

A PRELIMINARY ECOSYSTEM MODEL FOR THE ATLANTIC COAST OF MOROCCO IN THE MID-1980S

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ABSTRACT

This paper documents the construction of the model of the Atlantic coast of Morocco including the coast of Western Sahara (Tangier to Cape Blanc). The model includes 37 functional groups of which 23 are fishes, grouped by size and commercial importance. The balancing process is described and highlights knowledge gaps. Recommendations for improvements of the model are given.

INTRODUCTION

The rich fishing grounds of the Moroccan Coast, are largely the consequence of an upwelling zone driven by the Canary Current (Belvèze and Erzini, 1984). The northeast to southwest flow transports cold waters along the northwest African coast and, combined with the trade winds, causes an upwelling of nutrient rich water to the surface. As a result, primary production is increased, generating rich fishing grounds (Nehring and Holzlohner, 1982). Upwelling intensity varies according to location and season, due to the variation in the trade winds throughout the year. The upwelling is weak in winter, develops in spring and peaks in intensity during the summer, coinciding with maximum irradiance. The upwelling ranges from 12°N to 33°N (Wooster, 1976 in Belvèze and Erzini, 1984), but can be subdivided into 3 main areas. North of 25°N upwelling primarily occurs in the summer, south of 20°N it occurs during the winter and spring, and between 20°N and 25°N, upwelling occurs throughout the year (Figure 1). Coastal topography is a significant factor in determining upwelling location. For a more detailed analysis of upwellings off the northwest African coast, see Belvèze and Erzini (1984).

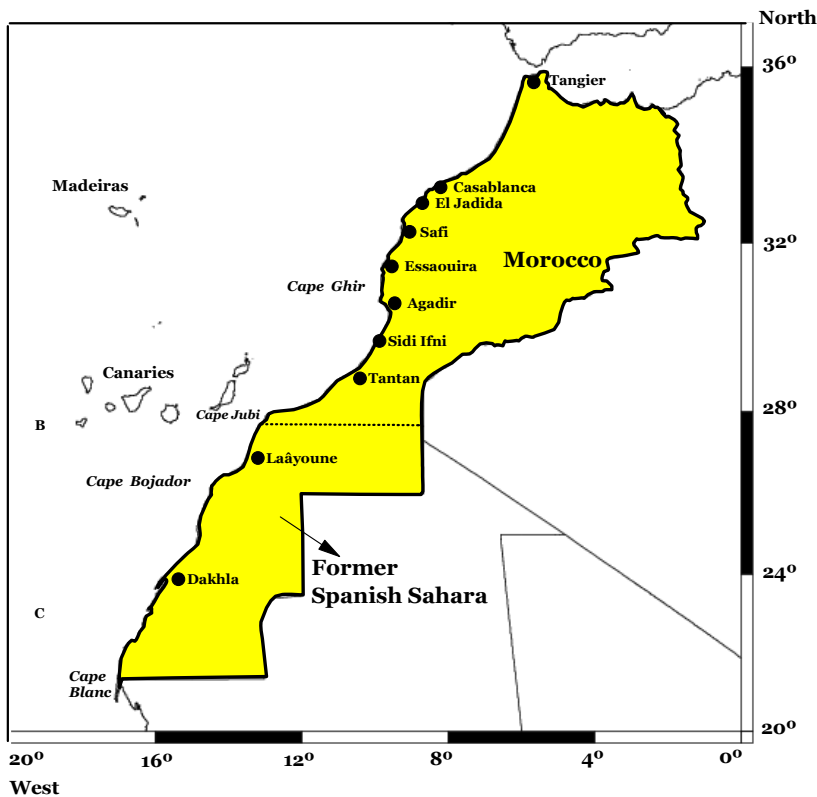


Figure 1. The Atlantic Moroccan coast showing the principal fishing ports, and the border of the former Spanish Sahara.

The ecosystem modeled here covers the Atlantic coast of Morocco extending from Tangier (36°N) to Cape Blanc (20°N) and is as wide as the EEZ. The resulting area is 586,900 km² (Figure 1). The mean annual water temperature, 19.4°C, was estimated by averaging over 1985-1986 from *www.noaa.gov*. At the time of the construction of the model, we did not have access to biomass estimates for the 1990s. Consequently, the model presented here represents the mid 1980s.

MODEL PARAMETERIZATION

Five key meters are required for Ecopath models: biomass, production per unit of biomass (P/B), consumption per unit of biomass (Q/B), ecotrophic efficiency (EE) and diet composition. The average biomass in the model area (586,900 km²) is given in t·km⁻². Since biomass estimates were extremely difficult to find for the coast of Morocco, they were left, for many groups, for Ecopath to estimate, by assuming an ecotrophic efficiency of 0.95. The ecotrophic efficiency is the fraction of production that is used in the system. Essentially, it refers to the mortality of a group explained by the model.

P/B expressed per year is equal to the instantaneous total mortality (Z), the sum of fishing mortality (F) and natural mortality (M). For commercial species, F was taken from stock assessment reports or obtained by dividing fisheries catch by biomass. Unless otherwise stated, the natural mortality for the fish groups in this model, were calculated from the following equation (Pauly, 1980):

$$M = K^{0.65} * L_{inf}^{-0.279} * T^{0.463} \quad \dots 1)$$

where K is the von Bertalanffy growth constant (per year), L_{inf} is the asymptotic length (in cm) and T is the average water temperature (in °C). For non-fish groups and when a K value was not available for the fish, different data sources were used and are recorded individually below. Generally, in absence of K values for a high proportion of the groups' species, natural mortality estimates from FishBase (Froese and Pauly, 2000) were used and labeled 'FishBase generic values'.

All Q/Bs, expressed per year, were calculated using an empirical equation derived by Palomares and Pauly 1989;

$$Q/B = 10^{6.37 * 0.0313^{Tk}} * Winf^{0.168} * 1.38^{Pf} * 1.89^{Hd} \quad \dots 2)$$

where, $Tk = 1000 \cdot (\text{Temperature in } ^\circ\text{C} + 273.1)^{-1}$, W_{inf} = asymptotic weight in g, $Pf = 1$ for predators and planktivores, zero for herbivores and detritivores, zero for omnivores $Hd = 1$ for carnivores and omnivores, zero for detritivores and herbivores. W_{inf} was calculated using the a and b parameters of length-weight relationships of the form $Winf = a \cdot Linf^b$, taken from the location closest to Morocco in FishBase (Froese and Pauly, 2000). In some cases, Q/B was estimated from an empirical equation in the 'Keyfact Table' of Fishbase (*www.fishbase.org*) which uses the aspect ratio of the fish' caudal fins as an input.

The majority of fish diet composition data was taken from FishBase (*www.fishbase.org*) and relevant literature for the most important species. Literature diet data for species from other areas included prey items that did not occur in Morocco. These prey items were placed in a functional group with similar species. For many species, existing diet data were qualitative (present/not present) or were measured as frequency of occurrence rather than measures based on weight or volume. In these cases, percentages were equally apportioned among groups. Unless otherwise stated, unidentified dietary components were split proportionally into the diet groups that were already present and combined values or entirely qualitative data were split equally between the identified groups. The detailed diet matrix is presented in Tables 1 to 3.

Description of functional groups

Primary producers (Group 1)

Benthic macroalgae and phytoplankton are the primary producers in the system. Little is known of the dominant species of phytoplankton. Phytoplankton biomass was calculated using the values given in Li (1994). Using a conversion factor of 32 gC = 1 g Chl a and 43 gC = 1 g wet weight, the wet weight was estimated as 94.1 t·km⁻². Lalli and Parsons (1993) gave a pictorial description of global phytoplankton production, with an approximate value of 150-250 gC·m⁻²·year⁻¹ for the Moroccan coast. Using the same conversion factor of 43 gC = 1 g wet weight·m⁻², we were able to estimate the P/B for phytoplankton at 91.4 year⁻¹.

Macrophyte biomass was calculated using data from Belvèze and Bravo de Laguna (1980). The authors listed the percentage of the total surface area (from 0-50 m depth) that can be trawled from Cap Spartel to Cap Blanc (the northern and southern limits of our study area). From these

Table 1. Source location and quality of the diet information for selected functional groups.

Scientific name	English name	Diet information	Location	Source
Small demersal (group 14)				
<i>Callionymus maculatus</i>	Dragonet	Quantitative	Scotland, Atlantic coast	Gibson and Ezzi (1987)
<i>Arnoglossus laterna</i>	Scaldfish	Quantitative	Scotland, Atlantic coast	Gibson and Ezzi (1987)
<i>Atherina boyeri</i>	Big-scale sand smelt	Quantitative	Black Sea	Zander (1986)
<i>Gobius niger</i>	Black goby	Quantitative	Norway	Fjøsne and Gjørseter (1996)
<i>Ctenolabrus rupestris</i>	Goldsinny wrasse	Quantitative	Norway	Fjøsne and Gjørseter (1996)
Medium demersal (group 15)				
<i>Coris julis</i>	Rainbow wrasse	Qualitative	Unknown	Fischer <i>et al.</i> (1987)
<i>Trachinus vipera</i>	Lesser weever	Quantitative	UK, Scotland	Gibson and Robb (1996)
<i>Parablennius gattorugine</i>	Tompot blenny	Qualitative	Unknown	Zander (1986)
<i>Callionymus lyra</i>	Dragonet	Qualitative	Unknown	Fricke (1986)
<i>Capros aper</i>	Boarfish	Qualitative	Unknown	Quéro (1986)
<i>Antigonia capros</i>	Deepbody boarfish	Qualitative	St Helena	Edwards (1990)
<i>Nezumia aequalis</i>	Atlantic grenadier	Qualitative	Namibia	MacPherson and Roel (1987)
<i>Labrus bimaculatus</i>	Cuckoo wrasse	Qualitative	Maritimes, Canada	Mérigoux and Ponton (1998)
<i>Caelorinchus caelorhincus</i>	Hollowsnout grenadier	Quantitative	Nova Scotia, Canada	Langton and Bowman (1980)
<i>Trisopterus minutus</i>	Poor cod	Quantitative	UK	Armstrong (1982)
<i>Lepidorhombus boscii</i>	Fourspotted megrim	Quantitative	North Tyrrhenian Sea, Italy	Mannini <i>et al.</i> (1990)
<i>Bothus podas</i>	Wide-eyed flounder	Qualitative	Azores	Nash <i>et al.</i> (1991)
<i>Syngnathus acus</i>	Greater pipefish	Quantitative	South Africa	Bennett (1989)
<i>Alepocephalus rostratus</i>	Risso's smooth-head	Quantitative	Namibia	Carrasson and Matallanas (1998)
Medium demersal commercial (group 16)				
<i>Diplodus vulgaris</i>	Common two-banded bream	Quantitative	Spain	Sala and Ballesteros (1997)
<i>Diplodus cervinus cervinus</i>	Zebra seabream	Qualitative	Unknown	Fischer <i>et al.</i> (1987)
<i>Balistes vetula</i>	Queen triggerfish	Quantitative	Puerto Rico	Randall (1967)
<i>Scorpaena notata</i>	Small red scorpionfish	Quantitative	France	Harmelin-Vivien <i>et al.</i> (1989)
<i>Brachydeuterus auritus</i>	Bigeye grunt	Qualitative	Senegal	Ben-Tuvia and McKay (1986)
<i>Mullus barbatus</i>	Red Mullet	Quantitative	Nova Scotia, Canada	Labropoulou and Eleftheriou (1997)
<i>Dicologlossa cuneata</i>	Wedge sole	Qualitative	Unknown	Quéro <i>et al.</i> (1986)
<i>Scorpaena porcus</i>	Black scorpionfish	Quantitative	France	Harmelin-Vivien <i>et al.</i> (1989)
<i>Oblada melanura</i>	Saddled seabream	Quantitative	France	Lenfant and Olive (1998)
<i>Pagellus acarne</i>	Axillary seabream	Quantitative	Central Eastern Atlantic	Domanevskaya and Patokina (1984)
<i>Solea lascaris</i>	Sand sole	Quantitative	France	Rodriguez (1996)
<i>Mullus surmuletus</i>	Striped Red Mullet	Quantitative	Spain	Olaso and Rodriguez-Marin (1995)
<i>Chelidonichthys lastoviza</i>	Longfin gurnard	Qualitative	unknown	Richards and Saksena (1990)
<i>Pagellus bellottii bellottii</i>	Red pandora	Qualitative	Senegal	Caverivière and Rabarison Andriamirado (1997)

