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THE NATURE, INVESTIGATION AND MANAGEMENT OF
TROPICAL MULTISPECIES FISHERIES

by

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ABSTRACT

Definitions are given of the major properties of multi-species stocks and fisheries.

Simple models for the simulation of two-species systems are discussed, including the "pedagogic" model of Pope. The applicability of complex, computer-based simulation models to tropical stocks is briefly assessed.

A method for the construction of quantitative "box models" is presented which requires limited data inputs, involving mainly crude information on the feeding habits of various fish groups and data generated by the fishery.

Some aims of fishery management are briefly discussed, and an "asymptotic" yield model is introduced which, having no real "MSY", might be better suited to managing tropical multispecies stocks than the commonly used "Schaefer" and "Fox" models.

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Introduction

With a few exceptions, the models commonly used in fish population dynamics and stock assessment are based on single species stocks, the assumption being that such things as growth, mortality and recruitment of a given single-species fish stock are little affected by what happens to the stocks of other species also occurring in the habitat of the species under investigation.

This approach may be justified in temperate waters, where some stocks (e.g., cods, pollock, herrings, salmons) sustain "aimed" fisheries, in which other species form only a minor part of the catch (i.e., the "bycatch").

In tropical, especially demersal fisheries, this approach is untenable because generally no one species is singled out. There is no "bycatch" according to the definition above except in shrimp fisheries when the fish caught (often 90% of the total weight of the catch) are usually thrown overboard.

The typical catch of a Southeast Asian trawler is depicted in Table 1. Note the large number of species, most of which occur in small numbers.

The goal of fishery biologists studying a fishery is generally to obtain information for use in conjunction with management measures (e.g., catch allocation, effort control). The objectives of these measures are either:

- to provide as high a sustained catch as possible
- to provide a reasonable income to as many people as possible
- to generate the greatest profits for those who have invested
in the fishery

These objectives are not necessarily compatible with each other and more often than not, they are mutually exclusive (see Clark 1976).

Table 1. A typical trawler catch (45 min haul) from the Java Sea (06°12'S 108°26'E, 34-35 m depth) made on 5 September 1976 by *R/V Mutiara IV* showing the diversity of tropical demersal multispecies stocks. (Asterisks refer to weight and number raised from a sorted sample of 1 out of 5 boxes. Invertebrates not included.)

No.	Family	Species	W (kg)	N	No.	Family	Species	W (kg)	N
1	Ariidae	<i>Osteogeniosus militaris</i>	3.4	17	29	Lutjanidae	<i>Lutjanus sanguineus</i>	4.0	1
2	Balistidae	<i>Abalistes stellaris</i>	0.5	1	30	Lutjanidae	<i>Lutjanus johni</i>	5.0	10*
3	Carangidae	<i>Seriolina nigrofasciata</i>	0.32	1	31	Lutjanidae	<i>Lutjanus lineolatus</i>	0.20	10*
4	Carangidae	<i>Scomberoides</i> sp.	0.15	5	32	Lutjanidae	<i>Caesio erythrogaster</i>	0.10	5*
5	Carangidae	<i>Alepes kalla</i>	5.0	90*	33	Mullidae	<i>Upeneus sulphureus</i>	75.0	6075*
6	Carangidae	<i>Alepes djedaba</i>	7.50	290*	34	Nemipteridae	<i>Nemipterus japonicus</i>	3.0	15*
7	Carangidae	<i>Megalaspis cordyla</i>	8.5	170*	35	Nemipteridae	<i>Nemipterus bathybius</i>	0.40	15*
8	Carangidae	<i>Selaroides leptolepis</i>	0.25	10*	36	Pentapodidae	<i>Pentapodus setosus</i> (?)	0.25	5*
9	Carangidae	<i>Carangoides</i> spp.	6.10	145*	37	Platycephalidae	not identified	0.25	5*
10	Carangidae	<i>Atropus atropus</i>	1.75	30*	38	Plectorhynchidae	<i>Plectorhynchus pictus</i>	0.40	15*
11	Chirocentridae	<i>Chirocentrus dorab</i>	0.80	5*	39	Pomadasyidae	<i>Pomadasys maculatus</i>	0.25	5*
12	Clupeidae	<i>Anadontostoma chacunda</i>	0.15	5*	40	Pomadasyidae	<i>Pomadasys</i> sp.	0.50	35*
13	Clupeidae	<i>Opisthopecterus valenciennensis</i>	1.10	15*	41	Priacanthidae	<i>Priacanthus macracanthus</i>	3.10	80*
14	Clupeidae	<i>Dussumieria acuta</i>	1.70	50*	42	Scombridae	<i>Scomberomorus guttatus</i>	7.20	65*
15	Clupeidae	<i>Ilisha</i> sp.	5.60	65*	43	Scombridae	<i>Scomberomorus commerson</i>	2.6	14*
16	Clupeidae	<i>Sardinella gibbosa</i>	0.30	10*	44	Scombridae	<i>Rastrelliger brachysoma</i>	3.0	50*
17	Dasyatidae	not identified	2.65	1	45	Stromateidae	<i>Pampus chinensis</i>	0.75	1
18	Drepanidae	<i>Drepane longimana</i>	0.35	5*	46	Stromateidae	<i>Pampus argenteus</i>	6.3	30*
19	Engraulidae	<i>Stolephorus</i> spp.	21.0	4175*	47	Synodontidae	<i>Saurida tumbil</i>	0.35	1
20	Gerridae	<i>Pentaprion longimanus</i>	15.25	1165*	48	Synodontidae	<i>Saurida elongata</i>	3.75	45*
21	Fistulariidae	not identified	0.15	10*	49	Synodontidae	<i>Saurida longimana</i>	0.90	105*
22	Formionidae	<i>Formio niger</i>	0.2	1	50	Sphyrinae	<i>Sphyræna obtusata</i>	0.60	10*
23	Lagocephalidae	not identified	4.0	95	51	Scienidae	not identified	0.25	5*
24	Leiognathidae	<i>Leiognathus splendens</i>	10.0	720*	52	Theraponidae	<i>Therapon</i> sp.	3.75	100
25	Leiognathidae	<i>Leiognathus leuciscus</i>	4.20	780*	53	Triacanthidae	not identified	1.0	25*
26	Leiognathidae	<i>Leiognathus bindus</i>	1.20	340*	54	Trichiuridae	<i>Trichiurus lepturus</i>	1.0	55*
27	Leiognathidae	<i>Secutor ruconius</i>	1.20	380*	55	Trichiuridae	<i>Lepturacanthus savala</i>	2.0	25*
28	Leiognathidae	<i>Secutor insidiator</i>	2.80	560*					
					Σ	29 families	43 genera 55 spp	231.02	15939

When the policy is to maximize yields, three forms of overfishing must be prevented:

- growth overfishing, i.e., taking fish that are too small).
(Yield-per-recruit analysis is a standard method to detect and quantify growth overfishing.)
- recruitment overfishing, i.e., taking so many adult fish that recruitment of young fish to the fishery is affected.
(Preventing this involves the study of "stock-recruitment relationships"; which is, at present, one of the most complicated areas of fisheries biology research.)
- ecosystem overfishing, i.e., inducing changes in stock composition through excessive fishing such that once abundant species decline without the subsequent compensatory increase of another (group of) species.

When unselective gear is used in heavily exploiting a community of widely different fishes, some large and long-lived, the others small and short-lived, it is not possible to prevent growth and recruitment overfishing of the more sensitive stocks. With increasing effort, some species will then decline rapidly resulting in complete alteration of the original food chain and catch composition and usually in ecosystem overfishing as well. These and related problems are reviewed in FAO 1978), Pope (1979), Pauly (1979) and in several papers included in Pauly and Murphy (in press).

Modelling multispecies systems

Two-species systems

Attempts by biologists to quantitatively model interacting species started, logically enough, by studying the two-species case (e.g., two

competing species, or a prey-predator system). The pioneers in this field were Lotka (1925) and Volterra (1926), who suggested independently what are now known as the Lotka-Volterra equations.

$$\frac{dN_1}{dt} = [r_{m1} - m_1 (C_1 N_1 + C_2 N_2)] N_1$$

$$\frac{dN_2}{dt} = [r_{m2} - m_2 (C_1 N_1 + C_2 N_2)] N_2$$

which describe the rate of numerical change in two competing species, where r_{m1} and r_{m2} are the intrinsic rates of increase of species 1 and species 2 respectively, m_1 and m_2 are positive proportionality constants, and C_1 and C_2 are interaction terms.

It can be shown (Gause, 1934) that the system represented by these equations is stable only in the unlikely case that $r_{m1}/m_1 = r_{m2}/m_2$. In all other cases, one species (that with the lowest r_m/m) will survive while the other will become extinct. This "competitive exclusion principle" of Gause (1934) was demonstrated to occur in micro-habitats, such as culture bottles and aquaria, in a wide variety of animals, including tropical fishes (Silliman, 1975).

A pair of Lotka-Volterra equations can also be formulated for a predator-prey system, i.e.

$$\frac{dN_1}{dt} = (r_m - c_1 N_2) N_1$$

$$\frac{dN_2}{dt} = (-g + c_2 N_1) N_2$$

where g is a coefficient of negative growth (the decline) of the predators (N_2) in the absence of prey (N_1), r_m is the intrinsic rate of increase of the prey population, and c_1 and c_2 are interaction terms.

