Trophic dynamics and fishery potentials of the Indian Ocean - critical assessment

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Abstract - A critical review of the status of the Indian Ocean marine fisheries reveals that the presently exploited annual catch is less than one third of the projected potentials as estimated from the biological productivity and exploratory fishery survey data. Such a wide gap between the estimated potential and the harvested yield necessitates reassessment of the potential fishery resources.

An attempt is made here, to examine the available potential fishery resource estimates against the background of the basic estimates from primary production; zooplankton-biomass and production; benthic and microbial production and the commonly used conversion efficiency at different trophic levels in relation to complexities of tropical marine food chain.

INTRODUCTION

Man's concept of the ocean is so elusive that there is a tendancy to consider marine living resources as being unlimited and inexhaustible. However, such type of pre-supposition is found to be far from realistic. There are already signs of depletion of fishery resources in some parts of the world. In this context, it is timely and appropriate to have a critical review of the status of the Indian Ocean fisheries.

Over the last two decades many workers (RYTHER, 1969; PRASAD et.al., 1970; MOISEEV, 1971; GULLAND, 1971; QASIM, 1977, FAO, 1979; PARULEKAR, 1985) have worked out the upper limits of the Indian Ocean fisheries from studies of food chains and exploratory fishery surveys. As might be expected, the range of the estimate is over 40 times the lowest. This range is, however, not representative. The recent estimates showed a strong convergence towards a range of 10.2 to 17 million tonnes per annum. The estimates of the upper limit are 3 to 5 times of the present exploited catch. In view of a wide gap between the potential and the yield, what seems necessary at the moment is to establish the degree to which the successive estimates have been based against the background of the basic estimates of various components of marine food chains.

An attempt is made here to examine the theoretical basis of potential fishery resources with specific relevance to the complexities of tropical food chain. Accordingly, a compartmental model, of energy flux, examining the potential for significant energy flow through detritus, micro-organisms and dissolved material to terminal consumers is presented. The reliability of the proposed model alongwith the inbuilt limitations are elaborated.

MATERIAL AND METHODS

The Indian Ocean, for the present study is considered to extend from 35°E as western boundary to the southern borders of the Mozambique; Eastern Boundary 115°E i.e. from Durban on the Africa coast to Green Horn on West Australian coast; the Northern boundary upto 25°N and the Southern boundary upto 35°S. The total area covered is 43.1 million km² which is 57 percent of the coventional Indian Ocean (SVERDRUP et.al., 1946).

The relevant basic data on primary production, zooplankton biomass and benthic biomass available at Data Centre of the National Institute of Oceanography (NIO) were taken and processed. The source of these data are the various cruises undertaken during the International Indian Ocean Expedition (IIOE) and other cruises of INS Darshak, RV Gaveshani and ORV Sagar Kanya during 1973 to 1986. For estimation of various biological components the entire study area was divided into two regions; the shelf (0-200 m depth) and the offshore (200m depth). The shelf occupies 3.3 million km² and the offshore 39.8 million km².

In view of complexity, of marine food web, the fishery production system in the present paper has been described by using systems approach. A comprehensive list of variables and pathways that seem to be of potential importance in determining the function of the system, were identified. The necessary computer programs were developed on ND-570. The limitations, however, in presenting this type of model are quite evident, because the deduction had to be based on many assumptions due to lack of experimental data on many variables used for the system. Nevertheless, the results of such study depict the processes involved in the productin of marine fisheries and brings the discrepancies in the reliability of available potential and exploitable resource estimates.

