Trophic Model of the Coastal Fisheries Ecosystem of the Southwest Coast of India

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Abstract

The Ecopath approach and software were used to construct a trophic model of the coastal fisheries ecosystem of the southwest (SW) coast of India. The model consisted of 11 ecological groups and used estimated landings from all areas along the southwest coast (based on the sample surveys conducted by Coastal Marine Fisheries Research Institute for the years 1994, 1995 and 1996). The trophic model suggests high catch levels, particularly for the large and medium predators, demersal feeders and detritivores. The biomass estimates in the trophic model were comparable to the biomass estimates from trawl surveys based on the swept area method for the southwest coast.

Introduction

There are numerous studies on the population dynamics of individual species of commercially important fishes and invertebrates of the Indian coast (Devaraj et al. 1994; Fernandez and Devaraj 1996; Vivekanandan and James 1986) with few extensions to multispecies cases (Murty et al. 1992). Pertinent models have been developed in applied ecology involving energy, nutrient and trophodynamics for temperate ecosystems (Andersen and Ursin 1977; Laevastu and Larkins 1981; Walsh 1981). Most of the earlier models are very data-demanding and therefore, not suitable for tropical fisheries where information is limited. (Polovina 1984) developed a relatively simple mass-balance trophic box model known as Ecopath, which provides a methodology for constructing models of trophic interactions in aquatic ecosystems. The model involves partitioning of the ecosystem into species/groups and, given a set of parameters as inputs, provides estimates of mean annual biomass, annual biomass production and annual biomass consumption for each species/group. These groups are defined based on similarity of life history parameters, physical habitat and diet. This approach was expanded upon by (Christensen and Pauly 1992; Christensen and Pauly 1993; Christensen et al. 2000; Pauly et al. 2000; Walters et al. 1997; Walters et al. 1999). Considering the need to gain insight into the functioning of the multispecies Indian fishery resources, this approach is particularly relevant considering that little work has been published on Indian coastal ecosystems.

The Study Area

The southwest coast of India was selected for the eco-system analysis because fish population and community structure analyses had been made in this area (see Srinath et al. this vol.). The southwest ecosystem extends from 8º N to 16º N comprising the maritime states of Kerala, Karnataka and Goa (Fig.1), covering a continental shelf area of 75 390 km^2. The environment of the southwest coast is influenced by monsoon and can be categorized into 3 seasons, *viz.,* monsoon or rainy season (June-September), post-monsoon (October-January) and pre-monsoon (February-May). The characteristics of the marine environment during the 3 seasons have been well studied and documented (Pillai et al. 1997).

Oceanographic Characteristics

During the monsoon, the southerly current spreads over the entire continental shelf. Isolines of water temperature, salinity, dissolved oxygen (DO), and density rise to the surface due to upwelling and occupy the area between the southerly current and the coast. Consequently, dense and cool water with low DO occupies the surface near the coast. During the post-monsoon period (October-January), there is a strong current with northerly flow. On the seaward side of the flow, there is a southerly flow, but only in the southern region of the southwest coast. During this period, the low salinity equatorial waters are advected northwards, causing sinking of high salinity Arabian water below the equatorial waters between 10º and 12º N latitude. During the pre-monsoon period (February-May), the northerly current disappears and the southerly flow is restricted to a narrow belt.

During the monsoon, the thermocline reaches the surface and the average sea surface temperature is around 24º C. During the post-monsoon period, the thermocline descends from the surface (October-November), and reaches deep waters (December-February). During the pre-monsoon, the thermocline remains deep, and the average surface water temperature increases to about 30º C.

During the monsoon, the mean sea surface salinity is relatively low (32.5 ppt) due to river runoff and the salinity maximum (35 ppt) occurs at 30 - 50 m depth. During the post-monsoon, the sea surface salinity is 33 ppt in the southernmost sector of the southwest coast off Cape Comorin and increases northwards up to Karwar (about 35 ppt). During the pre-monsoon period, as the temperature is high, the salinity also remains high in the entire shelf with mean surface salinity of 36 ppt. Oxygen-deficient water starts penetrating the shelf by May, and covers the entire bottom by June-July. By August, the oxycline becomes shallow and reaches the surface where it remains till September-October. It has been observed that the oxycline remains for a longer duration in the northern sector (Karwar: 6 months) than in the southern sector (Quilon: 2 months). However, the DO level is higher in the northern sector as the intensity of upwelling is low. During November-April, the shelf water is well aerated and the mean DO is 4.5 to 5.0 $ml \cdot L^{-1}$. Due to upwelling during the southwest monsoon, the southwest coast is characterized by a high level of nutrients such as phosphate, nitrate and silicate in the surface waters. The nitrate content in the surface waters is very high (3 to 4 µM) compared to < 1µM during the other months, which results in high productivity of 660 mg $C \cdot m^{-2} \cdot day^{-1}$ compared to 200 mg $C \cdot m^{-2} \cdot day^{-1}$ during the other months. The plankton biomass is significantly higher (0.9 to 1.2 $ml \cdot m^{-3}$) compared to < 0.5 $ml \cdot m^{-3}$ during the other months. The rate of primary production in the neritic waters, for instance, is as high as 1 g C $\cdot m^{-2} \cdot day^{-1}$ during upwelling off Cochin compared to only 0.1 g $C \cdot m^{-2} \cdot day^{-1}$ during the other seasons. The phytoplankton production along the southwest coast shows a strong north-south gradation, (Fig. 2). The production increases from 0.1 g $C \cdot m^{-2} \cdot day^{-1}$ off Goa to > 1 g $C \cdot m^{-2} \cdot day^{-1}$ off Cochin (Pant 1992).

In general, the southwest coast is rich in phytoplankton and zooplankton biomass compared to the other Indian coastal waters, see Figure 3. The secondary production along the southwest coast ranges from 10 to 57 mg $C \cdot m^{-2} \cdot day^{-1}$ with an average of 20 mg $C \cdot m^{-2} \cdot day^{-1}$ (Mathew et al. 1990) During upwelling, the minimum zooplankton biomass is > 1 $ml \cdot m^{-3}$ and at times attains up to 12 $ml \cdot m^{-3}$.

