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The stability of trophic mass-balance models of marine ecosystems: a comparative analysis

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Abstract

Dynamic simulations of 18 ECOPATH mass-balance marine trophic models are used to explore the stability of systems when briefly impacted by a fishery on the key 'wasp-waist' populations occurring at intermediate trophic levels. The results are related to different ecosystem goal functions previously identified as representative of three attributes of ecosystems development: community complexity, homeostasis and energetics. System recovery time, the time required for all functional groups to return to baseline level, and here used as a measure of model stability, was inversely correlated to Finn's Cycling Index, i.e. to the fraction of ecosystem throughput that is recycled, and to the mean length of trophic pathways in the systems. Systems with higher capacity to recycle detritus are systems with a higher ability to recover from perturbations. The results are in agreement with the E.P. Odum's theory of ecosystem development, where recycling is interpreted as a chief positive feedback mechanism that contributes to stability in the mature systems by preventing overshoots and destructive oscillations due to external impacts. © 1997 Elsevier Science B.V.

Keywords: Trophic models; Marine ecosystems; Fisheries Impact; Stability; Detritus Cycling

1. Introduction

Theoretical studies on behavior of ecological systems has put great effort on the character-

ization of systems response to stress, often measured by its stability. By definition, stability is the ability of a system to return to an equilibrium state after a temporary disturbance (Holling, 1973). The relation between various stability concepts and the structure of ecosystems has been widely discussed in the ecological literature, particularly in relation to the complexity of food

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webs (Elton, 1958; MacArthur, 1955; Odum, 1969; May, 1972, 1981; Pimm, 1984).

Many marine ecosystems of the world share a similar configuration of their biological community structure, characterized by a crucial intermediate trophic level often occupied by a small plankton-feeding pelagic species (Bakun, 1996). The major control of trophic dynamics in these wasp-waist ecosystems (sensu Rice, 1995) is neither 'bottom up' nor 'top down' but rather 'both up and down from the middle', as variations in size of these populations may have major effects on the trophic levels above, which depend on the wasp-waist species as their major food source, and also on the trophic levels below, which are fed upon by massive wasp-waist populations (Bakun, 1996). These large populations very often represent important fisheries resources, e.g. of anchovies, sardines and herrings (Csirke, 1988). Fisheries exploiting the wasp-waist populations, occurring at intermediate trophic levels, hence have a potential disrupting effect on marine ecosystems communities with direct impact on its stability. The presence of narrow waists in food webs make it possible to compare the impact of disturbances on functionally similar groups in different ecosystems, which then allow us to derive stability properties from inter ecosystems comparisons.

In the ecosystem development theory of Odum (1969), stability is viewed as one property of mature ecosystems, which tend, over time, to increase in size and diversity within the constraints of available resources. Hence, along with other characteristics, mature ecosystems, according to Odum (1969), should incorporate a high information content, attain high biomass, and have a high capacity to entrap and hold nutrients for cycling within the system. Although widely criticized (Maanson and McGlade, 1993), quantitative tests of Odum's theory have been rare due to insufficient comparative information about ecosystems structure and processes, and the lack of appropriate modelling tools. However, recent developments of the ECOPATH approach for the construction, analysis and comparisons of mass balance trophic models now allows quantification of most Odum's attributes of ecosystems develop-

ment (Christensen and Pauly, 1992; Christensen, 1995a). As the original ECOPATH approach provides only a static picture of ecosystems, we rely here on a recently developed model called ECOSIM, which uses ECOPATH files for dynamic simulations (Walters et al., 1997). ECOSIM thus allow us to explore the response of 18 previously constructed marine ecosystem models when fishing on their wasp-waist group is briefly increased. System recovery time, defined as the time required for all elements of a system to return to their baseline biomass values following a perturbation is used here as a measure of ecosystem internal stability, or resistance to external changes, and compared with other ecosystem structural and functional attributes output by ECOPATH (see Christensen, 1995a). This comparative approach seeks to identify the ecosystem attributes directly involved in the stability and to address their relation to ecosystem maturity.

