Comparative Modelling of Trophic Flows in four Large Upwelling Ecosystems: Global versus Local Effects

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ABSTRACT

Trophic flow models of productive subsystems of the four large eastern boundary current ecosystems, i.e., the Humboldt Current off northern and central Peru (4-14°S), the northern Benguela Current off Namibia (15-35°S), the Canary Current (12-25°N) off Senegal and Mauritania, and the California Current (28-43°N) were constructed to represent different regimes in these systems during the mid-1960s to the early 1980s. The models were then analysed and compared by means of flow network analysis. The present contribution summarizes the results of a more detailed study with emphasis on the five dominant fish species: anchovy, sardine, horse-mackerel, mackerel and hake, and on the distinction between local and global effects. Whereas the general structure of the systems is very similar, characteristics pertaining to their size are system specific. The systems are all rather inefficient in terms of energy transfer up the food web. Total catch is correlated with primary production, as well as with the trophic level of the fishery. Productivities of small pelagics, as well as favorable conditions for them, appear of global nature, whereas properties pertaining to the medium-sized fish, as well as the inhibition of all dominant fish groups, appear more similar within the systems. Properties related to the fishing regime, e.g., fishing mortality, or the fraction of available primary production required to sustain fishery catches, are highly variable among systems and regimes. A closer focus on time-series of flows in the plankton compartments is required to obtain a more detailed understanding of regime-specific properties at the ecosystem level.

RÉSUMÉ

Des modèles de flux trophiques de sous-systèmes productifs des quatre grands écosystèmes du bord est des océans, c'est-à-dire le courant de Humboldt devant le nord et le centre du Pérou (4-14 °S), le courant nord du Benguela devant la Namibie (15-35 °S), le courant des Canaries (12-25 °N) devant le Sénégal et la Mauritanie, et le courant de Californie (28-43 °N), sont construits afin de représenter les différents régimes de ces systèmes du milieu des années 60 au début des années 80. Les modèles sont analysés et comparés au moyen de l'analyse des réseaux de flux. La présente contribution synthétise les résultats d'une étude plus détaillée focalisée sur les cinq espèces dominantes : l'anchois, la sardine, le chinchard, le maquereau et le merlu, et sur la distinction entre effets locaux et globaux. Tandis que la structure générale des systèmes est similaire, les caractéristiques propres à la taille des systèmes sont spécifiques. Les systèmes sont presque tous inefficaces en termes de transfert d'énergie au travers du réseau trophique. Les productivités en petits pélagiques, de même que les conditions favorables pour elles, apparaissent de nature globale, tandis que les propriétés relatives aux poissons de taille moyenne ainsi que les effets d'inhibition de tous les autres groupes dominants de poisson apparaissent plus semblables à l'intérieur des systèmes. Les propriétés relatives au régime de pêche, c'est-à-dire à la mortalité par pêche, ou à la fraction de production primaire disponible et nécessaire pour maintenir les pêcheries, sont très fluctuantes d'un système ou d'un régime à l'autre. Une attention particulière est nécessaire pour analyser les séries temporelles de flux dans les compartiments planctoniques afin d'obtenir une compréhension plus détaillée des propriétés spécifiques de l'écosystème.

INTRODUCTION

Eastern boundary current systems, or upwelling ecosystems, are among the most productive marine areas of the world. The four largest of these are the Humboldt Current off South America, the Benguela Current off southern Africa, the Canary Current of northwest Africa and the California Current off North America. They support large fish stocks of a similar species composition (Table 1) and important fisheries, accounting for more than 25% of the world catch of marine fish (FAO, 1990). Major scientific attention has been devoted towards the management of these fisheries, but to date no tool exists which would be capable of dealing with the considerable interannual fluctuations, notably of the anchovies and sardines stocks. Recent approaches emphasize the necessity of managing fisheries a multispecies context (see, e.g., contributions in Daan and Sissenwine, 1991), giving expression to the need of understanding the ecology of the systems components and their interactions.

The productivity of the upwelling systems depends strongly on the oceanographic conditions (Parrish *et al.*, 1983; Cury and Roy, 1989), which are likely to change along with intensifying coastal winds due to global warming (Bakun, 1990, 1993). Additionally, upwelling systems are carbon sinks (Walsh, 1989; Siegenthaler and Sarmiento, 1993), which is relevant to our understanding of the global carbon cycle.

In line with the CEOS concept (Bakun *et al.*, 1993; Cury *et al.*, this vol.), and based on published results of research relevant to models of upwelling ecosystems and earlier modelling studies on the Peruvian upwelling system (Jarre *et al.*, 1991; Jarre-Teichmann, 1992), trophic flow models of subsystems of the four upwelling regions (Fig. 1) were constructed and analyzed, aiming at a comparison of energy flows and systems characteristics under different climatic and/or fishing regimes (Jarre-Teichmann and Christensen, in press). This contribution contrasts the results of this study relevant to global versus those relevant to local properties of the four upwelling ecosystems, with emphasis on the five commercially most important fish anchovy, sardine, horse mackerel, mackerel and hake.

Common name	Genus	Species			
		Peru	California	Benguela	Northwest Africa
Anchovy	*Engraulis*	*ringens*	*mordax*	*capensis*	*encrasicolus*
Sardine	*Sardinops*	*sagax*	*caeruleus*	*ocellatus*	*Sardina pilchardus*
Horse mackerel	*Trachurus*	*murphyi*	*symmetricus*	*capensis*	*trachurus,* *trecae*
Mackerel	*Scomber*	*japonicus*	*japonicus*	*japonicus*	*japonicus*
Hake	*Merluccius*	*gayi*	*productus*	*capensis,* *paradoxus*	*pollis,* *senegalensis*

Table 1: Dominant fish species in the four large upwelling systems (modified from Bakun and Parrish, 1980).

