

INDIA

Case Study Reports

Benchmarks for ecosystem assessment:
Indicators and guidelines for practical
Ecosystem Based Fishery Management (EBFM)



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Contents

- 1 A historical background of Kerala's marine fisheries
- 2 Development of fishery database for Kerala with species-level information
- 3 Determining target species for assessment in multispecies fisheries: insights from an expanded CMFRI-NMFDC database
- 4 Dynamics of marine fish landings in Kerala examined through Principal Component Analysis
- 5 Size spectrum model for the fishery in Kerala
- 6 MICE model for the fishery of selected marine fishery resources in Kerala
- 7 Ecosystem modelling and simulation of the Kerala marine fishery ecosystem
- 8 A fisher development index for assessing human development in marine fisheries of Kerala
- 9 Enhancing the quality and utility of India's Marine Fish Landing Data Collection and Processing System using spatial information
- 10 Social and Economic indicators – Ingrid's analysis
- 11 Composite ecological indices – BETH, Green Band etc – Beth's analysis

Ecosystem modelling using Ecopath and Ecosim (EwE) and simulation of the Kerala marine fishery ecosystem

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Introduction

Ecopath with Ecosim (EwE) is a type of ecosystem food web model that accounts for biomasses of species or species groups and energy flows between them (Polovina 1984, Christensen & Pauly 1992, Walters et al. 1997). Ecopath with Ecosim (EwE) is designed for straightforward construction, parameterization and analysis of mass-balance trophic models of aquatic and terrestrial ecosystems. EwE is based on principles of mass-balance, such that for each group in a model, the energy removed (i.e. predation or fishing) must be balanced by the energy consumed (Coll et al. 2009).

EwE can be selected to identify and quantify major energy flows in an ecosystem, describe the ecosystem resources and their interactions among species, evaluate the ecosystem effects of fishing or environmental changes, explore management policy options by incorporating economic, social and ecological considerations of fisheries, evaluate the placement and impact of marine protected areas, or predict the bioaccumulation of persistent pollutants (Plagányi, 2007). EwE models are also useful for testing ecosystem theories on resilience, stability and regime shifts (Pérez-España and Arreguín-Sánchez, 2001, Tomczak et al., 2013, Arreguín-Sánchez and Ruiz-Barreiro, 2014, Heymans and Tomczak, 2015).

The Ecopath mass-balance modelling system is built on an approach initially presented by J.J. Polovina for estimating biomass and food consumption of the elements (species or groups of species) of an aquatic ecosystem. Subsequently, it was combined with various approaches from theoretical ecology, notably those proposed by R.E. Ulanowicz, for the analysis of flows between the elements of ecosystems. However, the system has been optimized for direct use in fisheries assessment as well as for addressing environmental questions through the inclusion of the temporal dynamic model, Ecosim, and the spatial dynamic model, Ecospace. Full details of the EwE modelling approach, as well as the associated software, can be obtained from www.ecopath.org.

Study Area

The state of Kerala is situated on the west coast of Peninsular India between Latitude 8° 18' and 12° 48'N Longitude between 74° 72' and 77° 22'E, with a coastline of over 590 Km., and has an exclusive economic zone (EEZ) of 218,536 Sq Km. The habitat area for the present study was taken as 86,894 km², up to 2000m depth based on the exploitation pattern of fishing fleets.

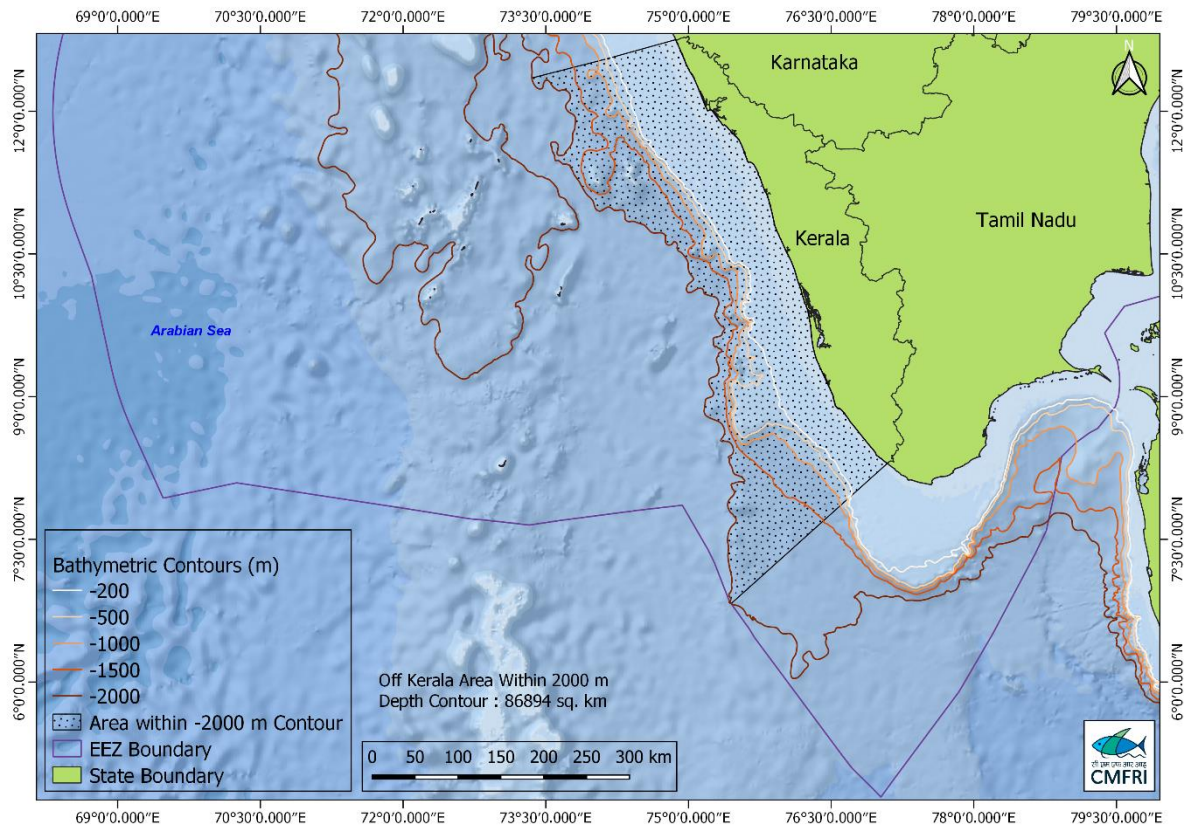


Fig.1. Map of area (stippled) modelled using EwE.

Methods

Ecological Groupings

A EwE model must represent the main species and trophic levels that are present in the modelled ecosystem and are of relevance for the policy or research question that is to be addressed. Ecological Groups are species or collections of species that share similar population dynamics and perform a similar function in the ecosystem, i.e. within a group, the species have approximately the same growth rates, consumption rates, diets, habitats, and predators. They should be based on species that occupy similar niches, rather than of similar taxonomic groups. Under these assumptions, the resources were grouped into 47 ecological groups for ECOPATH analysis. This ecological grouping is comprised of 740 species (Supplementary Table 1). The functional groups defined in the Ecopath model included 1 mammal, 28 fishes, 15 invertebrates 2 plants and one group of detritus. The detailed list of ecological groups is given in Table 1. Group information on P/B, Q/B ratios and diet information was mostly sourced from the Arabian Sea Model Karnataka¹⁰ and FishBase¹¹.

Marine mammals are large warm-blooded organisms that are important consumers in marine ecosystems. The biomass abundance was estimated as 0.019 t/km². The production per biomass

¹⁰ Mohamed K S, Zacharia P U, Muthiah C, Abdurahiman K P & Naik T H, Trophic model of the Arabian Sea ecosystem off Karnataka and simulation of fishery yields, CMFRI Bull, 51 (2008) 141p.

¹¹ Froese R & Pauly D, Fishbase World Wide Web electronic publication. <http://www.fishbase.org>, 2020.

(P/B) and consumption per biomass (Q/B) values of mammals are accordingly estimated as 0.100 and 12.750. The species belonging to sharks were classified into three ecological groups based on their habitat as sharks coastal, offshore sharks and demersal sharks. The sharks coastal group is constituted of 26 species belonging to 9 families. The estimated biomass abundance for sharks coastal was 0.042 t/km², and the catch level was 0.019 t/km². The group was dominated by Carcharhinidae with 12 species belonging to this family. The species that were recorded most was *Carcharhinus* spp. followed by *Stegostoma fasciatum*. The Offshore sharks group is comprised of eight species belonging to four families with *Carcharhinus falciformis* as the dominant species belonging to Carcharhinidae family. The biomass abundance for this group was 0.037 t/km² and the catch level was 0.016 t/km².

Table 1: Ecological groupings

Sl.No	Group Name	Sl.No	Group Name
1	Marine Mammals	25	Threadfin breams
2	Sharks coastal	26	Indian Mackerel
3	Sharks offshore	27	Oil Sardine
4	Sharks demersal	28	Other Clupeids inshore
5	Guitarfishes & Rays	29	Anchovies
6	Large pelagics-offshore	30	Crabs & Lobsters
7	Large Pelagics-inshore	31	Deep Sea Shrimps
8	Large Benthopelagic shelf	32	Coastal Shrimps
9	Large benthopelagic deep	33	Squids
10	Medium Benthopelagic shelf	34	Cuttlefishes
11	Medium benthopelagic deep	35	Octopus
12	Small Benthopelagic shelf	36	Commercial molluscs
13	Small benthopelagic deep	37	Benthic detritivore
14	Mesopelagics	38	Macrozoobenthos (Benthic carnivore)
15	Tunas coastal	39	Benthic grazers
16	Tunas offshore	40	Shelf filter feeders
17	Ribbonfishes	41	Deep filter feeders
18	Large Benthic Carnivores shelf	42	Gelatinous zooplankton
19	Large Benthic Carnivores deep	43	Large Zooplankton
20	Medium Benthic Carnivores shelf	44	Micro Zooplankton
21	Medium Benthic Carnivores deep	45	Phytoplankton
22	Small Benthic Carnivores shelf	46	Macroalgae
23	Small Benthic Carnivores deep	47	Detritus
24	Benthic omnivores shelf		

The ecological group Guitar fishes and Rays includes 42 species belonging to six families (Guitar fishes, Butterfly rays, Stingrays, Eagle rays and Electric rays). The biomass abundance was 0.077 t/km² and the estimated catch was 0.025 t/km². *Mobula* spp. comprises the major catch in the group and the single species dominating the catch is *Manta birostris*.

Bill fishes, sunfish and the swordfishes belonging to six families are grouped under large pelagics offshore, which are mainly caught using the hooks and lines. The biomass abundance for pelagics

offshore was found to be 0.342 t/km² and the catch level was 0.059 t/km². Landings of this group were dominated by *Istiophorus platypterus* followed by Dolphinfish (*Coryphaena hippurus*).

A total of 18 species belonging to families Rachycentridae, Albulidae, Carangidae, Scombridae, Belonidae, Latidae and Sphyraenidae were together taken as the large pelagics inhabiting the inshore waters of the study area. *Scomberomorus commerson* and *Sphyraena* spp dominated in the catch. The biomass abundance was estimated as 0.205 t/km² and the catch level from the study area was found to be 0.118t/km². The P/B value for these 18 species averaged 1.206 and the Q/B value was 5.091. The benthopelagics usually occupy the column of water above the seabed and 14 species were categorised as large benthopelagics occupying the shelf area. The major families included in this category are Carangidae, Belonidae, Lutjanidae, Latidae, Sphyraenidae, Polynemidae and Labridae with Carangidae dominating in the landings. The biomass abundance was estimated as 0.044 t/km² and the catch level was 0.014 t/km². The P/B and Q/B values were observed as 1.047 and 4.757.

The medium benthopelagics ecological group that primarily inhabits the shelf, comprise 39 species belonging to 23 families. Genus *Decapterus* dominated the group and was the major catch along the coast. Some important species included in the group are *Alepes djedaba*, *Decapterus russelli*, *Megalaspis cordyla*, *Chirocentrus* spp., *Scomber indicus*, *Arius* spp., *Chirocentrus dorab*, *Carangoides malabaricus* etc. The estimates of catch and biomass of the group were 0.495 t/km² and 1.519 t/km² respectively with a P/B value of 1.404 and the Q/B value of 8.904.

