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A GUIDE TO THE ECOPATH II SOFTWARE SYSTEM (VERSION 2.1)

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and

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SOFTWARE 6

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

A guide to the ECOPATH II software system (version 2.1)

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No fish is an island...

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APPENDICES

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Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem[1]

Astrid Jarre, Peter Muck, and Daniel Pauly

Jarre, A., Muck, P., and Pauly, D. 1991. Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. – ICES mar. Sci. Symp., 193: 171–184.

The major interactions between fish stocks of the Peruvian upwelling ecosystem are predation of anchoveta (Engraulis ringens) by the teleosts Trachurus murphyi, Scomber japonicus, Sarda chiliensis, and Merluccius gayi, by three species of guano birds, and by two pinniped species. Their distributions are mediated mainly by sea surface temperature. Predation levels are determined by relative population sizes and the temporal and spatial overlap of the distribution of these species. Balanced "box" models which quantify these, and other trophic interactions for the periods 1953–1959, 1960–1969, and 1973–1979 are presented, along with the basic structure of a spatial simulation model incorporating dynamic versions of these interactions. The interrelationships of the steady-state box models, and of the simulation models are outlined, as are their potential uses for research management.

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Introduction

The Peruvian upwelling ecosystem is a typical eastern boundary current area (Parrish *et al.*, 1983). During the 1960s and the early 1970s, it supported the largest single-species fishery in the world, that for the anchoveta (*Engraulis ringens*) (Cushing, 1969; Ryther, 1969; Pauly and Tsukayama, 1987). As defined here, this system has an alongshore extension of 2100 km, from 3.5°S to 18.5°S, and an offshore extension of 200 nautical miles (nm) or about 370 km, with a total area of about 780 000 km^2 (Fig. 1). The shelf is wider in the north than in the south; its mean width is 60 nm. This paper is based predominantly on data pertaining to the northern and central region of the system, i.e. from 4°S to 14°S, corresponding to a total area of approximately 82 000 km^2, which covers the main distribution area of anchoveta.

In the late 1970s, a cooperative fisheries research project was initiated between Peru and the Federal Republic of Germany, the Programa Cooperativo Peruano-Alémán de Investigacion Pesquera (PROCOPA), based at the Instituto del Mar del Perú (IMARPE), Callao, Peru, to construct a model of the pelagic fisheries of the Peruvian ecosystem. It was anticipated that this model would be used either for real time fishery management, i.e. for fleet deployment and the identification of optimum responses to complex occurrences such as El Niño events, or at least to help sensitize managers to environmental effects and their management implications.

Major results of the analyses of field data from the project are contained in two books, one edited by Pauly and Tsukayama (1987), the other by Pauly *et al.* (1989). The contributions in these books present numerous time series of oceanographic and climatic data, covering the period from 1953 to the mid-1980s on a monthly basis, as well as time series of primary production (Chavez *et al.*, 1989; Mendo *et al.*, 1989), and zooplankton and fish biomass (Fig. 2). Also included are documentations of the dynamics of various anchoveta predators and models of their anchoveta consumption. The species (groups) covered are: bonito (*Sarda chiliensis*) (Pauly *et al.*, 1987); mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*) (Muck and Sanchez, 1987); hake (*Merluccius gayi*) (Espino and Wosnitza-Mendo, 1989; Muck, 1989a); guano birds (cormorant (*Phalacrocorax bougainvillii*), booby (*Sula variegata*) and pelican (*Pelecanus thagus*)) (Muck and Pauly, 1987); pinnipeds (fur seal (*Arctocephalus australis*) and sea lion (*Otaria byronia*)) (Muck and Fuentes, 1987).

The estimates of predation on anchoveta, computed

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[1] ICLARM Contribution No. 563.

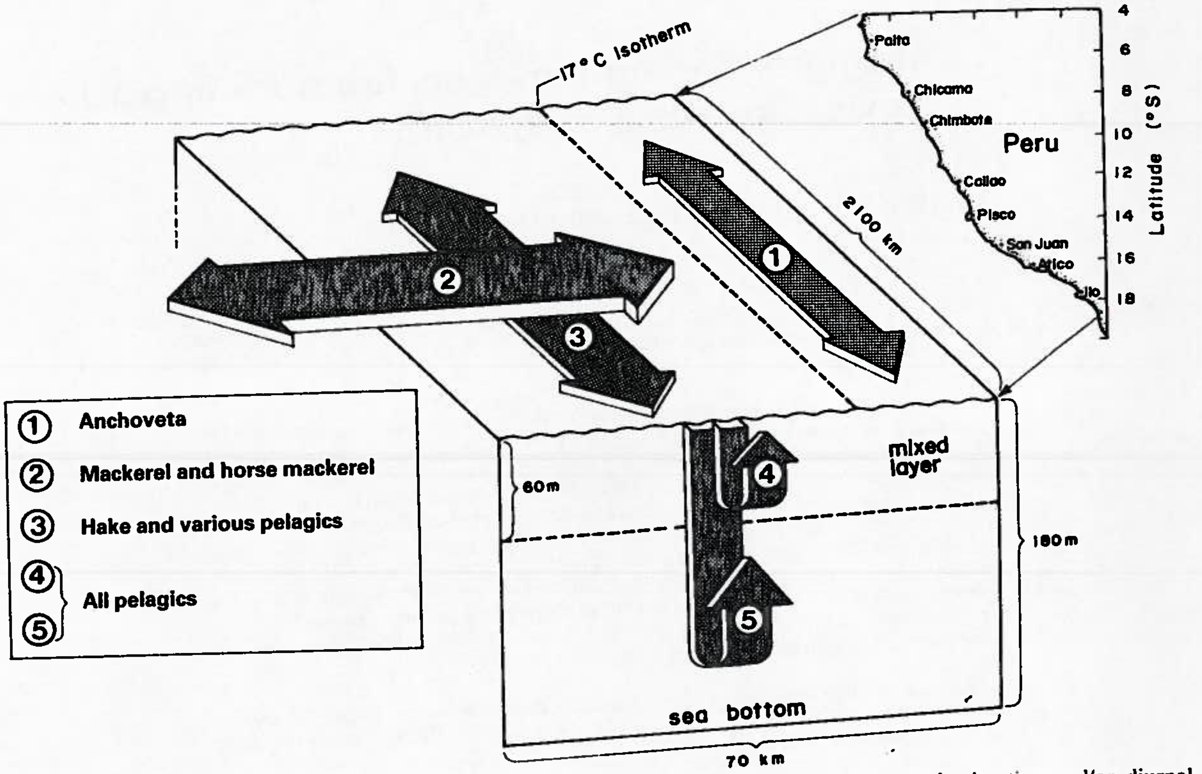

Figure 1. Schematic representation of the Peruvian upwelling system, showing axes of seasonal migration and/or diurnal movements of major resource species (see text).

on a monthly basis from 1953 to 1982 (and beyond), combined with fishery catch data, were used to reconstruct monthly anchoveta biomass and a number of derived variables, e.g. estimates of the part of natural mortality caused by the various predators (Fig. 3). These results have made it possible to model the Peruvian upwelling ecosystem as a whole. This paper briefly documents what has been achieved to date.