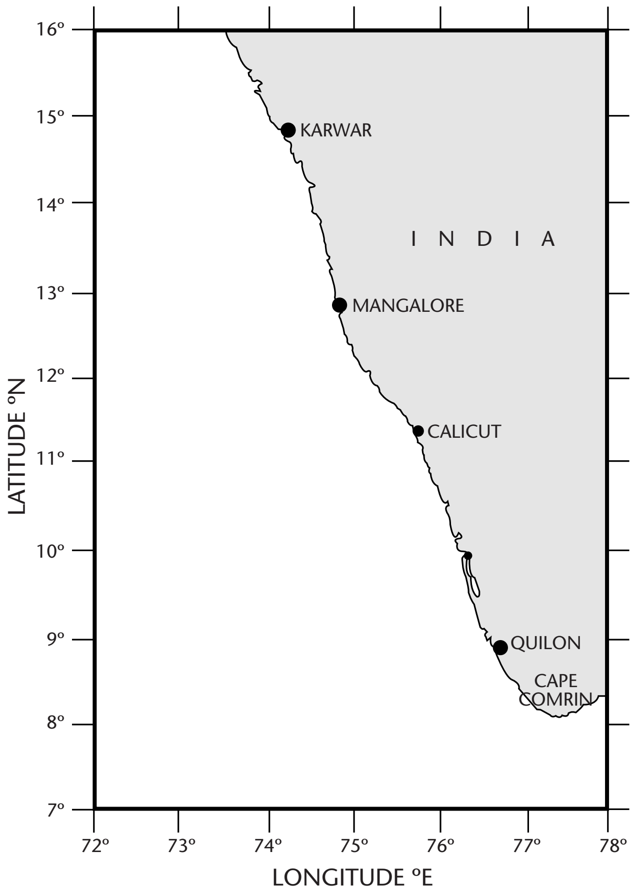

Fig. 1. Study area: the southwest coast of India.

Fig. 3. Primary productivity along the coasts of India during June-August 1998 showing high productivity along the southwestern coast. Scale and source are the same as Fig. 2.

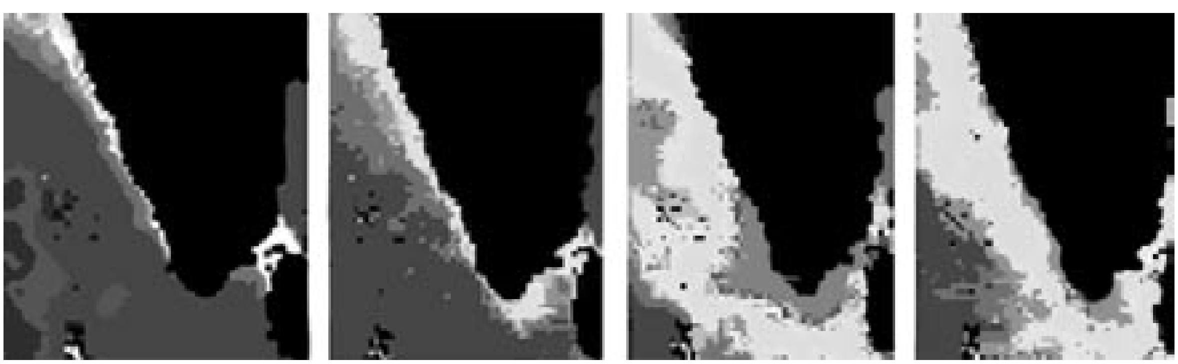

Fig. 2. Primary productivity along the southwest coast of India. The pictures cover 3-months periods starting from December 1997 through November 1998. The scale ranges from 0 (gray) to 150 (white) g C·m^{-2}·month^{-1}. Based on satellite data made available courtesy of the Marine Environment Unit, Space Applications Institute, of the Joint Research Centre of the European Union.

Fisheries

The fishing grounds along the southwest coast are quite extensive and very productive. The sea bottom is generally muddy and sandy. Most of the area is suitable for trawling barring the southern sector, which is characterized by coral and rocky grounds. The 50 m depth contour is at a distance of about 25 km from the coast in the southern sector (off Kerala) and at about 40 km from the coast in the northern sector (off Karnataka and Goa). The width of the continental shelf from the shore varies from about 65 km off Kerala to about 90 km off Karnataka and Goa.

The annual average fish landings along the southwest coast was 630 000 t during 1970 - 97 (see Pillai et al. this vol.), or 37% of total Indian landings. The southwest coast ecosystem is characterized by the abundance of oil sardine, Indian mackerel and penaeid prawns, which together contribute 45% of the landings. In addition to these groups, whitebaits, lizardfishes, threadfin breams, carangids, flatfishes and stomatopods also contribute a high percentage to the landings.

A variety of craft and gear combinations are being used by the commercial fishing sector along the southwest coast (Table 1). Among the mechanized vessels, trawlers are the most common, followed by gillnetters. Of the various traditional crafts, catamarans are prevalent only in the southern sector, while dugout canoes and plank-built boats are prevalent along the entire coast. Gillnets and boat-seines of various dimensions are the most common gears for the artisanal craft. In Kerala alone, 15 types of boat-seines and 26 types of gillnets of various mesh sizes are employed depending upon the fish target resources, which range from species with small body size such as whitebaits to large bodied groups such as rays.

Annual average fish catches along the southwest coast increased from 0.19 million t in 1950 to 0.80 million t in 1997 (Devaraj et al. 1997). The increase was largely due to research and development efforts by different organizations. Motorization of indigenous craft started in Kerala in the early 1980s, and became instantly popular. Consequently, most of the indigenous craft have been fitted with outboard motor and fishing with non-motorized craft has become rare.

Table 1. Major fishing vessel and gear types used along the southwest coast of India.

	Vessel	Vessel Length (m)	Gear	Mesh size (mm)
Mechanized	Trawler	12 - 16	Trawl	15 (codend)
	Gillnetter⁺	7 - 10	Drift gillnet	70 - 130
	Purse-seiner⁺	11 - 14	Purse-seine	8 - 10 & 20 - 30
Motorized/	Catamaran	5 - 10	Boatseine*	5 - 20
Artisanal	Dugout canoe	4 - 10	Ringseine*	5 - 15
	Plank built boat	6 - 14	Drift gillnet*	60 - 110
			Bottom set gillnet*	20 - 260
			Other gillnets*	5 - 100
			Hook and line*	
			Mini trawl*	10 - 15 (codend)
			Dragnet*	12
			Stake net*	8 - 10
			Shore seine	8 - 10

Note: $^{+}$ mechanization employed for propulsion only * operated from any of the 3 motorized/artisanal craft

Mechanization was introduced in the late 1950s and currently, there are about 14 000 mechanized vessels along the southwest coast, most of which are trawlers. Purse seine operation started experimentally in 1957 and was commercialized in the 1960s. There were about 700 purse seiners in the 1980s, but the number declined in the 1990s. At present there are only about 350 purse seiners operating along the southwest coast. The introduction of mechanized fishing vessels and modern gear occurred through 1951 - 60. The increase in the use of synthetic gear materials since 1960, introduction of purse seines in the 1960s, motorization of artisanal crafts in the 1980s, and the substantial growth in the mechanized and motorized crafts since 1985 are the major reasons for the significant increase in production.

However, the technological developments in craft and gear are becoming counterproductive. There is evidence that several fish stocks along the southwest coast are overexploited, and declining (Devaraj et al. 1997). Hence, implementation of appropriate management measures is imperative.

