

Trophic Modelling of Marine Ecosystems and Ecosystem-Based Fisheries Management

K. Sunil Mohamed

Head, Molluscan Fisheries Division
Central Marine Fisheries Research Institute [CMFRI]
PO Box 1603, Cochin 682018, Kerala
Email: ksmohamedfalvsnl.com; mfdcmfri@vsnl.com

Fish populations are an integral part of marine ecosystems. Historically, fish population dynamics have been studied in relation to a single species; for example, mackerel, shrimp or sardine, and almost always in isolation from the system in which they exist. In recent years, however, there has been growing awareness that the aforesaid traditional approach towards managing fisheries is incomplete and partially unsuccessful. Sustainable use of living marine resources must consider both the impacts of the ecosystem on the living marine resources, and the impacts of fishery on the ecosystem. This holistic approach to fisheries management has been termed as "ecosystem based fisheries management".

The Principles of Ecosystem-Based Fisheries Management are: 1) The focus for management of fisheries has to be maintained on natural structure and function of ecosystems, including the biodiversity and productivity of natural systems and identified important species; 2) Human use and values of ecosystems are central to establishing objectives for use and management of natural resources; 3) Ecosystems are dynamic; their attributes and boundaries are constantly changing and consequently, interactions with human uses also are dynamic; 4) Natural resources are the best managed within a management system that is based on a shared vision and a set of objectives developed amongst stakeholders; and 5) Successful management is adaptive and based on scientific knowledge, continual learning and embedded monitoring processes.

A lot of attention has been directed recently at assessing the impacts of fisheries on whole marine ecosystems (ICES, 1998, 2000; Frid *et al.*, 1999b; Hall, 1999a, b). This has in part been driven by the need to ensure conservation of biological diversity and sustainable use of the biosphere, and key provisions of the convention agreed at the UN Rio summit (Tasker *et al.*, ; 2000). The utilisation of

sound ecological models as a tool in the exploration and evaluation of ecosystem health and state has been encouraged and endorsed by the leading bodies in ecosystem-based fisheries research and management (NRC, 1999; ICES, 2000). The potential of the available dynamic ecosystem models to make measurable and meaningful predictions about the effects of fishing on ecosystems has not however been fully assessed.

Ecological Factors

Harvesting alters ecosystem structure in ways that are only beginning to be understood. It is argued that long-term heavy commercial harvesting is likely to shift the ecosystem to high-turnover species with low trophic levels (Pitcher and Pauly, 1998). The biological mechanism underlying species shifts is that the relatively large, long-lived fishes, which have low mortality rates, are more strongly affected by a given fishing mortality rate than are smaller fishes which are part of the same community. A second shift-inducing biological mechanism is due to habitat degradation, caused by various fishing gears, especially bottom trawls. Here, the effect is through destruction of bottom structure, depriving benthic fishes of habitats and prey.

Thirdly, the above and the fishery-induced predatory pressure by benthic fish may then lead to an increase of small pelagic fish and squids, which becomes available for exploitation. This may mask the decline in catches of the demersal groups. In the Gulf of Thailand, in Hong Kong Bay and other areas of the South China Sea, extremely heavy trawling pressure has resulted in a shift from valuable demersal table fish such as croakers, groupers and snappers to a fishery dominated by small pelagics used for animal feed and invertebrates such as jellyfish and squids.

These mechanisms almost often lead, through a positive feedback loop, to a

fourth biological mechanism: harvesting small pelagic fish species at lower trophic levels reduces the availability of food for higher trophic levels, which then decline further, releasing more of prey for capture by a fishery that finds its targets even lower down the food web, a process now occurring throughout the world (Pitcher and Pauly, 1998). Some examples of such documented species shifts in exploited multispecies fish communities are shown in Table-1.(Next page).

It has also been observed that fishes evolve or change their life histories in response to selective fishing mortality, for e.g., halving of the size of mature Chinook salmon. In this semelparous species early maturity means less time at risk of being caught and therefore, higher fitness. This species has been intensively managed for over 80 years using the best that single species quantitative science can offer, and yet Chinook salmon are on decline.

Socio-Economic Factors

One of the main socio-economic mechanisms, which contribute to species shift is increasing prices, both for traditional high-value species and for trash species. Such price increases are effective in masking the economic consequences of fishing at lower trophic levels.

Single Species Assessments

The tools developed for single species population dynamics are an essential part of any new methodology. Detailed information on growth, mortality and recruitment schedules and their associated errors and uncertainties are essential for the implementation of the ecosystem approach advocated in the Rio summit.

