Competition Between Fisheries and Marine Mammals for Prey and Primary Production in the Pacific Ocean

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Abstract

The degree of competition between fisheries and marine mammals in the Pacific Ocean was estimated for 7 statistical areas defined by the Food and Agriculture Organization of the United Nations (FAO). Catch statistics compiled from FAO sources show that the amount of fish caught in the Pacific Ocean rose from 2 million tons in the late-1940s to over 50 million tons in the early-1990s. Recent stagnation and declines occurring in some areas of the Pacific suggest that Pacific fisheries cannot continue to expand as they had previously.

Based on estimates of population size, total biomass and daily consumption rates, it was estimated that the 84 species of marine mammals inhabiting the Pacific Ocean consume about three times as much food as humans harvest. A large fraction (>60%) of the food caught by marine mammals consisted of deep sea squids and very small deep sea fishes not harvestable by humans, thus limiting the extent of direct competition between fisheries and marine mammals. Moreover, the most important consumers of commercially exploited fish are other predatory fish, not marine mammals.

Although direct competition between fisheries and marine mammals for prey appears rather limited, there may be considerable indirect competition for primary production. The primary production required to sustain marine mammals in each of the 7 FAO areas varies within a narrow range, suggesting that the diversity and abundance of marine mammals may have slowly evolved to fully exploit their niche and maximize their use of available primary production. This contrasts with the rapid expansion of fisheries and their relatively recent dependence on primary production, which may have led to what we call 'food web competition'.

Key words: competition, fisheries, food/feeding, marine mammals, Pacific Ocean

Introduction

The Pacific Ocean ranges from the high Arctic in the north to the Antarctic continent in the south, and is the largest of the world's oceans with a surface area of nearly 180 million km^2. It is rather homogeneous biogeographically, consisting largely of a central plate with a distinct and diverse load of co-evolved organisms and ecosystems. Eighty-four species of whales, dolphins, porpoises, seals and sea lions, totally over 20 million individuals, inhabit the Pacific Ocean – while over a billion people line its rim and draw upon its resources.

This study briefly explores the use and development of fishery resources in the Pacific Rim, and their relationship to marine mammals of the Pacific. The objective is to compare the fisheries catches of the early-1990s to the amount of food consumed by marine mammals, and to estimate the fraction of the primary production required to sustain the food web upon which the fisheries and the marine

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mammals depend. An attempt is also made to assess the extent of competition by estimating the overlap between marine mammal diets and fishery catches, and conclude with some implications of our findings for fisheries management and research.

Methods

Catch

The Food and Agriculture Organization of the United Nations (FAO) divided the world into 88 statistical regions, of which 7 are contained in the Pacific Ocean (Fig. 1, Table 1). The amounts of fish caught in each of these 7 regions over the period 1948 to 1992 were taken from the FAO FISHSTAT Database and from the FAO yearbook (FAO, 1994). Catches were compiled by FAO 'commodity' group (i.e. set of species with similar life history such as 'anadromous fishes', or habits such as 'small pelagics').

Consumption

Amounts of prey caught and consumed each day by marine mammals were estimated from

$$Q_i = \sum_s N_{i,s} W_{i,s} R_{i,s} \qquad (1)$$

where $N_{i,s}$ is the number of individuals (all age classes) by sex s of species i in the Pacific Ocean; $W_{i,s}$ is the mean individual weight by sex and species; and $R_{i,s}$ is the daily ration for an individual of weight $W_{i,s}$.

Estimates of total population sizes $(N_{i,s})$ and their distribution within the seven FAO areas are documented in Table 2. The proportion of marine mammals residing within the Pacific were estimated from distribution maps drawn by Reijnders et al. (1993) and Jefferson et al. (1993). Population estimates were largely drawn from Northridge (1984), Reijnders et al. (1993) and Jefferson et al. (1993) and appear to be reasonably accurate for pinnipeds, the great whales and some species of dolphins, but represent little more than educated 'order-of-magnitude' guesses for mid-sized cetaceans such as the beaked whales. When presented with 'order-of-magnitude' estimates (e.g. '00 000s), we conservatively chose a value that corresponds roughly to the geometric mean (i.e. 300 000) from the range of possible values (i.e. 100 000 to 1 000 000). We assumed the proportion of females in the total population to

be 0.5 for all species, except for sea lions and fur seals, for which a value of 0.6 was used (Trites and Pauly, 1997).

Sex specific mean weights $(W_{i,s})$ for 13 species of pinnipeds and 17 species of cetaceans were calculated from the product of average weight-at-age (determined from published growth curves) and the relative numbers alive (predicted from life history tables scaled by longevity, as described in Barlow and Boveng, 1991). This resulted in biomass-at-age curves (Trites and Pauly, 1997). Individual weights below which 50% of the cumulative biomass occurred were defined as $W_{i,s}$. Mean weights of species with unknown growth curves were estimated from measures of maximum body length $(L_{i,s})$ according to the relation

$$W_{i,s} = a L_{i,s}^b \qquad (2)$$

The functional relationship was derived for species i and sex s with known growth curves, and was estimated separately for pinnipeds and cetaceans (Trites and Pauly, 1997).

An individual's daily consumption or ration (kg per day) was estimated for each species using

$$R_{i,s} = 0.1 \, W_{i,s}^{0.8} \qquad (3)$$

where $W_{i,s}$ is the mean body weight in kg, 0.8 is from Equation 23 in Innes et al. (1987), and 0.1 is a downward adjusted value (from 0.123 in Innes et al. 1987) to account for the difference between ingestion for growth and ingestion for maintenance. Estimates of daily ration from Equation 3 range from 1.1% of body weight per day in a 50 000 kg baleen whale (i.e. 574 kg per day), to 4.5% of body weight per day in a small 50 kg dolphin (2.3 kg per day), and are compatible with present knowledge of the biology of large and small marine mammals (Bonner 1989).