2. Material and methods

2.1. The ECOPATH approach

Trophic mass-balance models in ECOPATH rely on a system of linear equations which for any given group (i) can be represented for any time interval by

$$0 = B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i - Y_i + \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} \quad (1)$$

where B_i is the biomass of (i) during the period in question; $(P/B)_i$ the production/biomass ratio, EE_i is the ecotrophic efficiency, i.e. the fraction of the production of (i) that is consumed within the system or harvested, Y_i is the yield (with $Y_i = F_i \cdot B_i$; and F as the fishing mortality), B_j is the biomass of consumers or predators, $(Q/B)_j$ is the food consumption per unit of biomass of (j), and DC_{ji} is the fraction of (i) in the diet of (j). The parametrization of this equation, which leads to quantified networks of trophic flows, is typically based upon observed data on species abundance, food and feeding habit studies and fisheries catch data. At equilibrium this system has the rate of biomass change (dB_i/dt) equal to zero, and hence

Table 1

Models used for analyses of ecosystem stability. Group trophic level is computed as 1 + (the weighted average of the prey's trophic level) (Christensen and Pauly, 1992)

Model	Location	Species	Trophic	F^a	Source
Bru	Brunei, South China Sea	Pelagic fish	2.9	0.2	Silvestre et al. (1993)
Cmp	Campeche Bank, Gulf of Mexico	<i>Opisthonema oglinum</i>	2.9	0.89	Vega-Cendejas et al. (1993)
Cel	Celestun Lagoon, Gulf of Mexico	<i>Eucinostomus</i> spp	3.1	0.04	Chávez et al. (1993)
GMx	Northern shelf, Gulf of Mexico	Pelagic fish	2.0	0.11	Browder (1993)
Lng	Lingayen Gulf, Philippines	Sergestids	2.5	0.31	Pauly and Christensen (1993)
Mpt	Maputo Bay, Mozambique	Small pelagics	2.1	0.35	Paula e Silva et al. (1993)
Mrey	Monterey Bay, California	Omnivorous fish	2.5	0.16	Olivieri et al. (1993)
Nsea	North Sea	Sandeel, <i>Ammodytes</i> spp	3.7	0.45	Christensen (1995b)
Peru 60	Peru upwelling, 1960–1969	<i>Engraulis ringens</i>	2.2	0.78	Jarre et al. (1991)
Peru 70	Peru upwelling, 1973–1979	<i>Engraulis ringens</i>	2.4	0.54	Jarre et al. (1991)
Sch	Schlei Fjord Germany	Planktivorous fish	3.1	0.28	Christensen and Pauly (1992)
Thai10	Gulf of Thailand, 10–50 m.	Small demersal fish	3.3	3.86	Pauly and Christensen (1993)
Thai50	South China Sea	Small demersal fish	3.2	3.70	Pauly and Christensen (1993)
Thau	Etang de Thau, France	Atherinids	2.8	0.02	Palomares et al. (1993)
Trg	Kuala Trengganu, Malaysia	Pelagic fish	3.2	2.71	Christensen (1991)
Venz	Venezuela shelf, 10–50 m	Small pelagics	2.6	0.08	Mendoza (1993)
WMx	Western Gulf of Mexico	<i>Eucinostomus</i> spp	3.0	0.06	Arreguin-Sánchez et al. (1993a)
Yct	Yucatan shelf, Mexico	<i>Opisthonema oglinum</i> , <i>Harengula jaguana</i>	3.2	0.01	Arreguin-Sánchez et al. (1993b)

^a F , Baseline (per year) refers to the wasp-waist group's fishing mortality estimated from the corresponding mass-balanced ECOPATH model

the initial emphasis on its steady nature (Polovina, 1984; Christensen and Pauly, 1992). Re-expressing the system of Eq. (1) in form of ordinary differential equations is straightforward, and leads to a system wherein the left terms expresses dB_i/dt , which can be integrated over time (Walters et al., 1997) and leads to fully functional simulation models.

2.2. Ecosystem model comparisons

Comparisons were carried out with 18 models of marine ecosystems (Table 1), all briefly described in Christensen and Pauly (1993a), Christensen (1995a). In each model a group or species was selected using a set of criteria allowing direct comparison of results among ecosystems. Basically these criteria define the characteristic role of wasp-waist species, which must: (i) occupy an intermediate trophic level; (ii) provide an important link between lower and higher trophic levels,

indicated by a high energy throughput compared to the other fish groups at similar trophic levels, and (iii) already be fished in the baseline ECOPATH model.