RESULTS AND DISCUSSION

Primary Production

Most of the data collected on primary production by various investigators have been published in one or the other form. By utilizing the available data at INODC, annual primary production of the Indian Ocean has been computed to be 0.8 X 10° tonnes and 2.8 X 10° tonnes for shelf and offshore regions respectively. KABONOVA (1968) based on the data prior to 1965 estimated the annual primary production to be 3.9 X 10° tonnes C. PRASAD *et al.*, (1970) after taking into consideration the various factors which might give rise to an error in the estimate of primary production, estimated the annual net production of the Indian Ocean as 3.9 X 10° tonnes of carbon. Based on 7000 observations KOBLENTZ-MISHKE *et.al.*, (1970) estimated the primary production to be between 3 to 5 X 10° tonnes C per annum. KREY (1973) estimated the primary production as 6 X 10° tonnes C per annum. PLATT and SUBBA RAO (1975) while reviewing various global estimates, projected the production of the Indian Ocean to be 6.6 X 10° tonnes C per annum. QASIM (1977) estimated the annual primary production as 4.42 X 10° tonnes C.

Using different techniques, earlier authors have concluded that phytoplankton have specific growth rates and therefore primary productions are much higher than estimates based on the C¹⁴ techniques, (SHELDON, 1978; GOLDMAN *et.al.*, 1979; SCHULENBERGER and REID 1981; JENKINS, 1982). In other words the existing estimates of primary production which are based on C¹⁴ technique are low by an order of magnitude.

Zooplankton Biomass

Based on 1622 samples collected during IIOE, PRASAD, et.al., (1970) estimated the total biomass for the Indian Ocean to be 0.5 X 10⁹ tonnes. After, IIOE, the data obtained in coastal as well as in offshore waters (NAIR, et.al., 1978; GOSWAMI, 1979; ACHUTANKUTTY, et.al., 1980; NAIR, et.al., 1980; MADHUPRATAP, et.al., 1981) indicate that the biomass is much higher in coastal waters than oceanic waters, suggesting that the estimates based on IIOE data are more likely to be an underestimate. By considering the data of IIOE and of post IIOE, the zooplankton biomass production

is estimated as 0.1 X 109 and 0.48 X 109 tonnes for shelf and offshore regions, respectively. A factor of 0.065 has frequently been used to convert zooplankton biomass into organic carbon and is primarily based on studies undertaken in temperate waters (CUSHING, 1971). It is shown that organic carbon content of tropical zooplankton is lower than in higher latitudes (LOVEGROVE, 1962; BEERS, 1966). Biochemical studies carried out in tropical waters (OSTAPENYA et.al., 1967; GUPTA, 1977; QASIM et.al., 1978; NAIR, 1980; MADHUPRATAP, et.al., 1981;) indicates that the ratio between dry weight and organic carbon varies between 31 and 41% and that between displacement volume and dry weight fluctuate 75.4 and 81.7 mg. Considering the mean values, the conversion factor for displacement volume to organic carbon works out to be 0.027, which is less than half as compared to the CUSHING (op.cit) factor of 0.065.

Using the factor 0.027, the zooplankton biomass production in terms of organic carbon, is estimated as 0.0035×10^9 and 0.0129×10^9 tonnes for shelf and offshore regions, respectively.

Benthic Production

There are almost no studies in which all the components of the benthos have been determined. SANDERS (1960), FENCHEL (1969) and Mc INTYRE (1969) have discussed the problems resulting from the lack of standard methods.

Based on IIOE data , NEYMANN *et.al.*, (1973) estimated the benthic biomass for different regions of the Indian Ocean. Probably because of the patchy data, they estimated the biomass seperately for various regions as given in Table 1. Most comprehensive work on the benthic production of the Indian Ocean is of PARULEKAR (1985). He divided the area into three regions viz. shelf, (0-200 m depth), slope (200-1000 m depth) and deep (>1000 m depth). The mean benthic biomass estimated for these three regions is given in Table 1.

Table 1. Marine benthic faunal biomass (g/m²)

NEYMANN et.al., (1973)		PARULEKAR (1985)	
AREA	BIOMASS	DEPTH RANGE (m)	BIOMASS
Arabian Sea	35	0-200	20.4
Bay of Bengal	10	200-1000	3.2
New Austrian Shelf	2.6-8		
Great Australian sight	16	>1000	1.6
5°-30°s	0.05		
South of 30°S	0.2-0.4		

The large difference in mean biomass values are (i) One is based on very scanty data and other on comparatively large data and (ii) the methods used for collection are different.

