biomass estimation. Therefore, different approaches had to be used to estimate 1950s biomasses in each model.

In the North Atlantic model, the biomasses of yellowfin, bigeye and skipjack were estimated based on the ratio between unexploited stock (i.e., 1950s biomass) and the current stock biomasses presented in the ICCAT stock assessment reports. The ratios were approximately 1.98 for yellowfin, 3 for bigeye and 3 for skipjack. For albacore, the reported ratio of 4 resulted in a biomass much smaller than the catch of 1950. Instead, albacore biomass was estimated from the catch and an F value of 0.1 year⁻¹. The same approach had to be used for swordfish since the reported ratio between the biomasses in the 1950s and the late 1990s (3.6) resulted in an F value of 0.5 year⁻¹ which was too high for the 1950s. For bluefin tuna, no information was available in

ICCAT reports to obtain a ratio between biomasses. Therefore, bluefin tuna biomass was also estimated based on the ratio between the catch and an F of 0.1 year^{-1} (F of 0.01 year^{-1} resulted in an estimated 40 times decrease in biomass from 1950 to the present, which seemed unrealistic).

Table 15. Final parameters of the North Atlantic model for the recent period. Values in bold were estimated by the model.

Functional group	B ($\text{kg}\cdot\text{km}^{-2}$)	P/B (year^{-1})	Q/B (year^{-1})	EE	Landings ($\text{kg}\cdot\text{km}^{-2}$)
Baleen whales	24.634	0.020	4.394	0.755	0.000
Toothed whales	51.144	0.020	6.689	0.657	0.000
Beaked whales	0.536	0.020	8.806	0.319	0.000
Seabirds	0.204	0.078	72.779	0.255	0.000
Pelagic sharks	6.643	0.390	10.000	0.900	1.731
Yellowfin	0.015	1.050	15.530	0.762	0.005
Bluefin	2.030	0.500	4.000	0.977	0.731
Skipjack	0.463	1.350	19.610	0.843	0.162
Albacore	0.000	0.800	9.600	0.625	0.000
Bigeye	26.944	0.750	17.160	0.557	9.430
Swordfish	0.059	0.700	4.000	0.730	0.030
Billfishes	0.051	0.404	4.690	0.528	0.010
Large planktivorous fish	6.490	0.112	1.800	0.100	0.006
Large epipelagic fish	13.777	0.690	8.938	0.900	0.661
Medium epipelagic fish	112.968	1.080	7.671	0.900	15.909
Small epipelagic fish	859.276	2.053	12.549	0.900	0.017
Large mesopelagic fish	0.001	0.150	3.550	0.900	0.000
Small mesopelagic fish	1724.369	1.980	18.250	0.706	0.000
Small bathypelagic fish	62.888	1.040	3.650	0.900	0.000
Medium bathypelagic fish	69.549	0.190	0.290	0.900	0.000
Large bathypelagic fish	23.169	0.270	0.490	0.900	0.662
Small bathydemersal fish slope	81.102	0.345	0.628	0.900	16.020
Large bathydemersal slope	53.246	0.175	0.318	0.689	5.582
Small bathydemersal abyss	121.430	0.378	0.687	0.448	0.000
Large bathydemersal abyss	189.631	0.209	0.380	0.467	0.000
Small squids	293.465	4.600	36.500	0.900	0.163
Large squids	80.386	4.600	36.500	0.900	0.000
Benthic cephalopods	8.791	1.150	2.300	0.900	0.000
Meiobenthos	1234.000	2.250	22.650	0.259	0.000
Macrobenthos	545.000	1.000	9.850	0.231	0.000
Megabenthos	493.000	1.100	6.700	0.112	0.000
Heterotrophic bacteria	28167.000	18.450	29.000	0.647	0.000
Small zooplankton shallow	90000.000	17.300	57.700	0.324	0.000
Large zooplankton shallow	7377.317	8.700	29.000	0.230	0.000
Small zooplankton deep	20000.000	17.300	57.700	0.123	0.000
Large zooplankton deep	1392.264	8.700	29.000	0.138	0.000
Phytoplankton	13500.000	259.274	–	0.898	0.000
Detritus	–	–	–	1.000	–

Table 16. Final parameters of the Central Atlantic model for the recent period. Values in bold were estimated by the model.

