

ECOSYSTEM MODELING OF THE RESETTLED MARITIME AREA OF THE BAY OF BENGAL, BANGLADESH THROUGH WELL-ADJUSTED ECOPATH APPROACH

EHSANUL KARIM^{1,2} – LIU, Q.^{1*} – XUE, Y.¹ – LIAO, B.³ – HASAN, S. J.² – HOQ, M. E.² – YAHIA MAHMUD²

¹*College of Fisheries, Department of Marine Fisheries, Ocean University of China
266003 Qingdao, China*

²*Bangladesh Fisheries Research Institute (BFRI), Mymensingh-2201, Bangladesh*

³*College of Mathematics and Statistics, Shandong University, Weihai 264209, China*

**Corresponding author*

e-mail: qunliu@ouc.edu.cn; phone: +86-532-8203-1715

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Abstract. This study was selected to assemble the current information in order to establish a mass-balanced ecosystem model within the resettled maritime limit zone of the Bay of Bengal, Bangladesh through ECOPATH approach covering over 90000 km². A total of 19 functional groups were considered demonstrating all trophic levels in the food web where the estimated trophic interactions between the groups were varied from 1 (primary producers and detritus) to 3.45 (sharks). The ecotrophic efficiency (EE) of most of the consumers was >0.80; indicating a largely exploited ecosystem and high energy transfer from lower to higher trophic levels. Moreover, the gross efficiency (0.0018) and transfer efficiency (11.12%) of the whole system symbolize the ‘developing systems’ with somewhat maturity. Ecosystem’s overhead (64.6) and ascendancy (35.4) also designate the ecosystem’s stability. Thus, this study concludes that the resettled maritime area of BoB reserves significant backup strength to face stress situations having capacity to rapid restoration to the original states.

Keywords: *Ecopath with Ecosim (EwE), Bay of Bengal (BoB), ecological groups, maritime ecosystem, mass balance*

Introduction

Ecosystems are superbly balanced although they are reasonably complex, non-linear and their structures are composed by the interconnection of living and non-living bodies with their habitat. In every portion of an ecosystem, has a significant role to play and if any alteration is occurred to any portion of a particular ecosystem, the whole ecosystem of that area can also be altered. This is not only dynamic but also hierarchically ascended. Ecosystems structures and processes are associated across the spatial and temporal balances. Due to their complication and the array of negative and positive response across balances, the predictability of these structures is inadequate (Gunderson, 1999). Sustainable usage of ecosystem components is unlikely in absence of a better understanding of balancing ecosystem dynamics that foster ecosystem capability (Bengtsson et al., 2003). Coastal and marine ecosystems are among the largest aquatic ecosystems of the world, covering 71% of the earth and fish populations are one of the most vital parts of these systems (BOBLME, 2011). Therefore, management approach that is based on fisheries ecosystem has reaped consideration for maintaining long-term sustainability to balance ecosystems (ICES, 2000). In recent, the ability of marine ecosystems to produce fish for supporting human interest is extremely degraded by

overfishing, excessive trawling, and loss of spawning and nursing grounds (McGlade et al., 2002). Noticeable limitation exists between single and multispecies fisheries management, which does not consider a comprehensive assessment of changes in ecosystem arrangement, and functions linked with the interactions of individuals (Mace, 2001; Pikitch et al., 2004). The concept of ecosystem-based fishery management needs the improvement of tools to gain perceptions in ecosystem functioning and the effect of fishing on ecosystem structure. Some of the critical issues like interspecies interactions within an ecosystem, effects of the enormous environmental and climatic alterations along with the fishing impacts should be incorporated to formulate an ecosystem based management strategy in any habitat (Browman et al., 2004; Pikitch et al., 2004).

Recent improvements in constructing multispecific ecosystem based modeling approach of aquatic ecosystems named “Ecopath with Ecosim (EwE)” are successfully used to evaluate the structure and ecosystem effects of fishing (Polovina, 1984; Christensen and Pauly, 1992). This approach provides a base for feasible and applied simulation model having actual predictive power that can be performed more rapidly and rigorously than ever before (Christensen and Pauly, 1993; Walters et al., 1997; Christensen and Walters, 2004). The construction of such mass-balance models of ecosystems are based mainly on food consumption, diet composition, biomass and mortality estimates. The ECOPATH packages of software have now been improved (Walters et al., 1997, 1999) through including ECOSIM (simulation module) and ECOSPACE (spatial module). These new modules have not only upgraded the quantitative command of the approach but also permitted qualitatively new inquiries.

Recently, Bangladesh has been settled maritime boundary with neighboring states Myanmar and India up to 200 nautical miles from the coastline comprising about 121110 km² (MoFA, 2014), whereas coastal and shallow shelf waters constitute about 20% and 35% respectively, the rest covers deeper waters (Khan et al., 1997). The entire shelf area of Bangladesh (up to 200 m depth contour) covers about 66440 km² and from the coastline to 10 m (0-10 m) depth zone comprises 24000 km² (Table 1). Nevertheless, in the context of fisheries resources, from the coastline to 200 m depth zone plays a significant role as it almost covers four major fishing grounds of Bangladeshi waters and also produces most of the marine catch (Lamboeuf, 1987; Khan et al., 1997). The declared areas of four major fishing grounds (Fig. 1b) are ‘South Patches’ and ‘South of South Patches’ covering an area about 6200 km². In addition, ‘Middle Fishing Ground’ contains 4600 km² area (Table 1) and ‘Swatch of No Ground’ covers 3800 km² (Khan et al., 1997). Among them ‘Middle ground’ and ‘South patches’ have been declared as ‘Fish sanctuaries’ in the Bay of Bengal. Still, the detailed ecological and oceanographic data of these areas are limited to determine the suitability of these areas as fish sanctuary.

In the context of the recent settlement of the maritime boundary, ‘Blue Economy’ recently turned into a buzzword for sustainable development, particularly in highlighting the vision of SDG (Sustainable Development Goals) for Bangladesh. The Government of Bangladesh emphasized those marine and coastal fisheries resources based blue economy might act as a driver for sustainable development, designating development not only for today but also for the upcoming years (Shamsuddoha and Islam, 2016). Moreover, this new relocated vast area could not be accessible to fishing due to the lack of vessel capability and suitable fishing technology (Hossain et al., 2014). The Bay of Bengal (BoB) defined as a temperately productive ecosystem among the world’s 64 Large Marine Ecosystems (Hussain and Hoq, 2010) has great potential

for fisheries because of the enormous nutrient input from the river flow of the Ganges and Brahmaputra (ESCAP,1988). A total of 475 species of finfish, 36 of shrimps, 15 types of crabs, 5 varieties of lobster, and over 300 species of mollusks were recorded (FRSS, DoF). The fishes which are presently exploited consist mainly of the shallow water estuarine species and some mid-water species. The average total marine industrial catch over the last decade (*Table 1*) was 540592 Mt (DoF, 2016). Functionally, marine fisheries are sub-divided into industrial and artisanal fisheries. The average production of the last ten years shows that the industrial fishery based on trawl fishery (shrimp and fish trawl) contributes only 5% of the total marine captures and the artisanal fisheries (mainly based on Set bag net and Gillnet fisheries) contributes 95%.

Table 1. The geographic location and covered areas of the major fishing grounds of the EEZ of the Bay of Bengal, Bangladesh (Khan et al., 1997)

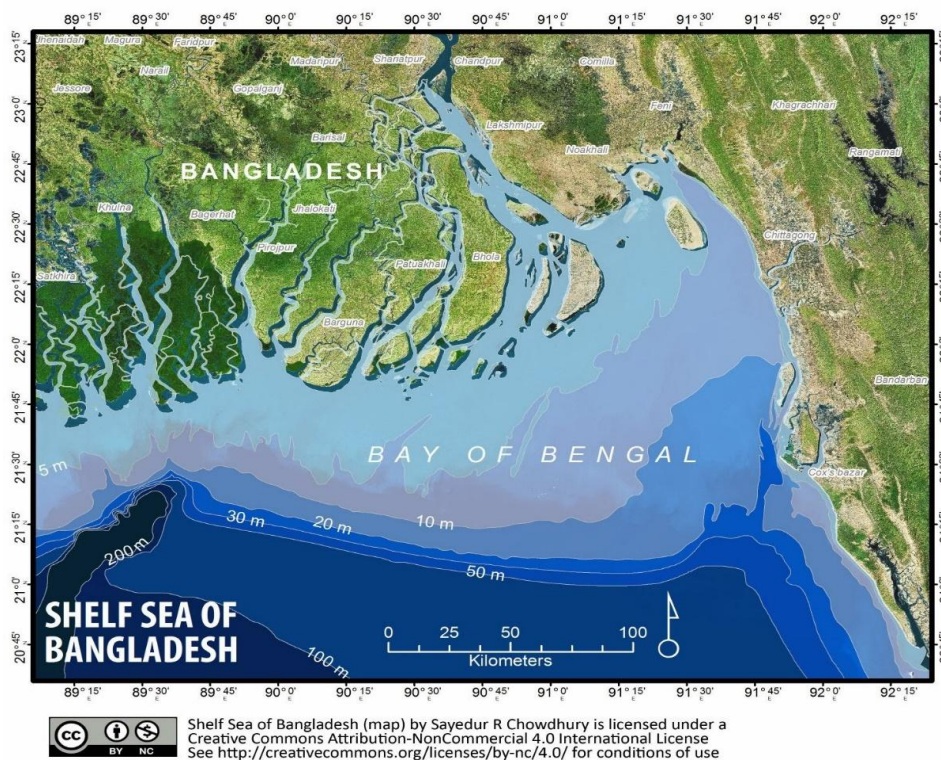
Depth zone (m)	Area (km ²)	Fishing grounds	Location	Depth
≤ 10	2400	South Patches	(Lat. 20°50'N to 21°40'N; Long. 91°00'E to 91°50'E)	10-40 m (depth)
10-24	8,400	(3400 km ²)		
25-49	4,800	South of South Patches	(Lat. 20°50'N to 21°40'N; Long. 91°00'E to 91°50'E)	10-100 m (depth)
50-74	5,580	(2800 km ²)		
75-99	13,410	Middle Ground	(Lat. 20°50'N to 21°20'N; Long. 90°00'E to 91°00'E)	10-100 m (depth)
100-199	10,250	(4600 km ²)		
All shelf	66,440	Swatch of No Ground	(Lat. 21°00'N to 21°25'N; Long. 89°00'E to 90°00'E)	10-100 m (depth)
		(3800 km ²)		