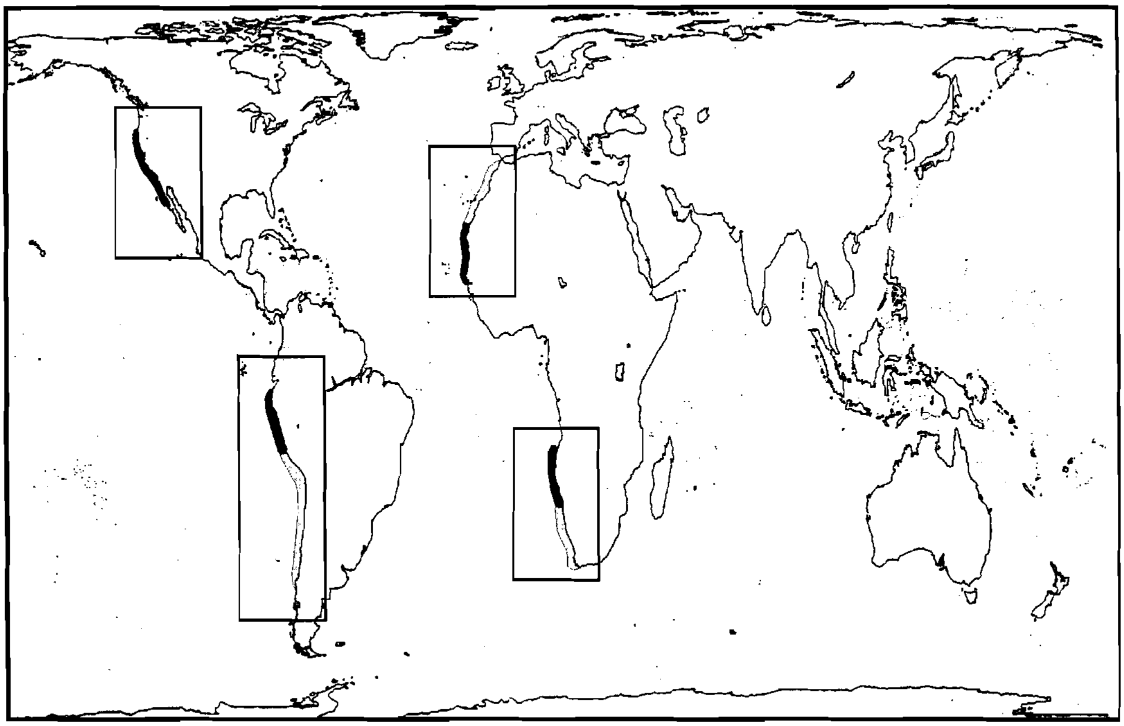


Fig. 1: The four large eastern boundary currents of the world (shaded) and the subsystems modelled for the present contribution (solid black). The subsystems were chosen such that they comprise the areas occupied by the dominant stocks of small pelagics.

1. MATERIAL AND METHODS

1.1. Model construction

A set of seven models was constructed of the four large upwelling ecosystems, averaging two periods each for the systems off Peru, Namibia and California, and one period for the upwelling system off Northwest Africa (Table 2). As the models are described in detail in Jarre-Teichmann and Christensen (in press), we confine ourselves here to a brief overview of their approach.

We used the Ecopath software (Christensen and Pauly, 1992), which based on the work of Polovina and associates (Polovina and Ow, 1983; Polovina, 1984, 1985). Assuming mass-balance over an appropriate period of time, trophic interactions between the components of an ecosystem (species or species groups) are described by a set of linear equations, wherein the production of each component equals its withdrawals by other components in the system (predation mortality), its export from the system (fishing mortality and other exports), and the baseline mortality, i.e.:

Production by (i) = All predation on (i) + nonpredatory biomass losses of (i) + fishery catches of (i) + other exports of (i)

The terms in this equation may be replaced by:

Production by (i) = B_i (P/B_i)

Predatory losses of (i) = $M_2 = \Sigma_j (B_j\ (Q/B_j)\ DC_{j,i})$

Other losses of (i) = $(1 - EE_i)\ B_i\ (P/B_i)$

and this leads, for any component in the system, to:

$$B_i\ (P/B_i)\ (EE_i - S_j)\ (B_j\ (Q/B_j)\ DC_{j,i}) - Ex_i = 0$$

where:

i indicates a component (stock, species, species group) of the model;
j any of its predators;
B_i its biomass;
P/B_i the production of a component per unit biomass (= total mortality under steady-state conditions);
Q/B_i the consumption of a component per unit biomass;
$DC_{j,i}$ the average fraction of i in the diet of j (in terms of weight);
EE_i its ecotrophic efficiency (the fraction of the total production consumed by predators or exported from the system);
Ex_i its export from the system (e.g., by emigration or advection, or fishery catch).

The energy balance of each component is given by:
Consumption = Production + Respiration + Non-assimilated food

wherein consumption is composed of consumption within the system and consumption of imports (i.e., consumption 'outside the system'), and production may be consumed by predators, exported from the system, or be a contribution to detritus.

This structure defines the necessary inputs to the model. These are, for each component, an estimate of its

- biomass;
- production per unit biomass;
- total food consumption per unit biomass;
- assimilation efficiency;
- diet composition;
- exports from the system;
- ecotrophic efficiency.

For each component, one of above parameters B, P/B, Q/B, or EE may be unknown and is estimated when solving the system, along with the respiration of that component. If an acceptable result for each of the unknowns is achieved from the inputs, the model is mass-balanced and may be analysed further.

In this study, the ecotrophic efficiencies were computed for most of the components (Table 3) and used to balance the models, where, for obvious reasons $0 \leq EE < 1$ served as a constraint. For components for which the biomasses were not available or proved erroneous during the modelling process, EEs were set and the biomasses estimated.

System (Latitude)	Period	Dominant[a] pelagic fish species	Regime characteristics, remarks
Peru, (4-14 °S)	1964-1971	Anchovy	Overwhelming anchovy biomass with world's largest single-species fishery; prior to collapse of anchovy
	1973-1981	Anchovy	Slow increase of anchovy stock
Northern Benguela, (15-35 °S)	1971-1977	Sardine	Sardine biomass lower than in the late 1960s, but still high. Strong fishery on sardine and hake.
	1978-1983	Horse mackerel	Sardine and hake biomasses strongly decreased, nevertheless heavily fished.
NorthWest Africa, (12-25 °N)	1970-1979	Sardine	System with least published information. Sardinella hold ecological niche occupied by anchovies in the other upwelling systems. Strong fishery for sardine and horse mackerel. Seasonal upwelling, system comprises several tropical fish species.
California, (28-43 °N)	1965-1972	Anchovy	Highly seasonal upwelling. Very low fish biomasses after breakdown of sardine and mackerel stocks. Fishing moratoria effective for both species.
	1978-1985	Anchovy	Fish biomasses recovering, end of fishing moratoria.

[a] in terms of production

Table 2: Major characteristics of the four large upwelling systems and the periods modeled.

1.2. Analysis of the models

After a model has been balanced, it is assured that the various estimates of biomass and turnover rates are mutually compatible, and hence represent a possible and consistent picture of energy flows in the system. Only then is it meaningful to perform further analyses of the model, e.g., for interactions between its components, or towards a holistic assessment of the system's structure based on the theories of Odum (1969) or Ulanowicz (1986). If shifts in biomass or catches in an ecosystem reflect transitions between alternative states of that system (Steele and Henderson, 1984; Lluch-Belda *et al.*, 1989), these changes should be reflected in such ecological properties.