In India, the maritime state governments are responsible for formulation and implementation of fisheries management measures. At present, the three maritime states in the southwest coast (*viz*. Kerala, Karnataka and Goa) observe closed fishing season for the mechanized vessels for a period of 45 to 60 days during the southwest monsoon (June-September). Also, mechanized vessels are banned from fishing within 5 km from the shore. However, the effectiveness of these restrictive management measures on the sustainability of the resources has not been demonstrated. These management measures, on the other hand, have resulted in inter and intra sectoral conflicts. Management measures, which are effective for sustainability of resources and are acceptable to all stakeholders need to be developed.

Materials and Methods

Ecopath Model

The Ecopath approach stems from work of (Polovina 1984; Polovina and Ow 1983). It is a trophic modeling approach and is based on the assumption of mass balance, i.e.

Production = fishing mortality + predation mortality + other mortalities + migration + biomass accumulation. (1)

In addition, it is based on the following relationship:

Consumption = production + unassimilated food + respiration. (2)

The Ecopath master equation takes in the following form (Christensen and Pauly 1993): (3)

$$B_i \frac{P_i}{B_i} - \sum_j B_j \frac{Q_j}{B_j} DC_{ij} - B_i \frac{P_i}{B_i}(1 - EE_i) - EX_i = 0$$

where: B_i = biomass of i; P/B = production/biomass ratio, which is equal to the instantaneous rate of total mortality (Z) under steady state conditions (Allen, 1971); EE_i = ecotrophic efficiency of i; B_j = biomass of predator j; Q_j/B_j = consumption/biomass ratio of predator j; DC_{ij} = fraction of prey i by weight in the average diet of predator j; EX_i = sum of fisheries catches of i plus net migration to adjacent ecosystems.

Ecological Groupings

The ecosystem along the southwest coast was categorized into 11 ecological groups based on feeding habit and the ecological niche of the component species/groups. The compositions of these groups are summarized in Table 2.

Landings and Biomass

The research trawler *M.F.V. Samudrika*, used had a codend mesh size of 35 mm and fished in waters more than 25 m depth off the southwest coast of India. Consequently, the crustaceans were not well-represented in the catches. Moreover, the survey did not consider pelagic resources (which are abundant along the southwest coast). Hence, biomass estimates based on the trawl survey data were not used as input parameters and the biomass values were obtained as outputs from Ecopath. For the present analysis, estimated landings from all gears operated by commercial vessels along the southwest coast (based on the sample survey conducted by CMFRI for the years 1994, 1995 and 1996) were used as inputs.

Table 2. The ecological groupings used for the Ecopath analysis of fishery resources along the southwest coast of India.

Group	Taxa
Large predators	Sharks, seerfishes, tunas, billfishes
Medium predators	Catfishes, lizardfish, snappers, pigface breams, ribbonfishes, barracudas, cephalopods
Large zoobenthic feeders	Skates, rays, eels, Indian halibut
Demersal feeders	Threadfin breams, other perches, goatfishes, threadfins, croakers, silverbellies, whitefish, pomfrets, flounders, soles, stomatopods
Mesopelagic feeders	Wolf herring, half beaks, full beaks, horse mackerel, leather jackets, other carangids
Molluscan feeders	Crabs, lobsters
Plankton feeders	Oil sardine, other sardines, hilsa shad, other shads, Coilia spp., *Stolephorus* spp., *Thryssa* spp., Indian mackerel, other clupeids, scads, gastropods
Zooplankton	
Phytoplankton	
Detritivores	Mullets, penaeid prawns, non-penaeid prawns
Detritus	

Production/biomass (P/B) and Consumption/biomass (Q/B) Ratios

The P/B ratio for each ecological group was obtained from Z estimates for representative species under each category occurring along the southwest coast, as consolidated in Appendix III (this vol.). The annual P/B ratios for phytoplankton and zooplankton were set at 70 and 40, respectively, and the EE's at 0.75 (Polovina 1984).

The Q/B for each ecological group was estimated following the empirical equation suggested by (Pauly et al. 1990):

$$Q/B = 10^{6.37} \cdot 0.0313^{Tk} \cdot W^{-0.168} \cdot 1.38Pf \cdot 1.87^{Hd} \qquad (4)$$

where:

Tk = 1000/(T° + 273) = 3.333;

T° = average annual sea surface temperature (27°C);

W_∞ = asymptotic weight (g) of the species which contributed maximum to the biomass;

Pf = 1 for large predators and zooplankton feeders and 0 for other feeding types; and

Hd = 0 for carnivores and 1 for herbivores and detritivores.

Diet Composition

Though there are studies on the diet composition of numerous species in Indian waters, many of these studies have over-aggregated the diet, and items are only mentioned as "fish", "crustaceans", etc. For the present analysis, wherever diet composition was not available, the general habitat characteristics of the group and information available in FishBase (see http://www.fishbase.org) were used to characterize the diet composition.

Ecotrophic Efficiency

It was assumed that the EE for different ecological groups ranged from 0.65 to 0.95 and a conservative value of 0.75 was assumed for phytoplankton, following (Mendoza 1993).

Assimilation in all the ecological groups (except zooplankton) was considered as 80% of consumption, which is the default value in the Ecopath software. For zooplankton an assimilation rate of 60% was used as this results in a more realistic respiration/biomass ratio for this herbivorous group (V. Christensen pers. comm.)

Primary Production

Phytoplankton primary production has been estimated along the southwest coast by several researchers. The average production in the neritic waters is estimated to be 0.5 g C•m^{-2}•day^{-1} (Pant 1992). A conversion factor of 0.06 g C = 1 g wet weight (Walsh 1981) was employed for transformation. Average total primary production for the ecosystem was estimated as 3042 t•km^2•$year^{-1}$.

Model Parameterization

Large Predators

The large predators include sharks, seerfishes, tuna and billfishes. The dominant species of shark along the SW coast are the large-sized *Carcharhinus* spp. and *Rhizoprionodon acutus* and the smaller *Scoliodon laticaudus*. As the carcharhinids contributed most of the biomass, the asymptotic weight of a medium-sized species, *C. dussumieri* (15 kg) (Compagno 1984) was considered as representative of the sharks. The total mortality (Z) reported for the most abundant species *S. laticaudus* (1.45; Devadoss 1998) was used as the P/B value. The major species of seerfishes and tunas and their representative W, Pf and Hd values are given in Table 3. The diet of the large predators was considered to consist mostly of plankton feeders (0.6) such as the clupeids (Table 4), which is the most abundant group along the southwest coast. The minor diet components were medium predators (0.2) such as the lizardfish, sea breams and cephalopods; young ones of their own group (0.1); large zoobenthic feeders (0.1) such as the perches; and a small quantity (0.01) of zooplankton, ingested along with other prey. It was also considered that import (0.08) would have occurred in the form of migration, especially of the tuna such as *Thunnus tonggol* from other ecosystems and the sharks such as *Carcharhinus* spp. from the offshore into the inshore fishing grounds. There is evidence that the seerfish, *Scomberomorus commerson*, undertakes coastal migration (Devaraj et al. 1997). The Q/B and P/B values for this group were estimated as 7.307 $year^{-1}$ and 2.231 $year^{-1}$, respectively for the large predators (Table 5).