Several surveys and studies have been piloted to assess and estimate the potentialities of marine fisheries resources of Bangladesh since 1970 to 1980 by the collaboration of National and International agencies, but no fresh assessment is available. Limited reports are found focusing on biological, environmental and resource management concerns of the Bay of Bengal (BoB) (Hossain, 2003; Huntington et al., 2007; Hussain and Hoq, 2010), but such pieces of evidences are insufficient to consider and manage of our marine resources systematically. Conversely, in the near future, there is a possibility of dropped off the fisheries role on people's livelihoods as the stocks of various fish and shrimps are showing diminishing trends due to effects of climatic change, water pollution and fishing pressure (BOBLME, 2011). In recent, Mustafa (2003) made an attempt to describe the ecosystem features of BoB based on trawl catch data but overlooked the most important artisanal fishing areas and Ullah et al. (2012) described the shallow coastal areas not exceeding the 10 m in depth. Therefore, the maritime waters of the BoB, Bangladesh remain to be one of the most unfocused areas in the world, thus limiting the exploitation, exploration, conservation and management of its marine, though this zone is recognized as one of the world's ample and diversified ecosystems considered by greater productivity (Islam, 2003). All of these studies considered only short-term available data that not elucidate long-term outputs properly. Hence, attempts are made by authors to drive a new study concerning management of the maritime resources of the BoB, Bangladesh using the ecosystem scheme. The EwE (ECOPATH with ECOSIM; version 6.5) routine package was used in the current study to develop the mass-balance ecosystem model. The aim of this study is to illustrate the interaction between the diverse ecological groups and to define the flow of energy in the maritime area of Bay of Bengal, Bangladesh. In addition, another aim of this study is to measure the existing capability of the maritime ecosystem of BoB, Bangladesh to cope with the emerging "blue economy" pressure.

Materials and methods

Study areas

The Bangladesh part of the Bay of Bengal is located between 20° N and 22°30' N latitude, and 89° E and 92°30' E longitudes (Fig. 1a). The current study mainly focuses on the ecosystem structures of the major fishing grounds of the BoB, which lies from the baseline to 200 m depth zone (Table 1) occupying about 90000 km² that covers not only 24000 km² of inshore area but also 66440 km² of all shelf areas. The demarcation line is used to illustrate the depth zone and fishing grounds in the current study (Fig. 1a, b). Nevertheless, this area of both offshore and inshore water covers more than 90% of fishing activities in the country (DoF, 2015a) and thus, this model can be designated as 'resettled maritime ecosystem of Bay of Bengal, Bangladesh'. The bottom topography of the shelf sea is usually coarse sandy and muddy with some rocky blotches, but the shallow inshore areas are dominated by muddy bottom. Moreover, the shelf zone down to about 150 m seems to be quite smooth with very limited obstacles to bottom trawling whereas due to existence of precipitous slope trawling is not possible into the waters deeper than 180 m (Khan et al., 1997). The oceanographic features in BoB mainly depend on three key factors: (i) precipitation, (ii) wind direction; and (iii) mass siltation from the river discharges (Lamboeuf, 1987) that have a strong influence on the abundance and distribution of fishes too. The annual average temperature is about 26°C and the yearly average rainfall of the BoB, Bangladesh is approximately 3800 mm where over 80% precipitation is received from June to September (DoEF, 2015). Hence, these areas are treated as a sole homogenous area as they cover a wide range of marine habitats. However, this zone has been carefully chosen for the present study because of the availability of fisheries landing data.



a

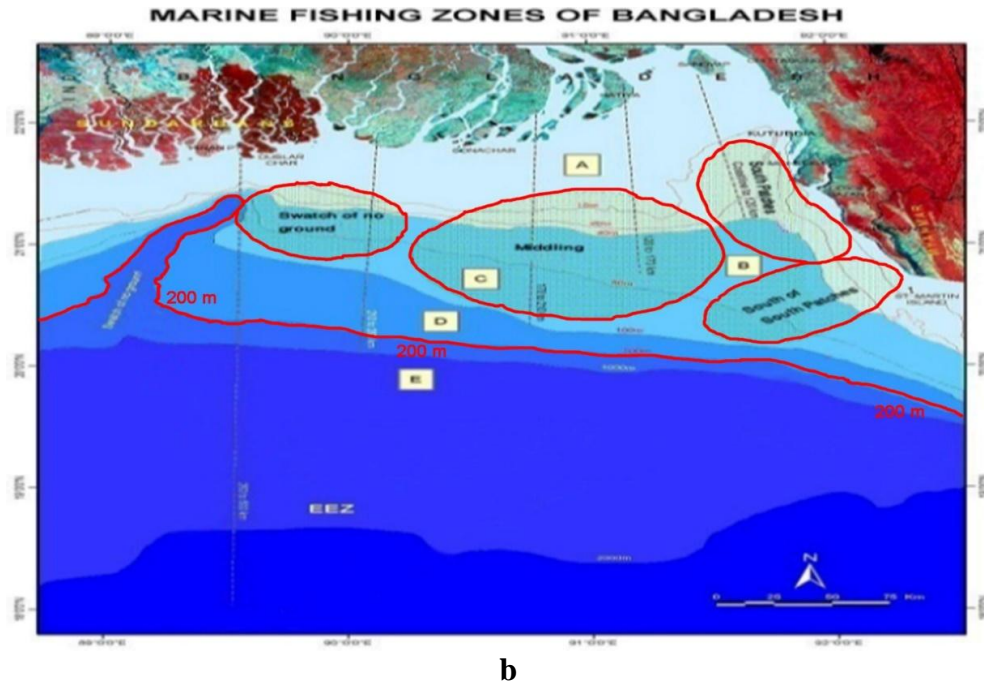


Figure 1. a. Total shelf area of the Bay of Bengal, Bangladesh highlighting the depth zones (Sayedur, 2014). **b.** Existing marine capture fisheries zones of Bangladesh focused on the major fishing grounds area

Overview of ECOPATH model (version 6.5)

The software 'ECOPATH' was designed for analyzing trophic dynamic interactions within the fisheries resources systems (Christensen and Pauly, 1992, 1995). This scheme is based on the previous work, which was first demonstrated by Polovina (1984), and it has been widely applied to aquatic systems after successive improvements (Christensen and Pauly, 1993; Pauly et al., 2000). Ecopath is basically a large spreadsheet that is instantaneously keeping track of all the individuals or species and entire feeding interactions occurring within the ecosystem (Christensen and Pauly, 1993). This approach designates an ecosystem at steady-state for a certain period and assumes mass balance in production of any specified prey that is equivalent to the biomass consumed by predators in combination with the estimated captured biomass (e.g. in fisheries) and any other exports from the system, i.e. (Eq. 1):

$$B_i (P/B)_i EE_i = Y_i + \sum (B_j) (Q/B_j) DC_{ij} + EX_i \quad (\text{Eq.1})$$

B_i represents the biomass of prey i group; P/B_i is the production/biomass ratio of that group; EE_i is the ecotrophic efficiency. Y_i symbolizes the yield (or catch rate of fisheries) of i groups; B_j is the biomass of predator j group and Q/B_j is the food export or consumption per unit biomass of j , DC_{ij} is the fraction of prey i in the diet of j and EX_i is the export of i . When the input values of the parameters of the model are delivered, ECOPATH assesses the missing parameters for each group within the model, e.g. the annual biomass production, the annual biomass consumption or ecotrophic efficiency for each functional groups of the ecosystem.

Model construction

Fisheries landing data

Existing marine capture fisheries of BoB are categorized into two major sub-divisions, i.e. industrial trawl captures and artisanal captures which put up about 95% of the total marine landings. The term ‘industrial captures’ indicate ‘large-scale’ which mainly focus on demersal fish and penaeid shrimps in the offshore waters. Artisanal consist of a number of diverse categories of traditional fishing gears and crafts i.e. gillnets, set bag nets (SBN), longline, trammel net, purse seine etc (*Table 2*).

Table 2. Gear wise landed total marine catches (metric ton) since 2005-06 to 2014-15 (10 years) of Bangladesh

Year	Fishing types (fleets/gears)						Total marine catch (MT)
	Industrial trawl catch	*Gillnet	*Set bag net (SBN)	*Longline	*Trammel net	*Others (Purse seine)	
2005-06	34084	264627	153687	16224	7399	3789	479810
2006-07	35391	265668	154736	15325	12883	3435	487438
2007-08	34159	274526	159043	13856	12466	3523	497573
2008-09	35429	296634	154164	16724	9680	2013	514644
2009-10	34182	297332	149142	18373	12608	5645	517282

*Fishing gears that used for large-scale commercial catch having different net mesh size (Gillnet, Trammel net and Purse seine consist of fine twin nylon net while Longline consist of hooks and rope lines and Set bag net having sack like bag at it's cod end)

Annual catch data of the last 10 years (from 2005-06 to 2014-15) from the Fisheries Resource Survey System (FRSS) of Department of Fisheries (DoF) of Bangladesh were considered in this study (*Table 2*). Due to the scarcity of an efficient data collecting and recording system, it is not possible to find the total species-wise annual landing data but group-wise data in FRSS. In addition, some of the reference reports (Mustafa, 1999; Nabi, 2007) and reports from the NGO organizations (eg. FAO country data) were also considered for this study.

Ecological or functional groups

Functional groups were characterized based on similarities in feeding habits, bulk body mass, life history parameters, physiological behavior and spatial distributions to keep homogeneous characteristics throughout the species within a group (Yodzis and Winemiller, 1999). More than 82 fish species and 20 types of shrimps and crustaceans are regularly collected by FRSS (DoF, 2015b), thus, over 77 taxonomic families of fish, shrimps, crustaceans, mollusks were included in this study. Representative species were selected based on their significance to fisheries and available information in the statistics (*Table 3*).

Greater preference was given to collect data from those pieces of literatures having local and regional data for every group when life history parameters, diet composition, food consumption, habitat and other information were considered for the modelling (*Table 4*). Where diet data were not available, information from similar ecosystems was

considered. Fishbase (www.fishbase.org; Fröese and Pauly, 2006) has also been applied to link up the gaps whenever possible. Data sources of non-fish groups are given in Table 5.