Functional group	B (kg·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	Landings (kg·km ⁻²)
Baleen whales	20.642	0.020	4.394	0.708	0.000
Toothed whales	42.856	0.020	6.689	0.432	0.000
Beaked whales	0.449	0.020	8.806	0.319	0.000
Seabirds	0.125	0.078	73.562	0.310	0.000
Pelagic sharks	1.724	0.390	10.000	0.900	0.372
Yellowfin	0.078	1.050	15.530	0.396	0.027
Bluefin	0.008	0.500	4.000	0.764	0.003
Skipjack	2.605	1.350	19.610	0.378	0.912
Albacore	0.155	0.800	9.600	0.963	0.078
Bigeye	8.942	0.750	17.160	0.555	3.130
Swordfish	0.302	0.700	4.000	0.715	0.151
Billfishes	1.657	0.416	4.137	0.481	0.331
Large planktivorous fish	1.539	0.112	1.800	0.100	0.000
Large epipelagic fish	11.114	0.693	8.938	0.900	2.026
Medium epipelagic fish	44.780	1.080	7.671	0.900	0.800
Small epipelagic fish	628.895	2.053	12.549	0.900	0.000
Large mesopelagic fish	0.558	0.150	3.550	0.900	0.000
Small mesopelagic fish	3253.854	3.757	18.250	0.155	0.000
Small bathypelagic fish	20.715	1.040	3.650	0.900	0.000
Medium bathypelagic fish	22.377	0.190	0.290	0.900	0.000
Large bathypelagic fish	5.535	0.270	0.490	0.900	0.000
Small bathydemersal fish slope	15.938	0.355	0.645	0.682	0.576
Large bathydemersal slope	18.835	0.160	0.291	0.607	1.075
Small bathydemersal abyss	93.452	0.343	0.623	0.521	0.000
Large bathydemersal abyss	145.938	0.202	0.368	0.526	0.000
Small squids	226.259	4.600	36.500	0.900	0.276
Large squids	67.357	4.600	36.500	0.900	0.000
Benthic cephalopods	5.099	1.150	2.300	0.900	0.000
Meiobenthos	984.000	2.250	22.650	0.244	0.000
Macrobenthos	369.000	1.000	9.850	0.181	0.000
Megabenthos	394.000	1.100	6.700	0.089	0.000
Heterotrophic bacteria	22542.999	18.450	29.000	0.624	0.000
Small zooplankton shallow	66000.000	17.300	57.700	0.704	0.000
Large zooplankton shallow	17567.677	8.700	29.000	0.123	0.000
Small zooplankton deep	18858.584	17.300	57.700	0.419	0.000
Large zooplankton deep	5931.747	8.700	29.000	0.060	0.000
Phytoplankton	20250.000	146.382	–	0.777	0.000
Detritus	–	–	–	1.000	–

Table 17. Final parameters of the South Atlantic model for the recent period. Values in bold were estimated by the model.