Steady-state modelling

Steady-state trophic models are commonly used to integrate biomass and rate estimates, to identify major energy pathways and gaps in one's knowledge of an ecosystem (see, e.g., Steele, 1974; Silvert, 1982). In view of the known variability of the Peruvian upwelling ecosystem (see, e.g., Bohle-Carbonell, 1989; Muck, 1989b), we have opted for constructing several models describing distinct periods during which the biomass of major species (groups) or "boxes" did not fluctuate so much as to render meaningless the estimation of mean values. Pending analyses on a shorter time scale, we present here results for three periods: (i) 1953–1959, during which anchoveta was moderately abundant and the fishery was limited; (ii) 1960–1969, during which anchoveta biomass and fishery efforts and catches were high, and (iii) 1973–1979, i.e., the period following the 1972/73 collapse of the fishery (Fig. 3, Table 1).

The basic concept of the ECOPATH model of J. J. Polovina and associates (Polovina, 1984a, b, 1985; Polovina and Ow, 1983; Grigg *et al.*, 1984) as further developed by Pauly *et al.* (1987), was used for model constructions.

In this formulation, for any species (group) (i) in a system, the rate of change of biomass dB/dt = 0, i.e.

Production by (i) = all predation on (i) + non-predatory biomass losses of (i) + fishery catches of (i) + other exports of (i) (1)

For each of the species (groups), its energy balance is given by

Consumption + import = predation mortality + export + contributions to detritus + respiration (2)

Equation (1), applied to all components of the model, leads to a system of linear equations which can be solved for a given set of unknowns. Polovina and Ow (1983) provide a computer program which implements this

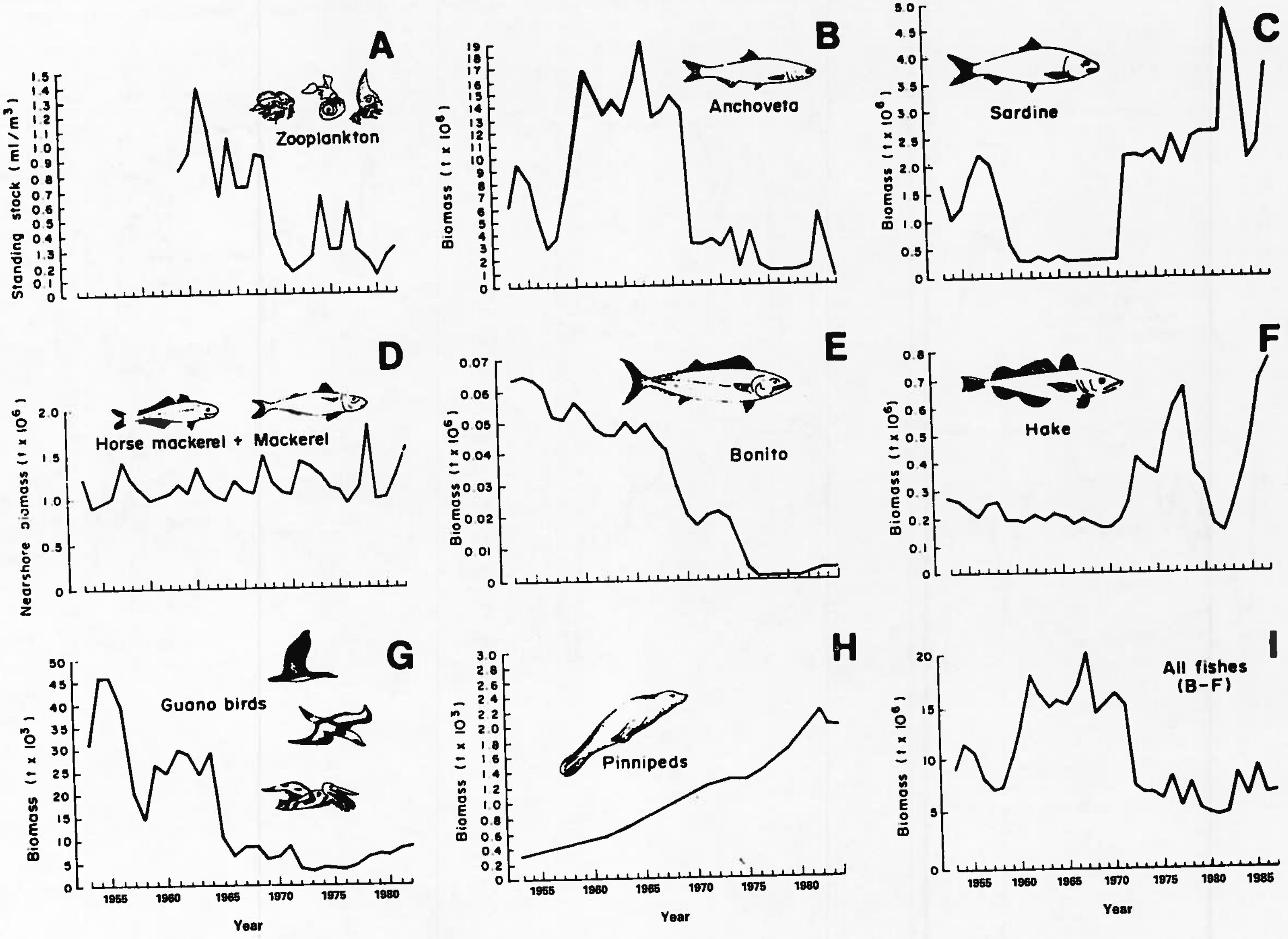

Figure 2. Biomass of major species of the Peruvian upwelling system, as estimated using approaches documented in Pauly and Tsukayama (1987) and in Pauly *et al.* (1989). Note different Y-scales.