An interesting property of this set of equations is that they can generate oscillations in time of the numbers of prey and predators independent of external (environmental) fluctuations. This feature may be used to explain the oscillating behavior of at least some terrestrial predator-prey systems. In the aquatic environment, such oscillations have been recently suggested for Baltic Sea cod and herring but have never been demonstrated from a tropical system, where the complexity of the food web possibly prevents such behavior.

The Lotka-Volterra equations, while providing insight into various aspects of the interactions between species, have been often criticized because of their extreme simplicity and lack of realism. Beverton and Holt (1957), for example, proposed a much more elaborate two-species model. However, bringing some realism into the Lotka-Volterra system of equations is relatively straightforward. Larkin (1966), who briefly reviewed some earlier variants of the Lotka-Volterra equations, suggested the following set for predator-prey interactions:

$$\frac{dN_1}{dt} = (r_{m1} - a_1N_1 - c_1N_2) \cdot N_1$$

$$\frac{dN_2}{dt} = (r_{m2} - a_2N_2 - c_2N_1) \cdot N_2$$

where r_{m1} and r_{m2} are the intrinsic rates of increase of the prey (N_1) and the predators (N_2), a_1 and a_2 are coefficients of intraspecific competition

and c_1 and c_2 are interaction terms, expressing decrease of prey in the presence of predators and increase of predators in the presence of prey. This system of equations, which is far more realistic than the original Lotka-Volterra formulation, has the following properties:

- the levels of abundance of predator and prey are mutually dependent
- the abundance of prey has an upper limit in the absence of predators
- the abundance of predators has a lower limit in the absence of prey (i.e., they switch to another prey and thus don't become extinct)

Larkin (1966) presented a discussion of the behavior of the predator-prey system under exploitation by a fishery. As this behavior is similar to that of the model developed by Pope (1979), we shall now go directly to the latter's model.

Pope (1979) presented an equation which is extremely helpful in making species-interaction visible. The model has the form

$$Y_T = \underbrace{aF_P - bF_P^2 + c_1F_PF_Q}_{Y_P} + \underbrace{dF_Q - eF_Q^2 + c_2F_PF_Q}_{Y_Q}$$

or $Y_T = Y_P + Y_Q$

where P and Q are interacting species, a , b , d and e are constants of parabolic yield curves, c_1 and c_2 are interaction terms, Y_P and Y_Q yields from species P and Q , respectively, given the fishing mortalities F_P and F_Q and where Y_T is the total yield from the two-species system.

Thus for example, we could have

$$Y_T = 200F_P - 100F_P^2 - 25F_PF_Q + 100F_Q - 50F_Q^2 + 25F_PF_Q$$

where P is an abundant prey, Q a less abundant predator and -25 and 25 are the interaction terms, positive for the predator whose yield increases in the presence of prey. (This example is illustrated in Fig. 2). Table 2 presents some combinations of values of a, b, d, e, and c_1 and c_2 and indicates the type of interaction that these values suggest. Based on the values in Table 2, Figures 1-4 have been drawn in the manner of Pope (1979) to demonstrate the effects of biological interaction on the combined yields of two interacting species.

Table 2. Constants used for drawing Figures 1 to 4

Fig. #	Constants of yield curve and interaction terms						System optimum		
	a	b	d	e	c_1	c_2	MSY	F_Q	F_P
1	200	100	200	100	-25	25	200	1.00	1.00
2	200	100	100	50	-25	25	150	1.00	1.00
3	100	50	50	25	10	25	146	2.25	1.79
4	100	50	50	25	5	10	94	1.36	1.20

Pope's model also allows precise definition of what he calls "technological interactions", i.e., the fact that in a multispecies fishery (and in "single" species fisheries also) catching a certain quantity of a given species necessarily implies catching certain quantities of other species (i.e., of another species in the two-species case).

Thus, when the ratio of the fishing mortalities (F_P/F_Q) of species P and Q remains constant for any level of F_P , this can be expressed as in Fig. 2 by a straight line starting from the origin and cutting through the yield isopleths (lines A, B and C on Fig. 2). The interesting thing about these lines, however, is that while any F-ratio necessarily generates a parabolic yield curve (see

Fig. 5 and Pope, 1979, for a mathematical proof), this yield curve does not necessarily go through the combined MSY of the whole system (Figs. 2 and 5).

As Pope (1979) demonstrated, his two-species system may be extended to any number of species with the overall conclusions remaining that

- for constant F-ratios, the total yield curve for any system composed of parabolic single species curves and linear interaction terms is itself a parabola, and
- the F-ratios in a given fishery do not necessarily generate the MSY, and the optimum F-ratios can be found only iteratively by changing F-ratios until MSY is reached.

Pope's model is of great teaching value as it enables one literally to see how the interactions affect the yields and to determine the absence or presence of species in the system. However, the parameters of the model cannot be estimated, so the model cannot be used directly for stock assessment purposes.

A calculator program is provided (Appendix 1) for the reader to calculate quickly values of Y_T , Y_p and Y_Q for any set of constants as well as to find the MSY and F_{opt} values of a hypothetical two-species system. It is hoped that exercises using this program with combinations of constants as in Table 2 will help the reader visualize the nature and effects of both technological and biological interactions.

Modeling systems with n species

It is only since the advent of electronic computers that it has become possible to model systems containing more than two species realistically.

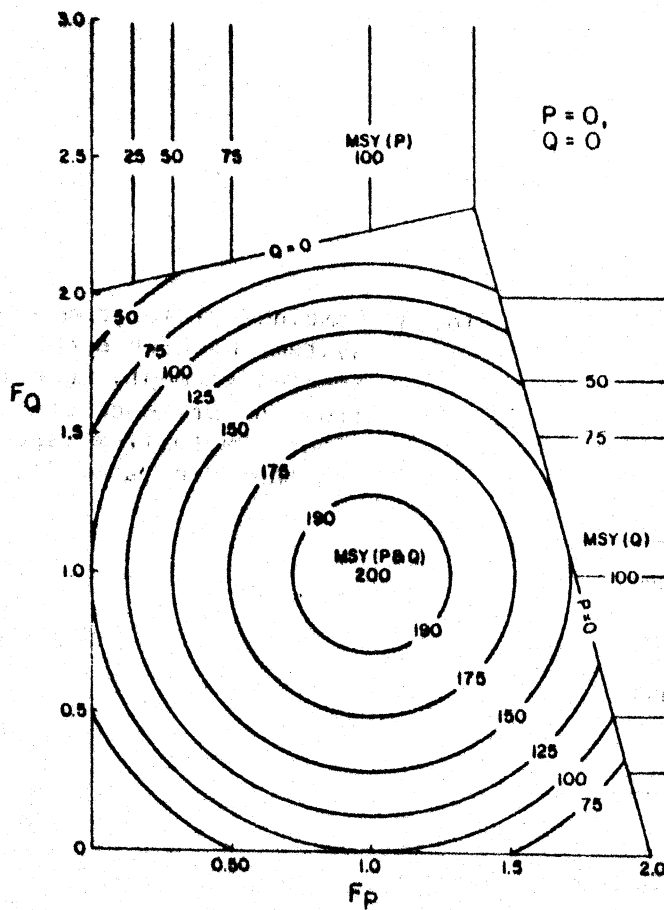
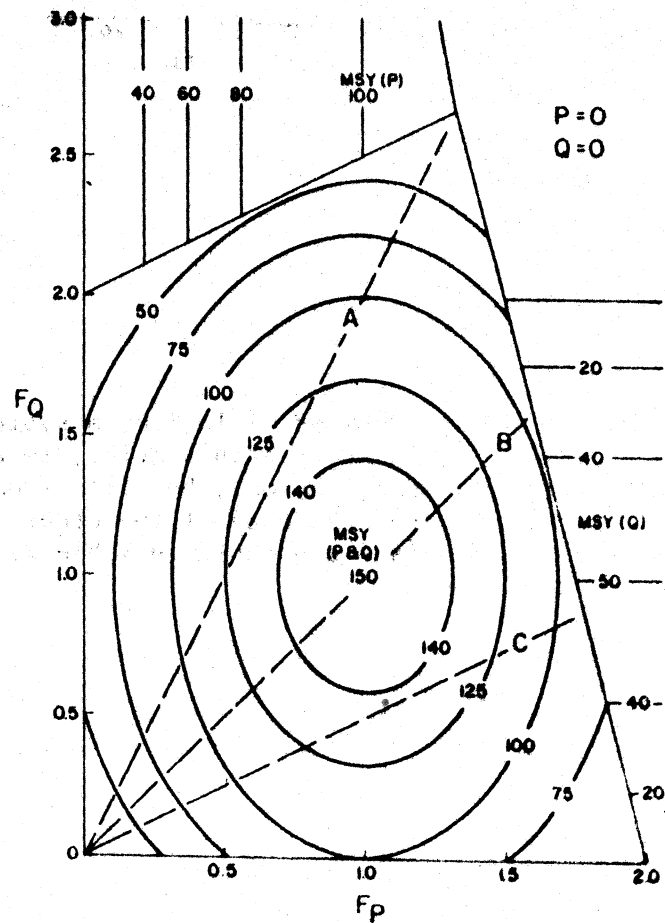


Fig. 1 Combined yield of two similar species, one nibbling on the other (see constants of Table 2).

Fig. 2 Combined yield from a predator-prey system (see constants in Table 2). Lines A, B and C refer to three fixed F-ratios (see Fig. 5).



