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

by

Andrew W. Trites[1], Daniel Pauly[1,2] and Villy Christensen[2]

[1] Marine Mammal Research Unit, Fisheries Centre, University of British Columbia
2044 Main Mall, Vancouver, B.C., Canada B6T 1Z4

[2] International Center for Living Aquatic Resources Management (ICLARM)
Manila, Philippines

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 2,000 mt in 1948 to over 50,000 mt in 1992. About 50% of the total Pacific catch has traditionally come from the mixed stock fisheries off the coasts of Russia, China and Japan. Recent declines occurring in some areas of the Pacific suggest that Pacific fisheries cannot continue to expand as they have previously.

Based on estimates of population size, total biomass and daily consumption rates, the 81 species of marine mammals inhabiting the Pacific Ocean consume three times as much food as humans harvest. However, the most significant consumer of commercially sought fish is other predatory fish, not marine mammals. A large fraction (>60%) of the food caught by marine mammals consists 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. The greatest dietary overlap with humans occurs among the pinnipeds, dolphins and porpoises.

Although direct competition between fisheries and marine mammals for prey appears rather limited, there may be considerable indirect competition through the food web for the primary productivity which sustains each of them. A mathematical model showed that amounts of primary productivity required to sustain marine mammals in each of the FAO areas varies within a narrow range, suggesting that the diversity and abundance of marine mammals may have slowly evolved to fully exploit their niches, and maximize their use of available primary production. This contrasts sharply with the rapid expansion of fisheries and their relatively recent dependence on primary productivity. An apparent relationship between the size of fishery catches and the amounts of primary productivity required to sustain fisheries and marine mammals implies that fisheries may reduce the amount of primary production accessible to marine mammals, thereby negatively affecting marine mammal numbers.

Introduction

The Pacific Ocean is the largest of the world's oceans with a surface area of nearly 180 million km^2. It ranges from the high Arctic in the north to the Antarctic continent in the south, and tends to be rather homogeneous biogeographically, consisting largely of a central plate with a distinct and diverse load of co-evolved organisms and ecosystems. Eighty-one species of whales, dolphins, porpoises, seals and sea lions, totalling over 12 million individuals, inhabit the Pacific Ocean; while over a billion people line its rim and draw upon its marine resources.

The following explores the use and development of fishery resources in the Pacific Rim, and their relationship to marine mammals of the Pacific. We show the amounts of fish caught in the Pacific for 7 statistical areas defined by the FAO - Food and Agriculture Organization of the United Nations (Fig. 1), and estimate the amount of food consumed in each area by the 81 Pacific species of marine mammals. We also use an approach recently developed by Pauly and Christensen (1995) to estimate the percentage of primary production required to sustain the food web upon which the fisheries and marine mammals depend. In this way we attempt to assess the extent of competition between humans and marine mammals. Finally, we present 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 contain the Pacific Ocean (Fig. 1). 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 most recent FAO yearbook (FAO, 1994). Catches were compiled by FAO 'commodity' group (*i.e.* ensemble 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 ($N_{i,s}$) were obtained from various sources documented in Trites and Pauly (1995a). They 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 (*e.g.* Northridge, 1984). When presented with 'order-of-magnitude' estimates (*e.g.* 00,000s), we conservatively chose the lower bound (*e.g.* 100,000) from the range of possible values (*e.g.* 100,000 to 1,000,000). Such an approach produced comparable estimates of abundance for the few species for which both guesses and subsequent population estimates existed. We assumed the sex ratio (proportion of females in the total population) was 0.5 for all species, except for sea lions and fur seals, for which a value of 0.6 was used (Trites and Pauly, 1995b).

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. Individual weights below which 50% of the cumulative biomass occurred was 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, 1995b).

An individual's daily consumption or ration (kg day^{-1}) 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 Eq. 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 Eq. 3 range from 1.1 % of body weight per day in a 50,000 kg baleen whale (*i.e.* 574.3 kg day^{-1}), to 4.5 % of body weight per day in a small 50 kg dolphin (2.3 kg day^{-1}), 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 81 species of marine mammals was derived from published accounts of stomach contents, as well as from morphological, behavioural and other information (Pauly *et al.*, 1995). Diet composition was grouped by 8 types of food (benthic invertebreates, large zooplankton, small squids, large squids, small pelagic fishes, mesopleagic fishes, miscellaneous fishes and higher vertebreates).

Primary Productivity

The total amount of primary production (P_T) in each of the 7 FAO Pacific regions was derived from a global analysis by Longhurst *et al.* (1995). The authors divided the world's oceans into 56 'provinces', estimating primary productivity for each from a large observational data base. We superimposed the 29 provinces of the Pacific Ocean onto the 7 FAO areas in the Pacific Ocean (Table 1, Fig. 2), to compute weighted mean estimates of primary productivity for each FAO area.

The amount of primary productivity (P_C) required to produce the fish caught by commercial fisheries was calculated 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 Table 1 in Pauly and Christensen (1995) and were based on 48 ecosystem models (ECOPATH II software from Christensen and Pauly 1992a,b, 1993). As illustrated in Figs. 3 and

4, groups with similar life history and habits have a trophic level equal to the mean trophic level of its prey (weighted by consumption) plus 1. Primary producers (mainly planktonic algae) and detritus are conventionally given a trophic level equal to 1. Transfer efficiencies between trophic levels tend to have a mean value of 0.10 in aquatic ecosystems (Fig. 4, Pauly and Christensen 1995). Further details are contained in Appendix 1.

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

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

where Q_i is the total amount of prey caught by species *i* (Eq. 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 81 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 2. Corresponding trophic levels occupied by each species of marine mammal were calculated using the ECOPATH II approach. They equaled the average trophic level of their prey plus one, and ranged from 4.6 in killer whales to 3.2 in right, blue, fin and bowhead whales (Pauly *et al.* 1995).

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

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

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 productivity required to sustain fisheries - Eq 4, or marine mammals -Eq. 5, divided by total available primary productivity).

We simplified the analysis by aggregating the marine mammals into five groups: baleen whales, beaked whales, dolphins and porpoises, pinnipeds, and all 81 species of marine mammals combined. Niche overlap indices were estimated between each of the five whale groups, and the fisheries by FAO area using the ECOPATH II software system (Vers. 2.2+).

Results and Discussion

Catch

The amount of fish caught in the Pacific Ocean rose from 2,000 mt in 1948 to over 50,000 in 1992 (Fig. 5). 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 until their collapse in 1972, and have recently undergone rapid increases in catches of sardines and horse mackerel. This contrasts with the steady build up in mixed stock catches reported in the South Pacific (see Fig. 4). Elsewhere in the Pacific, catches have been relatively small having been dominated by groundfish in the Gulf of Alaska and Bering Sea (Area 67) and tuna in the Central Pacific (Area 77).