Due to lack of sufficient data on various components the mean biomass values estimated by PARULEKAR (1985) were taken to estimate the total biomass of the Indian Ocean. The biomass for shelf and offshore regions is estimated as 0.64×10^9 and 0.95×10^9 tonnes respectively. In terms of organic carbon the biomass production is estimated as 0.005×10^9 and 0.007×10^9 tonnes for shelf and offshore regions respectively (PARULEKAR *et.al.*, 1980).

Microbial Production

The rate of microbial production in most of the biotope is unknown. The data available and the methods by which they have been obtained are still disputable

(STEEMANN-NIELSEN, 1972). The only estimate available based on patchy data is that of SOROKIN (1978). He estimated the world ocean microbial production as 2.4 X 10⁹ tonnes C per annum and of which 60 percent takes place in the warm waters of the tropical zone between 30^oN and 20^oS at temperature from 22^o to 28^oC. Due to lack of sufficient literature it is unwisely to extrapolate the estimates given by SOROKIN (op.cit) for the Indian Ocean regions. Further work is required.

Fishery Potentials

PRASAD et.al., (1970) estimated the potential yield of fish of the Indian Ocean based on the data on primary production and zooplankton biomass. The area of 51 million sq.km. considered by them lies between 20°-120°E longitude and from the Asian landmass to 45°S latitude. By assuming three variants, (10%, 15%, 20%) conversion ecological efficiency from primary to tertiary level between the production of different organisms, they estimated the fish production for the western and eastern Indian Ocean, seperately. From the estimated zooplankton biomass of 5.19 X 10⁸ tonnes, the potential yield of fish was estimated to be 29 million tonnes and 45 million tonnes by assuming 10% and 15% conversion coefficient, respectively. Based on the yield ratio of carbon production of 0.005% as well as the estimated potential yield derived from the results of the fishery exploratory surveys, PRASAD et.al., (op.cit)estimated the potential yield of fish to be 11 million tonnes.

GULLAND (1971), estimated the exploitable fish stock of pelagic, demersal and crustaceans, separately for eastern and western Indian Ocean. GULLAND's estimates for the areawise potential annual catches of fish are as follows:

Group	Western Ocean	n Indian	Eastern Indian Ocean	Total
	(X10 ⁶ Tonnes)		(X10 ⁶ Tonnes)	(X10 ⁶ Ton.)
Demersal Fish	4.50		3.00	7.50
Shoaling Pelagic Fish	4.00		2.00	6.00
Crustanceans	0.15		0.10	0.25
Tunas and Skipjack	_	0.30	-	0.30
Total	8.65	0.30	5.10	14.05

The estimates of exploited stocks are based on the data on catch/effort, length and age composition while the unexploited stock have been estimated from exploratory fishing, eggs and larval studies and echo-sounding survey data.

By considering the available data on four main factors viz. (i) light (ii) nutrients (iii) primary production and (iv) secondary production, QASIM (1977) has given an intergrated picture of the biological productivity in terms of exploitable resources. The area of the Indian Ocean considered by QASIM (op.cit) lies between 25° and 120°E longitude and 25°N to 40°S latitude totalling to about 46.8 million sq.km.

The column primary production of the Indian Ocean as estimated from 934 observations (available from the C¹⁴ technique) to be 4.42X10⁹ tonnes of carbon/annum. The estimated primary production has then been converted to tertiary production by taking 0.1% as the transfer coefficient. The value of 0.1% has been considered to be a more realistic figure, rather than coefficient of 1%, as suggested by CUSHING (1971, 1973) for the Indian Ocean, based on three reasons: (1) A large percentage of organic matter is lost during its transfer from primary to secondary level of the food chain and so 1% is on higher side; (2) There could be many unpredictable pathways in which the food energy is lost, as pointed out by RYTHER (1969) and (3) The estimated production is too high as compared to estimates derived from secondary production.

The tertiary production thus calcutated has been coverted to live weight by multiplying by a factor of 10 and thereafter the potential production of fish has been estimated to be 15 million tonnes by considering the yield ratio of 0.035% of carbon.

