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## Stratified Models of Large Marine Ecosystems: A General Approach and an Application to the South China Sea

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### Introduction

This contribution provides an approach for constructing models of large marine ecosystems (LMEs) as defined in Sherman (1990), Sherman and Alexander (1986, 1989), and Sherman and Gold (1990).

This contribution results from an attempt to follow up on some of the implications of the LME concept for ecological modeling, especially approaches that place emphasis on fish and other living resources, and hence on fisheries management. Conversely, we shall neglect models that emphasize only the lower part of food webs.

### Modelling of LMEs: The Need, the Constraints, and a Resolution

Given our inability to conduct controlled experiments<sup>1</sup> at the LME scale and the absence of a comprehensive theory that could predict interactions within LMEs and their evolution through time, modeling of such systems appears to be a necessary tool to link understanding of organism-level interactions with ecosystem dynamics (Toft and Mangel, 1991).

The ecological models that might be considered for describing LMEs can be grouped into two broad, nondistinct classes: (i) dynamic models, built of coupled differential equations describing major transfer and growth rates and integrated to provide time series of, for example, biomasses for key species/groups; and (ii) steady-state models, in which the species/groups compared are assumed to maintain their biomass (and related statistics) around some average level, valid for the period under

consideration.

Andersen and Ursin (1977) and Laevastu and Favorite (1977) developed models of the first type to describe resource dynamics in the North and Bering seas, respectively, and Larkin and Gazey (1982) developed the first simulation model of a tropical LME, the Gulf of Thailand.<sup>2</sup>

The latter model was used to illustrate that relatively simple simulation models can be rapidly constructed, parameterized, and used to test various competing hypotheses on the interactions among the resources of an LME, and between fisheries and their resources.

An often encountered problem with more comprehensive dynamic models is that the complex interactions among the simulated processes often lead to invalidation, even when using input data well within observed ranges. There are various routes for overcoming this constraint. One, briefly sketched by Larkin and Gazey (1982), consists of drastically reducing the number of processes that are simulated and increasing the number of external inputs. An example of this approach is the reduction of the North Sea model of Andersen and Ursin (1977) to Multispecies Virtual Population Analysis (MSVPA), which, for the fish in the system, requires the input of sizes at-age (rather than simulating individual fish growth) and which combines (externally inputted) catch-at-age data with numbers of consumed prey items to estimate biomasses using VPA (Sparre, 1991).

Another approach for dealing with the problem is to abandon all pretenses of being able to model LMEs realistically in the time domain, and to turn to the steady-state models described above.

Thus, Polovina (1984) reduced a dynamic

model, the Bering Sea model of Laevastu and Favorite (1977), to a static system of linear equations in which, for each species/group,

$$\text{Production} = \text{exports} + \text{mortality} \\ \text{due to predation} + \text{other mortality} \quad \dots 1)$$

or in more detailed fashion, for any species/group (i),

$$P_i = Ex_i + \sum_j (Q/B_j)(DC_{ji}) + B_j(P/B_j)(1-EE_j) \dots 2)$$

where  $P_i$  is the production during any nominal period (here, 1 year) of group  $i$ ;  $Ex_i$  represents the exports (fishery catches and emigration) of  $i$ ;  $\sum_j$  represents summation over all predators of  $i$ ;  $B_j$  and  $B_i$  are the biomass of the predator  $j$  and group  $i$ , respectively;  $Q/B_j$  is the relative food consumption of  $j$ ;  $DC_{ji}$  is the fraction that  $i$  constitutes of the diet of  $j$ ;  $B_i$  is the biomass of  $i$ ; and  $(1-EE_i)$  is the other mortality of  $i$ , that is, the fraction of  $i$ 's production that is not consumed within, or exported from, the system under consideration. (In the text below, we refer to  $EE$  as "ecotrophic efficiency"; its definition is inverse to that of "other mortality.")

Polovina and Ow (1983) implemented this approach in the form of a program called ECOPATH, which they used to estimate the biomasses of the major species/groups of French Frigate Shoals, a coral reef system north of Hawaii.

Since its original presentation, the ECOPATH approach has been extended to include estimation of not only biomasses, but also of other variables in equation (2), and description of the network of trophic flow between the "boxes" of a model using the theory of Ulanowicz (1986) and related concepts (Christensen and Pauly, in press, a).

These changes led to a much improved ECOPATH II software system (Christensen and Pauly, 1991). The ECOPATH II was applied to a wide variety of aquatic ecosystems, ranging from aquaculture ponds in China to the Antarctic Shelf (Christensen and Pauly, in press, b). This exercise allowed evaluation of various aspects of the approach. Notably, it led to the conclusion that steady-state models such as ECOPATH can be used to model systems that

are changing with time either: (i) by constructing models that apply to longer periods with no major changes in biomasses, and during which all rates and states can be averaged (see Walsh, 1981); or (ii) by constructing a model representing a "snapshot" of a rapidly changing situation, such as representing the midpoint of the growing period in an aquaculture pond, or a given month in a system subjected to strong seasonal oscillations (Jarre and Pauly, 1990<sup>3</sup>).

Our models are based on the first of these two approaches, with the bulk of the data used for model construction stemming from the decade from the mid-1970s to the mid-1980s.

### The South China Sea: The Reality and the Models

Figure 1 defines the South China Sea (SCS) as discussed here. We see the SCS as bounded in

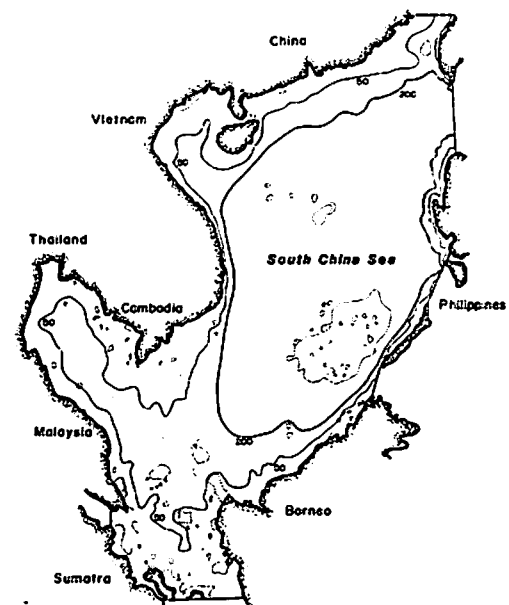
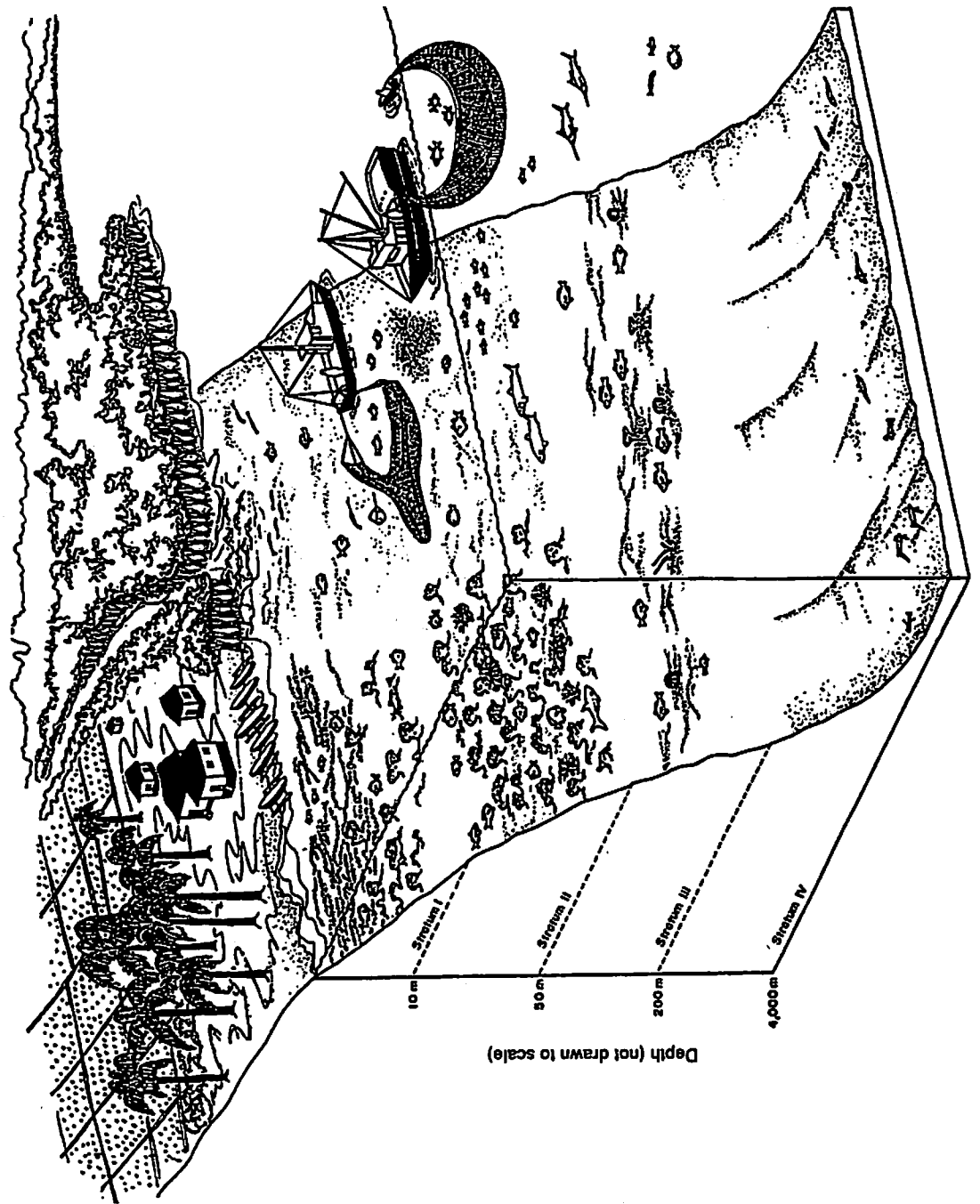