The ecological group medium benthopelagic deep consists of eight species belonging to five families with *Erythrocles schlegelii* (Japanese ruby fish), being the dominant species followed by *Hemiramphus lutkei* (Lutke's halfbeak) in terms of catch.

Small Benthopelagics from the shelf comprise 29 species belonging to 20 families. A sizable catch in the group was by *Ambassis* spp followed by the moonfish (*Mene maculata*). The catch level of the group was 0.068 t/km² and 1.550 t/km² is the biomass abundance. This group mainly includes species such as flying fishes, glass fishes, pufferfishes, halfbeaks, moon fishes, sickle fish, alligator pipefish, etc.

Five species belonging to five families are grouped as small benthopelagic deep. The biomass for this group was found to be 3.5 t/km² and *Bembrops caudimacula*, *Symphysanodon typus*, *Cubiceps whiteleggii*, *Odontanthias rhodopeplus*, and *Halietaea* spp among which the Opal fish (*Bembrops caudimacula*) leads in the catch. The Mesopelagic group includes the fishery of a single species *Diaphus* spp (headlight fishes) belonging to the family Myctophidae. Although this group includes a single species, it is not exploited commercially along the coast and is bycatch in shrimp trawls.

The group coastal tunas consist of seven species of coastal tunas belonging to the family Scombridae occupying the neritic zones of the ocean. This is one of the commercially important groups and the species that is most exploited is *Euthynnus affinis*. The other commercially important species included in the group are *Auxis rochei* and *Sarda orientalis*. The catch level for the group was 0.144 t/km² and the biomass was 0.44 t/km². Offshore tunas are represented by three species *Thunnus albacares*, *Katsuwonus pelamis* and *Thunnus obesus* belonging to the family Scombridae. Yellowfin tuna (*Thunnus albacares*) forms the dominant oceanic tuna in the area.

Ribbon fishes possess a significant role in the marine food chain as they form an important food to tuna and other marine carnivores. It consists of four species belonging to the family Trichiuridae. The genus *Trichiurus* contribute to the major catch from the study area. Anchovies are the major prey followed by scads. The species *Trichiurus lepturus* has high market demand with peak fishing from October to December. The catch level of the group was 0.195 t/km² and the biomass was 0.852 t/km².

The group of Large benthic carnivores from the shelf is represented by 59 species belonging to 14 families with a catch of 0.214 t/km². Some commercially important fish families included in the group are Carangidae, Synodontidae, Serranidae, Lethrinidae and Lutjanidae with *Saurida* spp dominating in abundance. The group Large Benthic Carnivores Deep comprises 12 species belonging to five families. Small benthic carnivores and octopuses are the major prey. *Pristipomoides typus* forms the major catch in the group followed by fishes of genus *Muraenesox*.

Major commercially important species included in Medium Benthic carnivores are *Priacanthus hamrur*, *Johnnieops* spp., *Alutera monoceros*, *Johnius* spp., *Pampus argenteus*, *Parastromateus niger*(=*F. niger*), *Otolithes ruber*, *Otolithes cuvieri*, *Johnius elongatus* and *Elagatis bipinnulata*.

The ecological group small benthic carnivores shelf consists of 83 species belonging to 26 families and the medium Benthic Carnivores inhabiting deep waters includes 14 species belonging to 10 families. The group Small Benthic Carnivores Deep consists of 13 carnivorous species belonging to 11 families inhabiting the deep benthic areas. It includes the deep-sea fishes belonging to the families Callionymidae, Bothidae, Chlorophthalmidae, Priacanthidae, Nomeidae, Blenniidae, Gobiidae, Cepolidae, Trigilidae, Setarchidae and Acropomatidae which are not commercially exploited. The group of benthic omnivores consists of 11 species belonging to two families, Mugilidae and Siganidae. The majority of the yield was contributed by Mugil spp.

The group threadfin breems are represented by 11 species belonging to the family Nemipteridae and form the bulk of the demersal finfish fishery in Kerala. The group has a major contribution to the overall catch from the coast with *Nemipterus* spp dominating the group. The catch level for the group was estimated as 0.4718916 t/km² and the biomass was found to be 1.364 t/km². This group forms the major fishery along the Kerala coast after Indian Oil sardine and Indian Mackerel.

Indian mackerel (*Rastrelliger kanagurta*) is considered a single group because of its commercial and economic importance. It forms a major pelagic fishery along with Indian oil sardine of the coast and shows interannual fluctuations with an estimated catch of 0.6263 t/km² and the biomass was 1.889 t/km². The P/B value for Indian mackerel was 2.257 and the Q/B value was 21.7. Mackerels are mainly caught using ring seines.

Indian oil sardine (*Sardinella longiceps*) is a commercially important species and forms a bulk part of the pelagic fishery along the study area and is also a major prey in the food chain. They usually inhabit the coastal waters and feeds on phytoplankton mainly diatoms and is eaten by larger pelagics. The estimate of catch for the oil sardine was 2.329 t/km² and the biomass in the habitat area was found to be 7.856 t/km². The P/B value and the Q/B value is estimated as 2.605 and 27.6 respectively.

The Other Clupeids Inshore group is represented by 41 species belonging to four families. They are shoaling fishes occupying the pelagic waters. This group includes the lesser sardines and *Sardinella gibbosa* holds the highest yield. The families that are included in the group are Clupeidae, Engraulidae, Dussumieriidae, Pristigasteridae in which the fishes of family Clupeidae and Engraulidae are of commercial importance. This group is mainly exploited using seine nets and mainly feeds on phytoplankton and zooplankton.

Anchovies comprise eight species belonging to the family Engraulidae which occupies a major part of pelagic fishery along the coast and *Stolephorus* spp forms a bulk catch in the group. These small pelagics are usually exploited using ring seines and purse seines.

The occurrence of 29 species of crabs and lobsters belonging to eight families were identified in the catch from the study area. *Portunus sanguinolentus* forms the major catch. This group includes 5 families of crabs with Portunidae being the major family and Palinuridae being the major among the 3 families of lobsters.

The ecological group Deep-Sea Shrimps consists of 18 species of shrimps from seven families that inhabit the deep sea. The resources of this group are exploited using trawlers. The deep-sea shrimp fishery is dominated by pandalid shrimps and the major species landed are *Metapenaeopsis andamanensis* followed by *Aristeus alcocki* (red ring) which has a targeted fishery in the study area.

Coastal Shrimps was represented by 24 species belonging to 3 families. Penaeid shrimps forms the bulk yield in coastal shrimps. The catch level for the group was 0.393 t/km² and the biomass was 5.3 t/km². *Metapenaeus dobsoni* forms the greatest individual component of shrimps caught from the study area followed by *Parapenaeopsis styliifera*.

The group Squids comprises 11 species belonging to two families (Loliginidae, Thysanoteuthidae) and genus *Uroteuthis* forms the bulk of yield with 6 species from this genus. The cephalopods are mainly caught by mechanised shrimp trawling. Squid jigging is also done to catch squids. The catch level for the group was 0.199 t/km² and biomass was 1.592 t/km². Squids feed on crustaceans and fishes and is a major component of the marine ecosystem.

The group Cuttlefishes was represented by nine species belonging to two families and the species that is landed the most is *Sepia* spp and the single species having maximum catch is *Sepia pharaonis*.

The group Octopus consists of seven species belonging to the family Octopodidae. The catch level for the group was 0.045 t/km² and the biomass was 0.15 t/km². *Octopus dollfusi*, *Cistopus indicus*, *Amphioctopus neglectus*, *Amphioctopus marginatus*, *Octopus globosus* are the few species that come under this group.

Commercial Molluscs is represented by 24 species of molluscs belonging to 18 families. The catch level was 0.009 t/km² and the biomass was 0.44 t/km². The most exploited species are from the genus *Babylonia*. The mussels and clams that are commercially important are also included in this group.

This group of Benthic Detritivore includes the benthic organisms that feed on detritus. The macrozoobenthos group consists of two species of stomatopods belonging to the family Squillidae, three marine molluscs belonging to the family Cassidae and one in the family Fascioliariidae.

The group Benthic Grazers consist of *Lambis* spp. some gastropods, sea urchins, abalones and chitons. The group Shelf Filter Feeders was comprised of many species of bivalves and other molluscs, cockles, oysters, mussels, barnacles, bryozoans in-sand zoobenthos/ sessile epifauna which is mostly filter feeding. The group Deep Filter Feeders is an aggregate of crinoids, bryozoans, ascidians, and fewer sponges. The Large Zooplankton group consists of jellyfishes which plays an important role in the marine ecosystem. They feed on zooplankton, crustaceans, fishes and are eaten by larger fishes (sunfishes) and turtles.

The group Micro Zooplankton forms a major prey for many commercially exploited species such as mackerel and other pelagic fishes and is a major part of the marine food chain. Phytoplanktons also form an important ecological group as many commercially important species feeds on them. They are the primary producers of the ocean ecosystem.

Macroalgae include the larger algal groups and form the food for larger herbivore fishes. Biomass for the group Detritus was estimated as 15 t/km². Benthic detritus which is usually found on the seafloor forms the major part of the benthic food web.

Estimates of landings

A variety of craft and gear combinations are used for commercial fishing along the Kerala coast, which are classified into mechanised, motorized and non-motorized sectors. Among the mechanised sector, trawlers, gillnetters, Hooks and Lines and Ring seiners account for the major share of catch while in the case of motorised vessels, ring seiners, gillnetters and liners form the major part. Trawl nets (multiday and single day) are primarily used for exploiting the demersal fishes while the seine nets, gill nets, hooks and lines etc. are used for exploiting the pelagic resources. The major fishes such as the Indian oil sardine (*Sardinella longiceps*) and the Indian mackerel (*Rastralleger kanagurta*) are caught mainly using ring seines vessels that are fitted with outboard engines. Estimates of landings for each species were obtained from the National Marine Fisheries Data Centre of CMFRI for the period 2008-17 and based on the ecological grouping the average landings were classified gear-wise (15 craft gear combinations or fleets) and expressed in tonnes per square km (Table 2.)

Table 2. Fleet wise landings of species groups (tonnes.km²)

Grp No.	Group name	MDTN	MGN	MHL	MOTHS	MPS	MRS
1	Marine Mammals	0	0	0	0	0	0
2	Sharks coastal	0.00114	0.00185	0.00103	0.01325		0.00000
3	Sharks offshore	0.00101	0.00203	0.00095	0.01017		0.00000
4	Sharks demersal	0.00129	0.00035	0.00041	0.00489		0.00000
5	Guitarfishes & Rays	0.00408	0.00165	0.00046	0.00935		0.00025
6	Large pelagics-offshore	0.00176	0.00570	0.00257	0.02813	0.00000	0.00010
7	Large Pelagics-inshore	0.02745	0.00202	0.00212	0.01749	0.00018	0.00427
8	Large Benthopelagics shelf	0.00513	0.00038	0.00044	0.00279	0.00017	0.00152
9	Large benthopelagic deep	0.00003			0.00000		
10	Medium Benthopelagics shelf	0.26165	0.00097	0.00039	0.02713	0.00542	0.07111
11	Medium benthopelagic deep	0.00009	0.00001	0.00000	0.00002		0.00000