Everything that is caught is not necessarily landed. In 1992 for example, the amount of fish discarded at sea averaged 34% of the total Pacific catch (Table 3). Rates of by-catch ranged from a low of 18% in South America (Area 87) to a high of 50% in the Central Pacific off the coast of North America (Area 77).

Recent fishery statistics (Fig. 4) suggest catches have been declining in some areas of the Pacific and may have stabilized in others. Declining catches 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 would appear however that the Pacific fisheries cannot continue to expand as they have previously.

Consumption

Pacific marine mammals, with a total biomass approaching 25 million mt, consume about 150 million tons of food per year (Table 4). This is about three times the nominal catch. The most important prey items are squids (26 and 41 million tons for small and large squids, respectively) and mesopelagics (25 million tons). Intermediate amounts of miscellaneous fishes (19 millions tons) and small pelagics (17 million tons) are consumed, while benthic invertebrates (3-4 millions tons) and higher vertebrates (marine mammals and birds, mainly penguins) contribute only 0.7 million tons for the Pacific as a whole.

Primary Productivity

The amount of primary productivity required to sustain marine mammals in each of the FAO Areas varied within a very narrow range of 20 to 30 g C m^{-2} $year^{-1}$ (see Fig. 6). This presumably reflects a long evolutionary history during which the various species of marine mammals occurring in a given area diversified to fully exploit the niche opened by their 'new' morphology and respiratory physiology. Primary productivity required to sustain the fisheries varied much more between different areas of the Pacific, depending on the level of fishing effort and the type of resource exploited (Fig. 6).

Resource Competition

Commercial fisheries target only 35% of the prey items sought by marine mammals (Fig. 7), a figure far less than might be expected considering the frequent complaints about marine mammals by some fisheries. Over 65% of the prey consumed by marine mammals is 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. 7).

Specialized feeding habits further imply that the observed overlap between the prey items of the marine mammals and the 'prey' of the fisheries is less than expected. For example, most of the squids 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 fishing gear currently in existence. Similarly the very small fish which make up the mesopelagic community 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 Gjφsaeter and Kawaguchi 1980). Marine mammals exploit mesopelagics by diving to deep depths where they occur during daytime, or by foraging at night when the millions of fish and associated invertebrates that make up the 'deep-scattering-layer' rise to the upper 100 m of the water column (Fig. 8).

The most significant consumer of fish and competitor of commercial fisheries is probably other predatory fish, and not marine mammals. For example, ECOPATH II model estimates of the amount of fish consumed by fish and marine mammals in the Eastern Central Pacific (FAO Area 77) indicate that predatory fish consume an order of magnitude more fish than the marine mammals (Figs. 1 and 3, Table 5). Thus it is likely that fish predation is more important to the fisheries than predation by marine mammals in all FAO Areas.

Although direct competition between fisheries and marine mammals for prey appears rather limited, there may be considerable indirect competition for the primary productivity which sustains each of them. Our estimates of required primary production (Fig. 6) suggest that Pacific fisheries in some FAO Areas may have entered into a 'food-web-competition' with the marine mammals. Such competition would occur at the *base* of the food web as shown in Fig. 4, and is the 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 3) and the amounts primary productivity required to sustain fisheries and marine mammals (Fig. 6) is explored in Fig. 9. The data imply that the amount of primary productivity used by marine mammals declines as the catch increases. Thus primary productivity of the fisheries may affect the food web upon which the marine mammals rely.

Management Implications

Our tentative results suggest 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.

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 (EEZ's) 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 from the Pacific, the trend is clear: the excessive build up of, and overcapitalization in the fishing fleets unavoidably leads to overfishing, and potentially threaten marine mammals with food web competition.

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Table 1. Key statistics of the 29 'provinces' used by Longhurst et al. (1995) to summarize primary production estimates in the Pacific Ocean (as defined by FAO areas 61-88).

Domain	Province	Area[a)] ($10^6 km^2$)	Annual PP (gC/m^2)	Total PP (GtC), by index of coastal turbidity 0 (%)	50 (%)	75 (%)
Coastal	AUSW	(0.27)	199	0.59	0.05	0.05
Coastal	ALSK	0.59	661	0.39	0.39	0.39
Coastal	CCAL	0.96	388	0.37	0.37	0.37
Coastal	CAMR	1.26	334	0.42	0.42	0.42
Coastal	CHIL	2.61	269	0.70	0.70	0.70
Coastal	CHIN	0.97	619	0.60	0.30	0.15
Coastal	SUND	6.33	328	2.08	1.04	0.52
Coastal	AUSE	1.14	323	0.27	0.27	0.27
Coastal	NEWZ	1.04	312	0.32	0.32	0.32
Westerlies	PSAE	3.20	199	0.64	0.64	0.64
Westerlies	PSAW	2.90	264	0.77	0.77	0.77
Westerlies	KURO	3.70	193	0.72	0.72	0.72
Westerlies	NPPF	3.02	172	0.52	0.52	0.52
Westerlies	NPSE	6.83	111	0.76	0.76	0.76
Westerlies	NPSW	3.93	109	0.43	0.43	0.43
Westerlies	OCAL	2.39	117	0.28	0.28	0.28
Westerlies	TASM	1.65	163	0.27	0.27	0.27
Westerlies	SPSG	37.29	87	3.23	3.23	3.23
Westerlies	SSTC	(7.74)	136	2.29	1.05	1.05
Westerlies	SANT	(15.59)	120	3.63	1.87	1.87
Trades	ISSG	(0.04)	71	1.37	0.00	0.00
Trades	NPTG	21.09	59	1.24	1.24	1.24
Trades	PNEC	8.17	107	0.87	0.87	0.87
Trades	PEQD	10.34	113	1.17	1.17	1.17
Trades	WARM	16.78	82	1.38	1.38	1.38
Trades	ARCH	8.84	100	0.88	0.88	0.88
Polar	BERS	3.89	363	1.41	1.41	1.41
Polar	ANTA	(4.29)	122	1.47	0.71	0.71
Polar	APLR	(1.06)	213	0.77	0.42	0.42
Total (mean)		177.91	(122)	29.84	22.49	21.82

[a] Areas in brackets refer to provinces of which only a part occurs in FAO areas 61-88; the total primary productivity for these provinces is reduced in proportion of the area reduction.

Table 2. Definition of prey groups and related information required to assess the trophic impact of marine mammals. Exampliay diet compositions are shown for 5 of the 81 species of Pacific marine mammals (adapted from numerous sources *e.g.* Evans ..., Klinowska 1991, Bonner 1989, King ...).

Feature / Group	Benthic inverts[a]	Large Zoopl[b]	Small squid[c]	Large squid[d]	Meso-pelagics[e]	Small pelagic[f]	Misc. fishes[g]	Higher vert.[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.