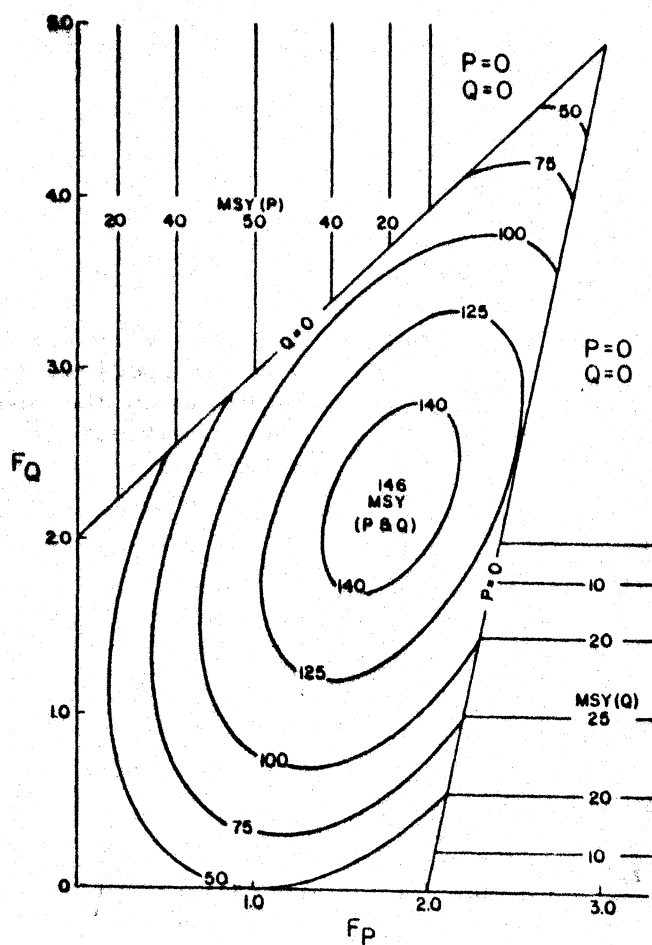
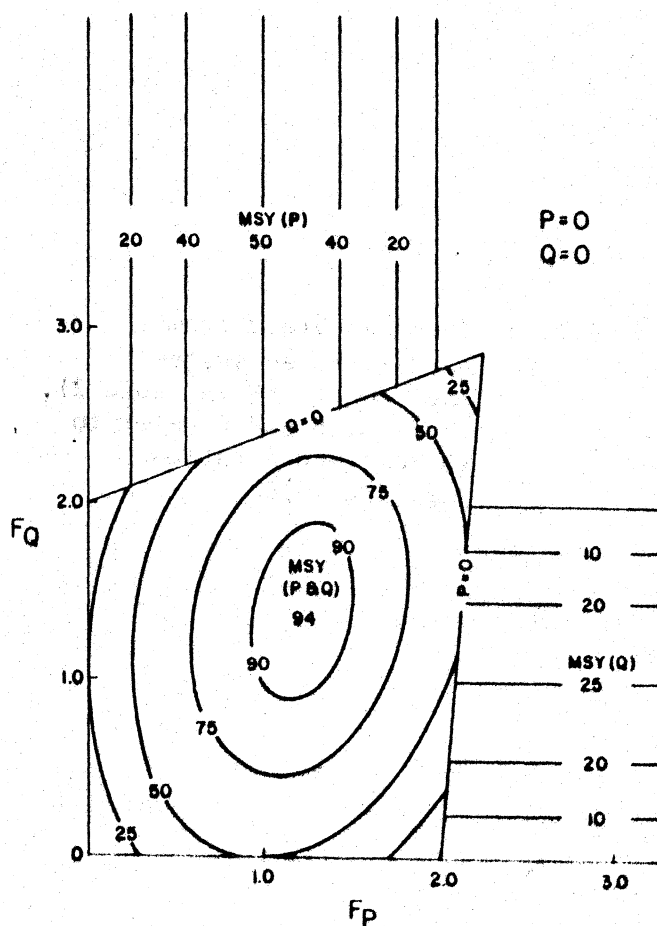


Fig. 3 Combined yield from a system in which each species strongly benefits from the presence of the other - mutualism (see constants in Table 2).

Fig. 4 Combined yield from a system in which each species, to a small extent, benefits from the presence of the other (see constants in Table 2).



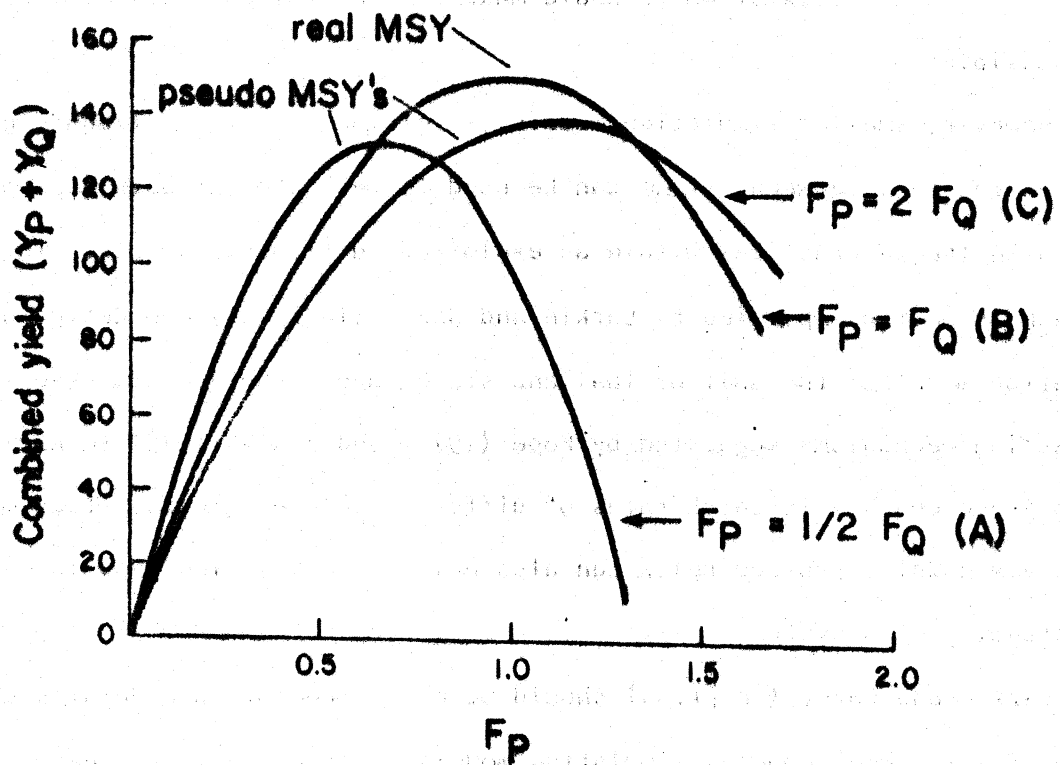


Fig. 5 Yield curves used to show how the selection of the F-ratios affects the shape of a yield curve; note that one optimum F-ratio leads to the real MSY of the 2-species system (see also Fig. 2).

Computers made it possible to depart from simplified approaches, such as represented by the equations presented above, and to incorporate into the models more realistic representations of growth, mortality, predation and other processes. This approach is best represented by the "North Sea model" of Andersen and Ursin (1977). At present, models such as the one presented by Andersen and Ursin (1977) cannot be applied to tropical stocks: the data base simply does not exist which would make such exercises meaningful or even possible.

However, smaller simulation models, involving only a few trophic groups and the transfers between them can be used to test and validate hypotheses concerning the interactions within an exploited multispecies stock. This approach is best exemplified by Larkin and Gazey (in press) who designed a simulation model of the Gulf of Thailand stocks and fisheries and used it for testing mechanisms suggested by Pope (1979) and Pauly (1979) to explain the observed changes in catch rates of different species groups. Such models as the box model discussed below can also help in identifying gaps in our understanding of a system.

Larkin and Gazey (in press) should be consulted for more details on the applicability of complex simulation models to tropical fisheries.

Method for constructing quantitative "box models"

While the mathematical simulation of multispecies systems is generally so complex as to discourage all but very mathematically-oriented biologists, constructing box models of an ecosystem is both rather easy and necessary, if only to identify the main energy pathways within a system under study. Fig. 6 may serve here as an example of a qualitative box model, in which the relative size of the boxes is used to suggest the importance of the various elements of the system.

Quantitative box models (see Walsh, 1981 for a very interesting example) consist of four elements, the first two of them structural, the others quantitative.

Those elements are:

- a) the taxa included in each box,
- b) the energy transfer between each box (i.e., the direction of the arrows linking the boxes with each other),
- c) the average biomass represented in each box, and
- d) the average energy transfer between boxes (i.e., the quantities represented by the arrows). (See Fig. 7)

Identifying the taxa to be included in the various boxes (a) involves criteria relating to the size of the animals, to their distribution and to their feeding habits. Generally, it will be possible to identify groups separated by all three criteria, e.g.

- large predators e.g., sharks, groupers (which are large, tend to occur in deeper water and feed on smaller fish),
- small, demersal, forage fish, e.g., slipmouths (which are small, occur in relatively shallow waters and feed on zooplankton or zoobenthos), or
- small pelagics ... etc.

and thus to place the animals concerned in the appropriate boxes. Since food and feeding habits cannot be determined for all species concerned, exhaustive use should be made of the available literature (Appendix 2) and of generalizations relating the morphology of fishes to their feeding habits.

