

Seasonal Changes in the Peruvian Upwelling Ecosystem*

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Abstract

A set of twelve balanced steady-state models is presented which quantify the seasonal changes in biomass and food consumption among major fish stocks of the Peruvian upwelling ecosystem, *Engraulis ringens*, *Sardinops sagax*, *Scomber japonicus*, *Trachurus murphyi* and *Merluccius gayi*, as well as three species of guano birds and three groups of marine mammals. The results are based on published series of monthly biomasses and vital statistics, covering the years 1973 to 1979, a period which did not include major El Niño events. The seasonality of network flow indices computed from these models is discussed, following the theory of R.E. Ulanowicz.

Introduction

The Peruvian ecosystem is one of the world's large upwelling ecosystems. During the 1960s it supported a huge industrial fishery for anchoveta *Engraulis ringens*, which collapsed in the early 1970s. The anchoveta fishery has however continued to the present on a reduced level, and was in part replaced by fisheries on other species such as sardine *Sardinops sagax* for reduction purposes, and mackerel *Scomber japonicus*, horse mackerel *Trachurus murphyi* and hake *Merluccius gayi* for human consumption. Data compiled and results published in the course of various research efforts in the 1970s and 1980s (among others: Dickie and Valdivia 1981, Arntz et al. 1985, Pauly and Tsukayama 1987,

Salzwedel and Landa 1988, Pauly et al. 1989) have now enabled us to model species interactions in this ecosystem. In the frame of an investigation of time series available from 1953 to 1982, and based on three models averaging the periods 1953-1959, 1960-1969 and 1973-1979 (Jarre et al. 1991), this contribution attempts to quantify monthly changes during the years 1973 to 1979, a period which did not include major El Niño events, and in which conditions were stable enough to allow the use of a steady-state approach.

Materials and Methods

The area included in this analysis extends along the Peruvian coast from 4 to 14°S, to about 55 nautical miles offshore, thus covering the main area of anchoveta distribution (see

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contributions of Pauly and Tsukayama 1987b, and Pauly et al. 1989). The ECOPATH approach originally developed by Polovina (Polovina 1984; 1985) and extended as ECOPATH II by D. Pauly and associates (Pauly et al., this vol.; Christensen and Pauly 1992a, this vol.) was used to quantify the interactions of a total of 20 boxes, including major components of the system with emphasis on the commercial fish species (Fig. 1). For each group, monthly averages of biomass, mortality, consumption/biomass rate and catch were entered into the program, as was the diet composition for each component. Primary production, zooplankton biomass and biomasses of anchoveta and its most important predators, as well as some vital

statistics were computed from the data made available in Pauly and Tsukayama (1987) and Pauly et al. (1989), and from other statistics and estimates of diet composition from the available Peruvian literature (see Tables 1 and 2 for details). Average values of the above statistics were used where seasonal data were not available. The program's default values of 20% of the consumption for unassimilated food were accepted. We further assumed no imports to the system and no exports from it, apart from fishery catch. For brevity's sake the input data are not listed in this paper in detail but are included in the files distributed with this volume (see Appendix 4).