When considering the management of single components of the ecosystem, such as the target fish stocks, it is possible to set target and limit reference points for particular measurable properties of the species. For example, the implementation

Table 1: Examples of documented shifts towards smaller, high-turnover species in exploited multispecies communities (modified from Pitcher and Pauly, 1998)

Fishing grounds/ Stocks (period)	Documented species shift
Gulf of Thailand Demersal stocks (1960-1980)	Overall biomass reduced by 90%; residual biomass dominated by trash fish
Philippine Shelf Small pelagics (1950-1980)	Gradual replacement of sardine-like fishes by anchovies
Carigara Bay, Philippines All fish (1970-1990)	Fish replaced by jellyfish, now an export item
Black Sea North Sea	Small pelagics and jellyfish replace large table fish Halibut and small sharks extinct; cod and haddock threatened; demersal omnivores and small pelagics favoured
Humboldt Current, Chile	Large hake depleted, small pelagics favoured
North Pacific	First marine mammal depletions, followed by huge trawl fisheries: Pollock favoured
South China Sea, Hong Kong	Croakers and groupers almost extinct; small pelagics form bulk of fishery

of precautionary fisheries management in the North Atlantic has progressed through the setting of reference points for various measures of the status of the exploited species, e.g. the spawning stock biomass (SSB). Two types of reference points are considered. These are; a limit reference points and a target reference point (Fig.1). Management measures are aimed at achieving the target reference point in the medium term and ensuring that the limit reference point is never exceeded.

In theory, it should be possible to apply reference points to any or all taxa in the ecosystem. ICES (2000) have contended that even if this was practical for a significant number of taxa, it may not ensure adequate protection of all the ecosystem components at risk. There is a need, therefore, to develop reference points for system level emergent properties as a measure of ecosystem health (Hall, 1999a; Gislason et al., 2000).

Ecosystem Modelling

There are many recent developments in the building of trophic models of aquatic ecosystems. Such modelling can now be performed more rapidly and rigorously than ever before, providing a basis for viable and practical simulation models that have real predictive power (Christensen and Pauly, 1993; Walters et al., 1997). This was made possible by the development of

ECOPATH (Polovina, 1984; Christensen and Pauly, 1992), for construction of mass-balance models of ecosystems, based mainly on diet composition, food consumption rates, biomass and mortality estimates.

Such ecosystem models can describe the biomass flows between the different elements of the exploited ecosystems, and can provide answers to 'what if' questions regarding the likely outcome of alternate

fishing policies. The ECOPATH route of software has now been modified (Walters et al., 1997, 2000) to include ECOSIM (simulation module) and ECOSPACE (spatial module). These new routes have not only increased the quantitative power of the approach, but have also allowed qualitatively new questions to be asked.

Ecopath applications to ecosystems, ranging from cold latitude areas to the tropics, and from ponds, rivers, and lakes to estuaries, coral reefs, shelves, and the open sea, but all using the same metrics, allowed identification of several general features of aquatic ecosystems:

Multivariate comparisons demonstrated the basic soundness of E. P. Odum's (1969) theory of eco-system maturation (Christensen, 1995b), including a confirmation of his detailed predictions regarding ecosystems near carrying capacity (Christensen and Pauly, 1998). Conversely, this theory can now be used to predict the effect of fisheries on ecosystems, which tend to reduce their maturity, as illustrated by the comparison of Ecopath models for the Eastern Bering Sea in the 1950s and early 1990s (Trites et al., 1999a, b), and to guide ecosystem rebuilding strategies implied in "Back to the Future" approaches (Pitcher, 1998; Pitcher et al, 2000).

The importance (relative to fishing) of predation by fish and marine mammals within marine ecosystems as suggested by complex models in a few areas (North Sea