Various types of favorable or inhibitive interactions are commonly described in ecology (see, e.g., Odum, 1971). Direct trophic interactions can be assessed by analysing partial mortality coefficients of the prey groups. In order to also consider indirect interactions between the components in an ecosystem, such as competition, we used the mixed trophic impact routine suggested by Ulanowicz and Puccia (1990). This approach assesses the relative impact that infinitissimally small changes in the biomass of a given group would have on the biomass of other groups, provided that the trophic structure in the system does not change. The latter is the reason why it cannot be used for predictive purposes; however, it can well be used as a sensitivity analysis for interspecific interactions.

	Estimated paramater			
Component	Peru	Northern Benguela	Northwest Africa	California
Phytoplankton	EE	EE	B	B
Benthic producers	B	B	B	B
Zooplankton	EE	B[a], EE[b]	EE	EE
Anchovy	EE	EE	EE	EE
Sardinella	—	—	EE	—
Sardine	EE	EE	EE	EE
Mackerel	EE	EE	EE	EE
Horse mackerel	EE	EE	EE	EE
Large scombrids	EE	EE	EE	EE
Other pelagics	B	B	B	B
Meiobenthos	B	B	B	B
Macrobenthos	EE	B	EE	EE
Hake	EE	EE	EE	EE
Demersals	B	B	B	B
Marine birds	EE	EE	EE	EE
Marine mammals	EE	EE	EE	EE
Mesopelagics	—	EE	EE	EE
Detritus	EE	EE	EE	EE

[a] Period 1971-1977

[b] Period 1978-1983

Table 3: Estimated parameters in the models of the four large upwelling ecosystems constructed. B: biomass, EE: ecotrophic efficiency; -: component not included in model. List refers to all time periods modeled if not stated otherwise.

Fractional trophic levels may also be reexpressed into discrete trophic levels sensu Lindemann (1942) (Ulanowicz, 1995). Thus, a given consumer is not placed on a single (fractional) trophic level according to its diet composition, but is perceived as finding on various (discrete) trophic levels simultaneously. The ratio between trophic flows consumed or exported from one trophic level and the flows entering it is defined as transfer efficiency.

Fisheries in different areas may have catches of similar size, but their species composition can be rather different, based, of course, on the availability of fish and on the fishing regime. The exploitation of fish on higher trophic levels in the food web is more costly in ecological terms than the exploitation of groups on lower trophic levels, because the energy transfer efficiency up the food web is far below unity. Hence, the maintenance cost of a fishery (or, generally, any system component) can only be compared across systems by using a common currency, e.g., primary production equivalents as implemented by Christensen & Pauly (1993). Following their approach, cycles in the system are removed first. The end flow of each path in the system (e.g., fishery catch) is then traced backwards to the primary producers, using, for each step, the ratio between consumption and production as a raising factor. Consequently, the sum of the primary production required at the basis of each path is the total primary production needed to sustain the system component in question, or the fishery.

2. RESULTS AND DISCUSSION

2.1. Trophic flow diagrams

Examples of trophic flow diagrams are given for the Peruvian upwelling ecosystem for the periods 1964-1971 and 1973-1981 (Fig. 2). The general structure of the trophic flow diagrams looks similar for all four upwelling systems. With the primary producers and detritus situated on trophic level 1 (by definition), the planktonic and benthic invertebrate groups are located at trophic levels 2.0 - 2.5. Small pelagics and other pelagics ranged next, with trophic levels between 2.5 and 3.0, while the predatory fish, as well as marine birds and mammals, were operate at trophic levels 3 and 4. Large scombrids and birds are the top predators in the system.

The major flows in all systems occurred in the plankton. Other important flows in the Peruvian ecosystem comprised anchovy and the benthic invertebrates, as well as sardine during the later period. Flows towards anchovy were reduced by a factor of more than four between the two periods, while those to sardine increased by a factor of seven, towards values similar to those for anchovy. Flows toward macrobenthos and hake also increased with the higher abundance of these groups. Due to the overall shortage of small pelagics in the system, the trophic level of predatory fish decreased (as they switched to a larger fraction of zooplankton) while that of hake, mammals and birds increased. Feeding of marine mammals 'outside' the system (i.e., on oceanic squid and mesopelagics) was important during both periods. In spite of the considerable changes in the ecosystem, the general structure of the pathways in the system was not altered.

2.2. Systems characteristics

The four upwelling systems ranked rather distinctly after the 'size' of their primary production, total biomass sustained in the system, catches and, consequently, total system throughput (Fig. 3). The Peruvian upwelling ecosystem was the largest of these four systems. It was also the system in which the most pronounced changes of system size occurred during the periods analysed. After the collapse of the anchovy stock, it became more similar to the northern Benguela system. The latter decreased in size from the mid-70s to the early 80s, due to the strong decrease of small pelagics (notably sardine), not compensated by the increased abundance of horse mackerel. The upwelling system off northwest Africa was similar in size to the northern Benguela system, despite the seasonality of its upwelling. The California system, whose upwelling is also highly seasonal, was the smallest of these four systems.

2.3. Productivity of small pelagics

The productivity (or P/B ratio, equivalent to total mortality) of small pelagics ranged between 1.1 year^{-1} and 2.7 year^{-1} for anchovy, and between 0.4 year^{-1} and 1.2 year^{-1} for sardine in the balanced models (Fig. 4). The productivity of anchovy was highest off Peru, followed by Namibia, northwest Africa and California. Their natural mortality (1.1 - 2.1 year^{-1}) was