Table 3. Ecological or functional groups used in ECOPATH model including estimated total catch and percent composition of the maritime ecosystem of BoB, Bangladesh

Ecological or functional group	Major families or species	Total catch (MT)	Catch composition (%)	Explanation (habitat/fishing type)
1. Sharks	Carcharihinidae Squalidae Sphyrnidae Rajidae	3245	0.97	Down to 30 m depth Mostly Longline, SBN and Gillnet
2. Rays	Rhinobatidae Dasyatidae	2005	0.001	Down to 30 m depth Mostly Longline, SBN
3. Diadromous (Pelagic)	<i>Tenualosa ilisha</i> <i>Tenualosa toli</i>	215500	39.8	0-100 m depth, mostly by Gillnet
4. Minor Pelagics	Mugilidae Gobiidae <i>Setipinna spp</i> <i>Coilia dusumieri</i> <i>Gudusia chapra</i> Other Clupeids (Sardines) Engraulidae (Anchovies) Exocoetidae (Flying fish)	17530	3.2	Down to 10 m depth Mostly SBN, Gillnet and few catch by trawls and purse seines
5. Medium Pelagics	Scombridae <i>Scomberomurus guttatus</i> <i>Rastrelliger kanagurta</i> Other Mackerals <i>Euthunnus affinis</i> <i>Parastromateus niger</i> <i>Megalaspis cordyla</i> <i>Pterotolithus maculatus</i> <i>Decapterus spp.</i>	29352	5.4	10-100 m depth Mostly Gillnet and few catch by trawls
6. Minor Mesopelagics	Leiognathidae	6240	1.15	10-100 m depth Mostly Gillnet catch
7. Medium Mesopelagics	<i>Lepturacanthus savala</i> <i>Pampus chinensis</i> <i>Pampus argenteus</i> Trichiuridae	27843	5.15	10-100 m depth Mostly SBN and Gillnet, slightly by trawls
8. Medium Demersal	<i>Lates calcarifer</i> Lutjanidae (Snappers) Synodontidae (Bombay duck) Sciaenidae (Jew fish)* Pomadasidae	141434	27.7	0-100 m depth Mostly SBN and Gillnet, slightly by trawls and trammel net *Longline also used in fishing

	<i>Johnius argenteus</i> <i>Polynemus indicus</i> <i>Acanthopagrus latus</i> Ariidae* Lethrinidae <i>Eleutheronema spp.</i> <i>Otolithes spp</i> <i>Protonibea diacanthus</i> <i>Otolithoides spp.</i>			
9. Minor Demersal	Nemipteridae <i>Harpodon nehereus</i> <i>Saurida tumbil</i> Serranidae (Groupers) <i>Agryrops spinifer</i> Sparidae <i>Cynoglossus spp</i> Tetradontidae Priacanthidae <i>Tricanthus spp</i> Platycephalidae	47528	8.8	0-100 m depth Mostly SBN and Gillnet, slightly by trawls
10. Penaeid Shrimp	<i>Penaeus monodon</i> Other Penaeids <i>Metapenaeus monceros</i> <i>Metapenaeus spinulatus</i> <i>Parapenaeopsis stylifera</i>	34523	6.4	0-90 m depth Mostly by SBN and major target species by shrimp trawls
11. Other Shrimp	<i>M. rosenbergii*</i> <i>Asctes indicus</i>	9019	1.67	0-40 m depth, Mostly by SBN *Estuarine catch
12. Other crustaceans	Lobstars Crabs	2017	0.37	10-50 m depth and Intertidal zone
13. Cephalopods	Loligo Sepia Octopus	4356	0.8	10-100 m depth Mostly by catch of various gear and some catch by Squid jiggers
14. Mollusks	Bivalves			
15. Benthos	Annelids, Polychaetes, worms	-	-	0-40 m depth
16. Aquatic Invertebrates	Meiobenthos, Jelly Fish etc	-	-	0-50 m depth
17. Zooplankton	Copepods etc.	-	-	
18. Phytoplankton				
19. Detritus				

Basic parameters of fish

Estimation of biomass (B): The biomass of each ecological group per unit area in the habitat area (i.e. t/km²) was estimated in average by using Gulland (1971) formula of $B = Y/F$, where Y represents the annual yield of each group and F symbolizes the coefficient of fishing mortality. Biomass of sharks and other unexploited groups, i.e. benthos, aquatic invertebrates, zooplankton, phytoplankton, and detritus were obtained from various reference data (Table 5). In addition, biomass of other crustacean, gastropod and cephalopod groups were obtained from Arreguin-Sanchez et al. (1993) and Christensen and Pauly (1993).

Estimation of production/biomass (P/B): Estimation of this ratio is equivalent to the total mortality (Z) (Pauly et al., 2000) as it was really hard to assess directly. Consequently, this parameter was calculated by obtaining the sum of the fishing (F) and natural (M) mortalities while the entry of P/B ratios is optional. The estimated P/B values and other population parameters are given in Table 4.

Table 4. Life history parameters of the functional fish groups that were selected for ECOPATH model in the maritime ecosystem of BoB, Bangladesh

Representative species	L_{inf} (cm)	K (yr)	Z (yr)	F (yr)	M (yr)	E	References
1. Sharks							
<i>Scoliodon laticaudus</i>	74	0.68	3.91	2.94	0.97	0.75	Mathew et al. (1997)
2. Rays							
<i>Rhinobatus granulosus</i>	97	0.38	2.56	1.02	1.44	0.4	Mohamed et al. (2005)
3. Diadromous (Pelagic)							
<i>Tenuailosa ilisha</i>	60.0	0.82	3.77	2.49	1.28	0.66	Amin et al. (2002)
<i>Ilisha filigera</i>	35.0	0.75	3.37	1.95	1.42	0.58	Mustafa (1999)
4. Minor Pelagics							
<i>Coilia dusumieri</i>	16.8	1.30	2.61	1.60	1.01	0.61	Mustafa (1999)
<i>Gudusia chapra</i>	11.03	1.72	3.43	1.7	1.73	0.49	Islam (2005)
<i>Setipinna spp</i>	17.33	1.8	8.34	5.33	3.01	0.64	Nabi (2007)
<i>Escualosa thoracata</i>	12.20	1.2	9.84	7.29	2.55	0.74	Nabi (2007)
<i>B. mccllellandii</i>	11.03	0.83	3.53	1.48	2.06	0.42	Nabi (2007)
5. Medium Pelagics							
<i>Rastrelliger kanagurta</i>	27.8	0.9	4.92	3.21	1.71	0.65	Mustafa (1999)
<i>Parastromateus niger</i>	41.0	0.59	3.05	1.66	1.39	0.54	Mustafa (1999)
<i>Megalaspis cordyla</i>	38.5	0.54	2.86	1.44	1.11	0.51	Mustafa (1999)
6. Minor Mesopelagics							
<i>Leiognathus eqqulus</i>	28.0	1.08	3.2	2.5	0.7	0.78	Haque (1998)
7. Medium Mesopelagics							
<i>Lepturacanthus savala</i>	108.0	0.75	2.96	1.72	1.24	0.58	Haque (1998)
<i>Pampus chinensis</i>	38.1	0.67	2.56	1.23	1.33	0.48	Haque (1998)
<i>Pampus argenteus</i>	29.8	0.53	2.40	1.10	1.3	0.46	Haque (1998)
8. Medium Demersal							
<i>Lates calcarifer</i>	87.5	0.6	1.62	0.95	0.67	0.58	Haque (1998)
<i>E. tetradactylum</i>	38.1	0.18	4.4	3.5	0.85	0.87	Islam et al. (1993)
<i>Polynemus pradiseus</i>	20.5	0.48	4.38	3.17	1.21	0.72	Nabi et al. (2007)
<i>Sillaginopsis panijus</i>	43.3	0.38	3.6	2.7	0.86	0.76	Islam et al. (1993)

9. Minor Demersal							
<i>Harpadon nehereus</i>	29.4	1.5	4.18	3.01	1.17	0.72	Mustafa et. al. (1998)
10. Panaeid shrimp							
<i>Penaeus monodon</i>	31.5	0.95	4.75	1.74	3.01	0.37	Mustafa (1999)
<i>M. Monoceros</i>	17.9	1.5	6.51	2.70	3.81	0.42	Mustafa (1999)
11. Other shrimp							
<i>M. rosenbergii</i>	35.5	0.34	8.5	4.57	3.94	0.54	Islam et al. (1993)
12. Other crustaceans							
Lobstars (<i>P. polyphagus</i>)	58.0	0.43	7.9	1.67	6.23	0.21	Islam et al. (1993)
Crabs (<i>S. serrata</i>)	96.5	0.55	6.9	2.41	4.49	0.35	Islam et al. (1993)
13. Cephalopods							
Squid (<i>Loligo</i>)	44.7	0.21	3.5	1.02	2.48	0.29	Islam et al. (1993)

Table 5. Production-consumption data sources for non-fish groups

Ecological groups	Production/biomass (P/B)	Consumption/biomass (Q/B)	Ecotrophic efficiency (EE)
Sharks	Mathew and Devraj (1997)	Mohamed et al. (2005)	Computed by ECOPATH
Rays	Mustafa (1999)	Calculated in this study	Computed by ECOPATH
Panaeid Shrimp	Calculated in this study	Calculated in this study	Computed by ECOPATH
Other Shrimp	Calculated in this study	Calculated in this study	Computed by ECOPATH
Other Crustaceans	Calculated in this study	Arreguin-Sanchez et al. (1993)	Computed by ECOPATH
Cephalopods	Calculated in this study	Christensen and Pauly (1993)	Computed by ECOPATH
Gastropods	Fishbase (2006)	Guénette (2013)	Computed by ECOPATH
Benthos	Silvestre et al. (1993)	Silvestre et al. (1993)	Computed by ECOPATH
Aquatic Invertebrates	Guénette (2013)	Guénette (2013)	Computed by ECOPATH
Zooplankton	Arreguin-Sánchez et al. (1993)	Arreguin-Sánchez et al. (1993)	Computed by ECOPATH
Phytoplankton	Computed by ECOPATH	-	Fixed Value

Estimation of relative food consumption (Q/B): Consumption/biomass (Q/B) ratio of each group was calculated through the following empirical relationship suggested by Palomares and Pauly (1999):

$$\log Q/B = 7.964 - 0.204 \log W_{inf} - 1.965.T + 0.083.A + 0.532.h + 0.398.d$$

where, W_{inf} represents the asymptotic weight that can be calculated from the asymptotic length L_{inf} (one of the VBGF parameter found from ELEFAN routine of FiSAT II package) and length–weight relationships (LWR) of the representative species derived

from various sources (Table 4). T symbolizes the average annual temperature of that habitat which is expressed as $1000/(T_c + 273.1)$. Here T_c represents the annual average temperature of sea surface (26°C) (DoEF, 2015). A signifies the ratio of the square of the caudal fin height and its surface area, and h and d are binary variables demonstrating the feeding class of the fish species, i.e. for detritivore ($h = 0, d = 1$) and herbivore ($h = 1, d = 0$) and for carnivore ($h = 0, d = 0$). The aspect ratio of the caudal fin (A), which is the indication of metabolic activity, was collected mostly from the FishBase (Fröese and Pauly, 2006) and also from the laboratory works that were conducted in the Population Dynamics laboratory of Bangladesh Fisheries Research Institute (BFRI) during the data collection period. For other functional groups, Q/B was assembled from various literatures (Table 5).