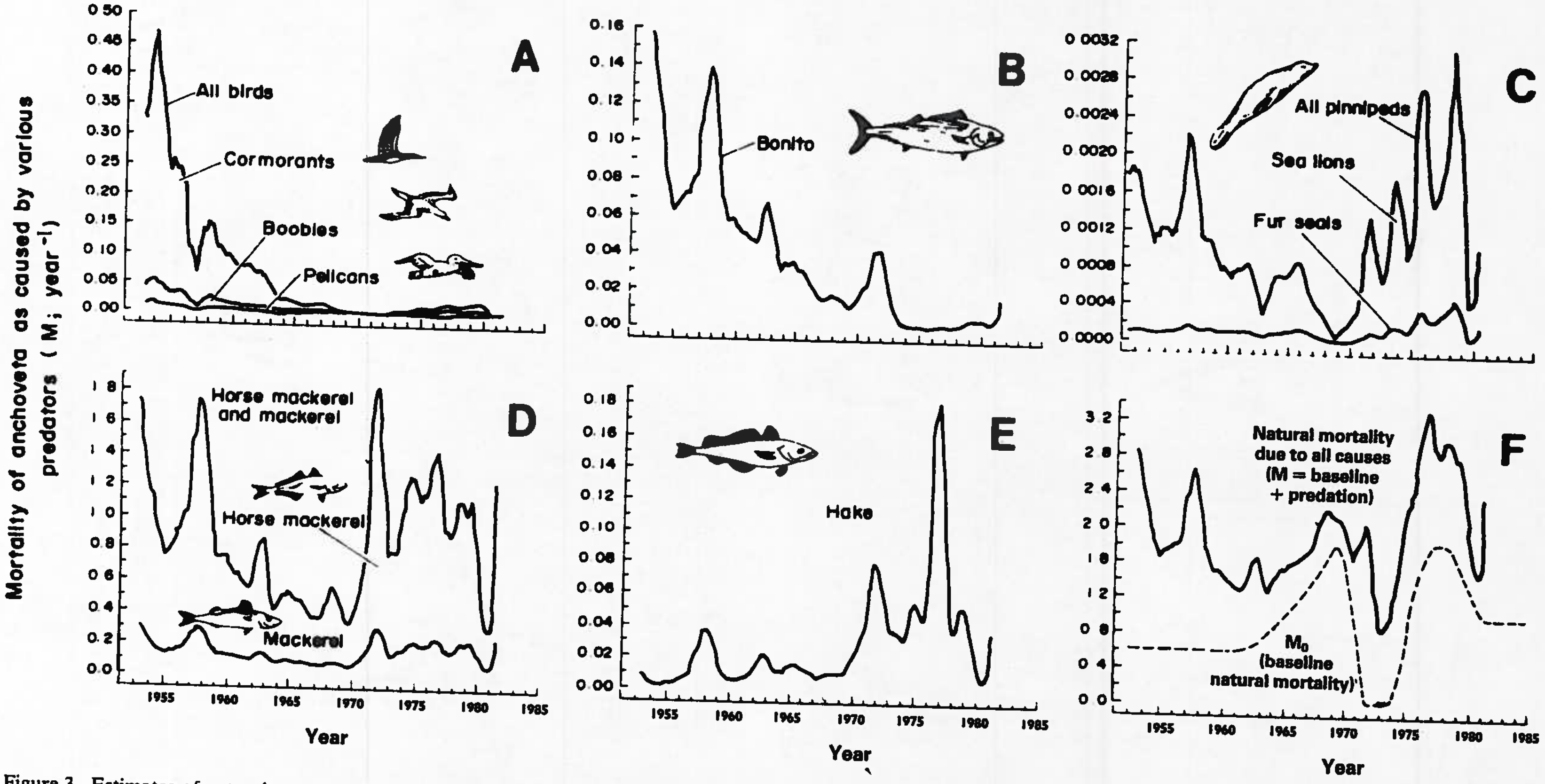

Figure 3. Estimates of natural mortality (M) of anchoveta (*Engraulis ringens*) as caused by its various predators. M is decomposed into its various components using estimates of predator-specific predation and a length-structured VPA technique. This was calibrated using acoustic estimates of biomass and allowed for estimation of baseline natural mortality (M_o) (adapted from Pauly and Palomares, 1989). Note relative constancy of overall M due to complementarity of some predators (A vs. D).

Table 1. Fishery catches (t × km^{-2}) used for construction of box models of the Peruvian upwelling ecosystem in Figures 4–6. Data from IMARPE (1987), contributions in Pauly and Tsukayama (1987) or Pauly *et al.* (1989).

Group	1953–1959	1960–1969	1973–1979
Macrobenthos	0.010	0.090	0.190
Anchoveta	6.820	110.240	32.150
Sardine	0.010	0.040	7.490
Mackerel	0.070	0.100	0.800
Horse mackerel	0.030	0.030	2.280
Bonito	0.060	0.050	0.060
Hake	0.070	0.070	1.610
Other pelagics	0.230	0.240	0.290
Other demersals	0.180	0.300	0.600
Other mammals	0.001	0.001	0.002

approach for the estimation of biomasses. The data requirements are:

- estimates of mean total mortality (Z, per year) for each box
- estimates of mean annual Q/B, the food consumption (Q) per unit biomass (B) for each box
- estimates of ecotrophic efficiency for each box (the fraction of the total production of a box that is consumed by predators included in the model)
- an estimate of catch or of biomass for the top predator(s), as needed to solve the system of equations from the "top down"
- a "diet-consumption matrix", in which the fraction (in weight) of each box in the diet of each other box is indicated and in which the rows must add up to unity.

Pauly *et al.* (1987) modified the program of Polovina and Ow (1983). Major changes are:

(i) The system of equations can be solved for unknowns other than the biomasses. Also, the routine used for matrix inversion (Mackay, 1981) computes least-squares estimates of the unknowns when the system is overdetermined, and provides (non-unique) solutions when the system is slightly underdetermined.

(ii) A number of physiological and ecological attributes of the species (groups) included in each box are automatically computed after their biomass, food consumption, and production have been estimated.

(iii) The computed flows between "boxes" are used to compute statistics relevant to Ulanowicz's (1986) theory of ecosystem phenomenology.

In this study, the biomasses were known (Fig. 2), or could be straightforwardly approximated, as were the mortalities and the food consumption estimates. Because of limited information on excretion and egestion values of most boxes, default values of 5% for excretion and 15% for egestion (Winberg, 1956) were accepted.

We used some of the attributes in (ii) above to assess the mutual compatibility of our inputs. These attributes were:

(a) Ecotrophic efficiency (see above), where $0 \leq EE < 1$ serves as constraint.

(b) Gross transfer efficiency (all production from a box/all inputs into that box); the range of which is usually between 0 and 0.3.

(c) Ivlev's electivity index, defined by:

$$I = (r_i - p_i)/(r_i + p_i) \qquad (3)$$

where r_i is the relative count or biomass of a species i in the diet of a particular predator, and p_i is its relative count or biomass in the ecosystem (i.e. included in the model) (Ivlev, 1961; Parsons and LeBrasseur, 1970). This index can range from −1 (prey is not consumed at all) to near +1 (prey is consumed exclusively).

The construction of the model involved: (1) preparation of an initial set of biomass and rate inputs and of an initial diet-composition matrix; (2) estimation of model parameters, and of the physiological and ecological attributes listed above; (3) performing small changes in the initial values and returning to item (2) until all attributes examined took values within a range considered acceptable. (The initial and modified values for each of the periods considered here are given in Jarre *et al.*, 1989.)

Figures 4, 5, and 6 give the results obtained. These three graphs and their associated parameters indicate that our quantifications of the biomasses and our concepts of the interactions between various species (groups) of the Peruvian ecosystem are mutually compatible within a factor of about two with their published value. Major changes had to be made only (i) in the initial estimate of the zooplankton biomass (by a factor of three) for the 1950s and 1960s, probably due to our limited knowledge on the actual mortality and consumption rates of this species group; (ii) the biomasses of the heterogeneous groups of "other pelagics" and "other demersals", for which the official catch statistics might not be the adequate basis for estimation of biomass; and (iii) the mortality of the sardine, which had to be raised from a published value that was very low to a value close to that of anchoveta.