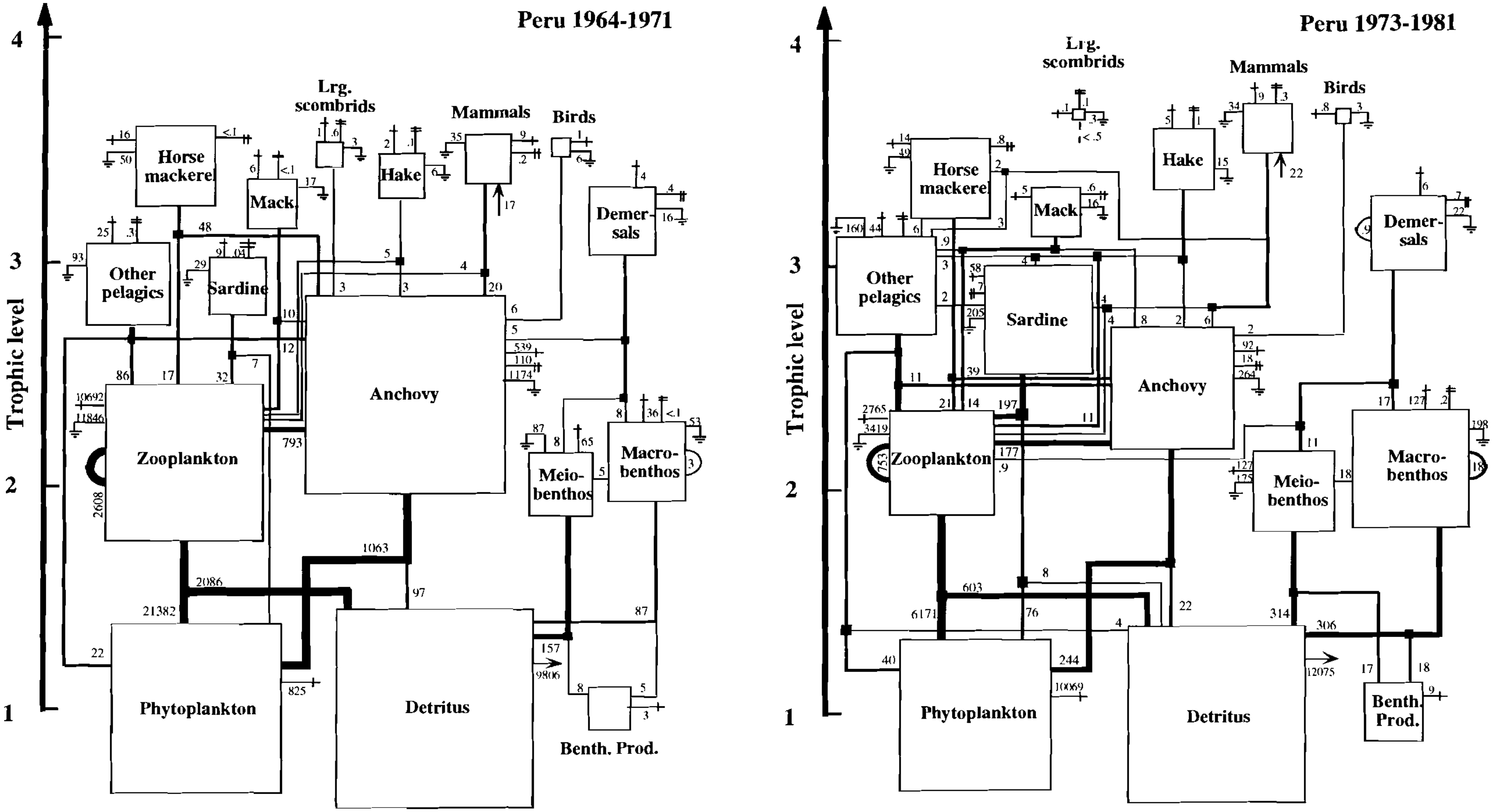


Fig. 2: Trophic flows in the Peruvian ecosystem, averaging the period 1964-1971, and the period 1973-1981. The size of the boxes is proportional to the biomass of the corresponding components in the models, if the boxes are imagined as cubes instead of squares. Boxes are arranged along the vertical axis according to their trophic level, defined as one for primary producers and detritus, and for consumers as one plus the mean trophic level of the prey items, weighted according to their fraction in the consumer's total diet. Flows are in units of t wet mass km^{-2} year^{-1}. Flows leave boxes on the upper half and enter them on the lower half, the width of the line indicates the order of magnitude of trophic flows. Flows of at least 1 t km^{-2} year^{-1} were rounded to integers, those below to one digit. Trophic flows of less than 0.1 ppt of the total consumption in the system, corresponding to about 3 t km^{-2} year^{-1} during 1964-1971 and to about 0.9 t km^{-2} year^{-1} during 1973-1981, were ommitted for clarity. Biomass of detritus is a rough guess only.

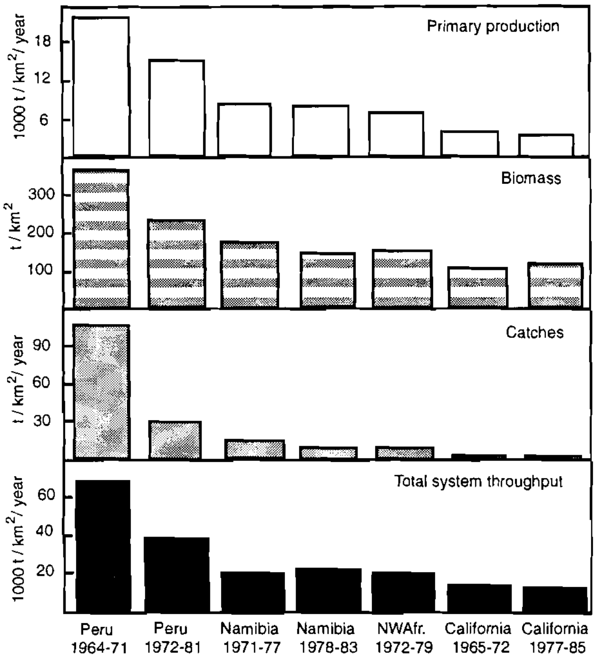


Fig. 3: Summary statistics of the seven balanced models constructed, referring to system size. Systems are arranged after decreasing primary production. Note that systems are set apart in geographic rather than in regime-specific order. Also note similar trend, in all four parameters, of primary production, total biomass (excl. detritus), total catches and total system throughput.

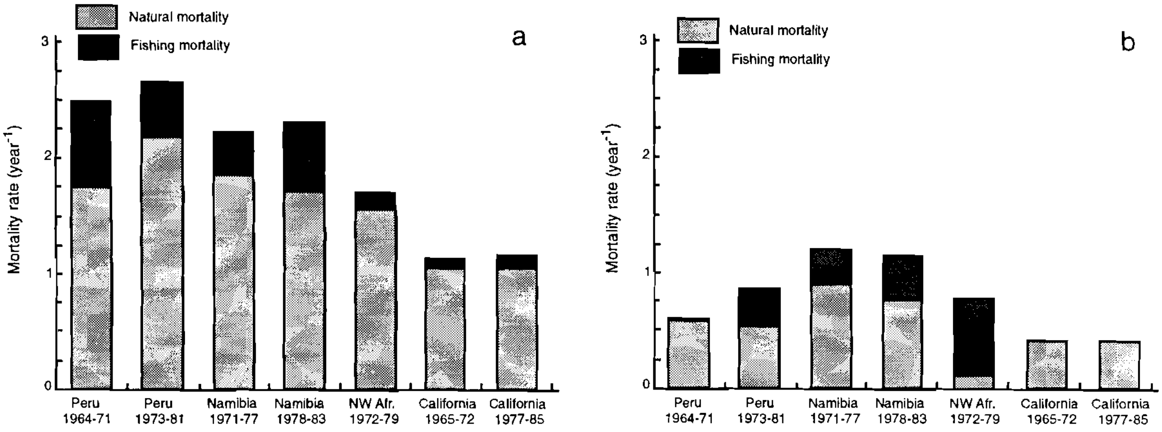


Fig. 4: Breakdown of total mortality rates for anchovy (a) and sardine (b). Note consistent scale of vertical axes. Systems are arranged after decreasing primary production.

always considerably higher than their fishing mortality (0.1 to 0.7 year^{-1}), indicating their importance as a food resource for other system components. Fishing mortality of anchovy was highest off Peru during the late 1960s, followed by Namibia in the early 1980s. The latter is remarkable as anchovy were not dominant off Namibia, neither in the system, nor in the landings. Anchovy fishing mortality was still high in the Peruvian and Namibian systems during the other periods, while it was lower in the northwest African and Californian systems, due to a lack of directed fishery in the former, and a more restrictive fishery management in the latter.