The composition of the diet for each of the 84 species of marine mammals was derived from published accounts of stomach contents, as well as from morphological, behavioural and other information (Klinowska, 1991; Pauly et al., 1997). Diet composition was grouped by 8 types of food: benthic invertebrates, large zooplankton, small squids, large squids, small pelagic fishes, mesopelagic fishes, miscellaneous fishes and higher vertebrates (Table 3).
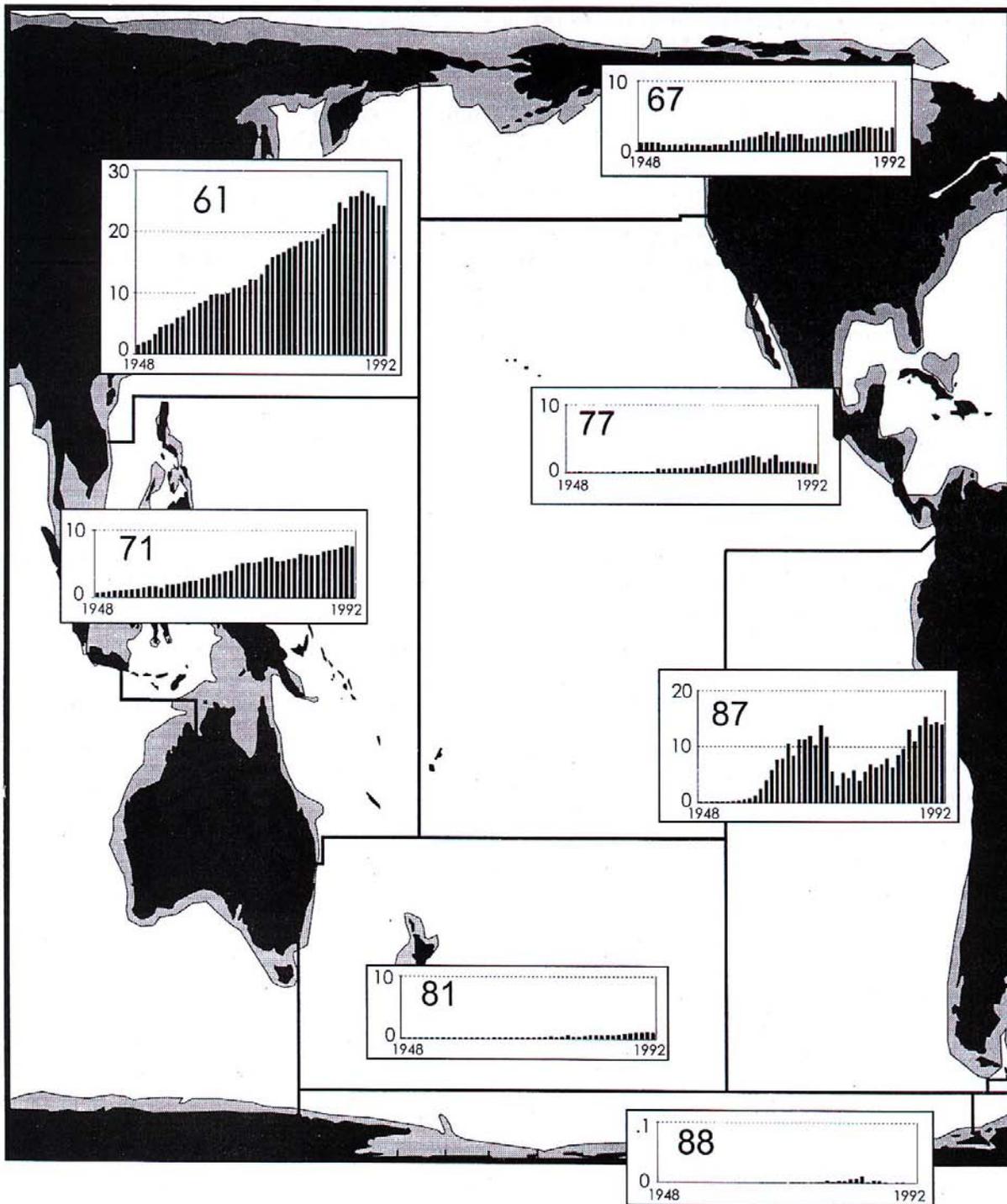
Fig. 1.   Time series of Pacific ocean fisheries catches (tons $\times 10^6$) by FAO area for the period 1948 to 1992. Note the stagnation or decline of catches in recent years. The projection (Peters 1983) allows direct comparisons of surface and shelve areas (shaded) from which the overwhelming bulk of the fisheries catches originate.

Primary production

The total amount of primary production in each of the seven FAO Pacific regions was derived from a global analysis by Longhurst *et al.* (1995), who divided the world's oceans into 56 'provinces', and estimated primary production for each from satellite

TABLE 1. Key features of the seven areas used by FAO to report fisheries statistics, with 1992 catches (FAO 1994). Percentage estimates of shelf areas are approximate.

FAO area	Region of the Pacific	Latitude	Area ($km^2 \times 10^3$) and % shelf	Catch in 1992 (ton $\times 10^3$)	By-catch[a] (% of catch)	Primary production (g C per m^2)
61	Northwest	65° N–15°N	20 476 (4.7)	24 199	39.8	215
67	Northeast	65°N–40°N	7 503 (12.9)	3 148	28.2	272
71	Western Central	15°N–25°S	33 233 (13.9)	7 710	43.0	128
77	Eastern Central	40°N–5°N	48 899 (0.9)	1 342	49.9	98
81	Southwest	30°S–50°S	28 375 (4.7)	1 114	29.7	118
87	Southeast	5°N–60°S	30 016 (1.3)	13 899	18.5	120
88	Antarctic	60°N–(75°S)	10 386 (21.7) [b]	<< 1 [c]	29.5	147
All	Total Pacific Ocean	65°N–(75°S)	178 888 (6.1)	51 412	33.9	135

[a] Adapted from Alverson *et al.* (1994).
[b] Approximate value.
[c] Consisting of 50 tons of krill (*Euphausia superba*) caught from 1 July 1991 to 30 June 1992.

TABLE 2. Global and Pacific population estimates for the 84 species of marine mammals inhabiting the Pacific Ocean during the 1980s and early 1990s. The proportions of animals within the Pacific and within each of the 7 Pacific FAO areas were estimated from range maps displaying the distribution of each species. Population estimates were largely drawn from Northridge (1984), Reijnders *et al.* (1993) and Jefferson *et al.* (1993). Order of magnitude estimates are indicated by an apostrophe (e.g. '000).