A fishing pattern was chosen which generate a 5-fold increase in fishing mortality on the wasp-waist group. Throughout the work we tested different levels of increase in F without noticing any substantial difference in results. We decided for a 5-fold increase to create a situation where the group is severely depleted or displaced from its original steady-state condition in a relatively short period of time. Such a extreme scenario is routinely applied to many small pelagic fish populations and very often associated with stock collapse (Patterson, 1992). The higher F values were kept constant for 10 years, then returned to the baseline, with the model running for further 80 years (Fig. 1). This allows estimating the time it took the system to return to its original state after having been impacted, that is, the time it takes the

last impacted group to return to its baseline biomass level (Fig. 1). The recovery time was considered as a measure of the internal stability of the model and hence an index of ecosystem stability.

A comparative analysis of systems behavior was carried out using a set of ecosystem goal functions previously identified as representative of Odum's attributes of ecosystem maturity (Christensen, 1995a). The attributes were chosen to represent three different aspects of ecosystem development: (i) complexity in community structure; (ii) community energetics and (iii) overall community homeostasis. A detailed description of the indices listed below can be found in Christensen and Pauly (1992), Christensen (1995a).

1. Complexity in community structure: Total

number of ECOPATH pools (Npools); The ratio of the number of actual trophic links to the number of possible links (Connectance Index, CI); A measure of how the feeding interactions are distributed between trophic levels (System Omnivory Index, SOI);

- Community energetics: Total primary production over biomass (Pp/B); Total activity of the system (System Throughput, SThr); Biomass over production (B/P); Biomass over system throughput (B/T); System respiration over biomass (R/B);
- Community overall homeostasis: Relative Ascendancy (Asc_d); System Internal flow Overhead (IO_{vh}); The Finn's cycling index (FCI) and Finn's Path length (Path).

The cycling index, developed by Finn (1976), measures the fraction of an ecosystem's throughput that is recycled. The degree of recycling of energy and nutrients in an ecosystem is assumed to increase as ecosystems mature and develop routes for nutrient conservation (Odum, 1969). The path length is defined as the average number of components or pools that a unit of flow passes through on its way from inflow to outflow (Finn, 1980). As diversity of flows and cycling is expected to increase with maturity, and as these tendencies should result in an increased path length it is assumed that the path length will be highest for more mature systems (Christensen, 1995a).

3. Results and discussion

Of the 18 models analyzed, 3 exhibited an unstable behavior, i.e. did not recover completely their original structure 80 years after the end of the perturbation. These were the Thai10 model, which did attain a stable structure but in a different state, and the Peruvian upwelling system models (Peru60 and Peru70) which did not stabilize again. Such unstable behavior is expected when ECOSIM is used to extrapolate to a state far away from that described by a given ECOPATH model (Walters et al., 1997).

System recovery time of the remaining models was correlated against the different ecosystem at-

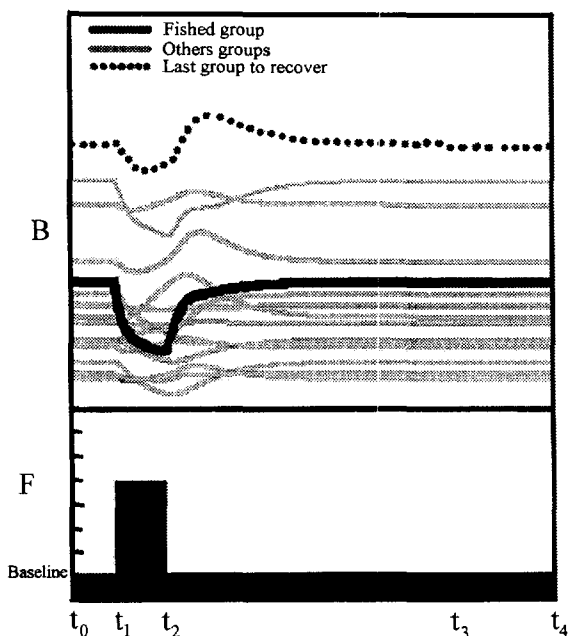


Fig. 1. Simulation of system recovery of the Venezuela shelf model after fishing impact imposing a 5 times increase in fishing mortality. Top graph shows changes in biomass (B) by group; fished group: small pelagics (*Sardinella aurita*); last group to recover: croakers (*Cynoscion* spp. and *Micropogonias furnieri*); t_0 start of simulation with F baseline; interval t_1-t_2 sets the time the system was kept under a higher fishing mortality rate (here 10 years); interval t_2-t_3 corresponds to the system recovery time or time it took the last impacted group to recover to its original biomass. Time t_4 equals 100 years.

