# LARGE MARINE ECOSYSTEMS: ANALYSIS AND MANAGEMENT 

D. PAULY*


#### Abstract

This contribution articulates a series of research issues concerning the definition, study and management of Large Marine Ecosystems (LMEs) and of the fisheries resources therein. The 57 biochemical provinces of Longhurst (1995, Progress in Oceanography 36) are suggested as standard for all global stratification of the world's oceans, because these "Longhurst areas", contrary to traditionally defined LMEs, permit direct comparisons of results from different disciplines. Examples of such comparisons, emphasizing the competition between fisheries and marine mammals, are given for the Pacific Ocean. The case is made that methods exist for rigorous descriptions of the trophic fluxes prevailing in such ecosystems, and based thereon, for dynamic modelling of at least the first-order impacts of fisheries on LMEs. Also, emphasis is given on the need to reconstruct the earlier, unexploited states of ecosystems so as to obtain baselines for correctly evaluating fisheries impacts, and to evaluate the benefits foregone by present exploitation patterns. The need for fisheries scientists to reconceive their work from one principally devoted to optimizing short- and medium-term returns to the fishing industry to one serving a broader set of clients is emphasized. A recent initiative, the Marine Stewardship Council, serves as an example of the many new approaches that will be required if the public at large is to become an active stakeholder in conserving the biodiversity of LMEs.


The world's marine fisheries currently generate a catch of about 150 million tons per year, about 90 million tons of nominal catch reported by individual countries to the Food and Agriculture Organization of the United Nations (Garcia and Newton 1997), 20-30 million tons of discarded by-catch (Alverson et al. 1994) and the remainder a (probably low) estimate of unreported/illegal catches. Detailed analyses of these figures, in view of understanding the dynamics of world fisheries, and predicting their future evolution, requires a stratification scheme permitting comparisons among areas. Large Marine Ecosystems (LMEs) may serve for this purpose, because many biological processes relevant to the sustainability of marine fisheries are ecosystem processes, occurring on a large scale.

However, the LME concept is rather amorphous, in spite of a series of proceedings having been devoted to it (Sherman and Alexander 1986, 1989, Sherman et al. 1990, 1991, 1993). This amorphous nature is not due to a lack of dictionary-type definitions - many have been proposed. Rather it is due to the lack of a functional definition, i.e. the type of definition that, in a given discipline, allows people to work, publish and understand what their colleagues are talking about, to do "normal science" sensu Kuhn (1970). Indeed, close study of the above-cited series of proceedings will show that, notwithstanding existing definitions and list of LMEs (Sherman 1993), their coverage is
entirely based on authors contributions, and not on $a$ priori definitions of LMEs based on, say, biogeographic or oceanographic considerations. This leads to minor irritants (e.g. the Gulf of Thailand being treated, in the same proceedings series, as an LME by Piyakarnchana [1989] and as a component of the South China Sea by Pauly and Christensen [1993]), and to serious problems when attempts are made to raise ocean fluxes estimated at the LME level to the world's oceans.

An important element of a functional definition of LMEs is that they must identify real ecosystems, i.e. entities with identifiable boundaries, internally homogenous, and whose internal fluxes are much higher than their exchanges with adjacent entities. These criteria exclude, for example, the 18 large areas which FAO uses to stratify the world's oceans (Fig. 1) and used to generate global figures such as those cited above.

To address these, and similar issues raised in Bakun (1985), Longhurst (1995) provided a framework for comparative studies of ocean processes in the form of 57 "biochemical provinces", with boundaries defined by oceanographic structures that generate distinctive patterns of nutrient fluxes. For comparative work on LMEs, there would be great benefit in the use of the framework provided by these 57 provinces (Fig. 2). Recent work by Longhurst et al. (1995) on global primary production, and by Fonteneau (1997) on global tuna catches, illustrate the usefulness of these standardized areas.