Scientific name	English name	Diet information	Location	Source
<i>Trisopterus luscus</i>	Pouting	Quantitative	Isle of Man, UK	Armstrong (1982)
<i>Chelidonichthys cuculus</i>	East Atlantic red Gurnard	Quantitative	Spain	Velasco <i>et al.</i> (1996)
<i>Micromesistius poutassou</i>	Blue whiting	Quantitative	Spain	Olaso and Rodriguez-Marin (1995)
<i>Scorpaena scrofa</i>	Largescaled scorpionfish	Quantitative	Marseilles, France	Harmelin-Vivien <i>et al.</i> (1989)
<i>Pagellus erythrinus</i>	Common pandora	Quantitative	Spain	Olaso and Rodriguez-Marin (1995)
Large demersal (group 17)				
<i>Malacocephalus laevis</i>	Softhead grenadier	Quantitative	South Africa	Meyer and Smale (1991)
<i>Hoplostethus atlanticus</i>	Orange roughy	Quantitative	Australia	Kotlyar (1980)
<i>Scophthalmus rhombus</i>	Brill	Qualitative	Unknown	Bauchot (1987)
<i>Arius parkii</i>	Guinean sea catfish	Partially Quantitative	Senegal	Diouf, 1996; Caverivière and Rabarison Andriamirado (1997)
<i>Cepola macrophthalma</i>	Red bandfish	Qualitative	Unknown	Stergiou (1993)
<i>Rhinobatos rhinobatos</i>	Common guitarfish	Partially quantitative	Senegal	Caverivière and Rabarison Andriamirado (1997)
<i>Phycis phycis</i>	Forkbeard	Quantitative	Greece	Papaconstantinou and Caragitsou (1989)
<i>Alepocephalus bairdii</i>	Baird's smooth-head	Qualitative	Unknown	Markle and Quéro (1984)
Large demersal commercial (group 18)				
<i>Diplodus puntazzo</i>	Sharpsnout seabream	Quantitative	Spain	Sala and Ballesteros (1997)
<i>Umbrina canariensis</i>	Canary Drum	Quantitative	Spain	van der Elst and Adkin (1991)
<i>Chelidonichthys gurnardus</i>	Grey gurnard	Quantitative	Spain	Moreno-Amich (1994)
<i>Dentex macrophthalmus</i>	Large eye Dentex	Quantitative	Area between Cap Blanc and Cap Bojador	Domanevskaya and Patokina (1984)
<i>Sparus aurata</i>	Gilthead seabream	Qualitative	Australia	Winstanley (1983)
<i>Beryx splendens</i>	Splendid alfonso	Quantitative	Russian Fed. Naska seamount	Dubochkin and Kotlyar (1989)
<i>Pagellus bogaraveo</i>	Blackspot seabream	Qualitative	Can Mart Qeb	Bauchot and Hureau (1990)
<i>Pagrus caeruleostictus</i>	Bluespotted seabream	Qualitative	Senegal	Caverivière and Rabarison Andriamirado (1997)
<i>Zeus faber</i>	John Dory	Quantitative	Greece	Stergiou and Fournouni (1991)
<i>Pagrus pagrus</i>	Red porgy	Quantitative	Greece	Papaconstantinou and Caragitsou (1989)
<i>Dicentrarchus labrax</i>	European seabass	Qualitative	Unknown	Fischer <i>et al.</i> (1987)
<i>Pseudotolithus typus</i>	Longneck croaker	Qualitative	Senegal	Diouf (1996)
<i>Pseudotolithus senegalens</i>	Cassava croaker	Qualitative	Senegal	Diouf (1996)
<i>Dentex dentex</i>	Common dentex	Quantitative	Spain, Balearic Is.	Morales-Nin and Moranta (1997)
<i>Phycis blenoides</i>	Greater forkbeard	Quantitative	Spain	Velasco <i>et al.</i> (1996)
<i>Epinephelus aeneus</i>	White grouper	Partially Quantitative	Unknown and Senegal	McCosker, 1988; Caverivière and Rabarison Andriamirado (1997)
<i>Anguilla anguilla</i>	European eel	Quantitative	Portugal	Costa <i>et al.</i> (1992)
Large bathypelagic fish (group 23)				
<i>Trachyearincus scabrus</i>	Roughsnout grenadier	Quantitative	Namibia	MacPherson and Roel (1987)
<i>Eurypharynx pelecanooides</i>	Pelican eel	Qualitative	California, USA	Eschmeyer <i>et al.</i> (1983)
<i>Mora moro</i>	Common mora	Qualitative	Australia	Coleman and Mobley (1984)
<i>Lepidocybium flavobrunneum</i>	Escolar	Qualitative	Cuba	Sierra <i>et al.</i> (1994)

Scientific name	English name	Diet information	Location	Source
Very large demersal commercial (group 20)				
<i>Merluccius merluccius</i>	European hake	Quantitative	Bay of Biscay, France	Guichet (1995)
<i>Seriola dumerili</i>	Greater amberjack	Qualitative	West Indies	Randall (1967)
<i>Lepidopus caudatus</i>	Silver scabbardfish	Quantitative	South Africa	Smale (1991)
<i>Argyrosomus regius</i>	Meagre	Qualitative	Senegal	Caverivière and Rabarison Andriamirado (1997)
<i>Trichiurus lepturus</i>	Largehead hairtail	Qualitative		
Mesopelagic prey fish (group 24)				
<i>Argyroleucus hemigymnus</i>	half-naked hatchetfish	Quantitative	Gulf of Mexico	Hopkins and Baird (1985)
<i>Benthoema glaciale</i>	glacier lanternfish	Qualitative	Unknown	Hulley (1990)
<i>Gadiculus argenteus argenteus</i>	silvery cod	Quantitative	Rockall area off Scotland	Conway (1980)
<i>Maurolicus muelleri</i>	pearlsides	Quantitative	South Atlantic	Gorelova and Krasil'nikova (1990)
<i>Sternoptyx diaphana</i>	diaphanous hatchet fish	Quantitative	Eastern Gulf of Mexico	Hopkins and Baird (1985)
<i>Vinciguerrria nimbaria</i>	oceanic lightfish	Quantitative	Tropical Atlantic	Shevchenko (1986)
<i>Atherina presbyter</i>	sand smelt	Qualitative	France	Billard (1997)
Tunas (group 29)				
<i>Katsuwonus pelamis</i>	Skipjack	Quantitative	Western Indian Ocean	Roger (1993)
<i>Thunnus albacares</i>	Yellowfin tuna	Quantitative	Western Indian Ocean	Roger (1993)
<i>Thunnus thynnus</i>	Bluefin tuna	Quantitative	Bay of Biscay	Ortiz de Zarate and Cort (1986)
<i>Thunnus alalunga</i>	Albacore	Quantitative	Bay of Biscay	Ortiz de Zarate and Cort (1986)
<i>Auxis thazard thazard</i>	Frigate tuna	Quantitative	Solomon Islands	Blaber <i>et al.</i> (1990)
<i>Auxis rochei rochei</i>	Little tunny	Quantitative	Indian Ocean	Kumaran (1964)
<i>Thunnus obesus</i>	Bigeye tuna	Quantitative	Northern Peru	Fuentes <i>et al.</i> (1988)
<i>Xiphias gladius</i>	Swordfish	Quantitative	Western Northern Atlantic	Scott and Tibbo (1968)
<i>Orcynopsis unicolor</i>	Plain bonito	Qualitative	Unknown	Collette and Nauen (1983)
<i>Sarda sarda</i>	Atlantic bonito	Qualitative	Unknown	Yoshida (1980)

values, it was determined that approximately 1,937 miles² (or 5,017 km²) of the total area (up to 50 m deep) was made up of non-trawlable rock bottom. Assuming the first 25 m depth to account for 50% of the area and that 75% of this rock surface could support algal growth up to 25 m, the total surface area used in our calculations of macrophyte biomass was 1,882 km². Macrophytes density in the Azores was 550 g·m⁻² dry weight or 2,619 g·m⁻² wet weight (Neto, 1997), using a dry weight to wet weight ratio of 0.21 as given in Mackinson (1996). Using the same density, the Moroccan macrophyte biomass was estimated at 8.4 t·km⁻². Combining the macrophyte and phytoplankton biomass gave a total of 102.5 t·km⁻² for this functional group. For macrophytes, we used a value of P/B = 15 based on a guesstimate (A. Jarre-Teichman, pers. comm.). A weighted average of the P/B values for

phytoplankton and macrophytes yielded an estimate of 84.6 t·km⁻².

Artisanal fishers collected red and brown seaweeds, listed separately in the catch data as 'red seaweeds and other aquatic plants'. The red seaweeds were *Celidium* and *Graciliaris* species, and the brown algae *Laminaria*. The total landing of seaweeds was reportedly 5,190 t or 0.00884 t·km⁻².

Small zooplankton (Group 2)

Zooplankton were separated into large and small groups to reduce cannibalism. Small zooplankton were assumed to be copepods, cladocerans and polychaete larvae.

For the outer shelf and slope north of Cap Blanc, Weikert (1982) gave the average wet weight of invertebrate plankton (copepods and related invertebrates) as 101 mg m^{-3} up to 200 m depth. By integrating this value over depth, we calculated the total wet weight for the area to be 20.2 g m^{-2} in 1968.

Banse and Mosher estimated P/B for small zooplankton (microzooplankton) at 25 year^{-1} , which is consistent with the values used both in the Labrador model by Bundy *et al.* (2000) and the Alaskan Gyre model (Purcell, 1996). Our estimate for the Q/B ratio of small herbivorous zooplankton (90.4 year^{-1}) was taken directly from the Alaskan Gyre model (Purcell, 1996). Small zooplankton was assumed to feed exclusively on phytoplankton (Bundy *et al.*, 2000).

Large zooplankton (Group 3)

Although zooplankton are a crucial link between primary production and fish production, there was little information on them from Morocco. The large zooplankton group included chaetognaths, euphausiids, amphipods, isopods, mysids and jellyfish.

We used the P/B ratio given for euphausiids in the Alaskan Gyre model by Polovina *et al.* (1996) as our estimate for this functional group (P/B=6 year^{-1}). The Q/B ratio for salps, tunicates, and euphausiids used in the Labrador model (Bundy *et al.*, 2000) was utilised as a basis for this model. The Labrador model estimated Q/B at 21 year^{-1} , but we used the slightly higher value of 25 year^{-1} to incorporate small jellyfish into our estimate. Jellyfish have very high Q/B ratios, (e.g., 110 year^{-1} in the Alaskan Gyre model - considered high by the authors - Arai, 1996). To the best of our knowledge, jellyfish do not make up an important component of the Moroccan coastal ecosystem and were therefore not weighted heavily in our Q/B estimate.

Large zooplankton can be herbivorous (some euphausiid species), omnivorous (most euphausiids, amphipods and mysids) or carnivorous (chaetognaths and jellyfish) (Bundy *et al.*, 2000). The proportions of these groups off the coast of Morocco were unknown. The diet of euphausiids was based on Mauchline and Fisher (1980). Diet for isopods and amphipods are from qualitative accounts from Florida (Venier and Pauly, 1997). The resulting diet was: 58% for primary producers, 5% for small zooplankton, 10% for large zooplankton, and 2.25% for other benthos. These data were treated as very approximate and later modified (Table 2).

Worms (Group 4)

This group was dominated by polychaetes, but also included other nematodes and flatworms. Because there are so many species of worms living on and in the sediment, this was a diverse group. Some worms are errant, and others sedentary, and some are deposit or suspension feeders, whilst others are carnivorous. No information was found specifically referring to worm populations off the coast of Morocco.

No estimate of biomass was available for this group. P/B (2 year^{-1}) and Q/B (22 year^{-1}) estimates for polychaetes were taken from the Labrador model (Bundy *et al.*, 2000). The worms were assumed to be entirely detritivorous (Nesis, 1965).

Other benthos (Group 5)

This group includes non-predatory echinoderms, mollusks, pycnogonids, porifera, tunicates and benthic species of amphipod, isopod and copepoda. No estimate of biomass was available for this group. Using an average value of 'other benthic invertebrates' and 'mollusks' from the Labrador model by Bundy *et al.* (2000), we calculated the average P/B ratio for this functional group as 1.55 year^{-1} . Using the same method Q/B was estimated at 9.4 year^{-1} . In accordance with Nesis (1965), this group was assumed to feed entirely on detritus.

Predatory echinoderms (Group 6)

This benthic group was created to avoid large intra-group cannibalism and includes the true starfish (Asteroidea) and some members of the brittle stars (Ophiuridae) that feed entirely carnivorously or omnivorously. The remainder of the echinoderms were placed in group 4 (other benthos).

No estimate of biomass was available for this group. The P/B value (1.1 year^{-1}) was obtained by averaging values given for sea stars (0.4 year^{-1}) and brittle stars (1.8 year^{-1}) given in the model of the southern BC shelf (Jarre-Teichmann and Guénette, 1996). The same procedure was used to estimate Q/B at 4.44 year^{-1} (Jarre-Teichmann and Guénette, 1996). Other benthos accounted for 80% of the diet (Sloan, 1980), while the rest was attributed to detritus.