An interesting aspect of Figures 4, 5, and 6 is their immediate visual impact, i.e. the strong difference in ecosystem structure which they indicate. This impact was achieved by two techniques, apparently not used previously for the graphical representation of box models, i.e.: (1) making the area of each box proportional to the logarithm of the biomass it represents, and (2) using the trophic level[1] of each box to arrange the boxes vertically.

The graphs thus allow a direct assessment of the

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[1] The trophic level of a species (group) is defined as one plus the mean of the tropic levels of its prey items, weighted by their fraction in the total diet.

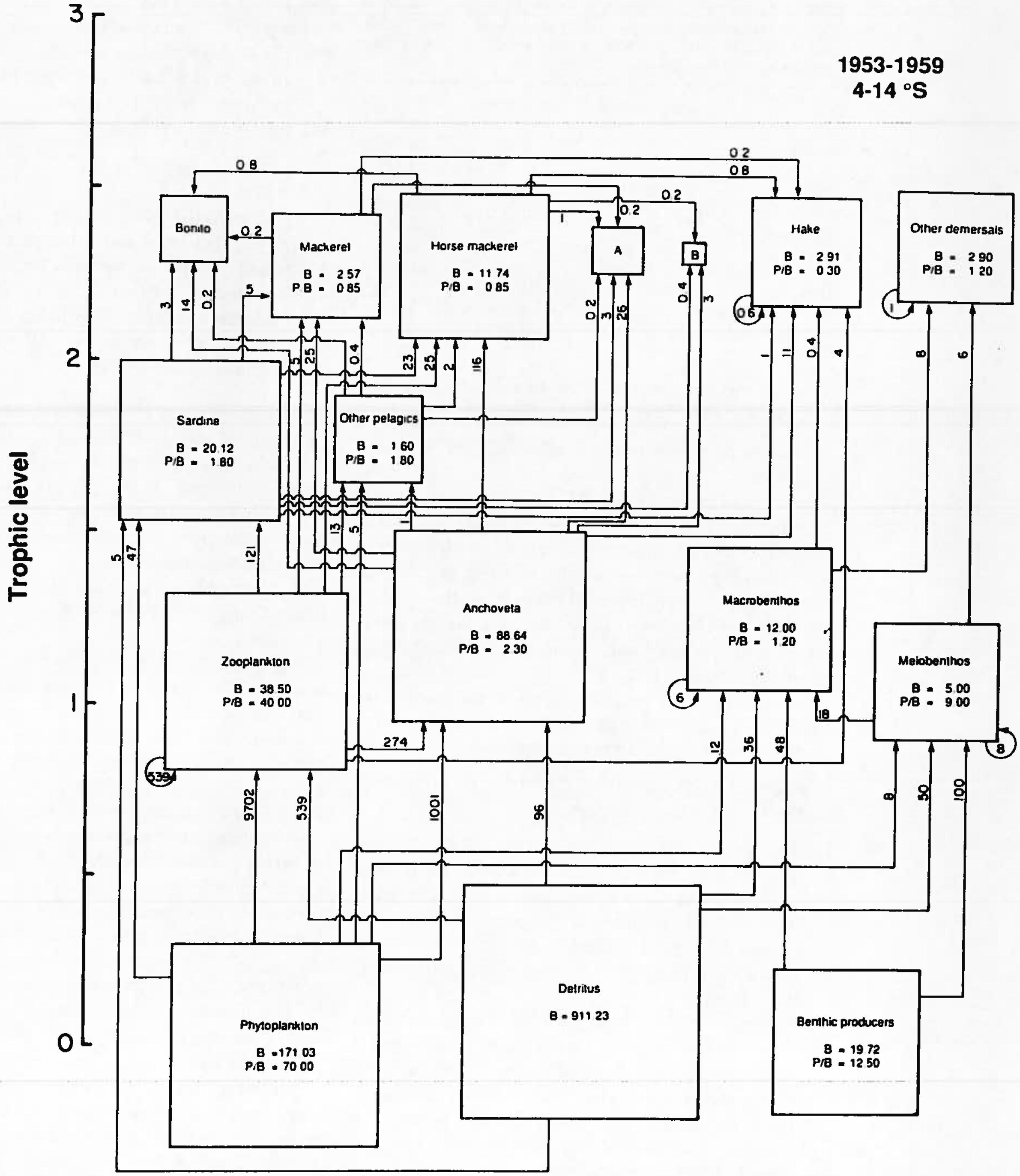

Figure 4. Box model of the Peruvian ecosystem for the period 1953–1959. A. Marine birds (cormorant, booby, pelican; $B = 0.40\,t \times km^{-2}$, $P/B = 0.04\,yr^{-1}$). B. Sea mammals (sea lion, fur seal, and others: $B = 0.07\,t \times km^{-2}$, $P/B = 0.09\,yr^{-1}$). Bonito: $B = 0.72\,t \times km^{-2}$, $P/B = 0.91\,yr^{-1}$. Flows greater than $1\,t \times km^{-2} \times yr^{-1}$ are rounded to integer numbers; those between 0.1 and $0.9\,t \times km^{-2}\,yr^{-1}$ are rounded to one digit. Flows of less than $0.1\,t \times km^{-2} \times yr^{-1}$, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

differences between the three periods considered here, e.g. anchoveta is more important in the 1960–1969 period than in the earlier and later periods; and sardine is more important in the 1973–1979 period than in the two earlier periods. The trophic level of the top predators is increased as a consequence of increased consumption of sardine instead of anchoveta as well as increased consumption of mackerel and horse mackerel.