[^0]

Fig. 1: Global system of statistical areas used by the Food and Agriculture Organization of the United Nations (FAO) to stratify the world's oceans, and here allows direct comparison of surface areas


Fig. 2: Stratification of the world's oceans proposed by Longhurst (1995) based on 57 "biochemical provinces" whose boundaries define Large Marine Ecosystems. As opposed to Mercator's, the Peter's projection used here allows direct comparison of surface areas

## STUDYING THE ECOSYSTEM NATURE OF LONGHURST AREAS

To study the ecosystem nature of LMEs and Longhurst areas, it is first necessary to deal with the internal fluxes of such ecosystems. What are these fluxes? In this paper, the focus will be on fluxes of organic carbon (and/or biomass, a close correlate) from primary producers up various foodwebs to top predators and fisheries.

The key input into LMEs, the flux generated by primary production, has been recently re-estimated as $45-50$ GtonsC•year ${ }^{-1}$ for the world's oceans as a whole (Longhurst et al. 1995), much higher than the 12-15 GtonsC•year- ${ }^{-1}$ estimated by Steemann Nielsen and Jensen (1957), and even than the much-cited 23 GtonsC•year ${ }^{-1}$ estimated by Koblents-Mishke et al. (1970; see, for example, FAO 1971). The key outputs of LMEs are the $150 \times 10^{6}$ tons year ${ }^{-1}$ mentioned above as taken by fisheries, and $400-500 \times 10^{6}$ tons•year ${ }^{-1}$ taken by marine mammals (see below).

To study how the primary production input into the world's oceans is turned into output, it is necessary to
study the foodwebs that turn primary production into harvestable biomass. This is illustrated herein through some preliminary studies pertaining to the Pacific Ocean, as stratified by FAO areas, and soon to be extended to the world's oceans, using Longhurst areas for stratification.

Figure 3 shows an example of the basic structure of the foodwebs in FAO area 77, the Central Eastern Pacific. This allows, among other things, differentiating the strands leading to the fisheries and the marine mammals. The transfer efficiency between trophic levels can be calculated from the quantified flows in such graphs (Christensen and Pauly 1992), as can a number of other important holistic features of the ecosystems so represented (Wulff et al. 1989).

Figure 4 illustrates the concept of primary production required to support top predators, and its implications in terms of what may be called "foodweb competition". This concept is developed in Figure 5, suggesting that, in the Pacific, the primary production required to sustain the fisheries is incompatible with the large biomass of marine mammals, which consume $150 \times 10^{6}$ tons $\cdot$ year ${ }^{-1}$ of food per year there (Trites et al. in press) and about three times that on a



Fig. 4: Schematic representation of the food pyramids that emerge when the fluxes required to sustain top predators (or a fishery) are followed, via transfer efficiencies of $10 \%$, all the way down to the primary producers. Note the potential overlap at the level of the primary production required (PPR), even in cases when, for example, marine mammals and fisheries do not exploit the same groups
global basis. An attempt is now being made to verify these results by re-expressing them on the basis of Longhurst areas (which should lead to more natural groupings of fisheries and mammal species assemblages), and for the world as a whole.

Studying LMEs as true ecosystems involves more, however, than input-output analyses: notably, it implies paying attention to the detailed structure of the foodweb mediating between the input and the outputs. Foodwebs quantifying the fluxes between a number of functional groups (i) can be straightforwardly constructed for any period for which sufficient data are available by the system of linear equations:

$$
\begin{equation*}
B_{i}(P / B)_{i} E E_{i}=Y_{i}+\sum_{j=1}^{k} B_{j}(Q / B)_{j} D C_{j i} \tag{1}
\end{equation*}
$$

where $B_{i}$ is the biomass of group $(i)$ and $B_{j}$ that of its consumers during the period in question;
$P / B_{i}$ is the production/biomass ratio of $i$, equivalent to its total mortality (Allen 1971);
$E E_{i}$ is the fraction of its production consumed (or caught) within the system;
$Y_{i} \quad$ is its fishery catch (equivalent to $F_{i} B_{i}$ );
$Q / B_{i}$ is the consumption/biomass ratio of its $k$ consumers; and
$D C_{j i}$ is the fraction of $i$ in the diet of $j$.
Such a system of equations consists (except for $E E_{i}$ ) of quantities that are routinely estimated by fishe-