Table 2. Final diet matrix for non-fish functional groups. The original value entered in Ecopath value is in italic on the second row of a cell. A value smaller than 0.001 is represented by zero, while S.=small; L.=large; V.L.=very large; dw=deep-water; C= commercial

Prey	Predator												
	2	3	4	5	6	7	8	9	33	34	35	36	37
1. Primary producers	1	0.579				0.007	0.32						
2. S. zooplankton		0.06				0.14	0.1		0.064				
		<i>0.05</i>							<i>0.056</i>				
3. L. zooplankton		0.1						0.11	0.136	1	0.125	0.71	
									<i>0.045</i>				
4. Worms						0.04	0.03		0.064				
									<i>0.056</i>				
5. Other benthos					0.986	0.25	0.2	0.667	0.1		0.05		0.01
		<i>0.022</i>				<i>0.45</i>		<i>0.66</i>	<i>0.16</i>				
6. Predatory echinoderms						0.003							
7. Crabs						0.02			0.197				0.01
						<i>0.09</i>			<i>0.16</i>				
8. Shrimps						0.006	0.02		0.183				0.01
									<i>0.16</i>				
9. Lobsters													
10. Detrital feeders									0.007				
11. S. dw benthic													
12. L. dw benthic													
13. L. dw C													
14. S. demersal						0.012		0.212	0.027		0.21	0.04	0.07
								<i>0.21</i>	<i>0.024</i>				
15. M. demersal												0.04	0.07
16. M. demersal C											0.15	0.04	0.07
									<i>0.015</i>				
17. L. demersal													0.03
18. L. demersal C													
19. V.L. demersal													
20. V.L. demersal C													
									<i>0.005</i>				
21. S. bathypelagic									0.058			0.03	0.045
									<i>0.051</i>				<i>0.04</i>
22. M. bathypelagic									0.001				0.045
									<i>0.015</i>				
23. L. bathypelagic									0.001				
									<i>0.009</i>				
24. Mesopelagic prey									0.041		0.225	0.03	0.045
									<i>0.036</i>				
25. M. pelagic												0.03	0.03
													<i>0.02</i>
26. M. pelagic C									0.067			0.03	0.03
									<i>0.059</i>				<i>0.02</i>
27. L. pelagic													
28. Sardines									0.02		0.04	0.03	0.022
													<i>0.02</i>
29. Tunas													
30. S. demersal sharks													
31. L. dem. sharks C													
32. Pelagic sharks													
33. Cephalopods								0.01	0.033		0.2	0.02	0.511
								<i>0.02</i>	<i>0.130</i>				
34. Turtles													
35. Seabirds													
36. Baleen whales													0.0001
37. Toothed whales													0.001
													<i>0.029</i>
Detritus		0.261	1	1	0.004	0.527	0.35						
					<i>0.2</i>	<i>0.27</i>							

Crabs (Group 7)

This functional group consists of macrobenthic crabs. Basic parameters were estimated using male and female edible crab (*Cancer pagurus*), green crab (*Carcinus maenas*), and spinous spider crab (*Maja squinado*). No estimate of biomass was available for this group. In absence of local estimates a P/B of 1.8 year⁻¹ and a Q/B of 10 year⁻¹ were used from Southern British Columbia (Jarre-Teichmann and Gu enette, 1996).

Diet information was based on juvenile green crab and velvet crab (*Necora puber*) (Gonzalez-Gurriaran *et al.*, 1995). Cannibalism in crabs was high (18.7%) because large crabs feed on small crabs. This value was halved with the difference split equally into the dominant prey items, other benthos and detritus. The resulting diet was composed of 45% other benthos, 27% detritus, 9% crabs, 4% worms, 1% small demersal fish, 14% small zooplankton, 0.6% shrimps, 0.4% Predatory echinoderms. Cannibalism and predation on other benthos were reduced to balance the model (Table 2).

Shrimps (Group 8)

The main species of shrimp found off the coast of Morocco are deepwater rose shrimp (*Parapanaeus longirostris*), and pink shrimp (*Penaeus notialis*) although scarlet shrimp (*Plesiopenaeus edwardsianus*), royal shrimp (*Pleoticus robustus*) and blue shrimp (*Aristeus antennatus*) are also present. No estimate of biomass was available for this group. There was no information for shrimp P/B in the waters off North Africa and a value of 1.7 was used from Norwegian waters (Hopkins, 1988). In absence of data for Q/B, P/Q was given a value of 0.15 year⁻¹ (Bundy *et al.*, 2000).

The shrimp diet was based on *Crangon crangon* (Pihl, 1985) and generic herbivorous and predatory shrimps (Venier and Pauly, 1997). Of the diet, 31% was allocated to primary production, 2% to worms, 10% each for other benthos, small and large zooplankton, 35% to the detritus and the remaining 2% to cannibalism.

Lobsters (Group 9)

Three species of lobster were present in Moroccan waters, the European lobster (*Homarus gammarus*), the spiny lobster (*Palinurus elephas*) and the Norwegian lobster (*Nephrops norvegicus*). No estimate of biomass was available for this group. Values for P/B and Q/B were taken from the Newfoundland-Labrador Model of

Bundy *et al.* (2000) as 2.82 year⁻¹ and 5.85 year⁻¹ respectively.

The frequency of occurrence of various items in the diet of the Norwegian lobster has been described as consisting of 66% other benthos, 11% large zooplankton, 21% small demersal fish and 2% cephalopods (Cristo, 1998).

Detrital feeders and herbivores (Group 10)

This small group is dominated by three species of mullet (Mugilidae) and also contains salemma (*Sarpa sarpa*) and planehead filefish (*Stephanolepis hispidus*). All of the mullet species were assumed to be commercially fished, although the catch data did not identify them. This demersal group inhabits coastal regions often forming shoals. No estimate of biomass was available for this group.

Natural mortality for this group was calculated from thinlip mullet (*Liza ramada*), thicklip grey mullet (*Chelon labrosus*) and golden grey mullet (*Liza aurata*) and averaged, equaling 0.368 year⁻¹. As a first attempt, an assumption was made that F was equal to half of M which yielded a value of 0.552 year⁻¹. This value may be overestimated. A Q/B of 7.161 year⁻¹ was estimated as an average for all species in this group.

The diet of mullet was described qualitatively in Fischer *et al.* (1987) and Billard (1997). Bennett provided diet composition data for *Sarpa salpa* from South Africa. Data for *Stephanolepis hispidus* came from Adams (1976), and is based on fish sampled off North Carolina, USA. All species were detritivores (37%) and herbivores (41%) although a small percentage of worms (1%) and other benthos (8%) were also assumed consumed.

Small deep-water benthic (Group 11)

The fish in this small, non-commercial group generally inhabit depths below 200 m, are 30 to 65 cm in total length and remain close to the bottom. Although this group is labeled as small, they actually are of similar body size as the medium demersal group. They differ by their diet consisting of a high proportion of small demersals. Comprehensive data were not available for argentine (*Argentina sphyreaena*), comber (*Serranus cabrilla*) and blackbelly rosefish (*Helicolenus dactylopterus*). Data were very scarce for deep-sea lizardfish (*Bathysaurus ferox*).

No estimate of biomass was available for this group. A natural mortality of 0.352 year^{-1} was used for P/B and was averaged from blackbelly rosefish and comber. The mean Q/B value of 6.167 year^{-1} was calculated using rough estimates from FishBase for blackbelly rosefish, comber and argentine.

Cohen's (1990) overview of Argentinidae provided the qualitative diet data for *Argentina sphyraena* from an unknown location. Diet composition data for *Serranus cabrilla* came from Greece (Labropoulou and Eleftheriou, 1997) and for *Helicolenus dactylopterus* from South Africa (Yap, 1988). Small deep-water benthic fish generally consumed mainly small demersals (33%) and other benthos (18%). Upon balancing the model, the proportion of lobsters in the diet had to be decreased from 3 to 0.1%, and that of small demersals to 24.9%, worms and other benthos have been augmented (Table 3), while the medium and large demersals were removed from the diet.

Large deep-water benthic (Group 12)

The fish in this commercially unimportant group reach total lengths larger than 1 m. This group consisted of Kaup's arrowtooth eel (*Synaphobranchus kaupii*), rabbitfish (*Chimaera monstrosa*) and pudgy cuskeel (*Spectrunculus grandis*).

No biomass estimate was available for this group. The average P/B was calculated for all species in the group and resulted in a value of 0.27 year^{-1} . Following the same procedure, Q/B was found to equal 2.985 year^{-1} .

Detailed diet information for *Synaphobranchus kaupii* was obtained from Gordon and Mauchline (1996) from a study on the Rockall Trough in the North Atlantic and for *Chimaera monstrosa* from the Western Mediterranean (MacPherson, 1980). Only presence/absence data for *Spectrunculus grandis* were available (Mauchline and Gordon, 1984). A first approximation to a diet composition was thus obtained by dividing equally the whole diet into the groups represented. Large deep-water benthic fish fed mainly on crabs (28%), shrimps (20%), medium demersal commercial fish (11%), cephalopods (12%) and other benthos (20%).

Large deep-water benthic – commercial (Group 13)

Fish in this group have the same characteristics as the large deep-water benthic fish, except that they

were caught commercially in 1984. The group includes alfonsino (*Beryx decadactylus*), wreckfish (*Polyprion americanus*), European conger eel (*Conger conger*), anglerfish (Lophiidae), black-bellied angler (*Lophius budegassa*), and angler (*Lophius piscatorius*).

Natural mortality was calculated for black-bellied angler, angler and conger eel. F was assumed to be half the natural mortality (0.355 year^{-1}) so a P/B value of 0.533 year^{-1} was used. Q/B was calculated for black-bellied angler, wreckfish and conger eel, yielding a mean of 4.47 year^{-1} .

Diet composition data were available from Spain for black-bellied angler, European conger eel (Olaso and Rodriguez-Marin, 1995) and angler (Velasco *et al.*, 1996). Dietary information for alfonsino was qualitative (Shimizu, 1984) and because it overlapped with other fish in the group, it was not used for the calculation. This group consumes a higher percentage of fish (63%) than the other deep-water benthic groups. Upon balancing the model, the percentage of medium demersal commercial fish and very large demersal commercial was decreased (from 63 to 28%), while medium pelagic and small sharks (group 30) were removed from the diet. To compensate, the other groups' percentages were increased (Table 3).

Small demersal (Group 14)

Small demersals, while remaining close to the seafloor, inhabit shallower water than the deeper water groups (11-13 above) with some even being classified as intertidal. This large group is composed of fish smaller than 30 cm, including seargent major *Abudelfduf scrutalis*, damselfish *Charis charis*, transparent goby (*Aphia minuta*), rocky goby (*Gobius paganellus*), black goby (*Gobius niger*), cardinal fish (*Apogon imberbis*), axillary wrasse (*Symphodus mediterraneus*), big-scale sand smelt (*Atherina boyeri*), scaldfish (*Arnoglossus laterna*), goldsinny wrasse (*Ctenolabrus rupestris*), longspine snipefish (*Macrorhamphosus scolopax*), Cadenat's rockfish (*Scorpaena loppei*), Madeira rockfish (*Scorpaena maderensis*) and corkwing wrasse (*Symphodus melops*).

None of these species were commercially fished and no biomass estimate was available for this group. P/B equaled natural mortality, estimated at 1.445 year^{-1} . Q/B was estimated at 10.957 year^{-1} .