12	Small Benthic Pelagics shelf	0.01587	0.00021	0.00001	0.00125	0.00013	0.00600
13	Small benthopelagic deep	0.00009		0.00000	0.00000		
14	Mesopelagics	0.00001					
15	Tunas coastal	0.00203	0.00263	0.00190	0.01322	0.00099	0.01150
16	Tunas offshore	0.00101	0.00738	0.00245	0.03514	0.00002	0.00016
17	Ribbonfishes	0.14591	0.00038	0.00421	0.01988	0.00000	0.00066
18	Large Benthic Carnivores shelf	0.15137	0.00193	0.00176	0.01777	0.00009	0.00283
19	Large Benthic Carnivores deep	0.00357	0.00024	0.00096	0.00486	0.00000	0.00000
20	Medium Benthic Carnivores shelf	0.12547	0.00103	0.00026	0.00656	0.00162	0.00905
21	Medium Benthic Carnivores deep	0.00129	0.00000	0.00000	0.00009		
22	Small Benthic Carnivores shelf	0.09105	0.00000	0.00001	0.00358	0.00002	0.00682
23	Small Benthic Carnivores deep	0.00082	0.00001	0.00000	0.00003		0.00000
24	Benthic omnivores shelf	0.00017	0.00001	0.00001	0.00002		0.00023
25	Threadfin breams	0.42785	0.00001	0.00000	0.02986		0.00009
26	Indian Mackerel	0.09374	0.00006	0.00000	0.01247	0.02257	0.22613
27	Oil Sardine	0.02295	0.00001		0.00367	0.00649	1.18484
28	Other Clupeids inshore	0.03335	0.00024		0.00121	0.00024	0.08349
29	Anchovies	0.05020	0.00001		0.00116	0.00000	0.07556
30	Crabs & Lobsters	0.02225			0.00034	0.00000	0.00000
31	Deep Sea Shrimps	0.09393			0.00143		
32	Coastal Shrimps	0.17790			0.00113	0.00003	0.03005
33	Squids	0.14732	0.00006	0.00160	0.01106	0.00001	0.00086
34	Cuttlefishes	0.14379	0.00006	0.00543	0.01587	0.00000	0.00003
35	Octopus	0.04208	0.00001	0.00000	0.00177		
36	Commercial molluscs	0.00253			0.00000		
37	Benthic detritivore						
38	Macrobenthos (Benthic carnivore)	0.00321			0.00000	0.00000	0.00000
39	Benthic grazers	0.00000					
40	Shelf filter feeders						
41	Deep filter feeders						
42	Gelatinous zooplankton						
43	Large Zooplankton						0.00003
44	Micro Zooplankton						
45	Phytoplankton						
46	Macroalgae						
47	Detritus						
	Sum	2.10335	0.02925	0.02696	0.29558	0.03799	1.71561

Table 2. (Contd.)

Grp No.	Group name	MTN	NM	OBBS	OBGN	OBHL	OBOHS
1	Marine Mammals	0	0	0	0	0	0
2	Sharks coastal	0.00011	0.00005	0.00000	0.00098	0.00006	0.00018
3	Sharks offshore	0.00004	0.00004		0.00099	0.00035	0.00065
4	Sharks demersal	0.00011	0.00000	0.00000	0.00068	0.00001	0.00009
5	Guitarfishes & Rays	0.00104	0.00018	0.00002	0.00610	0.00134	0.00040
6	Large pelagics-offshore	0.00007	0.00001	0.00007	0.01103	0.00739	0.00129
7	Large Pelagics-inshore	0.00124	0.00011	0.00251	0.04251	0.01465	0.00143
8	Large Benthopelagics shelf	0.00011	0.00006	0.00030	0.00138	0.00181	0.00004
9	Large benthopelagic deep				0.00000		0.00000
10	Medium Benthopelagics shelf	0.00830	0.00426	0.03243	0.02437	0.01314	0.00034
11	Medium benthopelagic deep	0.00001	0.00000	0.00000	0.00001	0.00005	
12	Small Benthopelagics shelf	0.00135	0.00044	0.00672	0.00275	0.00132	0.00006
13	Small benthopelagic deep		0.00000				
14	Mesopelagics						
15	Tunas coastal	0.00003	0.00006	0.00148	0.05902	0.04921	0.00110
16	Tunas offshore	0.00001			0.00962	0.00490	0.00145
17	Ribbonfishes	0.00580	0.00005	0.00525	0.01006	0.00214	0.00019
18	Large Benthic Carnivores shelf	0.00562	0.00107	0.00257	0.01813	0.00530	0.00009
19	Large Benthic Carnivores deep	0.00020	0.00001	0.00002	0.00184	0.00134	0.00004
20	Medium Benthic Carnivores shelf	0.01513	0.00546	0.01191	0.01808	0.00399	0.00009
21	Medium Benthic Carnivores deep	0.00001			0.00001	0.00000	0.00001
22	Small Benthic Carnivores shelf	0.07743	0.01173	0.00471	0.01696	0.00016	0.00000
23	Small Benthic Carnivores deep	0.00000			0.00002		
24	Benthic omnivores shelf	0.00009	0.00031	0.00003	0.00022	0.00002	
25	Threadfin breams	0.00811	0.00011	0.00114	0.00301	0.00165	0.00000
26	Indian Mackerel	0.00393	0.00617	0.00686	0.15378	0.00802	0.00021
27	Oil Sardine	0.01552	0.03085	0.00611	0.05595		0.00000
28	Other Clupeids inshore	0.01226	0.02467	0.02876	0.03387	0.00002	0.00001
29	Anchovies	0.00816	0.00479	0.02090	0.00092		0.00000
30	Crabs & Lobsters	0.01189	0.00243	0.00020	0.00156		0.00001
31	Deep Sea Shrimps	0.00017					
32	Coastal Shrimps	0.09190	0.00351	0.00504	0.00156		0.00001
33	Squids	0.00820	0.00069	0.01732	0.00153	0.00757	0.00006
34	Cuttlefishes	0.00246	0.00013	0.00001	0.00003	0.03692	0.00003
35	Octopus	0.00104	0.00000	0.00000	0.00000	0.00003	
36	Commercial molluscs	0.00571	0.00012		0.00018		0.00001
37	Benthic detritivore						

Grp No.	Group name	MTN	NM	OBBS	OBGN	OBHL	OBOTHS
38	Macrozoobenthos (Benthic carnivore)	0.01815	0.00000		0.00000		
39	Benthic grazers	0.00000					
40	Shelf filter feeders						
41	Deep filter feeders						
42	Gelatinous zooplankton						
43	Large Zooplankton	0.00005	0.00001				
44	Micro Zooplankton						
45	Phytoplankton						
46	Macroalgae						
47	Detritus						
	Sum	0.30428	0.09730	0.15438	0.47715	0.16141	0.00781

Table 2. (Contd.)

Grp No.	Group name	OBRS	OBTN	OBSS	Total
1	Marine Mammals	0	0	0	0
2	Sharks coastal	0.00001	0.00000		0.01864
3	Sharks offshore	0.00000			0.01624
4	Sharks demersal		0.00000		0.00784
5	Guitarfishes & Rays	0.00001	0.00002		0.02490
6	Large pelagics-offshore	0.00042	0.00000		0.05853
7	Large Pelagics-inshore	0.00188	0.00005	0.00000	0.11792
8	Large Benthic Pelagics shelf	0.00010	0.00000		0.01423
9	Large benthopelagic deep				0.00003
10	Medium Benthic Pelagics shelf	0.04313	0.00026	0.00248	0.49540
11	Medium benthopelagic deep	0.00009			0.00028
12	Small Benthic Pelagics shelf	0.03135	0.00029	0.00000	0.06775
13	Small benthopelagic deep				0.00009
14	Mesopelagics				0.00001
15	Tunas coastal	0.00085	0.00006	0.00031	0.14440
16	Tunas offshore	0.00005			0.06217
17	Ribbonfishes	0.00048	0.00021	0.00027	0.19548
18	Large Benthic Carnivores shelf	0.00491	0.00007	0.00028	0.21381
19	Large Benthic Carnivores deep	0.00000	0.00000		0.01307
20	Medium Benthic Carnivores shelf	0.02181	0.00239		0.22284
21	Medium Benthic Carnivores deep				0.00141
22	Small Benthic Carnivores shelf	0.01640	0.00859	0.00051	0.23797
23	Small Benthic Carnivores deep				0.00089
24	Benthic omnivores shelf	0.00035	0.00000		0.00147

Grp No.	Group name	OBRS	OBTN	OBSS	Total
25	Threadfin breams	0.00004	0.00001		0.47189
26	Indian Mackerel	0.09142	0.00006	0.00084	0.62627
27	Oil Sardine	1.00234	0.00007		2.32881
28	Other Clupeids inshore	0.09111	0.00147	0.00152	0.31223
29	Anchovies	0.27884	0.00111	0.00265	0.44429
30	Crabs & Lobsters	0.00008	0.00257		0.04133
31	Deep Sea Shrimps		0.00002		0.09555
32	Coastal Shrimps	0.04936	0.03279		0.39330
33	Squids	0.00109	0.00154	0.00014	0.19906
34	Cuttlefishes	0.00162	0.00086		0.20724
35	Octopus	0.00000			0.04493
36	Commercial molluscs				0.00855
37	Benthic detritivore				
38	Macrozoobenthos (Benthic carnivore)	0.00005	0.00397		0.02539
39	Benthic grazers				0.00000
40	Shelf filter feeders				
41	Deep filter feeders				
42	Gelatinous zooplankton				
43	Large Zooplankton	0.00002	0.00001		0.00011
44	Micro Zooplankton				
45	Phytoplankton				
46	Macroalgae				
47	Detritus				
	Sum	1.63784	0.05643	0.00900	7.11433

The primary data on landing centre prices were also converted into price per tonne per group for each gear (Supplementary Table 3).

Estimates of Biomass, P/B, Q/B and EE

The major input data provided for the Ecopath modelling includes the estimates of biomass (t/km²), production per biomass P/B (t/km² /year), consumption per biomass Q/B (t/km² /year), and ecotrophic efficiency EE for each functional groups. The amount of biomass in the habitat area is estimated using the equation of Gulland and is expressed in tonnes per square km. The P/B ratio is equivalent to the total mortality rate (Z) (Allen 1971, Merz and Myers 1998) and includes the mortality due to fishing (F), predation (M₂), net migration (NM), biomass accumulation (BA), and other mortality. The Q/B ratio is the ratio of annual food consumption to the biomass of each group and is only entered for secondary consumers as this value is not applicable for primary producers (Pauly et al. 2000). P/B and Q/B parameters required for the model were obtained from extensive literature reviews and other models (Karnataka model¹). (Table 3).

Table 4. Basic estimates of Biomass, P/B and Q/B for different Ecological groups

Grp No.	Group name	Hab area (proportion)	Biomass in habitat area (t/km ²)	Production / biomass (/)	Consumption / biomass (/)	Ecotrophic Efficiency
1	Marine Mammals	1	0.019	0.100	12.750	
2	Sharks coastal	0.5	0.042	1.181	3.700	
3	Sharks offshore	0.5	0.037	1.098	3.430	
4	Sharks demersal	1	0.018	0.930	4.463	
5	Guitarfishes & Rays	1	0.077	0.890	2.964	
6	Large pelagics-offshore	0.5	0.342	1.053	2.698	
7	Large Pelagics-inshore	0.5	0.205	1.206	5.091	
8	Large Benthic Pelagics shelf	0.5	0.044	1.047	4.757	
9	Large benthopelagic deep	0.5		0.834		0.98
10	Medium Benthic Pelagics shelf	0.5	1.519	1.404	8.904	
11	Medium benthopelagic deep	0.5		1.412	6.467	0.95
12	Small Benthic Pelagics shelf	0.5	1.550	2.184	10.950	
13	Small benthopelagic deep	0.5	3.500	1.553	13.000	
14	Mesopelagics	0.75	1.200	1.680	11.602	
15	Tunas coastal	0.5	0.440	1.552	13.600	
16	Tunas offshore	0.5	0.193	1.172	17.603	
17	Ribbonfishes	0.5	0.852	1.292	3.750	
18	Large Benthic Carnivores shelf	0.5	1.667	1.171	5.324	
19	Large Benthic Carnivores deep	0.5		1.023	4.320	0.95
20	Medium Benthic Carnivores shelf	0.5	1.687	1.856	7.697	
21	Medium Benthic Carnivores deep	0.5		1.100	4.538	0.95
22	Small Benthic Carnivores shelf	0.5	2.950	2.170	11.272	
23	Small Benthic Carnivores deep	0.5		1.256	4.484	0.95
24	Benthic omnivores shelf	1		0.940	26.980	0.98
25	Threadfin breams	0.5	1.364	2.038	10.938	
26	Indian Mackerel	0.5	1.889	2.257	21.700	
27	Oil Sardine	0.5	7.856	2.605	27.600	
28	Other Clupeids inshore	0.5	1.500	2.884	20.700	
29	Anchovies	0.5	8.000	4.000	17.133	