Table 3. Key features of the seven areas used by FAO to report fisheries statistics, with 1992 catches (FAO 1994)[a].

FAO Area	Region of the Pacific	Latitude (° N or S)	Area (% shelf) ($km^2 \cdot 10^3$)	Catch (1992; $t \cdot 10^3$)	By-catch (% of catch) [b]
61	North West	65 N - 15 N	20,476 (4.7)	24,199	39.8
67	North East	65 N - 40 N	7,503 (12.9)	3,148	28.2
71	Western Central	15 N - 25 S	33,233 (13.9)	7,710	43.0
77	Eastern Central	40 N - 5 N	48,899 (0.9)	1,342	49.9
81	South West	30 S - 50 S	28,375 (4.7)	1,114	29.7
87	South East	5 N - 60 S	30, 016 (1.3)	13,899	18.5
88	Antarctic[a]	60 N - (75 S)	(10,386 (21.7))	<< 1[c]	29.5
all	Total Pacific Ocean	65 N - (75 S)	178,888 (6.1)	51,412	33.9

[a] Approximate values in brackets.

[b] Adapted from Alverson et al. (1994).

[c] Consisting of 50 t of krill (*Euphausia superba*) caught from July 1, 1991 to June 30, 1992.

Table 4. Food consumption ($t \cdot 10^3 year^{-1}$) by the marine mammals (in $t \cdot 10^6$) in the Pacific Ocean, by FAO area and food type.

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

Table 5. Estimates (g m^{-2} $year^{-1}$) of fish consumed by fish, marine mammals or caught by fisheryies in 1992 the Eastern Central Pacific (FAO Area 77). Estimated from ECOPATH II *trophic model* (see Appendix 2).

		"Prey"			
"Predator"	Tuna, billfish	Misc. fish	Meso-pelagics	Benthic fish	Small pelagics
Fishery	0.01	0.01	0.00	0.00	0.01
M. mammals	0.00	0.10	0.14	0.00	0.09
Fish	0.00	0.23	0.55	0.07	2.09

FAO Statistical Areas

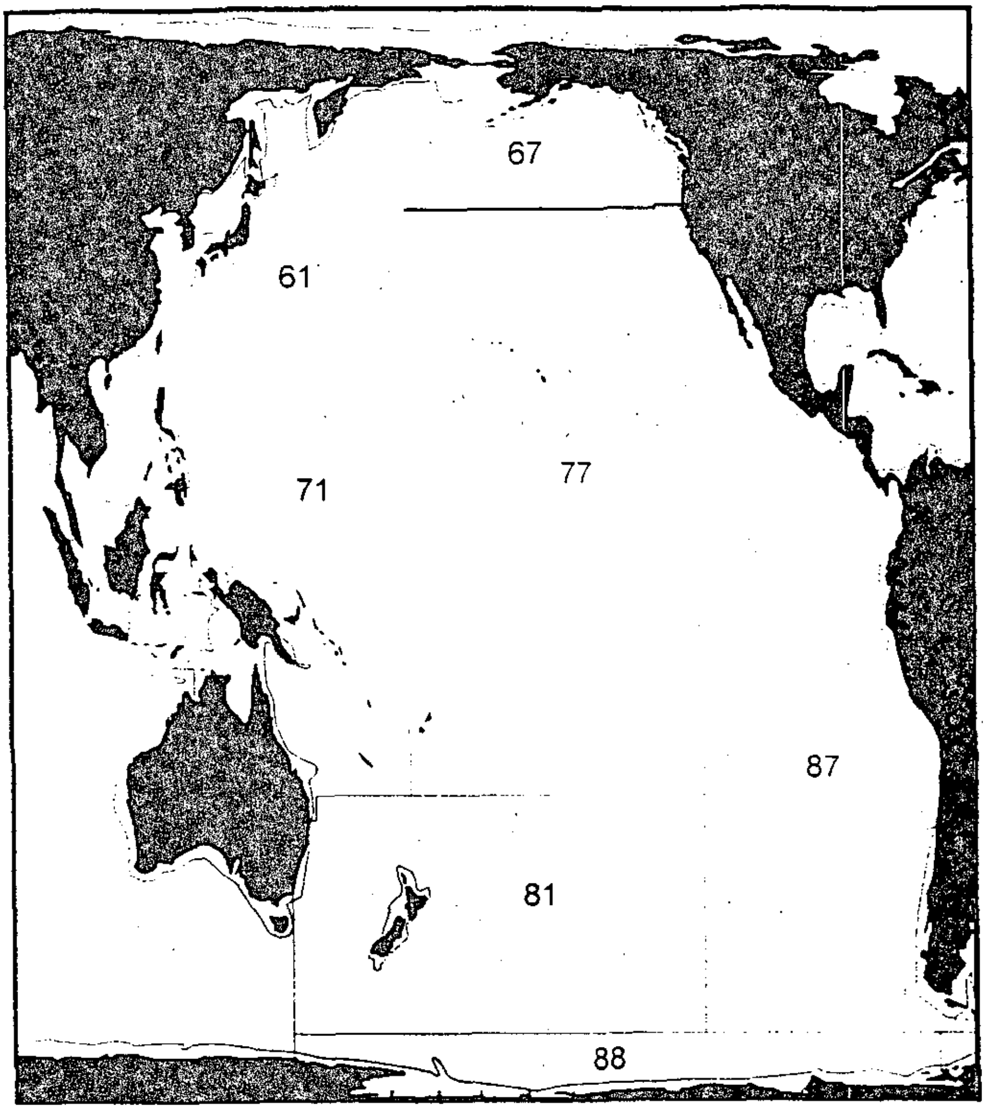

Fig. 1. The seven FAO areas used to report fish catches in the Pacific Ocean. The projection (Peters 1983) allows direct comparisons of surface areas, and of shelve areas (shaded) from which the overwhelming bulk of the fisheries catches originate.