Diet composition of every group

Still today, there are no complete investigations about trophic interactions of the coastal and marine ecosystem of Bangladesh. Only limited works have been done on diet composition of fishes in this area (Mustafa and Mansura, 1994; Mazid, 1998). Most of the studies are qualitative in nature where diet items of fish are frequently lumped together. Due to the deficiency of available data on diet composition of functional groups considered, Mustafa (2003), Fishbase (www.fishbase.org) data (Fröese and Pauly, 2006) and the study of Mohamed (2010) were used to complete the diet matrix of this study (Appendix I).

Ecotrophic efficiency (EE)

It provides the fraction of the yield of a group that is consumed within the system (i.e. transported through the trophic web) or caught by any fishery. In most cases, maintenance of the input values that provide the output fraction of EE between 0 and 1 are not possible as EE by definition, its fraction lies between 0 and 1. The EE is used to be computed from additional parameters in the Ecopath model since there is no field calculation to assess this parameter (Christensen et al., 2000).

Estimation of pedigree index

It categorizes the given input sources of an Ecopath through computing the type of source data on which it is based and specifying the probable uncertainty associated with the input. The main principles used here is that input estimated from native data (i.e. from the area covered by the model in question) as a rule is better than the data from elsewhere, be it a guesstimate, derived from other models or derived from empirical relationships. Three scales meet the above principles here, firstly for biomass assessing, second one for the estimating of P/B and Q/B and the rest for diet composition that are varied between 0 to 1. When the score is close to 0 that indicates the used input data is not rooted within local data, whereas value close to 1 means that are fully rooted within local data. The measure of fit (t^*) is also computed to define how well rooted the given model is in local data.

Evaluating the model through mass balancing method

The parametrization of Ecopath is based on its master equation (Eq. 1) which requires mass-balancing states of the functional groups. For this reason, the input

parameters need to be adjusted in a style to maintain the ecotrophic efficiency (EE) values less than 1. This practice depends on the understanding of which adjustments need to be done (Kavanagh et al., 2004). Primarily, input parameters like biomass, production-consumption rate, food consumption and fishing catch records were set into the basic input tools sheet of the package. Biomass accumulation value was taken as zero as the model was considered to describe an average for one year. Initial running of the routine provided the P/Q ratio and EE, but some of them were not balanced as EE values were greater than 1 which pointed out their higher demand in relation with sustainability. Initially EE values were found in case of diadromous pelagic (0.86), minor pelagic (0.96), medium mesopelagic (0.89), minor demersal (0.98), medium demersal (0.99), Gastropods (0.68) and benthos (1.26). On the other hand, some groups showed the exceeded value (one) of respiration/assimilation, which is not possible because respiration value cannot be exceeded from assimilation (Christensen et al., 2000). Thus, new run continues with the revised entries of biomass and diet composition values of the previous run, till to the achievement of mass balance. New run was also performed to obtain EE and gross efficiency values of all groups as it should be less than one. In order to get mass-balance, diet matrix needs to be adjusted because of its variation and instability of food sources and feeding habits throughout the groups. The foremost output of Ecopath modeling is the assessment of trophic levels which sometimes may be beyond expectation. In this case, one must check the diet matrix of the input data and also compare the data with the trophic levels of the same or similar species data of FishBase.

Results

The basic estimates of the mass-balanced models of maritime ecosystem of BoB, Bangladesh are given in *Table 6*. Life-history parameters and production-consumption data of non-fish groups are also presented in the *Tables 4* and *5*. Moreover, pre-balancing diagnostics of the maritime ecosystem BoB, Bangladesh model are presented in *Figure 2*.

Table 6. Input values and estimated parameters (bold) achieved after mass-balancing using auto-mass balance routine of ECOPATH model of BoB, Bangladesh

Group name	TL	<i>B</i> (t/km ²)	<i>P/B</i> (yr ⁻¹)	<i>Q/B</i> (yr ⁻¹)	<i>EE</i>	<i>P/Q</i>	<i>R/A</i>	<i>NE</i>	<i>OI</i>
1. Sharks and Rays	3.45	0.42	3.50	12.8	0.16	0.173	0.66	0.34	0.49
2. Rays	3.03	0.76	0.55	8.6	0.68	0.206	0.63	0.37	0.61
3. Diadromous (Pelagic)	2.02	1.11	3.77	13.1	0.77	0.287	0.64	0.36	0.11
4. Minor Pelagics	2.27	1.56	5.57	25.8	0.58	0.216	0.73	0.27	0.27
5. Medium Pelagics	2.34	0.42	3.76	18.9	0.80	0.198	0.75	0.25	0.31
6. Medium Mesopelagics	2.31	1.38	3.04	10.6	0.92	0.286	0.64	0.36	0.26
7. Minor Mesopelagics	2.36	1.05	3.2	12.8	0.81	0.25	0.69	0.31	0.27
8. Medium Demersal	2.80	1.3	3.5	13.1	0.86	0.267	0.66	0.33	0.48
9. Minor Demersal	2.54	1.65	4.18	14.1	0.46	0.296	0.63	0.37	0.43
10. Penaeid Shrimp	2.40	0.74	5.63	22.8	0.99	0.247	0.69	0.31	0.33

11. Other Shrimp	2.59	0.82	8.5	29.2	0.80	0.291	0.63	0.36	0.49
12. Other crustaceans	2.34	0.76	7.4	25.4	0.46	0.291	0.63	0.36	0.31
13. Cephalopods	2.65	0.7	3.5	22.9	0.98	0.153	0.81	0.19	0.43
14. Gastropods	2.85	0.85	5.3	23.5	0.29	0.225	0.72	0.28	0.50
15. Benthos	2.44	1.69	6.8	66.34	0.69	0.103	0.87	0.12	0.35
16. Aquatic Invertebrates	2.34	13	11	45	0.24	0.24	0.69	0.31	0.26
17. Zooplankton	2.11	27	34	119	0.61	0.286	0.64	0.36	0.11
18. Phytoplankton	1	58	100	0	0.57	-	-	-	0
19. Detritus	1	9.8	3.5	12.8	0.15	-	-	-	0

TL = trophic level, B = biomass, P/B = production rate, Q/B = consumption rate, EE = ecotrophic efficiency, R/A = respiration-assimilation ratio, NE = net efficiency and OI = omnivory index

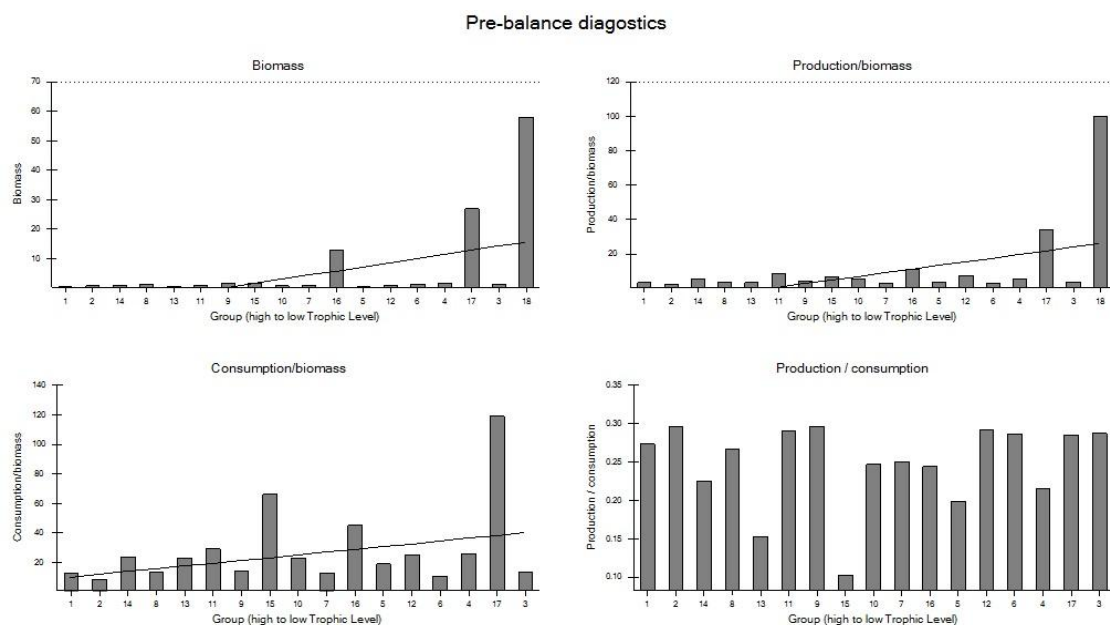


Figure 2. The figure represents the pre-balancing diagnostics of basic inputs for construction of mass-balanced marine ecosystem model of Bay of Bengal, Bangladesh

Mean trophic level was found 2.53, with the highest value obtained from sharks (3.45) and rays (3.04) groups followed by medium demersal (2.80) and gastropods (2.85), while the lowest value was obtained from phytoplankton (Table 6). In case of estimating ecotrophic efficiency, penaeid shrimps showed the higher EE value (0.99) followed by cephalopods (0.98) while diadromous pelagic showed lower value (0.202) and except minor pelagics and demersal all fish groups showed higher EE values ($EE > 0.8$). Benthos showed the highest rate of respiration–assimilation ratio (0.87) whereas shrimps and crustaceans showed lower. In this model, the maximum omnivory index was found in the apex predators like rays group (0.61) followed by sharks (0.49). The highest P/Q values was found in minor demersal group (0.296) while net efficiency was obtained from the rays and minor demersal groups (0.37). Most of the fish groups showed the lower fishing mortality rate over the predation mortalities. In addition,

maximum prey overlaps were detected for benthos and zooplankton groups. The relative and absolute results of flows and biomasses are showed in *Table 7* and *8*. In case of cycles and pathways, mean length of pathways from prey to predator was found 6.33 and the total number of pathway was 680.