Table 2
Correlation among the ecosystem attributes defined in the text^a

Attribute	Complexity				Homeostasis				Energetics			
	CI	SOI	Npools	FCI	Path	Ascd	IOvh	R/B	Pp/B	B/T	B/PS	Thr
Rec. time	-0.10	-0.15	0.12	-0.76	-0.67	0.09	-0.32	-0.10	0.33	-0.13	-0.14	-0.28
CI	—	0.28	-0.57	0.13	-0.09	-0.47	0.53	-0.25	-0.23	-0.13	-0.06	-0.28
SOI	—	—	0.29	0.23	0.48	-0.35	0.24	0.33	0.25	-0.45	-0.40	0.77
Npools	—	—	—	-0.14	-0.02	0.22	-0.51	-0.19	-0.05	-0.37	-0.16	-0.01
FCI	—	—	—	—	0.80	0.27	-0.04	-0.26	-0.34	0.20	0.24	0.49
Ascd	—	—	—	—	—	—	-0.83	-0.46	-0.36	0.44	0.50	-0.04
IOvh	—	—	—	—	—	—	—	0.29	0.38	-0.23	-0.32	0.27
R/B	—	—	—	—	—	—	—	—	0.63	-0.86	-0.83	-0.04
Pp/B	—	—	—	—	—	—	—	—	—	-0.55	-0.65	0.16
B/T	—	—	—	—	—	—	—	—	—	—	0.94	0.06
B/P	—	—	—	—	—	—	—	—	—	—	—	-0.07

^a Numbers in bold indicate significance at the 5% level (d.f. = 13). Recovery time (Rec. time) is the measure of stability utilized in the analysis.

tributes (Table 2). Only Finn's indices of cycling and path length are statistically correlated to recovery time ($r = -0.76$ and -0.67 , respectively). On the other hand, the assumption that ecosystem organization is a more important aspect of system stability (Ulanowicz, 1986) was not confirmed: none of the attributes of trophic web organization (Relative ascendancy and Internal flow Overhead) was correlated with recovery time. Community complexity and energetics attributes also showed low correlation, as may perhaps have been expected (Begon et al., 1990; Hansen and Jørgensen, 1990). May (1972) concluded that a simple relationship between stability and complexity may not be obtained, and in some cases, complex systems may fluctuate more than less complex ones. Here, we refute the hypothesis that stability and complexity (expressed in terms of connectance, web structure (SOI) and trophic groups richness) are correlated in the 18 models we compared.

Finn's cycling index showed a consistent negative relation with system recovery time (Fig. 2). Systems with a low percentage of energy recycled, simple recycling structures and short average path length (e.g. the upwelling systems off Venezuela and Monterey Bay) exhibit characteristically low resistance to changes. On the other hand, systems where recycling is important, such as coastal lagoons and fjords (e.g. Schlei Fjord and Etang de

Thau models), appeared more stable. To test the hypothesis that stability changes with recycling in a single system, we simulated the effect of an increase in the importance of detritus cycling to the Venezuela shelf model. The steps were as follows: first we gradually increased the diet component of detritus for heterotrophic benthos from 0 to 45% (thereby increasing the FCI from 0 to 2.8%); then we increased the diet component of detritus for zooplankton from 0 to 95% (the FCI thereby increased from 2.8 to 24.5%). Simulations were run for each level of recycling, leading to the results shown in Fig. 3. A negative relationship clearly emerge between the amount of detritus cycled and the recovery time of the model. Model stability does not appear very sensitive to increasing recycling up to a certain threshold from which small changes in recycling lead to substantial reductions in recovery time.