Primary Productivity 'Provinces'

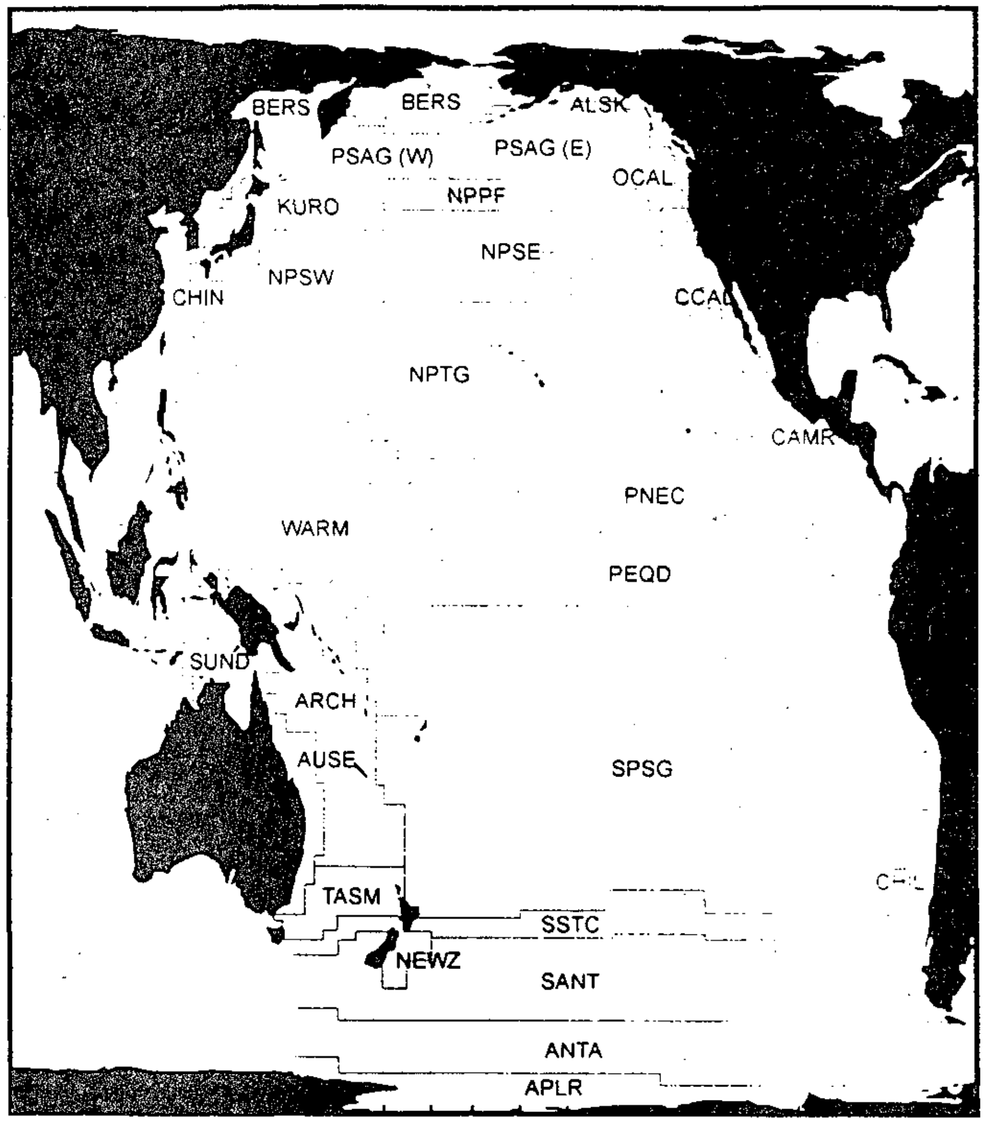

Fig. 2. The 'provinces' of the Pacific Ocean used by Longhurst et al. (1995) to summarize available data on primary production.

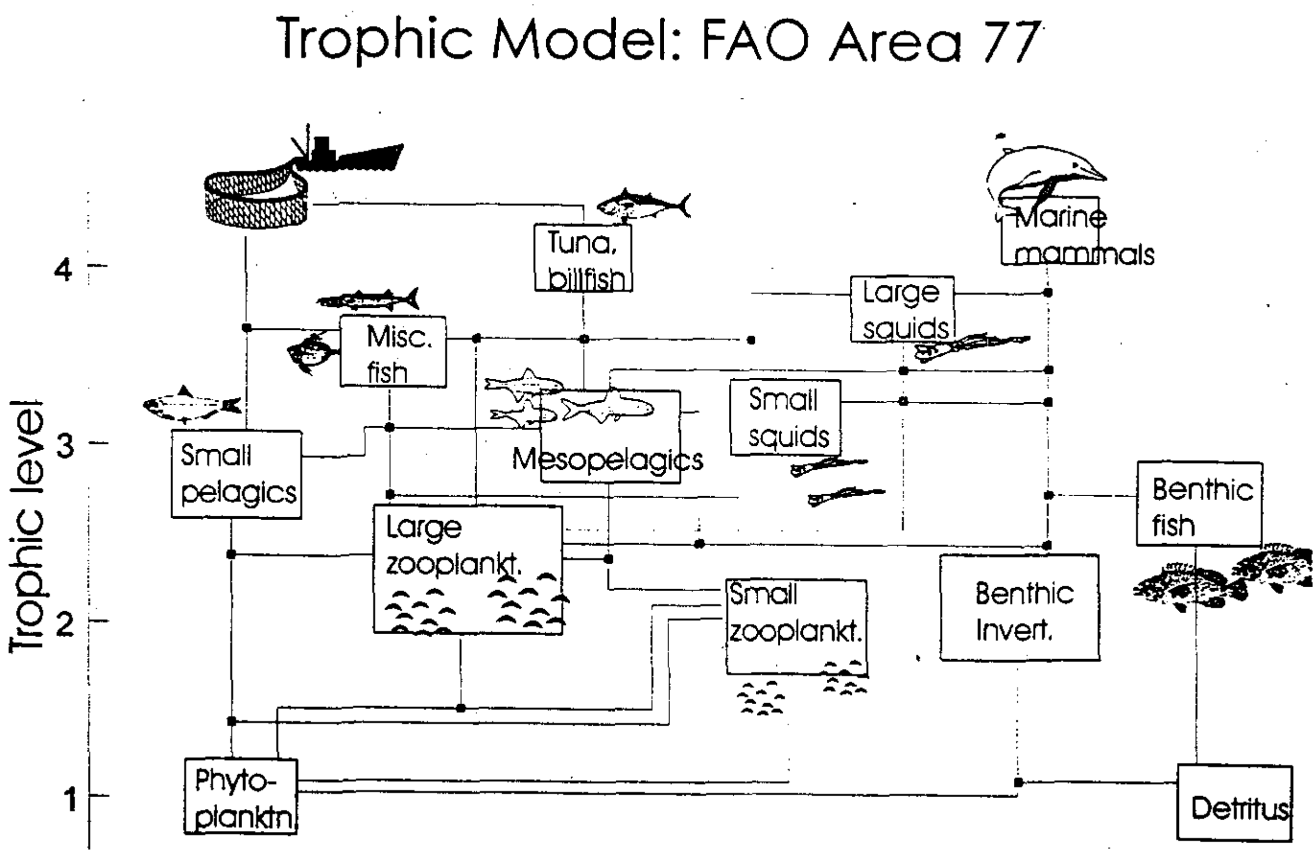

Fig. 3. Trophic model representing the pelagic ecosystem in FAO Area 77 (see Appendix 1 for details). Note the difference between those parts and pathways of the system leading to the fisheries, and those that lead to most of the marine mammals.