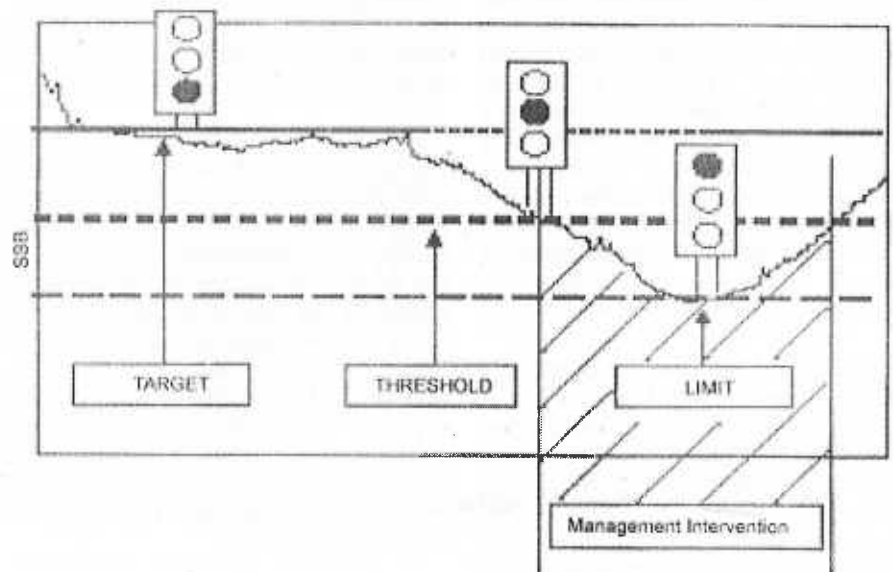


Fig.1: Illustration of target, threshold and limit reference points with regard to spawning stock biomass (from Hall and Mainprize, 2004)



- Andersen and Ursin, 1977; North Pacific - Laevastu and Favorite, 1977) was confirmed globally by Ecopath models (Christensen, 1996; Trites *et al*, 1997).

Identification of trophic levels as functional entities rather than as concepts for sorting species (Lindeman, 1942; Rigler, 1975) implied the use of non-integer values computed as 1+ the mean trophic level of the preys, as proposed by Odum and Heald, (1975) that express degree of omnivory (Christensen and Pauly, 1992a), i.e., the extent to which feeding occurs at different trophic levels (Pimm, 1982). Also, trophic level estimated from analyses of stable isotopes of nitrogen has been shown to correlate well with estimates from Ecopath models (Kline and Pauly, 1998).

Estimates of transfer efficiencies between trophic levels (Christensen and Pauly, 1993b; Pauly and Christensen, 1995), previously a matter of conjecture usually pertaining to single-species populations or even to studies of a few individual animals (Slobodkin, 1972), differed radically from earlier guesses by ecosystem types (Ryther, 1969) used for inferences on the potential yields of fisheries (Pauly, 1996), even though the mean was unsurprising (about 10%; Morowitz, 1991).

Performance Measures

It is generally agreed that reductions in single species fishing mortality levels is perhaps the most significant step one could

take towards ensuring the persistence of marine ecosystems (Hall and Mainprize, 2004). It is also clear that ecosystem based fisheries management is still in its formative years, although substantial developments have been seen in some countries and regions. Among these, North America, Antarctica, Europe, Australia and New Zealand are the most notable.

Unfortunately, despite the legislative imperative and clearly articulated principles (Table 2), arriving at an operational framework for an ecosystem-based approach to fisheries management is fraught with difficulties. This difficulty is due, not only to the inherent challenge in establishing and quantifying the effects of fishing at an ecosystem level, but also due to the social and political dimensions associated with harvesting fisheries at an environmentally sustainable level.

An Overview of ECOPATH & ECOSIM

The ECOPATH software is a simple approach for analysing trophic interactions in fisheries resources systems (Christensen and Pauly 1992 a,b, 1995). ECOPATH is based on the earlier work of Polovina (1984), and is being widely applied to aquatic systems (Christensen and Pauly 1993, Pauly and Christensen 1995). It is a mass-balance approach that describes an ecosystem at a steady-state for a given period. Further development of this steady-state model has resulted in a dynamic ecosystem model called ECOSIM that is capable of simulating ecosystem

changes over time (Walters *et al.*, 1997). ECOPATH and ECOSIM represent all of the major components of the ecosystem and their feeding interactions, but are relatively simple. These kinds of models readily lend themselves to answering simple, ecosystem wide questions about the dynamics and the response of the ecosystem to anthropogenic changes. Thus, they can help design policies aimed at implementing ecosystem management principles, and can provide insights into the changes that have occurred in ecosystems over time. ECOPATH models rely on the truism that:

$$\text{Production} = \text{biomass accumulation} + \text{fisheries catch} + \text{mortality due to predation} + \text{other mortality} + \text{loss to adjacent systems.}$$

This applies for any production (e.g., a given fish population) and time (e.g., a year or season). Groups are linked through predators consuming prey, where:

$$\text{Consumption} = \text{production} + \text{non-assimilated food} + \text{respiration.}$$