Table 3. Estimated annual landings and selected input parameters for species within the ecological groups (Table 2) for the Ecopath analysis covering the southwest coast of India.

Group	Taxa	Landings (t)			Input parameters				
		1994	1995	1996	W_∞(g)	Pf	Hd	Q/B	P/B
Large predators	Sharks	4 966	4 386	3 319	15 000	1	0	6.22	1.45
	Seerfishes	714	683	1 028					
	Scomberomorus commerson	8 644	9 009	6 621	7 500	1	0	6.99	
	Scomberomorus guttatus	617	479	635	6 000	1	0	7.26	4.08
	Euthynnus affinis	7 169	8 515	6 982	2 000	1	0	8.73	1.52
	Auxis spp.	8 802	3 139	9 700	1 500	1	0	9.16	2.20
	Thunnus tonggol	236	176	255	5 000	1	0	7.48	1.47
	Other tunas	601	933	1 655	10 000	1	0	6.66	
	Billfishes	169	173	436	10 000	1	0	6.66	1.50
Medium predators	Catfishes	779	2 510	783	8 000	0	0	5.01	3.00
	Lizard fishes	14 671	15 568	14 369	700	1	0	10.41	3.00
	Snappers	226	81	349	8 000	0	0	5.01	3.00
	Pig-face breams	446	445	676	6 000	0	0	5.26	3.00
	Ribbon fishes	25 273	7 619	27 270	1 250	0	0	6.84	3.40
	Barracudas	3 613	6 322	5 424	5 500	0	0	5.34	3.00
	Cephalopods	47 577	53 102	41 209	2 000	0	0	6.33	2.50
Large zoobenthic feeders	Skates	156	309	354	10 000	1	0	6.66	1.00
	Rays	2 438	1 731	2 042	15 000	1	0	6.22	1.00
	Eels	185	424	504	5 000	1	0	7.48	1.00
	Rock cods	4 242	6 652	8 470	10 000	0	0	4.83	1.00
	Halibut	343	437	584	3 500	0	0	5.76	1.00

Table 3. Estimated annual landings and selected input parameters for species within the ecological groups (Table 2) for the Ecopath analysis covering the southwest coast of India. (continued)

Group	Taxa	Landings (t)			Input parameters				
		1994	1995	1996	W_∞(g)	Pf	Hd	Q/B	P/B
Demersal feeders	Threadfin breams	49 390	35 132	60 650	450	0	0	8.13	3.50
	Other perches	18 448	16 380	16 128	1 000	0	0	7.11	3.50
	Goatfishes	416	179	106	200	0	0	9.31	3.50
	Threadfins	90	16	2	1 000	0	0	7.11	3.50
	Croakers	22 210	14 998	22 606	600	0	0	7.74	4.00
	Silverbellies	7 118	5 732	6 537	25	0	0	13.21	6.00
	Big-jawed jumper	2 341	1 794	3 012	200	0	0	9.31	5.00
	Black pomfret	5 564	4 564	3 829	2 000	0	0	6.33	4.20
	Silver pomfret	1 370	980	1 643	2 000	0	0	6.33	4.20
	Chinese pomfret	870	25	26	1 750	0	0	6.47	4.20
	Flounders	109	136	14	1 500	0	0	6.64	4.00
	Soles	28 792	17 141	22 606	500	0	0	7.98	5.00
	Stomatopods	69 373	34 487	29 858	100	0	0	10.46	5.00
Mesopelagic feeders	Wolf herring	2 433	1 632	2 011	3 500	0	0	5.76	2.00
	Half beaks & full beaks	728	3 928	734	800	1	0	10.18	2.00
	Horse mackerel	7 777	10 062	5 298	700	0	0	7.55	2.85
	Leather jackets	757	1570	869	500	0	0	7.98	2.50
	Other carangids	23 763	22 861	26 767	1 000	0	0	7.11	3.08
Molluscan feeders	Lobsters	447	97	112	2 000	0	0	6.33	1.20
	Crabs	6 691	3 086	3 086	750	0	0	7.46	4.50
Plankton feeders	Oil sardine	3 187	18 137	38 815	150	1	0	13.49	2.23
	Other sardines	23 129	54 923	13 851	200	1	0	12.85	5.00
	Hilsa shad	159	186	50	450	1	0	11.21	1.71
	Other shads	213	290	7	500	1	0	11.02	1.71
	Coilia	368	220	8	50	1	0	16.22	2.70
	Stolephorus	42 439	48 624	34 426	20	1	0	18.92	3.07
	Thryssa	12 777	10 184	9 127	150	1	0	13.49	3.07
	Other clupeids	17 663	14 613	23 940	200	1	0	12.85	3.00
	Scads	40 996	93 025	53 892	250	1	0	12.38	3.88
	Indian mackerel	147 165	105 103	204 282	400	1	0	11.44	4.50
	Gastropods	1 334	471	2 112	300	0	0	8.70	2.00
Zooplankton	Mullets	733	758	343	500	0	1	15.09	
	Penaeid prawns	82 906	52 830	56 489	70	0	1	20.99	10.00
	Non-penaeid prawns	278	182	137	10	0	1	29.11	12.00
	Miscellaneous	25 593	14 866	14 060					
	TOTAL	779 494	711 908	792 095					

Note:
W = asymptotic weight of the species which contributed maximum to the biomass, Pf = 1 for large predators and zooplankton feeders and 0 for other feeding types, Hd = 1 for herbivores and detritivores and 0 for carnivores, Q/B = Consumption/Biomass ratio (year^{-1}), P/B = Production/ Biomass ratio (year^{-1}).

Table 4. Diet composition input for the ecological groups of the Ecopath model of the southwest waters of India. This was assumed to be constant for all years.

	Predator								
Prey	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**10**
1. Large predators	0.01	–	–	–	–	–	–	–	–
2. Medium predator	0.20	0.01	–	–	–	–	–	–	–
3. Large zoobenthic feeders	0.10	0.02	0.01	–	–	–	–	–	–
4. Demersal feeder	–	0.04	0.15	0.01	–	–	–	–	–
5. Mesopelagic feeders	–	0.03	0.10	0.15	0.01	–	–	–	–
6. Mollusc feeders	–	–	–	–	–	0.010	–	–	–
7. Plankton feeders	0.60	0.75	0.70	0.75	0.80	0.75	0.05	–	–
8. Zooplankton	0.01	0.15	0.04	0.04	0.14	0.19	0.04	0.05	–
9. Phytoplankton	–	–	–	–	–	–	0.90	0.95	–
10. Detritivores	–	–	0.00	0.05	0.05	0.05	0.01	–	–
11. Detritus	–	–	–	–	–	–	–	–	1.00
Import	0.08	–	–	–	–	–	–	–	–
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Estimated annual average consumption/biomass (Q/B) and production/biomass (P/B) of ecological groups along the southwest coast of India during 1994 - 96.