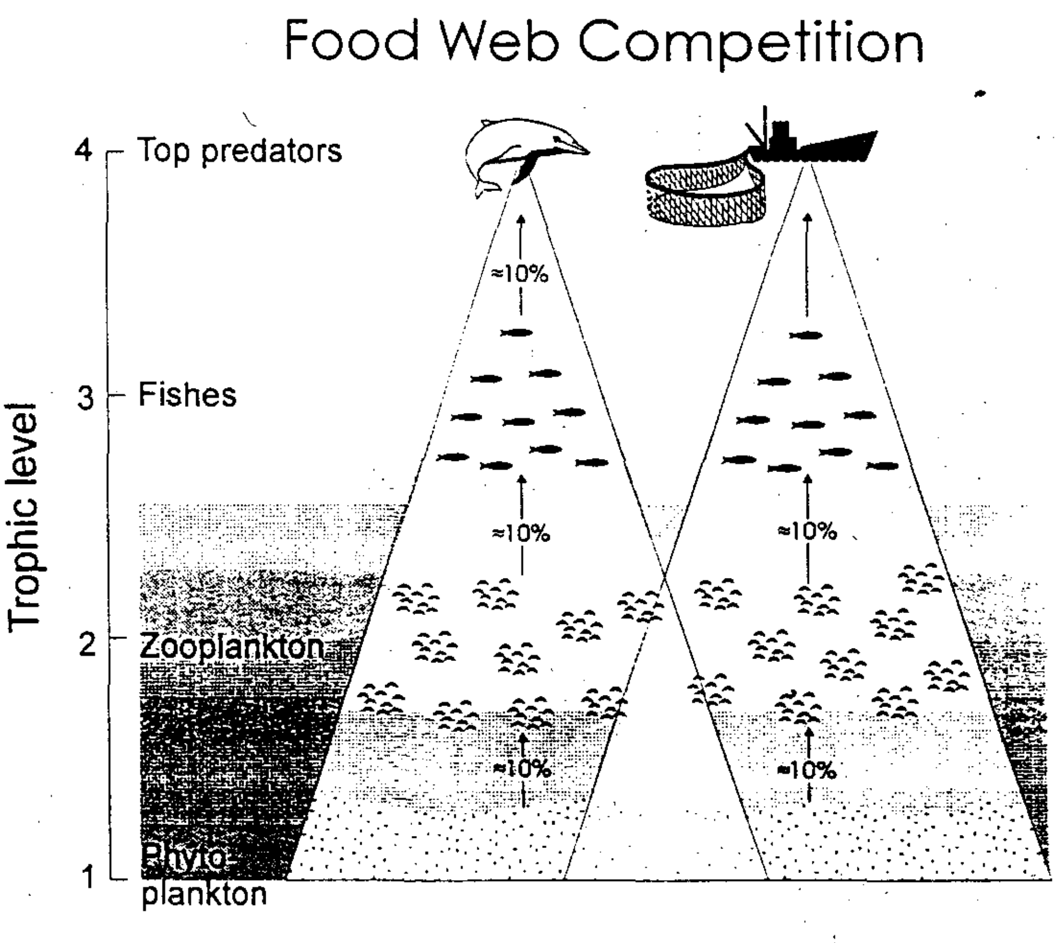

Fig. 4. Schematic representation of 'food web competition', a new concept proposed to explain why some groups of top predators, such as marine mammals, cannot sustain their biomasses when fisheries rely on food webs whose primary base overlaps with that of the group in question. Note that food web competition does not require the fisheries and the top predator to harvest the same prey.

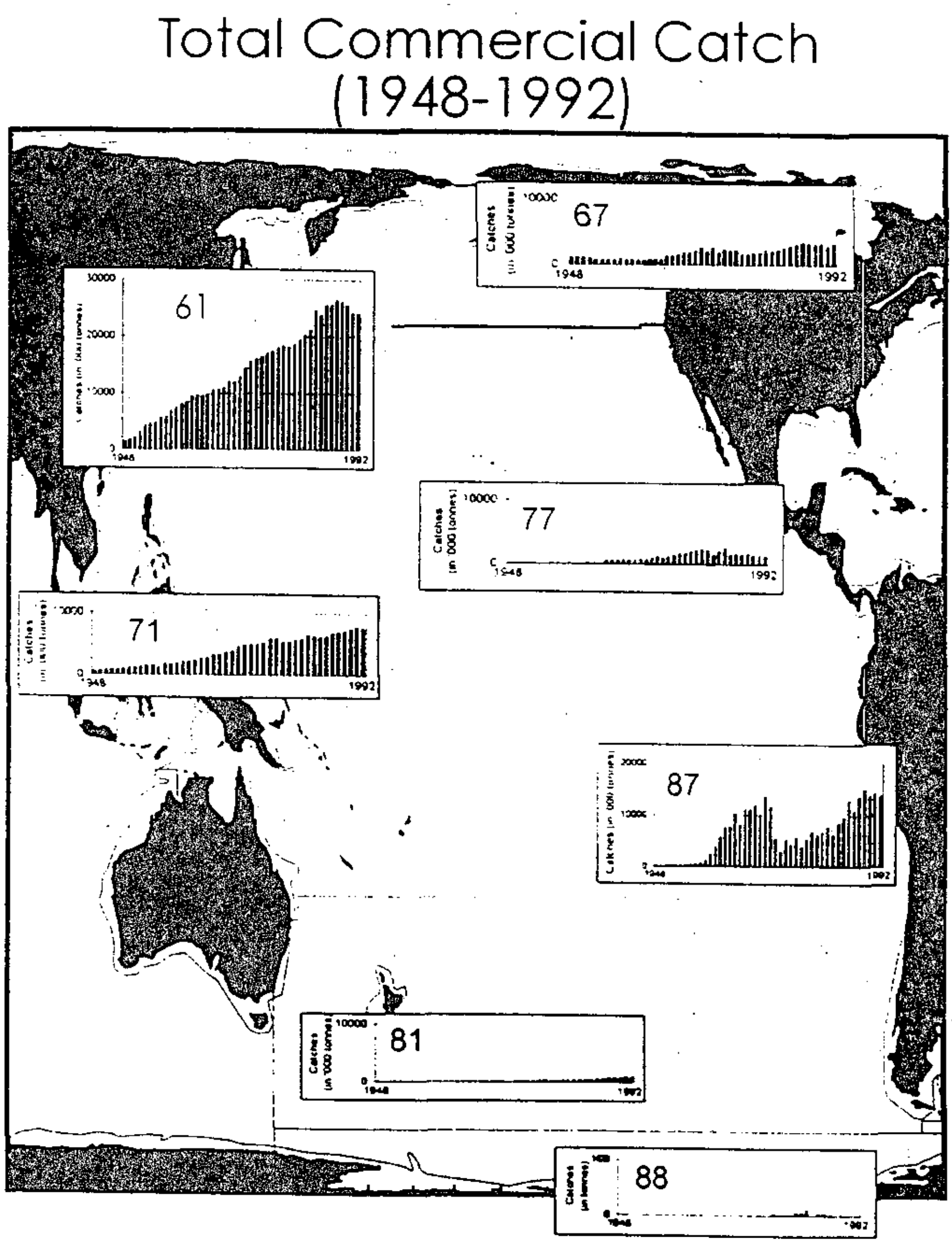

Fig. 5. Time series of Pacific ocean fisheries catches by FAO area. Note the recent decline or stabalization in catches reported in recent years.