Grp No.	Group name	Hab area (proportion)	Biomass in habitat area (t/km ²)	Production / biomass (/)	Consumption / biomass (/)	Ecotrophic Efficiency
30	Crabs & Lobsters	0.5	0.091	4.785	8.500	
31	Deep Sea Shrimps	0.5	0.750	3.941	10.900	
32	Coastal Shrimps	0.25	5.300	6.870	19.200	
33	Squids	1	1.592	4.250	16.640	
34	Cuttlefishes	1	0.590	3.552	16.640	
35	Octopus	0.5	0.150	3.810	12.500	
36	Commercial molluscs	0.5	0.440	4.301	12.500	
37	Benthic detritivore	1		2.900	9.000	0.95
38	Macrobenthos (Benthic carnivore)	1	15.000	3.100	12.482	
39	Benthic grazers	0.25		0.730	2.500	0.95
40	Shelf filter feeders	0.5	5.000	1.600	12.000	
41	Deep filter feeders	0.5	4.000	1.200	12.000	
42	Gelatinous zooplankton	1		4.850		0.75
43	Large Zooplankton	1		35.000	160.000	0.75
44	Micro Zooplankton	1	14.000	65.000	250.000	
45	Phytoplankton	1	58.500	70.000		
46	Macroalgae	0.005		2.780		0.95
47	Detritus	1	15.000			0

Diet Matrix

Information on the diet composition of the groups is an important requirement for understanding the dynamics of ecosystems, given that food networks connect different ecological groups. The diet matrix helps to identify the prey predator relationships existing in the marine ecosystem and forms the major input in Ecopath modelling. Diet composition of the ecological groups were estimated through stomach content analysis. Diet information was sourced from the literature^{1,2}. The final diet matrix used for the model is given in Supplementary Table.

Data Pedigree and Pedigree Index

A model's pedigree is a summary of the uncertainty related to the information sources as the input information was collected from a variety of sources with varying degrees of confidence. The pedigree index for the model was 0.326 (Table 5). The index values for input data scale from 0 for data that is not rooted in local data up to a value of 1 for data that are fully-rooted in local data. The measure of fit (t^*) is also calculated to describe how well rooted a given model is in local data.

Table 5. Ecopath Pedigree Index

Parameter	Pedigree fixed	index	default ci (+/-%)
Biomass	Approximate or indirect method	0.4	50
P/B	Same group/species, same system	1	10
Q/B	Empirical relationship	0.5	50
Diets	Quantitative but limited diet composition study	0.7	30
Catches	National statistics	0.5	50
Ecopath Pedigree Index		0.326	
Measure of fit (t*)		2.285	

Fleets

Fishing fleet wise information is used as a major input in the Ecopath model. The fishery along the coast is mostly supported by mechanized vessels with the primary gears being multiday trawl nets (MDTN), multiday gill nets (MGN), multiday hook and lines (MHL), multiday purse seines (MPS), multiday ring seines (MRS), single-day trawl nets (MTN), vessels fixed with outboard engines also contribute to the fishery with the major gears being boat seines (OBBS), gill nets (OBGN), hook and lines (OBHL), ring seines (OBRS), trawl nets (OBTN), shore seines (OBSS) and a variety of other gears belonging to mechanized, motorized and non-mechanized (NM) sectors are also utilized for fishing. The multiday fleets have a higher fixed cost involved as they operate for many days in deeper waters (fleet information in Supplementary Table).

Growth Input

The growth parameters of the groups are also used as an input in the model and the value is found out by taking the average of growth parameters of all individual species included in that group. The parameters used are 'a' and 'b' in the length-weight relationship and L_{∞} (asymptotic length), W_{∞} (asymptotic weight) and K (growth rates) in the von Bertalanffy growth equation (information in Supplementary Table).

Results

Balancing the model

A model is said to be mass-balanced if the catches, consumption, biomass accumulation and export do not exceed the production of a group. This is following the Ecopath equation (Eq.1). A balanced model is characterized by an EE value not exceeding 1. EE value exceeding 1 means that demand for the group is very high. Therefore, modification of diet composition and biomass (mean or maximum biomass) is conducted until a balanced model is achieved.

Mass-Balance Solution

The estimated output parameters (EE, P/Q ratio and trophic level) for 47 functional groups are summarized in Table 6.

Ecotrophic Efficiency (EE)

Ecotrophic Efficiency (EE) is a measure of the proportion of production that is utilized by the next trophic level through direct predation or fishing. EE values should be less than 1 as values above 1 show that the group is highly demanded to be sustainable. EE value close to 0 means that the group is not consumed by another group in the system, whereas an EE value close to 1 indicates that the group is highly consumed by its predators (another group) or caught by fishing activities. After balancing the model, our results showed that all the estimated EE values were less than 1, ranging from 0.269 to 0.99. The EE value of all commercially exploited groups was higher than 0.5. The EE value varied considerably for different functional groups in this ecosystem. Ecological groups that have high EE values include large pelagics inshore, Medium Benthic Pelagics shelf, Small benthopelagic deep, Other Clupeids inshore, Coastal Shrimps, Squids, Cuttlefishes, Octopus and Commercial molluscs.

P/Q ratio

It is the ratio of Production to Consumption and the value mostly ranged between 0.1-0.3 with a few exceptions where the marine mammals and benthic omnivore shelf showed a lower value and the group crabs and lobsters exhibited a higher value (0.5)

Trophic level of the catch

This value shows the position of ecological groups in the ecosystem and the relationship between the prey and predator species. The model indicated that there is 5 trophic levels. The fishery in the Kerala Arabian Sea ecosystem had a mean trophic level of 3.215, fluctuated between 1 (phytoplankton) and 5.07 (sharks offshore). The fishery of Kerala is highly dominated by species like oil sardine and Indian mackerel with trophic levels 2.2 and 2.49 respectively.

Table 6. Basic Estimates of the balanced model of Kerala Arabian Sea Ecosystem (KASE)

Grp No.	Group name	Trophic level	Hab area (proportion)	Biomass in habitat area (t/km ²)	Biomass (t/km ²)	Production / biomass (/)
1	Marine Mammals	4.031	1	0.02	0.02	0.10
2	Sharks coastal	4.760	0.5	0.04	0.02	1.18
3	Sharks offshore	5.078	0.5	0.04	0.02	1.10
4	Sharks demersal	4.842	1	0.02	0.02	0.93
5	Guitarfishes & Rays	4.396	1	0.08	0.08	0.89
6	Large pelagics-offshore	4.535	0.5	0.34	0.17	1.05
7	Large Pelagics-inshore	4.873	0.5	0.20	0.10	1.21
8	Large Benthic Pelagics shelf	4.557	0.5	0.04	0.02	1.05
9	Large benthopelagic deep	3.925	0.5	0.42	0.21	0.83
10	Medium Benthic Pelagics shelf	4.433	0.5	1.52	0.76	1.40
11	Medium benthopelagic deep	4.525	0.5	0.51	0.25	1.41
12	Small Benthic Pelagics shelf	4.055	0.5	1.55	0.78	2.18

Grp No.	Group name	Trophic level	Hab area (proportion)	Biomass in habitat area (t/km ²)	Biomass (t/km ²)	Production / biomass (/)
13	Small benthopelagic deep	3.781	0.5	3.50	1.75	1.55
14	Mesopelagics	3.595	0.75	1.20	0.90	1.68
15	Tunas coastal	4.268	0.5	0.44	0.22	1.55
16	Tunas offshore	4.371	0.5	0.19	0.10	1.17
17	Ribbonfishes	4.650	0.5	0.85	0.43	1.29
18	Large Benthic Carnivores shelf	4.449	0.5	1.67	0.83	1.17
19	Large Benthic Carnivores deep	4.490	0.5	0.09	0.04	1.02
20	Medium Benthic Carnivores shelf	3.748	0.5	1.69	0.84	1.86
21	Medium Benthic Carnivores deep	4.028	0.5	3.66	1.83	1.10
22	Small Benthic Carnivores shelf	3.121	0.5	2.95	1.48	2.17
23	Small Benthic Carnivores deep	3.822	0.5	5.94	2.97	1.26
24	Benthic omnivores shelf	2.600	1	0.26	0.26	0.94
25	Threadfin breams	3.866	0.5	1.36	0.68	2.04
26	Indian Mackerel	2.491	0.5	1.89	0.94	2.26
27	Oil Sardine	2.204	0.5	7.86	3.93	2.60
28	Other Clupeids inshore	3.364	0.5	1.50	0.75	2.88
29	Anchovies	3.505	0.5	8.00	4.00	4.00
30	Crabs & Lobsters	3.372	0.5	0.09	0.05	4.78
31	Deep Sea Shrimps	3.160	0.5	0.75	0.38	3.94
32	Coastal Shrimps	3.198	0.25	5.30	1.33	6.87
33	Squids	3.835	1	1.59	1.59	4.25
34	Cuttlefishes	4.322	1	0.59	0.59	3.55
35	Octopus	3.947	0.5	0.15	0.08	3.81
36	Commercial molluscs	2.400	0.5	0.44	0.22	4.30
37	Benthic detritivore	2.373	1	56.22	56.22	2.90
38	Macrobenthos (Benthic carnivore)	3.339	1	15	15.00	3.10
39	Benthic grazers	2	0.25	24.02	6.00	0.73
40	Shelf filter feeders	2	0.5	5	2.50	1.60
41	Deep filter feeders	2	0.5	4	2.00	1.20
42	Gelatinous zooplankton	2.65	1	3.00	3.00	4.85
43	Large Zooplankton	2.58	1	6.76	6.76	35.00
44	Micro Zooplankton	2	1	14	14.00	65.00
45	Phytoplankton	1	1	58.5	58.50	70.00
46	Macroalgae	1	0.005	1069.76	5.35	2.78
47	Detritus	1	1	15	15.00	

Basic Estimates Table Continued

Grp No.	Group name	Consumption / biomass (/)	Ecotrophic Efficiency	Production / consumption (/)	Biomass accumulation (t/km ²)	BA rate (/)
1	Marine Mammals	12.75	0.00	0.01	0	0
2	Sharks coastal	3.70	0.75	0.32	0	0
3	Sharks offshore	3.43	0.81	0.32	0	0
4	Sharks demersal	4.46	0.48	0.21	0	0
5	Guitarfishes & Rays	2.96	0.36	0.30	0	0
6	Large pelagics-offshore	2.70	0.63	0.39	0	0
7	Large Pelagics-inshore	5.09	0.99	0.24	0	0
8	Large Benthopelagics shelf	4.76	0.62	0.22	0	0
9	Large benthopelagic deep	3.34	0.98	0.25	0	0
10	Medium Benthopelagics shelf	8.90	0.99	0.16	0	0
11	Medium benthopelagic deep	6.47	0.95	0.22	0	0
12	Small Benthopelagics shelf	10.95	0.95	0.20	0	0
13	Small benthopelagic deep	13.00	0.99	0.12	0	0
14	Mesopelagics	11.60	0.89	0.14	0	0
15	Tunas coastal	13.60	0.60	0.11	0	0
16	Tunas offshore	17.60	0.74	0.07	0	0
17	Ribbonfishes	3.75	0.87	0.34	0	0
18	Large Benthic Carnivores shelf	5.32	0.85	0.22	0	0
19	Large Benthic Carnivores deep	4.32	0.95	0.24	0	0
20	Medium Benthic Carnivores shelf	7.70	0.91	0.24	0	0
21	Medium Benthic Carnivores deep	4.54	0.95	0.24	0	0
22	Small Benthic Carnivores shelf	11.27	0.95	0.19	0	0
23	Small Benthic Carnivores deep	4.48	0.95	0.28	0	0
24	Benthic omnivores shelf	26.98	0.98	0.03	0	0