A view of the role of recycling different from the presented here was proposed by R.E. Ulanowicz and co-workers who argues that it is perturbed systems which tend to do more recycling (Ulanowicz, 1984; Ulanowicz and Wulff, 1991; Baird et al., 1991); from this, they concluded that recycling is a measure of stress. Indeed, Ulanowicz and Wulff (1991) suggested that in ecosystem development, the number and length of the recycling routes is a more important attribute than the

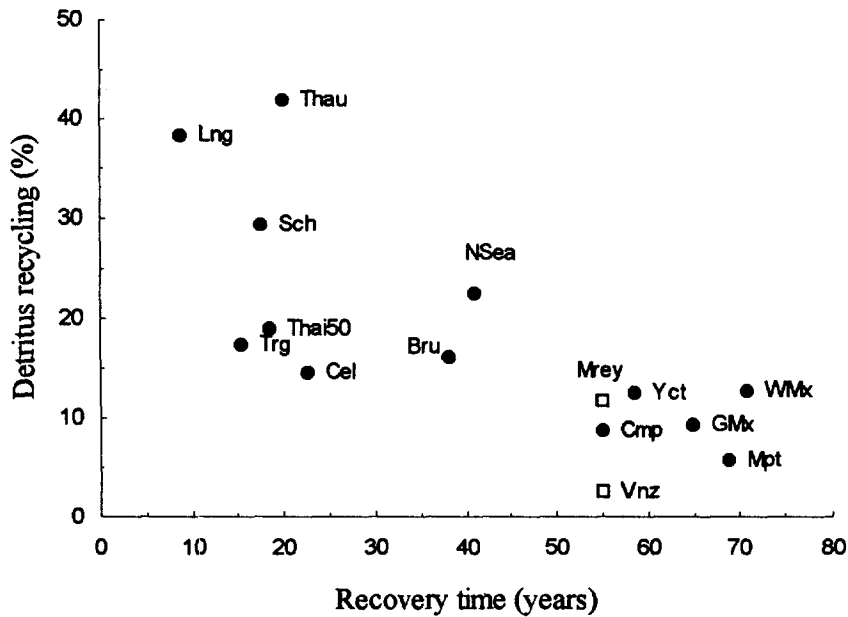


Fig. 2. Relation between Finn's index of detritus recycling and system recovery time ($r = -0.76$; $p = 0.001$; $df = 13$). See Table 1 for models descriptions. Empty squares indicate the recovery time of the models of upwelling systems (Monterey and Venezuela).

amount of cycling, thought in some ecosystems recycling occur over short benthic cycles and do not involve loops through various trophic levels. Here, the amount of energy and nutrients recycled may result in overevaluating the importance of recycling to the overall community. However, in the present study, recycling and path length were significantly correlated ($r = 0.80$) (Table 2), pointing to the substantial complexity and importance of the recycling routes for the marine ecosystem models analyzed.

We believe that Ulanowicz et al.'s interpretation of the role of detritus recycling as a result (and a measure) of stress to be due to they having selected a priori ascendancy as a strong and positive correlate of maturity, then evaluated all other system properties relative to ascendancy. This approach is problematic because ascendancy (or at least that of its two component meant to express the 'information content' of an ecosystem) is in fact negatively correlated with maturity (Christensen, 1995a). On the other hand, relative overheads, a measure of stability derived from Ulanowicz's theory does show a strong relationship with Finn's index (Christensen and Pauly, 1993b).

Thus we conclude that recycling does indeed have an important role in the maintenance of ecosystems stability. Basically, the higher the recycling the more quickly will the effects of perturbations be eliminated from the system (O'Neill, 1976; DeAngelis, 1980). Traditional view of ecosystem development consider that succession culminates in a stabilized ecosystem in which biomass and symbiotic functions between organisms are maintained per unit of available energy (Odum, 1969). Odum interpreted the strategy of succession as the one of increase control of or homeostasis with the physical environment in the sense of achieving maximum protection from its perturbations. The net result of community development would be symbiosis, nutrient conservation, stability, a decrease in entropy, and an increase in information. According to Odum, biotic control of grazing, population density and nutrient cycling provide the chief positive feedback mechanisms that contribute to stability in the mature systems by preventing overshoots and destructive oscillations. Our results are in agreement with the above theory to the extent it shows