Table 7. Tropic level flows from primary producers and detritus (t/km²/year)

Trophic level \ Flow	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
Tropic level flows from primary producers					
IX		0.000	0.000	0.000	0.000
VIII		0.000011	0.000006	0.000064	0.000120
VII		0.000273	0.000104	0.00138	0.00264
VI		0.00447	0.00192	0.0331	0.0584
V		0.0979	0.0416	0.469	0.868
IV		1.476	0.374	5.064	11.38
III		18.29	1.786	92.33	152.4
II		264.8	2.952	1154	1895
I	0.000	3317	0.000	2483	0.000
Sum	0.000	3601	5.155	3735	2060
Tropic level flows from detritus					
IX		0.000	0.000	0.000	0.000
VIII		0.000	0.000	0.000	0.000
VII		0.000011	0.000006	0.000062	0.000122
VI		0.000313	0.000097	0.00126	0.00249
V		0.00416	0.00183	0.0269	0.0476
IV		0.0804	0.0375	0.445	0.826
III		1.389	0.367	4.454	9.641
II		15.85	4.956	64.18	115.7
I	0.000	200.7	3603	0.000	0.000
Sum	0.000	218.0	3609	69.11	126.3

Table 8. Transfer efficiencies (%) for each TL of the maritime ecosystem of the Bay of Bengal, Bangladesh

Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX
Producer	12.17	12.53	10.11	9.451	6.528	8.563		
Detritus	7.873	10.01	8.490	7.444	9.865			
All flows	11.89	11.21	10.000	9.348	6.664	8.548	8.226	
Proportion of total flow originating from detritus: 0.30								
Transfer efficiencies (calculated as geometric mean for TL II-IV)								
From primary producers: 11.09%								
From detritus: 9.93%								
Total: 11.02%								

The resource biomass assembly of the BoB, Bangladesh maritime ecosystem model points out that it is predominantly a low trophic level driven ecosystem. However, the assessed pedigree index of the BoB maritime ecosystem was found 0.631 (*Table 9*) that conformed the developing stage of overall quality of an Ecopath approach as discussed by Christensen et al. (2005). In this study, Shannon diversity index of the maritime ecosystem of BoB was found 1.55 that was also within a satisfactory level (*Table 9*).

Table 9. The overall system statistics of the maritime ecosystem of BoB (no unit for indices and ratios)

Parameter	Value	Units
Sum of all consumption	4149.14	t/km ² /year
Sum of all exports	3613.73	t/km ² /year
Sum of all respiratory flows	2186.27	t/km ² /year
Sum of all flows into detritus	3803.94	t/km ² /year
Total system throughput	13753.08	t/km ² /year
Sum of all production	6933.04	t/km ² /year
Mean trophic level of the catch	2.53	
Gross efficiency (catch/net p.p.)	0.0018	
Calculated total net primary production	5800	t/km ² /year
Total primary production/total respiration	2.65	
Net system production	3613.73	t/km ² /year
Total primary production/total biomass	51.24	
Total biomass/total throughput	0.008	/year
Total biomass (excluding detritus)	113.2	t/km ²
Total catch	10.5	t/km ² /year
Connectance Index	0.325	
System Omnivory Index	0.285	
Ascendancy	35.4	
Overhead	64.61	
Ecopath pedigree index	0.631	
Measure of fit, t*	3.25	
Shannon diversity index	1.56	
Throughput cycled (excluding detritus)	328.2	t/km ² /year
Predatory cycling index	5.34	% of throughput without detritus
Throughput cycled (including detritus)	403	t/km ² /year
Finn's cycling index	2.93	% of total throughput
Finn's mean path length	2.47	

In addition, in the flow diagram of the systems, the greatest flows were observed from phytoplankton to zooplankton and from detritus to aquatic invertebrates, benthos, and others that are presented in *Figure 3*. The direct and indirect impacts throughout the groups including their exploiting gears are also shown in *Figure 4*.

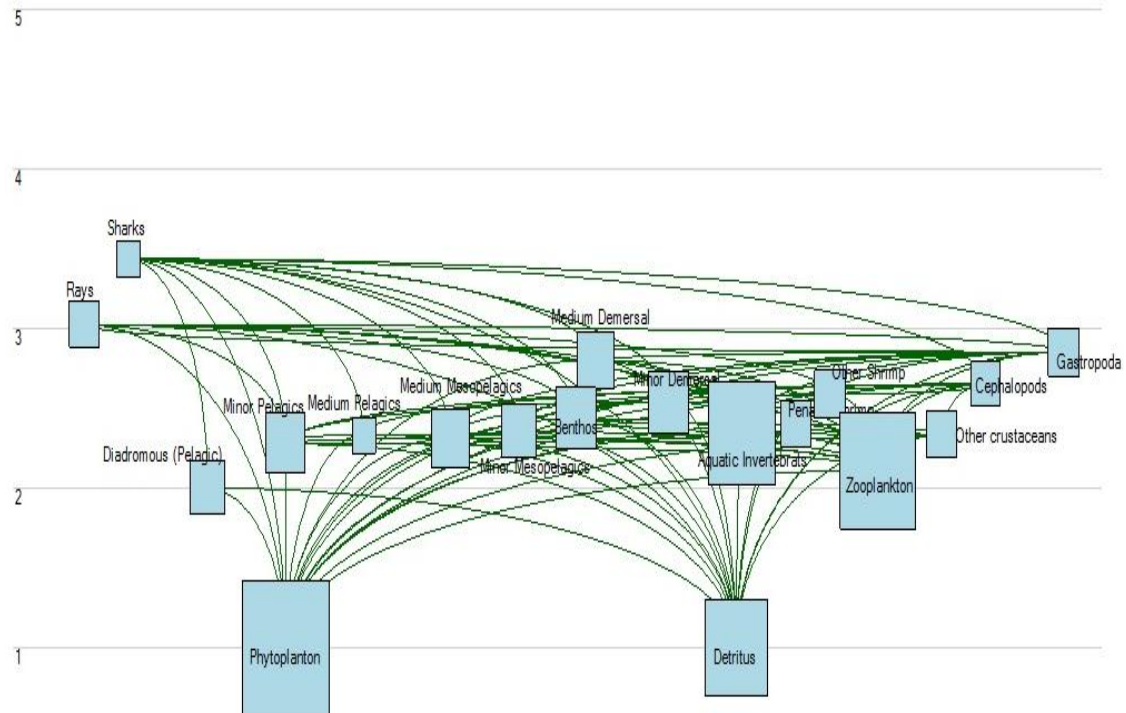


Figure 3. Flow diagram of trophic relationships in the marine ecosystem of the Bay of Bengal, Bangladesh

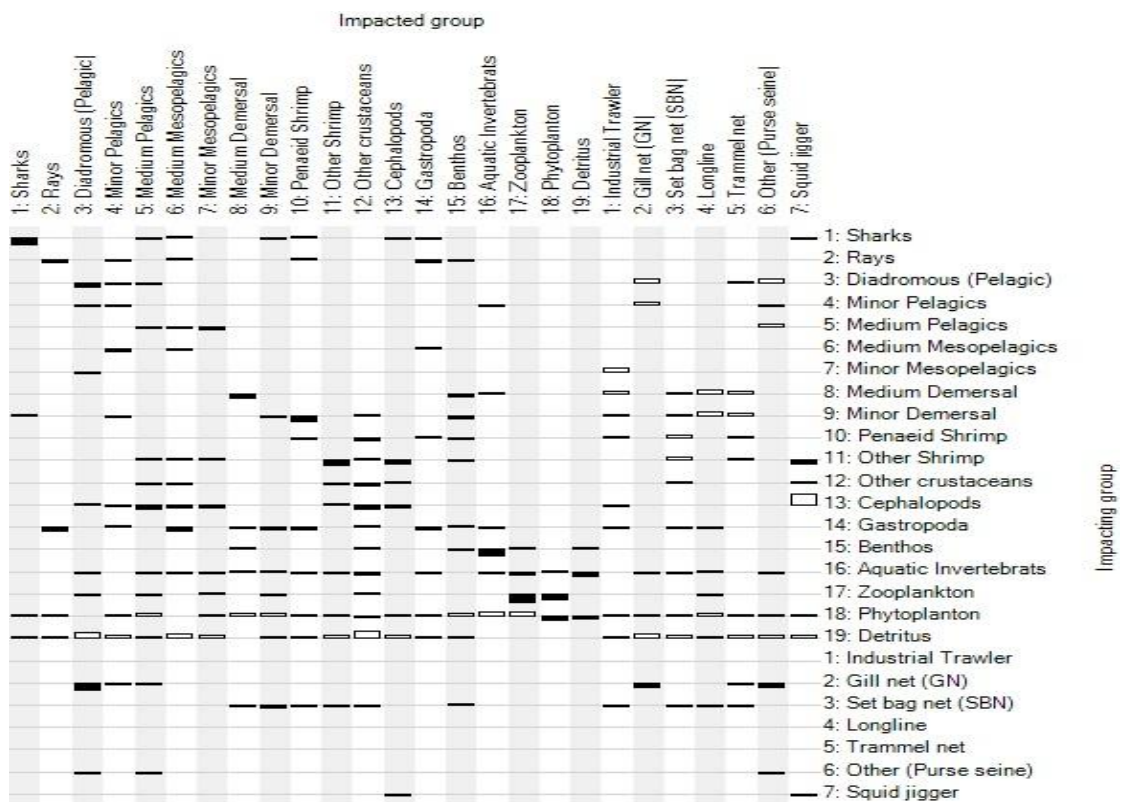


Figure 4. The diagram illustrates the direct and indirect impact of the groups and fishing fleets mentioned at the upper and right-side of the histograms (rows). The upward bars represent positive impacts and downwards reveal negative impacts

The summary of the total system statistics of the BoB maritime ecosystem model is given into the *Table 9*. Finally, comparative study of the functional characteristics of maritime ecosystem model of BoB, Bangladesh with some other marine ecosystem models are also presented in the *Table 10*.

Table 10. Comparison of the maritime ecosystem of BoB, Bangladesh with other ecosystems

Name of the ecosystems	Throughput	Catch/PP	PP/B	B/T	Net sys prod.	Omni. index	Ascendency	Cycling index	Path length
British Columbia Shelf ^a	1237.0	-	21.1	0.18	4106	0.14	40.1		2.03
Yacutan ^a	2362	0.003	27.4	0.036	370	0.134	44.0	2.8	2.84
Sarawak, Malaysia ^b	1414	0.004	19.37	0.02	273	0.22			
Brunei, SE Asia ^a	1816	0.0008	28.6	0.018	300	0.201	29.4	16.3	2.8
N. Gulf of Mexico ^a	1790	0.0002	7.0	0.015	19	0.195	39.1	2.1	3.03
San Pedro Bay, Leyte, Phillipines ^c	183960	0.0011	46.81	0.008	1879.8	0.29			
Peru 70 (upwelling) ^a	18800	0.0017	87.5	0.012	14709	0.169	38.1	8.7	3.63
Bering Sea 80's ^d	5692	0.0021	4.9	0.050	-356	0.157	30.9	11.1	3.51
Karnataka Arabian Sea ^e	11522	0.0016	29.9	0.012	904	0.299	33.0	6.03	2.81
Coastal Ecosys. of BoB ^f	2628	0.0015	14.69	0.026	264.24	0.224	38.7	10	2.58
Marine Ecosys. of BoB*	13753	0.0018	51.24	0.008	3614	0.285	35.4	2.93	2.47

a. Christensen and Pauly (1993); b. Garces et al. (2003); c. Campos (2003); d. Trites et al. (1999); e. Mohamed et al. (2005); f. Ullah et al. (2012); *Present study

Discussion

The relative biomass of the ecological groups of this study initially estimated from the Ecopath model that revealed considerable differences due to three issues. Firstly, all groups were not equally captured through all the gears and same catchability was not found in every gear types. Therefore, some may be under or over-exploited in the survey. Secondly, Ecopath computes the biomass by the data of given catch. So, the larger the catch, the greater the biomass estimate. Lastly, the estimated catch data was mostly on group-wise rather than species-wise which may led to comparatively diverge catch value for different species. The estimated biomass of the BoB maritime ecosystem varied from 0.42 to 1.65 mainly for targeted catch groups i.e. demersal fishery and lowest for the shark groups due to absence of large predators.