Grp No.	Group name	Consumption / biomass (/)	Ecotrophic Efficiency	Production / consumption (/)	Biomass accumulation (t/km ²)	BA rate (/)
25	Threadfin breams	10.94	0.89	0.19	0	0
26	Indian Mackerel	21.70	0.92	0.10	0	0
27	Oil Sardine	27.60	0.98	0.09	0	0
28	Other Clupeids inshore	20.70	0.99	0.14	0	0
29	Anchovies	17.13	0.99	0.23	0	0
30	Crabs & Lobsters	8.50	0.93	0.56	0	0
31	Deep Sea Shrimps	10.90	0.91	0.36	0	0
32	Coastal Shrimps	19.20	1.00	0.36	0	0
33	Squids	16.64	1.00	0.26	0	0
34	Cuttlefishes	16.64	0.98	0.21	0	0
35	Octopus	12.50	0.98	0.30	0	0
36	Commercial molluscs	12.50	0.97	0.34	0	0
37	Benthic detritivore	9.00	0.95	0.32	0	0
38	Macrobenthos (Benthic carnivore)	12.48	0.98	0.25	0	0
39	Benthic grazers	2.50	0.95	0.29	0	0
40	Shelf filter feeders	12.00	0.55	0.13	0	0
41	Deep filter feeders	12.00	0.27	0.10	0	0
42	Gelatinous zooplankton	16.17	0.75	0.30	0	0
43	Large Zooplankton	160.00	0.75	0.22	0	0
44	Micro Zooplankton	250.00	0.88	0.26	0	0
45	Phytoplankton		0.95		0	0
46	Macroalgae		0.95		0	0
47	Detritus		1.00		0	0

Summary Statistics

The Ecopath model uses several different statistics to describe the structure of the ecosystem in energetic terms, including total flows, consumption flows, respiration flows, exportation, detritus, and net primary production. Ecopath estimates two global indices: 1) the omnivory index, which represents the average diet breadth of the consumers based on the average consumption of each consumer, and 2) the connectance index, which estimates the proportion of the number of trophic ties with respect to the total number of possible connections. Several of these can be applied to assess the status and describe the developmental stages of an ecosystem. The System Statistics for Kerala Arabian Sea Model are given in Table 7.

The system statistic consists of total system throughput, which is the sum of all existing flows in the system. The flows consist of consumption, exports, respiration and flows into detritus. The total system throughput estimated for Kerala Arabian Sea Ecosystem is 10523.57 tonnes/km² /year. The value of the mean trophic level of the catch is 3.215 and its gross efficiency is 0.002. The maturity of the ecosystem is described by the value of the primary production/respiration (P/R) ratio. The P/R ratio of Kerala model is 1.002.

The value of net system production (or yield) for this ecosystem is 10.043 ton/km² /year while the PP/B value for the present model is 20.761. The system biomass/throughput ratio is 0.019 ton/km² /year. The Ecopath model also provides the Shannon diversity index, and the value of the diversity index is 2.289.

Total system throughput

The total system throughput expressed as t/km²/year is the total of all flows in the system, which is the sum of the four flow components: (1) sum of all consumption; (2) sum of all exports; i.e., exported from the system by fisheries or buried in the sediments; (3) sum of all respiration flows; and (4) sum of all flows into detritus. The total system throughput defines the size of the system in response to all flows (Ulanowicz 1986) and is crucial for comparing flow networks. The total system throughput of the Kerala system is 10523.57 t/km²/year, of which 55% was due to consumption, 39% from respiratory processes and 6% originated from backflows to detritus.

Mean trophic level of the catch

Mean trophic level is a critical index that indicates the overall level of exploitation of fishes which are low in the food web and its effect on prey and predator. The fishery in the Kerala Arabian Sea ecosystem had a mean trophic level of 3.215, fluctuated between 1 (phytoplankton) and 5.07 (sharks offshore). The fishery of Kerala is highly dominated by species like Oil sardine and Mackerel from trophic levels 2.2 and 2.49 respectively.

The major top predators in the ecosystem (TL > 4) include demersal sharks (4.8), coastal sharks (4.7), large pelagic inshore (4.8), large benthopelagic shelf (4.5), medium benthopelagic deep (4.5) and ribbon fishes (4.6). Groups with a trophic level value greater than 3.5 are included in higher trophic levels while the groups with value 1 are considered to be in lower trophic levels or as primary producers. The groups with value 1 in the Kerala system is phytoplankton, microalgae and detritus.

Gross efficiency of the fishery

The gross efficiency is the ratio of the total catch (including the discards) to total primary production of the ecosystem which can highly vary among systems. For the KASE model, the value obtained was 0.002 indicating a fishery harvesting fishes low in the food chain. The Arabian Sea ecosystem of Kerala will have a higher value as it is a part of the Malabar upwelling zones where lower trophic level pelagic fishes are highly exploited. Lower values are seen for systems that exploit top predators and higher values for systems exploiting lower trophic levels. Gross efficiency does not have a dimension as it is a ratio and generally has a much lower value than 1.

System primary production/respiration

This is the ratio between total primary production (Pp) and total respiration (R) in a system. This ratio provides information about the maturity of an ecosystem. The value of this ratio will be greater than 1 when production exceeds respiration which is usually expected to happen during the initial development stages of the ecosystem. The value will be less than one in organically polluted systems as the total respiration within the system is higher than the primary production, and a value close to 1 indicates that the system is mature. Energy fixed is approximately balanced by the cost of maintenance. This ratio is always positive and dimensionless. Since the TPP/TR for the Kerala system was 1.002, we can conclude that the ecosystem was mature.

Net system production

Net system production is also known as yield is the difference between total primary production and total respiration. As inferred from the discussion of ecosystem maturity, system production will be large in immature systems and close to zero in mature ones. Negative system production is seen in systems with large imports. It has the same unit as its inputs, the flows from which it is calculated, i.e., t/km²/year. A value of 10.043 t/ km² /year was obtained for KASE model which indicates the maturity of the ecosystem.

System primary production/biomass

This value is a function of systems maturity and is the ratio of the system's primary production (Pp) to total biomass (B). In immature systems, production is more than respiration for a majority of the groups, and hence, the biomass is expected to accumulate over time, which in turn can cause a decline in PP/B value. The dimension is per unit time. The ratio of the system behaves like that of single groups and can take any positive value. The value obtained for KASE is 20.761.

Total system biomass and total catches

The total system biomass is the sum of biomass of all ecological groups excluding the biomass of detritus. The total catch is the catch level of each group and these values are expressed in t/km² (biomass), and t/km² /year (catch). These values are used to find out the average size of organisms in the system.

Connectance index

The CI (connectance index) is the ratio between the numbers of actual links in a food web and the number of possible links in a food web. The CI value signifies the internal complexity of an

ecosystem. In the case of detritivorous organisms are taken into account while calculating CI but detritus feeding on others is not considered. The number of links is generally proportional to the number of ecological groups and how they are defined. A mature ecosystem tends to have CI values close to 1 (where there is interactions of all groups at some stage). The CI for our ecosystem is 0.212 indicates the low diversity of feeding interactions within the ecosystem. Alternate that can be taken for CI is the omnivory index which overcomes the drawbacks of CI (prey is given the same score for all levels of contribution to predators diet).

System omnivory index

The system omnivory index (SOI) is the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The logarithms are used as weighting factors because it can be expected that the intake rates are approximately log-normally distributed within the system. The system omnivory index shows the complexity and maturity of the system and is a measure of how the feeding interactions are broken down between trophic levels. A mature ecosystem tends to have OI values close to 1. The system omnivory index value of the KASE model is 0.325.

Table 7. Summary statistics of the KASE model.

Parameter	Value	Units
Sum of all consumption	5798.217	t/km ² /
Sum of all exports	10.0855	t/km ² /
Sum of all respiratory flows	4099.826	t/km ² /
Sum of all flows into detritus	615.4399	t/km ² /
Total system throughput	10523.57	t/km ² /
Sum of all production	5564.971	t/km ² /
Mean trophic level of the catch	3.214963	
Gross efficiency (catch/net p.p.)	0.001736	
Calculated total net primary production	4109.87	t/km ² /
Total primary production/total respiration	1.00245	
Net system production	10.04346	t/km ² /
Total primary production/total biomass	20.76057	
Total biomass/total throughput	0.018812	t/km ² /
Total biomass (excluding detritus)	197.9651	t/km ² /
Total catch	7.133595	t/km ² /
Connectance Index	0.21172	
System Omnivory Index	0.325283	
Total market value	802.3688	INR
Total value	802.3688	INR
Total fixed cost	91.9459	INR
Total variable cost	451.9712	INR
Total cost	543.9171	INR
Profit	258.4517	INR
Ecopath pedigree	0.325688	
Measure of fit, t*	2.284952	
Shannon diversity index	2.288502	

Key indices

The key indices of the Ecopath model for the KASE model are given below in Supplementary Tables. The net migration per year from the system is zero.

Flow to detritus

The flow to detritus includes the portion of food that is not assimilated, the dead (mortalities due to age and diseases) and decaying matters. The highest flow to detritus is contributed by the phytoplanktons followed by benthic detritivores organisms and micro zooplanktons. The lowest flow to detritus was from the organisms in higher trophic levels and the groups with the lowest flow in this system is sharks offshore followed by sharks coastal.

Net efficiency

The net food conversion efficiency is calculated using the P/B (production/biomass) ratio, Q/B (consumption/biomass) ratio and the amount of food that is not assimilated. The value of net efficiency is usually less than 1 and it is highest for the group Crabs and Lobsters.

Omnivory index (OI)

The Omnivory index (OI) is the variance in the trophic of the prey consumed by the predator. The omnivory index shows the pattern of feeding if the group possess a specialised feeding or not, if the value of OI is 0 then the group has a highly specific feeding habit (usually a single trophic level) while a larger value shows a varied feeding behaviour (many trophic levels). The larger value was found for small benthic carnivorous shelf followed by medium benthic carnivorous shelf.

Mortalities

The various mortality rates for the ecological groups are given in the supplementary table. The value Z indicates the instantaneous total mortality which is the ratio of production to biomass. The total mortality includes the mortalities due to fishing and natural mortalities (mortalities due to predation, old age, diseases). The fishing mortality rate is highest for larger pelagics inshore while the predation mortality rate is highest for phytoplankton. The net migration rate and the biomass accumulation rate is zero. The mortality rate by predation is further shown as a different table to show the impact of predators in each prey group. It was found that the ecological groups occupying the benthic regions had higher predation mortality than fishing mortality.

Consumption

The level of food intake of each group is given in the consumption supplementary tables. The flow of intake of food is expressed in $t / km^2 / year$. The consumption rate was higher in lower trophic levels. Microzooplankton had the maximum with $3500 t / km^2 / year$.

Respiration and Assimilation

The assimilation and the respiration rates and their ratios of the Kerala ecosystem are provided in the table. Consumption is the sum of production, respiration and assimilation and hence respiration rate is useful in finding the consumption. The part of food that is assimilated or absorbed is also

computed. Both the respiration and assimilation flows are expressed in t/km²/year. The ratio of respiration to assimilation cannot be more than zero as the respiration rate is always lesser than the assimilation rate. The respiration assimilation ratio is highest for marine mammals and is lowest for the group crabs and lobsters.

Electivity

Electivity refers to the selection index or the preference of the prey by a predator. The preference of ecological groups for their prey is given in the supplementary table. The value ranges from -1 to 1 and the value -1 shows that the particular species is not preferred as prey or avoiding the particular prey and the value 1 shows very high preference and is the most desired prey. The value zero indicates that it is preyed in accordance with the abundance of the prey species in the system. The offshore sharks have a higher preference for oceanic tunas and these tunas, in turn, prefer the medium benthopelagic deep. It is noticed from the table that the most desired prey of Indian mackerel is large zooplanktons.

Search Rates

The search rates for the ecosystem of Kerala is given in the supplementary tables. Search rates provide an estimate of the level of search by a predator for a particular prey species, and it is found that the organisms occupying the higher trophic levels exhibit higher search rates than the organisms in the lower trophic levels. The highest search rate is shown by oceanic tunas for the medium benthopelagic deep group.