Due to their small size and lack of commercial importance, relatively little is known on the diet composition of these species. Diet information

Table 3. Final diet matrix for fish groups. When modified, the original value entered in Ecopath value is in italic on the second row of a cell. S. =small; L.=large; V.L.=very large; dw=deep-water; C= commercial

Prey	Predator (by group number)																						
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1. Primary producers	0.41				0.008	0.036	0.05		0.041			0.045					0.04		0.1			0.006	0.005
2. S. zooplankton					0.11	0.026		0.050	0.011			0.238			0.569	0.159	0.201	0.097	0.4	0.010			0.085
3. Large zooplankton		0.039	0.016	0.001	0.077	0.032	0.048	0.03	0.049	0.03	0.318	0.084	0.32	0.572	0.17			0.35	0.043	0.025	0.003	0.0004	
4. Worms	0.011	0.161	0.075		0.061	0.155	0.103	0.059	0.043		0.05	0.084	0.069	0.011		0.023				0.005	0.017	0.003	
5. Other benthos	0.083	0.255	0.197	0.143	0.373	0.468	0.33	0.175	0.143	0.203	0.053	0.1	0.116	0.299	0.1				0.075	0.008	0.148	0.137	0.036
6. Pred. Echinoderms			0.002			0.036	0.029		0.006													0.123	0.032
7. Crabs		0.089	0.276	0.001	0.038	0.006	0.142	0.024	0.123		0.052				0.083					0.008	0.124	0.097	
8. Shrimps		0.06			0.084		0.136	0.040			0.037											0.087	
9. Lobsters		0.084	0.197	0.001	0.009	0.087	0.162	0.564	0.342	0.08		0.126			0.083	0.1			0.025	0.007	0.205	0.026	
10. Detrital feeders		0.06			0.089		0.155	0.466	0.311		0.113	0.100				0.222						0.024	
11. S. dw bent.		0.001				0.006	0.013																0.002
12. L. dw bent.																							0.001
13. L. dw bent. C																							0.09
14. S. demersal		0.03			0.05			0.088	0.27	0.007								0.057		0.02	0.027		0.004
15. M. demersal		0.33			0.123	0.090		0.074	0.222	0.030										0.065			0.003
16. M. demersal C		0.016			0.157		0.0002	0.004	0.27	0.188						0.05	0.024		0.047	0.018	0.037	0.07	
17. L. demersal		0.01			0.011			0.022	0.222	0.109												0.033	0.057
18. L. demersal C			0.114		0.21		0.008	0.005	0.005	0.055	0.04									0.097	0.030	0.055	0.004
19. V.L. demersal		0.08			0.632		0.063	0.029	0.052	0.222	0.127				0.007					0.052		0.050	
20. V.L. demersal C					0.09		0.001	0.031			0.12										0.004	0.038	0.006
21. S. bathypelagic					0.046						0.071											0.034	0.005
22. M. bathypelagic																					0.026	0.053	0.0004
23. L. bathypelagic		0.01																				0.048	
24. Mesopelagic prey spp																						0.029	
																							0.02
																							0.01
																							0.022
																							0.03
																							0.05
																							0.130
																							0.035
																							0.045
																							0.031
																							0.027
																							0.14
																							0.027
																							0.019
																							0.019
																							0.020
																							0.025

came from other countries (via FishBase), as no dietary studies were found for Morocco. The diet is dominated by other benthos (43%), shrimps (9%), crabs (8%), worms (6%) and small zooplankton (11%). Cannibalism was too high (13%) and this was halved with the remainder being allocated proportionally between the other groups (see Table 3). Upon balancing the model, the proportion of shrimps in the diet was found to be too high and was decreased to 0.9%.

Medium demersal (Group 15)

This large group consists of fish from 30 to 60 cm that are not commercially caught. The group includes Mediterranean rainbow wrasse (*Coris julis*), broadnosed pipefish (*Syngnathus typhle*), dragonet (*Callionymus lyeara*), painted comber (*Serranus scriba*), cuckoo wrasse (*Labrus bimaculatus*), poor cod (*Trisopterus minutus*), fourspotted megrim (*Lepidorhombus boscii*), East Atlantic peacock wrasse (*Symphodus tinca*), European flounder (*Platichthys flesus*), lesser African threadfin (*Galeoides decadactylus*), blotched picarel (*Spicara maena*), common Atlantic grenadier (*Nezumia aequalis*), hollowsnout grenadier (*Caelorinchus caelorhincus*), slender rockfish (*Scorpaena elongata*) and ballan wrasse (*Labrus bergylta*). The threshold (30 cm) between small and medium demersals was based mainly on the diet, the present group consuming very small demersal fish. The lesser weever (*Trachinus vipera*) was placed in the medium demersal group along with the greater weever (*Trachinus draco*), although it is small, because 92% of its diet is 'other fish' (Gibson and Robb, 1996), assumed to be small demersals.

No biomass estimate was available for this group. P/B, assumed equal to natural mortality, was estimated at 0.69 year⁻¹. Q/B was estimated at 8.558 year⁻¹.

Of the 18 medium demersal fish species that diet data was available for, 10 merely provided presence/absence of food items. Table 1 highlights these data, which originate from a number of unknown locations and from North Carolina and Namibia. The diet of medium demersal (non-commercial) feeders is dominated by other benthos (32%), crabs (14%), shrimps (16%), worms (10%) and fish (15%).

Medium demersal – commercial (Group 16)

Medium demersal commercial species are caught in large numbers by trawling. The group is

primarily represented by bogue (*Dentex maroccanus*), common two-banded bream (*Diplodus vulgaris*), Senegal seabream (*Diplodus bellotti*), common pandora (*Pagellus erythrinus*), axillary seabream (*Pagellus acarne*) and *Pagellus bellottii* Moroccan white seabream (*Diplodus sargus cadenati*), zebra seabream (*Diplodus cervinus cervinus*), spiny gurnard (*Lepidotrigla dieuzeidei*), longfin gurnard (*Chelidonichthys obscurus*), small red scorpionfish (*Scorpaena notata*), saddled seabream (*Oblada melanura*), and narrowhead grey mullet (*Mugil capurrii*) as well as some Mugilidae (grey mullets), Mullidae (mulletts) and Soleidae (soles). Of these, the Sparidae have traditionally constituted the most significant proportion of the catch.

The estimate of fishing mortality (1.219 year⁻¹) published in Mennes (1985) and based on length structure estimated for *Boops boops*, *Dentex maroccanus*, *Diplodus vulgaris*, *Diplodus bellotti*, *Pagellus erythrinus*, *Pagellus acarne* and *Pagellus bellottii* was considered an overestimate. Instead, we assumed an F value of 0.6 year⁻¹, roughly equal to natural mortality (M=0.66 year⁻¹). Landings of 1.1149 t·km⁻² divided by fishing mortality result in a biomass of 1.858 t·km⁻². Q/B was estimated at 7.924 year⁻¹.

Although many of the fish in this group are common commercial species, few studies on diet composition has been found for the region (Table 1). Diet composition was very diverse in this group as 19 of the models' functional groups were represented. Other benthos, crabs, shrimps and worms composed 68% of the diet, the remainder being mostly fish (see Table 3). Upon balancing the model, cannibalism had to be reduced from 6.3% to 0.8% and the remainder redistributed to other groups (Table 3).

Large demersal (Group 17)

The non-commercial large demersal group was composed of fish from 60 to 120 cm total length. Although present in catch statistics, these species are not common in Morocco. The group included parrot seaperch (*Callanthias ruber*), brill (*Scophthalmus rhombus*), common guitarfish (*Rhinobatos rhinobatos*), forkbeard (*Phycis phycis*) and red bandfish (*Cepola macrophthalmia*). Much is known about species such as orange roughy (*Hoplostethus atlanticus*) for other areas, however, since Morocco is at the extreme end of this species' North Eastern Atlantic range (Nakamura *et al.*, 1986). Few data relevant to Morocco were available.

No biomass estimate was available for this group. Natural mortality was calculated for four species yielding an averaged value of 0.494 year^{-1} . A value of $Q/P = 7.450 \text{ year}^{-1}$ was obtained based on orange roughy, brill, red bandfish and forkbeard.

Large demersals fed primarily on shrimps and other benthos although smaller fish were also consumed. The diet information came from a wide geographical range (Table 1) and the result is that many of the species in the diet information were not indigenous to Morocco. The qualitative diet data of *Scophthalmus rhombus* was allocated as 40 % to shrimp, 20 % to crab, 20 % to other benthos and the final 20 % was split between the two medium demersal groups. *Alepocephalus bairdii* ate other benthos (60 %), zooplankton (20 %) and the 20% fish were split between medium demersal groups. *Cepola macrophthalmus* diet was distributed between zooplankton (small 45 %, large 45 %), worms (5%) and other benthos (5%). Large demersals were thus assumed to consume 5% and 7.2% small and large zooplankton, 0.6% worms, 12% other benthos, 47% shrimps, 1.3% cephalopods, 10% very large demersals, and small amounts of 5 other fish groups. To balance the model, the amount of demersal fish consumed was decreased and the proportion of large invertebrates and small pelagic fish increased (Table 3).

Large demersal – commercial (Group 18)

Large demersal (commercial) fish are generally caught by trawling and include canary drum (*Umbrina canariensis*), grey gurnard (*Chelidonichthys gurnardus*), false scad (*Caranx rhonchus*), common dentex (*Dentex dentex*), large-eye dentex (*Dentex macrophthalmus*), brown meagre (*Sciaena umbra*), splendid alfonso (*Beryx splendens*), blackspot seabream (*Pagellus bogaraveo*), gilthead seabream (*Sparus aurata*), bluespotted seabream (*Pagrus caeruleostictus*), John dory (*Zeus faber*), red porgy (*Pagrus pagrus*), European seabass (*Dicentrarchus labrax*), longneck croaker (*Pseudotolithus typus*), greater forkbeard (*Phycis phycis*) and European eel (*Anguilla anguilla*). The majority of the species in this group remain at the bottom in water depths greater than 10 m for their entire lives but some such as gilthead and European seabasses live in the surf zone, lagoons or up rivers, while *Caranx rhonchus* is mainly pelagic.

The value of fishing mortality (1.77 year^{-1}) published in Mennes (1985) and based on length structure estimated for only two species, *Dentex macrophthalmus* and *Spondyliosoma cantharus*

was considered an overestimate. Instead we assumed an F value of 0.4 year^{-1} that is, roughly equal to natural mortality ($M=0.422 \text{ year}^{-1}$). Landings of $0.8952 \text{ t}\cdot\text{km}^{-2}$ divided by fishing mortality result in a biomass of $2.236 \text{ t}\cdot\text{km}^{-2}$. Q/B was estimated at 5.987 year^{-1} .

Of the 26 species in this group, there were diet data for 17 fish and only 5 of these were qualitative studies (Table 1). Many of these data sets were from the coast off Spain and there can be some confidence in the diet values for this group. Diet items listed are very diverse with representatives of 17 functional groups. Shrimps (31%) dominated the diet, while sardine, small demersal and medium demersal commercial dominated the fish portion with 5-7% of the weight each. To balance the model, two prey items had to be reduced: the medium demersal commercial and small demersal sharks (group 30) to one tenth of their original proportion of the diet (Table 3).

Very large demersal (Group 19)

Very large demersal were distinguished from large demersal by their extremely large size. This small group in term of biomass consists of blue ling (*Molva dypterygia*), oilfish (*Ruvettus pretiosus*), smalltooth sawfish (*Pristis pectinata*) and Mediterranean moray (*Muraena helena*).

None of these species were reported as being caught commercially and no biomass estimate was available for this group. A natural mortality estimate of 0.157 year^{-1} ($=P/B$) for blue ling was used to represent the entire group. An averaged value for Q/B of 3.881 year^{-1} was calculated based on blue ling and smalltooth sawfish.

Diet information for very large demersals was qualitative and expressed in general terms. However, the work of Cohen *et al.* (1990) on blue ling and Sierra *et al.* (1994) on oilfish were sufficient to determine the importance of fish in the diets. Qualitative values were equally allocated to small demersal, medium demersal and medium demersal commercial groups (22% each), the remaining was apportioned equally between cephalopods and other benthos (16.7% each). To balance the model, the proportion of medium demersal commercial (group 16) was subsequently reduced to one tenth of the original value (Table 3).

Very large demersal – commercial (Group 20)

Very large demersal commercial fish generate significant revenue, although they are not landed in vast quantities (Abdelali, 1995). Senegalese and European hakes, *Merluccius senegalensis* and *M. merluccius*, are also members of this group along with bluefish (*Pomatomus saltatrix*), dusky grouper (*Epinephelus marginatus*), goldblotch grouper (*Epinephelus costae*), silver scabbardfish (*Lepidopus caudatus*), meagre (*Argyrosomus regius*), largehead hairtail (*Trichiurus lepturus*) and greater amberjack (*Seriola dumerili*). *Merluccius senegalensis* undergoes latitudinal migration, but was here assumed to be in this area for the whole year.

Natural mortality, estimated at 0.316, plus fishing mortality yields a P/B value of 0.716 year⁻¹. Q/B was estimated at 4.89 year⁻¹. The fishing mortality for European hake has been estimated at 0.4 year⁻¹ (Anon., 1986). Assuming that all the species of this group are exploited at the same rate and landings of 0.716 t·km⁻², biomass was estimated at 0.3937 t·km⁻². This estimate was increased to 0.5 t·km⁻² in an attempt to account for the other species in the group.

Diet data were available for each of the five species in the group. It is notable that cannibalism within the group was caused by European hake (Guichet, 1995) and that large pelagics were consumed by the largehead hairtail (Meyer and Smale, 1991), which migrate vertically so that during the day they feed at the surface (Nakamura and Parin, 1993). Silver scabbardfish also migrate to the surface but do so during the night to feed on sardines (Meyer and Smale, 1991).