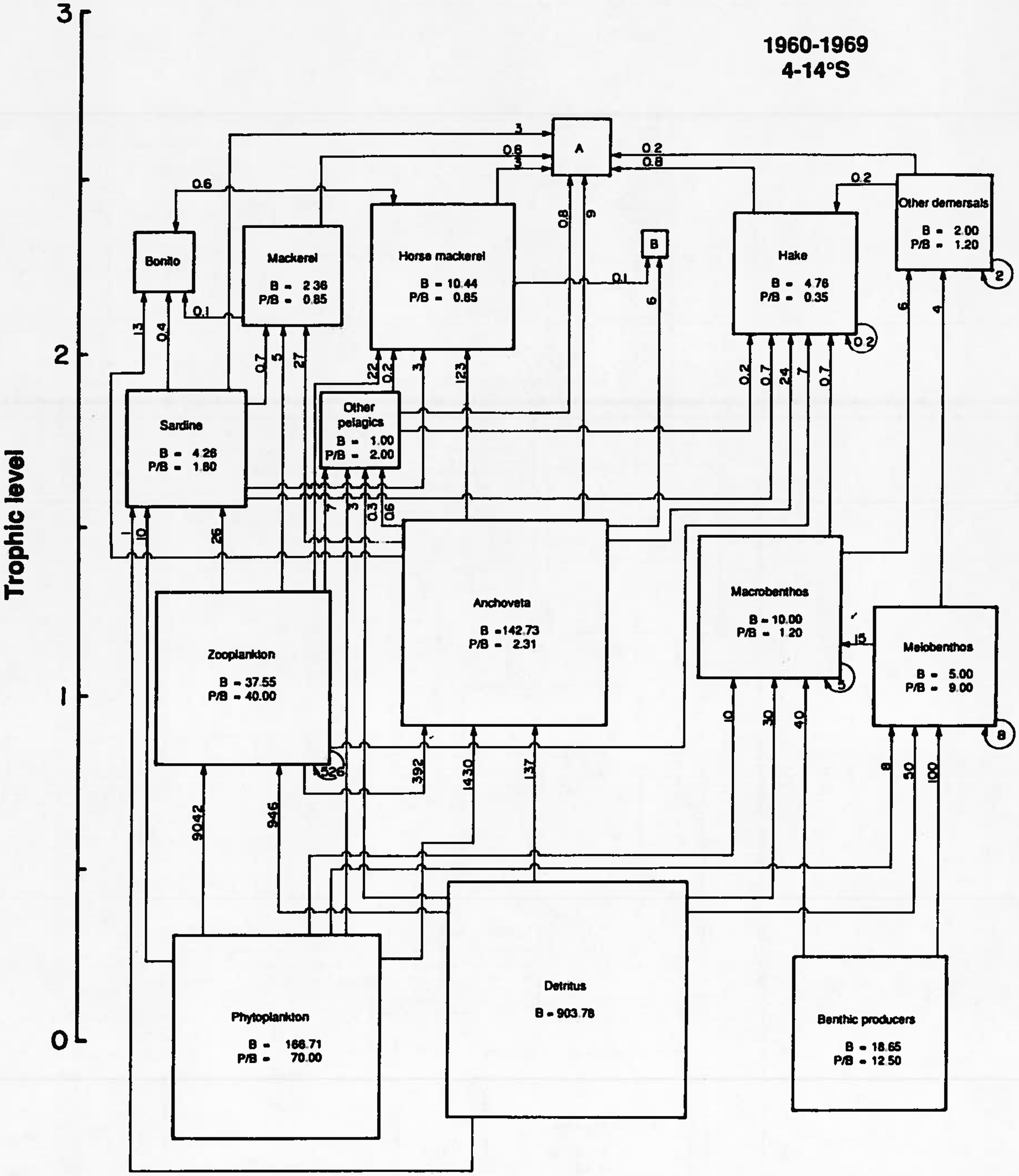

Figure 5. Box model of the Peruvian ecosystem for the period 1960–1969. A. Marine birds (cormorant, booby, pelican; $B = 0.21\,t \times km^{-2}$, $P/B = 0.04\,yr^{-1}$). B. Sea mammals (sea lion, fur seal, and others: $B = 0.07\,t \times km^{-2}$, $P/B = 0.09\,yr^{-1}$). Bonito: $B = 0.55\,t \times km^{-2}$, $P/B = 0.93\,yr^{-1}$. Flows greater than $1\,t \times km^{-2} \times yr^{-1}$ are rounded to integer numbers; those between 0.1 and $0.9\,t \times km^{-2} \times yr^{-1}$ are rounded to one digit. Flows of less than $0.1\,t \times km^{-2} \times yr^{-1}$, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

Another approach for the interpretation of the "weighted graphs" in Figures 4–6 is via the theory of Ulanowicz (1986), who introduced a set of single-number characteristics of ecosystems. The "ascendancy" of an ecosystem is defined as the product of the total system throughput (sum of all flows within the system) and the "average mutual information"; the latter index is computed from the network structure, and