Figure 1. Map of the South China Sea, as defined in this paper (i.e.,  $3.5 \times 10^6$  km<sup>2</sup>), with 50 and 200 m isobaths and major coralline areas (thin dotted lines).

- (1) We are aware that various uncontrolled experiments have been and continue to be conducted at the scale of the LME, for example, through overfishing or massive pollution.
- (2) Walsh (1975) developed another early simulation model of a tropical LME, the Peruvian upwelling system; this is not discussed further here because it dealt mainly with phytoplankton production and consumption (i.e., with the lower part of the food web) and hence could not be used to deal with fishery management issues (as opposed, for example, to the model of the same system documented in Jarre *et al.*, 1991).
- (3) This paper will appear in revised form in Christensen and Pauly (in press, b), together with other contributions from the same meeting cited here.



the north by the 25th parallel linking Taiwan and the Chinese mainland, and to the east by the Taiwanese coast, the 121° line between Taiwan and Luzon, by straight lines from Luzon to Mindoro and from Mindoro to Palawan, and by a line linking Palawan to northwestern Borneo (Shindo, 1973).

The southern limit is defined by a line crossing the Bangka and Karimata straits between Sumatra and Borneo at 3° S, while the western limit is the line crossing the Malacca Strait at 103° E, slightly west of Singapore.

The western border of the SCS includes a number of large subsystems, such as the Gulf of Thailand and the Gulf of Tonkin. These gulfs are completely open to the SCS proper. The SCS, as we have defined it, is an ecosystem bounded by rather narrow straits and sills. This system can be conceived as having negligible biological exchanges with other marine ecosystems. A point illustrating this is that the surface salinity in the SCS proper is relatively low because of large inflow from rivers and limited water exchange with open oceans (Wyrki, 1961).

Overall, the SCS covers  $3.5 \times 10^6 \text{ km}^2$ , or about 15 times the minimum size of an LME as conventionally defined (Sherman and Alexander, 1989). One implication of our choice of system is that we could not construct any single, manageable trophic box model reflecting the biological diversity of the subsystems (mangrove, coral reefs, soft-bottom communities, open seas) composing the SCS as a whole.

The approach we used was, therefore, to represent the overall system by a series of interlinked models representing subsystems (i.e., strata) as identified in Table 1. Here, the stratification ensures that the estimated biomasses of various species/groups and the extent of their trophic interactions remain biologically meaningful. Yet the interconnections between subsystems ensure that the overall system functions as an ecosystem, that is, with its various parts interacting (via export or import of production or detritus).

As a compromise between ecological reality and actual availability of data, we used the

Table 1. Summary statistics for 10 subareas of the South China Sea (SCS).

Model	Depth (m)	Area ( $10^3 \text{ km}^2$ )
A. Shallow waters	0 - 10	172
B. Reef-flats/seagrass	0 - 10	21
C. Gulf of Thailand	10 - 50	133
D. Vietnam/China	10 - 50	280
E. NW Philippines	10 - 50	28
F. Borneo	10 - 50	144
G. SW SCS	10 - 50	112
H. Coral reef	10 - 50	77
I. Deep shelf	50 - 200	928
J. Open Ocean	200 - 4,000	1,605
Total SCS	0 - 4,000	3,500

following strata for our overall SCS model (from inshore to offshore, see also Fig. 2):

- (Ia) Estuarine, mangrove-lined, shallow waters down to 10-m depth
- (Ib) Reef-flats/seagrass-dominated shallow waters down to 10-m depth
- (IIa) Soft-bottom communities, from 10 to 50 m
- (IIb) Coral reef communities, from 10 to 50 m
- (III) Deep shelves, from 50 to 200 m
- (IV) Oceanic waters, all areas deeper than 200 m.

The surface area of each stratum was determined by planimetry, whereas the separation of stratum I into Ia and Ib and of stratum II into IIa and IIb was done on the basis of a 9:1 ratio estimated by visual assessment of mangrove and coral maps in White (1983). This results, for the corals, in a total area for the SCS, which closely matches the estimate of Smith (1978) for the northern part of the "Southeast Asian Mediterranean."

We have further divided the most productive stratum (IIa) by describing soft-bottom communities from 10 to 50 m depth, into six substrata as follows (Table 1):

**Figure 2.** Schematic representation of a "slice" of the South China Sea (SCS) illustrating major elements considered in our 10 submodels of the SCS. Stratum I (0-10 m) comprises two subareas (mangrove-lined, "estuarinized" coasts, right, and reef-flats/seagrasses, left). Stratum I is exploited mainly by small-scale fishermen, including gleaning by women and children. Stratum II (10-50 m) also comprises two subareas (soft-bottom communities, right, and coral reefs, left). The former of these two subareas supports extensive trawl fisheries. Stratum III (50-200 m) represents the deep shelf, generally trawlable, but often unexploited because of technological or economic constraints. Stratum IV (200-4,000 m) represents the oceanic part of the SCS, in which only the large pelagics (tuna, billfishes) are exploited. (See text for details and quantitative estimates relating to this graph [kindly drawn by Mr. Chris Bunao, International Center For Living Aquatic Resources Management ICLARM Manila, Philippines]).

- (i) Gulf of Thailand
- (ii) Vietnam/China (the Vietnamese coast and southern China including Taiwan)
- (iii) Northwest Philippines (entire Philippine SCS Coast)
- (iv) Borneo (the northwestern coast of Borneo)
- (v) Southwest SCS (representing the coast of eastern peninsular Malaysia, especially Kuala Terengganu, and southeastern Sumatra).

Each stratum or substratum is represented by a steady-state model constructed using the ECOPATH II software with the data documented briefly below. The following major biological interactions were assumed.

- The detritus (especially mangrove leaf litter), and the fish and invertebrate production not consumed inshore are exported from stratum I to the detritivores and carnivores of stratum II.
- The detritus, and the fish and invertebrate production not consumed in stratum II are exported to stratum III.
- The detritus, and the fish and invertebrate production not consumed in stratum III are exported to stratum IV.
- Only stratum IV exports detritus out of the South China ecosystem (for burial on the sediments covering bottoms deeper than 200 m).

The "real" SCS is characterized by far more interactions among its subsystems; however, we believe it appropriate at this stage to present a simplified implementation of our approach—one that would allow us to retain simplicity and ease of application.

### Source of Data and Model Construction

For all consumer groups in all models, it is assumed that 20% of the consumption is not assimilated (Winberg, 1956). Throughout, wherever biomasses are not known, it is assumed that 95% of the production is eaten or caught (Ricker, 1968). A diskette with the 10 data sets is available from the authors, along with the ECOPATH II software and a user's manual (Christensen and Pauly, 1991).

#### *Model A: Shallow waters (0–10 m, all around SCS)*

This model for shallow waters (Fig. 3) is based on data from the Gulf of Thailand. The catches from the Gulf of Thailand in 1979 (SEAFDEC,

1981) were separated into two depth ranges (0–10 m and 10–50 m), based on the assumption that the large-scale fishery (excluding bamboo stake traps) operates between 10- and 50-m depth, whereas the small-scale fishery operates in the shallower parts of the gulf, where the bamboo stake traps are also located.

The biomass of the apex predators (mainly tuna) is from Olson and Boggs (1986) and originally pertained to a stock of eastern Pacific tuna. The diet matrix and estimates of production and consumption were nearly identical to that of the Gulf of Thailand model (below) with only minor adjustment to reflect differences in abundances.

The estimates of production and consumption rates were also taken from model C.