Examples of such generalizations are:

- large fish with strong, pointed teeth (sharks, conger eels, barracuda) are piscivorous

- piscivorous fish tend to eat fish about one-quarter to one-fifth of their length (Ursin, 1973; Cushing, 1978)
- fish with long, coiled guts (longer than 3-4 times their body length) are generally detritivorous
- fish with an extremely small mouth are generally zooplanktivorous
- generalist-type fish (e.g., such as snappers) are omnivorous
- the size of the spaces between the gill-rakers of pelagics gives a direct indication of their favorite food.

This list is not exhaustive but indicates some of the methods which can be used to group fish into feeding niches and hence into the various boxes of a model. Obviously, when detailed data are available on the food and feeding habits, ecological similarity (\approx niche overlap) indices can be computed to quantify objectively the similarity in the diet of different fishes to assist grouping. One such index is:

$$c_{ij} = 1 - 1/2 \sum |p_{ij} - p_{hj}|$$

where p_{ij} and p_{hj} are the percentages of a certain food item j in the food of fish species i and h , respectively, the index having a value of zero when the two fish species (i, h) have no food item in common, and of unity when both fish species have the same food items in the same percentage composition (see Colwell and Futuyama, 1971, and Pianka, 1971, for another index).

Obviously, grouping fish (and invertebrates) into boxes on the basis of their food and feeding habits makes the drawing of the arrows which link the various boxes quite easy, such that task (b) above becomes part of task (a).

Putting numbers into the boxes and along the arrows is a little more complicated

The first step is to obtain the mean standing stock in each box (or at least in most of them). The most straightforward method to obtain standing stock estimates is to conduct a trawl survey, in the case of demersal stocks, or an acoustic survey, in the case of pelagic stocks. In both cases, tagging-recapture experiments can also be conducted from which biomass and a number of other important parameters can be estimated.

These methods, however, are rather expensive, and in the following a method to bypass the problem is shown - at least as a first approach. For this it will be necessary to make a brief excursion into fish mortalities.

Early in this stock assessment course, methods have (presumably) been presented by which the annual catch (Y) from a fishery is estimated, as well as methods from which fishing mortality (F) is estimated. It will be recalled that in fishery biology, mortalities are generally expressed as exponential rates, i.e.

$$N_t = N_0 \cdot e^{-Zt}$$

which states that the number of fishes (N_t) left after a certain time (t) is a function of N_0 , the original number of fish, and Z , the total mortality rate. Z is defined as

$$Z = F + M$$

where M is the natural mortality rate.

Methods to estimate Z from the mean length of the fish in the catch, or from length-converted catch curves are discussed in a variety of papers, including Pauly (1980a). Methods to obtain reasonable estimates of F are

the swept-area method in the case of demersal fisheries (Gulland, 1969; Pauly, 1980b), and the subtraction from Z of an independent estimate of M, e.g., as obtained from the empirical equations of Pauly (1980c). (See Table 3 for a hypothetical data set).

Table 3. Hypothetical example of data from a multi-species fishery for use in the construction of a quantitative box model

<u>Trophic groups</u>	Catch (Y) (arbitrary units)	Z	<u>Mortalities</u> [*]	
			M	F
Large predators	3	0.5	0.2	0.3
Intermediate predators	30	1.1	0.5	0.6
Zooplanktivorous fish	120	2.7	1.5	1.2
Zoobenthivorous fish	300	2.4	1.2	1.2
Detritivores (fish & shrimps)	105	5.5	2.0	3.5

* pertaining to representative species within each group.

The interesting thing about the values of F is that now they can be used to estimate, in conjunction with the yield data, the mean standing stock, or biomass (\bar{B}) via the equation

$$Y/F = \bar{B}$$

(see Sekharan, 1974) which can be used to put numbers into our boxes. It will generally not be possible to obtain estimates of \bar{B} for all fishes included in each box; as a first approximation, however, all the fishes in a given box may be assumed to have the same fishing mortality (they will have similar sizes and occur at similar places, so it's not a completely unreasonable assumption). Putting numbers along the arrows linking boxes with each other is now relatively simple:

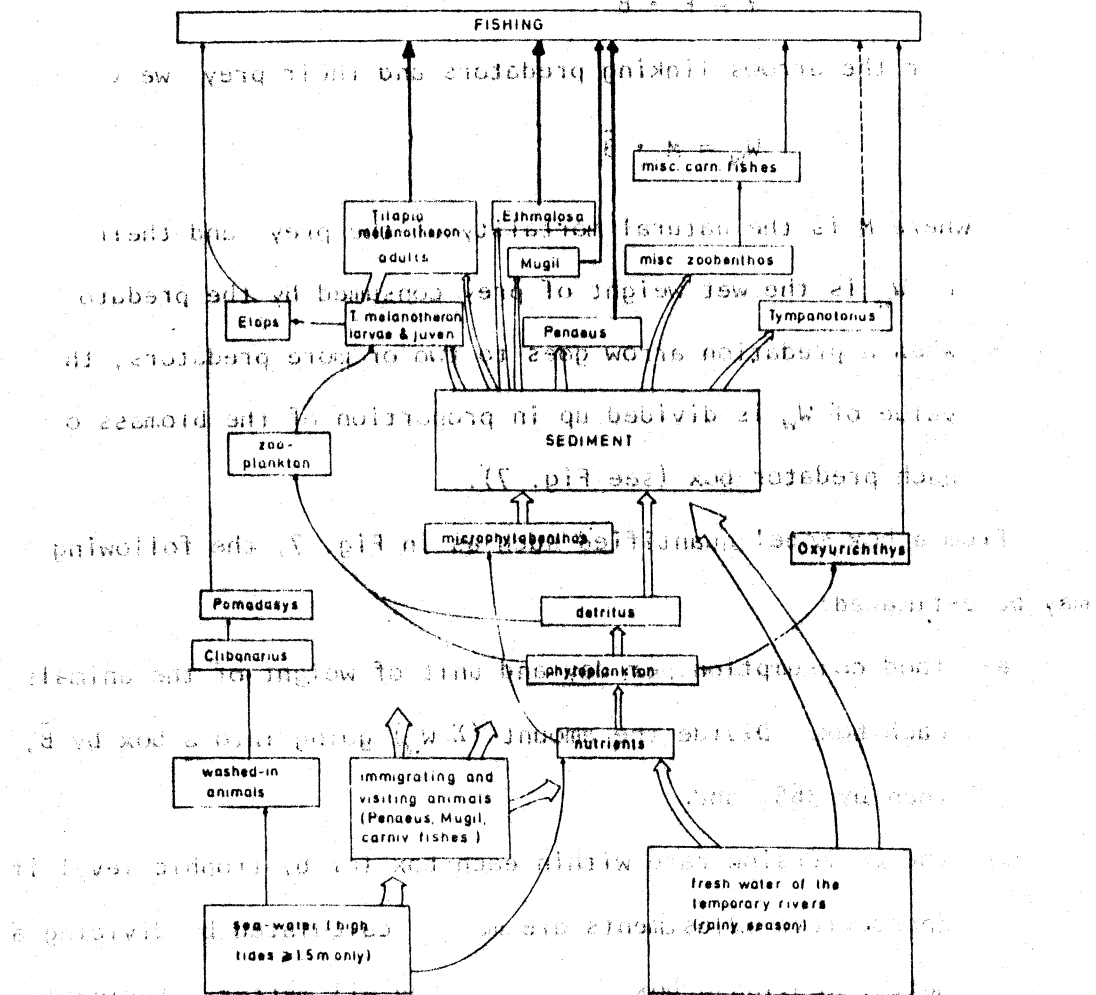


Fig. 6 Qualitative box model of a semi-enclosed small West African lagoon. Note central role of both sediment (as energy storage of the whole system) and of animals feeding on sediment and associated detritus (tilapia, mullets, shrimps).

The model, although qualitative, allows for an assessment of the role played by the various organisms in the lagoon, and thus helps understanding of the mechanisms supporting and limiting the fishery (adapted from Pauly, 1975).

- for the arrow linking fishes with the fishery, we use the yield data themselves, i.e.,

$$Y = F \cdot \bar{B}$$

- for the arrows linking predators and their prey we use

$$W_w = M \cdot \bar{B}$$

where M is the natural mortality of the prey and their biomass and W_w is the wet weight of prey consumed by the predators

- when a predation arrow goes to two or more predators, the value of W_w is divided up in proportion of the biomass of each predator box (see Fig. 7).

From a box model quantified such as in Fig. 7, the following quantities may be estimated:

- a) food consumption per day and unit of weight of the animals in each box. Divide the amount (ΣW_w) going into a box by \bar{B} , and then by 365, and
- b) the conversion rate within each box (or by trophic level if appropriate adjustments are made), calculated by dividing all matter leaving a box ($\Sigma[Y + W_w]$) by all matter entering it.

The values of a) generally should fall between 3% and 6%/day, and those of b) 5% to 25%. These ranges can also be used to complete empty boxes in the model, when values of Y and F are unobtainable, e.g., for zooplankton (see Fig. 7).