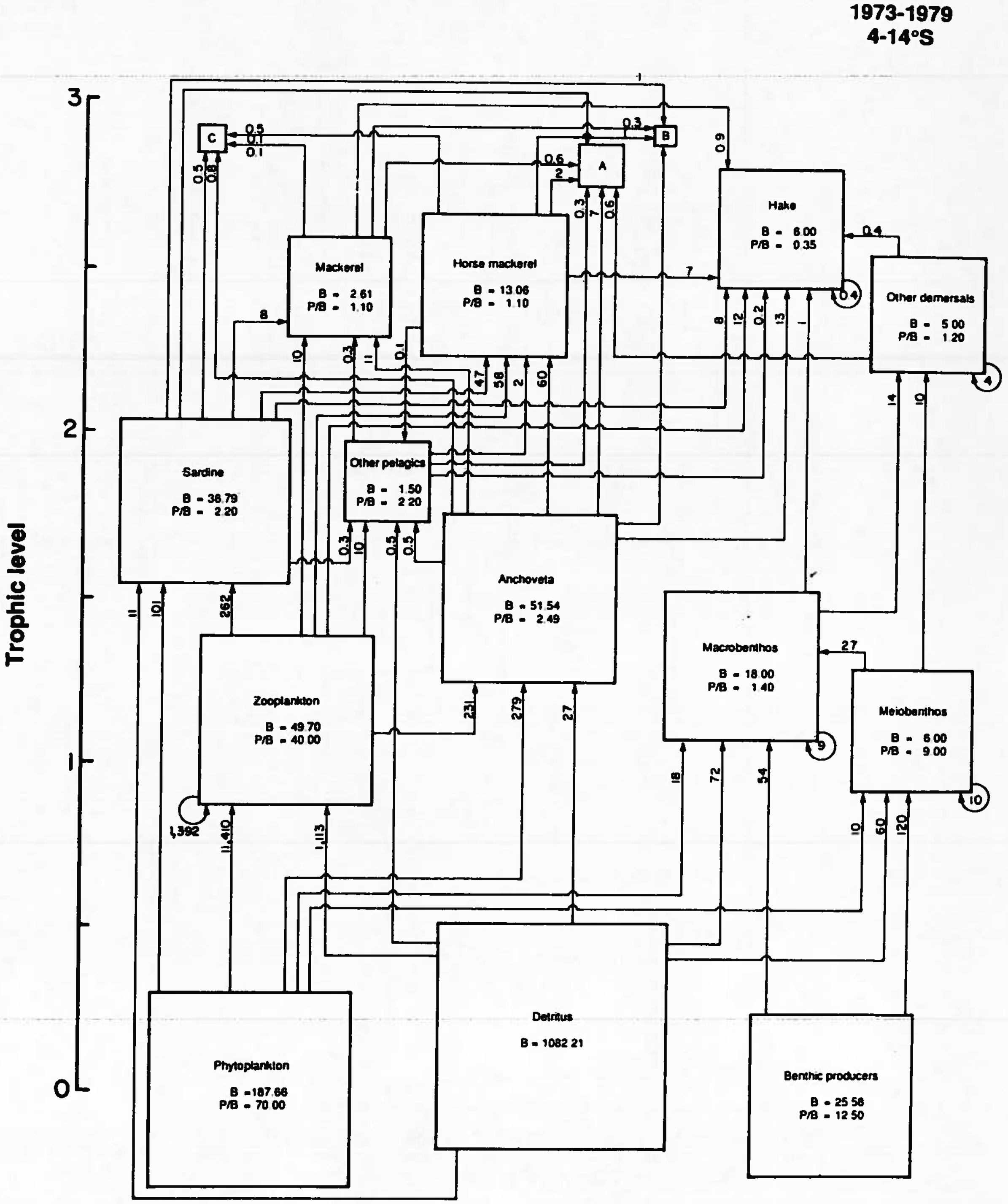

Figure 6. Box model of the Peruvian ecosystem for the period 1973–1979. A. Marine birds (cormorant, booby, pelican; B = 0.28 t × km^{-2}, P/B = 0.04 yr^{-1}). B. Sea mammals (sea lion, fur seal, and others; B = 0.09 t × km^{-2}, P/B = 0.09 yr^{-1}). C. Bonito (B = 0.09 t × km^{-2}, P/B = 0.93 yr^{-1}). Flows greater than 1 t × km^{-2} × yr^{-1} are rounded to integer numbers; those between 0.1 and 0.9 t × km^{-2} × yr^{-1} are rounded to one digit. Flows of less than 0.1 t × km^{-2} × yr^{-1}, backflows to the detritus box, respiration, and fishery catches are omitted for clarity (see text for interpretation).

Table 2. Whole-system indices of the box models in Figures 4–6, and indices computed by Pauly (1987) from the models in Walsh (1981).

Index	This study			Walsh's model	
	1953–1959	1963–1969	1973–1979	before 1972	after 1972
Number of boxes[a]	19	19	19	12	12
Total system throughput (t wet weight × km^{-2})	29 600	29 382	33 539	37 027[b]	34 591[b]
Full development capacity (t wet weight × km^{-2})	57 521	57 358	61 905	81 529[b]	73 484[b]
Full ascendency (%)	39.4	37.4	36.4	64.6	61.6
System redundancy (%)	27.5	30.6	34.4	12.8	15.1
Fishery "trophic level"	2.4	2.2	2.7	–	–
Fishery gross efficiency	0.0006	0.0093	0.0034	–	–

[a] Excluding fishery.

[b] The estimates of Walsh (1981) were converted from carbon to wet weight using 1 gC = 13.93 g wet weight (average of Cushing (1971) and Ryther (1969)).

is maximized if (i) flows are equally distributed among the boxes and (ii) each box has only one input and one output (i.e. origin and destination of any flowbit are determined). The "system redundancy" describes the loss of information due to multiple flows between the boxes of the ecosystem (i.e. the existence of multiple ways of connecting any two boxes).

These summary statistics, computed for the three models presented here, are given in Table 2. The throughput of the system was similar during the 1950s and 1960s, and increased in the 1970s, partly due to an increase in primary production in the upwelling system (Mendo *et al.*, 1989). The ascendency decreased, which in this case means a loss in "mutual information", also shown in the decrease of 12% of the corresponding index from the 1950s to the 1970s. The increase in redundancy is due to the fact that the anchoveta, previously of overwhelming importance to piscivores, was in part replaced by other components of the system, including anchoveta predators. This led to an increase in parallel energy transfer, as mentioned above. Our preliminary conclusion, based on the three periods considered here, is that the Peruvian ecosystem is less mature (*sensu* Odum, 1969, see Ulanowicz, 1986, p. 122) after the decline of the anchoveta than it was before.

The fishery fits in the model as an almost pure "anchoveta predator" in the 1950s and 1960s. Its "trophic level" increased in the 1970s, after the anchoveta collapse, due to the increased catch of anchoveta predators mackerel, horse mackerel, and hake. The increase in fishing effort from the 1950s to the 1960s is clearly reflected in the 15-fold increase of the fishery's gross efficiency (total catch/primary production), and the collapse of the fishery after 1972 in the decline of its efficiency to only 36% of the high value of the 1960s. It should be noted, however, that the fishery still retained an efficiency which is more than five times higher than the value from the 1950s. The partitioning of the total fish predation among fishes, birds, mammals, and the fishery (Fig. 7) shows the same pattern, albeit less pronounced.

Pauly *et al.* (1987) computed the above summary statistics from the model of the Peruvian upwelling ecosystem presented by Walsh (1981). Since Walsh's models set focus on different parts of the ecosystem, and hence had a different basic structure than the models in the present study, it is difficult to directly compare the values of ascendency and redundancy obtained. The changes in the system, i.e. the decrease of mutual information, the decline of ascendency and the increase in redundancy, however, are apparent from Walsh's (1981) approach as well (Table 2).

Simulation modelling

Our simulation model of the fish resources and fisheries of the Peruvian upwelling ecosystem is not complete. However, its basic structure with regard to spatial resolution and the role of sea surface temperature (SST) as driving factor is established. SST is used as a key factor because it has been shown by various authors to determine the distribution, hence the overlap and potential for trophic interactions, of the various pelagic species of the Peruvian upwelling ecosystem as follows:

1. When coastal SSTs are low, i.e. when the upwelling is strong, anchoveta occur near the surface on the shelf along the coast of Peru. Hake stay in the north because the bottom O_2 concentration in the upwelling area is low. Mackerel and horse mackerel stay offshore as they are oceanic species requiring temperatures of at least 20°C.
2. When coastal SSTs are high, anchoveta tend to crowd within a few remaining pockets of cold water and/or

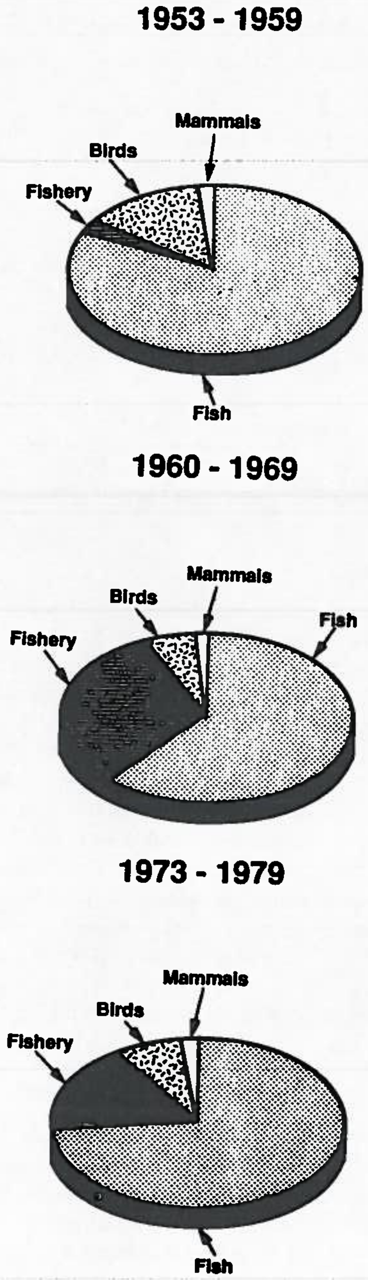

Figure 7. Partitioning of total fish production among fishes, birds, mammals, and the fishery, from the models in Figures 4–6. Contributions to detritus are disregarded.

to escape to greater depths, hence out of reach of guano birds and purse seiners. Hake migrate southward and feed on anchoveta, and mackerel and horse mackerel move inshore and consume large quantities of anchoveta.