#### *Model B: Reef-flats/seagrasses (0–10 m all around SCS)*

The model for reef-flats/seagrasses (Fig. 4) is based on a model of areas near Bolinao, north-west Luzon, Philippines, described by Aliño *et al.* (1990).

The Bolinao model is characterized by extremely high primary production of seagrass and seaweeds, comparable to that of the most productive terrestrial ecosystems (Rodin *et al.*, 1975). This type of ecosystem is common only in the Philippine part of the SCS (White, 1983). We have therefore reduced the production of benthic producers in our model of reef-flats/seagrasses to 20% of the Bolinao model, so that the resulting primary production becomes similar to that of the other shallow water area (model A).

#### *Model C: Gulf of Thailand (soft bottom, 10–50 m)*

The groupings for this model of the Gulf of Thailand soft-bottom community (Fig. 5) are mainly based on information in Pauly (1979), assuming that only the tuna fishery operates in areas of the gulf that are deeper than 50 m. Zooplankton biomasses were adopted from Piyakarnchana (1989), assuming a mean water depth of 30 m and leading to a rather high estimate of  $17.3 \text{ g} \cdot \text{m}^{-2}$ . The benthic biomass is from Piyakarnchana (1989); those for the demersal fish groups are from Pauly (1979).

No reliable estimates of biomass were available for pelagics; the biomass of apex predators was based on information from Olson and Boggs (1986).

Only a few estimates of production/biomass ratios (P/B) are available from the Gulf of Thailand. For phytoplankton, the total produc-

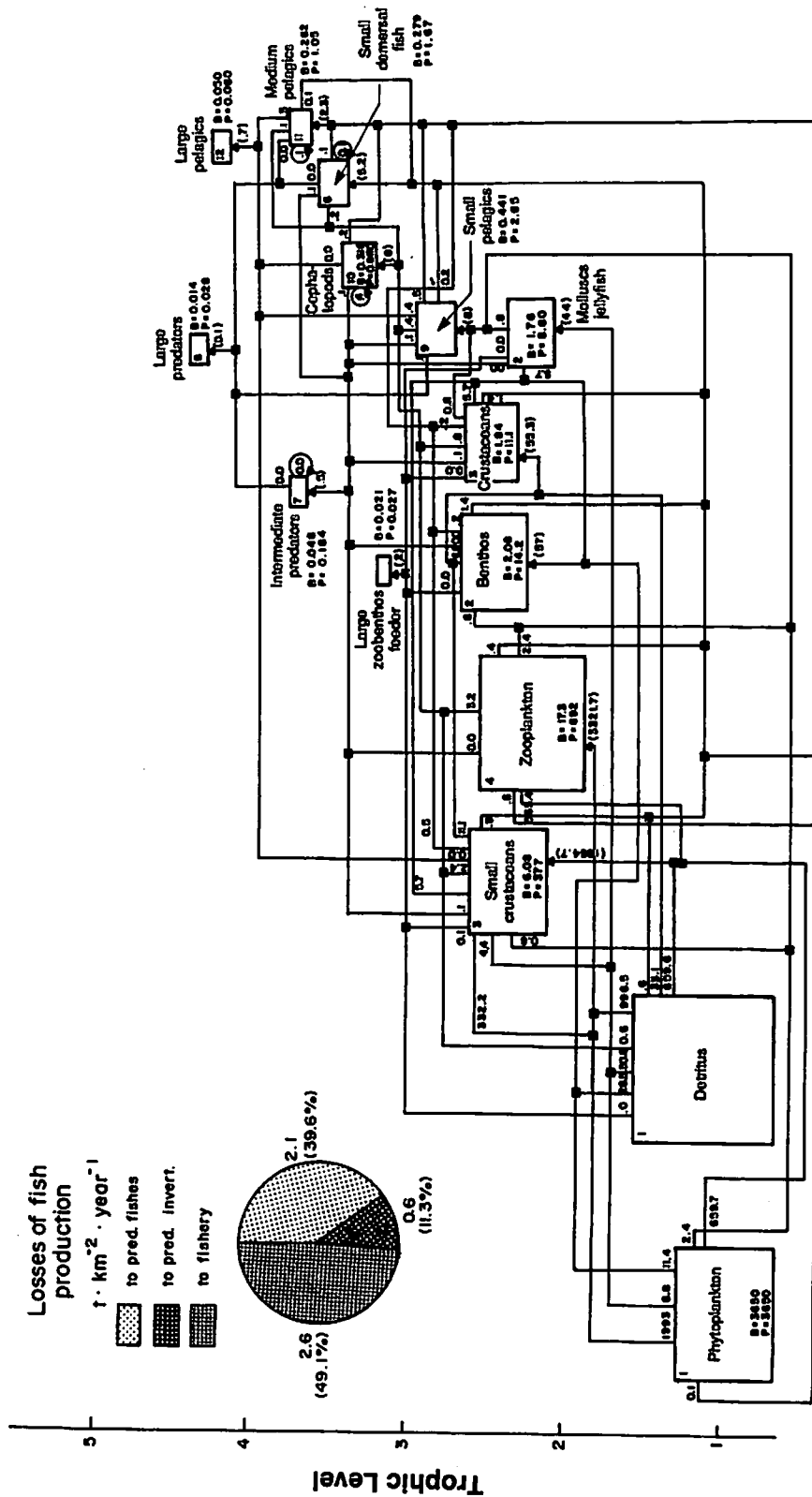


Figure 3. Model (A) of shallow waters (0-10 m) around the SCS, excluding reef-flat/seagrasses. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes  $\cdot km^2 \cdot year^{-1}$ ; catches, respiration, and detrital backflows are omitted; see text for details on construction; based on miscellaneous data, including catches in SEAFDEC, [1981].)