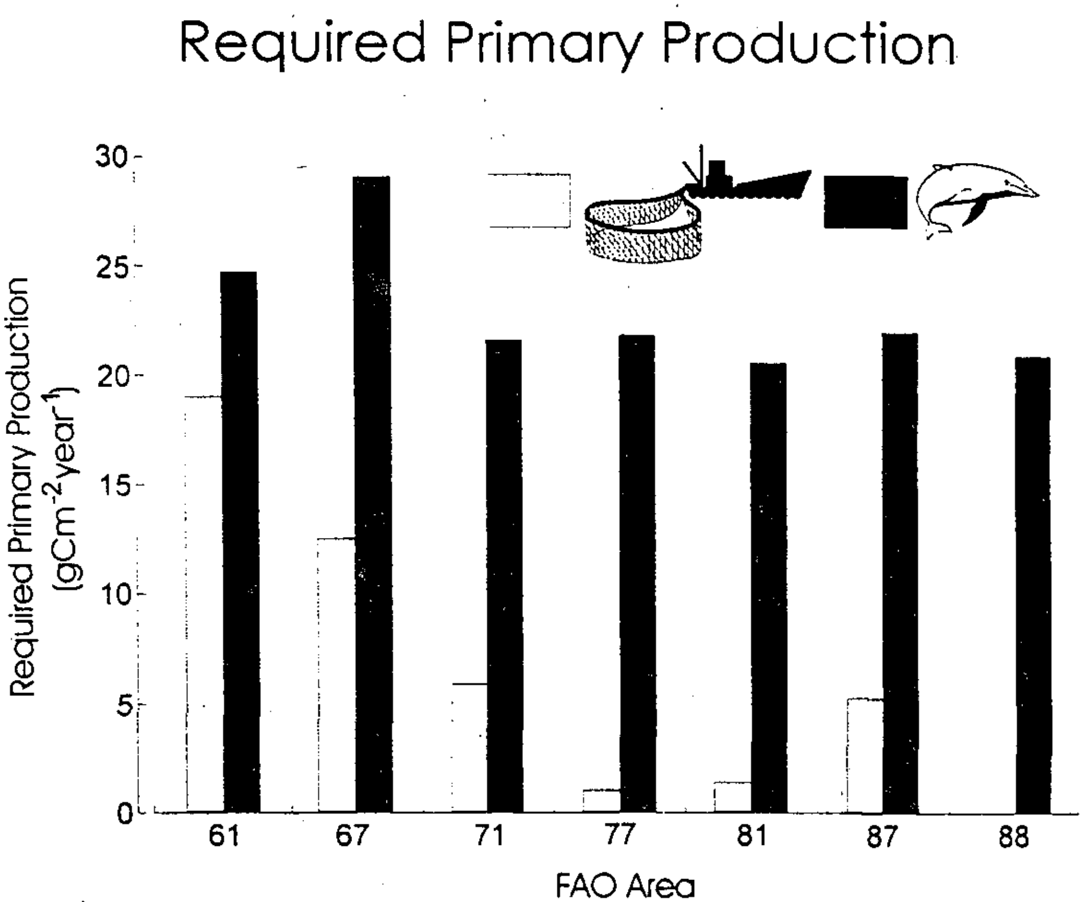

Fig. 6. Primary production required to sustain marine mammals and fisheries in the Pacific ocean, by FAO area.