Fishery-catch

The catch level of different ecological groups in the Kerala ecosystem using different gears utilised along the coast are provided in the supplementary table. The maximum catch was landed using multiday trawl nets with threadfin breams being the major catch followed by mechanised ring seines with Indian oil sardine forming the major catch. The fishery value is also given in supplementary tables.

Network Analysis

Trophic Level Decomposition

In addition to the routine for calculation of fractional trophic levels, a module is included in Ecopath, which aggregates the entire system into discrete trophic levels. This routine, based on an approach suggested by Ulanowicz (1995), reverses the routine for the calculation of fractional trophic levels. Thus, for the example where a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, the relevant fractions of the flow through the group are attributed to the herbivore level and the first consumer level.

The result of these analyses is presented in the supplementary tables, which shows that the flow occurs in 12 levels and the majority of the flow was in the first six trophic levels where the import (on trophic level I only), consumption by predators, export, flows to the detritus, respiration, and throughput are given by trophic levels. The majority of the organisms in the system belonged to the lower trophic levels. The throughput is the sum of the flows in the other columns.

Transfer Efficiency

Transfer efficiency is the proportion of energy passed between nodes in food webs. It is an emergent, unitless property that is difficult to measure and responds dynamically to environmental and ecosystem changes. Because the consequences of changes in transfer efficiency compound through ecosystems, slight variations can have large effects on food availability for top predators¹². Based on the network tables above, the transfer efficiencies between the successive discrete trophic levels can be calculated as the ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput on the trophic level. This is presented in a table of transfer efficiencies (%) by trophic levels. The efficiency of detritus transfer is not defined since detritus is a non-living group.

Further, the outputs include the ratio of total flow originating from the detritus to the total flow originating from both primary producers and detritus. This ratio, which may be viewed as an index of the importance of detritus in a system, is the quantitative form of yet another of Odum's (1969) measures of ecosystem maturity. The index is complementary to the proportion of the total flow that originates from the primary producers. The proportion of total flow originating from the detritus is 0.13 and the transfer efficiency of detritus is 21.11%. The transfer efficiencies are higher in the lower trophic levels than the higher trophic levels (Table 8). Other trophic level transfers are given in supplementary tables.

Table 8. Transfer efficiencies of the KASE model.

Transfer efficiency-Kerala Arabian Sea											
Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Producer	22.01	17.67	20.58	18.88	16.69	15.78	15.98	15.66			
Detritus	22.61	21.72	19.14	15.83	16.06	15.84	15.66				
All flows	22.09	18.23	20.35	18.44	16.62	15.78	15.95	15.61	15.1	14.73	25.82
The proportion of total flow originating from detritus: 0.13											
Transfer efficiencies (calculated as the geometric mean for TL II-IV)											
From primary producers: 20.00%											
From detritus: 21.11%											
Total: 20.16%											

¹² Eddy, Tyler D., et al. "Energy flow through marine ecosystems: confronting transfer efficiency." Trends in Ecology & Evolution (2020)

Mixed Trophic Impact

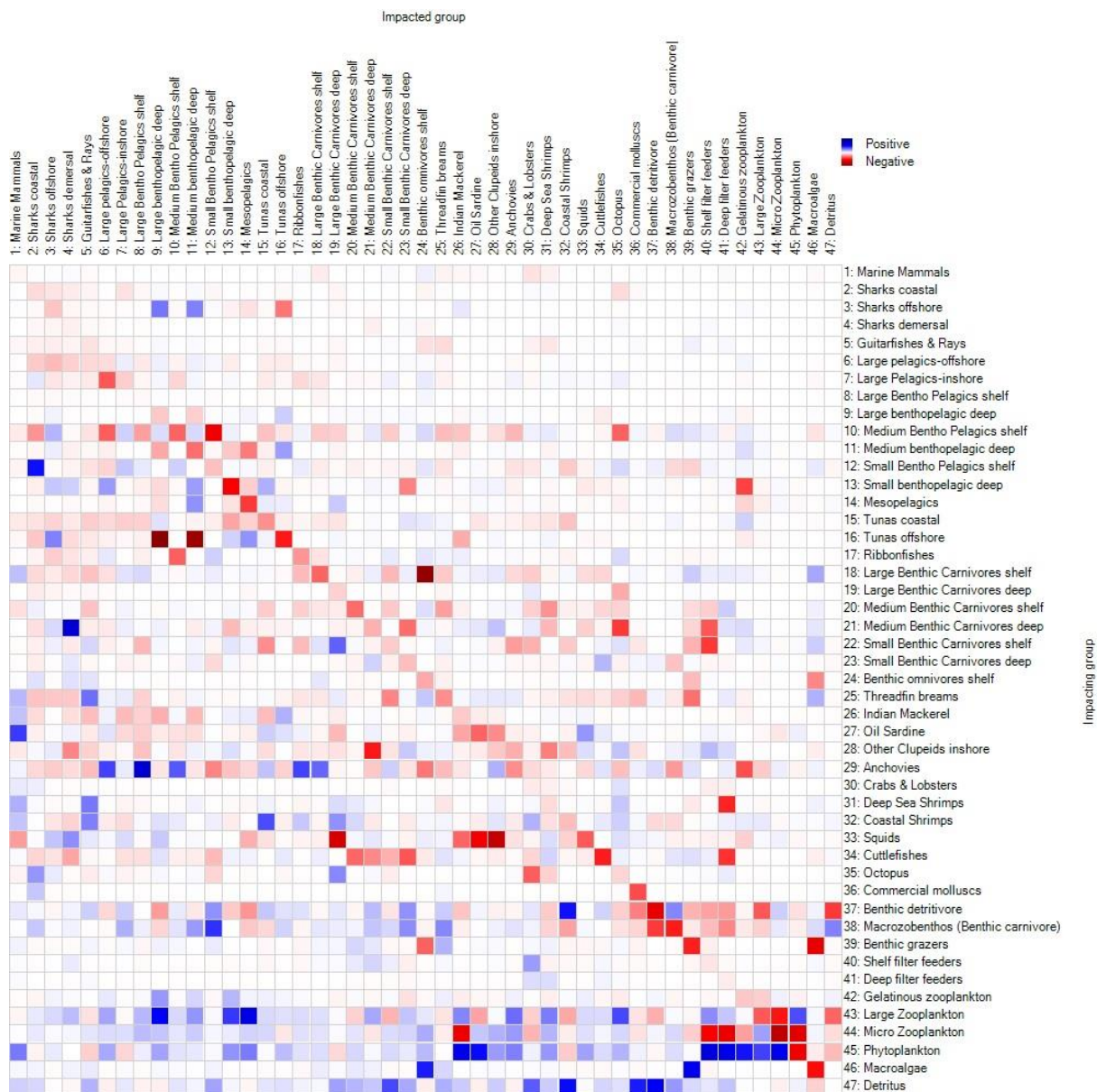
Mixed trophic impact (TI) is a measure of the relative impact of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia, 1990). It quantifies the net effects of one species on every other species in a system, taking into account positive effects of a prey species on its predator (weighted relative to its proportion in the diet), negative effects of a predator on its prey (weighted according to the fraction of the production of a prey that is consumed by the predator), and the indirect effects one species may have on another through trophic interactions. Matrices are constructed of relative net impacts of each group on every other, scaled between -1 and 1 . An assumption is that the trophic structure remains constant, implying that TI should not be used in a predictive sense, but rather as a type of sensitivity analysis, to identify those groups that may have large trophic impacts on others, and so there might be suitable indicators for monitoring fisheries effects across an ecosystem. The mixed trophic impact routine can also be regarded as a form of an 'ordinary' sensitivity analysis (Majkowski 1982). One can also, therefore, regard the impact routine as a tool for indicating the possible impact of direct and indirect interactions (including competition) in a steady-state system.

In the KASE model, phytoplankton has a positive impact on majority groups as they are the primary producers and the food for many groups except a few as shown in the supplementary tables. The impact of phytoplankton is the highest for pelagic fishes like Oil sardine, Indian mackerel, anchovies and larger zooplankton. Most groups have a negative impact on themselves, showing competition for the same food resources within the groups. Gears used also negatively impact many groups. Trawl nets negatively impact some of the economic groups such as Ribbonfishes, Demersal sharks, guitarfishes and rays, fishes of the group large benthopelagic shelf, large pelagics inshore and threadfin brems. The ring seines also have a negative effect on oil sardines, mackerels and anchovies. The increasing fishery activities in the Kerala system would have a negative impact on the economically important groups of the coast. Medium benthopelagic deep is the most negatively impacted by the oceanic tunas.

From the mixed trophic impact analysis, it is observed that the ecological groups occupying the lower trophic levels of the ecosystem have a higher positive impact than the organisms occupying the higher trophic levels of the ecosystem. The relatively small negative impact observed in the exploited groups can be seen as a result of a system that evolved over a long time. The negative impacts on a group can be mainly due to predation, competition among the groups for food, competition among the predators preying on the same groups etc. If the ecological group is food for the other group or if a particular group feeds on the predator of the ecological group then it can have a positive impact on the group.

The MTI (Fig.2) indicated that large zooplankton had a positive impact on pelagic groups and an indirect positive impact on sharks, because coastal sharks largely feed on medium pelagic while zooplankton constitutes a major portion in the diet of small benthopelagic group and mesopelagic group. However, zooplankton showed a significantly negative impact on themselves which may be due to the presence of a large proportion of carnivorous zooplankton. It is noteworthy that life histories of common zooplankton organisms (e.g. copepods) reveal that zooplankters are herbivorous only at juvenile stages, while they are frequently omnivores or carnivores during the

adult stage. A moderate negative impact on phytoplankton by zooplankton also indicated the presence of a smaller amount of herbivore zooplankton in the ecosystem. The Coastal Tunas had a negative impact on large benthopelagic deep and medium benthopelagics deep. The positive impact of detritus was evident on most of the functional groups especially for groups living in the benthic environment (i.e. snappers, grunts, groupers, shrimps, and other crustaceans), commercial molluscs and cephalopods. There was a significant positive impact by detritus since other crustaceans (mostly crabs and shrimps), molluscs and cephalopods fed largely on them. However, the KASE model showed an indirect positive impact of zooplankton on sharks, as sharks mainly prey upon schooling pelagic fishes which are mainly planktivorous (Sardines, mackerels, needlefish). Among the fish groups, demersal species showed a negative impact on most of the groups as they are mainly piscivorous and feeds on most other groups. Most fish groups had very minimal or less impact on themselves either positive or negative. But, all other functional groups at the lower trophic level except detritus had a negative impact on themselves, showing competition for the same resources within the group. However, detritus had neither positive nor negative impact on itself in the Arabian Sea waters. Based on the results is not possible to observe any kind of control of the food web, top-down or bottom-up. Fig 2. Mixed trophic impacts of the KASE model.



Keystoneness

Through MTI analysis, the Ecopath model provides information related to key species. Keystone species plays a pivotal role in the ecosystem. The key species are represented by plot points approaching or greater than 0. The key species groups in Kerala waters are phytoplanktons, zooplanktons (large and micro), anchovies and squids. The table showing the keystone species in the Kerala ecosystem is provided in the supplementary tables and the graphical representation is shown in Fig.3.