Species common names	World population	Proportion in Pacific	Pacific population	Proportion of Pacific population in each FAO area						
				61	67	71	77	81	87	88
Balaenidae										
Northern right whale	3 155	0.13	410	0.40	0.40	–	0.10	–	–	–
Southern right whale	2 900	0.10	290	–	–	–	–	0.60	0.40	–
Bowhead whale	4 000	0.10	400	0.80	0.20	–	–	–	–	–
Pygmy right whale	3 000	0.55	1 650	–	–	–	–	0.60	0.40	–
Eschrichtidae										
Gray whale	21 113	1.00	21 113	0.40	0.50	–	0.10	–	–	–
Balaenopteridae										
Fin whale	115 500	0.39	45 045	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Blue whale	14 000	0.34	4 760	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Minke whale	860 000	0.14	120 400	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Sei whale	39 000	0.45	17 550	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Bryde's whale	112 000	0.86	96 320	0.10	–	0.20	0.35	0.15	0.20	–
Humpback whale	22 000	0.25	5 500	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Ziphiidae										
Tasman beaked whale	'000	0.90	2 700	–	–	–	–	0.50	0.50	–
Arnoux's beaked whale	'0 000	0.34	10 200	–	–	–	–	0.50	0.25	0.25
Baird's beaked whale	'0 000	1.00	30 000	0.50	0.30	–	0.20	–	–	–
Longman's beaked whale	'000	0.50	1 500	–	–	1.00	–	–	–	–
Blainville's beaked whale	'000	0.55	1 650	0.15	–	0.20	0.35	0.10	0.20	–
Strap–toothed whale	'000	0.34	1 020	–	–	–	–	0.60	0.40	–
Hector's beaked whale	'000	0.80	2 400	–	–	–	0.10	0.70	0.20	–
Gray's beaked whale	'000	0.40	1 200	–	–	–	–	0.60	0.40	–

TABLE 2. (Continued). Global and Pacific population estimates for the 84 species of marine mammals inhabiting the Pacific Ocean during the 1980s and early 1990s. The proportions of animals within the Pacific and within each of the 7 Pacific FAO areas were estimated from range maps displaying the distribution of each species. Population estimates were largely drawn from Northridge (1984), Reijnders *et al.* (1993) and Jefferson *et al.* (1993). Order of magnitude estimates are indicated by an apostrophe (e.g. '000).

Species common names	World population	Proportion in Pacific	Pacific population	Proportion of Pacific population in each FAO area						
				61	67	71	77	81	87	88
Ziphiidae (continued)										
Stejneger's beaked whale	'000	1.00	3 000	0.40	0.50	–	0.10	–	–	–
Andrews' beaked whale	'000	0.50	1 500	–	–	–	–	1.00	–	–
Ginkgo–toothed beaked whale	'000	0.95	2 850	0.10	–	0.30	0.45	0.05	0.10	–
Hubb's beaked whale	'000	1.00	3 000	0.05	0.40	–	0.55	–	–	–
Pygmy beaked whale	'000	1.00	3 000	–	–	–	0.10	–	0.90	–
Cuvier's beaked whale	'0 000	0.55	16 500	0.15	0.10	0.15	0.25	0.15	0.20	–
Southern bottlenose whale	'0 000	0.34	10 200	–	–	–	–	0.50	0.25	0.25
Physeteridae										
Sperm whale	1 900 000	0.62	1 178 000	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Pygmy sperm whale	'0 000	0.55	16500	0.10	0.05	0.20	0.30	0.15	0.20	–
Dwarf sperm whale	'0 000	0.55	16500	0.15	0.05	0.20	0.35	0.10	0.15	–
Monodontidae										
White whale	60 000	0.24	14 400	0.70	0.30	–	–	–	–	–
Delphinidae										
Rough–toothed dolphin	'0 000	0.60	18 000	0.10	0.05	0.25	0.40	0.05	0.15	–
Indo–Pac. humpbacked dolphin	'0 000	0.30	9 000	0.10	–	0.85	–	0.05	–	–
Irrawaddy dolphin	'0 000	0.75	22 500	–	–	1.00	–	–	–	–
Melon–headed whale	'0 000	0.50	15 000	0.20	–	0.30	0.30	0.05	0.15	–
Pygmy killer whale	'0 000	0.50	15 000	0.15	–	0.25	0.40	0.05	0.15	–
False killer whale	'00 000	0.50	150 000	0.10	0.05	0.20	0.35	0.10	0.20	–
Killer whale	80 000	0.32	25 600	0.11	0.04	0.19	0.27	0.16	0.17	0.06
Short–finned pilot whale	'00 000	0.60	180 000	0.15	0.05	0.20	0.35	0.10	0.15	–
Dusky dolphin	'00 000	0.65	195 000	–	–	–	–	0.50	0.50	–
Hourglass dolphin	'00 000	0.34	102 000	–	–	–	–	0.50	0.30	0.20
Peale's dolphin	'0 000	0.30	9 000	–	–	–	–	–	1.00	–
Pacific white–sided dolphin	100 000	1.00	100 000	0.45	0.40		0.15	–	–	–
Fraser's dolphin	'0 000	0.40	12 000	0.10	–	0.35	0.30	0.05	0.20	–
Bottlenose dolphin	'000 000	0.80	2 400 000	0.15	–	0.35	0.30	0.05	0.15	–
Risso's dolphin	'00 000	0.60	180 000	0.15	0.05	0.20	0.25	0.15	0.20	–
Spinner dolphin	'000 000	0.55	1 650 000	0.15	–	0.25	0.40	0.05	0.15	–
Striped dolphin	'000 000	0.55	1 650 000	0.15	0.05	0.20	0.35	0.10	0.15	–
Pantropical spotted dolphin	1 000 000	0.96	960 000	0.15	–	0.25	0.40	0.05	0.15	–
Common dolphin	'000 000	0.55	1 650 000	0.10	0.05	0.20	0.30	0.15	0.20	–
Southern right whale dolphin	'00 000	0.34	102 000	–	–	–	–	0.60	0.35	0.05
Northern right whale dolphin	'00 000	1.00	300 000	0.45	0.35	–	0.20	–	–	–
Hector's dolphin	5 500	1.00	5 500	–	–	–	–	1.00	–	–
Phocoenidae										
Harbour porpoise	'000 000	0.34	1 020 000	0.45	0.50	–	0.05	–	–	–
Vaquita	250	1.00	250	–	–	–	1.00	–	–	–
Burmeister's porpoise	'00 000	0.60	180 000	–	–	–	–		1.00	–
Spectacled porpoise	'000	0.25	750	–	–	–	–	0.70	0.30	–
Dall's porpoise	1 150 000	1.00	1 150 000	0.50	0.40	–	0.10	–	–	–
Finless porpoise	'00 000	0.30	90 000	0.30	–	0.70	–	–	–	–

TABLE 2. (Continued). Global and Pacific population estimates for the 84 species of marine mammals inhabiting the Pacific Ocean during the 1980s and early-1990s. The proportions of animals within the Pacific and within each of the 7 Pacific FAO areas were estimated from range maps displaying the distribution of each species. Population estimates were largely drawn from Northridge (1984), Reijnders *et al.* (1993) and Jefferson *et al.* (1993). Order of magnitude estimates are indicated by an apostrophe (e.g. '000).