The implication of these two relationships is that the system or model is mass balanced (i.e., biomass is 'conserved', or accounted for in the ecosystem). This principle of mass conservation provides a rigorous framework formalised through a system of linear equations through which the biomass and trophic fluxes among different consumer groups within an ecosystem can

Table 2. The six principles for an ecosystem based fisheries management approach (adapted from Inter-agency Marine Fisheries Working Group, 2002)

Principle	Description
Ecosystem identification	The ecosystem that fisheries will be managed within need to be defined on the basis of the main physical, biological and human dependency relationships.
Clear objectives	Objectives for fisheries management shall have regard to local and national needs, and management should be decentralized to the maximum extent possible
Long term benefits	Ecosystem based management should aim at long term benefits - management should look to restore stocks to levels that are capable of delivering optimal yields over the long term; and achieving such yields should not compromise other marine species and habitats. Management should also aim to support biological biodiversity.
Incentives aligned with an Ecosystem based approach	Incentives should be realigned to support aims of the approach. Incentives and financial support needs to be redirected from fisheries that aim at increasing fishing efficiency to those that make concerted efforts to those that promote the restoration of fish stocks to optimal yield levels and which support responsible fishing practices in sensitive marine areas
Easily assessed information and alternate management options	Information necessary to implement the ecosystem- based approach should be made available to all. Where information is insufficient, adaptive management and the precautionary approach should be followed. If the outcome falls short of what was intended, the management decisions should be suitably altered - proactive management.

be estimated (Christensen and Pauly 1995). Constructing an ECOPATH model emphasises ecological relationships rather than mathematical equations. All that is required are the types of data that is routinely collected by fisheries scientists and marine biologists. The model can incorporate and standardise large amounts of scattered information, information that might have otherwise languished in scattered journals, reports and filing cabinets (Christensen and Pauly 1995).

ECOPATH is essentially a large spreadsheet that is simultaneously keeping track of all the species and all the feeding interactions occurring within the ecosystem. It describes the ecosystem at one point in time. ECOSIM, which is based on the ECOPATH equation, simulates how a change in one or more components might affect the ecosystem over time.

ECOPATH and ECOSIM have been widely applied in recent years. Over 80 ECOPATH systems have so far been published world-wide. They span a diversity of systems including upwelling, shelves, lakes and ponds, rivers, open oceans and even terrestrial farming systems (see Christensen and Pauly 1992a,b, 1995; Walters *et al.* 1997; and the ECOPATH home page at <http://www.ecopath.org>).

Principles of the ECOPATH Model

The core routine of ECOPATH is derived from the ECOPATH programme of Polovina (1984), and since modified to make superfluous its original assumption of steady state. ECOPATH no longer assumes a steady state but instead bases the parameterisation on an assumption of mass balance over an arbitrary period, usually a year. In its present implementation, ECOPATH parameterises models based on two master equations, one to describe the production term and one for the energy balance for each group.

The first ECOPATH equation describes how the production term for each group (i) can be split in components. This is implemented with the equation, Production = catches + predation mortality + biomass accumulation + net migration + other mortality;

or, more formally,

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1-EE_i)$$

Eq.1 where P_i is the total production rate of (i), Y_i is the total fishery catch rate

of (i), $M2_i$ is the total predation rate for group (i), B_i the biomass of the group, E_i the net migration rate (emigration - immigration), BA_i is the biomass accumulation rate for (i), while $MO_i = P_i \cdot (1-EE_i)$ is the other mortality rate for (i).

This formulation incorporates most of the production (or mortality) components in common use, perhaps with the exception of gonadal products. Gonadal products however nearly always end up being eaten by other groups, and can be included in either predation or other mortality. Eq. 1 can be re-expressed as

$$P_i \cdot (P/B)_i - EE_i - \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0$$

where: P/B_i is the production/biomass ratio, Q/B_j is the consumption / biomass ratio, and DC_{ji} is the fraction of prey (i) in the average diet of predator (j).

Of the terms in Eq. 2 the production rate, P_i , is calculated as the product of B_i , the biomass of (i) and P_i/B_i , the production/biomass ratio for group (i). The P_i/B_i rate under most conditions corresponds to the total mortality rate, Z [see Allen 1971], commonly estimated as part of fishery stock assessments. The other mortality is a catch-all term including all mortality not elsewhere included, e.g., mortality due to diseases or old age, and is internally computed from,

$$MO_i = P_i(1-EE_i)$$

Where EE_i is called the ecotrophic efficiency of (i), and can be described as the proportion of the production that is utilised in the system. The production term describing predation mortality, $M2$, serves to link predators and prey as,

$$M2_i = \sum_j Q_j \cdot DC_{ji}$$

Eq.3 Where the summation is over all (n) predator groups (j) feeding on group (i), Q_j is the total consumption rate for group (j), and DC_{ji} is the fraction of predator (j) diet contributed by prey (i). Q_j is calculated as the product of B_j , the biomass of group (j) and Q_j/B_j , the consumption / biomass ratio for group (j).