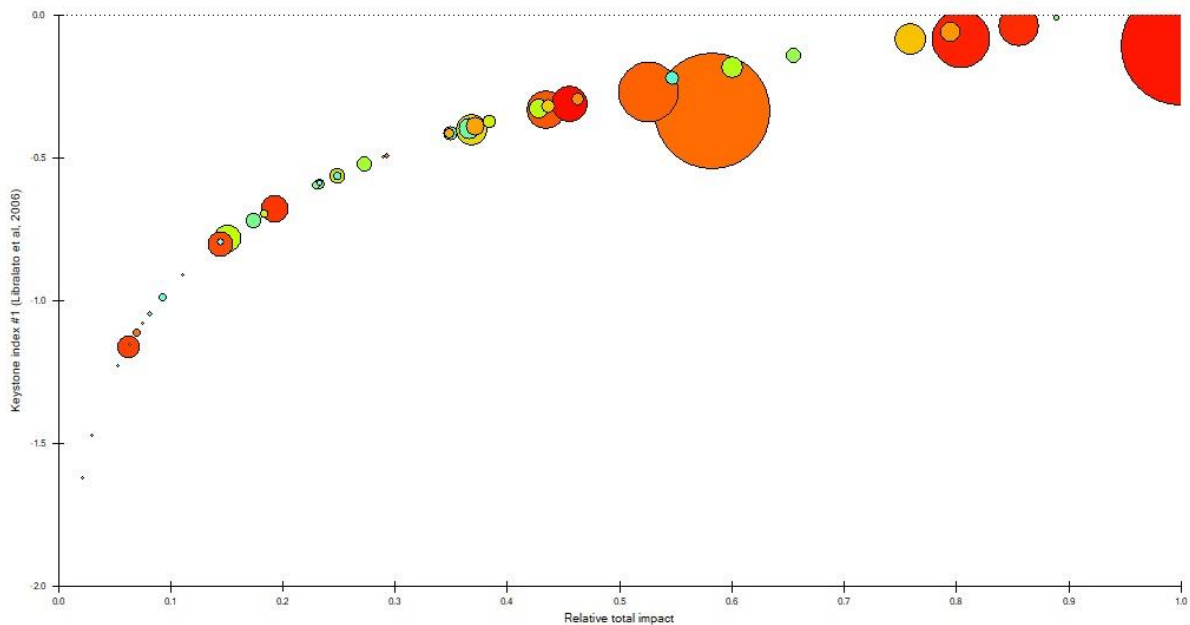


Fig.3. Major keystone species in the Kerala ecosystem are phytoplanktons, zooplanktons (large and micro), anchovies and squids (bubbles scaled by the impact).

Ascendancy

Ascendancy is the average mutual information in a system, a measure of the growth and development of the system. It is derived from the theory of information and scaled using throughput of the system. The upper limit of ascendancy is development capacity and the difference between the development capacity and ascendancy is overhead. Overhead is the amount of energy available in a system to resist the perturbations such as human activities (energy reserve of a system). It shows the strength a system can take from reserve to counteract perturbations. Ascendancy and overheads are related to the stability and maturity of the ecosystem. The value of ascendancy observed for the Kerala system is 31.34% and the overhead value for the system is 68.66%. These values are measured in flow bits ($t/km^2/year \cdot bits$). The Kerala system has low ascendancy and the system overhead signifies that the Kerala ecosystem is resilient or resistant to disturbances and can soon attain its original level. The ascendancy by the ecological groups is also provided in supplementary tables. Table 9 shows the total ascendancy and overheads in the Kerala marine ecosystem.

Table 9. Total ascendancy and overhead in the Kerala marine ecosystem.

Source	Ascendancy (flowbits)	Ascendancy (%)	Overhead (flowbits)	Overhead (%)	Capacity (flowbits)	Capacity (%)
Import	0	0	0	0	0	0
Internal flow	8329	21.84	16454	43.14	24783	64.98
Export	41.14	0.108	95.06	0.249	136.2	0.357
Respiration	3581	9.389	9640	25.27	13221	34.66
Total	11951	31.34	26189	68.66	38140	100

Ecosim Trials

The KASE model constructed was further used for temporal simulations. Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. This is done using a system of differential equations that express biomass flux rates among pools as a function of time-varying biomass and harvest rates. It also calculates the growth rate of a Functional Group during a specific time interval based on the net growth efficiency, the consumption rate of a prey FG by a predatory FG, the immigration and emigration rates and the other natural and fishing mortality rates (Christensen et al., 2005)

The inclusion of time series data in EwE facilitates its use for exploring policy options for ecosystem-based management of fisheries. An important preliminary conclusion from applications to various ecosystems is that the model is capable of producing a reasonable fit, for all available time series related to the ecological resources of an ecosystem in one go. This indicates a capability or at least a potential to replicate the known history of the ecosystems. In turn, this provides some insight to use the model fishery management and policy exploration.

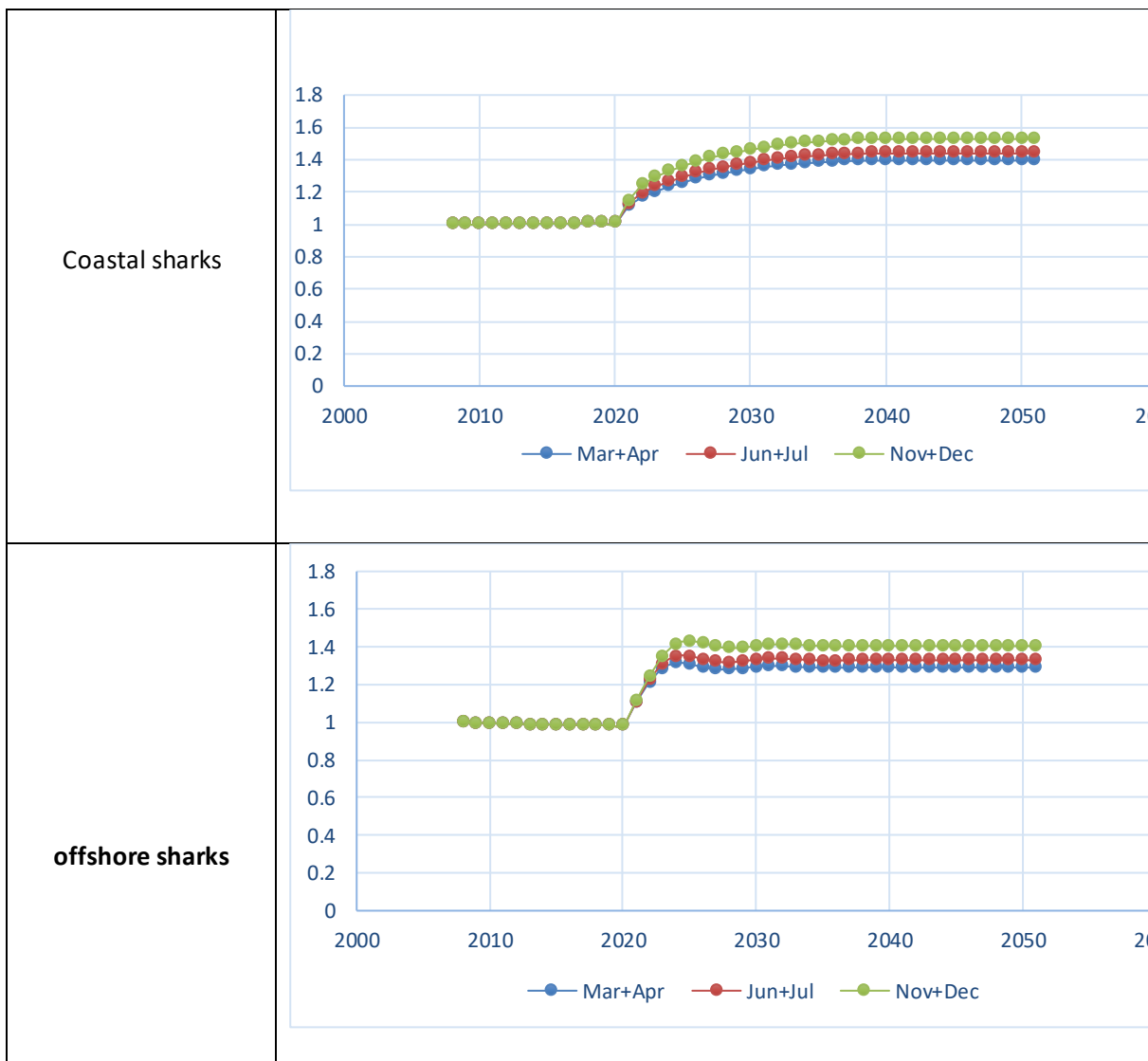
Ecosim routine in Ecopath was used to investigate how the changes in the fishing effort of different fleets operating in the Kerala Coast and closure of fishery in different seasons affect yields and biomass of different functional groups. The different scenarios considered were

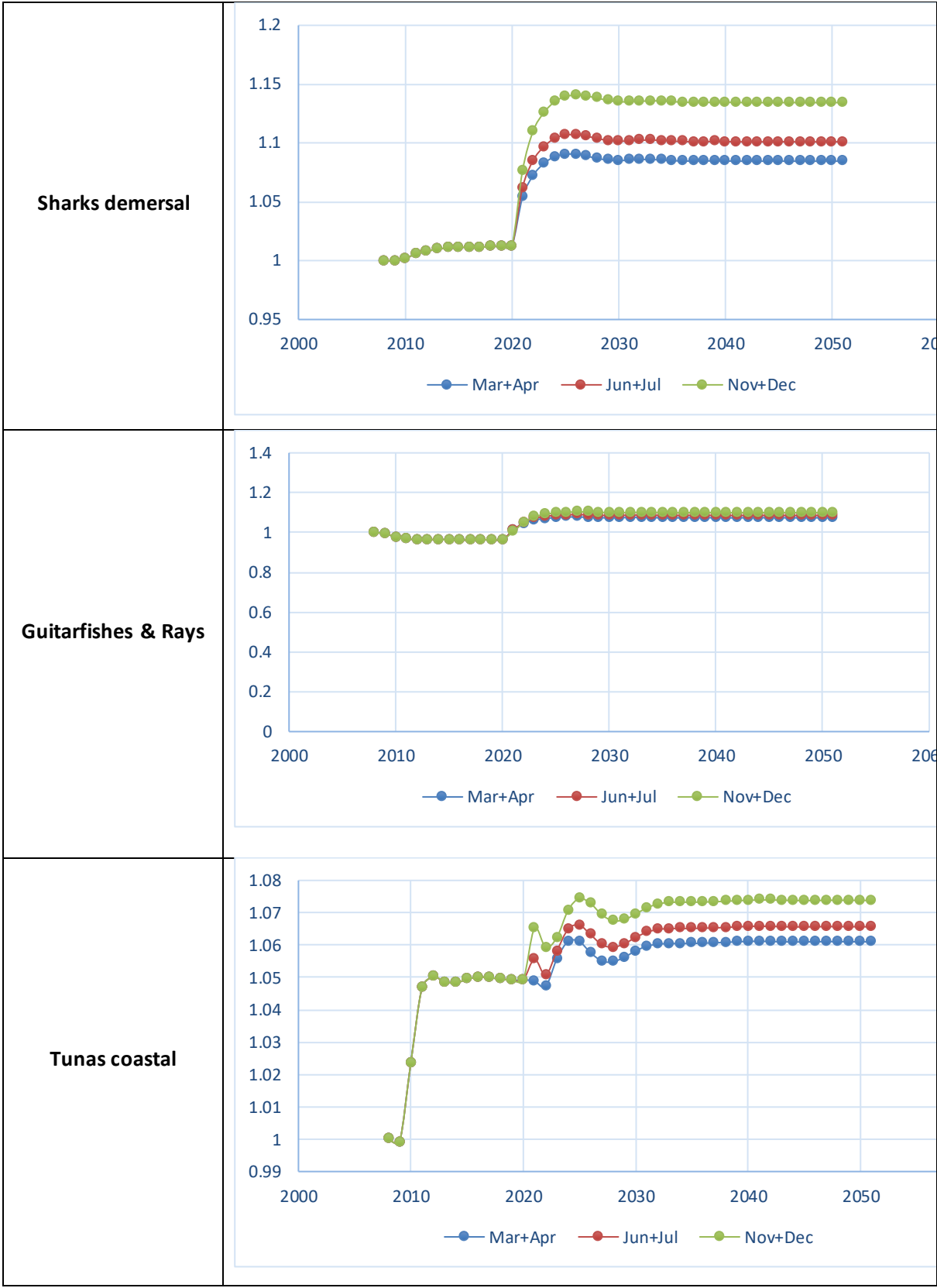
1. Closure of mechanized fishing in different seasons from 2020
 - March & April
 - June & July
 - November & December
2. Closure of ring seine fishery in different seasons
 - April & May
 - June & July

- November & December
3. Doubling the fishing effort of gillnet and hook and line with a gradual reduction in fishing effort of trawls from 2020
 - 4.