Species common names	World population	Proportion in Pacific	Pacific population	Proportion of Pacific population in each FAO area 61	67	71	77	81	87	88
Otariidae										
Steller sea lion	110 000	1.00	110 000	0.35	0.60	–	0.05	–	–	–
California sea lion	175 000	1.00	175 000	–	0.20	–	0.75	–	0.05	–
South American sea lion	230 000	0.50	115 000	–	–	–	–	–	1.00	–
Hooker's sea lion	12 000	1.00	12 000	–	–	–	–	1.00	–	–
Northern fur seal	1 200 000	1.00	1 200 000	0.40	0.55	–	0.05	–	–	–
Guadalupe fur seal	6 000	1.00	6 000	–	–	–	1.00	–	–	–
Juan Fernandez fur seal	12 000	1.00	12 000	–	–	–	–	–	1.00	–
Galapagos fur seal	40 000	1.00	40 000	–	–	–	–	–	1.00	–
South American fur seal	595 000	0.55	327 250	–	–	–	–	1.00	1.00	–
Australian fur seal	40 000	0.15	6 000	–	–	–	–	1.00	–	–
New Zealand fur seal	67 000	0.60	40 200	–	–	–	–	–	–	–
Odobenidae										
Walrus	230 000	0.80	184000	0.4	0.60	–	–	–	–	–
Phocidae										
Harbour seal	368 000	0.60	220 800	0.30	0.50	–	0.20	–	–	–
Larga seal	230 000	1.00	230 000	0.75	0.25	–	–	–	–	–
Ringed seal	6 500 000	0.15	975 000	0.70	0.30	–	–	–	–	–
Ribbon seal	216 000	1.00	216 000	0.70	0.30	–	–	–	–	–
Bearded seal	800 000	0.50	400 000	0.65	0.35	–	–	–	–	–
Hawaiian monk seal	1 500	1.00	1 500	0.10	–	–	0.90	–	–	–
Southern elephant seal	750 000	0.05	37 500	–	–	–	–	0.45	0.25	0.30
Northern elephant seal	125 000	1.00	125 000	0.15	0.75	–	0.20	–	–	–
Crabeater seal	11 900 000	0.11	1 309 000	–	–	–	–	0.25	0.15	0.60
Ross seal	130 000	0.50	65 000	–	–	–	–	0.20	0.10	0.70
Leopard seal	300 000	0.33	99 000	–	–	–	–	0.25	0.15	0.60
Weddell seal	750 000	0.33	247 500	–	–	–	–	0.30	0.20	0.50
Mustelidae										
Sea otter	150 000	1.00	150 000	0.40	0.50	–	0.10	–	–	–
Marine otter	10 000	1.00	10 000	–	–	–	–	–	1.00	–

and field measurements. We superimposed these 29 provinces of the Pacific Ocean onto the seven FAO areas in the Pacific Ocean to compute weighted mean estimates of primary production for each FAO area (Table 1).

The primary production (P_c) required to produce the fish caught by commercial fisheries was calculated, based on the 10% transfer efficiency between trophic levels estimated in Pauly and Christensen (1995), from

$$P_c = \sum_{g=1}^{14} C_g \, 10^{(L_g - 1)} \qquad (4)$$

where C_g is the catch and L_g is the trophic level of 'commodity' group g. Trophic levels were adapted from the 48 ECOPATH ecosystem models documented in Pauly and Christensen (1995; see also Christensen and Pauly, 1992a,b; 1993; and Pauly and Christensen, 1993). Trophic levels were calculated for each group from the mean trophic level of

its prey (weighted by consumption) plus 1, starting from primary producers (mainly planktonic algae) and detritus, both with a definitional trophic level equal to unity. This is illustrated by the trophic representation of FAO Area 77 in Fig. 2 (see Appendix 1 for details). Transfer efficiencies between

TABLE 3. Definition of prey groups and related information required to assess the trophic impact of marine mammals. Examples of diet compositions are shown for 6 of the 84 species of Pacific marine mammals (see Pauly *et al.*, 1997).

Feature/Group	Benthic invertebrates[a]	Large Zooplankton[b]	Small squids[c]	Large squids[d]	Meso- pelagics[e]	Small pelagics[f]	Misc. fishes[g]	Higher vertebrates[h]
Trophic levels[i]	2.2	2.2	3.2	3.7	2.7	3.3	3.3	4.0
Diet composition								
Southern right whale	–	1	–	–	–	–	–	–
Gray whale	0.8	0.1	–	–	–	0.1	–	–
Longman's beaked whale	–	–	0.4	0.4	0.2	–	–	–
Spinner dolphin	–	–	0.2	0.2	0.4	–	0.2	–
Antarctic fur seal	–	0.5	0.1	0.1	0.1	–	0.2	–
Leopard seal	–	0.3	0.1	–	–	0.1	0.1	0.4