Sardine were subjected to the highest fishing mortality off Northwest Africa, followed by the northern Benguela system and Peruvian system during the 1970s. Due to the closure of the sardine fishery off California, fishing mortality of sardine off California was negligible. The natural mortality of sardine was highest off Namibia during both periods, followed by the Peruvian and the Californian systems.

2.4. Productivity of mackerel, horse mackerel and hake

Mackerel tended to be more productive than horse mackerel, with productivities ranging from 0.5 year^{-1} to 0.9 year^{-1}, and 0.3 year^{-1} to 1.1 year^{-1}, respectively (Fig. 5). Total mortality of mackerel was lowest off California due to the closure of its fishery, and similar in the other systems. Total productivity of horse mackerel was rather low in the Peruvian upwelling system, where they grew relatively large. It was more than three times as high off Northwest Africa, were also the highest fishing mortalities were observed. Apart from the Namibian system in the early 1980s, fishing mortalities were generally low reflecting the lack of major directed fisheries.

The productivity of hake ranged from 0.4 year^{-1} to 0.9 year^{-1} (Fig. 5). It was lowest off Peru in the 1960s, reflecting the focus of the fishery on small pelagics. During the 1970s, hake were more strongly exploited off Peru.

The natural mortality of horse mackerel was similar in all systems except off Northwest Africa, where it was twice as high as in the other systems. For mackerel and hake, both components were approximately equal off Peru during the 1970s, as well as in the Namibian and Northwest African systems, reflecting their strong exploitation.

In general, the results from our balanced ecosystem models confirm that the rates of natural mortality are not system-specific (see also Beverton and Holt, 1959; Pauly, 1980). The fishing mortalities, however, showed marked differences among systems and regimes. In consequence, a fishing regime should be regarded as a local property of a system, whereas the productivities of each of the major fish components are probably more similar on the global scale.

2.5. Interactions between ecosystem components

Recruitment success is largely determined by the dynamics of primary production (Cushing, 1982; Parrish *et al.*, 1983), and moderate upwelling conditions are most favorable for small pelagics in upwelling regions (Cury and Roy, 1989; Cury *et al.*, 1995). Cushing (1982) also linked recruitment success to competition and stressed the need for information on how recruitment is affected by predation, although he considered the latter a minor process.

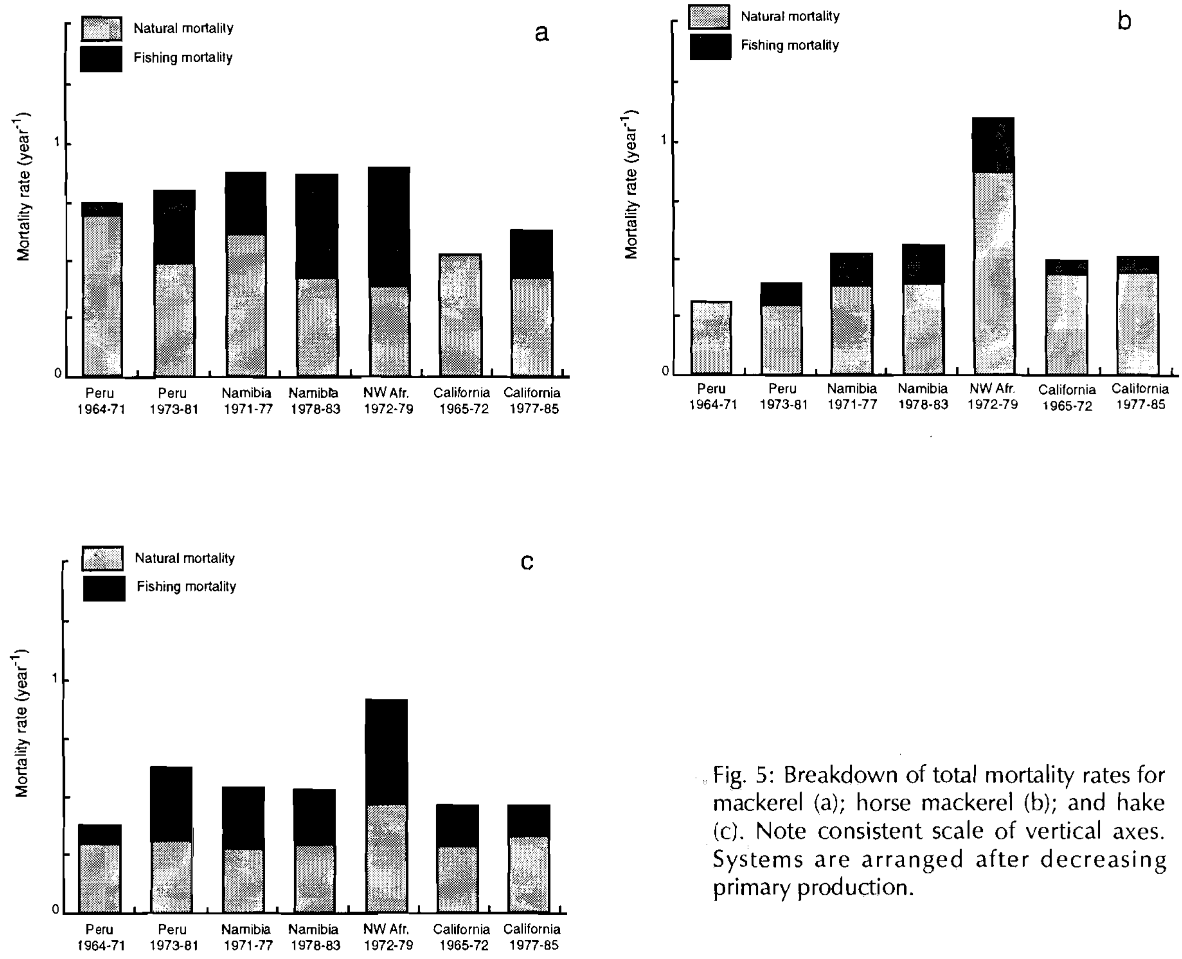


Fig. 5: Breakdown of total mortality rates for mackerel (a); horse mackerel (b); and hake (c). Note consistent scale of vertical axes. Systems are arranged after decreasing primary production.