Functional group	B kg·km ⁻²	P/B year ⁻¹	Q/B year ⁻¹	EE	Landings kg·km ⁻²
Baleen whales	21.580	0.020	4.394	0.693	0.000
Toothed whales	44.804	0.020	6.689	0.357	0.000
Beaked whales	0.470	0.020	8.806	0.319	0.000
Seabirds	0.137	0.081	73.757	0.273	0.000
Pelagic sharks	0.466	0.390	10.000	0.900	0.094
Yellowfin	0.066	1.050	15.530	0.350	0.023
Bluefin	0.003	0.500	4.000	0.749	0.001
Skipjack	3.988	1.350	19.610	0.331	1.396
Albacore	0.446	0.800	9.600	0.893	0.223
Bigeye	0.100	0.750	17.160	0.677	0.035
Swordfish	0.291	0.700	4.000	0.715	0.145
Billfishes	0.586	0.409	4.212	0.489	0.117
Large planktivorous fish	0.415	0.113	1.800	0.100	0.000
Large epipelagic fish	2.479	0.690	8.938	0.900	0.062
Medium epipelagic fish	5.958	1.080	7.671	0.900	0.043
Small epipelagic fish	569.886	2.053	12.549	0.900	0.000
Large mesopelagic fish	1.603	0.150	3.550	0.900	0.000
Small mesopelagic fish	1164.093	2.445	18.250	0.639	0.141
Small bathypelagic fish	0.649	1.040	3.650	0.900	0.000
Medium bathypelagic fish	2.150	0.190	0.290	0.900	0.000
Large bathypelagic fish	2.093	0.270	0.490	0.900	0.000
Small bathydemersal fish slope	7.509	0.412	0.748	0.994	0.965
Large bathydemersal slope	8.874	0.207	0.376	0.650	0.571
Small bathydemersal abyss	109.387	0.378	0.687	0.414	0.000
Large bathydemersal abyss	170.823	0.209	0.380	0.454	0.000
Small squids	221.587	4.600	36.500	0.900	0.000
Large squids	70.418	4.600	36.500	0.900	0.000
Benthic cephalopods	3.799	1.150	2.300	0.900	0.000
Meiobenthos	1073.000	2.250	22.650	0.246	0.000
Macrobenthos	414.000	1.000	9.850	0.150	0.000
Megabenthos	429.000	1.100	6.700	0.094	0.000
Heterotrophic bacteria	24562.000	18.450	29.000	0.551	0.000
Small zooplankton shallow	65000.000	17.300	57.700	0.291	0.000
Large zooplankton shallow	3537.318	8.700	29.000	0.320	0.000
Small zooplankton deep	16000.000	17.300	57.700	0.113	0.000
Large zooplankton deep	986.818	8.700	29.000	0.131	0.000
Phytoplankton	13500.000	192.982	–	0.871	0.000
Detritus	–	–	–	0.986	–

In the Central Atlantic model the biomass of bluefin was estimated as the ratio between catches and an F of 0.1 year^{-1} . Since there were no catches reported for the other species, the biomass of yellowfin, albacore, skipjack, bigeye and swordfish were estimated base on the ratios between unexploited stock and the current stock. The biomasses in the South Atlantic model were calculated using the ratios between unexploited stock and current stock sizes.

3. The P/B ratios of tunas and swordfish were adjusted according to total mortality rates estimated with the F values for 1950.
4. The EE values of the high trophic level groups that are exploited and that had EE entered as an input parameter in Ecopath (Pelagic sharks, Large Epipelagic fish and Large Bathypelagic fish) were also adjusted. For instance, an EE of 0.9 was entered for Pelagic sharks in the model for the late 1990s to reflect the fact that the group was heavily fished. In the 1950s, EE had to be adjusted to reflect that fisheries were less intensive and that predation is low for the group. Thus, for the 1950s model, EEs of these groups were set according to the contribution of the predation mortality to the total natural mortality rate (M) in the late 1990s model; EE was set to 0.31 for Pelagic sharks; 0.81 for Large epipelagic fish; and 0.79 for Large bathypelagic fish. An EE of 0.03 (calculated in the same way) was used to estimate the biomass of Billfishes in the 1950s model.
5. The biomass of whales were also adjusted. The biomass of whale groups was probably higher in the 1950s than in the present time period. For instance, based on genetic work, Roman and Palumbi (2003) estimated that there were approximately 400,000 humpbacks, 480,000 fins and 300,000 minke in the North Atlantic. However, in order to use his estimates, some type of adjustment had to be made (as proposed by Kaschner *et al.* (2001) to account for the fact that not all whales were present in the oceanic areas all the time. In the absence of other information, it was tentatively assumed that the biomass of whales in 1950 was twice the current level.