Fish of this group are assumed to consume shrimps (11.2%), cephalopods (4.4%), medium demersal commercial (13.2%) and non-commercial (10%), sardines (12%). The remaining is divided in seven other fish groups. Predation on commercial demersal fish was later reduced by about half. (Table 3).

Small bathypelagic (Group 21)

Small bathypelagic fish range in length from the 2.9 cm for humpback anglerfish (*Melanocetus johnsoni*) to the 30 cm black slimehead. The group inhabits oceanic water between 200 and 1000 m and is dominated by lanternfishes (Myctophidae), but also include highlight hatchetfish (*Sternoptyx pseudoscura*), Warming's lanternfish (*Ceratoscopelus*

warmingii), humpback anglerfish (*Argyroteleus olfersi*), brownsnout spookfish (*Dolichopteryx longipes*) and black slimehead (*Hoplostethus cadenati*). Small bathypelagics migrate vertically, feeding on zooplankton during the night. Although they are widely distributed, little has been recorded on the precise diet or biomass for this group and the results from this group are a combination of pieces of information from many species.

Natural mortality data from FishBase were only available for three species. The value for humpback anglerfish was 3.9 year⁻¹, which seemed high but was included in the average of 1.768 year⁻¹. Q/B was estimated at 12.648 year⁻¹.

There were precise diet composition data for only 2 of the 10 species in this group. Hopkins and Baird (1985) showed the stomachs of the highlight hatchetfish to contain worms, other benthos, zooplankton, bathypelagic fish and mesopelagic fish in the Gulf of Mexico. The qualitative description found for the Warming's lanternfish was similar to the latter species (Duka, 1986). Thus, 27 % was assigned to other benthos, 25 % to large zooplankton, 13 % to small zooplankton, 4% to small deep-water benthic fish, 7 % to small bathypelagic fish, 11 % to mesopelagic prey species and 3 % to phytoplankton. During the balancing process, the predation on other benthos and small deepwater (group 12) were reduced by half or more and the resulting surplus redistributed among other groups (Table 3).

Medium bathypelagic (Group 22)

This group was distinguished from the small bathypelagic by generally being larger (39 cm mean length) and consuming more fish and less zooplankton. It is composed primarily of Stomiidae (viperfish and dragonfish) and Paralepididae (barracudina), but also includes hammerjaw (*Omosudis lowei*), black snake mackerel (*Nealotus tripes*), rosy dory (*Cyttopsis rosea*), longnose tapirfish (*Polyacanthonotus challengerii*), ribbon barracudina (*Arctozenus risso*), rosy dory (*Cyttopsis rosea*), Dana viperfish (*Chauliodus danae*), and Atlantic pomfret (*Brama brama*). Although Atlantic pomfret grow to 1 m total length, it was placed in this group because most pomfret caught in Morocco tend to be very small, much smaller than their maximum length (K. Erzini, University of Algarves, Portugal, pers. comm. 2000). No biomass estimate was available for this group. P/B and Q/B were estimated at 0.525 year⁻¹ and 7.482 year⁻¹.

Of the 11 species in this group, diet data were only available for 5 of them. The stomachs of Dana viperfish (Sierra *et al.*, 1994) and the ribbon barracudina (Post, 1984) contained unidentified benthic crustaceans and fish. Black snake mackerel fed mainly on anchovies (Grove and Lavenberg, 1997). The longnose tapirfish consumed benthic and planktonic invertebrates. Atlantic pomfret consumed cephalopods, euphausiids and “bony fish” (Sierra *et al.*, 1994). The diet data for medium bathypelagic is dubious because most of them are qualitative and general (unknown locality). This group was assumed to consume 22% other benthos, 10% shrimps, 13.3% large zooplankton, 6.7% worms and 11.6% cephalopods. Unidentified fish were evenly split between small bathypelagic, small demersals and sardines. In order to balance the model, predation on other benthos and sharks was reduced by half or more and the surplus redistributed among other groups, especially small bathypelagics (Table 3).

Large bathypelagic (Group 23)

Large bathypelagic fish contained roughsnout grenadier (*Trachyearincus scabrus*), common mora (*Mora moro*), slender snipe eel (*Nemichthys scolopaceus*), pelican eel (*Eurypharynx pelecanooides*) and escolar (*Lepidocybium flavobrunneum*). These species, and particularly the pelican eel, are widely distributed although none are commercially fished. Only escolar migrates vertically at night.

The biomass of large bathypelagics was not available, but was necessary to start balancing the Ecopath model. Consequently a value of 0.02 year⁻¹ was initially used, before being increased to 0.24 year⁻¹ when balancing. Natural mortality was calculated from mean generic value from FishBase, yielding a value of 0.435 year⁻¹. Q/B was estimated at 4.34 year⁻¹.

Qualitative stomach contents information was located for 4 of the 5 species in the group and were obtained from a wide geographical range (see Table 1). Benthic invertebrates, including cephalopods dominated the diet composition and more precisely 6% worms, 27% other benthos, and 24% cephalopods. Fish were represented by small bathypelagics (17%), medium pelagic commercial and large pelagic (7% each), and cannibalism was estimated at 14%. In order to balance the model, cannibalism had to be reduced to 2% and the remainder redistributed mostly to medium pelagic commercial and large pelagic (Table 3).

Mesopelagic prey species (Group 24)

Mesopelagic prey species are very small (3-20 cm total length), numerically significant fish inhabiting high oceanic water. They are not caught commercially but are an important prey item for pelagic species. This group of 15 species is dominated by Myctophidae and Sternoptychidae, but also includes garrick (*Cyclothone braueri*), silvery cod (*Gadiculus argenteus argenteus*), veiled anglemouth (*Cyclothone microdon*), oceanic lightfish (*Vinciguerria nimbaria*) and sand smelt (*Atherina presbyter*). There are similarities between this group and small bathypelagics, but members of the latter group seem located slightly higher in the water column; more importantly, the mesopelagics are preyed upon by small bathypelagics. Myctophidae and oceanic lightfish undertake daily vertical migrations and feed at night in surface layers, hiding at depth during the daylight hours.

There was no biomass estimate available. P/B was estimated at 2.377 year⁻¹ while a Q/B value of 13.04 year⁻¹ was based on two species, silvery cod and sand smelt.

Diet data were only available for 7 of the 15 species in this group from various regions (Table 1). The qualitative diet information of *Benthosema glaciale* was equally split between large and small zooplankton and for *Atherina presbyter* went entirely to large zooplankton. The group primarily ate zooplankton (small 47%, large 26%), worms 1% and other benthos 26%. When balancing the model, this last item has been reduced to 10% and the remainder redistributed into the other groups.

Medium pelagic (Group 25)

Medium pelagic fish range in size from 40-110 cm and are not commercially caught. The group is composed of derbio (*Trachinotus ovatus*), pilotfish (*Naucrates doctor*), African threadfish (*Alectis alexandrinus*), the Atlantic saury (*Scorpaenopsis saurus saurus*), the Mediterranean flyingfish (*Cheilopogon heterurus*), the Cornish blackfish (*Schedophilus medusophagus*), the slender sunfish (*Ranzania laevis*) and the driftfish (*Cubiceps gracilis*). The pilotfish has a semi-obligate commensal relationship with sharks, rays, other bony fishes and turtles (Cervigón *et al.*, 1992).

No estimate of biomass was available for this group. Using the generic values from FishBase,

P/B and Q/B were estimated at 1.31 year⁻¹ and 8.47 year⁻¹ respectively.

Diet composition data were available for the Mediterranean flyingfish from the Eastern Pacific (Lipskaya, 1987) and for the driftfish (Gorelova *et al.*, 1994) from an unknown location, both indicating that feeding was almost entirely on zooplankton. Similarly, qualitative information for saury identified their diet to consist entirely of zooplankton (Frimodt, 1995). Derby consumed unknown proportions of crab, shrimp and small bathypelagics in Senegal (Diouf, 1996) so diet values were allocated evenly between these preys. Thus, this group was assumed to consume 57% large zooplankton, 16% small zooplankton, 8% each crabs and shrimps, and 10% mesopelagics.

Medium pelagic - commercial (Group 26)

This valuable commercial group consisted of Atlantic and Mediterranean horse mackerels (*Trachurus trachurus* and *T. mediterraneus*), chub mackerel (*Scomber colias*) crevalle jack (*Caranx hippos*), allis and twaite shads (*Alosa alosa* and *A. fallax*) and spotted seabass (*Dicentrarchus punctatus*), West African Spanish mackerel (*Scomberomorus tritor*) and Atlantic mackerel (*Scomber scombrus*). Mediterranean horse mackerels do spend some time amongst demersal fish but, because the majority of their biomass is in pelagic shoals (Smith-Vaniz, 1986), they have been included in this group. The Scombridae and Carangidae in this group form large shoals close to the shore (Collette and Aadland, 1996). The shads and spotted seabass remain close to the shore and are even caught in rivers (Whitehead, 1985).

No estimate of biomass was available for this group. An averaged natural mortality of 0.627 year⁻¹ was obtained from almost all species. The fishing mortality was estimated as one third of natural mortality yielding a P/B of 0.941 year⁻¹. Q/B was estimated at 6.314 year⁻¹.

Data on food items were available for 8 of the 9 species in the group, but comprehensive diet composition data for only 2 species, Atlantic mackerel (Wosnitza, 1975) and chub mackerel (*Scomber colias*). Both scombrids were shown to primarily consume zooplankton (Peru; Mendo, 1984). *Scomberomorus tritor* consumed only sardines (Cayré *et al.*, 1993).

Mediterranean horse mackerels feed on worms, sardines and plants (Smith-Vaniz, 1986) but worms were limited at 20% of the diet to favor pelagic species. Twaite shad consumed shrimps,

plankton and sardines (Moreira *et al.*, 1992), which we assumed had equal weight in the diet. Allis shad ate unspecified finfish, insects and benthic invertebrates (Billard, 1997). Finfish were equally apportioned to mesopelagic prey species and sardines. Atlantic horse mackerels consume zooplankton, benthic invertebrates and unspecified finfish (Frimodt, 1995). We assumed that the diet of this group was dominated by sardines (26%), and invertebrates (25%), the remaining being distributed among 6 groups of fish (see Table 3). The modifications to the diet were minor and involved decreasing the proportion of lobster in favor of zooplankton.

Large pelagic (Group 27)

Large pelagic fish are restricted to the agujon needlefish (*Tylosurus acus acus*), leerfish (*Lichia amia*) and common dolphinfish (*Coryphaena hippurus*). Tunas, the other large pelagics in the model, consume both agujon needlefish and the common dolphinfish.

No estimate of biomass was available for this group and none of these fish are harvested commercially. Using generic values from FishBase yielded an average natural mortality (M) of 0.467 year⁻¹. In absence of data, fishing mortality was assumed to equal 2/3 of M or 0.31 year⁻¹. Thus P/B was estimated at 0.777 year⁻¹. Q/B (=3.206 year⁻¹) was based on common dolphinfish and leerfish.

Leerfish feed uniquely on fish (unspecified) (Bennett, 1989). The diet composition of common dolphinfishes were used as representative for the whole group (Palko *et al.*, 1982). Their diet is dominated by medium pelagic, commercial (22.6%) and non-commercial (40%), and tunas (11%). The remainder of the diet is composed of 4% large pelagics, 5% sardines, small demersal (5.6%), medium demersal (2%). The tuna had to be removed from the diet composition in favor of sardines (Table 3).

Sardines (Group 28)

There are four species of Clupeidae along the coast of Morocco, the European sprat (*Sprattus sprattus*), the European pilchard (*Sardina pilchardus*), the round sardinella (*Sardinella aurita*), the Madeiran sardinella (*Sardinella maderensis*), and the European anchovy (*Engraulis encrasicolus*). The grouping of sardines in the catch data meant that all have been classified as commercially fished although the European pilchard is by far the most important pelagic species caught off Morocco. All

of the Clupeidae in this group rise to the surface at night.

The biomass of pilchard (15.53 t·km⁻²) was taken from Lamboeuf (1997). As sardines constitute only 88% of the group landings, the pilchard estimate was augmented proportionally to 17.647 t·km⁻². A P/B value of 1.1 year⁻¹ was obtained by summing natural (0.6 year⁻¹) and fishing mortality (0.5 year⁻¹; García Santamaría, 1995). Q/B was estimated at 11.081 year⁻¹.

Quantitative diet composition data for the European sprat off the Atlantic coast of England showed 100% of its diet were zooplankton (Last, 1987). Qualitative information showed that European pilchards and European anchovies consumed only zooplankton (Whitehead, 1985). Round sardinella consumed phytoplankton, zooplankton, shrimp and other benthos (Venezuela; Rincon *et al.*, 1988) while Madeiran sardinellas (Senegal; Diouf, 1996) fed on zooplankton, phytoplankton and detritus. Thus we assumed that this group consumed 44% small zooplankton, 35% large zooplankton, 7.5% other benthos, 2.5% shrimps, and 5% detritus.