Quantitative box models, constructed along principles such as outlined here can serve the following purposes:

- summarizing the data available on a multispecies system
- allowing for an integration of fishery with ecological data

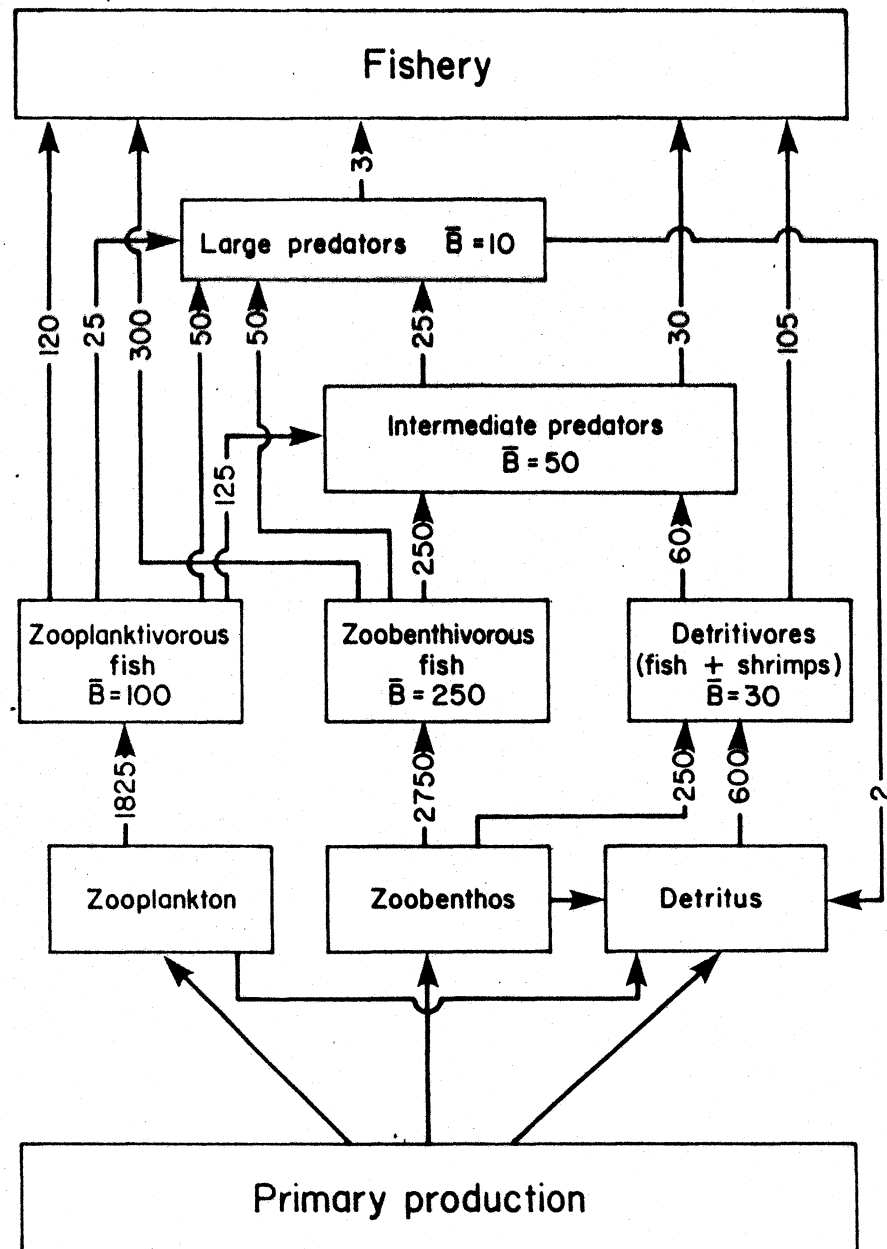


Fig. 7 Quantitative box model of a multispecies system exploited by a fishery, based on the data of Table 3 and the methods of computation outlined in the text. Note that while zooplankton and zoobenthos consumption (by fish and shrimps) could be estimated, their production and standing stock could not. Also, to achieve some internal consistency, the natural mortality of the large predators is assumed to be caused by the intermediate predators. It should be noted that this model applies only to those parts of the stocks that are accessible to the fishery, as implied in the equations used for the various computations. Thus, the fact is not considered in this model that fish "change boxes" in the course of their ontogeny.

- identifying those parts of the system where gaps in knowledge occur
- assessing the possible impact of exploiting one stock or the other.

Useful references that may be consulted when dealing with food chains and box models are Slobotkin (1974), Winberg (1971), Steele (1973), Boje and Tomczak (1978) and Pauly (1979); the last mentioned contains an application of such models to the management of the Gulf of Thailand and other fisheries.

Managing multispecies fisheries

Fortunately, finding out what is necessary to meaningfully manage a multispecies fishery is most often less complicated than trying to understand how the system works in biological terms. Throughout much of the world, as a rule, once exploitation of a stock has begun, the fishery rapidly moves toward overfishing, because, in the absence of effective regulations, the point of equilibrium of a fishery occurs when the average costs of fishing are as high as the gross returns from the fishery (see Fig. 8; Clark, 1976; Smith, 1980).

Thus, managing a fishery (as opposed to developing one) is for most purposes synonymous with attempting to reduce or redirect fishing effort, in order either to increase the catch and/or to reduce losses due to overcapitalization, i.e., increase the income of those remaining in the fishery (see Fig. 8 and Smith, 1980).

The work of Pope (1979) suggests that fitting a parabolic yield curve to time series of catch and effort data from a multispecies fishery

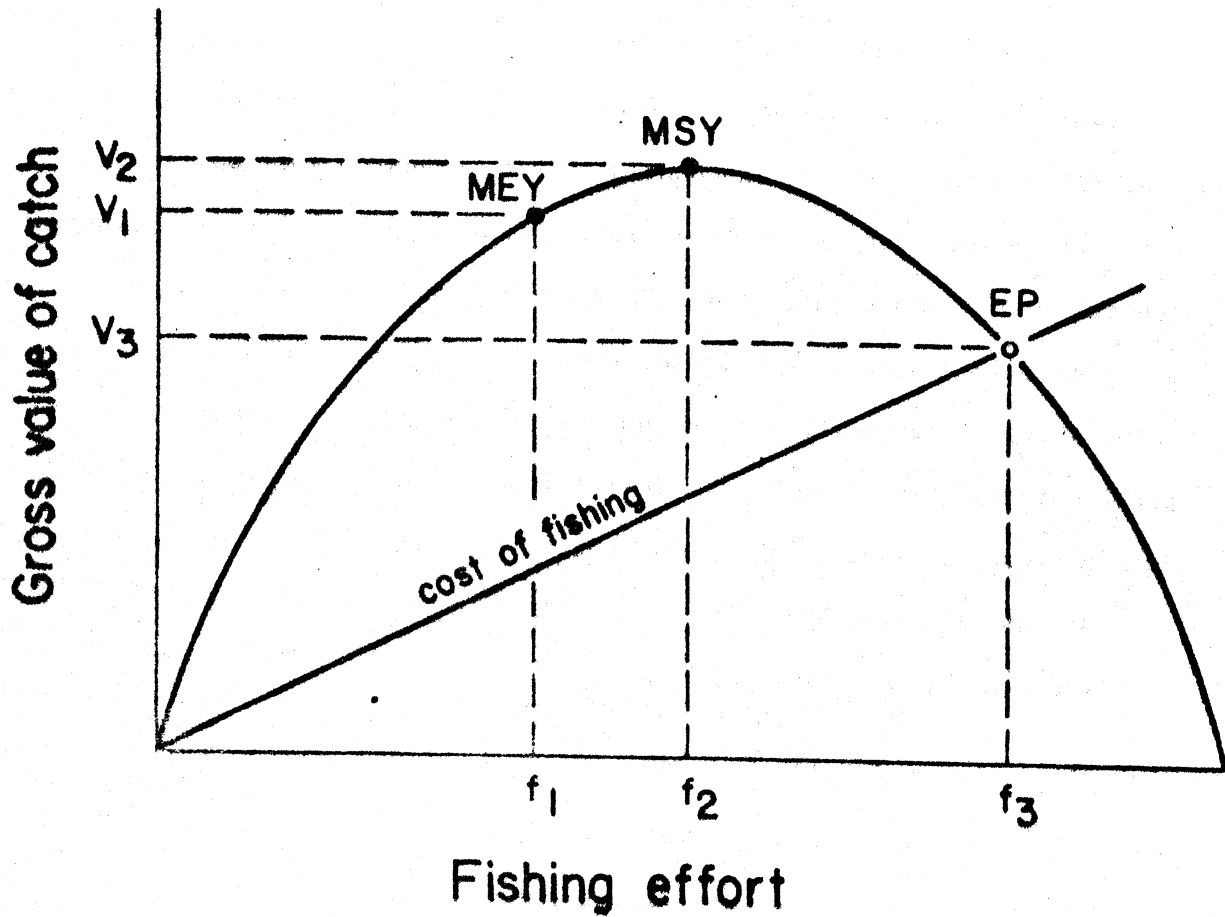


Fig. 8 A simple economic model of a fishery with fishing costs linearly proportional to effort. Note that MEY (maximum economic yield, i.e., the maximum difference between gross value of catch and cost of fishing) is achieved at a level of effort lower than needed to obtain MSY (maximum sustainable yield). Under conditions of open access to fishing, fishing effort will increase until total costs equal the gross value of the catch (i.e., the fishing reaches f_3 , and the equilibrium point, EP) and at which profit for the average fishing unit is zero. Note also that lowering the cost line (e.g., by subsidizing the fishery lowers the point at which equilibrium is reached, and thus lowers the catch (Smith, 1980).

although it may underestimate MSY, may be an appropriate method to identify an optimum level of aggregate effort, and this is in fact what is done in practice whenever appropriate time series are available.