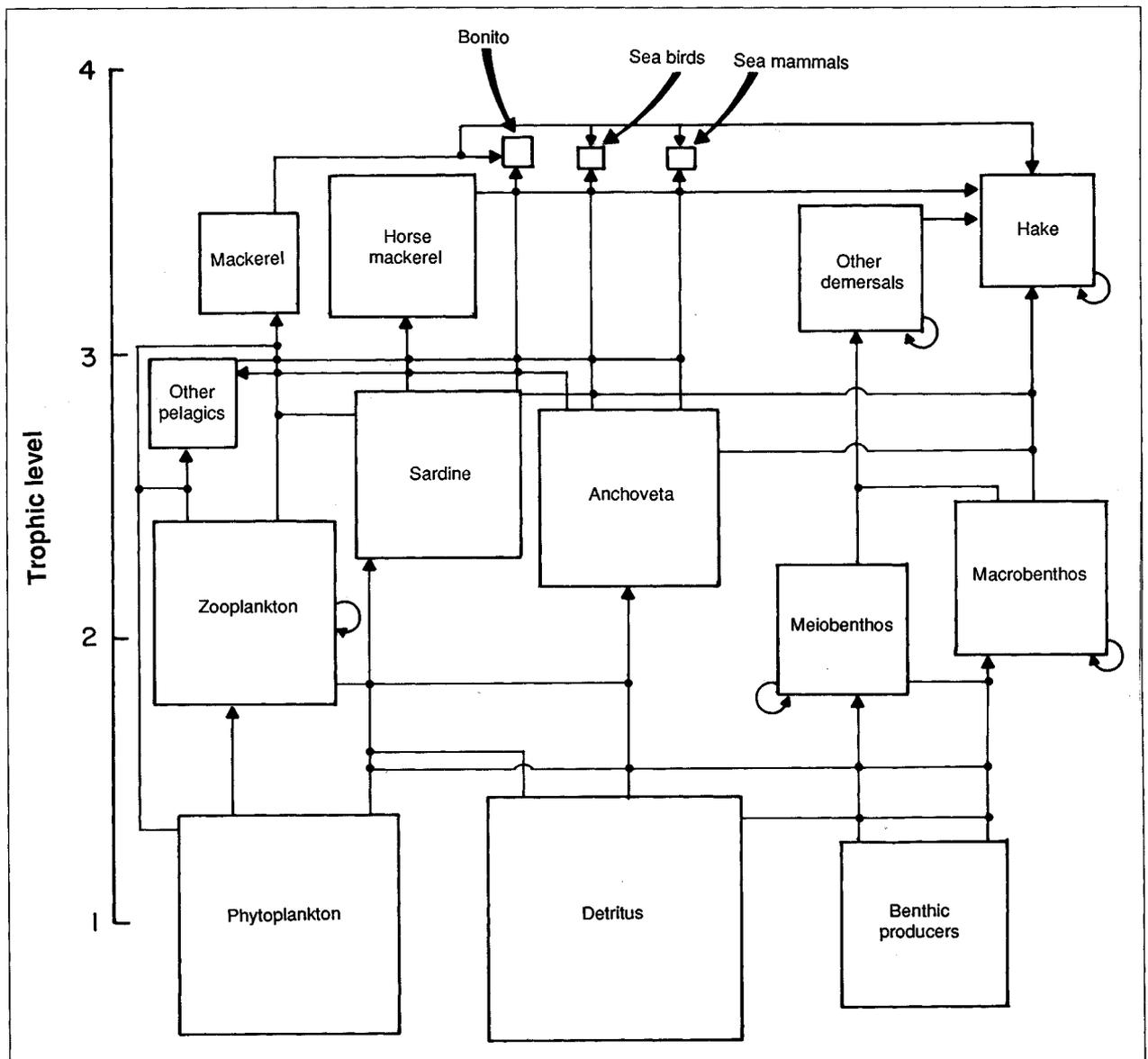


Fig. 1. Overview of the boxes used for the 12 monthly ECOPATH II models described in the text, arranged according to average annual trophic level. Note that the box "sea birds" is comprised of cormorants, boobies and pelicans which are computed with separate parameters, and the box "sea mammals" is comprised of sea lions, fur seals and other mammals also kept separate in model construction.

Table 1. Sources for biomass, mortality and catch inputs for ECOPATH II models of the Peruvian upwelling ecosystem.

Group	Biomass	P/B or mortality	Catch
Zooplankton	Carrasco and Lozano (1989)	Shushkina et al. (1978)	-
Meiobenthos	guesstimate	Gerlach (1971)	-
Macrobenthos	Rosenberg et al. 1983, Arntz et al. 1991	Walsh (1981)	IMARPE (1987)
Anchoveta	Pauly and Palomares (1989)	Pauly and Palomares (1989)	Tsukayama and Palomares (1987), Castillo and Mendo 1987
Sardine	Muck and Sánchez (1987) and Serra and Tsukayama (1988)	Serra and Tsukayama (1988)	Serra and Tsukayama (1988)
Mackerel	Muck (1989b and unpubl. data)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Horse mackerel	Muck (1989b and unpubl. data)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Bonito	Muck (1989b)	Jarre et al. (1991), based on Muck and Sánchez (1987)	IMARPE (1987)
Hake	Espino and Wosnitza-Mendo (1989) and Muck (1989a)	Espino and Wosnitza-Mendo (1989)	Espino and Wosnitza-Mendo (1989)
Other pelagics	guesstimate, based on IMARPE (1987)	guesstimate (Jarre et al. 1991)	IMARPE (1987)
Other demersals	guesstimate, based on IMARPE (1987)	guesstimate (Jarre et al. 1991)	IMARPE (1987)
Cormorant	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Laugksch and Duffy (1984)	-
Booby	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	-
Pelican	Muck and Fuentes (unpubl. data), based on Tovar et al. (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	-
Sea lion	Muck and Fuentes (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Fur seal	Muck and Fuentes (1987)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Other mammals	guesstimate (Jarre et al. 1991)	Jarre et al. (1991), based on Lindstedt and Calder (1981)	guesstimate, based on Majluf and Reyes (1989)
Phytoplankton	computed output; production values from Mendo et al. (1989)	Polovina (1985)	-
Benthic producers	computed output	Polovina (1985)	-
Detritus	regression in Pauly et al. (this vol.)	-	-