The balancing of the 1950s model relied as much as possible on biomass adjustments leaving the diet matrix similar to the late 1990s model. In this sense, the 1950s model served as a way to address the question of how much biomass could be supported by the current system structure. For the North Atlantic model, two groups became unbalanced with the new input parameters: Skipjack tuna and Small mesopelagic fish. Predation by albacore was the main source of mortality of skipjack tuna. Instead of decreasing the biomass of Albacore (which would bring the F for group too high for the 1950), the biomass of Skipjack was increased by approximately 4 times. In the case of mesopelagic fish, the main source of predation was Small and Large squids, which had their biomass estimated based on predation pressure (mainly of Toothed whales) and an EE value of 0.9. To balance the model the biomass of Toothed whales was decreased from 0.102 to $0.079 \text{ t}\cdot\text{km}^{-2}$, the EE of squids increased to 0.95. To bring the model to balance the proportion of Small squids in the diet of Large squids was decreased to 0.15 and the proportion of Mesopelagic fish in the diet of Small squids decreased to 0.15, the remaining diet proportions allocated to Large zooplankton groups.

For the Central Atlantic model, the EE of Pelagic sharks was decreased to 0.25 because biomass estimated with an EE of 0.3 was approximately the same as in the present time model. Because of the predation by Toothed whales the Bathydemersal fish groups had EEs slightly over 1 in the Central Atlantic. To balance the model the biomass of Toothed whales was decreased from 0.085 to $0.078 \text{ t}\cdot\text{km}^{-2}$.

The model of the South Atlantic could not be balanced unless a biomass value was entered for Pelagic sharks. Biomass of Pelagic sharks was therefore set to $0.0009 \text{ t}\cdot\text{km}^{-2}$ (approximately twice the present time model), with EE being estimated at 0.23. Two groups remained unbalanced: Small mesopelagics and Small bathydemersal slope fish. The model was balanced by decreasing the biomass of Toothed whales to $0.078 \text{ t}\cdot\text{km}^{-2}$, increasing the biomass of Small mesopelagics from 1.16 to $1.3 \text{ t}\cdot\text{km}^{-2}$, increasing the biomass of Small Bathydemersal fish from 0.007 to $0.008 \text{ t}\cdot\text{km}^{-2}$, and by decreasing the proportion of Small mesopelagics in the diet of Large squids from 0.2 to 0.15. The remaining diet proportions were allocated to Deepwater large zooplankton. The final parameters for the 1950s models are presented in Tables 18 to 20.

Table 18. Final parameters of the North Atlantic model for 1950. Values in bold were estimated by the model.

Functional group	B kg·km ⁻²	P/B year ⁻¹	Q/B year ⁻¹	EE	Landings kg·km ⁻²
Baleen whales	49.268	0.020	4.394	0.693	0.000
Toothed whales	79.000	0.020	6.689	0.357	0.000
Beaked whales	1.072	0.020	8.806	0.319	0.000
Seabirds	0.204	0.078	72.779	0.273	0.000
Pelagic sharks	9.986	0.390	10.000	0.900	0.265
Yellowfin	0.030	0.700	15.530	0.350	0.000
Bluefin	98.667	0.240	4.000	0.749	0.987
Skipjack	6.000	1.030	19.610	0.331	0.046
Albacore	18.900	0.400	9.600	0.893	1.852
Bigeye	80.831	0.400	17.160	0.677	0.052
Swordfish	1.080	0.300	4.000	0.715	0.109
Billfishes	0.082	0.404	4.690	0.489	0.000
Large planktivorous fish	12.302	0.112	1.800	0.100	0.038
Large epipelagic fish	22.194	0.690	8.938	0.900	0.394
Medium epipelagic fish	306.364	1.080	7.671	0.900	1.759
Small epipelagic fish	1437.178	2.053	12.549	0.900	0.032
Large mesopelagic fish	67.879	0.150	3.550	0.900	0.000
Small mesopelagic fish	1724.369	1.980	18.250	0.639	0.000
Small bathypelagic fish	197.122	1.040	3.650	0.900	0.000
Medium bathypelagic fish	247.122	0.190	0.290	0.900	0.000
Large bathypelagic fish	67.239	0.270	0.490	0.900	0.109
Small bathydemersal fish slope	108.154	0.345	0.628	0.994	1.119
Large bathydemersal slope	53.246	0.175	0.318	0.650	1.597
Small bathydemersal abyss	121.430	0.378	0.687	0.414	0.000
Large bathydemersal abyss	189.631	0.209	0.380	0.454	0.000
Small squids	344.755	4.600	36.500	0.900	0.052
Large squids	113.264	4.600	36.500	0.900	0.000
Benthic cephalopods	20.184	1.150	2.300	0.900	0.000
Meiobenthos	1234.000	2.250	22.650	0.246	0.000
Macrobenthos	545.000	1.000	9.850	0.150	0.000
Megabenthos	493.000	1.100	6.700	0.094	0.000
Heterotrophic bacteria	28167.000	18.450	28.500	0.551	0.000
Small zooplankton shallow	90000.000	17.300	57.700	0.291	0.000
Large zooplankton shallow	7377.317	8.700	29.000	0.320	0.000
Small zooplankton deep	20000.000	17.300	57.700	0.113	0.000
Large zooplankton deep	1392.264	8.700	29.000	0.131	0.000
Phytoplankton	13500.000	259.274		0.871	0.000
Detritus				0.986	