At a recent workshop on the theory and management of tropical multispecies stocks (Pauly and Murphy, in press), it emerged, however, that fitting parabolic or exponential yield curves to just any set of catch and effort data might be in fact inappropriate. Thus, for example, the catch and effort data of the Gulf of Thailand Demersal Trawl Fishery are generally fitted with a Schaefer model (e.g., SCS 1978) or a Fox model (FAO, 1978) although the data do not really suggest a downward trend of total catch at high levels of effort (although the catch-per-effort data decrease dramatically). For this reason, an asymptotic model would fit the data as well (see Fig. 9).

The model can be described by

$$Y = Y_{\infty} (1 - e^{-Kf})$$

where Y_{∞} is the "asymptotic yield" i.e., the yield that would be taken with infinite effort, K a coefficient and f a measure of effort. (The equation can be fitted to catch and effort data in the same fashion that the von Bertalanffy growth equation is fitted to length-at-age data, with t_0 set equal to zero).

Obviously, when this model is used to reduce a set of catch and effort data, the need arises to define an optimal level of effort (since infinite effort, giving Y_{∞} , would clearly be an unreasonable proposition), especially when economic data are not available from which the equilibrium point and maximum economic yield could be defined.

In analogy to the $F_{0.1}$ concept used for managing several temperate fisheries, a level of catch and effort may be defined at which the slope of the yield curve is one-tenth of the slope of the origin ($Y_{0.1}$, $f_{0.1}$), as follows:

The slope at $f = 0$ in the equation above is given by

$$\text{slope (at } f = 0) = Y_{\infty} \cdot K$$

while for all positive values of f , the slope is given by

$$\frac{dy}{df} = Y_{\infty} K \cdot e^{-Kf}$$

Thus, $f_{0.1}$ can be obtained from

$$Y_{\infty} \cdot K/10 = Y_{\infty} \cdot K \cdot e^{-Kf_{0.1}}$$

or

$$\frac{\log_e 10}{K} = f_{0.1}$$

while $Y_{0.1}$ is obtained from

$$Y_{0.1} = Y_{\infty} \cdot 0.9$$

"The selection of 10% [and the $Y_{0.1}$ concept are] arbitrary, but once the 10% figure is accepted, the corresponding catch can be calculated objectively. Thus it can be used to provide a commission or other management body objective guidance based on scientific grounds" (Gulland and Boerema, 1973). An application of this model to a set of catch and effort data is given in Fig 9.

Reliable techniques on how to exploit a multispecies stock to obtain a desired species mix or avoid an undesired one are not available (Daan, 1980; Pauly and Murphy, in press).

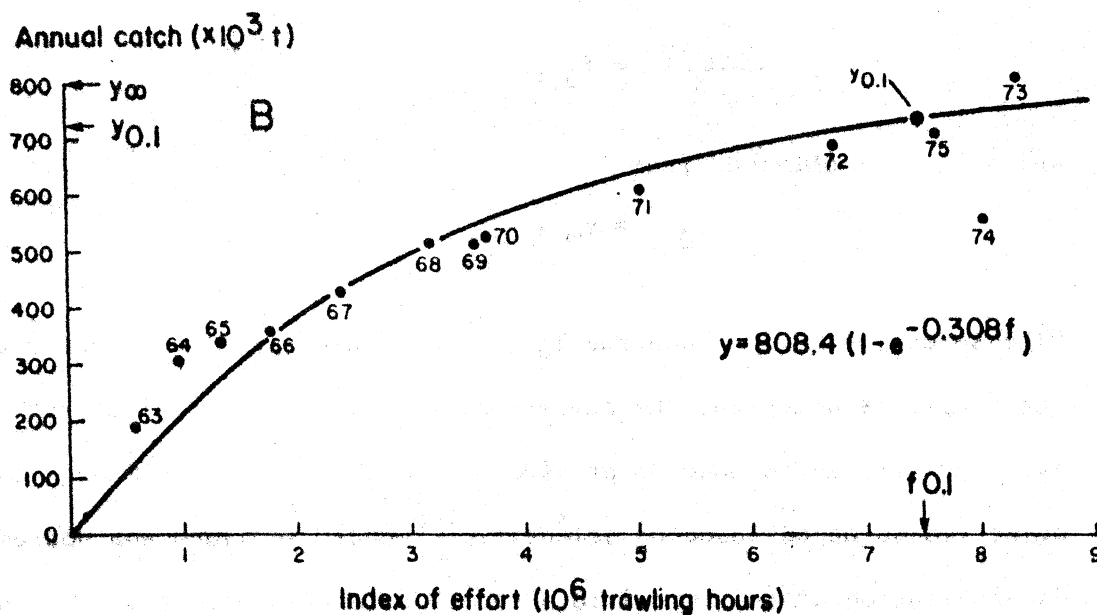
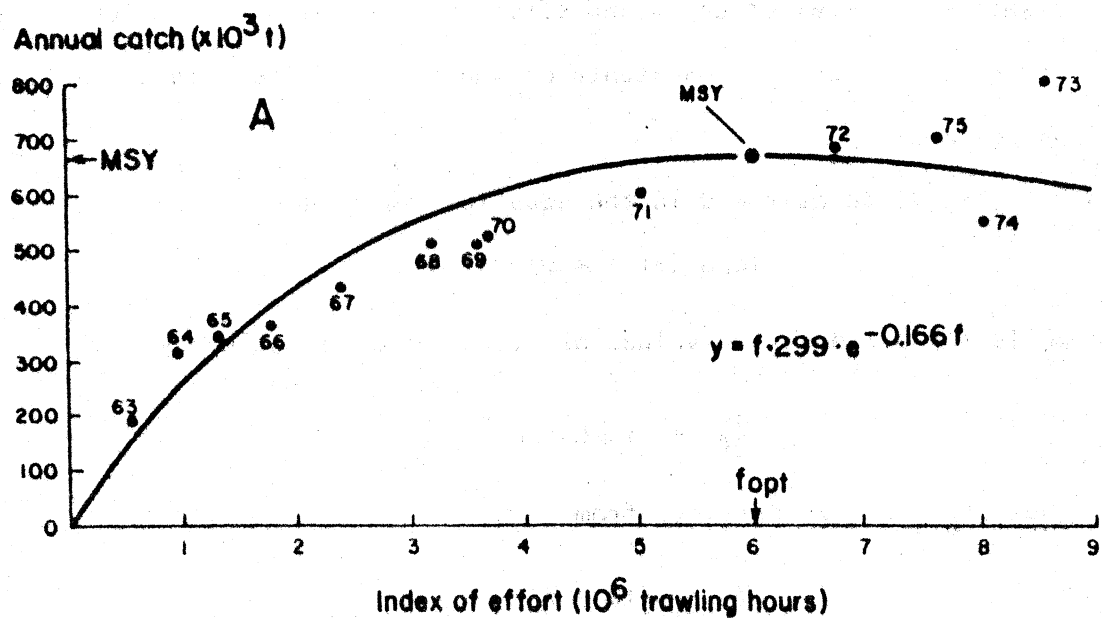


Fig. 9 Catch and effort data from the Gulf of Thailand demersal trawl fishery, with two alternative shapes for the yield curves.
A: Fox model; B: asymptotic yield model.

At least some of the following changes may be expected, however, with a steadily increasing effort in a demersal multispecies fishery:

- a decline in catch-per-effort (although not necessarily of the total catch, see above)
- a decrease and virtual extinction of the larger species
- a decrease in average size of the fish caught
- an increase of the relative contributions of low-value, small-sized fish
- the increase of previously insignificant components of the catch (e.g., squids or jelly-fish).

Fishery research in tropical multispecies systems

Evidently, it is difficult to define a research program that applies to all multispecies stocks. However, the following elements should be included in any basic fishery research program:

- monitoring total catch and catch-per-effort of the fishery
- monitoring catch-per-effort of various "indicator" species representing various groups of fish (e.g., large, medium- and small-sized)
- thorough study of the biology and population dynamics of the most abundant and of the most valuable species
- an attempt to construct a "box model" of the system in question (see above)
- an attempt to identify gear that would selectively remove certain groups of species (i.e., attempt to identify the best F-ratios in the system in question).

The various reviews included in Pauly and Murphy (In press) should be helpful in defining such a research program.

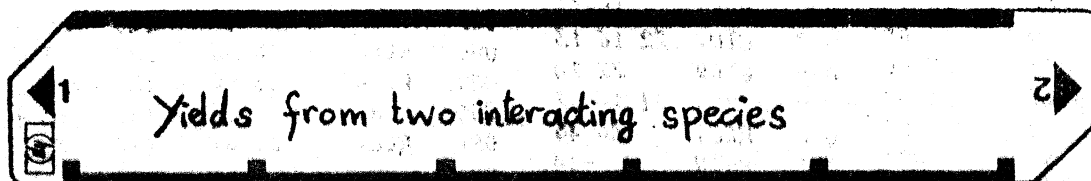
REFERENCES

- Andersen, K.P. and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Medd. fra Danm. Fisk. og Havunders. (N.S.)* 7:319-435.
- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. *U.K. Min. Agric. Fish., Fish. Invest. (Ser.2)* 19:533 p.
- Boje, R. and M. Tomczak, Editors. 1978. *Upwelling ecosystems*. Springer Verlag, Berlin. 303 p.
- Clark, C.W. 1976. *Mathematical bioeconomics: the optimal management of renewable resources*. Wiley Interscience, New York. 352 p.
- Colwell, R.K. and D.G. Futuyama. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-76.
- Cushing, D.H. 1978. Upper trophic levels in upwelling areas, p.101-110. In R. Boje and M. Tomczak (eds.) *Upwelling ecosystems*. Springer Verlag, Berlin. 303 p.
- Daan, N. 1980. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacements, p.405-421. In A. Saville (ed.) *The assessment and management of pelagic pelagic fish stocks*. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer.* 177. 517 p.
- FAO, 1978. Some scientific problems of multispecies fisheries, Report of the Expert Consultation on Management of Multispecies Fisheries. *FAO Fish. Tech. Pap.* 181. 42 p.
- Gause, G.F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore. 163 p.
- Gulland, J.A. and L.K. Boerema. 1973. Scientific advice on catch levels. *U.S. Fish. Bull.* 71:325-335.
- Larkin, P.A. 1966. Exploitation in a type of predator-prey relationship. *J. Fish. Res. Board Can.* 23:349-356.
- Larkin, P.A. and W. Gazey. Applications of ecological simulation models to management of tropical multispecies fisheries. In D. Pauly and R.I. Murphy (eds.) *Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks*. *ICLARM Conference Proceedings*. (In press).