Fig. 5: Primary production (PP) required in the Pacific Ocean to sustain the fisheries and marine mammals they are inversely related (after Trites et al. in press)
ries and/or marine biologists, and a large published database of generic values exists to complement locally derived data sets. Solving this system of equations (which for example allows estimation of the $E E_{i}$ value, by leaving them as unknowns) can be done by the use of any matrix inversion routine, such as that incorporated in the Ecopath software, which includes numerous routines for the analysis of the fluxes and biomass so estimated (Christensen and Pauly 1992, 1995). The straightforwardness of this approach is the reason why nearly 100 Ecopath models now exist, describing freshwater and marine systems, with the latter ranging from smaller areas to LMEs.
A number of generalizations has emerged from these models that are relevant to an understanding of their functioning. For, example, Figure 6 shows that, in LMEs, it is mostly fish that consume the bulk of fish production, although there are exceptions, e.g. the upwelling ecosystem off Namibia, where the fisheries catch is more than is consumed internally. Another generalization is that, in aquatic ecosystems, $10 \%$ is a good estimate of mean transfer efficiency between trophic levels (Pauly and Christensen 1995), so confirming earlier guesses by, for example, Slobotkin
(1980). On the other hand, this invalidates earlier guesses, e.g. by Ryther (1969), of 15 and $20 \%$ for coastal and upwelling systems respectively. Indeed, it is the upwelling ecosystems which tend to have low transfer efficiencies (Jarre-Teichmann 1992, Pauly 1996).

Yet another generality is that the trophic levels of exploited organisms in LMEs range from 2 (for strict herbivores) to 4 for tuna and other near-top predators. This value, combined with global catches by group of species (FAO 1996), the $10 \%$ transfer efficiency alluded to above and the principle illustrated in Figure 4 , allows estimation of the primary production required to sustain global fisheries as $8 \%$ of global primary production. However, this value is computed from two very unequal parts, one of $2 \%$ for large oceanic systems, in which about $10 \%$ of global catches are taken, the other of $25-35 \%$ for the smaller shelves and upwelling systems, from which the other $90 \%$ of global fisheries catches originate (Pauly and Christensen 1995). The latter figure, pertaining to systems fully exposed to human impacts, is close to the estimate of $35-40 \%$ of terrestrial primary production currently appropriated by humans (Vitousek et al. 1986), a


Fig. 6: Fate of fish production in four large marine ecosystems, as assessed using Ecopath models of their foodwebs (see Pauly and Christensen [1995] for sources). Note large role of "internal" consumption by fish
frightening reminder that the Earth's carrying capacity is not only finite, but that we are closing in on it.

Another way of assessing human impacts on LMEs, once they are described using the system of massbalance equation in (1), is to re-express them as a system of ordinary differential equations, viz:

$$
\begin{equation*}
d B / d t=\left(B_{i}\left\{P / B_{i}\right\} E E_{i}\right)-\left(F_{i} B_{i}+\sum_{j=1}^{k} B_{j}\{Q / B\}_{j} D C_{j i}\right),(2 \tag{2}
\end{equation*}
$$

whose parameters, defined as in Equation 1, can be estimated, for any period without biomass change, by setting $d B / d t$ to 0 , solving as for Equation 1, then integrating over time, with $F$ changing such as to simulate different fishing regimes (Walters et al. 1997).
A software package named Ecosim has been recently developed to read Ecopath files, and it implements Equation 2 in the form of dynamic simulation models that can be used to investigate the behaviour of any LME; first results of comparative studies based on this approach are already available (Mackinson et al. in press, Vasconcellos et al. in press).

For example, the effects were studied of a 10-year
pulse ( $5 \times$ baseline $F$; Fig. 7) applied to the small pelagic group of 15 marine ecosystems, i.e. to the group that, in most of these systems, transfers the bulk of primary and secondary production to the upper trophic levels (Csirke 1988, Bakun 1996).

Figure 8 shows that, in these systems, recovery time is closely related to the percentage of total detritus flux recycled (Vasconcellos et al. in press), a finding predicted by the leading theory of ecosystem development (Odum 1969). This is encouraging enough to make one disagree with those who question the present ability to understand even first-order ecosystem responses to perturbations, and hence the ability to manage ecosystems.