Table 19. Final parameters of the Central Atlantic model for 1950. Values in bold were estimated by the model.

Functional group	B kg·km ⁻²	P/B year ⁻¹	Q/B year ⁻¹	EE	Landings kg·km ⁻²
Baleen whales	41.284	0.020	4.394	0.664	0.000
Toothed whales	78.000	0.020	6.689	0.537	0.000
Beaked whales	0.898	0.020	8.806	0.290	0.000
Seabirds	0.125	0.078	73.562	0.598	0.000
Pelagic sharks	6.401	0.390	10.000	0.250	0.046
Yellowfin	0.155	0.700	15.530	0.065	0.000
Bluefin	0.009	0.240	4.000	0.714	0.001
Skipjack	7.813	1.030	19.610	0.130	0.000
Albacore	0.622	0.400	9.600	0.385	0.000
Bigeye	26.825	0.400	17.160	0.166	0.000
Swordfish	1.088	0.300	4.000	0.002	0.000
Billfishes	0.051	0.416	4.137	0.030	0.000
Large planktivorous fish	5.715	0.112	1.800	0.100	0.000
Large epipelagic fish	14.206	0.693	8.938	0.810	0.289
Medium epipelagic fish	98.111	1.080	7.671	0.900	0.125
Small epipelagic fish	1177.740	2.053	12.549	0.900	0.039
Large mesopelagic fish	2.233	0.150	3.550	0.900	0.000
Small mesopelagic fish	3253.854	3.757	18.250	<u>0.292</u>	0.000
Sm. Bathypelagic fish	62.940	1.040	3.650	0.900	0.000
Medium bathypelagic fish	70.743	0.190	0.290	0.900	0.000
Large bathypelagic fish	23.487	0.270	0.490	0.790	0.000
Small bathydemersal fish slope	15.938	0.355	0.645	1.000	0.188
Large bathydemersal slope	18.835	0.160	0.291	0.659	0.064
Small bathydemersal abyss	93.452	0.343	0.623	0.962	0.000
Large bathydemersal abyss	145.938	0.202	0.368	0.957	0.000
Small squids	426.664	4.600	36.500	0.900	0.000
Large squids	122.700	4.600	36.500	0.900	0.000
Benthic cephalopods	11.064	1.150	2.300	0.900	0.000
Meiobenthos	984.000	2.250	22.650	0.246	0.000
Macrobenthos	369.000	1.000	9.850	0.266	0.000
Megabenthos	394.000	1.100	6.700	0.095	0.000
Heterotrophic bacteria	22542.999	18.450	28.300	0.624	0.000
Small zooplankton shallow	66000.000	17.300	57.700	0.710	0.000
Large zooplankton shallow	17567.677	8.700	29.000	0.162	0.000
Small zooplankton deep	18858.584	17.300	57.700	0.419	0.000
Large zooplankton deep	5931.747	8.700	29.000	0.067	0.000
Phytoplankton	20250.000	146.382		0.777	0.000
Detritus				1.000	

Table 20. Final parameters of the South Atlantic model for 1950. Values in bold were estimated by the model.