Niche Overlap Indices

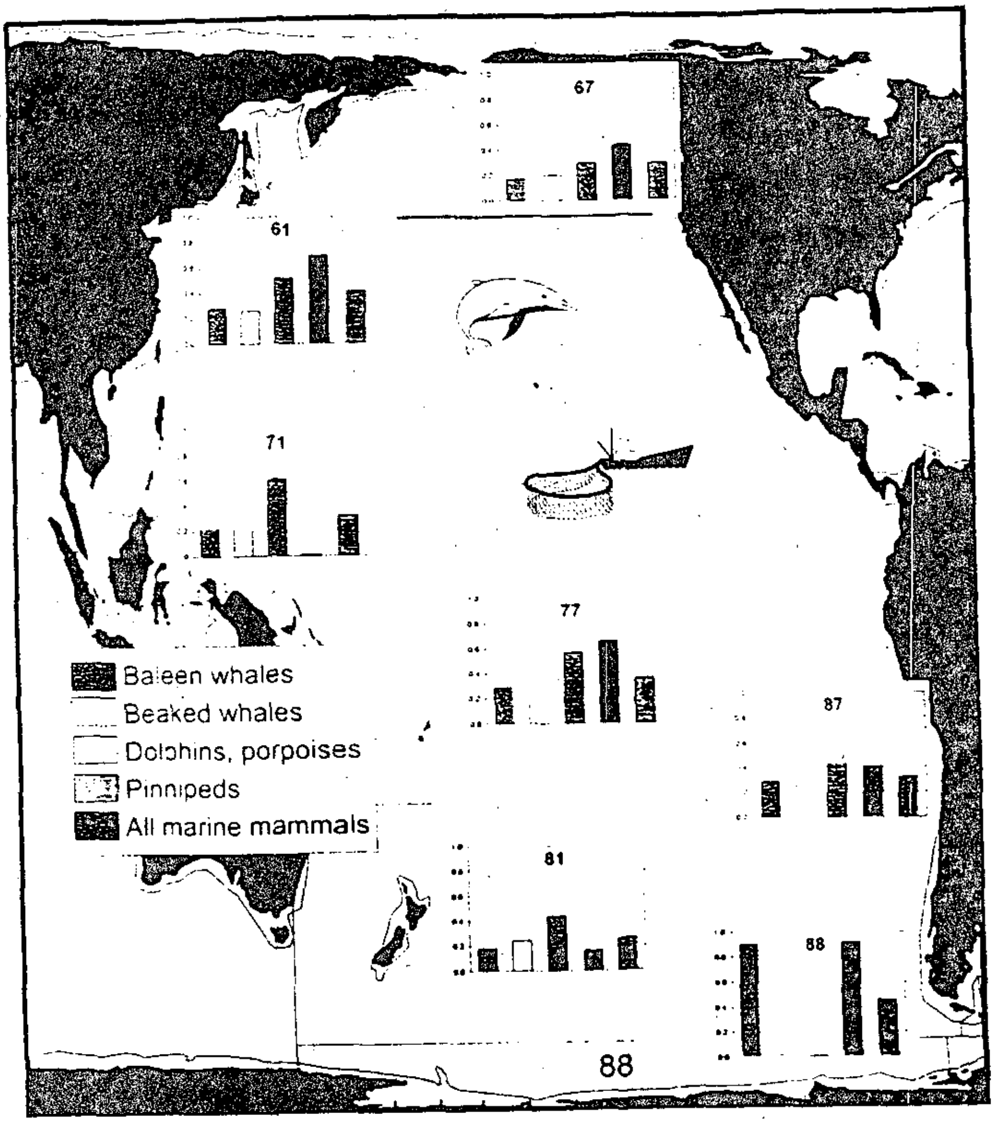

Fig. 7. Overlap between the prey composition of four groups of marine mammals (plus all marine mammals combined), and the catch composition of the fisheries by FAO area.

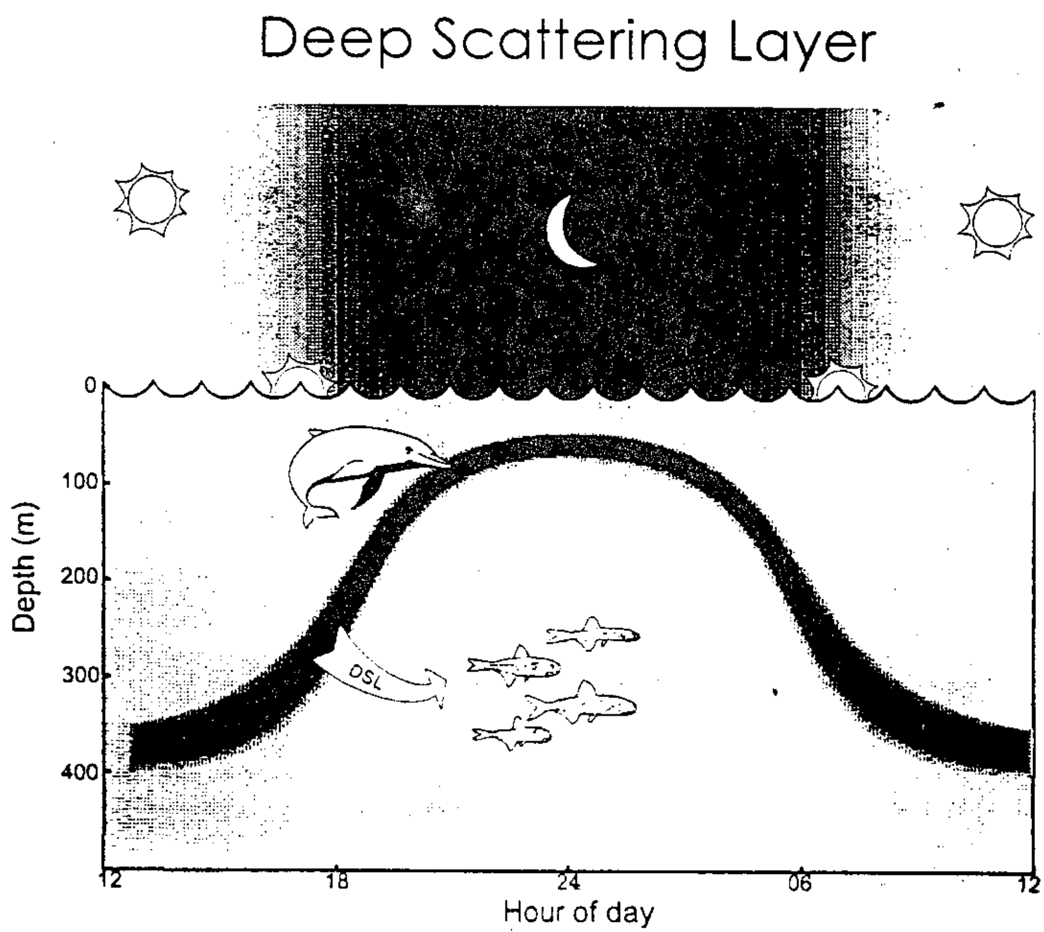

Fig. 8. Schematic representation showing how small cetaceans (*e.g*, spinner dolphin) exploit the small mesopelagic fishes of the Deep Scattering Layer (DSL).