The models were balanced using the ecotrophic efficiencies computed by the program (i.e., the proportion of the production that is consumed by predators or taken by the fishery, and the value of which, for obvious reasons, must be between zero and one), and computed values of Ivlev's electivity index (Ivlev 1961, Parsons and LeBrasseur 1970). The Q/B estimates of the anchoveta predators from the literature were reduced by 10%; further adjustments for balancing the models were achieved exclusively by changes in the diet composition matrix.

Summary Statistics

In an attempt to derive some system-level generalizations from steady-state models, a number of ecosystem attributes and goal functions have been proposed (Odum 1969; Mejer and Jørgensen 1979; Ulanowicz 1986; Jørgensen 1992). Discussions have recently occurred as to the appropriateness of those proposed attributes and goal functions to actually describe ecosystem maturity and stability (Baird et al. 1991; Jarre-Teichmann 1992; Christensen, in press). This

Table 2. Sources of consumption rate and diet composition inputs for ECOPATH models.

Group	Consumption/biomass	Diet composition
Zooplankton	Polovina (1985)	guesstimate
Meiobenthos	Walsh (1981)	guesstimate
Macrobenthos	Walsh (1981)	guesstimate
Anchoveta	Alamo (1989), Rojas de Mendiola (1989), Jarre et al. (1991)	Alamo (1989), Rojas de Mendiola (1989)
Sardine	Jarre et al. (1991)	Alamo et al. (1988)
Mackerel	Jarre et al. (1991), based on Muck and Sánchez (1987)	adapted from Muck and Sánchez (1987)
Horse mackerel	Jarre et al. (1991), based on Muck and Sánchez (1987)	adapted from Muck and Sánchez (1987)
Bonito	Palomares (unpubl. data)	guesstimate
Hake	Muck (1989a), based on Espino and Wosnitza-Mendo (1989)	guesstimate, based on Muck (1989a)
Other pelagics	guesstimate, between anchoveta and sardine	guesstimate
Other demersals	guesstimate	guesstimate
Cormorant	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Booby	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Pelican	Muck and Pauly (1987)	guesstimate, based on Muck and Pauly (1987)
Sea lion	Muck and Fuentes (1987)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Fur seal	Muck and Fuentes (1987)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Other mammals	guesstimate of Jarre et al. (1991)	guesstimate, based on Muck and Fuentes (1987) and Majluf and Reyes (1989)
Phytoplankton	-	-
Benthic producers	-	-
Detritus	-	computed output

shall, however, not be elaborated further in the present contribution but will instead be investigated in a larger context (Jarre-Teichmann and Christensen, in press). For the present contribution, we focus on the network flow indices based on Ulanowicz (1986): based on the "maximum power principle" (Odum 1983). Ulanowicz proposed to link the size of an ecosystem, computed as the sum of all flows in the ecosystem, with its internal structure, computed as a "factor of average mutual information" from the distribution of flows in this ecosystem. This factor of average mutual information is a probability by nature, and describes the reduction in uncertainty associated with a given unit of flow being channelled in a flow network. The product of these two parameters, i.e., of total system throughput and average mutual information, is called ascendancy. As Ulanowicz (1986) based his studies on the attributes of ecosystem maturity described in Odum (1969), he postulated that ecosystems evolving towards maturity optimize this goal function.

For mathematical-theoretical as well as for biological-practical reasons, there exists an upper bound of ascendancy, named development capacity. This bound is based on the reasoning that the total throughput of a given system, being limited by the inputs to the system, cannot exceed certain limits, and the number of components cannot increase without limits either: a high number of compartments would necessarily result in low throughput per compartment and, consequently, in high vulnerability to random environmental perturbations. The difference between development capacity and ascendancy is called system overhead, and may be understood as a measure of a system's ability to cope with random perturbations.

As a measure for the importance of cycling in an ecosystem, an index giving the fraction of the total throughput that is recycled in the system (Finn 1976) is commonly used. This index is strongly dependent on the way a particular model is constructed (i.e., on the number of compartments included and/or the degree of

resolution of the model), and can only be compared between similarly structured models, as is the case here.