- Lotka, A.J. 1925. Elements of mathematical biology. Dover Publications. New York. 465 p.
- Pauly, D. 1975. On the ecology of a small West African lagoon. Ber. Dt. Wiss. Komm. Meeresforsch. 24(1):46-62.
- Pauly, D. 1979. Theory and management of tropical multispecies stocks: a review with emphasis on the Southeast Asian demersal fisheries. ICLARM Studies and Reviews 1, 35 p. International Center for Living Aquatic Resources Management, Manila.
- Pauly, D. 1980a. A selection of simple methods for the assessment of tropical fish stocks. FAO Fish. Circ. No. 729. 54 p.
- Pauly, D. 1980b. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth mortality and stock-recruitment relationships, p. 154-172. In S. Saila and P. Roedel (eds.) Stock assessment for tropical small-scale fisheries. Proceedings of an international workshop held September 19-21, 1979 at the University of Rhode Island. Intern. Centr. Mar. Res. Dev., Univ. of Rhode Island. 198 p.
- Pauly, D. 1980c. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. du Conseil 39(3):175-192.
- Pauly, D. 1981. Stock assessment packages for programmable calculators and microcomputers: two examples, with a discussion of their potential usefulness in developing countries. ICES C.M. 1981/D:2 Statistics Committee. 19 p. (Mimeo)
- Pauly, D. and G.I. Murphy (eds.) Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks. ICLARM Conference Proceedings (in press)
- Pianka, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53-74.
- Pope, J.G. 1979. Stock assessment in multispecies fisheries, with special reference to the trawl in the Gulf of Thailand. SCS/DEV/79/19, 106 p. South China Sea Fisheries Development and Coordinating Programme, Manila.
- SCS. 1978. Report of the Workshop on the demersal resources of the Sunda Shelf, Part II. SCS/GEN/77/13, 120 p. South China Sea Fisheries Development and Coordinating Programme, Manila.

- Sekharan, K.V. 1974. Estimates of the stocks of oil sardine and mackerel in the present fishing grounds off the west coast of India, Indian J. Fish. 21(1):177-182.
- Silliman, R.P. 1975. Experimental exploitation of competing fish population. U.S. Fish. Bull. 73:872-888.
- Slobotkin, L.B. 1965. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York. 184 p.
- Smith, I.R. 1981. Improving fishing incomes when resources are over-fished. Mar. Policy 5:17-22.
- Steele, J.H., Editor. 1973. Marine food chains. Oliver and Boyd, Edinburgh. 552 p.
- Ursin, E. 1973. On the prey size preference of cod and dab. Medd. Danm. Fisk.-og Havunders. N.S. 7:85-98.
- Volterra, V. 1926. Variations and fluctuations of individuals of animals living together, p. 409-448. In R.N. Chapman (ed.). Animal Ecology. MacGraw-Hill, New York.
- Walsh, J.J. 1981. A carbon budget for overfishing off Peru. Nature 290(5804):300-304.
- Winberg, W.W., Editor. 1971. Methods for the estimation of production in aquatic animals. Academic Press, New York, 175 p.

Appendix 1 HP 67/97 Program: "Yield from two interacting species"



STEP	INSTRUCTIONS	INPUT DATA/UNITS	KEYS	OUTPUT DATA/UNITS
1	Enter constants	α	STO A	
		b	STO B	
		d	STO D	
		e	STO E	
		c_1	STO 2	
		c_2	STO 3	
	for step 2 do also	F_Q	STO 0	
2	Calculate yields from two interacting species	F_p	A	Y_p
				Y_Q
				Y_T
3	Calculate F_{popt} , F_{Qopt} and MSY			
	enter starting value of F_p	F_p'	STO 1	
	enter starting value of F_Q	F_Q'	STO 2	
	enter ΔF and TOL^*	ΔF	\uparrow	
		TOL	f a	F_{Qopt}
				F_{popt}
				MSY
	* ΔF = initial step size			
	TOL = tolerated error of F estimates,			
	e.g. 0.001			

LABELS					FLAGS	SET STATUS			
A	B	C	D	E	0	FLAGS		TRIG	DISP
→ Y's	used	used	used	used	0	ON OFF		DEG <input checked="" type="checkbox"/>	FIX <input checked="" type="checkbox"/>
→ MSY	used	used			1	0 <input checked="" type="checkbox"/> <input checked="" type="checkbox"/>		GRAD <input type="checkbox"/>	SCI <input type="checkbox"/>
used	used	used	used		2	1 <input checked="" type="checkbox"/> <input checked="" type="checkbox"/>		RAD <input type="checkbox"/>	ENG <input type="checkbox"/>
					3	2 <input checked="" type="checkbox"/> <input checked="" type="checkbox"/>			n <u>2</u>
						3 <input type="checkbox"/> <input type="checkbox"/>			

Program Title Yields from two interacting species

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Program Description, Equations, Variables, etc. Pope (1979) showed that, if single-species yield curves can be described by parabolas, the total yield (Y_T) of a system of two interacting species P and Q should, as long as the ratio $F_P:F_Q$ remains constant, also correspond to a parabola, i.e.

$$Y_T = \underbrace{aF_P - bF_P^2 + c_1F_PF_Q}_{Y_P} + \underbrace{dF_Q - eF_Q^2 + c_2F_PF_Q}_{Y_Q} \quad \dots 1)$$

$$Y_T = Y_P + Y_Q \quad \dots 2)$$

where a & b , and d & e are constants of the yield curves of two different species (e.g. predator & prey) and where c_1 and c_2 express the intensity and character of the interactions occurring between the two species (c_1 and c_2 have opposite signs in cases of predator-prey interactions). Pope (1979) also generalized equation (1) to a system of n -species and showed that the overall yield curves of such systems remain parabolic as long as the F -ratios remain constant and no species drop out of the system.

This program estimates values of Y_P , Y_Q and Y_T for any combination of constants, as well as the MSY and the optimal values of F_P and F_Q of the 2-species system.

The iterative subroutines included in this program are adapted from program #02831 D, submitted by B.W. Clare to the ICP 67/97 (US) Users' Library

Reference: Pope, J.G. 1979 SCS/DEV/79. FAO. 106 p

Operating Limits and Warnings a) There might be combinations of constants and of F_P , F_Q for which MSY cannot be located by the algorithm provided here. In either case, iteration time is quite long; don't be impatient.

b) When computing Y_P , Y_Q and Y_T , the contributions of the interaction terms (c_1 , c_2) are omitted if one of the species drops out of the system; "dropping out" occurs when one of the partial yields (including interaction term) has a negative value

Appendix 2. A short bibliography on the food and feeding habits of tropical and subtropical marine fish

1. Apparao, T. 1966. On some aspects of the biology of Lactarius lactarius (Schneider). Indian J. Fish. 13(2):334-349.
2. Bapat, S.V. and D.V. Bal. 1952. The food of some young fishes from Bombay, Proc. Indian Acad. Sci. 35B(2):78-92.
3. Basheeruddin, S. and K.N. Nayar. 1962. A preliminary study of the juvenile fishes of the coastal waters off Madras City. Indian J. Fish. 8(1):169-188.
4. Bell, J.D. 1979. Observations on the diet of red morwong, Cheilodactylus fuscus Castelnau (Pisces: Cheilodactylidae. Aust. J. Mar. Freshwater Res. 30:129-13.
5. Ben-Yami, M. and T. Glaser. 1974. The invasion of Saurida undosquamis (Richardson) into the Levant Basin - an example of biological effect of interoceanic canals, U.S. Fish. Bull. 72(2):359-373.
6. Berkeley, S.A. and E.D. Houde. 1978. Biology of two exploited species of halfbeaks. Hemiramphus brasiliensis and H. balao from Southeast Florida. Bull. Mar. Sci. 28(4):624-644.
7. Bograd-Zismann, L. 1965. The food of Saurida undosquamis in the Eastern Mediterranean in comparison with that in Japanese waters. Rapp. P-V. Réun. Comm. Int. Explor. Sci. Mer. Medit. 18:251-252.
8. Capape, C. and J-P Quignard. 1977. Contribution à la biologie des Rajidae des côtes tunisiennes. 6. Raja asterias Delaroche, 1809, Régime alimentaire. Bull. Inst. Natl. Sci. Tech. Océanogr. Pêche Salâmmo 4(2-4):319-332.
9. Chacko, P.I. 1949. Food and feeding habits of the fishes of the Gulf of Manaar. Proc. Indian Acad. Sci. 29B(3):83-97.
10. Chan, E.H. and T.E. Chua. 1979. The food and feeding habits of greenback grey mullet, Liza subviridis (Valenciennes), from different habitats and at various stages of growth. J. Fish. Biol. 15:165-171.
11. Conacher, M.H., W.J.R. Lanzing and A.W.D. Larkin. 1979. Ecology of Botany Bay. II. Aspects of the feeding ecology of the fanbellied leatherjacket, Monacanthus chinensis (Pisces: Monacanthidae), in Posidonia australis seagrass beds in Quibray Bay, Botany Bay, New South Wales. Aust. J. Mar. Freshwater Res. 30:387-400.
12. Croker, R.A. 1962. Growth and food of the gray snapper, Lutjanus griseus in Everglades National Park. Trans. Amer. Fish. Soc. 91(4):379-383.