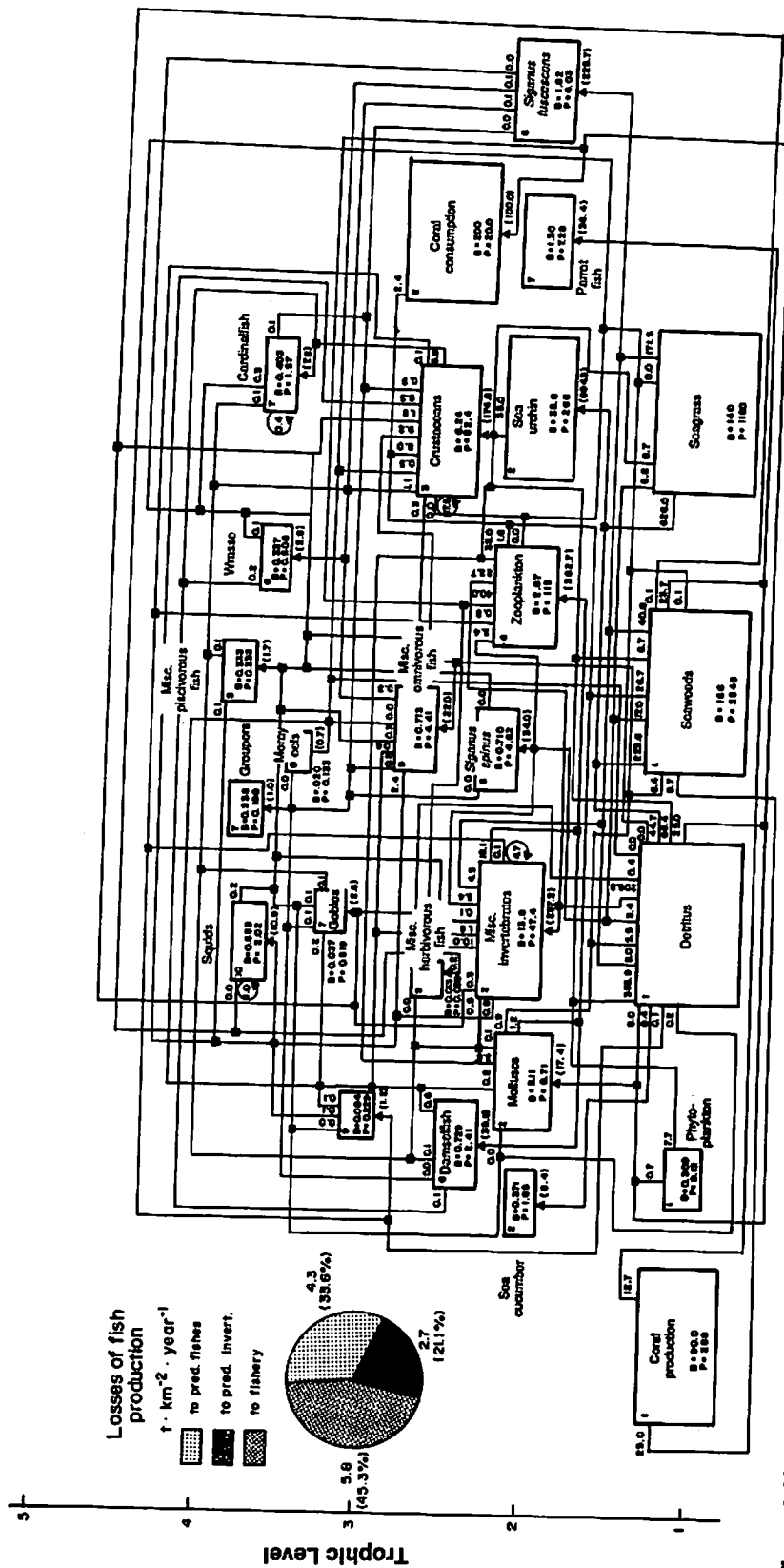
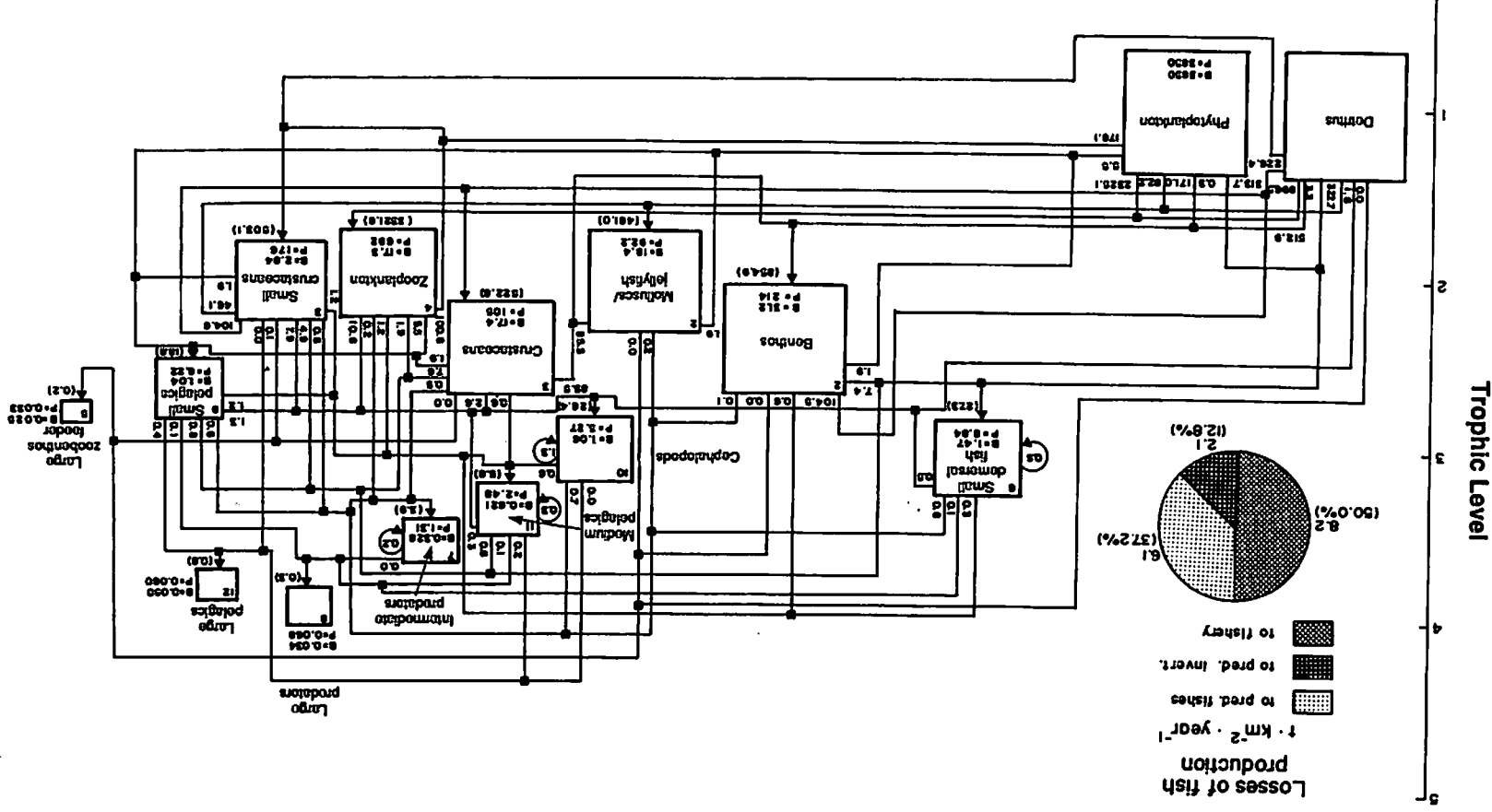


Figure 4. Model (B) of reef-flat/seagrasses areas (0-10 m) around the SCS. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes  $\cdot km^2 \cdot year^{-1}$ ; catches, respiration, and detrital backflows are omitted; see text for details on construction; based on Alfaro *et al.*, [1990].)

Figure 5. Model (C) of the Gulf of Thailand 10-50 m soft-bottom community. (The surface area of the boxes is proportional to the log of the biomass; all flows are in  $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ ; catches, respiration, and detrital backflows are omitted; based on various information, with emphasis on data in Pauly [1979] and Piyakarnchana [1989].)





tion is approximately  $1 \text{ g wet weight} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  (Piyakarnchana, 1989). Jellyfish and molluscs were assumed to have a P/B ratio that is intermediate between the values reported by Silvestre *et al.* (1990) for heterotrophic benthos and the value for shrimps/crabs used here. The estimates for cephalopods and zooplankton are based on Buchanan and Smale (1981) and Polovina (1984), respectively. The P/B ratio for shrimp is based on Chullasorn and Martosubroto (1986), and the P/B ratio for benthos is from Liew and Chan (1987). The estimate for crustaceans is from Silvestre *et al.* (1990).

For the rays (i.e., our "large zoobenthos feeders") and for large predators, we have used the P/B estimates of Liew and Chan (1987). The P/B ratio for intermediate predators is within the range reported by Pauly (1980); the estimates for small pelagics and for small demersal fishes are based on Chullasorn and Martosubroto (1986).

The P/B value for medium-sized pelagics was assumed to be intermediate between those for large predators and for small pelagics. The P/B ratio for large pelagics was again from Olson and Boggs (1986).

For most fishes, consumption/biomass ratios (Q/B) were estimated from the regression of consumption as a function of temperature, weight, and feeding mode given by Pauly *et al.* (1990). Weights were estimated from mean lengths given by Pauly (1979). Mean Q/B values were estimated from the biomass-weighted means of Q/B values of the various species/groups.

For jellyfish, molluscs, and crustaceans, Q/B was estimated based on an assumption of a gross food conversion efficiency (production/consumption) of 0.2.

Q/B ratios of 29 and 16.6 were used for shrimp and cephalopods, respectively (Sambily *et al.*, 1990). For zooplankton, a Q/B estimate of 192 was adopted from Ikeda (1977). The Q/B value for large pelagics was adopted from Olson and Boggs (1986).

There are a number of sources for diet compositions of the abundant fishes in Gulf of Thailand waters. Menasveta (1980) provides qualitative but useful information. Quantitative information is available in Menasveta (1986) for cephalopods, in Browder (1990) for shrimp, and in Liew and Chan (1987) for large zoobenthos feeders and large predators. Their diet compositions have been adapted here, in slightly modified form, to reflect local conditions.

The diet composition of small demersal prey fish is based on Yamashita *et al.* (1987), who give quantified diets for seven species/groups in this category, and on Menasveta (1980), who reports on the diet of two species. Yamashita *et al.* (1987) describe the diet of six

intermediate predators. These, together with data in Siti and Taha (1986), Menasveta (1980), and Pauly (1979) were used to derive an average diet composition.

The sources of SCS diet compositions are as follows: small pelagics from Yamashita *et al.* (1987) and Menasveta (1980); medium-sized pelagics from Menasveta (1980); and large pelagics from Olson and Boggs (1986) and Tandog-Edralin *et al.* (In press).

#### *Model D: Vietnam/China (Cape Cambodia-China, 10-50 m)*

This is a very productive area for which primary production and phytoplankton biomass estimates are given by Nguyen (1989).

From the mid-1970s to the mid-1980s great changes occurred in Vietnam; thus, information on the fisheries is limited. Menasveta *et al.* (1973) reported that a substantial fraction of Vietnamese catches were taken by artisanal, nonmechanized boats in coastal and estuarine areas. Therefore, Vietnamese catch data are not included in the present (more offshore) model (Fig. 6). Yeh (1981) reports that the demersal resources off southern Vietnam were exploited primarily by Taiwanese vessels, and gives catch and effort data. Based on this information, catches and biomasses for the demersal fish groups could be estimated. These data are assumed to be representative for the whole Vietnam/China area.