[a]   Echinoderms (sea urchins and some sea stars), molluscs (abalone, bivalves and some octopi) and macrobenthic crustaceans.
[b]   Mainly of crustaceans, notably euphausiaceans (e.g. Krill, *Euphausia superba*).
[c]   Squids with mantle length of up to 50 cm, e.g. Gonatidae.
[d]   Squids with mantle length of above 50 cm, e.g. Onychoteuthidae.
[e]   Lanternfish (Myctophidae) and other members of the deep scattering layer (DSL) community.
[f]   Anchovies, sardines, mackerels and allied groups.
[g]   Miscellaneous species, predominantly bottom fishes.
[h]   Marine mammals and birds (e.g. penguins), and some turtles.
[i]   The trophic levels are weighted means taken from Table 1 in Pauly and Christensen (1995), except for the higher vertebrates, whose values is taken as the mean trophic level of all Pacific marine mammals species, minus those which feed on higher vertebrates.
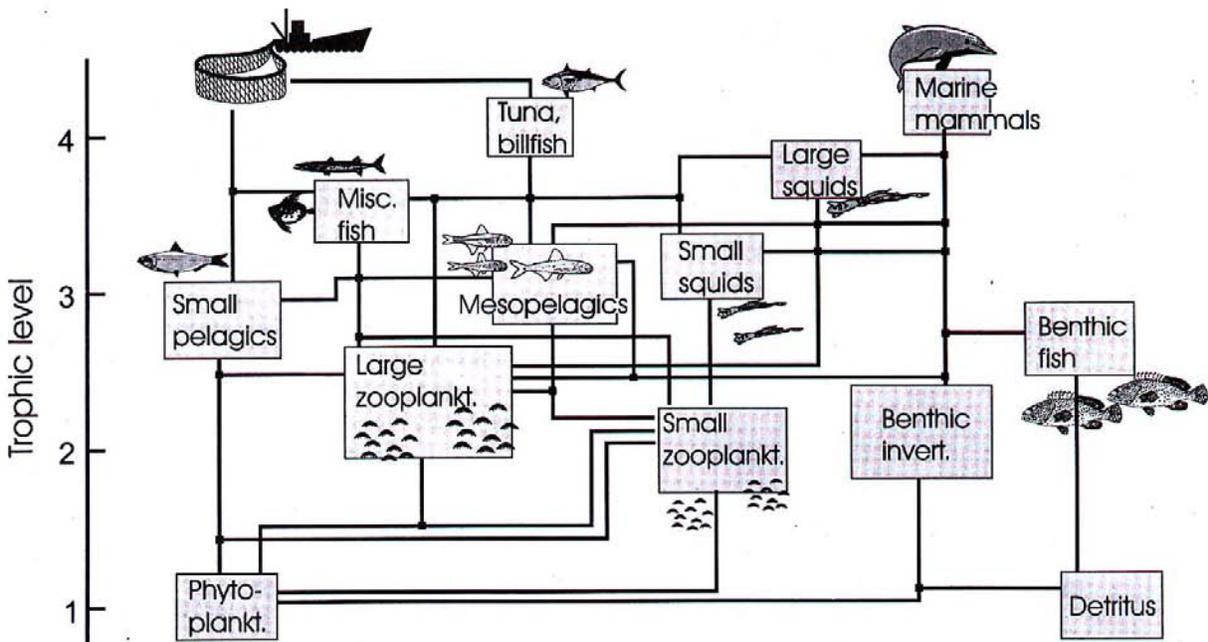

Fig. 2.   Trophic model representing the pelagic ecosystem in FAO Area 77 (see Appendix 1 for details). The lines entering the lower half of the boxes indicate consumption flows. Production exits through the upper half of the boxes. Respiration and backflows to the detritus are not shown. Note the difference between those parts and pathways of the system leading to the fisheries, and those leading to the marine mammals.

trophic levels tend to have a mean value of 0.10 in aquatic ecosystems (Fig. 3; Pauly and Christensen, 1995).

The amount of primary production (P_i) required to produce the prey consumed by marine mammals was estimated from

$$P_i = Q_i \sum_{g=1}^{8} d_{i,g} \, 10^{(L_{i,g}-1)} \qquad (5)$$

where Q_i is the total amount of prey caught in kg by species i (Equation 1), $d_{i,g}$ is the proportion of their total diet consisting of prey group g, and $L_{i,g}$ is the trophic level of the prey group. Diets of the 84 Pacific species of marine mammals were taken from published reports of food and feeding habits, and re-expressed in terms of the 8 prey groups defined in Table 3 (details in Pauly *et al.,* 1997). The few species (mainly *Mesoplodon* spp.) for which diet composition were not available were assumed to have the same feeding habits as their conspecifics. Trophic levels of marine mammals (see above) were calculated from the trophic level of their prey (in Table 3) and ranged from 4.6 in killer whales to 3.2 in right, blue, fin and bowhead whales (Pauly *et al.,* 1997).
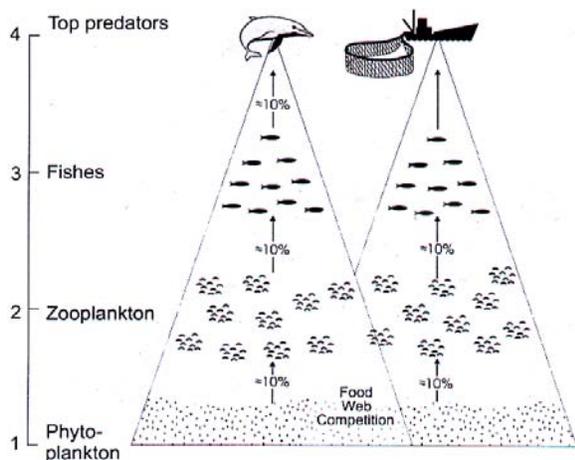
Fig. 3.   Schematic representation of 'food web competition', proposed to explain how some groups of top predators, such as marine mammals, may be affected by fisheries even when the prey and catch species do not overlap. Food web competition occurs at the base of the food pyramids, and involves the primary production required to sustain these pyramids.

Resource overlap

The degree of resource overlap between fisheries and the major groups of marine mammals in each of the seven Pacific FAO areas were calculated using a niche-overlap index modified from MacArthur and Levins (1967) of the form

$$\alpha_{i,j} = \frac{2 \sum_k p_{i,k} p_{j,k}}{\sum_k \left(p_{i,k}^2 \, p_{j,k}^2 \right)} \qquad (6)$$

where $\alpha_{i,j}$ (ranging from 0 to 1) expresses how species and/or fisheries i and j share the resource k, and $p_{i,k}$ and $p_{j,k}$ express the proportions that each of the k resources contributes to the diets or catches (*i.e.* the amount of primary production required to sustain fisheries – Equation 4, or marine mammals – Equation 5, divided by total available primary production).