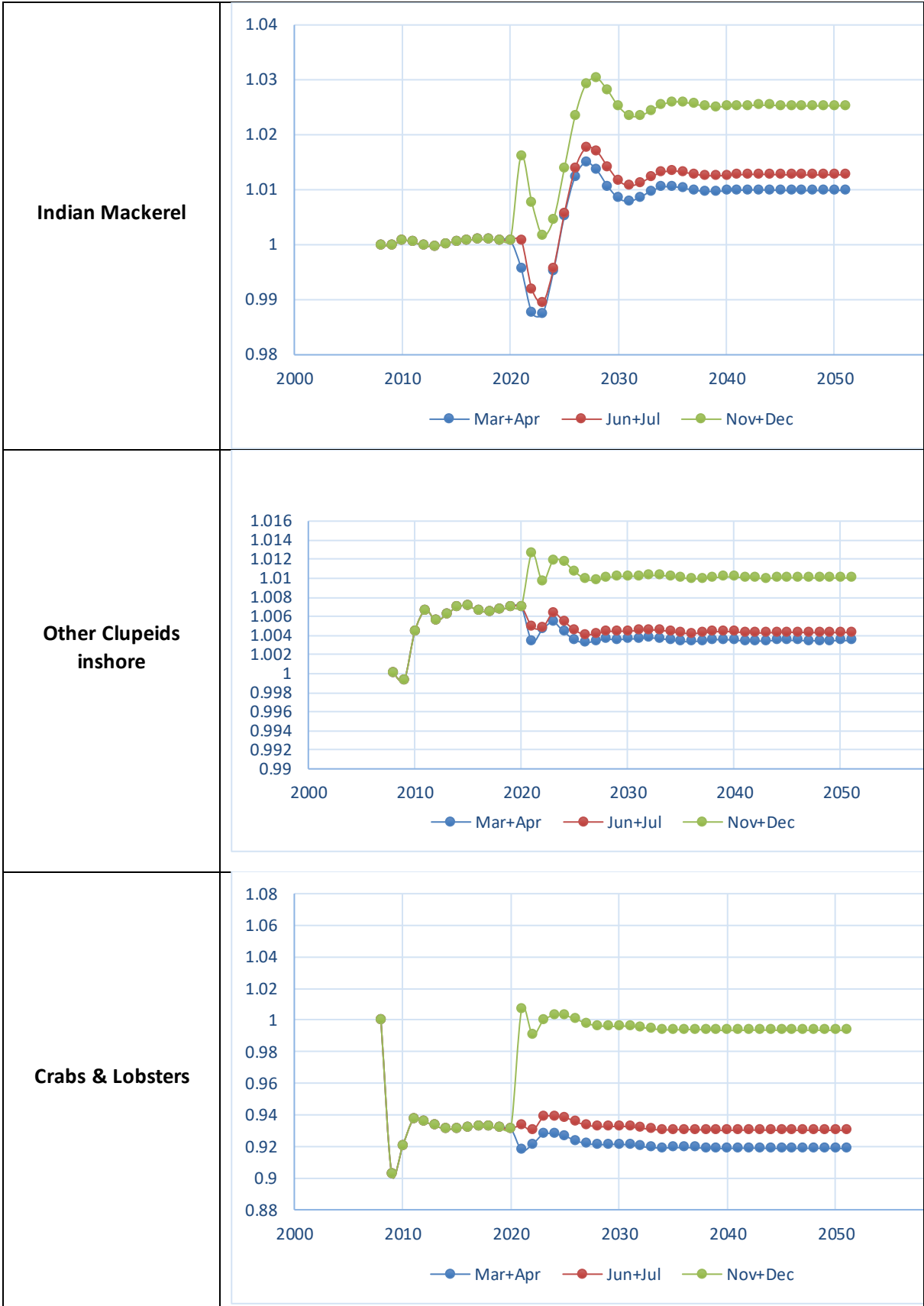
Scenario 1 Closure of mechanized fishing in different seasons

Under this scenario, the relative biomass of most of the commercially important groups are maximum when the fishery is closed during November and December

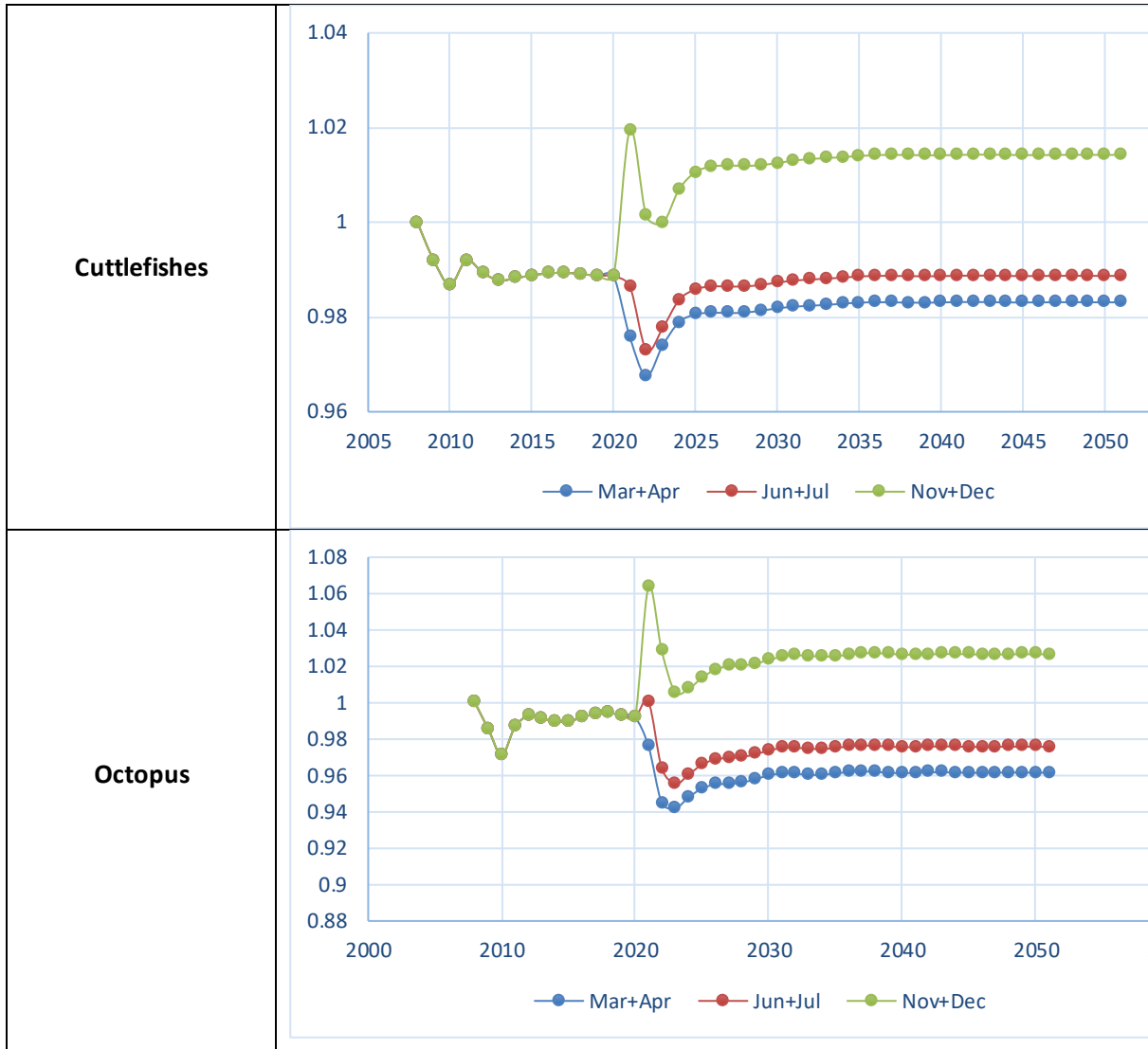




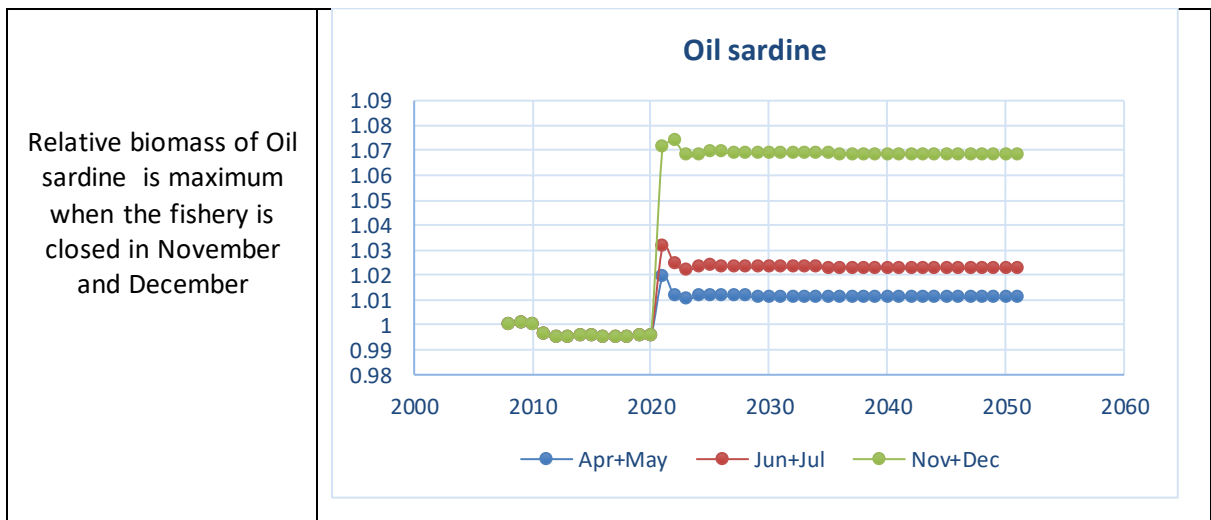


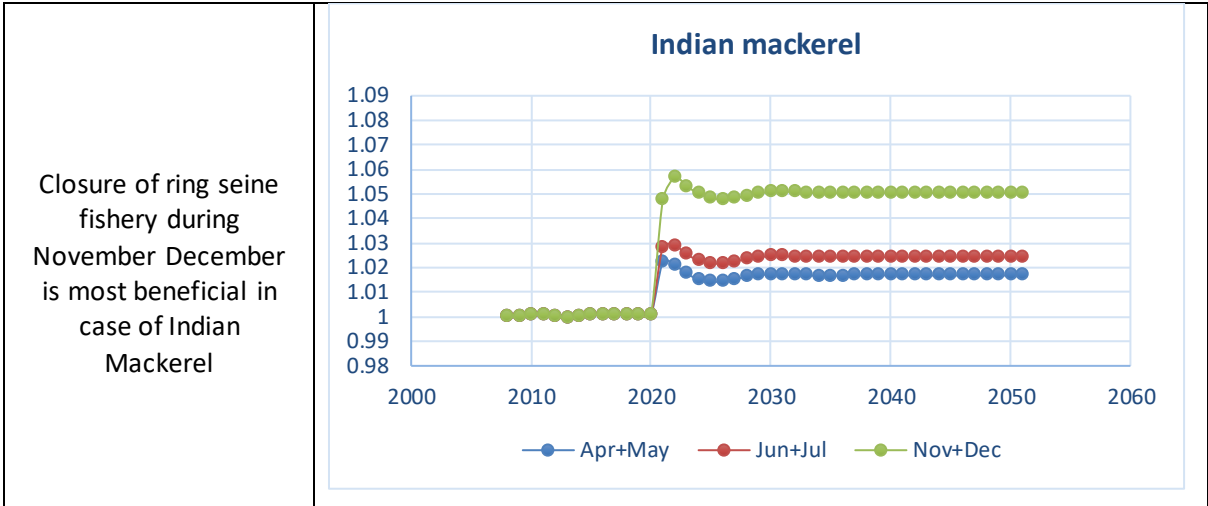






Scenario: 2 Closure of ring seine fishery in different Seasons





Scenario 3: Doubling the fishing effort of gillnet and hook and line with a gradual reduction in fishing effort of trawls from 2020