Functional group	B kg·km ⁻²	P/B year ⁻¹	Q/B year ⁻¹	EE	Landings kg·km ⁻²
Baleen whales	43.160	0.020	4.394	0.604	0.000
Toothed whales	78.000	0.020	6.689	0.360	0.000
Beaked whales	0.939	0.020	8.806	0.278	0.000
Seabirds	0.137	0.081	73.757	0.475	0.000
Pelagic sharks	0.900	0.390	10.000	0.232	0.000
Yellowfin	0.131	0.700	15.530	0.010	0.000
Bluefin	0.015	0.240	4.000	0.025	0.000
Skipjack	11.965	1.030	19.610	0.080	0.000
Albacore	1.785	0.400	9.600	0.233	0.000
Bigeye	0.300	0.400	17.160	0.141	0.000
Swordfish	1.046	0.300	4.000	0.000	0.000
Billfishes	0.007	0.409	4.212	0.030	0.000
Large planktivorous fish	0.800	0.113	1.800	0.100	0.000
Large epipelagic fish	1.755	0.690	8.938	0.810	0.000
Medium epipelagic fish	7.136	1.080	7.671	0.900	0.120
Small epipelagic fish	992.731	2.053	12.549	0.900	0.000
Large mesopelagic fish	6.412	0.150	3.550	0.900	0.000
Small mesopelagic fish	1300.000	2.445	18.250	0.952	0.000
Small bathypelagic fish	2.139	1.040	3.650	0.900	0.000
Medium bathypelagic fish	7.324	0.190	0.290	0.900	0.000
Large bathypelagic fish	6.151	0.270	0.490	0.790	0.000
Small bathydemersal fish slope	8.000	0.412	0.748	0.981	0.005
Large bathydemersal slope	8.874	0.207	0.376	0.870	0.016
Small bathydemersal abyss	109.387	0.378	0.687	0.721	0.000
Large bathydemersal abyss	170.823	0.209	0.380	0.791	0.000
Small squids	390.712	4.600	36.500	0.900	0.000
Large squids	122.754	4.600	36.500	0.900	0.000
Benthic cephalopods	6.699	1.150	2.300	0.900	0.000
Meiobenthos	1073.000	2.250	22.650	0.247	0.000
Macrobenthos	414.000	1.000	9.850	0.165	0.000
Megabenthos	429.000	1.100	6.700	0.097	0.000
Heterotrophic bacteria	24562.000	18.450	29.000	0.551	0.000
Small zooplankton shallow	65000.000	17.300	57.700	0.297	0.000
Large zooplankton shallow	3537.318	8.700	29.000	0.484	0.000
Small zooplankton deep	16000.000	17.300	57.700	0.114	0.000
Large zooplankton deep	986.818	8.700	29.000	0.193	0.000
Phytoplankton	13500.000	192.982		0.871	0.000
Detritus				0.990	

FINAL COMMENTS

The models constructed in this report can be improved in many different ways. Particular attention has to be given to obtaining better biomass estimates for whales and seabirds for both time periods in all areas of the Atlantic. More information on biomass distribution of bathydemersal fish and invertebrate fauna, particularly for the Central and South Atlantic, will also improve considerably the representation of regional differences through the mass-balance models. The 1950s model is still preliminary and should be used ultimately only as a possible scenario for changes in biomasses of selected groups between the 1950s and the present time. In this sense, more efforts should be put in using the available biomass time series of exploited groups (mainly tunas and swordfish) and time series of primary productivity to construct and test more realistic scenarios of change in oceanic ecosystems over time.

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