Tunas (Group 29)

The tunas group included yellowfin (*Thunnus albacares*), bluefin (*Thunnus thynnus*), bigeye (*Thunnus obesus*), albacore (*Thunnus alalunga*), frigate tuna (*Auxis thazard*), little tunny (*Euthynnus alletteratus*), skipjack (*Katsuwonus pelamis*), Atlantic bonito (*Sarda sarda*) as well as related species, longbill spearfish (*Tetrapturus pfluegeri*), Atlantic white marlin (*Tetrapturus albidus*), Atlantic blue marlin (*Makaira nigricans*) and swordfish (*Xiphias gladius*).

Although the majority of the species in this group are highly migratory, it was unknown how long they spend on the coast of Morocco. They were assumed to be present only 4 months. All species aside from longbill spearfish were commercially caught off the coast of Morocco. To accommodate the catches, tuna migration was set at 0.06 t·km⁻²·year⁻¹ for immigration and 0.06 t·km⁻²·year⁻¹ for emigration.

Natural mortality of 0.533 year⁻¹, added to fishing mortality of 0.109 year⁻¹ (assessment reports, www.iccat.es) yielded a P/B value of 0.642 year⁻¹. Q/B was estimated at 3.774 year⁻¹. Using the catch (0.006 t·km⁻²·year⁻¹) and fishing mortality, the biomass was estimated at 0.058 t·km⁻².

Diet information from various oceans and localities was available for 11 of the species in this

group of 14 (see Table 1). The resulting diet for this group is quite diverse, including 21 functional groups. The most important prey items are medium pelagic commercial (14.4%), sardines (19.3%) and cephalopods (15%) (see Table 3). To balance the model, the proportion of small demersal and very large demersal commercial were decreased in favor of medium demersal commercial species (Table 3).

Small demersal sharks and rays-commercial (Group 30)

Small deep dwelling sharks and rays included elasmobranchs from 40 cm to 150 cm in length living on, or close to, the sea bottom. Although some species are caught commercially their identity is uncertain which ones as most landings are not reported by species. Dogfishes (Dalatiidae) and rays (Rajidae) compose the majority of this large group, which includes catsharks (Scyliorhinidae), common crampfish (*Torpedo torpedo*), longnose spurdog (*Squalus blainville*), birddeak dogfish (*Deania calcea*), sharpnose sevengill shark (*Heptranchias perlo*), starry smooth-hound (*Mustelus asterias*), African sawtail catshark (*Galeus polli*), smooth lanternshark (*Etmopterus pusillus*), great lanternshark (*Etmopterus princeps*), cuckoo ray (*Leucoraja naevus*), spotted ray (*Raja montagui*), small-eyed ray (*R. microocellata*), smallspotted catshark (*Scyliorhinus canicula*), thornback ray (*R. clavata*) shagreen ray (*Leucoraja fullonica*), and undulate ray (*Raja undulata*).

Biomass data was not available but to initiate the balancing process, an estimated value of 0.07 t·km⁻² (based on other groups) was entered into Ecopath. Fishing mortality was assumed to equal natural mortality (0.329 year⁻¹), resulting in a P/B of 0.658 year⁻¹. A Q/B value of 5.707 year⁻¹ was calculated based on 14 of the 25 species of this group.

Diets were available for 20 fish with different level of details and in various localities (Table 1). Fish of this group consumed 20.3% shrimps, 13.2% cephalopods and 14.6% other benthic invertebrates and various other fish.

Large demersal sharks and rays-commercial (Group 31)

The 20 species of this group, ranging from 150 cm to 850 cm in length, belong to 15 different families (Rajidae, Squalidae, Centrophoridae, Triakidae, Myliobatidae, Torpedinidae, Hexanchidae, Dalatiidae, Scyliorhinidae,

Squatinae, Chlamydoselachidae, Echinorhinidae, Odontaspidae, Carcharhinidae, Sphyrnidae). These were assumed to be commercially fished although there was no information to determine which members of the group were actually caught.

Using generic values from FishBase, natural mortality was estimated at 0.157 year^{-1} and fishing mortality was given a value equal to natural mortality, resulting in a P/B of 0.32 year^{-1} . The averaged Q/B value of 3.196 year^{-1} was based on 10 species. Biomass information for this group was not available but was necessary to start balancing the model using Ecopath; an estimate based on $B = \text{Catch}/F$ was used as an initial value ($= 0.06 \text{ t}\cdot\text{km}^{-2}$). Upon balancing, this was raised to $0.2 \text{ t}\cdot\text{km}^{-2}$ to balance the model (Table 6).

The diet information for this group was based on a larger proportion of quantitative information than the preceding group (see Table 1). The diet items were distributed in 29 of the model's groups, mainly on cephalopods (23%) and other benthos (12.3%) and a combination of demersal fish (22.3%). Modifications of the diet composition were minor and consisted in decreasing predation on small sharks (group 30) to a fourth of its original value, and decreasing predation on whales (Table 3).

Pelagic sharks – commercial (Group 32)

This group included 12 species among which are sandbar shark (*Carcharhinus plumbeus*), blue shark (*Prionace glauca*), porbeagle (*Lamna nasus*), shortfin mako (*Isurus oxyrinchus*), hammerhead (*Sphyrna lewini*), dusky shark (*Carcharhinus obscurus*), oceanic whitetip shark (*Carcharhinus longimanus*), thintail thresher (*Alopias vulpinus*) and basking shark (*Cetorhinus maximus*). Their body lengths range from 250 cm to 980 cm. They inhabit the pelagic to mesopelagic zone although the sandbar shark and the oceanic whitetip shark can go to very deep water. The sharks are highly migratory but little information was known concerning their migratory patterns around Morocco or their biomass. They are fished commercially off the coast of Morocco. The sharks in this group have a high trophic level of 4.0-4.5 except for the basking shark which feeds more like a baleen whale but cannot be placed in the 'whale' group because its Q/B and P/B ratios are considerably different. It was kept in this group because it was not deemed significant enough either to be placed in a group of its own.

Because sharks were thought to be strongly exploited, fishing mortality was estimated to be equal to natural mortality (0.182 year^{-1}) for a total mortality of 0.36 year^{-1} ($=P/B$). A biomass estimate was not available for this group so a value of $0.05 \text{ t}\cdot\text{km}^{-2}$ (based on the ratio Catch/F) was used. The value was increased to $0.2 \text{ t}\cdot\text{km}^{-2}$ to balance the model. Q/B was estimated at 2.574 year^{-1} .

Quantitative diet composition data were available for *Carcharhinus plumbeus* (Northeast Atlantic Stillwell and Kohler, 1993), *Carcharhinus brachyurus* and *Carcharhinus obscurus* (South Africa Smale, 1991) and *Isurus oxyrinchus* (Northwest Atlantic Stillwell and Kohler, 1982). These data indicated quite a range of prey types for *Carcharhinus plumbeus*, which consumes both benthic and pelagic prey. Cephalopods were abundant in the stomachs of *Carcharhinus* and *Isurus* species, along with sardines, and it is noteworthy that although these sharks are pelagic, they do not remain at the surface all of the time like the medium pelagic group. The remainder of the diet information was largely qualitative (Cortés, 1999) and the unidentified fish were equally allocated to the medium deep-water benthic, large deep-water benthic, medium demersal, very large demersal commercial, medium pelagic commercial and sardines. This reflected the lack of information concerning the position in the water column these sharks were feeding at. The basking shark consumed 100% large zooplankton (Cortés, 1999). The final diet composition for this group was cephalopods (26.4%), sardines (12.1%) and very large demersal commercial (13%) as the main dietary components. Modifications of the diet composition upon model balancing were minor and consisted in decreasing predation on small sharks (group 30) to a fourth of its original value, and decreasing predation on whales (Table 3).

Cephalopods (Group 33)

Cephalopods are commercially important off the coast of Morocco and catches of octopus (*Octopus vulgaris*), cuttlefish (*Sepia officinalis hierredda*) and squid (*Loligo vulgaris*) significantly increased after the 1960s (Balguerías *et al.*, 2000). Also included in this group is the broadtail short-fin squid (*Illex coindetii*).

Estimates of biomass were not available for this group. P/B was assumed to 3.1 based on a similar group in a Caribbean model (Opitz, 1993). This value is similar to the value estimated for *Octopus vulgaris* in the Azores (Gonçalves, 1991). Q/B (11.7 year^{-1}) was also taken from Opitz (1993).

The diet information was exclusively qualitative for this group. *Illex coindetii* consumed other benthos, worms, shrimps, large and small zooplankton, small demersal fish, medium demersal commercial fish, small and large bathypelagic fish, medium pelagic commercial fish, sardines and other cephalopods (Sánchez *et al.*, 1998). *Octopus vulgaris* preyed on other benthos, crabs, shrimps, very large demersal commercial fish, small and medium bathypelagic fish and cephalopods (Guerra, 1978). *Loligo vulgaris* consume other benthos, shrimps, crabs, medium pelagic commercial fish and cephalopods were eaten (Baddy, 1989). *Sepia officinalis* ate other benthos, worms, shrimps, small zooplankton, detrital feeding fish, medium demersal commercial fish and cephalopods. Only *Sepia officinalis heirredda* was not cannibalistic (Boletzky and Hanlon, 1981). Cephalopods were assumed to consume 16% each of shrimps, crabs and other benthos, 13% of cephalopods (cannibalism). The remaining was distributed among zooplankton and 10 groups of fish. Cannibalism had to be reduced to 3.3% during the process of balancing the model.

Turtles (Group 34)

There was a large degree of uncertainty about the distribution of turtles off Morocco. General information was obtained from the Azores model (Guénette and Gomez, this volume) and www.exeter.ac.uk/telematics/EuroTurtle. The website suggested that the loggerhead sea turtle (*Caretta caretta*), the green turtle (*Chelonia mydas*), the leatherback turtle (*Lepidochelys kempii*) and Kemp's Ridley turtle (*Dermochelys coriacea*) should be seasonally present, although there was no information indicating the length of time spent off Morocco. The loggerhead is known to spend their juvenile stage (8 years) in the Northeast Atlantic, transported by the Gulf Stream from Florida (Bolten *et al.*, 1998; Riewald *et al.*, 1999). They are included in the model but nothing specific to Morocco is known about them.

A very low 'guesstimate' of biomass, 0.005 t·km⁻² was used. P/B and Q/B values of 0.15 year⁻¹ and 3.5 year⁻¹ were taken from the Azores model for the loggerhead turtle (Guénette and Gomez, this volume). Turtles, represented by the loggerheads, were assumed to feed entirely on large zooplankton, i.e., jellyfish (H. Martins, Dept. of Fisheries and Oceanography, University of the Azores, Portugal, pers. comm.).

Seabirds (Group 35)

The following species are known to inhabit the coast of Morocco (E. Balguerías, Institute of

Oceanography, Canary, pers. comm.) and were thus included in this model: great shearwater (*Puffinus gravis*), Leach's storm-petrel (*Oceanodroma leucorhoa*), gannet (*Morus bassanus*), pomarine skua (*Stercorarius pomarinus*), Arctic skua (*Stercorarius parasiticus*), long-tailed skua (*Stercorarius longicaudus*), great skua (*Catharacta skua*), common tern (*Sterna hirundo*), great cormorant (*Phalacrocorax carbo*), little gull (*Larus minutus*), black-headed gull (*Larus ridibundus*) and shag (*Phalacrocorax aristotelis*). Only the two *Phalacrocorax* species were thought to be permanent residents in the area; the others were either known, or assumed, to be non-breeding visitors. There are almost certainly other seabird species in our study area, but either there was too little information available about them to be considered, or they were only found in the area for a very short time each year.

As a first estimate, the biomass was assumed equal to 25% of the bird biomass in a similar upwelling area off Peru (Jarre-Teichmann and Pauly, 1993). Assuming that our study area would be similar to that of Mauritania, we used the same biomass estimate of 0.015 t·km⁻² for our seabird functional group. P/B (=0.04 year⁻¹) was taken from the Azores model (Guénette and Gomez, this volume).

Seabird consumption was derived from the equation

$$\log R = -0.293 + 0.85 \log W \quad \dots 1)$$

where R is the daily ration and W is the bird weight, both in grams (Nilsson and Nilsson, 1976, in Wada, 1996). This value was divided by the mass of the bird and multiplied by 365 days to calculate an annual Q/B value. The Q/B value of 52.143 year⁻¹ was based on great cormorant and common tern.