The biomass of planktivorous fish was estimated by Nguyen (1989) as  $3 \text{ g} \cdot \text{m}^{-2}$  for the whole Vietnamese shelf area and was separated into small and medium-sized pelagics based on an assumed 2:1 ratio. The catches for these groups were set at zero.

For the fish groups mentioned above, the P/B ratios were then estimated using the ECOPATH II program, assuming an ecotrophic efficiency of 0.95.

Zooplankton biomass and P/B were taken from Nguyen (1989) and the cephalopod biomass and catches from Yeh (1981).

For other groups, P/B and Q/B values are assumed to be similar to the values of model C.

#### *Model E: Northwest Philippines (all Philippine coast, 10-50 m)*

This model of the soft-bottom community along the northwestern Philippine coast (Fig. 7) is based on data recently assembled by Guarín (1991) for an ECOPATH II model of the Lingayen Gulf, northwestern Philippines. This is a soft-bottom area fished intensively, mainly by trawlers (Silvestre *et al.*, 1989).

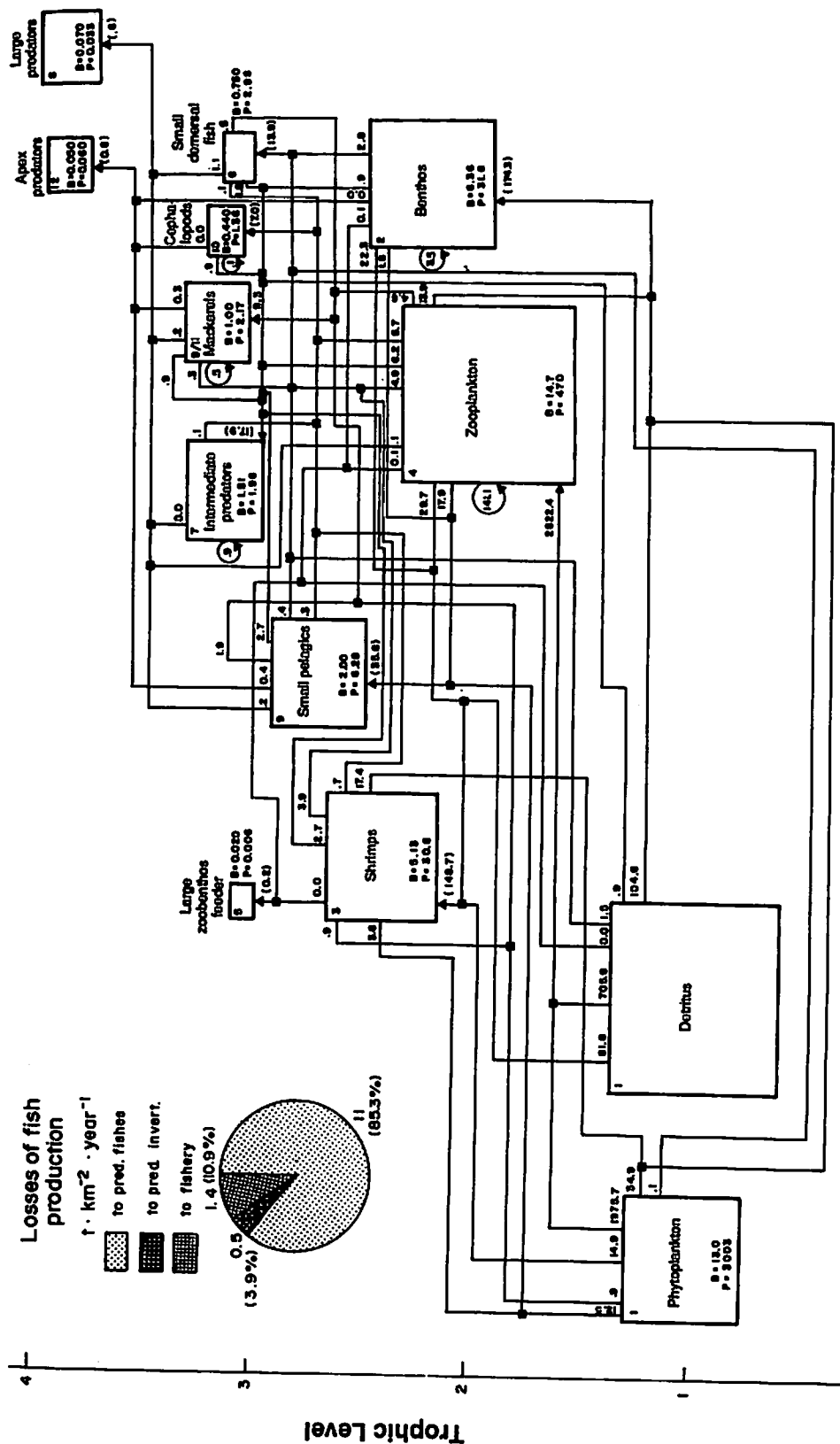


Figure 6. Model (D) of the soft-bottom community (10-50 m) off the coast of Vietnam and southern China, including Taiwan. (The surface area of the boxes is proportional to the log of the biomass; all flows are in tonnes · km<sup>-2</sup> · year<sup>-1</sup>; catches, respiration, and detrital backflows are omitted; see text for details on construction; based on various data sets, with emphasis on Nguyen [1989] and Yeh [1991]).

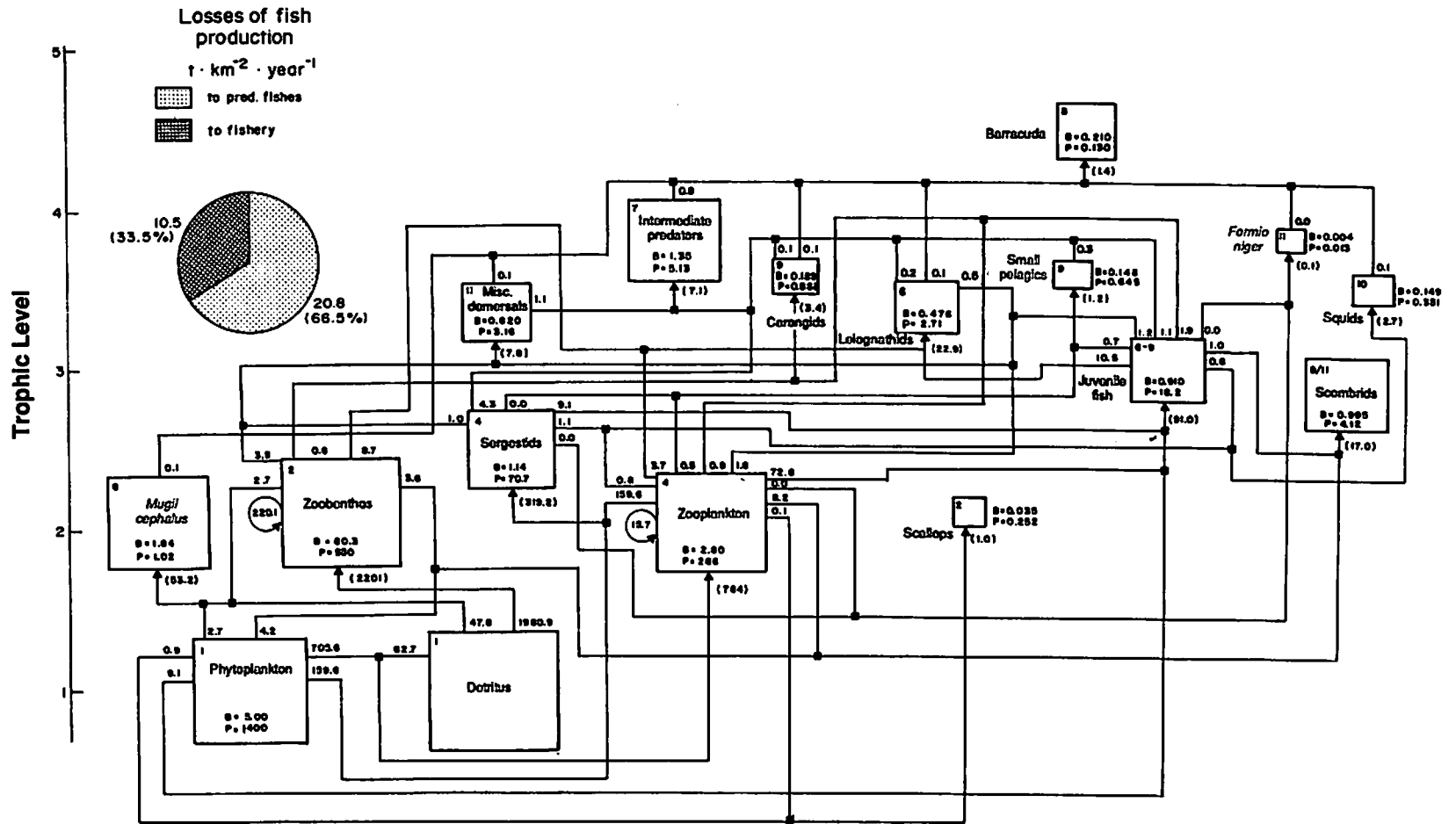


Figure 7. Model (E) of the 10–50 m soft-bottom community along the northwestern Philippine coast. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes  $\cdot km^{-2} \cdot year^{-1}$ ; catches, respiration and detrital backflows are omitted; see text for details on construction; based on preliminary information from the Lingayen Gulf, assembled by Ms. F. Y. Guarin [pers. com.] .)