The dominant food items in the diet of the five commercially most important fish are given in Table 4. All of them were essentially planktivores. Anchovy fed largely on phytoplankton, except off California, where they ingested a larger fraction of zooplankton. Sardine were predominantly phytoplanktivores in the Atlantic, and zooplanktivores in the Pacific. However, due to the well-known ambiguities in assessing the diet composition (see, e.g., James, 1988 for a review), this geographic division should be viewed with caution. Mackerel and hake fed predominantly on zooplankton throughout, and horse mackerel fed mostly on zooplankton except off Peru, where they fed mainly on anchovy.

Although the dominance of planktivores suggests a food web of rather simple structure, mixed trophic impact analysis suggested some indirect effects, as some of the groups most strongly favoring those five fish species differed from the most important food items. For anchovy, sardine and mackerel off California, primary production was the most enhancing factor. This also held true for the Peruvian system after the collapse of anchovy, where phytoplankon became the dominant factor for all fish groups. Hake off Namibia were also favored most strongly by primary production.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Peru 1973-1981	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Namibia 1971-1977	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
Namibia 1978-1983	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
NW Africa 1972-1979	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
California 1965-1972	Zooplankton	Zooplankton	Zooplankton	Zooplankton	Zooplankton
California 1978-1985	Zooplankton	Zooplankton	Zooplankton	Zooplankton	Zooplankton

Table 4a: Dominant food item (by weight) in the diet of the five commercially most important fish species by system and regime.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Phytoplankton	Zooplankton	Zooplankton	Anchovy	Zooplankton
Peru 1973-1981	Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton Anchovy	Phytoplankton
Namibia 1971-1977	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Phytoplankton
Namibia 1978-1983	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Phytoplankton
NW Africa 1972-1979	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton	Zooplankton
California 1965-1972	Phytoplankton	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton
California 1978-1985	Phytoplankton	Phytoplankton	Phytoplankton	Zooplankton	Zooplankton

Table 4b: Strongest trophic enhancement of the five commercially most important fish species by system and regime, based on mixed trophic impact analysis. Components that differ from the most important diet components, and thus point at indirect effects in the system, are shaded.

In general, the small pelagics appeared to be similarly favored in all systems, whereas the enhancement of mackerel, horse mackerel and hake was more system-specific. Within a system, the positive impacts were generally similar between regimes, except for pronounced changes in ecosystem structure, such occurred off Peru in the early 1970s.

The groups causing the highest mortality of the five most important commercial fish species differed more strongly among systems and regimes. Anchovy were heavily exploited by the fishery in the late 1960s off Peru, while horse mackerel caused most of its mortality during the 1970s. Hake was the dominant predator on anchovy off Namibia, other pelagics off Northwest Africa, and horse mackerel and mackerel off California. Sardine were preyed upon intensively by mammals and heavily fished off Peru; they were preyed upon most strongly by hake off Namibia, and by other pelagics off Northwest Africa. Mackerel were more strongly exploited by the fisheries off Peru, Namibia, and (after its reopening) off California than subjected to predation by any single group. Horse mackerel were preyed upon by mammals and other pelagics, except off Namibia, where predation by hake and exploitation by the fishery were the most important causes of mortality in the first and second periods, respectively. Hake was either influenced by cannibalism or by the fishery, except off California, where cannibalism was less important because the hake population consisted mainly of juveniles, preyed upon by the abundant marine mammals.

Whereas anchovy was inhibited rather directly, indirect effects of trophic interactions were more pronounced for the other groups. It is worth noting, though, that intraspecific competition apparently had a larger effect on anchovy during the 1960s than food limitation. Competition with anchovy was more important for sardine off Peru than predation by mammals. Inhibition by mackerel, exclusively based on indirect effects, was more important for sardine off Namibia in the 1970s than predation by hake. Competition for food could also have been limiting for sardine off northwest Africa. All in all, our results are thus supported by the competition model of Silvert and Crawford (1988).

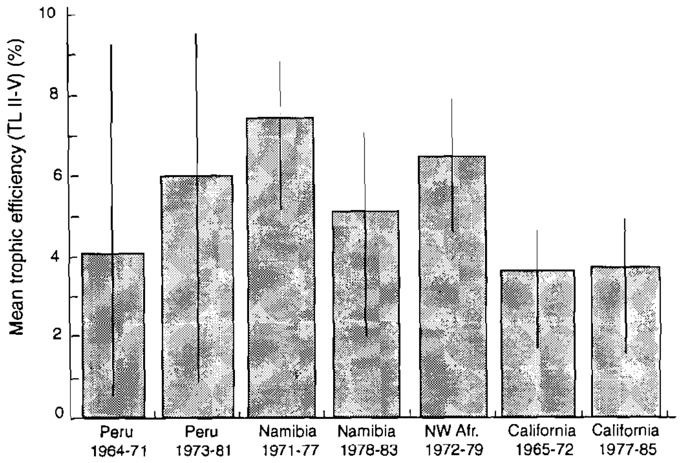
Mackerel were subjected to more direct effects rather than indirect ones, except off California during the early 1980s, where intraspecific competition for food inhibited its population growth more than any other group. Horse mackerel competed with the fishery during the period of high anchovy abundance off Peru, and with each other after the collapse of its major food resource. Off Namibia, horse mackerel were inhibited by hake to the same extent as by the fishery. Inhibition by other pelagics was more important to horse mackerel than direct predation by mammals off California during the late 1960s. Hake were generally predator-controlled, either by each other, by the fishery, or (off California) by marine mammals. Indirect interaction with anchovy turned out to be strongly inhibiting for hake off California during the early 1980s.

These results supplement earlier work by Korrubel (1992), who suggested that fisheries may induce species dominance shifts while emphasizing the need for further assessment of the role of other ecosystem components, based on improved knowledge of their interactions. In general, the components the Peruvian system were indeed most strongly inhibited by the fishery, but those in the northern Benguela system most strongly by hake. The cross-impacts included more groups in the two systems with seasonal upwelling, off California and Northwest Africa. However, all in all, the inhibition of these five groups appeared to be a highly local property.

2.6. Transfer efficiency

Restructuring of the fractional trophic levels (as used for the trophic flow diagrams) yielded six discrete trophic levels, i.e., producers, herbivores, and first- to fourth-order carnivores, for all of the models except Northwest Africa which had seven trophic levels. As the absolute flows on the topmost level were negligible, we computed the average transfer efficiency of the consumer levels II to V (i.e., herbivores to third-order carnivores) (Fig. 6). The grand mean of all models yielded a transfer efficiency of slightly above 5% (range 3.6 - 7.4%), much lower than the general mean of about 10% computed for a cross-section of aquatic ecosystems (Christensen and Pauly, 1993; Pauly and Christensen, 1995). Hence, upwelling systems are all relatively inefficient systems regardless of the prevailing fishing regime. Moreover, despite relatively large changes of the transfer efficiencies between different regimes in a given system, there is some suggestion that the systems might be slightly different from each other, the California system being the least, and the two Atlantic systems the most efficient ones.