## LMEs AS (MIS)MANAGED ECOSYSTEMS

Criticism of the concept of ecosystem management, besides noting its undeniable buzzword nature, generally focuses on:


Fig. 7: Simulation of pulse fishing, i.e. a five-fold increase of baseline fishing mortality of a given group (here the small pelagics), for 10 years, using the Ecosim routine of Ecopath (Walters et al. 1997). System recovery time $\left(t_{3}\right)$ is defined as that required by the slowest group to return to baseline level of biomass ( $B$ )
(i) the "general lack of knowledge" about ecosystem functioning;
(ii) a history of failure to predict simple processes such as that which generates the production of single-species stocks;
(iii) the lack of tools with which to explore alternative management options and to quantify their benefits;
(iv) the lack of formal explicit goals for such management.

Rebutting such criticisms is not difficult. It is, for example, always true that knowledge is incomplete, and that the conceptual tools are inadequate to the task. Indeed, when knowledge is perfect, and the tools adequate, there is no Science, only Technology and Engineering, devoted to applying the codified knowledge and a set of standard tools to a specific job, e.g. building a bridge. The point about science is how irreducible uncertainty and a lack of adequate data and tools are dealt with creatively (Medawar 1967).

One ecosystem-based approach for dealing with problems (i) - (iii) above is to implement marine protected areas (MPAs) whenever fisheries have devel-
oped that are capable of exploiting the natural refuges that sustained earlier, less-developed fisheries, e.g. deep waters in the case of the recently collapsed cod around Newfoundland, Canada (Hutchings and Myers 1994), or heavily-structured sea bottom areas, now often flattened by heavy ground trawls. For such areas, suitably placed and sized MPAs should help rehabilitate most stocks, despite items (i) - (iii) above (Roberts et al. 1995). Thus, MPAs may be seen as an ecosystem management tool par excellence and the biological research agenda implied by MPAs (how large should they be, where should they be, how should they be monitored) is ecosystem management research.

As for item (iv), the lack of explicit goals for ecosystem management, I believe a major goal, even though many fisheries scientists are not yet ready to open their eyes to it, is the maintenance of marine biodiversity. Many governments have already committed themselves to this issue by signing and ratifying the International Convention on Biodiversity, and related documents.

Given the traditional clients of fisheries scientists, governments and the fishing industry, this goal may be viewed as contentious or even too "green" to be


Fig. 8: Relationships between Finn's index of detritus recycling (\% recycled relative to overall detritus flux) and system recovery time as defined in Figure 7. The 15 marine ecosystems represented by the dots are documented in Vasconcellos et al. (in press)
taken seriously. Yet the overwhelming bulk of the world's fisheries having overfished their resources base, increasing catches or even maintaining them can only be achieved by rehabilitating stocks, which itself can only contribute to maintaining and, in many cases, re-establishing marine biodiversity to those parts where excess fishing has reduced it. Indeed, a vision for fisheries science and for the work of individual fisheries scientists would be that, for all systems studied, all historical sources be identified which may help reconstruct the earliest possible stage of these ecosystems. Then, this information could be used, together with the biomasses and fluxes it implies, as baseline for evaluation of present management options. The reason for this suggestion is that currently it is the converse which applies. Every generation of (fisheries) scientists uses ecosystem states at the start of their careers as baseline, and largely ignores (or dismiss as "anecdotal") the work of the preceding generations (Pauly 1995). The result is a steady shift of baseline (Fig. 9).

Using earlier stages of ecosystem states as baseline for ecosystem rehabilitation would not only lead to
more biodiversity, but also to larger exploitable biomasses for most of the resources we fish. Indeed, "anecdotal" evidence suggests pre-exploitation biomass in many systems to be one order of magnitude higher than the biomass now (see, for example, MacIntyre et al. 1995).

It is straightforward to conceive high-biomass systems which would lead to larger yields than can be now obtained. These, given well regulated and smaller fisheries, would generate far more net social benefit then the present subsidy-guzzling overfisheries. In Figure 10, industrial overfisheries are contrasted with the smallscale fisheries of the past, and which should be brought back again. Such a transition could be particularly appropriate for the new, democratic South Africa.