The estimates of zooplankton biomass given by PRASAD, et.al., (1970) for an area of 51 million sq.km. of the Indian Ocean are used as such by QASIM (op.cit) for estimating the secondary production. The biomass values were converted to secondary production by multiplying with a factor of 0.065 and by the generation time of zooplankton calculated from the relationship D=71.72 t^{-1.22} (D is generation time and t is temperature) as suggested by CUSHING (1971). The computed values for secondary prodution (69.3 million tonnes of carbon per annum) have then been converted to tertiary prodution by taking 10% value of transfer coefficient as suggested by CUSHING (1971). Further by assuming that 25% of the total catch can be safely exploited without depleting the stock, QASIM estimated the potential fish yield to be 17 million tonnes (op.cit).

An estimate of 10.2 million tonnes, of which 4.5 million tonnes are demersal and 5 million tonnes are pelagic has been reported by FAO, (1979). Recently, PARULEKAR (1985) has given the estimate of potential demersal fishery resources of the Indian Ocean, from benthic production data, to be 5.9 million tonnes with a split-up of: shelf - 3.4 million tonnes; slope - 0.4 million tonnes and deep or abyssal plains - 2.1 million tonnes. However, the basis of estimation are not clearly defined.

The deduction that emerge from the available potential estimates bring to light discrepancies in the reliability of potentials and exploitable resource estimates. The analyses also suggest that the applications have not differed from one another very much in basic data. On the contrary, the marine fishery production system is always described in very general terms as an ecosystem with a linear transfer of energy from phytoplankton to zooplankton to fish. Secondly, the estimates differ primarily in the productivity weightage given to various trophic levels and the yield ratio of carbon to fish. The calculations are not supported by proven conversion coefficients for animal products from one trophic level to another, so that in the final stage, the authors make arbitrary corrections to obtain reality in their opinion. GULLAND's (1971) estimates which are based on catch effort and exploratory fish survey data, forms another category of assessment of potential resource. However, such estimates lack ecological considerations.

In view of all these facts and some recent findings: i.e. role and magnitude of picoplankton (LI, et.al., 1983) and benthos (PARULEKAR, 1985) to the end product (fish); concept of trophic levels, (DALAL, 1985), and validity of zooplankton estimates (DALAL and PARULEKAR, 1986); the available fishery production estimates except possibly that of GULLAND (1971) are not more than guessess based on certain assumptions and therefore open to criticism and needs to be reassessed.

Fishery production system

Marine fishery production system is a limited system and can be defined by its inputs, its outputs and the internal transformations which convert input to output. The main input to the system is primary production. The output from the system are seafood harvest and waste matter. Detritus is recycled; it is both input and an output. This is an extreme simplification of the system.

The most popular form of fishery production system is the use of some form of energy budget in which standing stocks, production and ecological (transfer) coefficients are determined and model built around the various interactions.

Historical reviews of mechinistic models have been prepared by RILEY (1963), PATTEN (1968), MARGALEF (1973), STEELE (1974), WIEGERT (1975) and KREMER and NIXON (1978). The proceedings of several recent conferences have also emphasised the use of models in understanding estuarine (CRONIN, 1975) and marine (NIHAUL, 1975) ecosystems, as well as the role of models in ecosystem analysis and prediction (LEVIN, 1975). A recent volume of 'Sea' is also devoted to discussions of the numerical modelling of physical, chemical, geological and biological processes in estuarine and open ocean waters (GOLDBERG, et.al., 1977).

Earlier production models assumed a simple linear food chain of the LINDEMAN (1942) type, consisting of diatoms, copepods, benthos and fishes, (CLARKE, 1946; RILEY, et.Ual., 1949) and the acceptance of this type of model still persists. However, exceptional models by PETIPA, et.al., (1970) for the Black Sea and STEELE (1974) for the North Sea do exist. The compartments of such models generally are equated with trophic levels and ecological transfer efficiencies.