The diet information is based on great shearwater (Prince and Morgan, 1987) and great cormorant (Gremillet *et al.*, 1999). For great cormorant, unidentified fish were assumed to be sardines. It was assumed that for great shearwater, the "major" dietary component accounted for 40 %, the "moderates" for 25 % and the "minor" for 10 %. Of the 25 % of fish, 10 % were allocated to sardines and 15 % to small demersals. The diet of this group was dominated by mesopelagic prey species, small demersals and cephalopods, which altogether accounted for more than 60 % of the diet.

Baleen whales (Group 36)

Based on distribution maps provided in Carwardine (1995), we included the following species in our baleen whale group: sei whale (*Balaenoptera borealis*), fin whale (*B. physalus*), humpback whale (*Megaptera novaeangliae*), and Bryde's whale (*B. edeni*). Minke whales (*Balaenoptera acutorostrata*) were added to match records from the data base constructed within the *Sea Around Us* project (Kaschner *et al.*, 2001).

Relative biomasses were taken from the data base constructed within the *Sea Around Us* project (Kaschner *et al.*, 2001). All biomasses were adjusted with the fraction of the year they were thought to be present in the area based on their habitat preferences and their migration patterns (Table 4). Natural mortality was estimated at 0.02 year⁻¹ (Trites and Heise, 1996). The daily consumption per animal (R) was calculated using the formula of Innes *et al.* (1987):

$$R = 0.1 * W^{0.8} \quad \dots 2)$$

where W is mean body weight in kg; R is the ration in kg/day. The daily rate was multiplied by 365 days to obtain the annual consumption rate and divided by the body weight (Trites and Pauly, 1998) to obtain a Q/B of 4.652 year⁻¹.

Baleen whales feed primarily on large zooplankton like euphausiids and pelagic crustaceans (Pauly *et al.*, 1998). Their diet is dominated by large zooplankton (71%). General diet items from this source have been attributed to relevant functional groups in the following manner: small pelagics (9%) were apportioned into groups 25, 26, and 28; mesopelagics (6%) into groups 21 and 24; and miscellaneous fish to demersal fish of the groups 14 to 16. Small squids constitute only 2% of the diet.

Table 4. Estimated biomass and residence time off Morocco for baleen whales

Species	Biomass (t·km ⁻²) ^a	Residence time (days)
Minke	0.0012	20
Bryde's	0.0001	90
Sei	0.0003	90
Blue	0.0002	90
Humpback	0.0012	60
Fin	0.0270	90
Total	0.0309	-

^aAdjusted for period spent in the area.

Toothed whales and dolphins (Group 37)

Distribution maps in Carwardine (1995) showed the following toothed whale and dolphin species spending at least part of the year in Morocco: sperm whale (*Physeter macrocephalus*), short-finned pilot whale (*Globicephala macrorhynchus*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), Cuvier's beaked whale (*Ziphius cavirostris*), Risso's dolphin (*Grampus griseus*), bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), false killer whale (*Pseudorca crassidens*), and killer whale (*Orcinus orca*).

The biomass of each species in Morocco was estimated based on the distribution maps given in Carwardine (1995) and Kaschner *et al.* (2001). The estimated number of whales was multiplied by the average body mass (Trites and Pauly, 1998) and weighted according to the number of days these species were thought to reside in the area (Table 5). This led to a total biomass estimate of 0.0536 t·km⁻². P/B was assumed to be 0.07 year⁻¹ (Trites and Heise, 1996). Q/B was estimated at 12.116 year⁻¹ following the same procedure as for the previous group.

Table 5. Estimated biomass and residence time off Morocco for toothed whales

Species	Biomass (t·km ⁻²)	Residence (days)
Sperm whales	0.0176	60
Long-finned pilot whale	0.0406	182
Short-finned pilot whale	0.0007	90
Common dolphin	0.0005	182
Striped dolphins	0.0001	7
Cuvier's beaked whale	0.0007	180
Pantropical spotted dolphin	0.0001	90
Northern bottlenose whale	0.0005	180
Risso's dolphin	0.0011	365
Bottlenose dolphin	0.0005	180
Harbour porpoise	0.00006	180
False killer whale	0.00002	90
Killer whale	0.00007	90
Sum	0.062	-

Diet data were available for four species of dolphin: common, striped, Risso's and bottlenose, and for Cuvier's beaked whale, false killer whale, and sperm whale (Trites and Pauly, 1998). Cephalopods were the primary diet item (51 %). General diet items from this source have been attributed to relevant functional groups in the following manner: small pelagics (6%) were

apportioned into groups 25, 26, and 28; mesopelagics (13%) into groups 21, 22 and 24; miscellaneous fish (24%) to demersal fish of the groups 14 to 16 and small portion to group 17; and benthic invertebrates into groups 5, 7 and 8. Marine mammals contributed 2.9% to the initial

diet, which was considered too high and prevented us from balancing the model. Thus, the percentage of marine mammals in the diets had to be reduced to 0.5% apportioned to the two groups of whales and the remainder divided among the groups of fish (Table 2).

Table 6. Matrix of parameters after balancing. Parameters estimated by the model are in **bold**.

Group name	Trophic level	Biomass (t·km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	P/Q
1 Primary producers	1.0	102.459	84.551	-	0.32	-
2 Sm. zooplankton	2.0	20.2	25	90.4	0.59	0.277
3 Lg. zooplankton	2.2	56.304	6	25	0.95	0.24
4 Worms	2.0	21.963	2	22.2	0.95	0.09
5 Other benthos	2.0	155.756	1.55	9.4	0.95	0.165
6 Predatory echinoderms	2.8	2.510	1.1	4.44	0.95	0.248
7 Crabs	2.5	12.414	1.8	10	0.95	0.18
8 Shrimp	2.5	28.369	1.7	11.333	0.95	0.15
9 Lobsters	3.2	1.876	0.282	5.85	0.95	0.048
10 Detrital feeders	2.1	0.326	0.552	7.161	0.95	0.077
11 Sm. deep water benthic	3.4	3.054	0.352	6.167	0.95	0.057
12 Lg. deep water benthic	3.6	0.225	0.27	2.985	0.95	0.09
13 Lg. deep water comm.	4.0	0.109	0.533	4.47	0.95	0.119
14 Sm. demersal	2.8	12.302	1.445	10.957	0.95	0.132
15 Med. demersal	3.1	5.591	0.69	8.558	0.95	0.081
16 Med. demersal comm.	3.2	1.858	1.26	7.921	0.96	0.159
17 Lg. demersal	3.4	1.900	0.494	7.45	0.95	0.066
18 Lg. demersal comm.	3.4	2.236	0.822	5.987	0.64	0.137
19 V. lg. demersal	3.9	0.395	0.157	3.881	0.95	0.04
20 V. lg. demersal comm.	4.1	0.5	2.305	4.887	0.93	0.147
21 Sm. bathypelagic	3.3	3.632	1.768	12.648	0.95	0.14
22 Med. bathypelagic	3.8	0.290	0.525	7.482	0.95	0.07
23 Lg. bathypelagic	4.0	0.240	0.435	4.34	0.86	0.1
24 Mesopelagic prey	3.1	5.719	2.377	13.036	0.95	0.182
25 Med. pelagic	3.3	3.025	1.131	8.471	0.95	0.134
26 Med. pelagic comm.	3.5	6.396	0.941	6.314	0.95	0.149
27 Lg. pelagic	4.2	2.321	0.777	3.206	0.95	0.242
28 Sardines	2.9	17.647	1.1	11.081	0.99	0.099
29 Tunas	4.3	0.058	0.642	3.774	0.66	0.17
30 Sm. demersal sharks/rays	3.8	0.329	0.658	5.707	0.89	0.115
31 Lg. demersal sharks/rays	4.1	0.20	0.32	3.196	0.84	0.1
32 Pelagic sharks	4.3	0.20	0.36	2.574	0.72	0.14
33 Cephalopods	3.5	2.112	3.1	11.7	0.95	0.265
34 Turtles	3.2	0.005	0.15	3.5	0.09	0.043
35 Seabirds	4.0	0.015	0.04	52.143	0.09	0.001
36 Baleen whales	3.5	0.031	0.176	4.652	0.20	0.004
37 Toothed whales/dolphins	4.4	0.062	0.02	12.116	0.23	0.006
38 Detritus	1.0	-	-	-	0.35	-

THE FISHERY

This section gives a brief description of the fisheries occurring along the coast of Morocco. Baddy and Guénette (2001) provide more details on the fishery and its catch.

The Moroccan fishery, previously a purely small scale affair, began to expand in the 1920s, under French influence. Nowadays, the fishing industry is economically significant for Morocco, providing 60,000 jobs and accounting for 45 % of agricultural exports in 1994 (Abdelali, 1995). The small-scale fishery relies on small wood dories, now motorized, which use a broad range of gear and catch various species depending on stock availability. Their catches are landed fresh or preserved on ice. The coastal fleet consists of wooden boats that usually stay out less than three days because they often lack refrigeration and storage facilities. Their main target species are small pelagics (sardines, mackerel, anchovies and horse mackerel) and some trawlers are equipped to catch demersal fish and cephalopods (Abdelali, 1995) The industrial fleet started in the 1970s and increased rapidly in size until 1998. The fleet consists of large bottom trawlers mainly targeting demersal fish and cephalopods.

Spanish vessels, based in the Canaries as well as continental Spain, have been fishing the Moroccan coast since the fifteenth century

(Balguerías *et al.*, 2000). In addition to the Spanish, Asian, west African and eastern European (mainly Russian) vessels were very active along the coast. The foreign fleet target both pelagic and demersal species. Since 1975, when Morocco annexed the former Spanish Sahara, fishing activities of the foreign fleet became increasingly confined to the southern part of the Sahara and have since been almost totally displaced by the growing Moroccan fishing industry.

Allocating catches to functional groups

The raw landing data obtained from Baddy and Guénette (2001) were allocated in each functional group according to the procedure outlined in Tables 7 to 9. First, the catch data (Table 9) that could obviously be assigned to a single functional group in the model are listed in Table 7. The other groups were apportioned to functional groups according to the rules described in Table 8. Generally, the landings of a given group was allocated to the pertinent functional groups proportionally to their importance, defined by the landings allocated to them as described in Table 8. In absence of data, 60% of unspecified shark catches were attributed to small demersal sharks and rays (Group 30) and the remainder was equally divided between the large demersal sharks and rays (Group 31) and the Pelagic sharks (Group 32).

Table 7. List of the functional groups to which the landing is directly attributable. The line number referred to the raw landing data in table 9.

Code	Functional group	Origin of catch data (in table 9)
A	Primary production	Line 7.
B	Other benthos	Line 111.
C	Crabs	Line 17.
D	Shrimps	Line 134.
E	Lobsters	Line 57.
F	Detrital feeders (<i>Det. /herb</i>)	Line 23.
G	Large deep-water benthic commercial (<i>LdeepbenthC</i>)	Line 27.
H	Medium demersal commercial (<i>MdemC</i>)	Line 91.
I	Large demersal commercial (<i>LdemC</i>)	Line 53.
J	Very large demersal commercial (<i>VLdemC</i>)	Line 53.
K	Medium bathypelagic (<i>Mbathypel</i>)	Line 65.
L	Medium pelagic commercial (<i>MpelC</i>)	Line 109.
M	Large pelagic commercial (<i>LpelC</i>)	Line 61.
N	Sardines	Line 121.
O	Tunas	Line 143.
P	Small demersal sharks and rays (<i>Sdeepsharkray</i>)	Line 127.
Q	Pelagic sharks (<i>Pelsharkray</i>)	Line 115.
R	Cephalopods	Line 14.

Table 8. Rules for allocating the catch to functional groups.

Catch group	Line ^a	Allocation to functional groups ^b	Comments
Crustacea	19	= Line 19 * C/(C+D+E)	Catch split proportionally to the reported catch between crabs, shrimps and lobsters.
Marine animals	4	= Line 4 * D/(D+E+H+I+J+R)	Catch split proportionally on the basis of the coastal catch of shrimp, lobsters, demersal fish and cephalopods.
Mugilidae	23	75 % to detrital feeders (F) 25% to medium demersal commercial (H)	The majority of the Mugilidae are in the detrital feeders group so a high percentage of the catch was allocated there.
Beryx	51	= Line 51 * G/(G+I)	The catch was split proportionally between large deep-water benthic commercial and large demersal commercial because there was one species in each.
A mixed demersal group	96	= Line 96 * H/(H+I)	<i>Dentex</i> spp., Sparidae, Soleidae and Pleuronectiformes were present in two functional groups so the catch was split proportionately
Gadiformes	98	= Line 98 * H/(H+I+J)	'Gadiformes' includes species in medium, large and very large demersal commercial groups so the catch is split proportionally between these.
Demersal fish	4	= Line 4 * H/(H+I+J)	The catch was split proportionally
Marine fish	3	= Line 63 * H/(F+G+H+I+J+K+L+M+N+O+P+Q)	The catch was split proportionally between all fin-fish functional groups.
Elasmobranchii	123	= 60% of Line 123 to small demersal sharks and rays. = 20% to large demersal sharks and rays. = 20% to pelagic sharks.	'Elasmobranchii' could not be split proportionately because there were no catch data for large demersal sharks. Hence it was assumed that 60 % of the catch would be small demersal sharks and rays and both large demersal sharks and pelagic sharks would receive 20%.
Total sharks	129	= 60% of Line 126 to small demersal sharks and rays. = 20% to large demersal sharks and rays. = 20% to pelagic sharks.	"Total sharks" were allocated identically as the "Elasmobranchii" above.
Total Rays	125	same as the preceding	

^aLine identification from table 9;^bletters refers to codes in table 7.