An important implication of the equation above is that information about predator consumption rates and diets concerning a given prey can be used to estimate the predation mortality term for the group, or, alternatively, if the predation mortality for a given prey is known the equation can be used to estimate the consumption rates for one or more predators instead.

For parameterisation, ECOPATH sets up a system with (at least in principle) as many linear equations as there are groups in a system, and it solves the set for one of the following parameters for each group:

- biomass;
- production/biomass ratio;
- consumption/biomass ratio; or
- ecotrophic efficiency.

while the other three parameters along with following parameters must be entered for all groups:

- catch rate;
- net migration rate;
- biomass accumulation rate;
- assimilation rate; and
- diet compositions.

It was indicated above that ECOPATH does not rely on solving a full set of linear equations, i.e., there may be less equations than there are groups in the system. This is due to a number of algorithms included in the parameterisation routine that will try to estimate iteratively as many missing parameters as possible before setting up the set of linear equations.

ECOSIM - Dynamic mass-balance approach for Ecosystem Simulation

By converting the linear equations of ECOPATH models to differential equations, ECOSIM provides a dynamic mass-balance approach, suitable for simulation (Walters *et al.* 1997). In constructing a dynamic model from equation (1) there are three changes viz; (a) replace the left side with a rate of change of biomass; (b) for primary producers, provide a functional relationship to predict changes in (P/B_i) with biomass B_i (representing competition for light, nutrients and space); and (c) replace the static pool-pool consumption rates with functional relationships predicting how consumption will change with changes in biomass of B_i and B_j . The basics of ECOSIM consist of biomass dynamics expressed through a series of coupled differential equations. Using equilibrium simulations, where equilibrium biomass is plotted over a range of F values, ECOSIM provides the facility to predict the potential equilibrium yield for the fished group.

Trophic Modelling Studies in India

Trophic modelling studies in Indian aquatic ecosystems are few. The first preliminary attempt was made in small ecosystem in Veli Lake near Thiruvananthapuram. Subsequently another preliminary attempt was made to model the



Ecosystems	Through Put	Catch pp	PP/B	Table- 3		Net syst. prod	Omnivory Index	Ascen- dency	Cycling Index	Path length
				B/T						
Yacutan	2362	0.0029	27.4	0.036		370	0.134	44.0	2.8	2.84
N. Gulf of Mexico	1790	0.0002	7.0	0.015		19	0.195	39.1	2.1	3.03
Venezuela(upwell.)	5309	0.0016	27.0	0.023		831	0.135	39.9	2.2	4.05
Brunei, SE Asia	1816	0.0008	28.6	0.018		300	0.201	29.4	16.3	2.80
Peru 70(upwell.)	18800	0.0017	87.5	0.012		14709	0.169	38.1	8.7	3.63
Monterey	17513	0.0012	1.2	0.012		2208	0.324	66.2	4.4	3.63
Alaska Gyre	5946		38.1	0.015		407	0.103	42.3		2.03
British Columbia Shelf	1237		21.1	0.180		4106	0.140	40.1		2.03
Bering Sea 50's	6535	0.0002	5.9	0.050		-115	0.183	32.5	13.2	3.47
Bering Sea 80's	5692	0.0021	4.9	0.050		-356	0.157	30.9	11.1	3.51
Karnataka	11522	0.0016	29.9	0.012		904	0.299	33.0	6.03	2.81
Arabian Sea										

At present the scientists of the CMFRI are engaged in modelling two major ecosystems, namely, the Gulf of Mannar and Northwest Coast of India including the Gulf of Kutch.

southwest coast ecosystem using already existing data and many assumptions (Vivekanadan *et al.*, 2003). The first major targeted attempt to study was that of the model for the Arabian Sea off Karnataka (Mohamed *et al.* 2005). This ECOPATH model had a pedigree index of 0.521 (scale from 0 for data that is not rooted in local data up to a value of 1 for data that are fully rooted in local data). The Karnataka model encompassed an area of 27,000 km² (from the shore to the edge of the continental shelf) and had 24 functional ecological groups (species assemblages) of which 23 were living groups and one dead group (detritus). Ecological groups ranged from apex predators like marine mammals, sharks and tunas to micro zooplankton and phytoplankton.