Ecological group	Q/B ($year^{-1}$)	P/B ($year^{-1}$)
Large predators	7.31	2.23
Medium predators	6.83	2.99
Large zoobenthic feeders	6.19	1.00
Demersal feeders	8.16	4.28
Mesopelagic feeders	8.34	2.41
Molluscan feeders	6.89	2.85
Plankton feeders	13.23	2.74
Zooplankton	133.30	40.00
Phytoplankton		70.00
Detritivores	21.73	11.00

Medium Predators

The medium predators include the lizardfish *Saurida tumbil,* major perches such as snappers (*Lutjanus* spp.), pig-face breams (*Lethrinus* spp.), ribbonfishes (*Trichiurus* spp., *Lepturacanthus savala*), barracudas (*Sphyraena* spp.) and cephalopods (*Sepia pharaonis, Sepia elliptica, Sepiella inermis,* etc.). The annual average Q/B and P/B values estimated were 6.827 and 2.986, respectively.

Large Zoobenthic Feeders

The large zoobenthic feeders include skates, rays, eels, groupers (*Epinephelus* spp.) and Indian halibut (*Psettodes erumei*). The annual Q/B and P/B were 6.19 and 1.0, respectively (Table 5). Though this group is a major predator on demersal feeders such as threadfin breams and croakers, available information suggests that plankton feeders such as the Indian mackerel, which descend to the bottom and contribute to the trawl catches, constitute the major part of the diet (0.7).

Demersal Feeders

The demersal fish groups such as the threadfin breams, croakers, silverbellies and pomfrets constitute this group. The Q/B and P/B values for the group are given in Table 5. The demersal feeders consume large quantities of plankton feeders (0.75), mesopelagic feeders (0.15) and detritivores (0.05).

Mesopelagic Feeders

This ecological group includes the carangids such as *Caranx* spp., *Alepes* spp., *Selar* spp., *Chorinemus*, the horse mackerel *Megalaspis cordyla,* the wolf herring *Chirocentrus* spp, half beaks and full beaks. They feed mainly on the plankton feeders (0.80), zooplankton (0.14) and detritivores (0.05). The annual Q/B and P/B were 8.336 and 2.405, respectively.

Molluscan Feeders

The crabs *Portunus* spp. and *Charybdis* spp. and the spiny lobsters *Panulirus* spp. feed primarily (0.75) on bivalves such as the mussels and clams. The annual Q/B and P/B ratios were 6.892 and 2.850, respectively.

Plankton Feeders

The plankton feeders are mostly small pelagics such as the clupeids *Sardinella* spp., *Stolephorus* spp. and *Thryssa* spp.; the scads *Decapterus* spp. and the Indian mackerel *Rastrelliger kanagurta* contribute the maximum biomass to the southwest ecosystem. The information on the diet composition of the small pelagics has been reviewed by (Devaraj et al. 1997). The lesser sardines *Sardinella fimbriata* and *Stolephorus devisi* feed primarily on phyto-plankton whereas *S. gibbosa* and *S. bataviensis* (*S. waitei* in FishBase 2000) feed mainly on zooplankton.

Ontogenetic changes in the feeding habits are also observed in several species. The oil sardine *S. longiceps,* for instance, feeds on diatoms and microalgae when it is a postlarva, on zooplankton when it is a juvenile, and once again on diatoms after becoming adult. The mackerel *R. kanagurta* feeds on zooplankton when it is a juvenile, and on phytoplankton after becoming adult. Thus it is difficult to categorize such species as exclusive phytoplankton feeders or zooplankton feeders. Nevertheless, it is considered that phytoplankton and zooplankton constitute a major share (0.94) in the diet of this ecological group, and the juveniles of the plankton feeders themselves contribute the rest.

The total mortality coefficient values (Z) available for several species of the plankton feeders along the SW coast were collected, and the average Z was used as the P/B of each species/group. The estimated annual Q/B and P/B values for this ecological group were 13.233 and 2.739, respectively.

Detritivores

The penaeid and non-penaeid prawns and the mullids are categorized as the detritus feeders. The detritivores feed almost exclusively on detritus (1.0). The Z values of several penaeid (10.0) and non-penaeid (12.0) prawns are very high (Table 3) as they are preyed upon by several ecological groups. Moreover, the penaeid prawns are a target group for the commercial fisheries. The annual Q/B and P/B values of this ecological group were estimated as 21.733 and 11.0, respectively (Table 5).

Zooplankton

This group includes mostly copepods and fish larvae. Following (Polovina, 1984), the P/B value was set at 40 $year^{-1}$ and the diet vector based essentially on phytoplankton (0.95) and on cannibalism to a lesser extent (0.05). The zooplankton biomass was estimated as 10 $t{\cdot}km^{-2}$.

Phytoplankton

The annual P/B was set at 70 (Polovina, 1984) and the estimated biomass was 129.87 $t{\cdot}km^{-2}$.

Detritus

There was no available information regarding the detritus component along the southwest coast. The detritus biomass of 426 $t{\cdot}km^{-2}$ was estimated by employing the following empirical relationship suggested by (Pauly et al. 1993):

$$\text{Log } D = 0.954 \log PP + 0.863 \log E - 2.41 \quad (5)$$

where:

D = detrital biomass in g $C{\cdot}m^{-2}$;

PP = primary production (182 g $C{\cdot}m^{-2}{\cdot}year^{-1}$ for the southwest coast; after (Pant 1992), and

E = the euphotic layer depth (40 m).

Results and Discussion

The trophic model as devised using Ecopath for the southwest coast of India is presented in Fig. 4. The estimated parameters for the trophic model are summarized thus: 1994 in Table 6, 1995 in Table 7 and 1996 in Table 8. Most of the fish biomass and production is within the domain of plankton feeders, i.e. the small pelagic fishes (Table 9). Among the demersal resources, most of the biomass and production are associated with the detritus and detritivores.

Figure 5 illustrates the impact of each ecological group on the other ecological groups during 1994, as obtained through mixed impact analysis. The phytoplankton and plankton feeders are impacted by a large number of ecological groups. It is interesting that the fishery has a positive impact on large zoobenthos feeders and mesopelagic feeders. This is because this fishery, even though it has a direct negative impact on these groups, also has an indirect positive impact, by removing predators on the groups, (notably large and medium predators in the case of the large zoobenthos feeders).