The situation in (1) is typical of (austral) winter conditions; that in (2) is typical of summer conditions, and particularly of El Niño events, during which the crowding of anchoveta and their consumption by hake, mackerel, and especially by horse mackerel, become extremely pronounced. A brief account is given below of a simulation model which incorporates these features.

The large area of the Peruvian upwelling ecosystem was divided into manageable units by grouping administrative "fishing areas" (*areas de pesca*) as defined by IMARPE. This resulted in a total of 150 approximately rectangular "local areas", each of which extend one degree latitude southwards (covering the range from 3.5°S to 18.5°S) and 20 nm offshore, parallel to an idealized coastline (Fig. 8A). To estimate the size of the fish stock in each subarea at a particular time (month), a "local potential distribution volume" has been defined. Its size is assumed to depend on (i) the physical properties of this subarea; and (ii) the specific physiological requirements of each species with respect to temperature and oxygen content of the water column (Fig. 8B, C, D). We assume that the fish are homogeneously distributed inside this volume. Species-specific "local shelf preference indices" are introduced to account for the depth preference of coastal and demersal species, food related preferences and other factors. The size of a population in a given subarea is proportional to the local potential distribution volume divided by the total distribution volume of the ecosystem.

For the calculation of the local potential distribution volume, temperature tolerance limits were obtained from field observations (Jordan, 1971; Zuta *et al.*, 1983; Espino *et al.*, 1985; Serra and Tsukayama, 1988); they are 14–21°C for anchoveta, 16–23°C for sardine, 15–25°C for mackerel, 16–26°C for horse mackerel, and 14–22°C for hake. Oxygen tolerance limits were taken as 1.8 ml O_2/l for anchoveta, mackerel, and horse mackerel (Villavicencio and Muck, 1985; Mathisen, 1989), 2 ml O_2/l for sardine (Serra and Tsukayama 1988), and 0.4 ml O_2/l for hake (see Fig. 1 in Espino and Wosnitza-Mendo, 1988).

Temperature and oxygen concentration vertical profiles were computed from SST based on relationships given in Espino *et al.* (1985). SSTs were estimated from the data from nine Peruvian shore stations (Muck *et al.*, 1989) and the offshore temperature series in Bakun (1987), yielding a regression which was used to estimate local SST within 70 nm from the coast. Coastal SSTs are linearly interpolated between shore stations. For distances of more than 70 nm, SST is assumed constant along offshore transects.

In any given subarea, the vulnerability of a particular fish species to its predators (i.e. the degree of overlap of water volume inhabited by predator and prey) and to the fishery is determined by their distribution within the entire water column (Fig. 8E). The amount actually consumed is determined by the biomass of the predators, their temperature-mediated food requirements, and the biomass and vulnerability of the prey, following

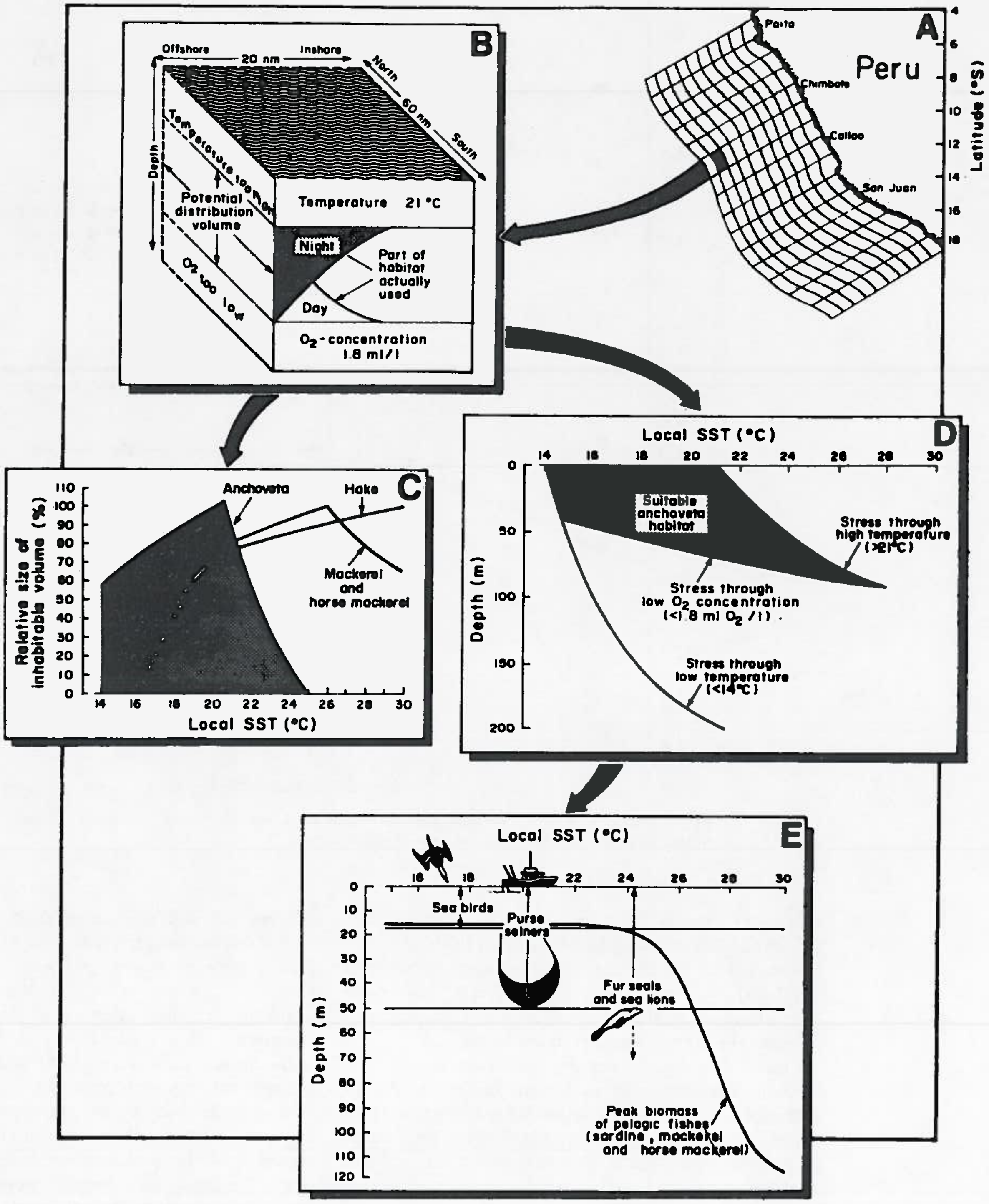

Figure 8. Schematic representation of submodels incorporated in large simulation model of the Peruvian upwelling ecosystem. A. Definition of the 15×10 subareas used for spatial modelling. B. The volume potentially inhabited by a given species within each subarea is a function of SST, O_2 concentration, and time of the day; C. Each species has different physiological requirements which, given changing SST, result in different fractions of a subarea's water column being occupied by that species. D. The effects in (C) cause vertical changes in distribution, all of which occur within a narrow range of temperature and above a critical O_2 concentration. E. Combined, these effects determine whether the fish will be high enough in the water column to be caught by guano birds, marine mammals, or purse seiners.