Fig. 6: Mean transfer efficiencies between discrete trophic levels II to V, i.e., herbivores to third-order carnivores, in seven models of the four major upwelling ecosystems. Thin lines indicate ranges. Systems are arranged after decreasing primary production.



2.7. Primary production required to sustain the fishery

Figure 7 gives the primary production required to sustain the fishery in the seven models constructed both in absolute terms, and relative to the primary production available in the corresponding system. In absolute terms, the flows from the primary producers required to sustain the fishery reflected the size of the catches, with high catches implying high primary production requirements. The systems could thus be ranked in the same way as after the 'size' parameters (Fig. 3). However, changes in the fishing regime must be considered as well: although the magnitude of the catches off Peru was reduced by a factor of more than three between the two periods analysed, the primary production required to sustain the fishery in the 1970s decreased only by about 10%, as sardine and hake, both situated on higher trophic levels, accounted for a considerable fraction of total catches.

The fraction of the available primary production used to sustain the catches, however, showed a rather different picture. Although the catches decreased significantly between the two periods analysed in the Peruvian system, a larger fraction of the available primary production was used in the later period. The fishery off Namibia during the early 1970s required the largest share of the available primary production, whereas the fishery off California took only a minor share. Comparing the 1970s as a period modelled for all four upwelling areas, we conclude that the primary production required to sustain the fishery is a local characteristic of the system, depending on the intensity of fishing and the trophic levels of its target species. It cannot straightforwardly be linked to species dominance, as the differences between sardine-dominated systems, such as the Northwest African and the northern Benguela systems during the 1970s, were larger than the differences between an anchovy-dominated system (off Peru during the late 1960s) and a horse-mackerel dominated one (off Namibia, during 1978-83).

The grand mean of the primary production used to sustain the fishery amounted to 9.5% of the available primary production in our models. This figure is higher than the global average of 8% estimated by Pauly and Christensen (1995), but seems strikingly low if compared with their results for upwelling regions of 25%. This apparent discrepancy is

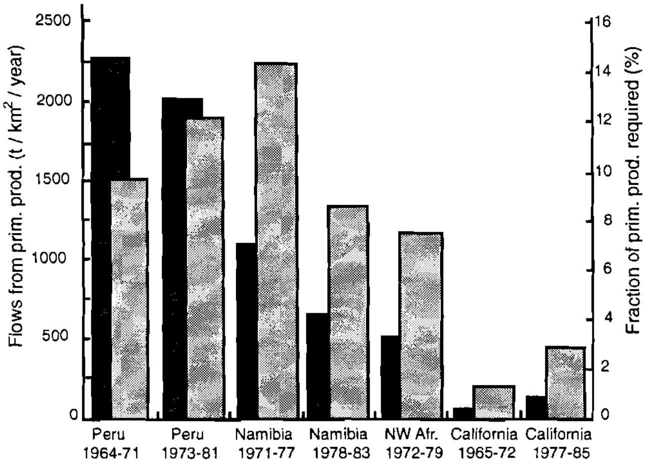


Fig. 7: Flows from the producers's level to the fishery, both in absolute (light shading) as well as in relative (dark shading) terms. Systems are arranged after decreasing primary production.

explained as follows: Pauly and Christensen (1995) used primary production estimates similar to the 1970s conditions in our models, but (i) catches of small pelagics were considerably higher in 1990 than they were during the 1970s; (ii) we used, except for Peruvian anchovy, nominal catches in our models, whereas Pauly and Christensen (1995) accounted for additional 15% of discards for each group; and (iii) catches of horse mackerel were disproportionally large in the southern part of the Humboldt Current, not included in the present comparisons. We have, thus, been looking at very productive subsystems in the four upwelling regions, but not necessarily at those parts of the systems and/or periods subjected to the highest rate of exploitation by the fishery. Using the respective raising factors for the catches, we would, too, arrive at relative requirements of 6-8% to sustain the fishery of anchovy and sardine, 15-17% for the fishery of horse mackerel and mackerel, and <1% for other pelagic groups, indicating the considerable degree of present exploitation of these systems. Additionally, it should be kept in mind that another 3-4% of the primary production are required to sustain the fishery of hake, not explicitly attributed to upwelling regions in the above study.

2.8. Primary production required to sustain the five major fish groups

About 20% - 35% of the available flows from the producers' level were generally used to sustain the five dominant fish groups in the system (Fig. 8 and Table 5), with the exception of the Namibian system during the 1970s, where almost half of the available flow was required. The latter seemed particularly high at first glance, but went along with a slightly elevated mean trophic efficiency in the system, and was also consistent with the high fraction of primary production required to sustain the fishery. The shift in species dominance in the Peruvian system between the late 1960s and the 1970s was clearly reflected, and it is worth noting that — in spite of the considerably smaller total biomass in the system — a similar fraction of primary production was required to sustain the dominant fish species.

It was also striking that the fraction of primary production used to sustain the fish in the Californian system was not much lower than in the other systems, indicating that the structure of the Californian system was indeed very similar to the other systems, despite their large differences in size. We should thus moderate the statement of Ware (1992) on the particular inefficiency of the Californian ecosystem with respect to fish production.

Within the systems where anchovy were the dominant fish by production (i.e., off Peru and California, see Table 2), it was also anchovy which required the largest single fraction of primary production among the fish groups. The same held true for horse mackerel off Namibia in the early 1980s. Strikingly, within the two systems dominated by sardine (the Namibian and northwest African systems during the 1970s), hake and horse mackerel required the single largest share of primary production, respectively, but not sardine. It would be premature to draw any conclusion from this inconsistency with respect to the persistence of species dominance or the diversity of flows in the systems (see also Shannon *et al.* (1988), and LeClus (1991)).

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Fishery	Mammals	Fishery	Mammals	Hake
Peru 1973-1981	Horse mackerel	Fishery	Fishery	Mammals	Fishery
Namibia 1971-1977	Hake	Hake	Hake	Hake	Fishery
Namibia 1978-1983	Hake	Hake	Fishery	Fishery	Hake
NW Africa 1972-1979	Other pelagics	Other pelagics	Lrg. scombrids	Other pelagics	Fishery
California 1965-1972	Horse mackerel	—a)	Marine birds	Mammals	Mammals
California 1978-1985	Mackerel	—a)	Fishery	Other pelagics	Mammals

a) The biomass of sardine was so low that it could only be a marginal component in the diet of its predators. It was hence impossible to determine the main predator on sardine.

Table 5a: Strongest predator group of the five commercially most important fish species by system and regime.