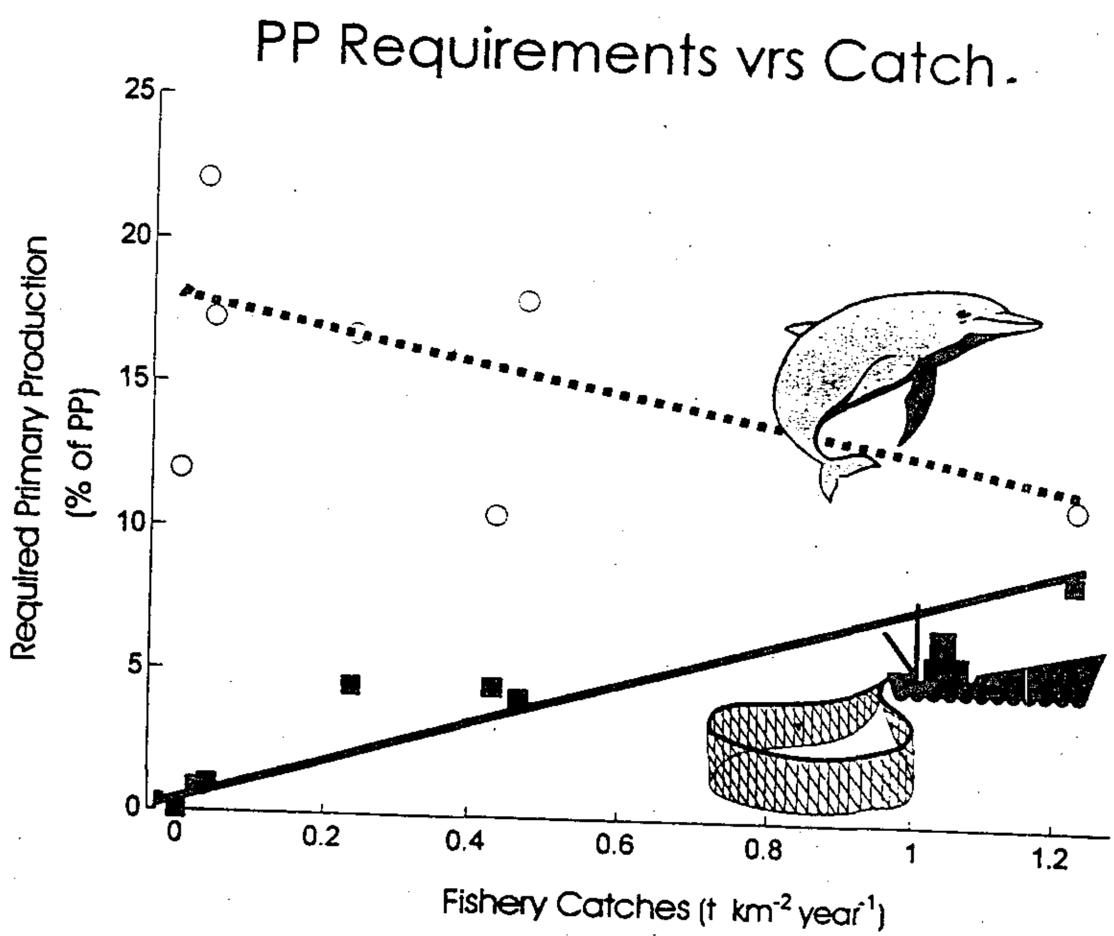

Fig. 9. Primary productivity requirements relative to fishery catches. Primary production required by the marine mammals of the Pacific ocean appears to decline when fisheries catches (and hence the primary productivity required by the fisheries) increases. This implies food web competition as defined in Fig. 8.

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

To exemplify 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 II 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 II, and of the parameters it requires).

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 groups:

1. Marine mammals, whose biomass was estimated as described in the text above (see also Table 4). The consumption/biomass ratio (Q/B) was estimated, while the production/biomass ratio (P/B) was assumed to be 0.10 $year^{-1}$, implying an average longevity of about 10 years. Their diet composition was obtained as a weighted average of the diet composition all species of marine mammals reported from area 77.

2. Tuna and billfishes, comprising ISSCAAP group 36, the top predators among the fishes. Based on Olson and Boggs' (1986) studies in the eastern Pacific, the biomass is estimated to approximately 0.05 g m^{-2}, while the P/B ratio was 1.2 $year^{-1}$, and the Q/B, 15 $year^{-1}$. The diet composition was estimated based on information for yellowfin tuna given by Olson and Boggs, and for skipjack by Tandog-Edralin et al. (1990).

3. Miscellaneous fish, including ISSCAAP groups 21-34 and 36-39. The biomass of the group is assumed to be 0.5 g m^{-2}, as used by Mann (1984) for epipelagic nekton in oceanic areas in general. Mann (1984) also estimated the production of epipelagic nekton to range between 0.5 and 1.3 g m^{-2} $year^{-1}$. This gives a P/B ranging from 1.0-2.6 $year^{-1}$, and we adopted a value of 2.0 $year^{-1}$. The Q/B estimate was assumed to be 9.3 $year^{-1}$ as used by Pauly and Christensen (1993) for mackerel. The diet composition is based mainly on information in Menasveta (1980) and Yamashita et al. (1987).

4. Mesopelagics, including myctophids, gonostomatids, and sternoptychids, occurring between 200 and 1000 m during daytime, while feeding primarily on zooplankton in the epipelagic zone during nighttime. The biomass was assumed to be 2.6 g m^{-2} based on data in Gjøsaeter and Kavaguchi (1980) for the western central Pacific. Mann (1984), similarly found the biomass of mesopelagics to range from 1.75 to 3.0 g m^{-2} $year^{-1}$. Following Mann (1984) we used a Q/B value of 2.9 $year^{-1}$, and a P/B of 0.6 $year^{-1}$. Hopkins and Baird (1977) found that more than 70% by volume of the diet of mesopelagics consisted of crustaceans; the diet composition of mesopelagics was assumed based on this plus qualitative information from various sources.

5. Small pelagics, including ISSCAAP group 35, herrings, sardines, anchovies, etc. The Q/B ratio was adapted from Pauly (1989), P/B was then estimated from an assumed gross food conversion efficiency (P/Q) of 0.15, while the biomass was estimated by the ECOPATH II program based on an assumed ecotrophic efficiency of 0.80, i.e. it is assumed that 80% of the production of small pelagics is used for catches and predation. Information about the diet of small pelagics came from Menasveta (1980) and Yamashita et al. (1987).

6.-7. Small and large squids are those with mantle length smaller and larger than 50 cm, respectively. The catches of small squids are assumed to be 2/3 of the total catch of squids in the area. The Q/B for small squids are based on Pauly et al. (1993), while the Q/B for the larger squids is assumed to be half of the Q/B of the smaller. The P/B is estimated based on an assumed gross food conversion efficiency of 0.20, and 0.10 for small and large squids, respectively. The biomasses for both groups are estimated based on an assumed ecotrophic efficiency, EE, of 0.80. The diet compositions are assumed, based on general knowledge of the biology of squids (Roper et al. 1984).

8. Benthic fish, living in the deep sea, and scarcely known. Mann (1984) gave biomasses for the group as a whole ranging from 1.0-2.0 g m^{-2}, we therefore used 1.5 g m^{-2}. Their P/B was given by Mann (1984) as 0.05 to 0.10 $year^{-1}$, and we used 0.075 $year^{-1}$. The Q/B value was estimated from an assumed gross food conversion efficiency of 0.25, while the diet was assumed based on information given by Mann (1984).

9.-10. Zooplankton: the large zooplankton consists of copepods, euphausiids, and decapods. Blackburn (1981) estimated their biomass and P/B as 8-13 g m^{-2} (we used 10 g m^{-2}), and 0.5 $year^{-1}$, respectively. Based on an assumed gross food conversion efficiency of 0.2 the Q/B is estimated to 2.5 $year^{-1}$. The diet compositions are assumed. For the small zooplankton...

11. Benthic invertebrates (amphipods, shrimps, and other decapods): Mann (1984) gives a mean biomass of 5.0 g m^{-2}, and a P/B estimate of 0.1 $year^{-1}$. With an assumed gross conversion efficiency of 0.25 the Q/B is then 0.4 $year^{-1}$. The diet composition is assumed.

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

13. Detritus. Includes all dead material. All egesta, excreta and dead organisms are directed to this group.

The model resulting from these estimates and assumption is tentative, and is presented here as a *possible* scenario. Interested readers may consult DP or VC for details on the ECOPATH II modelling approach and software, of which a window version has recently been released which includes a Monte-Carlo simulation routine allowing verification of assumption such as presented above, and evaluating their impact on final estimated trophic flows.