The analysis was simplified by aggregating the marine mammals into five groups: baleen whales, beaked whales, dolphins and porpoises, pinnipeds, and all 84 Pacific species of marine mammals combined.

Results and Discussion

Catch

The amount of fish caught in the Pacific Ocean rose from 2 million tons in 1948 to over 50 million tons in 1992 (Fig. 1). About 50% of the total Pacific catch has traditionally come from the mixed stock fisheries off the coasts of Russia, China and Japan (FAO Area 61). Major fisheries have also occurred in Areas 87 (South America) and 71 (Philippines). South American fisheries primarily targeted anchoveta (*Engraulis ringens*) until their collapse in 1972, and shifted thereafter toward sardines (*Sardinops sagax*) and horse mackerel (*Trachurus murphyi*). Elsewhere in the Pacific, catches have been relatively small, and dominated by groundfish in the Gulf of Alaska and Bering Sea, and tuna in the Central Pacific (Fig 1).

Levels of by-catch differed among areas (Alverson *et al.*, 1994), ranging from a low of 18% of total catch off South America (Area 87) to a high of 50% in the Central Pacific off the coast of North America (Area 77). Overall, by-catch averaged 34% of the total 1992 Pacific catch (Table 1).

Catches have declined in some areas of the Pacific and may have peaked in others (Fig. 1). Declining catches in Areas 61 and 77 may be due to overfishing, decreasing fishing effort, or both. Unfortunately, it is difficult to draw firm conclusions when no reliable estimates exist of the level of fleet sizes and effort in the Pacific as a whole. It appears however that the Pacific fisheries cannot continue to expand as they have previously.

Consumption

Pacific marine mammals, with a total biomass of approximately 25 million tons (over half of which were sperm whales), were estimated to consume about 150 million tons of food per year (Table 3), i.e. about three times the nominal catch. Over half of the total biomass can be attributed to sperm whales. The most important prey items for the Pacific as a whole were squids (26 and 41 million tons for small and large squids, respectively) and mesopelagic fishes (25 million tons). Intermediate amounts of miscellaneous fishes (19 million tons) and small pelagics (17 million tons) were consumed, while benthic invertebrates contributed 3-4 millions tons, and higher vertebrates (marine mammals and birds, mainly penguins) only 0.7 million tons.

Primary production

The primary production required to sustain marine mammals in each of the FAO Areas varied within a very narrow range of 20 to 30 g C per m^2 per year (Fig. 4). This consistency between areas suggests that marine mammals may be fully exploiting their marine environments, which may reflect a long evolutionary history that has seen marine mammals adapt their morphology and respiratory
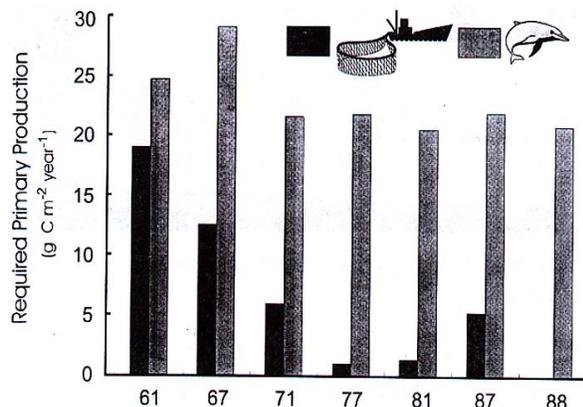

Fig. 4.   Primary production required to sustain marine mammals and fisheries in the Pacific ocean, by FAO area.

physiology to fully exploit the available feeding niches (e.g. in the deep-scattering-layer). Levels of primary production required to sustain fisheries varies much more between the different areas of the Pacific, depending upon the level of fishing effort and the type of resource exploited (Fig. 4).

Resource competition

Commercial fisheries target only 35% of the prey items sought by marine mammals (Fig. 5) – a figure far less than might be expected considering the frequent complaints about marine mammals by some fishers. Over 65% of the prey consumed by marine mammals are, as a whole, not of current commercial interest. The greatest overlap with fisheries for all areas of the Pacific combined occurs with pinnipeds (60%) and dolphins and porpoises (50%). The least overlap is with baleen whales and beaked whales (Fig. 5).

Specialized feeding habits further imply that the observed dietary overlap between the prey items of marine mammals and the 'prey' of the fisheries is less than expected. For example, most of the squids and fish which make up such a substantial part of the marine mammal diet are deep-water species not fit for human consumption, nor indeed catchable in commercial quantities using current fishing gear. Similarly, the small fish which make up the mesopelagic community consumed by marine mammals in oceanic areas contain high levels of wax esters (i.e. alkoxydigliceridae) that renders them unfit for human consumption even if their size, appearance and consistency allowed for such (see Gjøsaeter and Kawaguchi, 1980).

The most significant consumer of fish and competitor of commercial fisheries is probably other predatory fish, and not marine mammals. For example, the documented biomass fluxes in the ecosystem model (Fig. 2, Table 4, and Appendix 1) imply that the amount of fish consumed by fish in the Eastern Central Pacific (Table 5) is an order of magnitude higher than the amount consumed by the marine mammals (Christensen, 1996). Thus fish predation should be of greater concern to the fisheries than predation by marine mammals.