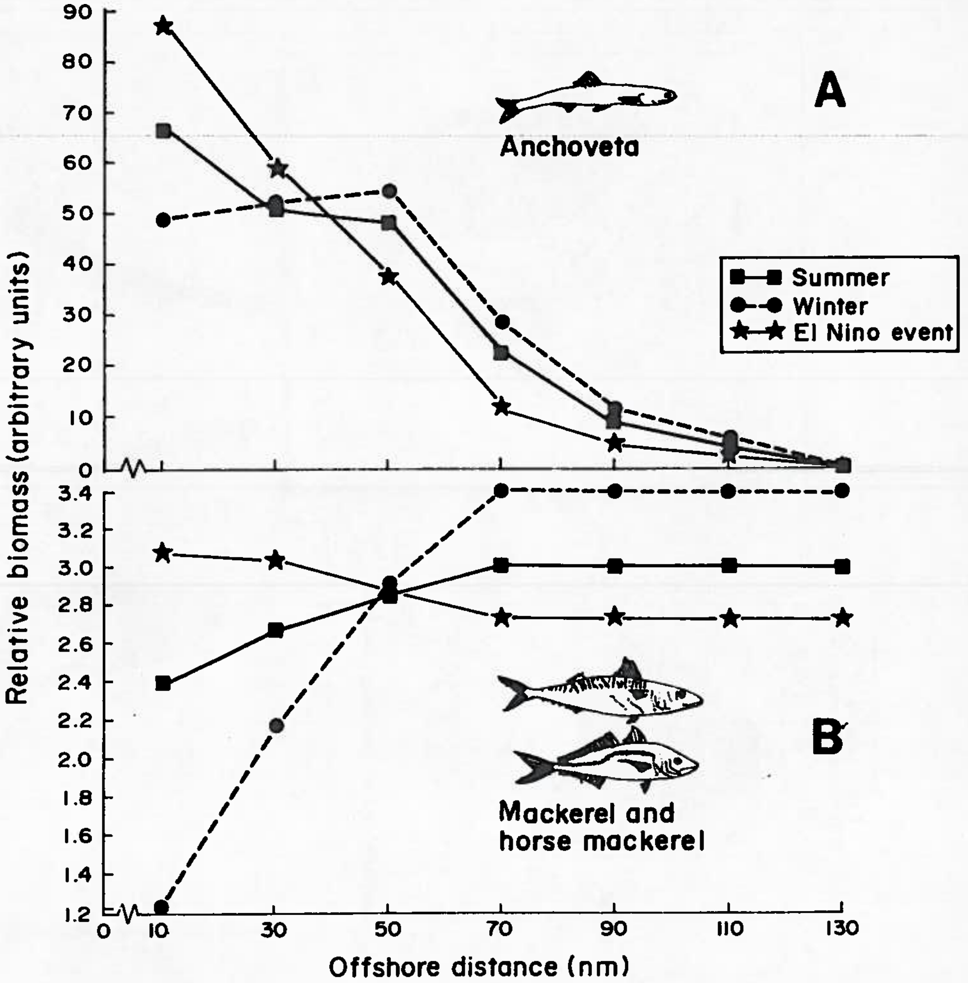

Figure 9. Relative biomass of anchoveta, mackerel, and horse mackerel off Peru as a function of distance offshore and SST regime, as estimated from the simulation model presented in the text.

Ursin (1967) and Andersen and Ursin (1977). The fishery catches are modelled for any given subarea as a function of (i) the biomass of the fish species; (ii) their depth distribution, i.e. their vulnerability to purse seines (Fig. 8E); and (iii) the fishing effort, i.e. the deployment of purse seiners and trawlers in that area.

Figure 9 gives, as some preliminary results, the offshore distribution of anchoveta and mackerels for different SST regimes. The model will eventually be parameterized using spatial distribution data based on fisheries operation in the 1960s and 1970s, and it is ntended to be interfaced with an economic submodel, based on Agüero (1987).

Discussion

The usefulness of top-down steady-state models of the type described above lies particularly in the identification of knowledge gaps, and of states or rate estimates that are mutually consistent (Silvert, 1981, 1982). In the case of the three models derived here, no major inconsistencies with previously published biomass estimates were noted except for zooplankton. Also, most of the available published estimates of key rates (food consumption, total mortality, etc.) for the groups included in the models did not have to be altered significantly to balance the model (except for sardine, see above). Hence, these models show the consistency of the concepts and estimates used for their construction. Future emphasis will be put on a more detailed representation of the planktonic and benthic groups in the model, and use of a shorter time interval.

The approach used to construct a spatially structured simulation model of the fish and fisheries of the Peruvian upwelling system may be as robust as our top-down model. Temperature is a variable which has, off Peru, an extremely strong impact on the distribution of major groups of organisms. Thus any model which uses SST as forcing variable is likely to be able to reproduce the key features of the distribution of the biota and the fishery, and the overlap of major predator and prey species.

Note that the model described here is still overly simplistic, and it will be refined after testing. For example, temperature distribution may need to be modified to take account of seasonal oscillations, and the offshore distribution of the major fish species may need to be related to plankton occurrence.

A similar approach in which SST and parameters directly dependent on SST were used to identify areas of potential availability of tuna to purse seiners and other gears has been presented by Sharp (1979) for the Indian Ocean. The concept of the simulation model presented here also corresponds, albeit indirectly, to the ideas of McCall (1984) concerning the tendency of a fish population to concentrate itself where conditions are optimal, such that, overall, conditions for individual fishes are similar over the whole area of distribution of that population.

One potential use of the simulation model is to optimize spatial deployment of the Peruvian purse seiner fleet, based on SST data from coastal stations. Even if the model is not used for real time management, it may lead to an improved understanding by Peruvian fishing managers and administrators of the factors that determine fishing success, and the consequences of fleet deployment strategies particularly during El Niño events, when anchoveta tend to become highly vulnerable.

Both models will allow us to follow up on some implications of Ulanowicz's theory. We will use the simulation model to generate the biomasses within boxes and some flows between boxes for various "steady-states" representing various environmental and fishing regimes. This will allow us to identify how Ulanowicz's indices (see Table 2) actually track environmental stress, or stress due to overexploitation.

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