A comparison of ecosystem parameters from other parts of the world is given in table below (modified from Trites *et al.*, 1999). The total throughput for the Arabian Sea ecosystem of Karnataka ranks third after Peru and Monterey Bay and is double of that of Bering Sea and Venezuela upwelling ecosystem. The gross efficiency of the fishery (catch/PP) value obtained for Karnataka is close to that of the Peruvian ecosystem, which is also an upwelling ecosystem, harvesting fishes low in the food chain. The omnivory index is quite high comparatively for the Karnataka ecosystem indicating the complex feeding interactions in the ecosystem. The estimated ascendancy values for the Arabian Sea ecosystem of Karnataka indicate that it has not reached its full development capacity, unlike the Yacutan and Monterey Bay ecosystems. The recycling capacity of the ecosystem throughput as indicated by the cycling index shows that recycling in Arabian Sea ecosystem of Karnataka is only moderate

as compared to ecosystems like those in Brunei and Bering Sea.

References

- CHRISTENSEN, V. 1995b. Ecosystem maturity -towards quantification. *Ecol. Modelling* 77:3-32.
- CHRISTENSEN, V. 1996. Managing fisheries involving predator and prey species. *Reviews in Fish Biology and Fisheries*, 6:417-442.
- CHRISTENSEN, V. and PAULY D. (eds.) 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings No. 26. ICLARM Manila, Philippines, 390p.
- CHRISTENSEN, V. and PAULY, D. 1992a. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Modelling* 61:169-185.
- CHRISTENSEN, V. and D. Pauly. 1992b. A guide to the ECOPATH II program (version 2.1). ICLARM Software 6, 72 p.
- CHRISTENSEN, V. and PAULY D. 1993. Flow characteristics of aquatic ecosystems, p. 338-352. In V. CHRISTENSEN and D. PAULY (eds.) Trophic models of aquatic ecosystems. ICLARM Conference Proceedings No. 26, 995.
- CHRISTENSEN, V. and PAULY, D. 1995. Fish production, catches and the carrying capacity of the world oceans. *Naga*, The ICLARM Quarterly 18(3):34-40.
- CHRISTENSEN, V. and Pauly, D. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. *Ecological Applications*, 8(1), (Suppl): 104-109.
- CHRISTIANSEN, V., WALTERS, C.J and D. PAULY, 2000. ECOPATH with ECOSIM: A User's Guide, October 2000, Fisheries Centre, University of British Columbia, Vancouver, Canada and International Center for Living Aquatic Resources Management (ICLARM), Penang, Malaysia. 125p.
- FINN, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol.* 56: 363-380.
- FRID CLJ, HANSSON RAGNARSSON SA, RIJNSDORPA, and (SA) RIJNSDORPA, and STEINGNMSSON, (SA) 1999b. Changing levels of predation on benthos as a result of exploitation of fish populations. *Ambio* 28: 578-582.
- HALL, S.J. 1999a. The effects of fishing on marine ecosystem and community. Blackwell Science, Oxford.
- HALL, S.J. 1999b. Managing fisheries within ecosystems: can the role of reference points be expanded? *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 579-583.
- HALL, S. J and B. MAIRIPRIZE. 2004. *Towards ecosystem-based fisheries management* Blackwell Ltd. Fish and Fisheries, 5, 1-20.
- HANNON, B. and C. JOIRIS. 1989. A seasonal analysis of the southern North Sea ecosystem. *Ecology* 70(6):1916-1934.
- HANNON, B., 1973. The structure of ecosystems. *J. Theor. Biol.* 41:535-546.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59:67-77.
- ICES. 1998. Report of the Working Group on the Ecosystem Effects of Fishing Activities ICES, Copenhagen, ICES CM 1998/ACFM/ACME: 01 Ref. E, 263pp.
- ICES 2000. Ecosystem effects of fishing. In: *ICES Marine Science Symposia*. 210. ICES Journal of Marine Science 57, 791.
- IVLEV, V.S. 1961. Experimental ecology of the feeding of fishes (Transl. by D. Scott). Yale University Press, New Haven, 302 p.
- KAVANAGH, P. 2002. Automated Mass Balance Procedure for ECOPATH Ecosystem Models User's Guide. Fisheries Centre, University of British Columbia. 28p.
- KLINE, T.C. Jr, and D. PAULY. 1998. Cross-validation of trophic level estimates from a mass-balance model of Prince William