For those who think such ideas are unrealistic, how realistic is it to assume that, in our greenhouse future, fisheries that burn up 80 tons of diesel fuel to catch 100 tons of fish, of which $80 \%$ consist of water, can be afforded? Further, how would the economy of these overfisheries look if they had to pay a carbon tax on top of the immense subsidies they generally now require to keep operating?


Fig. 9: Schematic representation of the shifting base syndrome of fisheries (Pauly 1995), wherein the rapid decline that occurred at low initial fishing mortalities, reported upon by an earlier generation of naturalists, or the first fisheries scientists, remains outside the experience of subsequent generations of fisheries scientists, who use later, already depleted states as reference for "unexploited stocks"

## TOWARDS A TRANSITION: A CONCLUSION AND A PLEA

A precondition for a change in the way fisheries are allowed to impact marine ecosystems is for the taxpaying public to be informed and involved, i.e. for fisheries scientists to realize that, ultimately, there are more clients for their services than the governments which employ them, and the industry which the governments try to regulate.
The public can be dismissed, but it can dismiss fisheries scientists too, for instance by electing politicians that will close down the government agencies employing fisheries scientists. Alternatively, the public, along with those NGOs that articulate public sentiments about the need to protect and rehabilitate marine resources, and that part of industry that lets its actions be guided by the enlightened form that self-interest can take, can be taken seriously.

To illustrate how this may occur, it is worth briefly mentioning an initiative, the Marine Stewardship Council (MSC), patterned after the Forestry Stewardship Council which, jointly with a multitude of other
initiatives, may help turn fisheries around and help rehabilitate marine ecosystems. The MSC, co-sponsored by the World Wildlife Fund for Nature (WWF) and Unilever, an Anglo-Dutch corporation heavily involved in the international fish market, was created to ensure that as much as possible of the fish products reaching consumers (mainly in the developed world) are labelled as having been caught in fisheries certified as sustainable.

A three-day workshop was held in October 1996 near London for an invited group of fisheries scientists to develop the first draft of a set of principles and criteria to be used by certifiers acting on behalf of the MSC. These criteria, to be refined in regional workshops, considered the state of the art in fisheries ecology (including concepts relative to ecosystem management, as presented above) and social sciences, while remaining realistic, i.e. implementable in the field. Biological considerations were crucial when deriving these principles and criteria (because maintenance of the stocks and the ecosystems that sustain them is the key to the sustainability), but economic, social and governance issues were also considered which, if implemented, should also lead to more equitable fisheries.

| BENEFITS <br> FISHERY | LARGE SCALE | SMALL SCALE |
| :---: | :---: | :---: |
| Number of fishers employed | $\begin{array}{r} 8 \\ \hline \text { 右 } \\ \pm 500000 \\ \hline \end{array}$ |  |
| Annual catch of marine fish for human consumption |  |  |
| Capital cost of each job on fishing vessels | \$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$ <br>  \$\$\$\$\$\$\$\$\$\$\$\$ \$30 000-\$300 000 \$\$\$\$\$\$\$\$\$\$ \$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$ \$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$\$ | $\begin{gathered} \$ \\ \$ 250-2500 \end{gathered}$ |
| Annual catch of marine fish for industrial reduction to meal and oil, etc. |  | Almost none |
| Annual fuel oil consumption |  | 1-2.5 million tons |
| Fish caught per ton of fuel consumed |  |  |
| Fishers employed for each \$1 million invested in fishing vessels | $\begin{gathered} 1 \\ 5-30 \\ 5 \end{gathered}$ |  |
| Fish destroyed at sea each year as by-catch in shrimp fisheries |  | None |

Fig. 10: Comparison between large-scale (industrial) and small-scale (artisanal) catches, ecological impacts and social benefits (after Thomson and FAO 1988)

Clearly, marine ecosystems can and should be analysed and managed, even if currently doing a less than adequate job is being made of it.

## ACKNOWLEDGEMENTS

I thank Dr T. J. Pitcher of the Fisheries Center, University of British Columbia, Mr C. G. Attwood of Sea Fisheries, Cape Town, and an anonymous reviewer for helpful comments on the draft of this contribution.

## LITERATURE CITED

ALLEN, K. R. 1971 - Relation between production and biomass. J. Fish. Res. Bd Can. 28: 1573-1581.