Table 9. Original landing data by functional group from Baddy and Guénette (2001). Abbreviations follow the same system as in Table 7.

Line	Groups	Species	Artisanal	Coastal	Industrial	Foreign
1	Plants	Marine animals nei	5119.9			
2		Total plants	5119.9			
3	Unidentified fish	Demersal fishes nei			5210	
4		Total unident.			5210	
5	Benthic plants	<i>Celidium graciliaris</i>	4590			
6		<i>Laminaria</i> spp	600			
7		Total Benthic plants	5190			
8	Cephalopods	<i>L.vulgaris</i> , <i>S.officinalis</i> , <i>O.vulgaris</i>		3316		
9		Loliginidae, Ommastrephidae			3316	700
10		<i>Loligo</i> spp				32
11		Octopodidae			31082	2876
12		<i>Octopus vulgaris</i>				37818
13		Sepiidae, Sepiolidae			11306	8605
14		Total cephalopods		3316	45704	50031
15	Crabs	<i>Brachyura</i>				50
16		<i>Maja squinado</i>		12		
17		Total crabs		12		50
18	Crustaceans	crabs; shrimp; lobsters				1366.2
19		Total crustaceans				1366.2
20	Detrit/ herb	<i>Mugil cephalus</i>				12
21		Total Detrit/ herb				12
22	Detrit/ herb; MdemC	Mugilidae		339		643
23		Total Detrit/ herb; MdemC Total		339		643
24	LdeepwbottC	<i>Conger conger</i>		1975		130
25		Lophiidae		192		417
26		<i>Polyprion americanus</i>	293.2			
27		Total LdeepwbenthC	293.2	2167		547
28	LdemC	<i>Anguilla anguilla</i>		2		
29		<i>Argyrosomus regius</i>		2498		
30		Ariidae				1185
31		<i>Campogramma glaycos</i>	0.6			
32		<i>Caranx rhonchus</i>				2075
33		<i>Dentex dentex</i>			4591	45
34		<i>Dentex gibbosus</i>	554			
35		<i>Dentex macrophthalmus</i>	0			5814
36		<i>Lepidorhombus whiffiagonis</i>				326
37		<i>Pagrus caeruleostictus</i>	1.6			
38		<i>Pagrus pagrus</i>	5		4473	376
39		<i>Pagrus</i> spp		14		34
40		<i>Phycis blennoides</i>				165
41		<i>Pseudolithus senegalensis</i>				5
42		<i>Pseudolithus</i> spp				2166
43		Sciaenidae				471
44		<i>Solea solea</i>			1648	6899.2
45		<i>Sparus aurata</i>	0	217		64
46		<i>Spondylisoma cantharus</i>	219.7	78		
47		<i>Umbrina cirrosa</i>				1
48		<i>Zeus faber</i>	0.1	172		9
49		Total LdemC	781	2981	10712	19635.2
50	LdemC LdeepbottC	Beryx				90
51		Total LdemC LdeepbenthC Total Ldeep				90
52	LdemC	<i>Pseudocaranx dentex</i>	0			

53		Total LdemC	0		
54	Lobsters	<i>Homarus gammarus</i>		23	
55		<i>Nephrops norvegicus</i>		15	117
56		<i>Palinurus spp</i>		68	192
57		Total Lobsters		106	
58	Lpel	<i>Lichia amia</i>			1087
59		<i>Rachycentron canadum</i>			64
60		<i>Sphyræna spp</i>	0		237
61		Total Lpel	0		1388
62	Marine fishes nei	Marine fishes nei		57615	50261.2
63		Total Marine fishes nei Total		57615	50261.2
64	Mbathypel	<i>Brama brama</i>	0		201
65		Total Mbathypel	0		201
66	MdemC	<i>Boops boops</i>		717	1860
67		<i>Brachydeuterus auritus</i>			88
68		<i>Cynoglossidae</i>			412
69		<i>Dentex angolensis</i>			0.2
70		<i>Diplodus sargus</i>			1177
71		<i>Diplodus spp</i>	4.9	650	1
72		<i>Diplodus vulgaris</i>	18.8		
73		<i>Haemulidae (=Pomadasyidae)</i>		371	235.2
74		<i>Lutjanidae</i>			48
75		<i>Macroramphosus scolopax</i>			12398
76		<i>Mullus spp</i>		123	54
77		<i>Pagellus acarne</i>	1.6		50
78		<i>Pagellus bellottii</i>			493
79		<i>Pagellus erythrinus</i>			267
80		<i>Pagellus spp</i>		3023	510
81		<i>Perciformes</i>			3637
82		<i>Plectorhinchus mediterraneus</i>	211.8		
83		<i>Pomadasys incisus</i>	0		
84		<i>Pseudolithus elongatus</i>			425
85		<i>Scorpaena scrofa</i>	0.3		
86		<i>Scorpaenidae</i>		171	20
87		<i>Stromateus fiatola</i>			4
88		<i>Trachurus trecae</i>			3142
89		<i>Triglidae</i>	1	912	381
90		<i>Trisopterus luscus</i>		1660	
91		Total MdemC	238.4	7627	1589
92	MdemC LdemC	<i>Dentex spp</i>			882
93		<i>Pleuronectiformes</i>		980	687
94		<i>Soleidae</i>		529	1145
95		<i>Sparidae</i>	3.2		1531
96		Total MdemC LdemC	3.2	1509	2218
97	MdemC LdemC	<i>Gadiformes</i>			800
98		Total MdemC LdemC VLdemC			800
99	MdemC	<i>Polynemidae</i>			76
100		Total MdemC			76
101	MpelC	<i>Alosa spp</i>		17	
102		<i>Caranx hippos</i>			0.2
103		<i>Caranx spp</i>			2
104		<i>Perciformes</i>			55
105		<i>Scomber japonicus</i>	20	127348	77722
106		<i>Scombroidei</i>	0.1		501
107		<i>Trachurus spp</i>		8996	180598
108		<i>Trachurus trachurus</i>			2193

109		Total MpelC	20.1	136361		261071.2
110	Other benthos	Mollusca	24			73.4
111		Total other benthos	24			73.4
112	pelagic	<i>Selene dorsalis</i>				1
113		Total pelagic				1
114	Pelsharkray	<i>Isurus oxyrinchus</i>	0			
115		Total Pelsharkray	0			
116	Sardines	<i>Engraulis encrasicolus</i>		10676	58	22640
117		<i>Sardina pilchardus</i>		150766	5742	371047
118		<i>Sardinella aurita</i>				30888
119		<i>Sardinella maderensis</i>				676
120		<i>Sardinella spp</i>				3549
121		Total Sardines		161442	5800	428800
122	Sdeepdwshark	Elasmobranchii	16.9	824		1628
123		Total Sdeepdwshark Ldeepdwshark Pels	16.9	824		1628
124	Sdeepdwsharkray	Rajiformes		1092		
125		Total Sdeepdwsharkray		1092		
126	Sdeepsharkray	<i>Mustelus spp</i>	0.2			
127		Total Sdeepsharkray	0.2			
128	Sharks	Selachimorpha(Pleurotremata)				490
129		Total Sharks				490
130	Shrimp	Natantia				334
131		<i>Parapenaeopsis atlantica</i>				430
132		<i>Parapenaeus longirostris</i>		1376		5152
133		<i>Penaeus kerathurus</i>				175
134		Total shrimp		1376		6091
135	Tunas	<i>Auxis thazard</i>		198		
136		<i>Euthynnus alletteratus</i>		15		
137		<i>Katsuwonus pelamis</i>	2	885		
138		<i>Sarda sarda</i>		310		
139		<i>Thunnus albacares</i>	6.5	614		
140		<i>Thunnus obesus</i>		120		
141		<i>Thunnus thynnus</i>		171		
142		<i>Xiphias gladius</i>		81		
143		Total Tunas	8.5	2394		
144	VLdemC	<i>Epinephelus aeneus</i>				120
145		<i>Epinephelus spp</i>				5
146		<i>Merluccius merluccius</i>		2124		8920
147		<i>Merluccius polli + M. senegalensis</i>				4872
148		<i>Merluccius senegalensis</i>			5121	9107
149		<i>Merluccius spp</i>				154
150		<i>Muraena helena</i>	8.1			
151		<i>Pomatomus saltatrix</i>	0	130		1862
152		Serranidae				1
153		<i>Trichiurus lepturus</i>		153		20021
		Total VLdemC	8.1	2407	5121	45062

Unreported landings in the 1980s represented 23% of the total landings (Baddy and Guénette, 2001), as based on estimates from each functional group. Discard rates, given as the percentage of the total catch, were taken from Baddy and Guénette (2001). The artisanal fishery was assumed to have no discards, as all its catch is used (Baddy and Guénette, 2001). A discard rate of 3 % of the total catch was applied to small pelagics (sardines) caught by the coastal fleet. The coastal demersal fishery was assigned a rate of 12%, while foreign and industrial demersal fleets were assigned discard rates of 30%. In absence of detailed studies on the specific composition of discards that could be extrapolated to the entire demersal fishery, we assumed that half the discards were non-commercial functional groups including benthos, in equal quantities. The other half was allocated to the commercial functional groups in proportion of their catch.

BALANCING THE MODEL

Before beginning to balance the model, guesstimates of biomass were entered for the following functional groups: very large demersal ($0.02 \text{ t}\cdot\text{km}^{-2}$), large bathypelagic ($0.02 \text{ t}\cdot\text{km}^{-2}$), tunas ($0.04 \text{ t}\cdot\text{km}^{-2}$), small demersal sharks and rays ($0.03 \text{ t}\cdot\text{km}^{-2}$), large demersal sharks ($0.01 \text{ t}\cdot\text{km}^{-2}$) and pelagic sharks ($0.04 \text{ t}\cdot\text{km}^{-2}$). They were all subsequently adjusted.

When attempting to balance the model, many of the Ecotrophic Efficiencies were greater than 1 meaning that more of the group was being consumed than produced, and thus had to be reduced. The main source of that problem reside in the allocation of prey items based on qualitative diets or to the species chosen to represent the functional groups. Also some estimates of biomass based on guesses or dubious data were modified (e.g. Mesopelagic prey species). In this sense, the balancing process leaves much to the discretion of the modeler. The resulting parameters are presented in Table 6.

DISCUSSION

The Ecopath model presented here summarizes much of the information that is available on the Moroccan marine ecosystem. It gives an indication of the relationships between 38 functional groups and of the influence that fishing has on the ecosystem. It is by no means a finished model and there are a number of recommendations made below that should result in a future model reflecting the ecosystem more accurately.

Biomass data were very scarce and only the estimates for primary producers, small zooplankton, large demersal commercial, sardines and seabirds could be entered into the model and left unchanged. During balancing, it was necessary to guess biomasses for many groups and this meant there was little anchorage to the model. A data deficiency in this area leaves the model open to take a wide range of shapes and a priority would be to get biomass data for more groups. Biomass time series would also be important if the model was to be used for policy analysis.

The functional groups could be designed differently depending on the modeler, but it would be useful to segregate the juveniles of the commercial fish species. Generally, there was a degree of confidence in the fish groups because even though data specific to Morocco was lacking, the species list and groupings have been verified (K. Erzini, University of Algarve, Portugal, pers. comm.) while P/B and Q/B values could be calculated from empirical relationships. The same was not true for non-fish groups. Many assumptions were made based on other models for the lower trophic level groups, for seabirds and turtles. Furthermore, there was no information readily available on the migration of tuna and cetaceans.

The allocation of unidentified fish in the diets of many species is a classic example of a case for which there was no single correct option. These decisions have been documented above and the pedigree component of the Ecopath model testifies to these gaps in knowledge.

This model presents a snapshot for the mid 1980s. A more informative approach would be to build an Ecosim model which would include time series of catch and biomass estimates as well as indices of upwellings strength. To this end, it is recommended that, since permanent upwellings occur mainly in the Western Sahara region, the model be divided into two components, a strictly Moroccan model and another one for the region that was formerly known as the Western Sahara.

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