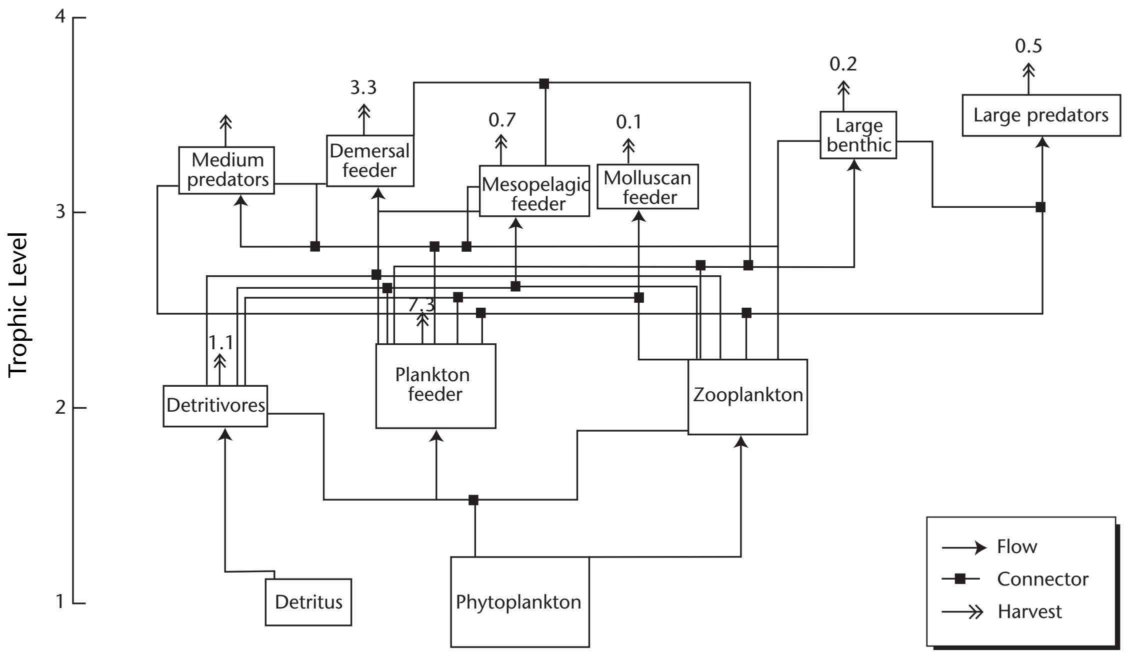

Fig. 4. Flowchart showing the trophic interactions in the ecosystem model of the southwest coast of India.

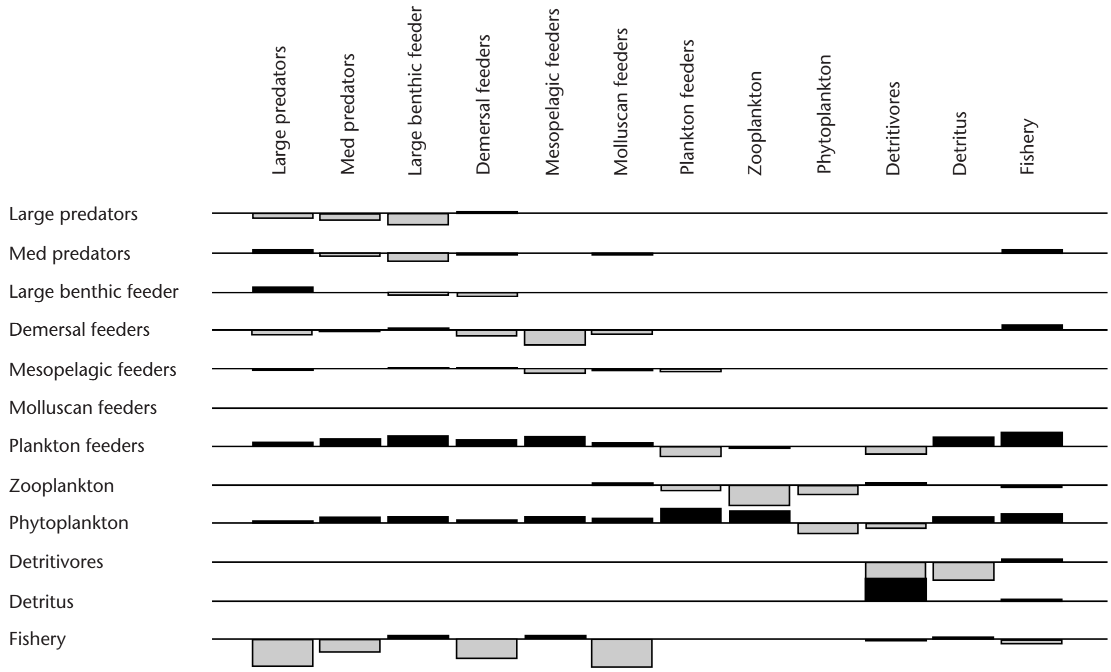

Fig. 5. Mixed trophic impact in the 1994 ecosystem model for the southwest coast of India. The graph shows the impact that each of the groups on the left (rows) is predicted to have on each of the groups on top (columns). Positive impacts are shown above the baseline, and negative below it. The impacts are relative but comparable between groups.

Table 6. Basic input and output parameters (in parentheses) for the Ecopath model of the southwest waters of India for the year 1994.

Ecological group	Biomass (t·km^{-2})	P/B	Q/B	EE	Catch (t·km^{-2} ·year^{-1})	Trophic Level	Flow to Detritus	Net Efficiency	Respiration (t·km^{-2}·year^{-1})	Assimilation (t·km^{-2}·year^{-1})
Large predators	(0.44)	2.23	7.31	0.65	0.61	(3.50)	(0.99)	(0.38)	(0.002)	(0.003)
Medium predator	(1.12)	2.99	6.83	0.75	1.78	(3.21)	(2.36)	(0.55)	(0.003)	(0.006)
Large zoobenthic. feeders	(0.35)	2.50	6.19	0.85	0.24	(3.39)	(0.56)	(0.51)	(0.001)	(0.002)
Demersal feeder	(1.18)	4.28	9.50	0.80	3.30	(3.26)	(3.25)	(0.56)	(0.004)	(0.009)
Mesopelagic feeders	(0.85)	4.00	8.34	0.85	0.71	(3.10)	(1.94)	(0.60)	(0.002)	(0.006)
Mollusc feeders	(0.05)	2.85	6.89	0.80	0.10	(3.10)	(0.09)	(0.52)	(0.000)	(0.000)
Plankton feeders	(14.64)	3.00	15.00	0.95	7.25	(2.11)	(46.12)	(0.25)	(0.132)	(0.176)
Zooplankton	10.00	40.00	133.30	0.19	0.00	(2.05)	(0.00)	(0.50)	(6.609)	(5.575)
Phytoplankton	(129.87)	70.00	–	0.75	0.00	(1.00)	(0.00)	–	(0.00)	(0.000)
Detritivores	(0.37)	12.00	60.00	0.95	1.13	(2.00)	(4.70)	(0.25)	(0.01)	(0.018)
Detritus	1.00	–	–	(0.37)	0.00	(1.00)	–	–	(0.00)	(0.000)

Note: P/B = Production/Biomass ratio (year^{-1}), Q/B = Consumption/Biomass ratio (year^{-1}), EE = Ecotrophic efficiency.