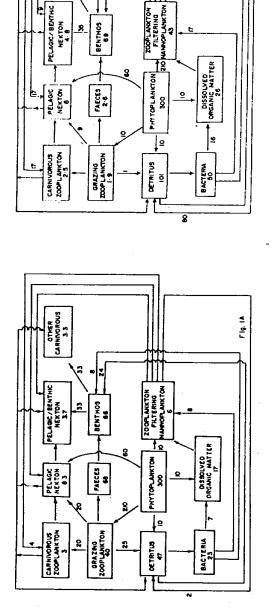
The existing models are not flawless as there is no excess energy at terminal consumer levels. It has been intuitively troublesome to see how a more complex food web model with compartments rather than trophic levels with additional energy transfer could satisfy the fundamental criterion of supporting the consumers. In the real terms there are other energy pathways involving such entities as micro-organisms, detritus and dissolved organic material (DOM) (POMEROY, 1974). The major evidence offered is the null hypothesis that longer food chains cannot work because not enough energy reaches the end. The other evidence is that alternative pathways not only exist but may sometimes dominate marine food webs (POMEROY, 1974).

Given the difficulties of unravelling the intricacies of trophic relationship, it is perhaps not surprising to find that attempts have been made to find some valid simplifying assumptions that could make the problems more testable. SHELDON, et.al., (1977) based on a relatively simple concept demonstrated that how the knowledge of the production of a trophic level can be predicted from the knowledge of biomass or production at some other trophic level. They took as their first example, the fish yield of the Gulf of Maine and showed that their results are agreeable with that of actuals. However, when predictions from theory agree reasonably well with observations, it does not necessarily mean that the two are perfectly in agreement. The question of accuracy has to be considered and this is not a particularly easy question to answer.

A compartmental model of an ecosystem presented here is based on the assumption that there are alternative energy pathways and that energy fluxes may vary substantially.

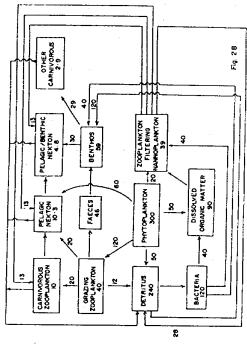
The model presented here is not of the linear LINDEMAN type, rather it follows the structural concept of WIEGERT and OWEN (1971). In the present model, classically defined trophic levels are obscured by omnivory and microbial processes and the most realistic values assigned to energy transfers between compartments are those of gross growth efficiencies. The data on gross growth efficiencies for various compartments is taken from the published literature (RAO, 1953; McLAREN, 1963; CORNER and COWEY, 1968; PETIPA, et.al., 1970; LASKER, 1970; HEMPEL, 1970; SOROKIN, 1971 & 1973 and GREEZE, 1978).

In following the route of energy supplied by primary producers through the food web, the number of horizontal links in the web is an important factor in determining the degradation of energy (STEELE, 1974). The relative transfer and loss of energy at these links that ultimately enables the most important pathways to be identified; assuming that the proportion of the losses which are available for recycling in one

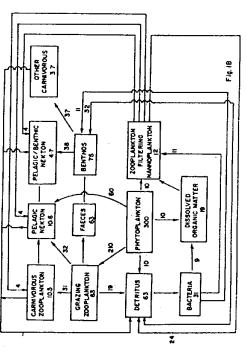


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Model of energy flow through the food web under the circumstances in which (Fig. 1 A&B) the grazing zooplankton consuming microphytoplankton receive all but a minor portion of the total phytoplanktonic production (set at 300 g C m⁻² per annum), and (Fig. 2 A&B) the filtering zooplankton are relatively important, feeding either on nanoplankton or on bacteria. The values inside the compartments are the average biomass in g C m⁻², those alongside the arrows are the flow rates in g C m⁻² per annum. (A) with relatively low efficiencies of energy transfer through intermediate food links; (B) with higher efficiencies of flow through those links (see text).

form or another, is known. The loss can be measured by the ecological efficiency, which is assumed to be 10% (SLOBODKIN, 1960 & 1961). However, such an anastomosing model will not carry enough energy to the terminal consumers.