Diet matrix preparation for this ECOPATH model was the most difficult task due to lack of earlier studies on feeding ecology. In order to make the study realistic some stomach content studies and diet isolations have been done. But most of the qualitative data provided by external studies were converted into a quantitative form for preparing the diet matrix. Although this model contains many groups (19 groups), the diet matrix

comprises some low proportions. In fact, these values are hard to determine from field data. This nature might be significantly influenced the ultimate result.

Production-consumption (P/Q) rate of less than 0.3 may assist as a diagnostic feature in a balanced model. In most cases, the P/Q values of all possible functional groups range from 0.05 to 0.3, but some exceptions may happen in case of coral reefs, fish larvae, nauplii, bacteria and other minute, fast-growing organisms. The present study supports this concept for all groups which was 0.103 to 0.296. Demersal groups showed higher P/Q ratio than most of the pelagic groups (*Table 6*), this may be due to higher consumption rate of benthic communities and some predatory behavior of few demersal species. Nevertheless, pelagic species are typically herbivores and generally dependent on phytoplankton and detritus.

One of the most significant feature of an ecosystem is to assess ecotrophic efficiency (EE) (Christensen et al., 2000) which is mainly the fraction of production consumed by predators. In the BoB model, the EE values varied extensively from 0.24 to 0.99 (*Table 6*). Normally, just over the zero value points out the 'group' was not consumed until now by any other groups throughout the system while close or equal to 1 designates a heavily preyed group, where there are no individuals left to die of old age. Only sharks (0.16) showed lower EE value which was realistic and expected as for the top predators (Christensen et al., 2000). In addition, in both cases of phytoplankton and detritus, the EE values were less than 1.0 that was settled with the systems proposed by Christensen and Pauly (1992) that indicates more producers would have entered than left. However, the estimated EE value of detritus (0.15) was the lowest among the groups probably due to absence of typical primary consumers in the ecosystem. Out of all targeted groups, the estimated EE value of penaeid shrimps and cephalopods were shown the highest values over 0.9 (*Table 6*) that were likely the consequence of greater fishing pressure and predation. Similar reports were found from Islam et al. (1993) that penaeid shrimps were highly exploited throughout the maritime waters of BoB.

Mean trophic level (TL) is the vital index of the complete exploitation level of fisheries groups low in the food web and its effect on predator and prey species. Fishing down the marine food web, in which fishing fleets gradually target species minimum in the food web, may or may not be the reason for decline in global mean trophic levels of catches. The BoB maritime ecosystem had a mean trophic level of 2.53, with the highest 3.45 (sharks) and lowest being 1 (phytoplankton and detritus) (*Fig. 3*). Except the predators' maximum group biomass and ecological production occupied the place at around TLIII (*Table 6*). Ecopath generally computes trophic levels higher than IV (Ulanowicz, 1995). A total of 9 TLs were counted in this study (*Table 8*), which may be due to the cannibalistic characters of the peak trophic levels (Haputhantri et al., 2008). Therefore, the trophic accumulation routine in Ecopath gathered the 19 groups in a normal food chain with ten trophic levels where primary producers (TLI) comprised detritus and phytoplankton (*Table 7*). The result displayed that the maximum flow of the system was transferred from secondary consumers mainly composed of zooplankton group followed by TLI where phytoplankton was the single contributor. This output reveals the significance of zooplankton for the activation of trophic level of the BoB maritime ecosystem which is dominated by lower trophic level of fisheries resources as reported by Hossain (2003). For each group, the flow to the detritus contains non-absorption rate of diet and those components of the group that die of old age, diseases, etc. The detritus flow indicates that almost every functional group of the BoB maritime

ecosystem are severely exploited by either excessive fishing pressure or predation along with other mortalities, i.e. cannibalism (*Table 7*).

Gross efficiency of the system was 0.0018 indicates less crowd of target fisheries in the food chain. Actually increasing trend of gross efficiency index represents the fisheries 'development' which is generally much lesser than 1.0 as globally it is about 0.0002. This results is almost similar with the by Mohamed et al. (2005) and Ullah et al. (2012). In addition, the average transfer efficiency (TE) was 11.02% where flows from phytoplankton were demonstrated more essential than flows from detritus demonstrating a significant planktonic food chain throughout the maritime ecosystem of BoB (*Table 8*). Actually, transfer efficiency acts as an index of the significance of detritus in a system. The TEs for TLII, as suggested by Ryther (1969), are 15% for marine areas, but the most common range is 10–20% (Odum, 1971; Barnes and Hughes, 1988). However, the accounted of all flows was 11.89% (*Table 8*) which covers the above range demonstrating ecosystem maturity (Odum, 1971). In addition, estimated TEs of the trophic levels III, IV and V of this study were within the standardize range of 10–20% for coastal zones (Odum, 1971; Barnes and Hughes, 1988). Hence, the existence of some dominating fish groups having higher EE value around TL III may be the basis of the higher TE in TLIII.

Mixed trophic impacts may be direct or indirect i.e. as for a prey; a group causes a positive impact on others while as a direct predator, impact is negative. In the current observation, zooplankton, phytoplankton, and detritus were showed to have a positive impact on most other groups. The impact was greater on their direct consumers, i.e. most of the pelagic fishes depend on either phytoplankton or detritus or both. Negative impacts were due to benthos or zooplankton as a consumer of aquatic invertebrates, phytoplankton, and detritus or as a competitor for the same food source. Phytoplankton and detritus were shown a significant positive impact on pelagic groups and moderately positive on some of the demersal groups whereas barely any impact was found on penaeid shrimps and cephalopods (*Fig. 4*). The system package designated that the impact on detritus would be negative since detritus normally accompanied by phytoplankton in the regimes of several primary consumers. Thus, upsurge of phytoplankton would stimulate primary consumers to forage more detritus. Zooplankton had significant negative impact on themselves due to the existence of greater quantity of carnivorous zooplankton and relatively low negative impact on phytoplankton, which also indicates the existence of herbivory zooplankton in that ecosystem. Remarkable positive impact of detritus was observed on most of the functional groups whereas detritus had neither positive nor negative impact on itself in that ecosystem. Comparable results are also observed in other ecosystems (Christensen and Pauly, 1993). Fishing fleets also negatively affected several groups i.e. pelagic groups were negatively impacted by Gill net whereas demersal by SBN operations. Thus, it can be concluded that increased fishing pressure by gillnet and SBN in the BoB maritime ecosystem would have generated more negative impacts on fish groups, especially on the demersal and predators.

Total system throughput (*TST*) is the sum of all flows (e.g. total consumption, total respiration, total export and total flows to detritus) in a system which represents the 'size' of the entire system in relation to flow (Ulanowicz, 1986). The estimated *TST* for BoB was relatively higher 13753 t/km²/year (*Table 9*) but consistent with tropical marine ecosystems with much turnover. This result was also similar (*Table 10*) with the

studies of San-Pedro Bay, Phillipines by Campos (2003) and Karnataka, India by Mohamed et al. (2005).

The ratio of total primary production and total respiration (PP/R) is considered by Odum (1971) to be a significant ratio to describe the 'maturity' of an ecosystem. Previously, a system needs to be developed for being balanced as the production is expected to exceed respiration that provides a ratio greater than 1. Finally, in 'mature' systems, the PP/R ratio should be 1; when energy is constant that is roughly balanced by maintenance (Odum, 1971). The PP/R value was found 2.65 which was higher than 1, thus, it is concluded that the BoB marine ecosystem is not so developed or still in developing stage. The net system production value of 3613.7 t/km²/year was assessed for the BoB maritime ecosystem, which again points out the BoB is still developing but also little bit matured comparing with the other studies. Generally, system production is greater in immature systems and nearby zero in maturity stages. The net system production value of British Columbia shelf ecosystem were also provided 4106 t/km²/year (Table 10) which was greater than the current value. This may be happened due to absence of large predators as well as lower trophic level as this system completely based on TLII to TLIII. Moreover, the ratio between a system's primary production (PP) and total biomass (B) was 51.24, which was higher and also indicates some sorts of immaturity. Production exceeds respiration largely in immature systems and therefore it will influence the system's PP/B ratio which dimension is per unit time, and it can take any positive value.

The available ecosystem energy flow directly supports the total system biomass which can be expected to rise maximum for the utmost maturity stages of a system (Odum, 1971). The ratio of B/TST is directly proportional to the system maturity, where the estimated value tends to be low during the ecosystem development stage and increases as a purpose of maturity (Christensen, 1995). From the present study, system biomass/throughput ratio was found 0.008 being lower compared with those given by Ullah et al. (2012); Mohamed et al. (2005); Garces et al. (2003), which showed the status of comparative maturity of the ecosystem (Table 10). The yield of a group throughout a system is size-specific that has been revealed that the inverse of a group's production/biomass ratio is a degree of size (Christensen and Pauly, 1993). However, the estimated total biomass (excluding detritus) 113.2 t/km² was higher than the study of Ullah et al. (2012) but lower than the value of Mohamed et al. (2005), as their study based on the adjacent area of BoB. But the total catch (10.5) was comparatively higher than the above studies which may be due to excessive artisanal fishing pressure in Bangladeshi waters.