Table 7. Basic input and output parameters (in parentheses) for the Ecopath model of the southwest waters of India for the year 1995.

Ecological group	Biomass (t·km^{-2})	P/B	Q/B	EE	Catch (t·km^{-2} ·year^{-1})	Trophic Level	Flow to Detritus	Net Efficiency	Respiration (t·km^{-2}·year^{-1})	Assimilation (t·km^{-2}·year^{-1})
Large predators	(0.40)	2.23	7.31	0.65	0.55	(3.50)	(0.89)	(0.38)	(0.001)	(0.002)
Medium predator	(1.05)	2.99	6.83	0.75	1.70	(3.21)	(2.22)	(0.55)	(0.003)	(0.006)
Large zoobenthic. feeders	(0.30)	2.50	6.19	0.85	0.19	(3.39)	(0.49)	(0.51)	(0.001)	(0.001)
Demersal feeder	(0.96)	4.28	9.50	0.80	2.61	(3.26)	(2.63)	(0.56)	(0.003)	(0.007)
Mesopelagic feeders	(0.77)	4.00	8.34	0.85	0.80	(3.10)	(1.75)	(0.60)	(0.002)	(0.005)
Mollusc feeders	(0.03)	2.85	6.89	0.80	0.06	(3.10)	(0.06)	(0.52)	(0.000)	(0.000)
Plankton feeders	(13.04)	3.00	15.00	0.95	6.86	(2.11)	(41.10)	(0.25)	(0.117)	(0.157)
Zooplankton	10.00	40.00	–	0.90	0.00	(2.05)	(0.00)	(0.50)	(6.634)	(5.595)
Phytoplankton	(129.91)	70.00	0.00	0.75	0.00	(1.00)	(0.00)	–	(0.000)	(0.000)
Detritivores	(0.33)	12.00	60.00	0.95	1.07	(2.00)	(4.21)	(0.25)	(0.012)	(0.016)
Detritus	1.00	(0.37)	–	–	0.00	(1.00)	–	–	(0.000)	(0.000)

Note: P/B = Production/Biomass ratio (year^{-1}), Q/B = Consumption/Biomass ratio (year^{-1}), EE = Ecotrophic efficiency.

Table 8. Basic input and output parameters (in parentheses) for the Ecopath model of the southwest waters of India for the year 1996.

Ecological group	Biomass (t·km^{-2})	P/B	Q/B	EE	Catch (t·km^{-2} ·year^{-1})	Trophic Level	Flow to Detritus	Net Efficiency	Respiration (t·km^{-2}·year^{-1})	Assimilation (t·km^{-2}·year^{-1})
Large predators	(0.44)	2.23	7.31	0.65	0.61	(3.50)	(0.99)	(0.38)	(0.002)	(0.003)
Medium predator	(1.12)	2.99	6.83	0.75	1.78	(3.21)	(2.36)	(0.55)	(0.003)	(0.006)
Large zoobenthic. feeders	(0.35)	2.50	6.19	0.85	0.24	(3.39)	(0.56)	(0.51)	(0.001)	(0.002)
Demersal feeder	(1.18)	4.28	9.50	0.80	3.30	(3.26)	(3.25)	(0.56)	(0.004)	(0.009)
Mesopelagic feeders	(0.85)	4.00	8.34	0.85	0.71	(3.10)	(1.94)	(0.60)	(0.002)	(0.006)
Mollusc feeders	(0.05)	2.85	6.89	0.80	0.10	(3.10)	(0.090)	(0.52)	(0.000)	(0.000)
Plankton feeders	(14.64)	3.00	15.00	0.95	7.25	(2.11)	(46.12)	(0.25)	(0.132)	(0.176)
Zooplankton	10.00	40.00	–	0.90	0.00	(2.05)	(0.00)	(0.07)	(6.609)	(5.575)
Phytoplankton	(129.87)	70.00	0.00	0.75	0.00	(1.00)	(0.00)	–	(0.000)	(0.000)
Detritivores	(0.37)	12.00	60.00	0.95	1.13	(2.00)	(4.70)	(0.25)	(0.013)	(0.018)
Detritus	1.00	(0.37)	–	–	0.00	(1.00)	–	–	(0.000)	(0.000)

Note: P/B = Production/Biomass ratio (year^{-1}), Q/B = Consumption/Biomass ratio (year^{-1}), EE = Ecotrophic efficiency.

Table 9. Comparison of average reported catch from commercial vessels and biomass estimates from the Ecopath model during 1994 - 96 along the southwest coast of India.

Group Name	Catch ($t \cdot year^{-1}$)	Catch ($t \cdot km^{-2} \cdot year^{-1}$)	Biomass ($t \cdot km^{-2}$)
Large predators	30 83	0.60	0.44
Medium predators	91 63	1.78	1.12
Large zoobenthic feeders	9 85	0.19	0.35
Demersal feeders	172 48	3.35	1.18
Mesopelagic feeders	37 97	0.74	0.85
Molluscan feeders	5 30	0.10	0.05
Plankton feeders	346 57	6.74	14.64
Detritivores	66 55	1.29	0.37
TOTAL	761 17	14.80	19.00

Some of the results of the trophic models for the years 1994 to 1996 can be summarized as follows:

- The total system throughputs were 14 083, 14 078 and 14 083 $t \cdot km^{-2} \cdot year^{-1}$ (see Table 10) for the years 1994, 1995 and 1996, respectively. The throughputs were higher than that (7 621 $t \cdot km^{-2} \cdot year^{-1}$) reported for the northeastern (NE) Venezuela shelf ecosystem (Mendoza, 1993);
- The ecosystem off the southwest coast of India has very high net primary production (9 091 $t \cdot km^{-2} \cdot year^{-1}$ during 1996) and consequently high detritus biomass (426 $t \cdot km^{-2}$) compared to the detritus biomass (135 $t \cdot km^{-2}$) off northeastern Venezuela.
- However, the total biomass (excluding detritus) was only marginally higher off the southwest coast of India (158.9 $t \cdot km^{-2}$) than that off the northeastern coast of Venezuela (122.1 $t \cdot km^{-2}$).
- The biomass of commercially exploited fishery resources was estimated as 19.0 $t \cdot km^{-2}$ off the southwest coast of India (Table 9). The gross efficiency (total catch/primary production) was 0.0017.

Mean Trophic Level

Ecopath estimates the mean trophic level of the exploited fishery from the diet composition by placing primary producers and detritus on trophic level 1 and the consumer groups on trophic levels estimated as the weighted average trophic level of their prey groups plus one (Christensen and Pauly 1992). The mean trophic levels of commercial catches along the southwest coast were estimated as 2.61, 2.59, and 2.61 during 1994, 1995 and 1996, respectively. Comparatively, the trophic level of catches in the Gulf of Thailand ecosystem is reported to have declined from 3.12 in 1963 to 3.01 in 1980 (Christensen 1998). This difference appears to be due to the greater abundance and catches of pelagics low in the food chain off the southwest coast of India.