**Model F: Borneo (all Borneo coast, 10–50 m)**

This model of the soft-bottom community (Fig. 8) is based on the model by *Silvestre et al.* (1990) of the moderately exploited Brunel Shelf and is also considered representative of the areas off Sarawak and Sabah, which have nearshore (0–10 m) fisheries, but where the more offshore areas only began to be exploited during the time period considered here.

**Model G: Southwestern South China Sea (eastern peninsula of Malaysia and southeastern Sumatra, 10–50 m)**

This model of the soft-bottom community (Fig. 9) is a modification of that of Liew and Chan (1987), who constructed a model of the area off Kuala Terengganu, on the eastern coast of western peninsular Malaysia. For this model, primary production is two-thirds of that in the Gulf of Thailand. This is supported by the pattern of primary production given by Lieth (1975) and the Food and Agriculture Organization of the United Nations (FAO) (1981).

**Model H: Coral reefs (all around SCS, 10–50 m)**

The model of coralline areas (Fig. 10) is based on Polovina's (1984) model of the French Frigate Shoals (FFS), north of Hawaii. This "import" of an entire model in the SCS appears legitimate because their latitudes are compatible. However, to render this model compatible with the other nine, we added detritus and detritivory by heterotrophic benthos.

FFS is an unfished ecosystem, whereas coral reefs in the SCS tended, in the 1970s, to be at least moderately exploited. To adjust for this, we deleted three apex predators (birds, monk seals, and tiger sharks) from the original model and treated their prey consumption as fishery catches. This adjustment resulted in a catch composition roughly similar to that observed from coral reef fisheries in the Philippines (Murphy and Ferraris, 1980).

**Model I: Deep shelf (all around SCS, 50–200 m)**

The deep shelf area utilized in this deep shelf model (Fig. 11) occupies more than one-quarter of the total SCS area. Yeh (1981) reported that the predominant fishing activity in this area is by Taiwanese vessels.

The primary production for this sub-

system was estimated to be  $0.2 \text{ g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$  or approximately  $730 \text{ g wet weight} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  (Nguyen, 1989). In line with this relatively low primary production, the biomass of zooplankton is assumed to be 25% of that off Vietnam/China (10–50 m), whereas its P/B and Q/B values were taken as equal to those in model C.

For shrimp and crabs there are no catch or biomass data, and other parameters are assumed to be identical to those in model C. The benthos parameters were adopted from model D.

Information on catches of demersal fish groups is sparse. Based on the South China Sea Programme (SCSP) (1978), the catches in 1975 in two deep offshore areas (Gulf of Thailand, depths over 50 m, and Natuna Islands–Central Sunda Shelf) were estimated as 45,100 tonnes from  $318,000 \text{ km}^2$  (i.e.,  $0.11 \text{ tonnes} \cdot \text{km}^{-2}$ ). This estimate reflects a low fishing pressure and is assumed to be representative of the whole area. The biomasses of the demersal groups and cephalopods were estimated using data in Yeh (1981); the Q/B estimates were from model C.

No information seems available on the pelagic stocks in this subsystem. We have therefore assumed that the biomasses of small and medium-sized pelagics are 50% of those in model D. For both groups, the Q/B values were assumed to be similar to those in model C. The large pelagics group was assumed to have the same parameters as the other models.

**Model J: Oceanic waters (central SCS, 200–4000 m)**

This stratum covers nearly one-half of the SCS ( $1.6 \text{ million km}^2$ ). The fisheries are limited to catching large pelagic fishes, mainly tunas.

The system represented by this open-ocean community model (Fig. 12) is divided into the following components based on Blackburn (1981), Rowe (1981), and Mann (1984):

- Apex predators (tuna, billfish, swordfish, sharks, and porpoise) occurring in the upper 200–300 m. Olson and Boggs (1986), based on studies conducted in the eastern Pacific, estimated the biomass of this group as approximately  $0.05 \text{ g wet weight} \cdot \text{m}^{-2}$ ; the corresponding P/B was  $1.2 \text{ year}^{-1}$  and the Q/B,  $15 \text{ year}^{-1}$ . Their paper also presents the diet composition of yellowfin tuna, used here as representative of the whole group. In the absence of reliable data for the SCS, the catch per area was also taken from this source.

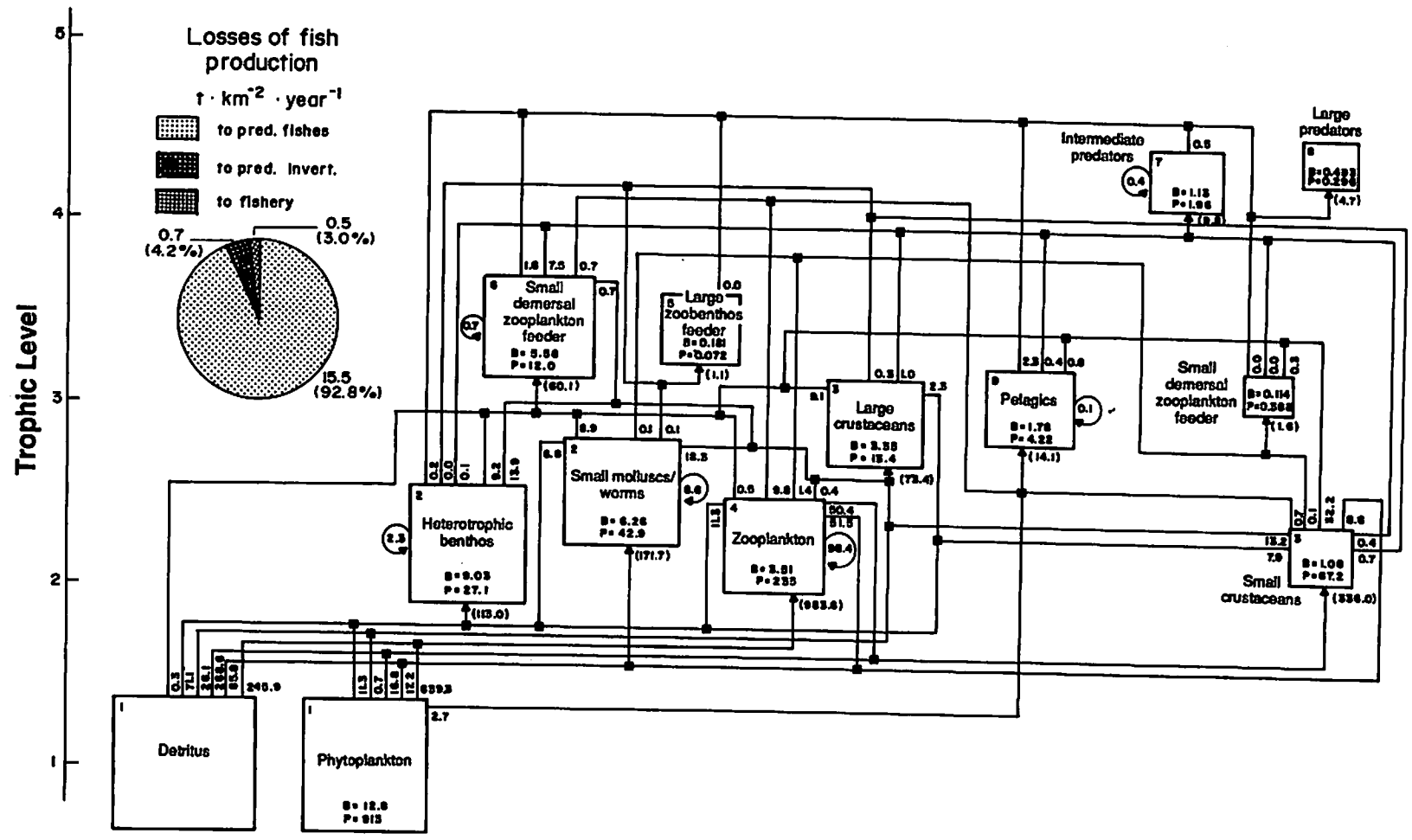


Figure 8. Model (F) of the 10–50 m soft-bottom community along the northwestern coast of Borneo. (The surface area of the boxes is proportional to the log of the biomass; all flows are in tonnes  $\cdot km^{-2} \cdot year^{-1}$ ; catches, respiration, and detrital backflows are omitted; see also Table 1 and text for details on construction; adapted from a model of the Brunei Shelf assembled by Silvestre *et al.* [1990].)