In order to be able to compare the efficiency of biomass transfer in the system at different points in time, it is useful to look at discrete trophic levels *sensu* Lindeman (1942). An algorithm that, after removal of all cycling in the system, assigns each predator to (several of) these discrete trophic levels according to its diet composition has been proposed by Ulanowicz and Kemp (1979) and Ulanowicz (in press) and is applied to illustrate the structure of energy flows throughout the different seasons, in the Peruvian upwelling ecosystem.

Results and Discussion

Species Interactions

The annual cycles of sea surface temperature and primary production are given in Fig. 2a and

the annual course of zooplankton biomass and the fraction of zooplankton consumed by anchoveta in Fig. 2b. The results show a clear seasonality of temperature and production, the former with a maximum in (southern) summer and a seasonal temperature difference of about 4°C, the latter with a maximum in winter, where monthly production is about 2.5 times higher than in the summer months. The seasonality of zooplankton biomass roughly follows the temperature trajectory, and is reflected in the diet of anchoveta. Fig. 2c gives the seasonal biomass fluctuations of major fish species in the system, and Fig. 2d shows the amounts of anchoveta consumed by its major predators, and taken by the fishery (note that the fishery was usually closed during the months June to September, hence the strong seasonality of catches). Natural predation on anchoveta as estimated in the relevant papers in Pauly and Tsukayama (1987), however, is considerably lower than the inputs that were necessary to balance the models, given the biomasses and vital