The present analysis has to be viewed as a preliminary approximation of the fisheries ecosystem off the southwest coast of India. Inadequacies of the present analysis could be classified under the following categories: (i) data inadequacy; (ii) categorization of ecological groups; and (iii) incomplete analysis.

a. Data Inadequacy: The tropical ecosystem is complex and inhabited by numerous species with diverse biological characteristics. For instance, there are 15 species of sardines, 24 species of whitebaits, 15 species of hilsa and other shads, 10 species of *Thryssa* and 40 species of other clupeids, which contribute to the ecological group of plankton feeders (Devaraj et al. 1997). It may be difficult to estimate the required input parameters such as W_∞ , Q/B, P/B and diet composition of all the species in an ecosystem to estimate the biomass of that ecological group. Hence, several assumptions and compromises had to be made in completing the model.

b. There are several default values in Ecopath, the reliability of which should be tested for each ecological group in different ecosystems. For instance, the assimilation efficiency will be different for large predators and for detritivores. Hence, it is crucial for future work to examine the impact of changes to the default parameter settings on the outputs.

Categorization of Ecological Groups

a. Maximum body size (W_∞ or L_∞) of individual species in each ecological group varies so much that categorization of fishes into ecological group is subject to individual bias. For instance, the asymptotic weight of the bullet tuna *(Auxis rochei)* is only 5 kg whereas that of the migratory yellowfin tuna *(Thunnus albacares)* is 170 kg. Hence, it is possible that the small coastal tunas *Euthynnus affinis, Auxis thazard)* and *A. rochei* should be categorized as medium predators, rather than be included with other tunas as large predators, as has been done in the present analysis.

b. Ontogenetic shifts in feeding habits also could greatly influence the categorization. The thread fin bream *Nemipterus japonicus,* for instance, feeds primarily on detritus when young but preys upon small demersal fishes when adult (Vivekanandan, unpublished data). A reverse feeding pattern is observed for the lizardfish, *Saurida tumbil.* The Ecosim module of the Eco path Software incorporates ontogenetic shifts by modeling adult and juveniles separately; Ecosim analysis will however have to await further studies.

Incomplete Analysis

a. Predators on fishes such as marine mammals, reptiles and birds have not been included due to lack of data. For the same reason, invertebrates such as jellyfishes and starfishes, which are abundant and prey on small fishes, and holothurians, which play a significant role in detrital turnover, have been left out.

b. The contribution of benthic biota to biomass flow could not be accounted for. As the detrital biomass is large along the southwest coast, the benthic biomass consisting of meiofauna (body size < 0.5 mm) and macrofauna (> 0.5mm) is also expected to be high. (Parulekar 1985) estimated that the biomass varies from 0.1 to 601 g•m^{-2} with an average of 38.5 g•m^{-2}, and concluded that the benthic biota play a significant role in demersal fish production.

Table 10. Biomass flows in the southwest Indian coast ecosystem.

Index	1994	1995	1996
Sum of all consumption (t•km^{-2}•year^{-1}):	7 242.62	7 237.22	7 242.62
Sum of all exports (t•km^{-2}•year^{-1}):	15.12	13.84	15.12
Sum of all respiratory flows (t•km^{-2}•year^{-1}):	6 765.70	6 773.36	6 765.70
Sum of all flows into detritus (t•km^{-2}•year^{-1}):	60.01	53.34	60.01
Total system throughput (t•km^{-2}•year^{-1}):	14 083.44	14 077.76	14 083.44
Sum of all production (t•km^{-2}•year^{-1}):	9 553.07	9 548.86	9 553.07
Mean trophic level:	3.61	3.59	3.61
Gross efficiency (catch/net primary production):	< 0.01	< 0.01	< 0.01
Calculated total net primary production (t•km^{-2}•year^{-1}):	9 090.89	9 093.68	9 090.89
Total primary production/total respiration:	1.34	1.34	1.34
Net system production (t•km^{-2}•year^{-1}):	2 325.19	2 320.32	2 325.19
Total primary production/total biomass:	57.22	57.99	57.22
Total biomass/total throughput (year):	0.01	0.01	0.01
Total biomass (excluding detritus) (t•km^{-2}):	158.87	156.80	158.87
Total catches (t•km^{-2}•year^{-1}):	15.12	13.84	15.12
Connectance Index:	0.36	0.36	0.36
System Omnivory Index:	0.10	0.109	0.10

c. Diverse habitats such as coral reefs provide shelter for unique fishes, which feed on coral polyps. Information is not available on these biologically rich ecosystems, which is a habitat for diverse ecological groups. The southern part of the present study area is rocky with coral reefs. The biomass in this habitat along with the associated fauna and flora has not been included in the biomass budget.

d. Another shortcoming is that imports and exports (barring the catches) are not known. Biomass estimates for species/groups from adjacent ecosystems may be necessary. In the present analysis, import was set only for large predators (8% of diet), assuming that interactions with adjacent ecosystems are very low.

Summary

Nevertheless, the Ecopath biomass estimates are comparable to the biomass estimates based on the swept area method for the southwest coast (Matthew et al. 1990). In the trawl survey, penaeid prawns (detritivores), spiny lobsters and crabs (molluscan feeders) and plankton feeders (clupeids) were not well represented in the catch. The biomass of the remaining resources was estimated at 3.71 t•km^{-2} during 1994 - 96. In the Ecopath analysis, the estimated total biomass was 19.0 t•km^{-2}, and the biomass of the ecological groups represented in the trawl survey was 3.94 t•km^{-2}. Hence, the biomass of the top 5 ecological groups (large and medium predators, large zoobenthos feeders, demersal feeders and mesopelagic feeders) estimated by employing the two different methods (namely, Ecopath and swept area) are very close to each other.

Ecopath is a powerful tool not only for understanding ecosystem functioning but also for fisheries management. The present analysis suggests that the annual average catches have exceeded estimated biomass in the case of the large and medium predators, demersal feeders and detritivores (Table 9). It appears that there is scope for increasing the catch of large zoobenthic feeders, mesopelagic feeders such as the carangids, and plankton feeders such as sardines, shads, whitebaits, *Thryssa* spp. and other clupeids and scads. Gear employed for exploitation of demersal resources, particularly bottom trawl, is probably in excess. The trawlable biomass appears to be overexploited and a reduction in trawl effort may be necessary to sustain the trawl fisheries along the southwest coast of India. On the other hand, there appears room for increasing gear employed for the exploitation of pelagic resources considering the abundance of plankton feeders. However, as the present analysis has limitations, further research and consolidation of available data are required to improve the model, refine the analysis and enhance the accuracy of the results.

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