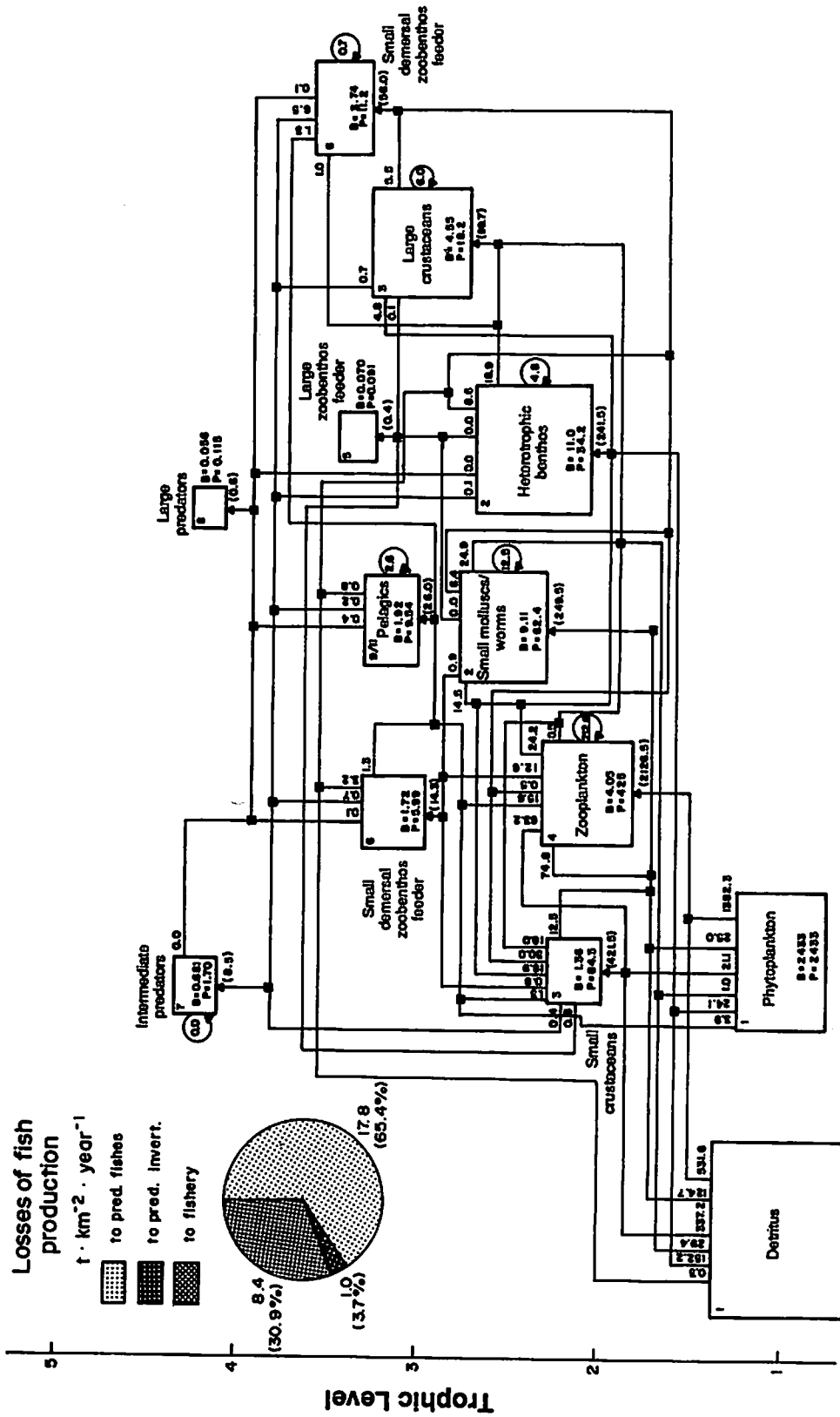


Figure 9. Model (G) of the 10-50 m soft-bottom community along the eastern coast of peninsular Malaysia and southeastern Sumatra. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes  $\cdot \text{km}^2 \cdot \text{year}^{-1}$ ; catches, respiration, and detrital backflows are omitted; see text for details on construction; modified from model of Kuala Terengganu, Malaysia, of Liew and Chan [1987].)

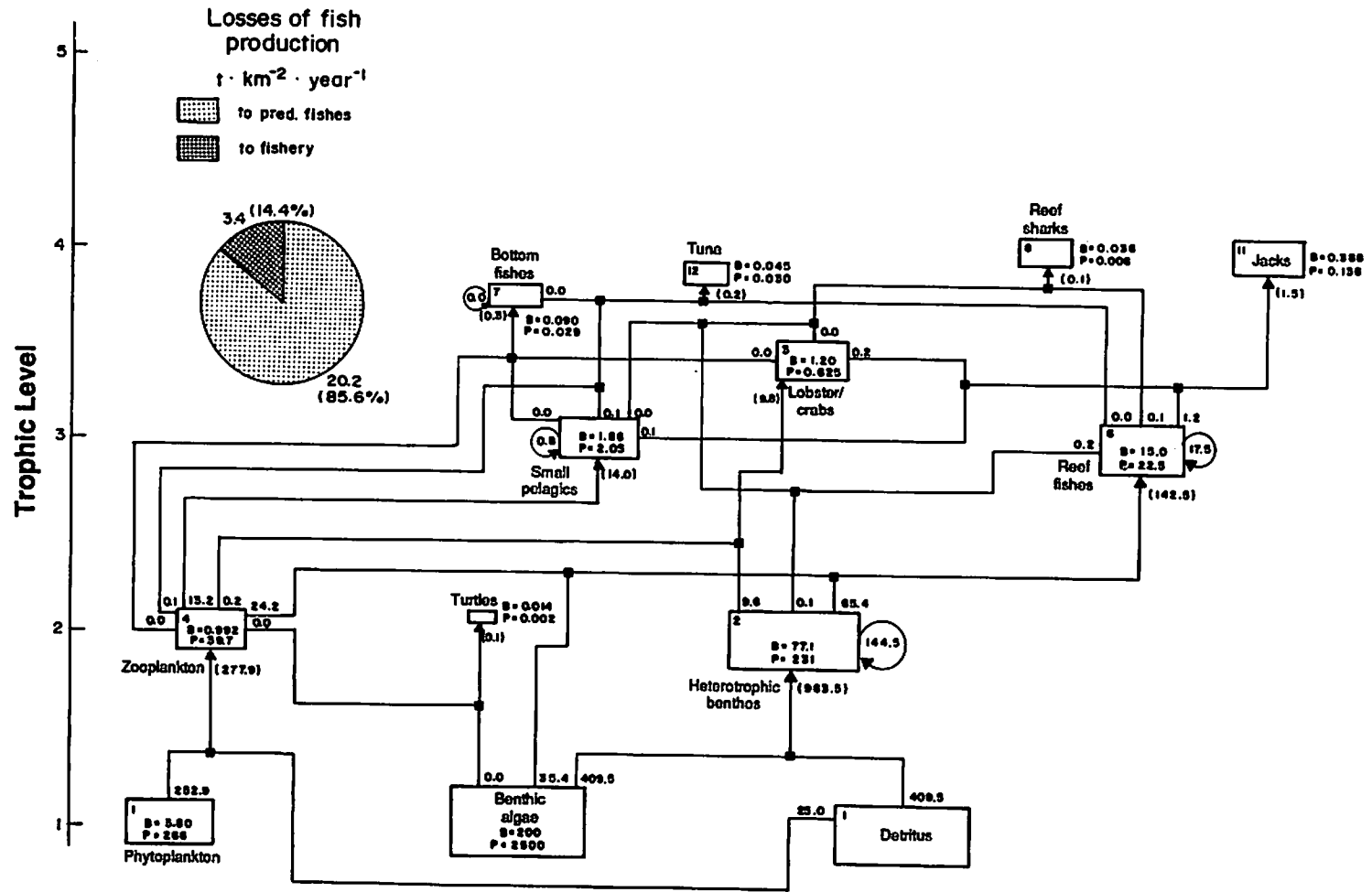


Figure 10. Model (H) of 10–50 m coralline areas around the SCS. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes  $\cdot km^{-2} \cdot year^{-1}$ ; catches, respiration, and detrital backflows are omitted; see text for details on construction; adapted from Polovina [1984], through deletion of three top predators and their replacement by the fishery, and the addition of detritus and detritivory by heterotrophic benthos.)