The trophic flows to detritus were observed highest for zooplankton and smallest for top predators. For each group, the flow to the detritus contains non-absorption rate of diet and those components of the group that die of old age, diseases, etc. The detritus flow indicates that almost every functional group of the BoB maritime ecosystem are severely exploited by either excessive fishing pressure or predation along with other mortalities, i.e. cannibalism (Table 7). The cycling matter and energy flow is considered as a vital process of any active natural ecosystems (Odum, 1969). The percentage of 'cycling index' is the fraction of an ecosystem's throughput that was developed by Finn (1976). It was basically intended to calculate Odum's (1969) system maturity. However, its explanation was not as simple as originally conceived that intensify recycling as a system matures. Detritus played a supreme role in all flows (cycled) in the BoB model where the total cycled flow was 328.2 t/km²/year. The Finn's cycling index was

obtained 2.93%, which was lower compared with the study by Mohamed et al. (2005) for Karnataka, India and Ullah et al. (2012) for coastal ecosystem of BoB. Similar close output was reported by Christensen and Pauly (1993) for Yacatan and Northern Gulf of Mexico. Actually, Finn's cycling index gives the proportion of flow in a system that is recycled compared with total system throughput and immature systems give lower value while matured provide higher. Finn's mean path length is the measurement of the mean quantity of groups that a unit of flux will experience from its entry into the system until it leaves the system. Over-all 680 pathways was obtained from the BoB maritime ecosystem and the mean length of pathways was computed as 6.33, was found a little bit higher when compared with the range (2.86–4.95) reported by Baird and Ulanowicz (1993) for the four estuaries. Nevertheless, the lower number of pathways proves the simplified feature of that ecosystem and it is cycled through detrital pathways.

The connectance (CI) and system omnivory index (SOI) of the BoB maritime ecosystem was 0.322 and 0.285 respectively. In fact, the CI can be predictable and associated with maturity, which can be define by the ratio of 'the quantity of actual links with the number of possible links'. The connectance index is mostly determined by the level of taxonomic aspect used to characterize prey groups. On the other hand, the system omnivory index is proposed as a substitute which is defined as the mean omnivory index of all consumer's weight-mass by the logarithm of each consumer's consumption. The SOI is a measurement of how the diet interactions are scattered between trophic levels. The SOI is stimulated by apparent drawbacks of the CI. In the development stage of an ecosystem, CI would be close to 1 in most systems and increase maturity reduce the value of connectance. Moreover, a prey having the same 'score' in case of connectance index whether it supports 1, 10 or 100% of its higher trophic's diet.

Another important fact is ascendancy, which is a measurement of system growth, and development of network links whereas proportion of a system's capacity not considered. When the system's capacity is considered, it is known as system's overhead, which was the reserved energy of an ecosystem (Ulanowicz and Norden, 1990). The relative values of ascendancy (35.4) and system's overhead (64.6) of the maritime ecosystem of BoB indicated the ecosystem's stability and some sorts of maturity. This proved that maritime ecosystem of BoB have significant backup strength also have the capacity to control any pressure situations through fast reformation to the original stages.

Conclusion

The software outputs indicate that the maritime ecosystem of BoB is steadily reaching maturity, although it is still considered to be in a developing phase. Excessive artisanal fishing pressure is the main hindrance to develop ecosystem quality. One of the major challenges for this multispecies ecological modelling was the scarce of studies on the feeding ecology of the various functional groups. Therefore, further studies should be required in order to get more specific estimations for a multispecies approach to improve basic inputs of the system and also improve the catch landing statistics of the national record.

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Conflict of interest. We declare that there is no conflict of interest.

REFERENCES

- [1] Amin, S. M. N., Rahman, M. A., Haldar, G. C., Mazid, M. A., Milton, D. (2002): Population dynamics and stock assessment of hilsa shad, *Tenualosa ilisha* of Bangladesh. – Asian Fish Sci. 15(2): 123–128.
- [2] Arregum-Sánchez, F., Seijo, J. C., Valero-Pacheco, E. (1993): An Application of Ecopath II to the North Continental Shelf Ecosystem of Yucatan, Mexico. – In: Christensen, V., Pauly, D. (eds.) Trophic Models of Aquatic Ecosystems. ICLARM, Manila.
- [3] Baird, D., Ulanowicz, R. E. (1993): Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. – Mar. Ecol. Prog. Ser. 99: 221–237.
- [4] Barnes, R. S. F., Hughes, R. N. (1988): An Introduction to Marine Ecology, 2nd ed. – Blackwell Scientific Publications, Oxford.
- [5] Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nyström, M. (2003): Reserves, resilience, and dynamic landscapes. – Ambio 32(6): 389–96.
- [6] BOBLME (2011): Bay of Bengal Large Marine Ecosystem-Program: Country report on pollution in the BOBLME – BOBLME- 2011, Ecology, Bangladesh, pp. 0–53.
- [7] Browman, H. I., Cury, P. M., Hilborn, R., Jennings, S., Lotze, H. K., Mace, P. M., Murawski, S., Pauly, D., Sissenwine, M., Stergiou, K. I., Zeller, D. (2004): Perspectives on ecosystem-based approaches to the management of marine resources. – Mar Ecol Prog Ser 274: 269–303.
- [8] Campos, W. L. (2003): An ecosystem model of San Pedro Bay, Leyte, Philippines: initial parameter estimates. – Working Papers, The WorldFish Center, Number 37743.
- [9] Christensen, V. (1995): Ecosystem maturity—towards quantification. – Ecol. Model. 77: 3–32.
- [10] Christensen, V., Pauly, D. (1992): Ecopath II—software for balancing steady-state ecosystem models and calculating network characteristics. – Ecol. Model. 61: 169–185.
- [11] Christensen, V., Pauly, D. (1993): Trophic Models of Aquatic Ecosystems. – ICLARM Conference Proceedings, Manila 26: 390.
- [12] Christensen, V., Pauly, D. (1995): Fish production, catches and the carrying capacity of the world oceans. – Naga, ICLARM Q 18(3): 34–40.
- [13] Christensen, V., Walters, C. (2004): Ecopath with Ecosim: methods, capabilities, and limitations. – Ecol. Model. 172: 109–139.
- [14] Christensen, V., Walters, C. J., Pauly, D. (2000): Ecopath with Ecosim: A User's Guide. – Fisheries Center, University of British Columbia, Vancouver and ICLARM, Malaysia.
- [15] DoEF (2015): Fifth National Report to the Convention on Biological Diversity. – Department of Environment, Ministry of Environment and Forests, Government of the People's Republic Bangladesh, Dhaka.
- [16] DoF (2015a): National Fish Week 2015 - Compendium (in Bengali). – Department of Fisheries, Ministry of Fisheries and Livestock, Bangladesh. <http://www.fisheries.gov.bd/site/page/cc02ff66-b470-4b76-aadd-25c7f18a09a7/Sonkolon>.

- [17] DoF (2015b): The Ecosystem-Based Management Fishery in the Bay of Bengal. – Ministry of Agriculture and Cooperatives, Thailand, 250.
- [18] DoF (2016): National Fish Week 2016 - Compendium (in Bengali). – Department of Fisheries, Ministry of Fisheries and livestock, Bangladesh. <http://www.fisheries.gov.bd/site/page/cc02ff66-b470-4b76-aadd-25c7f18a09a7/Sonkolon>.
- [19] ESCAP (1988): Coastal Environmental Management Plan for Bangladesh. – Final Report 2, Bangkok, Thailand.
- [20] Finn, J. T. (1976): Measures of ecosystem structure and function derived from analysis of flows. – *J. Theor. Biol.* 56: 363–380.
- [21] Fröese, R., Pauly, D. (eds.) (2006): Fishbase 2006. – World Wide Web electronic publication. www.fishbase.org.
- [22] FRSS (2016): Fisheries Resources Survey System: Fisheries statistical report of Bangladesh. – Department of Fisheries (DoF), Ministry of Fisheries and Livestock (MoFL), Bangladesh 31: 1–57.
- [23] Garces, L. R., Alias, M., Abu Talib, A., Mohamad-Norizam, M., Silvestre, G. T. (2003): A Trophic Model of the Coastal Fisheries Ecosystem off the West Coast of Sabah and Sarawak, Malaysia. – In: Silvestre, G., Garces, L., Stobutzki, I., Ahmed, M., Valmonte-Santos, R. A., Luna, C., Lachica-Aliño, L., Munro, Christensen, V., Pauly, D. (eds.) Assessment, Management and Future Directions for Coastal Fisheries in Asian Countries. WorldFish Center Conference Proceedings, pp. 333–352.
- [24] Guénette, S. (2013): An exploratory ecosystem model of the Bay of Bengal Large Marine Ecosystem. – Bay of Bengal Large Marine Ecosystem Project Report, pp. 23–25. www.booblme.org/.
- [25] Gulland, J. A. (1971): The Fish Resources of the Oceans. – Fishing News (Books), Ltd. for FAO, West Byfleet, Surrey.
- [26] Gunderson, L. H. (1999): Resilience, flexibility and adaptive management: antidotes for spurious certitude? – *Conservation Ecology* 3: 7.
- [27] Haque, M. A. (1998): Population dynamics of five commercially important marine fishes in north-eastern part of the Bay of Bengal. – M.Sc. Thesis. Institute of Marine Sciences, University of Chittagong, Chittagong, Bangladesh.
- [28] Haputhantri, S. S. K., Villanueva, M. C. S., Moreau, J. (2008): Trophic interactions in the coastal ecosystem of Sri Lanka: an ECOPATH preliminary approach. – *Est. Coast Shelf Sci.* 76(2): 304–318.
- [29] Hossain, M. M. (2003): National Report of Bangladesh on the Sustainable Management of the Bay of Bengal Large Marine Ecosystem. – BOBLME, FAO GCP/RAS/179/WBG, Chennai, India.
- [30] Hossain, M. S., Roy, K., Datta, D. K. (2014): Spatial and Temporal Variability of Rainfall over the South-West Coast of Bangladesh. – *Climate* 2(2): 28–46. doi:10.3390/cli2020028.
- [31] Huntington, T., Khan, G., Islam, S., Brakel, M. V., Miller, A. (2007): Towards sustainable coastal and marine fisheries in Bangladesh: initiating a precautionary approach. – Report to WorldFish Center, Dhaka, Bangladesh.
- [32] Hussain, M. G., Hoq, M. E. (2010): Sustainable Management of Fisheries Resources of the Bay of Bengal-Compilation of national and regional workshop (Report No. SBOBLMEP Pub. Rep. 2). Support to Sustainable Management of the BOBLME Project. – Bangladesh Fisheries Research Institute, Dhaka.
- [33] ICES (2000): Ecosystem effects of fishing. – *ICES J. Mar. Sci.* 57(3): 1–791.
- [34] Islam, M. S. (2003): Perspectives of the Coastal and Marine Fisheries of the Bay of Bengal, Bangladesh. – *Ocean Coast Manag.* 46: 763–796.
- [35] Islam, M. S., Khan, M., Quayum, G. S. A., Sada, M. N., Chowdhury, Z. A. (1993): The Estuarine Set Bagnet Fishery. – Reports of Interactive Marine Fisheries of Bangladesh. DoF, Bangladesh.