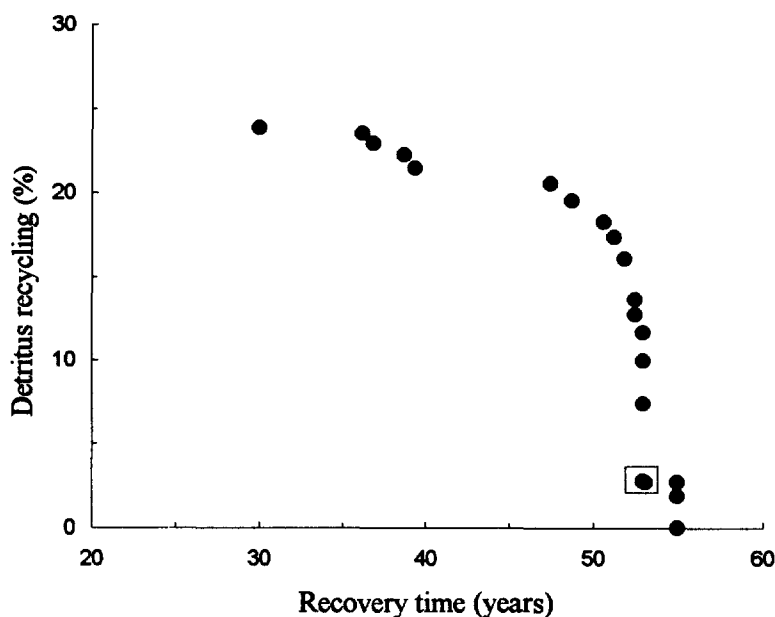


Fig. 3. Effect of increasing detritus cycling on the stability of the Venezuela shelf model (see text for procedure). The square corresponds to the system recovery time (t_3 on Fig. 1) for the baseline Finn cycling index value (2.7%).

that systems with higher capacity to recycle detritus are systems with a higher ability to recover from perturbations. Taking, therefore, stability and recycling as directly related attributes during ecosystem development the results of this analysis provide support to Odum's theory and to previous comparative studies of marine food webs (Christensen and Pauly, 1993b; Christensen, 1995a).

Very often ecosystems develop what Odum called pulse stability, where a more or less regular physical perturbation can maintain an ecosystem at some intermediate point in the development sequence toward maturity. Connell (1978) showed that in fact intermediate levels of disturbances are essential for the maintenance of certain ecosystem characteristics, such as species diversity, even in highly mature systems. Evidence gained in ecological studies, mainly of terrestrial ecosystems, has shown that change during ecosystem development is not continuous and gradual, but it is episodic with slow accumulation of biomass and nutrients punctuated by sudden releases and reorganization (Holling et al., 1995). According to Holling et al. (1995) the structure of biological communities is

therefore controlled through the balance of destabilizing and stabilizing forces. While destabilizing forces are important in maintaining diversity, resilience and opportunity, stabilizing forces, such as nutrient recycle, are important in maintaining productivity and biogeochemical cycles.

The role of destabilizing forces may be particularly important in pelagic marine ecosystems. Thus, for example, in the sea, short-term variability is damped out by very large heat capacity of the ocean. In turn, this large thermal capacity and the long period exchange rates between deep and near-surface waters leads to relatively large-amplitude changes at the long term scales (Steele, 1985). As a result, less robust internal ecosystem processes are needed to handle the smaller amplitude variability at short periods. The possible absence of such mechanisms, combined with increase variance with period, can mean that pelagic marine populations or ecosystems have to continually adapt to physical variability in the short as well as the long term (Holling et al., 1995). The absence of well structured recycling routes, the low recycling and reduced stability of upwelling ecosystems (Fig. 2) can be considered a result of a

longer-term adaptation of biological community to the physical variability and transitory nature of these systems. Bakun (1996) considered variability itself a key asset for the massive small pelagic wasp-waist populations inhabiting upwelling systems, which must rely on pulsing its abundance to cope with the temporal and spatial patterns presented by their prey, while simultaneously presenting patterns to their predators that overcome growth of intolerable levels of predation.