Although direct competition between fisheries and marine mammals for prey appears rather limited, indirect competition might occur for the primary production which sustains each of them. As shown in Fig. 3, food web competition occurs when
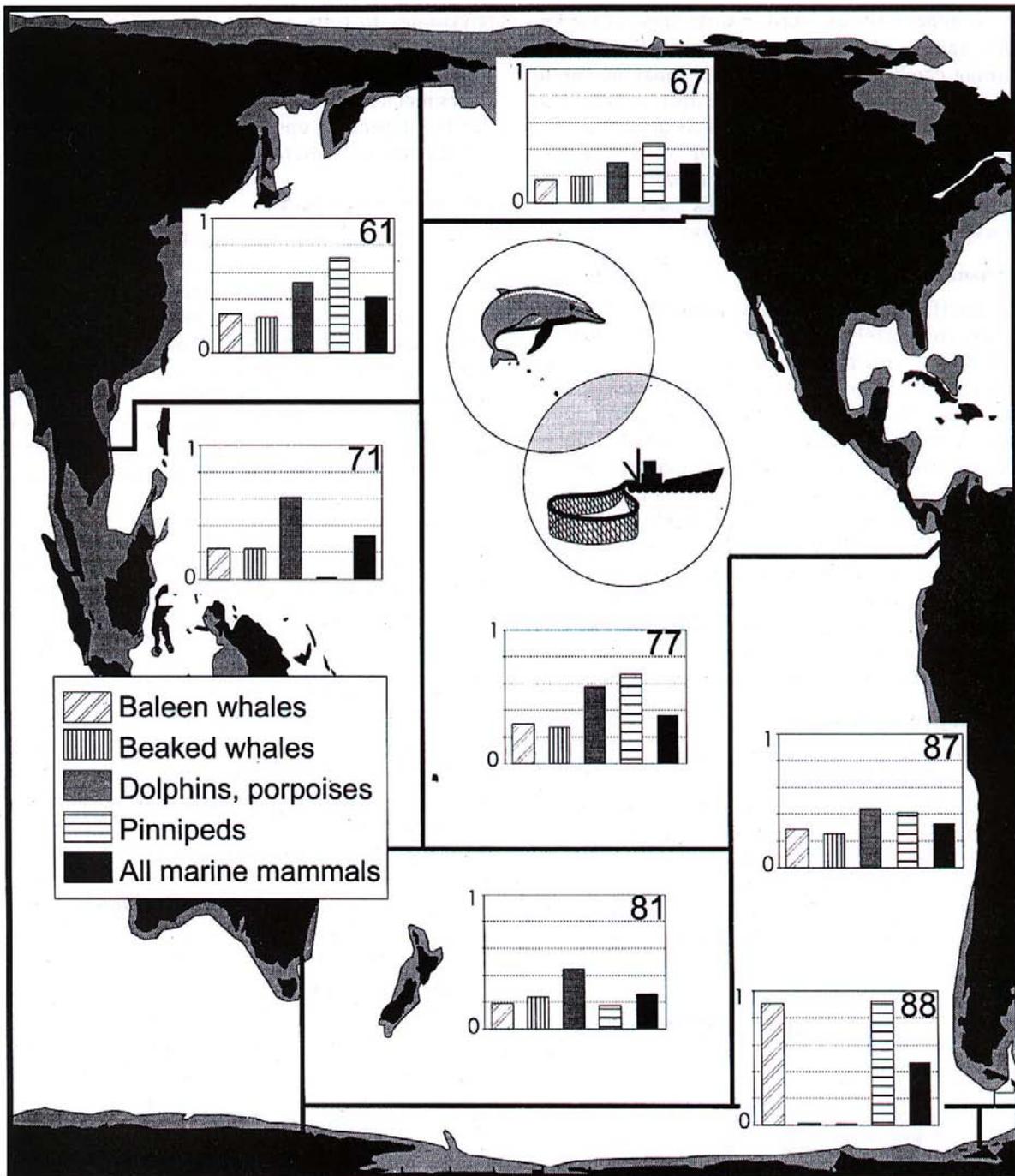
Fig. 5.   Overlap between the prey composition of four groups of marine mammals (plus all marine mammals combined) and the catch composition of the fisheries by FAO area.

there is potential overlap of the trophic flows supporting a given group (such as marine mammals) with the trophic flows supporting another group (such as fisheries). The relationship between the size of fishery catches (Table 1) and the amounts of primary production required to sustain fisheries and marine mammals suggests that the primary production available to marine mammals may decline as catches increase (Fig. 6). This raises the possibility that Pacific fisheries in some FAO areas may

TABLE 4. Food consumption (tons $\times 10^3$ per yr) by marine mammals (biomass in tons $\times 10^6$) in the Pacific Ocean, by FAO area and food type.

FAO Area	Biomass marine mammals	Benthic invertebrates	Large zooplankton	Small squids	Consumption Large squids	Small pelagics	Meso-pelagics	Misc. fishes	Higher vertebrates	Total
61	3.22	1 568	1 956	3 402	5 043	2 299	3 240	2 770	99	20 378
67	1.35	1 473	681	1 442	2 066	961	1 455	1 170	85	9 334
71	4.61	28	2 853	4 820	7 595	2 994	4 432	3 520	79	26 320
77	6.88	204	4 364	6 989	11 270	4 351	6 828	4 972	131	39 108
81	3.88	57	3 190	3 680	6 261	2 368	3 660	2 421	92	21 729
87	4.23	168	3 199	4 267	6 891	2 787	4 037	3 095	130	24 573
88	1.49	55	2 548	1 332	2 219	980	1 161	883	108	9 286
Total	25.67	3 552	18 791	25 931	41 345	16 741	24 814	18 831	723	150 728

TABLE 5. Estimates (g per m^2 per yr) of fish consumed by fish, marine mammals or caught by fisheries in 1992 the Eastern Central Pacific (FAO Area 77). Estimated from the Ecopath trophic model in Fig. 2 and Appendix 1.

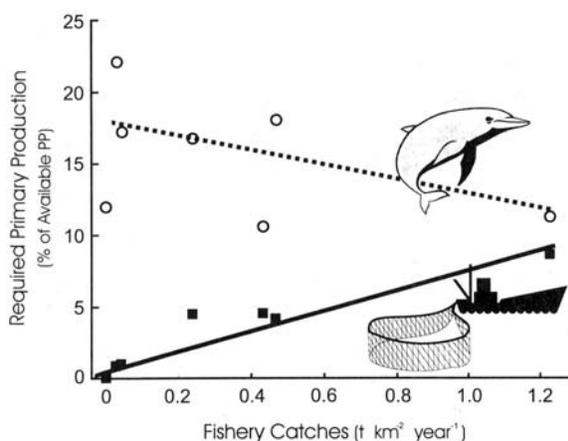| Predator	Tuna, billfish	Miscellaneous fish	Prey Mesopelagics	Benthic fish	Small pelagics
Fishery	0.01	0.01	0.00	0.00	0.01
Marine mammals	0.00	0.10	0.14	0.00	0.09
Fish	0.00	0.23	0.55	0.07	2.09

Fig. 6. Primary production requirements relative to fishery catches. Primary production required by the marine mammals of the Pacific ocean is low where fisheries catches (and hence the primary production required by the fisheries) is high. This may indicate food web competition as defined in Fig. 3.

have entered into 'food web competition' with marine mammals.