System / Group	Anchovy	Sardine	Mackerel	Horse mackerel	Hake
Peru 1964-1971	Anchovy	Anchovy	Fishery	Fishery	Hake
Peru 1973-1981	Horse mackerel	Anchovy / Fishery	Fishery	Horse mackerel	Fishery
Namibia 1971-1977	Hake	Horse mackerel	Hake	Hake	Hake
Namibia 1978-1983	Hake	Hake	Fishery	Hake / Fishery	Hake
NW Africa 1972-1979	Other pelagics	Zooplankton	Lrg. scombrids	Other pelagics	Demersals
California 1965-1972	Horse mackerel	—a)	Marine birds	Other pelagics	Mammals
California 1978-1985	Mackerel	—a)	Mackerel	Other pelagics	Anchovy/Mammals

a) The biomass of sardine was so low that it could only be a marginal component in the diet of its predators. It was hence impossible to account for its proper role in the mixed trophic impacts routine.

Table 5b: Strongest inhibition of the five commercially most important fish species by system and regime, based on mixed trophic impact analysis. Components that differ from the strongest predator, and thus point at food limitation or competitive inhibition of the respective fish group, are shaded.

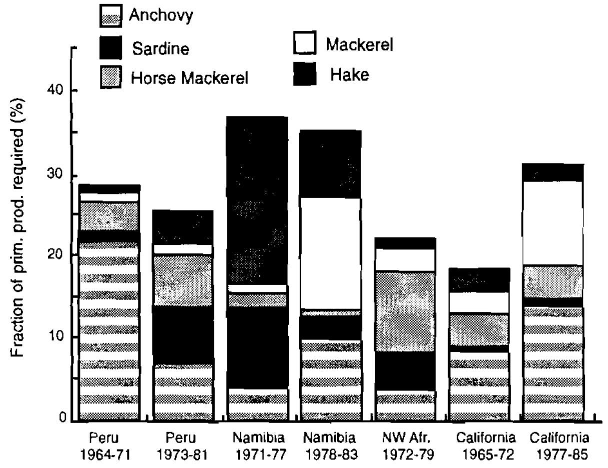


Fig. 8: Fraction of flows from the producers' level required to sustain the five dominant groups in the system. For the Northwest Africa system, the requirements of anchovy and sardinella have been combined, as sardinella occupies, in part, the ecological niche of anchovy. Systems are arranged after decreasing primary production.

CONCLUSION

The different aspects of our analysis with respect to global versus local properties are summarized in Table 6. The consistent set of species dominating the flow on the higher trophic levels is one of the obvious global characteristics of upwelling ecosystems. Also, the distribution of the major flows in the models is also quite similar among systems.

However, it is necessary to keep in mind that all flows among the fish groups and toward the warm-blooded top predators are small in comparison to those in the plankton. Hence, for improved comparison of the systems with respect to system-level properties (maturity, ascendency, etc.) under different environmental regimes, time-series of flows in the plankton compartments, as well as the microbial food web, will need to be assembled and analysed in more detail than it has been possible for the present contribution.

The productivity of the small pelagics, as well as the natural mortality of all dominant fish stocks, was also similar between systems, and can thus be regarded global properties. This should not be regarded as a pure artifact of model construction, as the models were balanced prior to any comparisons.

It also emerged clearly that small pelagics increase with primary production regardless of system and regime. This does not appear, at first glance, to go along with the findings of Cury and Roy (1989) and Cury *et al.* (1995) that moderate conditions are most beneficial to successful recruitment, but it should be kept in mind that the present approach dealt only with trophic interactions, and not with the transport processes that determine the survival of eggs and larvae.

The fraction of primary production used to sustain the five most important fish groups in the ecosystems was also quite similar between the systems (with exception of the Namibian ecosystem during the 1970s) and may thus be regarded as a global property. Furthermore, our results suggest that flows from the primary producers' level required to sustain the dominant fish species (in terms of production) may be a regime-specific property, anchovy using the largest fraction in anchovy-dominated systems, but hake or horse-mackerel using the largest fraction in sardine-dominated systems.

Characteristic / Property	'Global'[a]	'Local'[b]
General system structure	Species composition Major flow patterns	System size
Productivity of major fish species	Natural mortality of all dominant fish stocks, total mortality of small pelagics	Fishing mortality
Species interactions	Favoring of small pelagics	Favoring of medium-sized fish; Inhibition of all major fish groups; Strongest predators of all major fish groups
Sustenance of the major fish groups Sustenance of the fishery	Total fraction of primary production required (in general)	Fraction of primary production required by the dominant species Fishing regime, primary production required to sustain the fishery
Relation between production and fishery	Total catch vs. trophic level of fishery Total catch vs. primary production	–
System transfer efficiency	Low mean efficiency of energy transfer up the food web	Efficiency on 'medium scale' (?)
Goal functions	Overall low maturity; similar information content of flows, low relative ascendency	–

[a] Similar between systems through time, i.e., (i) regime-dependent, or (ii) independent of system and regime

[b] More similar within systems through time (i.e., regime-independent), or system- and regime-specific

Table 6: Summary of global versus local properties of the four upwelling ecosystems analysed.

Most system-level properties of these ecosystems, such as their generally low transfer efficiency, were also of global nature. Further attributes are discussed in detail in Jarre-Teichmann and Christensen (in press), notably those pertaining to the theories of Odum (1969) and Ulanowicz (1986). The generally low maturity, and low relative ascendency of these systems are global properties as well, and corroborate the grouping of upwelling systems in Christensen's (1992) maturity ranking of aquatic ecosystems. It should further be pointed out that the total catch was correlated with the trophic level of the fishery, and also with the primary production of the systems.

The most obvious local properties of the systems were related to system size, as primary production, total system biomass, or total catches. Furthermore, the factors most strongly favoring the medium-sized fish were more similar within systems through time. The strongest predators of the five most important fish species were rather variable, but their inhibition appeared to be a system-specific property, independent of the prevailing regime. Lastly, all properties related to the fishery, as fishing mortality of the groups, or the primary production required to sustain the fishery, were highly variable, not only among systems, but also among different regimes.

There are a number of inconsistencies in the properties that we have categorized as 'global'. In terms of multispecies management models, care should be taken before these estimates are transferred from one system to another. Additionally, all aspects related to the fishing regime will need to be modelled specifically for the system and period in question.

The complexity and interaction of the various factors influencing fish populations in upwelling ecosystems have been highlighted earlier (Crawford, 1991), implying blurred borderlines that have also made it difficult for us to categorize a given aspect as global or local. Nevertheless, time series, long required for improved understanding of any kind of variability in upwelling systems (see, e.g., Bakun and Parrish, 1980; Pauly, 1987; Sharp, 1991) are becoming increasingly suited for ecosystem approaches such as the one presented here, and may justify optimism that they will subsequently allow for refined future assessment of climatic effects on these four eastern boundary currents.

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