In face of the scale of human impact on marine ecosystems and the increasing evidences of regime shifts in many exploited areas (Pauly et al., 1989; Steele, 1996), fisheries research has to find ways and tools to account for ecological interactions, especially those of a trophic nature. The ECOPATH and ECOSIM systems provide a rigorous and relatively simple framework that is capable of accounting for the major components and trophic interactions of the ecosystem, tracking ecosystem changes over time, and produce results coherent with ecological theory on ecosystem development properties. These models may provide new insights into the understanding of how marine ecosystems have evolved, specifically on the balance between stability, resilience and food web organization, and hence support the design of policies aimed at implementing ecosystem management principles. For instance, while the internalization of system activity by recycling renders resistance to change (increasing stability), the lack of redundancy in the recycling pathways could make it very difficult for a highly organized system to reestablish broken pathways (Ulanowicz and Wulff, 1991). In this sense, the cost of stability would be a decrease in the resilience of ecosystems (Holling, 1973), that is of their ability to absorb changes and still persist in a state of high biomass. This seems to be the case for heavily depleted marine ecosystems, for which model simulations have shown that increased recycling of detritus by a variety of detritivores and omnivores now absent or reduced in abundance, could lead to substantially higher biomass and certainly higher and more valuable catches than are now being taken (Christensen and Pauly, 1996). Convincing fisheries managers to understand and consider the dynamics of stability and resilience of

marine ecosystems might be, therefore, a major challenge toward achieving sustainable use of marine resources.

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References

- Arreguín-Sánchez, F., Seijo, J.C., Valero-Pacheco, E., 1993a. An application of ECOPATH II to the north continental shelf ecosystem of Yucatan, Mexico. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 269–278.
- Arreguín-Sánchez, F., Valero-Pacheco, E., Chávez, E.A., 1993b. A trophic box model of the coastal fish community of the Southwestern Gulf of Mexico. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 197–205.
- Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine ecosystems. *Phil. Trans. R. Soc. Lond.* 333, 15–29.
- Bakun, A., 1996. *Patterns in the Ocean. Ocean Processes and Marine Population Dynamics*. California Sea Grant College System, CA.
- Begon, M., Harper, J.L., Townsend, C.R., 1990. *Ecology: Individuals, Populations and Communities*. Blackwell, London.
- Browder, J.A., 1993. A pilot model of the Gulf of Mexico continental shelf. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 279–284.
- Chávez, E.A., Garduño, M., Arreguín-Sánchez, F., 1993. Trophic dynamic structure of Celestun Lagoon, Southern Gulf of Mexico. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 186–192.
- Christensen, V., 1991. On ECOPATH, fishbyte, and fisheries management. *Fishbyte* 9 (2), 62–66.
- Christensen, V., 1995a. Ecosystem maturity—towards quantification. *Ecol. Model.* 77, 3–32.
- Christensen, V., 1995b. A model of trophic interactions in the North Sea in 1981, the year of the stomach. *Dana* 11 (1), 1–28.