Management and research implications

Catches by the Russian Federation, both in the Pacific and elsewhere, have decreased since the breakdown of the USSR, which along with the world-wide introduction of 200 nautical mile exclusive economic zones caused the demise of the subsidized, long-distance Soviet fishery. However, the best global estimates show that the fishing fleets elsewhere have more than compensated for this decrease (FAO, 1995). While proofs are lacking in the Pacific, the trend is clear: the excessive build up, and overcapitalization in the fishing fleets leads unavoidably to overfishing, and potentially threatens marine mammals with food web competition.

We wish to stress that our results are tentative and will be refined as better estimates of diets, abundance and biomass become available. As a whole, our study implies an uncertain future for

fisheries and marine mammals in the Pacific Ocean, and will need further investigation and testing by extension to the Atlantic and Indian Oceans. It is clear, however, that the Pacific fisheries cannot continue to expand as they have previously.

Acknowledgments

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APPENDIX 1. Construction of a model of trophic interaction in FAO Area 77 (Eastern Central Pacific).

To illustrate the method for construction of balanced trophic flow models, an ecosystem model was constructed for the Eastern Central Pacific (FAO area 77) using the Ecopath software (Christensen and Pauly, 1992a, b). The model was based on published information, supplemented by various approximations. A number of the estimates used are discussed by Pauly and Christensen (1993). The description below assumes a basic knowledge of the structure of Ecopath, and of the parameters required.

Catches are based on the FAO statistics for Area 77 in 1992 (FAO, 1994). The model included a total of 12 living groups, plus a detritus group:

1.   *Marine mammal* biomass (B) and consumption/biomass ratio (Q/B) were estimated as described in the text above. The production/biomass ratio (P/B) was assumed to be 0.1 per year, implying an average longevity of about 10 years. Diet composition was obtained as a weighted average of the diet composition of all species of marine mammals reported from Area 77.

2.   *Tuna and billfishes*. Biomass of these top predators among fishes was estimated as approximately 0.05 g m^2, while the P/B ratio was set at 1.2 per yr, and the Q/B at 15 per yr, based on Olson and Boggs (1986). Diet composition was based on information for skipjack (Tandog-Edralin *et al.* 1990) and yellowfin tuna (Olson and Boggs 1986).

3.   *Miscellaneous fish*. Biomass was assumed to be 0.5 g per m^2, as suggested by Mann (1984) for epipelagic nekton in oceanic areas. Mann (1984) also estimated that the production of epipelagic nekton ranged from 0.5 to 1.3 g per m^2 per yr, yielding P/B values ranging from 1.0–2.6 per yr. We adopted a value of 2.0 yr, and assumed Q/B = 9.3 per yr as in for mackerel. (Pauly and Christensen, 1993) Diet composition was based largely on information in Menasveta (1980) and Yamashita *et al.* (1987).

4.   *Mesopelagics* include myctophids, gonostomatids and sternoptychids. They occur between 200 and 1 000 m during daytime and rise into the upper 200 m (epipelagic zone) at night to feed primarily on zooplankton. Biomass was assumed to be 2.6 g per m^2 based on data in Gjøsaeter and Kawaguchi (1980) for the western central Pacific. Similarly, estimates of mesopelagic biomass were calculated by Mann (1984) to range from 1.75 to 3.0 g per m^2 per yr. Following Mann (1984), we used a Q/B value of 2.9 per year, and a P/B ratio of 0.6 per yr. We followed Hopkins and Baird (1977), who found that more than 70% by volume of the diet of mesopelagics consisted of crustaceans.

5.   *Small pelagics* include fish such as herrings, sardines and anchovies. Their Q/B ratio was adapted from Pauly (1989), while P/B was estimated from an assumed gross food conversion efficiency (P/Q) of 0.15. Biomass was estimated by the Ecopath software, based on an assumed ecotrophic efficiency of 0.80, i.e. 80% of the production of small pelagics was assumed to be caught by the fishery or consumed by predators. The diet of small pelagics was as described by Menasveta (1980) and Yamashita *et al.* (1987).

6.–7. *Small and large squids* were those with mantle length smaller and larger than 50 cm, respectively. The catches of small squids were assumed to be 2/3 of the total catch of squids in the area. The Q/B for small squids were based on Pauly *et al.* (1993), while the Q/B for the larger squids was assumed to be half that of the smaller squids. The P/B was estimated based on assumed gross food conversion efficiencies of 0.20, and 0.10 for small and large squids, respectively. Biomasses for both groups was estimated using an assumed ecotrophic efficiency of 0.80. Diet compositions were based on data in Roper *et al.* (1984).

8.   *Benthic fish*   are those living in the deep sea. Mann (1984) gave biomass estimates for the group as a whole ranging from 1.–2. g per m^2. We therefore used 1.5 g per m^2. Their P/B was given by Mann (1984) as 0.05 to 0.10 per yr, and we used 0.075 per yr. The Q/B value was estimated from an assumed gross food conversion efficiency of 0.25, while the dietary composition was based on information given by Mann (1984).

9. *Large zooplankton* such as copepods, euphausiids, and decapods had an estimated biomass of 10 g per m^2, and a P/B of 0.5 per yr (Blackburn, 1981). Based on an assumed gross food conversion efficiency of 0.2, Q/B was estimated as 2.5 per yr.

10. *Small or micro-zooplankton* were assumed to have a biomass equal to about 25% of the biomass of large zooplankton (Blackburn, 1981). Their P/B and Q/B ratios were adjusted to account for their smaller sizes.

11. *Benthic invertebrates* (amphipods, shrimps, and other decapods). Mann (1984) gives a mean biomass of 5.0 g per m^2, and a P/B estimate of 0.1 per yr. With an assumed gross conversion efficiency of 0.25, Q/B was 0.4 per yr. A diet composition was input which led to mass-balance, given the constraints in 1–12.

12. *Phytoplankton*. The primary production was derived as explained in the text.

13. *Detritus*. This includes all dead material, egesta, excreta and dead organisms.

The model resulting from these estimates and assumption (Fig. 2) is tentative, and is presented here as a *possible* scenario. Interested readers may obtain further details (including the complete file and the Ecopath software to run it) from Daniel Pauly or Villy Christensen. The latest (Windows 3.1) version of Ecopath includes a Monte-Carlo simulation routine allowing verification, in a Bayesian context, of assumptions such as those presented above.

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