- [36] Kavanagh, P., Newlands, N., Christensen, V., Pauly, D. (2004): Automated parameter optimization for Ecopath ecosystem models. – *Ecol. Model.* 172: 141–149.
- [37] Khan, M. G., Alamgir, M., Sada, M. N. (1997): The coastal fisheries of Bangladesh. – In: Silvestre, G., Pauly, D. (eds.) *Status and Management of Tropical Coastal Fisheries in Asia*. ICLARM Conference Proceedings 53: 26–37.
- [38] Khan, M. G., Islam, M. S., Chowdhury, Z. A., Paul, S. C. (1998): Shrimp resources of Bangladesh—Four crates of exploitation and its comparative effect on the stock. – *Marine Fisheries Research Management & Development Project, DoF*.
- [39] Lamboeuf, M. (1987): Bangladesh demersal fish resources of the continental shelf. – *Marine Fisheries Research Management and Development Project. FAO/BGD. FE: DP/BGD/80/075*.
- [40] Mace, P. M. (2001): A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. – *Fish and Fisheries* 2: 2–32.
- [41] Mathew, C. J., Devraj, M. (1997): The biology and population dynamics of the spade nose shark *Scoliodon laticaudus* in the coastal waters of Maharashtra State, India. – *Indian J. Fish.* 44: 11–27.
- [42] Mazid, M. A. (1998): Hilsa fisheries research in Bangladesh. *Proceedings of BFRI/ACIAR/CSIRO Workshop*. – In: Mazid, M. A., Blaber, S. J. M. (eds.) *BFRI/ACIAR/CSIRO Workshop on Hilsa Fisheries Research in Bangladesh*, Dhaka, Bangladesh, Bangladesh Fisheries Research Institute, Mymensingh, Bangladesh.
- [43] McGlade, J. M., Cury, P., Koranteng, K. A., Hardman-Mountford, N. J. (2002): *The Gulf of Guinea large marine ecosystem: environmental forcing and sustainable development of marine resources*. – Elsevier Science B. V., Amsterdam.
- [44] MoFA (2014): Ministry of Foreign Affairs Press Release: Press statement of the Hon'ble Foreign Minister on the verdict of the Arbitral Tribunal/PCA. Dhaka, 08 July 2014. – <http://www.mofa.gov.bd/PressRelease/PRDetails.php?TxtUserId= & PRid=854/> 2014.
- [45] Mohamed, K. S. (2010): Trophic modelling of marine ecosystems and ecosystem based fisheries management. – *Fish Chime.* 30(9): 35–39.
- [46] Mohamed, K. S., Zacharia, P. U., Muthiah, C., Abdurahiman, K. P., Nayak, T. H. (2005): A Trophic Model of the Arabian Sea Ecosystem off Karnataka and Simulation of Fishery Yields for its Multigear Marine Fisheries. – CMFRI publication. Central Marine Fisheries Research Institute. Kerala, India.
- [47] Mustafa, M. G. (1999): Population dynamics of penaeid shrimps and demersal finfishes from trawl fishery in the Bay of Bengal and implications for the management. – Ph. D. Thesis. Department of Zoology, University of Dhaka, Dhaka, Bangladesh.
- [48] Mustafa, M. G. (2003): Trophic model of the coastal ecosystem in the waters of Bangladesh, Bay of Bengal. – In: Silvestre, G., Garces, L., Stobutzki, I., Ahmed, M., Valmonte-Santos, R. A., Luna, C. et al. (eds.) *Assessment, Management and Future Directions of Coastal Fisheries in Asian Countries*. World Fish Center Conference Proceedings 67: 263–280.
- [49] Mustafa, M. G., Khan, M. G. (1993): The bottom trawl fishery. *Studies of interactive marine fisheries of Bangladesh*. – BOBP/WP/89. Bay of Bengal Programme, Madras, India.
- [50] Mustafa, M. G., Mansura, B. (1994): Some aspects of the biology of the Ribbon fish *Lepturacanthus savala* Cuvier in the Bay of Bengal. – *Proceedings of Ninth National Zoology Conference, Dhaka, Bangladesh*.
- [51] Mustafa, M. G., Zafar, M., Matin, A. K. M. A., Amin, S. M. N. (1998): Population dynamics of *Harpodon nehereus* (Ham-Buch.) from the Kutubdia channel of Bangladesh. – *Bangladesh J. Fish Res.* 2(1): 83–90.
- [52] Nabi, M. R. (2007): *Management of Estuarine Set Bag Net Fisheries of Bangladesh: Application of Traditional Scientific Method, Local Indigenous Knowledge and Sustainable Livelihood Approach*. – PhD Thesis. Borneo Marine Research Institute, University Malaysia Sabah, Malaysia.

- [53] Odum, E. P. (1969): The strategy of ecosystem development. – *Science* 104: 262–270.
- [54] Odum, E. P. (1971): *Fundamentals of Ecology*, 3rd ed. – W. B. Saunders, Philadelphia.
- [55] Palomares, M. L. D., Pauly, D. (1999): Predicting the food consumption of fish populations as functions of mortality, food type, morphometrics, temperature, and salinity. – *Mar. Freshwater Res.* 49: 447–453.
- [56] Pauly, D., Christensen, V., Walters, C. J. (2000): Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impacts of fisheries. – *ICES J. Mar. Sci.* 57: 697–706.
- [57] Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J., Sainsbury, K. J. (2004): Ecosystem-based fishery management. – *Science* 305: 346–347.
- [58] Polovina, J. J. (1984): Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. – *Coral Reefs* 3: 1–11.
- [59] Ryther, J. H. (1969): Photosynthesis and fish production in the sea. – *Science* 166: 72–76.
- [60] Sayedur, R. C. (2015): Map of the Coastal Zone of Bangladesh. – University of Chittagong, Chittagong, Bangladesh. <http://mapsmaps.blogspot.in/2015/01/map-of-coastal-zone-of-bangladesh.html>.
- [61] Shamsuddoha, M., Islam, M. M. (2016): Bangladesh National Conservation Strategy: Coastal and Marine Resources. – Department Forest and International Union for Conservation of Nature. http://fd.portal.gov.bd/sites/default/files/files/fd.portal.gov.bd/notices/c3379d22ee624dec9e2975171074d885/24%20Coastal%20and%20Marine%20Resources_NCS.pdf.
- [62] Silvestre, G. T., Selvanathan, S., Salleh, A. H. M. (1993): Preliminary trophic model of the coastal fisheries resources of Brunei Darussalem, South China Sea. – In: Christensen, V., Pauly, D. (eds.) *Trophic Models of Aquatic Ecosystems*. ICLARM Conference Proceedings, Manila, Philippines, pp. 300–306.
- [63] Trites, A. W., Livingston, P. A., Vasconcellos, M. C., Mackinson, S., Springer, A. M., Pauly, D. (1999): Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses. – *Fish. Centre Res. Rep.* 7(1): 106.
- [64] Ulanowicz, R. E. (1986): *Growth and Development: Ecosystem Phenomenology*. – Springer, New York.
- [65] Ulanowicz, R. E. (1995): The Part-Whole Relation in Ecosystems. – In: Patten, B. C., Jørgensen, S. E. (eds.) *Complex Ecology*, pp. 549–560. Prentice-Hall, Englewood Cliffs, New Jersey.
- [66] Ulanowicz, R. E., Norden, J. S. (1990): Symmetrical overhead in flow and networks. – *Int. J. Syst. Sci.* 21(2): 429–437.
- [67] Ullah, M. H., Nabi, M. R. U., Mamun, M. A. A. (2012): Trophic model of the coastal ecosystem of the Bay of Bengal using mass balance Ecopath model. – *Ecol. Model.* 225: 82–94.
- [68] Walters, C., Christensen, V., Pauly, D. (1997): Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. – *Rev. Fish. Biol. Fish.* 7: 139–172.
- [69] Walters, C., Pauly, D., Christensen, V. (1999): Ecospace: predicting of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. – *Ecosystems* 2: 539–554.
- [70] Yodzis, P., Winemiller, K. O. (1999): In search of operational tropho-species in a tropical aquatic food web. – *Oikos* 87: 327–340.

APPENDIX

Appendix 1. Estimates of diet consumption for ecological or functional groups in the maritime ecosystem of Bay of Bengal, Bangladesh

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Sharks	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Rays	0	0.14	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0
3 Diadromous (Pelagic)	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Minor Pelagics	0.005	0.05	0	0	0.031	0.071	0	0	0.04	0	0	0	0.076	0	0	0	0
5 Medium Pelagics	0.06	0	0	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0
6 Medium Mesopelagics	0.042	0	0	0	0.054	0	0	0	0	0	0	0	0.08	0.08	0	0	0
7 Minor Mesopelagics	0.08	0	0	0	0.085	0	0	0	0	0	0	0	0.055	0.01	0	0	0
8 Medium Demersal	0.067	0	0	0	0	0	0	0.1	0	0	0	0	0	0.05	0	0	0
9 Minor Demersal	0.182	0.04	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0
10 Penaeid Shrimp	0	0	0	0	0	0	0	0	0.065	0	0	0.009	0	0.08	0	0	0
11 Other Shrimp	0	0.05	0	0	0	0	0	0	0	0	0.13	0.052	0	0	0	0	0
12 Other crustaceans	0	0	0	0	0	0	0	0	0	0.034	0	0.01	0.08	0	0	0	0
13 Cephalopods	0.134	0	0	0	0	0	0	0	0	0	0.06	0	0	0	0	0	0
14 Gastropoda	0.05	0.08	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0
15 Benthos	0.06	0.1	0	0	0	0	0	0.155	0.081	0.046	0.048	0.02	0.01	0	0	0	0
16 Aquatic Invertebrates	0	0.1	0	0.125	0	0	0	0.119	0.152	0.049	0.018	0	0.118	0.03	0.175	0	0
17 Zooplankton	0	0.1	0	0.1	0.1	0.2	0.321	0.216	0.072	0.2	0.171	0.177	0.05	0.25	0.181	0.31	0.1
18 Phytoplankton	0.1	0.18	0.3	0.327	0.45	0.239	0.315	0.285	0.338	0.358	0.109	0.014	0.217	0.2	0.388	0.55	0.9
19 Detritus	0.05	0.16	0.7	0.448	0.28	0.49	0.364	0.125	0.252	0.313	0.464	0.718	0.284	0.18	0.256	0.14	0
20 Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22 (1 - Sum)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0