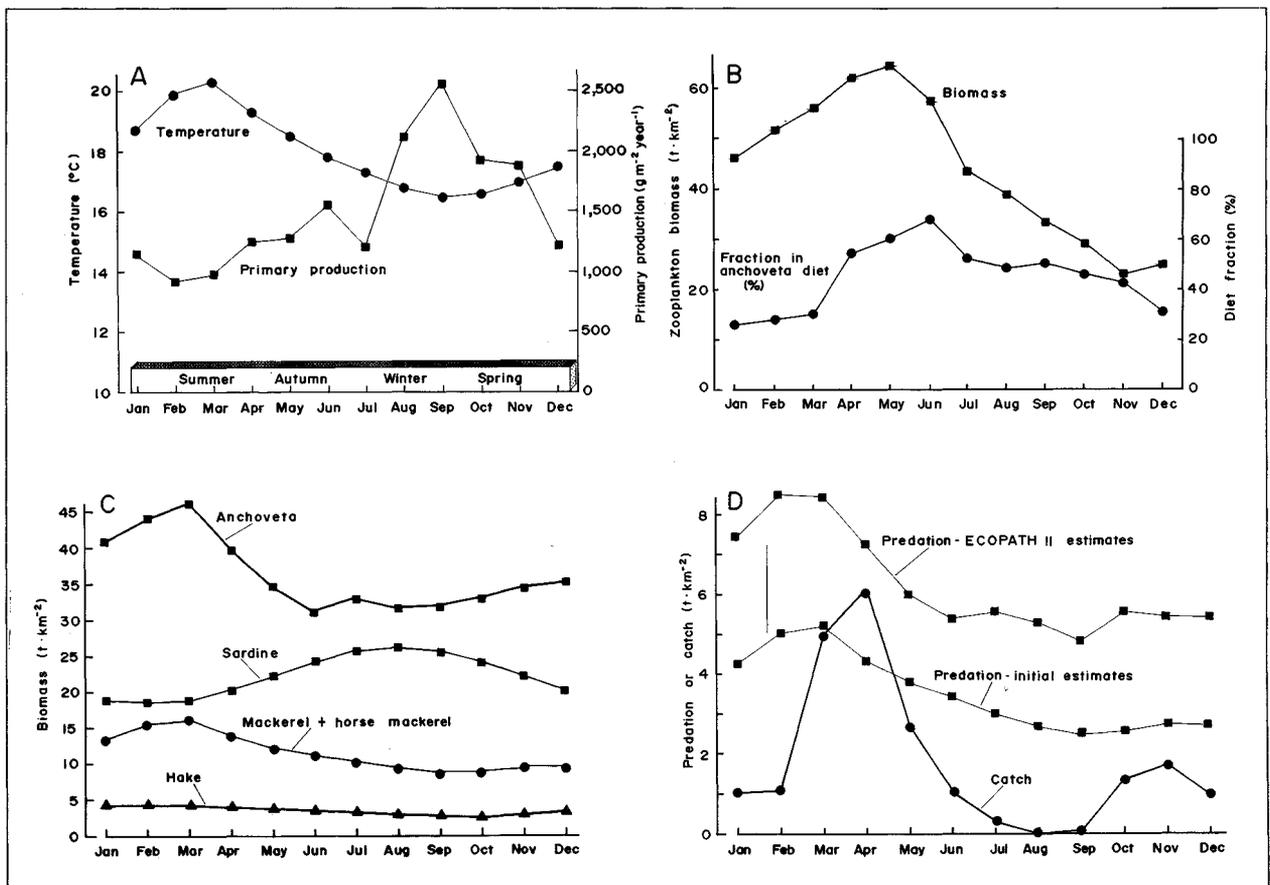


Fig. 2. Seasonal temperature and primary production changes in the Peruvian upwelling ecosystem, 1973-1979. Sea surface temperature averaged from Pauly and Tsukayama (1987b, Table 2). New primary production ($\text{g wet mass} \cdot \text{m}^{-2} \cdot \text{month}^{-1}$) based on Mendo et al. (1989) (variable depth model, mean of coastal and oceanic estimates), using a conversion factor of 13.6 from carbon to wet mass.

- Temperature and primary production.
- Zooplankton biomass and fraction of zooplankton on the diet of anchoveta.
- Biomass of dominant fishes; note contrary courses of sardine and anchoveta, and temperature-dependence of hake and mackerel, due to their usual location at the thermal periphery of the system.
- Total predation and catch of Peruvian anchoveta, *Engraulis ringens*, 4-14°S.

statistics of other species which could have replaced the anchoveta as prey items, mainly in the diets of horse mackerel and hake. Assuming that the consumption rates of these species are of the right order of magnitude, we therefore have to conclude that either the anchoveta fraction in the diet of its predators has been larger than assumed before (i.e., an average fraction of about 40% as compared to about 26% estimated earlier), or sardine and "other pelagics" biomass and production values have been considerably higher. The following discussion of summary statistics assumes the former to be true.

Summary Statistics

The seasonality of system throughput, ascendancy and development capacity are given in Fig. 3 and roughly follow the trajectory of primary production with a maximum in winter.

Fig. 3 shows the annual course of ascendancy normalized by total system throughput, the factor of "average mutual information" (Ulanowicz 1986, equation 6.9) with a bimodal seasonality (one maximum in late summer, the second in spring). As the value of this factor changes only slightly, we conclude that the system's content of mutual information is roughly constant throughout the year, and that the change of ascendancy is mainly due to changes of the size of the ecosystem, based on the seasonality of primary production. This corresponds well to the findings of Baird and Ulanowicz (1989) for Chesapeake Bay.

The seasonality of cycling in the Peruvian upwelling ecosystem as computed by Finn's cycling index (Finn 1976), however, is more pronounced (Fig. 3). This index is generally low (less than 10%), but clearly indicates a higher fraction of cycling in the system in summer (when upwelling is low) than in winter (when