13. Cummings, W.C., D.B. Bradley and J.J. Spires. 1966. Sound production, schooling, and feeding habits of the margate, Haemulon album Cuvier, off North Bimini, Bahamas. Bull. Mar. Sci. 16(3):626-640.
14. Davis, W.P. and R.S. Birdsong. 1973. Coral reef fishes which forage in the water column. Helgol. Wiss. Meeresunters. 24:292-306.
15. Devadoss, P. and P.K. Mahadevan Pillai. 1973. Observations on the food of juveniles of Psettodes erumei (Bloch). Indian J. Fish. 20(2):664-667.
16. Eggleston, D. 1972. Patterns of biology in the Nemipteridae. J. Mar. Biol. Ass. India 14(1):357-364.
17. Fagade, S.O. and C.I.O. Olaniyan. 1973. The food and feeding inter-relationship of the fishes in the Lagos Lagoon. J. Fish. Biol. 5:151-156.
18. Gygi, R.A. 1975. Sparisoma viride (Bonnaterre), the spotlight Parrotfish, a major sediment producer on coral reefs of Bermuda? Eclogae Geol. Helv. 68(2):327-359.
19. Haitt, R.W. and D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65-127.
20. Hobson, E.S. 1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. U.S. Fish. Bull. 70:715-740.
21. Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. U.S. Fish. Bull. 72:915-1031.
22. Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. Amer. Sci. 63:382-392.
23. Hobson, E.S. and J.R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. U.S. Fish. Bull. 76:133-153.
24. Jakob, P. 1950. The bionomics of ribbon fishes (Trichiurus spp.) and their fishery on the West Coast of Madras Province. J. Bombay Nat. Hist. Soc. 48(2):261-264.
25. James, P.S.B.R. 1966. Notes on the biology and fishery of the butterfly ray, Gymnura poecilura (Shaw) from the Palk Bay and Gulf of Manaar. Indian J. Fish. 13(1-2):150-157.
26. James, P.S.B.R. 1967. The ribbon fishes of the Family Trichiuridae of India. Mem. Mar. Biol. Ass. India (1):226 p.
27. James, P.S.B.R. 1973. Sharks, rays and skates as a potential fishery resources off the east coast of India: 483-494. In Proceedings of the Symposium on Living Resources of the Seas Around India. Spec. Publ. Cent. Mar. Fish. Res. Inst., Cochin, 748 p.

28. Kawanabe, H., T.T. Saito, T. Sunaga and M. Azuma. 1968. Ecology and biological production of Lake Naka-Umi and adjacent region.
IV. Distribution of fishes and their food. Spec. Publ. Seto Mar. Biol. Lab., Ser. 2. Part 2 (415):45-73.
29. Konchina, Y.V. 1977. Some data on the biology of grunts (Family Pomadasyidae). J. Ichthyol. 17(4):548-558.
30. Kuthalingham, M.D.K. 1955. Food and feeding habits of juveniles and adults of four fishes of Madras. J. Madras Univ. 25B(3):235-253.
31. Kuthalingham, M.D.K. 1958. The food and feeding habits of some young silver bellies. J. Madras Univ. 28B(1):13-22.
32. Kuthalingham, M.D.K. 1959. Development and feeding habits of Saurida tumbil. J. Zool. Soc. India 11:116-124.
33. Kuthalingham, M.D.K. 1960. Observations on the life history and feeding habits of the Indian sardine, Sardinella longiceps. Treubia 25:207-213.
34. Kuthalingham, M.D.K. 1965. Notes on some aspects of the fishery and biology of Nemipterus japonicus (Bloch) with special reference to feeding behavior. Indian J. Fish. 12 A & B (2):500-506.
35. Kuthalingham, M.D.K. 1966. A contribution of the life history and feeding habits of Mugil cephalus (Linn.) Treubia 27(1):11-32.
36. Lee, C.K.C. 1973. The feeding of Upeneus moluccensis (Bleeker) on fishing grounds near Hong Kong. Hong Kong Fish. Bull. (3):47-53.
37. Lewis, J.B. 1961. The growth, breeding cycle and food of the flying fish Parexocoetus brachypterus hillianus (Gosse). Bull. Mar. Sci. Gulf and Caribbean 11(2):258-266.
38. Longhurst, A.R. 1957. The food of the demersal fish of a West African estuary. J. Anim. Ecol. 26(2).
39. Longhurst, A.R. 1965. A survey of the fish resources of the eastern Gulf of Guinea. J. du Conseil 29(3):
40. Michaelson, D.M., D. Sternberg and L. Fishelson. 1979. Observations on feeding, growth and electric discharge of newborn Torpedo ocellata (chondrichthyes, batoidei). J. Fish. Biol. 15:159-169.
41. Nakamura, H. 1936. On the food habit of yellowfin tuna N. macropterus (Schlegel) from the Celebes Sea. Trans. Nat. Hist. Soc. Formosa, 26: and Pac. Oceanic Fish. Inv. Translations (17) (1949)
42. Nursall, J.R. 1977. Speculation concerning speciation in coral reef fishes. Mar. Res. Indones. (17):133-139.

43. Pearson, J. and A.H. Malpas. 1926. A preliminary report on the possibilities of commercial trawling in the sea around Ceylon. Ceylon J. Sci. Sect. C 2:1-165.
44. Prabhu, M.S. 1955. Some aspects of the biology of the ribbonfish Trichiurus haumela (Forskål). Indian J. Fish. 2(1):132-163.
45. Rajan, S. 1964. Environmental studies of the Chilka lake. I. Feeding spectrum of fishes. Indian J. Fish. 11(2):521-532.
46. Randall, J.E. 1967. Food habits of reef fishes of the West Indies Stud. Trop. Oceanogr. Miami 5:665-847.
47. Randall, J.E. 1977. Contribution to the biology of the whitetip reef shark (Triaenodon obesus). Pac. Sci. 31(2):143-164.
48. Rao, K. Srinivasan. 1967. Food and feeding habits of fishes from trawl catches in the Bay of Bengal with observations on diurnal variations in the nature of the feed. Indian J. Fish 11(1):277-314.
49. Ronquillo, I.A. 1954. Food habit of tuna and dolphins based upon the examination of their stomach contents. Philipp. J. Fish. 2(1):71-83.
50. Sarojini, K.K. 1954. The food and feeding habits of the grey mullet Mugil parsia Hamilton and M. speigleri Bleeker. Indian J. Fish. 1(1/2):67-93.
51. Sreenivasan, P.V. 1974. Observation on the food and feeding habits of the 'torpedo trevally' Megalaspis cordyla (Linnaeus) from Vizhinjam Bay. Indian J. Fish. 21(1):76-84.
52. Suseelan, C. and K.V. Somasekharan Nair. 1969. Food and feeding habits of the demersal fishes of Bombay. Indian J. Fish. 16:56-74.
53. Thomson, J.M. 1959. Some aspects of the ecology of Lake Macquarie, N.S.W., with regard to an alleged depletion of fish. IX. The fishes and their food. Aust. J. Mar. Freshwater Res. 10(3):365-374.
54. Tiews, K., P. Divino, I.A. Ronquillo and J. Marques. 1972. On the food and feeding habits of eight species of Leiognathus found in Manila Bay and San Miguel Bay. Proc. Indo-Pacific Fish. Counc. 13(3):93-99.
55. Tiews, K., J.A. Ordonez and I.A. Ronquillo. 1972. On the benthos biomass and its seasonal variations in Manila Bay and San Miguel Bay and a comparison of their foraminiferan fauna. Proc. Indo-Pacific Fish. Counc. 13(3):121-138.
56. Tiews, K., I.A. Ronquillo and P. Caces-Borja. 1972. On the biology of roundscads (Decapterus Bleeker) in the Philippine waters. Proc. Indo-Pacific Fish. Counc. 13(2):82-106.

57. Tiews, I., A. Mines and I.A. Ronquillo. On the biology of Saurida tumbil (Bloch, 1801) family Synodontidae in Philippine waters. Proc. Indo-Pacific Fish. Council. 13(3):100-120.
58. Tham, Ah Kow. 1950. The food and feeding relationships of the fishes of Singapore Straits. Colonial Office Fishery Publ. 1(1):35 p.
59. van der Elst, R.P. 1976. Game fish of the east coast of Southern Africa. I. The biology of the elf, Pomatomus saltatrix (Linnaeus) in the coastal waters off Natal. Ocean Res. Inst. Invest. Rep. South Africa (44):1-59.
60. Venkataraman, G. 1960. Studies on the food and feeding relationships of the inshore fishes off Calicut on the Malabar Coast. Indian J. Fish. 7(2):275-306.
61. Venkataraman, R.S. 1944. Food of ribbon fishes. Curr. Sci. (India) 13(9):239.
62. Westerhagen, H. von. 1973. The natural food of the rabbitfish Siganus oramin and S. striolata. Mar. Biol. 22:367-370.