ALVERSON, D. L., FREEBERG, M. H., MURAWSKI, S. A. and J. G. POPE 1994 - A global assessment of fisheries bycatch and discards. F.A.O. Fish. tech. Pap. 339: 233 pp.
BAKUN, A. 1985 - Comparative studies and the recruitment problem: searching for generalizations. Rep. Calif. coop. oceanic Fish. Invest. 26: 30-40.
BAKUN, A. 1996 - Patterns in the Ocean. Ocean Processes and Marine Population Dynamics. California Sea College System, NOAA, San Diego, California, U.S.A., in cooperation with Centro de Investigaciones Biológicas del Noroeste, La Paz, Mexico: 323 pp.
CHRISTENSEN, V. and D. PAULY 1992 - Ecopath II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61: 169-185.
CHRISTENSEN, V. and D. PAULY 1995 - Fish production, catches and the carrying capacity of the world oceans. Naga 18(3): 34-40.
CSIRKE, J. 1988 - Small schooling pelagic fish stocks. In Fish Population Dynamics, 2nd ed. Gulland, J. A. (Ed.). New York; Wiley: 271-301.
F.A.O. 1971 - The living resources of the seas: an illustrated atlas. F.A.O. Fish. Circ. 126: 6 pp. +30 charts.
F.A.O. 1996 - FISHSTAT-PC-Data Retrieval and Analytical Software for Microcomputers Rome; F.A.O.
FONTENEAU, A. 1997 - Atlas of Tropical Tuna Fisheries: World Catches and Environment. Paris; ORSTOM 192 pp.
GARCIA, S. and C. NEWTON 1997 - Current situation, trends and prospects in world capture fisheries. In Global Trends: Fisheries Management. Pikitch, E. K., Ruppert, D. D. and M. P. Sissenwine (Eds). Bethesda, Maryland; American Fisheries Society Symposium 20: 3-27.
HUTCHINGS, J. A. and R. A. MYERS 1994 - What can be learned from the collapse of a renewable resource? Atlantic cod, Gadus morhua, of Newfoundland and Labrador. Can. J. Fish. aquat. Sci. 51(9): 2126-2146.

JARRE-TEICHMANN, A. 1992 - Steady-state modelling of the Peruvian upwelling ecosystem. Ph.D. thesis, University of Bremen: 153 pp.
KOBLENTZ-MISHKE, O. J., VOLKOVINSKY, V. V. and J. G. KABANOVA 1970 - Plankton primary production of the world ocean. In Scientific Exploration of the South Pacific. Wooster, W.S. (Ed.). Washington, D.C.; National Academy of Sciences: 183-193.
KUHN, T. 1970 - The Structure of Scientific Revolutions. 2nd