The compartments in the model are neither guilds nor trophic levels, but trophic groups. STEELE's (1974) model is a subset of the present model. However, not all energy now passes down that chain. Instead, variable amounts of energy may pass through DOM or faecal detritus to microbial populations. Some fraction of both phytoplankton and microbes is utilised by mucous-net feeders. The question is one of the relatively significant pathways. The answer to this question has been searched by varying the flux of energy with different assumptions about its fate. The zooplankton population have been divided into grazers and mucousnet feeders in the model because of the importance of nannoplankton and bacteria in the estuaries and coastal waters (PAFFENHOFER, 1975). All the essential information on gross growth efficiencies and alternative pathways have been condensed in Fig. 1 and 2. Initially the model was tested with efficiencies similar to those used in the model of North Sea (STEELE, 1974) to ascertain the addition of detrial and DOM pathways. Nominal values were assigned to DOM production and consumption of nano-plankton by mucous-net feeders. Then each of these in turn was assigned a major portion of primary production. DOM production might be as high as 30% if conditions were adverse for the phytoplankton production (THOMAS, 1971). Higher efficiencies were then assumed for grazers and carnivorous zooplankters, as deduced from the published literature. Again the flux of energy from primary producers was divided in various ways.

The model was fueled by an input of 300gC/m²/annum of phytoplankton production. This input was influenced by two parallel series of variables: (1) The proportion consumed when alive or deriving from differently sized phytoplankton species; and (2) different level of energy transfer from consumed to consumer. The first set of variables comprised two alternatives namely: (1) transfer of energy from microphytopalnkton to grazing herbivores dominate the energy flow; and (2) mucousnet filterers are the dominant consumers taking abundant nannoplanktonic species or bacteria. The efficiency of energy transfer to bacteria was set at 50% throughout the analysis, (PAYNE, 1970) and that to nektonic and benthic carnivores remained constant at 10%. But two alternative sets of efficiencies were applied to the other links in the food web, a generally low series of mucous-net filters (17%), grazing zooplankton (19%), carnivorous zooplankton (13%) and benthic detritivores (33%); and a higher set of 30% for all these four groups. These values of efficiency were gathered from published literature.

Combining these two sets of variables whilst a fixed input of 300 gC/m2 as annual yield, four different energy flow patterns, each with individual values of steady-state biomass in the various interacting compartments, dependent on energy receipt and loss (Fig. 1A, 1B, 2A, 2B) could be established. Each of the four is realistic in the sense that the division of basic energy supply between the four compartments radiating from the phytoplankton (grazers, filters, dissolved organics, and detritus) is in accordance with known field measurements in shelf waters. Comparison of derivations shows that when most production is in the form of the larger members of the phytoplankton, not only is the grazing zooplankton abundant but so also are the benthic consumers which feed on the rain of faecal pellets. Dividing primary production in two ways among energy pathways results in comparable figure of exploratory catch percentage of pelagic and demersal production.

The model shows that it is possible for sufficient energy to flow through either the grazers or the alternate pathways to support all major trophic groups at a reasonable

level, even assuming rather low gross growth efficiencies. However, if all gross growth efficiencies between compartments in the model were assumed to be 10%, energy flux would be insufficient. The efficiencies assumed by STEELE (1974) for North Sea seems to be reasonable.

The model shows that, large changes in energy flux from one pathway to another result in changes in the amount of energy available to various terminal consumers.

The model cannot tell us whether all the above assumptions occur in the real terms or not. These are to be decided by mailing observations only. The model helps in defining conditions and reveals some gaps in our knowledge of energy flux in marine ecosystem.

Due to lack of experimental data on many variables which have been used for model, it was not possible to test the statistical significance of the alternate energy pathways. While this modelling exercise in no way proves that alternative energy pathways are important, it shows that there is no underlying reason why they should not be. By altering the patterns in which energy flows, for example by decreasing greatly the importance of some links, the effects on the remainder of the system can be gauged by relatively simple laboratory simulation, an operation impossible to perform in the field. It is important to remember, however, that any such model is only as good as the assumptions on which it is based and its efficacy and reality will depend on the data fed into it.

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