- Christensen, V., Pauly, D., 1992. ECOPATH II—A software for balancing steady-state models and calculating network characteristics. *Ecol. Model.* 61, 169–185.
- Christensen, V., Pauly, D. (Eds.), 1993a. Trophic Models of Aquatic Ecosystems. ICLARM Conf. Proc., 26, pp. 390.
- Christensen, V., Pauly, D., 1993b. Flow characteristics of aquatic ecosystems. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 338–352.
- Christensen, V., Pauly, D., 1996. Rehabilitating fished ecosystems: insights from the past. *Naga*, ICLARM Q. 19 (2), 13–14.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199 (24), 1302–1310.
- Csirke, J., 1988. Small shoaling pelagic fish stocks. In: Gulland, J.A. (Ed.), *Fish Population Dynamics: the implications for management*, Wiley, New York, pp. 271–302.
- DeAngelis, D.L., 1980. Energy flow, nutrient cycling and ecosystem resilience. *Ecology* 61, 764–771.
- Elton, C.S., 1958. *The Ecology of Invasion by Animals and Plants*. Methuen, London.
- Finn, J.T., 1976. Measures of ecosystems structure and function derived from analysis of flows. *J. Theor. Biol.* 56, 363–380.
- Finn, J.T., 1980. Flow analysis of models of the Hubbard-Brook ecosystem. *Ecology* 61 (3), 562–571.
- Hansen, P.E., Jørgensen, S.E. (Eds.), 1990. *Introduction to Environmental Management. Developments in Environmental Modelling*, 18, Elsevier, Amsterdam.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4, 1–23.
- Holling, C.S., Schlindler, D.W., Walker, B., Roughgarden, J., 1995. Biodiversity and the function of ecosystem. In: Perrings, C., Göran-Mäler, K., Folke, C., Holling, C.S., (Eds.), *Biodiversity loss*. Cambridge University Press, Cambridge.
- Jarre, A., Muck, P., Pauly, D., 1991. Two approaches for modelling fish stocks interactions in the Peruvian upwelling ecosystem. *ICES Mar. Sci. Symp.* 193, 178–184.
- MacArthur, R.H., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36, 533–536.
- Maanson, B.A., McGlade, J.M., 1993. Ecology, thermodynamics and H.T. Odum's conjectures. *Oecologia* 93 (4), 582–596.
- May, R.M., 1972. Will a large complex system be stable?. *Nature* 238, 413–414.
- May, R.M., 1981. Patterns in multi-species communities. In: May, R.M. (Ed.), *Theoretical Ecology: Principles and Applications*, Blackwell, Oxford.
- Mendoza, J.J., 1993. A preliminary biomass budget for the Northeastern Venezuela shelf ecosystem. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 285–297.
- O'Neill, R.V., 1976. Ecosystem persistence and heterotrophic regulation. *Ecology* 57, 1244–1253.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Olivieri, R.A., Cohen, A., Chavez, F.P., 1993. An ecosystem model of Monterey Bay, California. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 315–322.
- Palomares, M.L., Reyes-Marchant, P., Lair, N., Zainure, M., Barnabé, G., Lasserre, G., 1993. A trophic model of a Mediterranean Lagoon, Etang de Thau, France. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 224–229.
- Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. *Rev. Fish. Biol. Fisheries* 2, 321–338.
- Paula e Silva, R., Sousa, M.I., Caramelo, A.M., 1993. The Maputo Bay ecosystem (Mozambique). In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 214–223.
- Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.), 1989. *The Peruvian upwelling ecosystem: dynamics and interactions*. ICLARM Conf. Proc., 18, pp. 438.
- Pauly, D., Christensen, V., 1993. Stratified models of large marine ecosystems: a general approach, and an application to the South China Sea. In: Sherman, K., Alexander, L.M., Gold, B.D. (Eds.), *Stress, Mitigation and Sustainability of Large Marine Ecosystems*. AAAS Press, Washington, DC, pp. 148–174.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326.
- Polovina, J.J., 1984. Model of a reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3, 1–11.
- Rice, J., 1995. Food web theory, marine food webs, and what climate changes may do to northern marine fish populations. In: Beamish, R.J. (Ed.), *Climate Change and Northern Fish Populations*. Can. Special Publ. Fish. Aquat. Sci., 121, 561–568.
- Steele, J.H., 1985. A comparison of terrestrial and marine ecological systems. *Nature*, 313 (6001) 355–358.
- Steele, J.H., 1996. Regime shifts in fisheries management. *Fish. Res.* 25, 19–23.
- Silvestre, G., Selmanathan, S., Salleh, A.H.M., 1993. Preliminary Trophic Model of the Coastal Fisheries Resources of Brunei Darussalam, South China Sea. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 300–306.
- Ulanowicz, R.E., 1984. Community measures of marine food networks and their possible applications. In: Fasham, M.J.R. (Ed.), *Flows of Energy and Materials in Marine Ecosystems*, Plenum, New York, pp. 23–47.
- Ulanowicz R.E., 1986. *Growth and development: Ecosystems Phenomenology*. Springer-Verlag, New York.

- Ulanowicz, R.E., Wulff, F., 1991. Comparing ecosystem structures: The Chesapeake Bay and the Baltic Sea. In: Cole, J., Lovett, G., Findlay, S. (Eds.). *Comparative analysis of ecosystems. Patterns, mechanisms and theories*, Springer-Verlag, Berlin, pp. 140–166.
- Vega-Cendejas, M.E., Arreguín-Sánchez, Hernández, M., 1993. Trophic fluxes on the Campeche Bank, Mexico. In: Christensen, V., Pauly, D. (Eds.), *Trophic Models of Aquatic Ecosystems*, ICLARM Conf. Proc., 26, 206–213.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* (in press).