Edition, Chicago; University Press: 210 pp.
LONGHURST, A. [R.] 1995 - Seasonal cycles of pelagic production and consumption. Prog. Oceanogr. 36(2): 77-167.
LONGHURST, A. [R.], SATHYENDRANATH, S., PLATT, T. and C. CAVERHILL 1995 - An estimate of global primary production in the ocean from satellite radiometer data. $J$. Plankt. Res. 17(6): 1245-1271.
MacINTYRE, F., ESTEP, K. W. and T. T. NOJI 1995 - Is it deforestation or desertification when we do it to the ocean? Naga 18(3): 4-6.
MACKINSON, S., VASCONCELLOS, M., SLOMAN, K., PITCHER, T. and C. WALTERS (in press) - Ecosystem impacts of harvesting small pelagic fishes in upwelling systems using a dynamic mass balance model. In Ecological Role of Forage Fishes, Alaska Sea Grant Symposium, November 1996.
MEDAWAR, P. 1967 - The Art of the Soluble. London; Methuen: 160pp.
ODUM, E. P. 1969 - The strategy of ecosystem development. Science, N.Y. 164: 262-270.
PAULY, D. 1995 - Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol. Evolution 10(10): p. 430.
PAULY, D. 1996 - One hundred million tonnes of fish, and fisheries research. Fish. Res. 25(1): 25-38.
PAULY, D. and V. CHRISTENSEN 1993 - Stratified models of large marine ecosystems: a general approach and an application to the South China Sea. In Large Marine Ecosystems: Stress, Mitigation, and Sustainability. Sherman, K., Alexander, L. M. and B. D. Gold (Eds). Washington, D.C.; AAAS Press: 148-174.
PAULY, D. and V. CHRISTENSEN 1995 - Primary production required to sustain global fisheries. Nature 374: 255-257 (Erratum 376 p. 279).
PIYAKARNCHANA, T. 1989 - Yield dynamics as an index of biomass shifts in the Gulf of Thailand ecosystems. In Biomass Yields and Geography of Large Marine Ecosystems. Sherman, K. and L. M. Alexander (Eds). Boulder, Colorado; Westview Press: 95-142. (AAAS Selected Symposium 111).
ROBERTS, C., BALLANTINE, W. J., BUXTON, C. D., DAYTON, P., CROWDER, L. B., MILON, W., ORBACH, M.K., PAULY, D. and J. TREXLER 1995 - Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. NOAA tech. Meто. NMFS-SEFSC- 376: 8 pp. + Appendices.
RYTHER, J. H. 1969 - Photosynthesis and fish production in the sea. Science, N.Y. 166(3091): 72-76.
SHERMAN, K. 1993 - Large marine ecosystems as global units for marine resources management - an ecological perspective. In Large Marine Ecosystems: Stress, Mitigation, and Sustainability. Sherman, K., Alexander, L. M. and B. D. Gold (Eds). Washington, D.C.; AAAS Press: 3-14.
SHERMAN, K. and L. M. ALEXANDER (Eds) 1986 - Variability and Management of Large Marine Ecosystems. Boulder, Colorado; Westview Press: 319 pp. (AAAS Selected Symposium 99).
SHERMAN, K. and L. M. ALEXANDER (Eds) 1989 - Biomass Yields and Geography of Large Marine Ecosystems. Boulder, Colorado; Westview Press: 493 pp. (AAAS Selected Symposium 111).
SHERMAN, K., ALEXANDER, L. M. and B. D. GOLD (Eds) 1990 - Large Marine Ecosystems: Patterns, Processes and Yields. Washington, D.C.; AAAS Press: 242 pp.
SHERMAN, K., ALEXANDER, L. M. and B. D. GOLD (Eds) 1991 - Food Chains, Yields, Models, and Management of Large Marine Ecosystems. Boulder, Colorado; Westview Press: 320 pp .
SHERMAN, K., ALEXANDER, L. M. and B. D. GOLD (Eds) 1993 - Large Marine Ecosystems: Stress, Mitigation, and Sustainability. Washington, D.C.; AAAS Press: 376 pp.

SLOBOTKIN, L. B. 1980 - Growth and Regulation of Animal Populations, 2nd ed. New York; Dover Publications: 234 pp.
STEEMANN NIELSEN, E. and E. A. JENSEN 1957 - The autotrophic production of organic matter in the oceans Galathea Rep. 1: 49-124.
THOMSON, D. and FAO 1988 - The worlds two marine fisheries - how they compare. Naga 11(3): p. 17.
TRITES, A., PAULY, D. and V. CHRISTENSEN (in press) Competition between fisheries and marine mammals for prey and primary production in the Pacific ocean. J. NW. Atl. Fish. Sci.
VASCONCELLOS, M., MACKINSON, S., SLOMAN, K. and D. PAULY (in press) - The stability of trophic mass-balance
models of marine ecosystems: a comparative analysis. Ecological Modelling.
VITOUSEK, P. M., EHRLICH, P. R., EHRLICH, A. H. and P. A. MATSON 1986 - Human appropriation of the products of photosynthesis. Biosci. 36(6): 368-373.
WALTERS, C., CHRISTENSEN, V. and D. PAULY 1997 Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7: 139-172.
WULFF, F., FIELD, J. G. and K. H. MANN (Eds) 1989 - Network analysis in marine ecology: methods and applications. New York; Springer Verlag: 289 pp.(Coastal and Estuarine Studies 32).


[^0]:    * Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver B.C., Canada, V6T $1 Z 4$ and International Center for Living Aquatic Resources Management (ICLARM), M.C. P.O. Box 2631, 0718 Makati, Philippines. Email: pauly @ fisheries.com