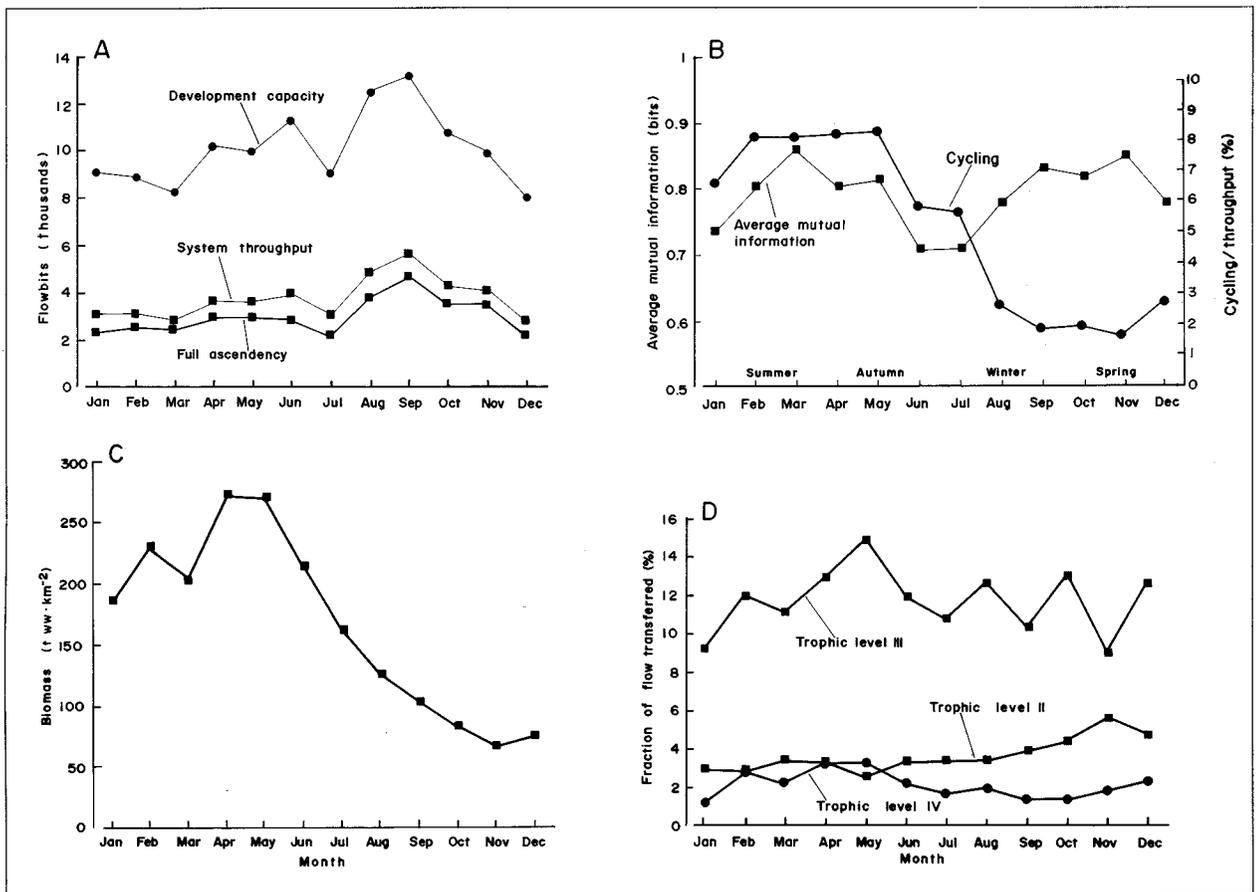


Fig. 3. Seasonality of basic features of the Peruvian upwelling ecosystem, 4 to 14°S, 1973 to 1979:

- Summary statistics of the 12 ECOPATH II models constructed in this paper, following the theory of Ulanowicz (1986).
- Seasonality of the factor of "average mutual information" (Ulanowicz 1986), i.e., full ascendancy divided by system throughput, and seasonal changes of the Finn cycling index (Finn 1976), i.e., the fraction of total throughput that is recirculated within the system.
- Seasonality of cycling in the Peruvian upwelling ecosystem as constructed in the 12 ECOPATH II models.
- Monthly transfer efficiencies computed from the 12 ECOPATH II models, flows based on producers and on detritus combined.

upwelling is high). This increase in the Finn's cycling index is not only due to the increased system throughput (the denominator of this index) in winter, but also to the reduced amount of organic matter cycled in the system in winter and spring (Fig. 3), due to the seasonal decrease in biomass and activity of zooplankton and benthos as the principal consumers of detritus.

The transfer efficiencies of all flows as computed using ECOPATH II and shown in Fig. 3D range from 1% for trophic level IV (in October) to 15% for trophic level III in May; a clear seasonal pattern is not apparent. Whereas the monthly transfer efficiencies from trophic level II to level III average at about 12%, corresponding very closely to the 10% literature "rule of thumb," the transfer efficiencies from level II to III and III to IV appear rather low. As the transport from levels II to III is dominated by zooplankton, a closer look at this box reveals that the largest fraction of its ecotrophically efficient production is consumed within the box itself and hence does not enter the computation of transfer efficiency as used here. Although a certain decrease in trophic efficiency with trophic level is observed in many ecosystems (see, e.g., Baird and Ulanowicz 1989), the low value of the transfer efficiency of the other levels (III to IV) can be additionally explained with the fact that the activity of the fishery (trophic level about 3.6) as an export, is not included in the computation but may account, e.g., in the case of the anchoveta, for up to 83% (April) of the withdrawals from the system.

Summarizing, our results indicate that the Peruvian upwelling ecosystem shows a clear seasonality not only as far as the vital parameters of each of its components are concerned, but also on the system level. This seasonality is mainly expressed in the change of system throughput (dominated by the upwelling intensity) but also, albeit to a less extent, in a change in the topology of the system.

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