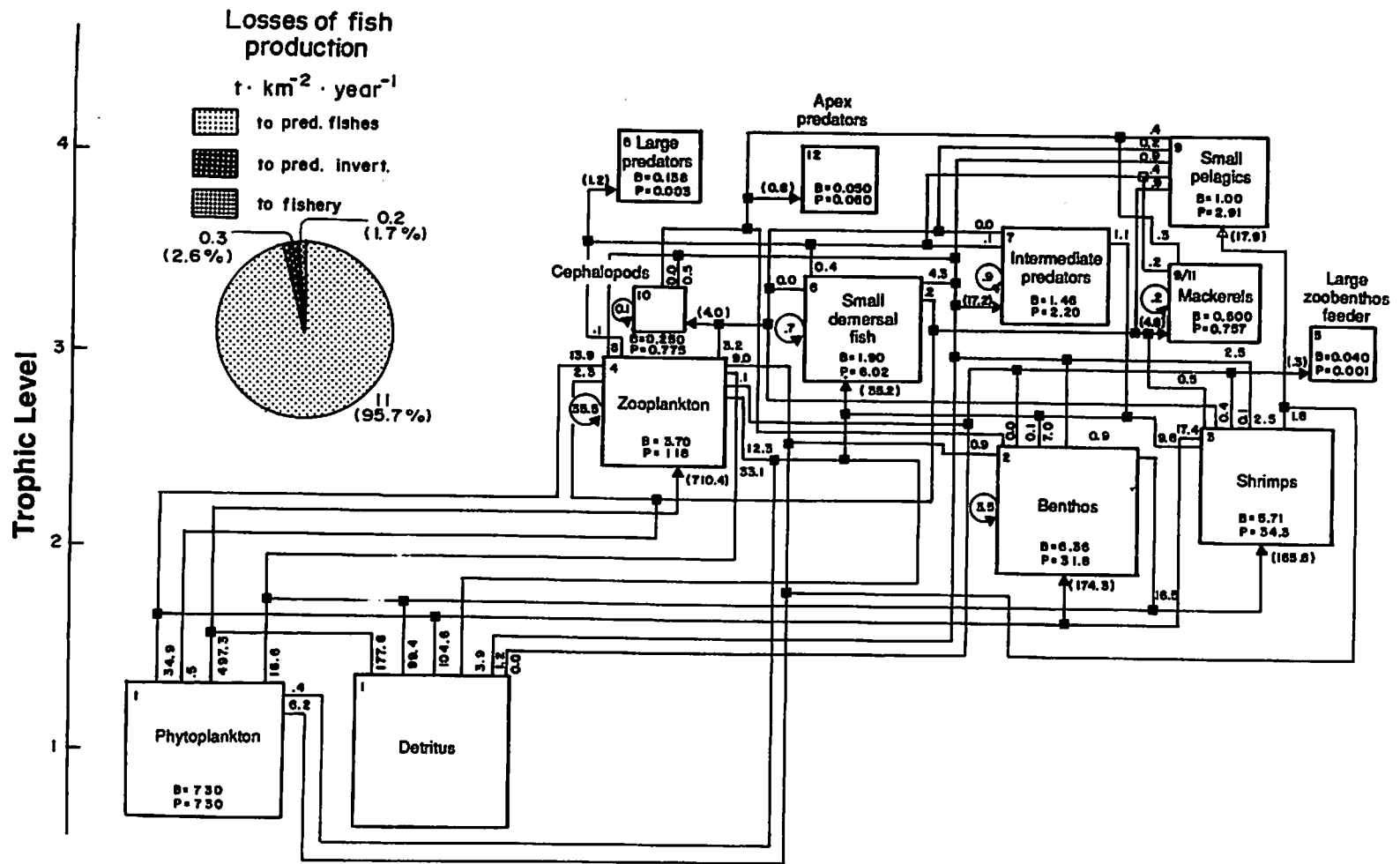


Figure 11. Model (I) of the 50–200 m soft-bottom, deeper shelf communities around the SCS. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes · km<sup>-2</sup> · year<sup>-1</sup>; catchac, respiration, and detrital backflows are omitted; see text for data sources and details on construction.)



- Epipelagic nekton (mackerel, small tuna, nomeids, flyingfish, cephalopods) occurring in the upper 200–300 m. Mann (1984), considering oceanic areas in general, gives a biomass of  $0.5 \text{ g} \cdot \text{m}^{-2}$  and a production of  $0.5\text{--}1.3 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  (i.e., a P/B of 1.0–2.6  $\text{year}^{-1}$ ). We adopted a P/B value of 2  $\text{year}^{-1}$  and assumed a Q/B value of 9.3  $\text{year}^{-1}$ , as for mackerel in model C. The diet composition is based mainly on Mann (1984).
- Mesopelagics (myctophids, gonostomatids, and sternoptychids) occurring between 200 and 1,000 m during daytime. At night, a large proportion of the mesopelagics migrate to the epipelagic zone to feed, mainly on zooplankton. The biomass of this group is assumed to be  $2.6 \text{ g} \cdot \text{m}^{-2}$  based on data from the western central Pacific in Gjøsaeter and Kawaguchi (1980). Mann (1984) estimated the biomass to be in the range of  $1.75\text{--}3.0 \text{ g} \cdot \text{m}^{-2}$ . As in Mann (1984), who used a bioenergetic model and derived a Q/B value of 2.9  $\text{year}^{-1}$  for the mesopelagics, we set the P/B value to 0.6  $\text{year}^{-1}$ . Hopkins and Baird (1977) estimated that more than 70% (by volume) of their food consists of crustaceans.
- Bathypelagics (anglerfish and Cyclotone) occurring at depths greater than 1000 m. These fish tend to minimize their energy expenditure and are capable of taking prey over a large size range. Mann (1984) reported a biomass of  $0.02 \text{ g} \cdot \text{m}^{-2}$  and a P/B of 0.1  $\text{year}^{-1}$ . We used a Q/B value of 0.4  $\text{year}^{-1}$ .
- Benthic fish (Bathysaurus, Chlorophthalmidae, Macrouridae, Moridae, and Brotulidae) for which there is scarce quantitative information. According to Mann (1984), their joint biomasses range from  $1.0\text{--}2.0 \text{ g} \cdot \text{m}^{-2}$  (we used 1.5), and their P/B values from 0.05 to 0.10  $\text{year}^{-1}$  (we used 0.075); Q/B was assumed to be 0.3  $\text{year}^{-1}$ . The diet composition was assumed based on scattered information in Mann (1984) and constrained the limited number of boxes used to describe the system.
- Benthos (amphipods, shrimp, and other decapods). Mann (1984) reported biomass as  $5.0 \text{ g} \cdot \text{m}^{-2}$ , with a P/B value of 0.1  $\text{year}^{-1}$ ; Q/B was assumed as 0.4  $\text{year}^{-1}$ .
- Zooplankton (larger copepods, euphausiids, and decapods). Blackburn (1981) reported biomasses as  $8\text{--}13 \text{ g} \cdot$

$\text{m}^{-2}$  (we used  $10 \text{ g} \cdot \text{m}^{-2}$ ), and Mann (1984) reported a P/B ratio of 0.5  $\text{year}^{-1}$ . Q/B was assumed to be 2.5  $\text{year}^{-1}$ .

- Phytoplankton. Blackburn (1981) reported primary production rates from oceanic areas of  $0.1\text{--}0.5 \text{ g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ . We adopted a value of  $400 \text{ g wet weight} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ , corresponding to a value in the lower part of the range given by Blackburn (1981).
- Microzooplankton. Blackburn (1981), in a review of low-latitude gyral regions, summarized information suggesting that the biomass of microzooplankton (which is usually not sampled) may be about 25% of that of net-caught zooplankton. The P/B and Q/B ratios were assumed to equal only half the P/B and Q/B values of inshore zooplankton, because of lower primary production.

## Results and Discussion

### The models

Each of the 10 models in this study has been drawn so that the area of a box is proportional to the logarithm of the biomass of the box. All boxes included the biomass (B) and production (P), in tonnes wet weight  $\cdot \text{km}^{-2}$  and tonnes  $\cdot \text{km}^{-2} \cdot \text{year}^{-1}$ , respectively. To minimize the number of "wires" needed to draw the connections (i.e., energy flows) between groups, we used the following rules: (i) flows exiting a box do so from the top half of a box, whereas flows entering a box do it in the lower half, and (ii) flows exiting a box cannot branch, but they can be combined with flows from other boxes, if they all go to the same box.

Backflows to the detritus box, respiration, and fishery catches have been omitted on Figures 3–12 for the sake of clarity. Nonetheless, all boxes have been balanced by the ECOPATH II system so that inputs equal outputs.

Based on these models, some generalizations can be made. They are presented in Table 2, which includes the total primary production of each of the 10 areas. This varies between  $4,000 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  in the highly productive reef-flat/seagrass area down to  $400 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  in the open-ocean waters.

### Primary production

The general pattern of primary production indicates high production in coastal and gulf areas and decreasing production with

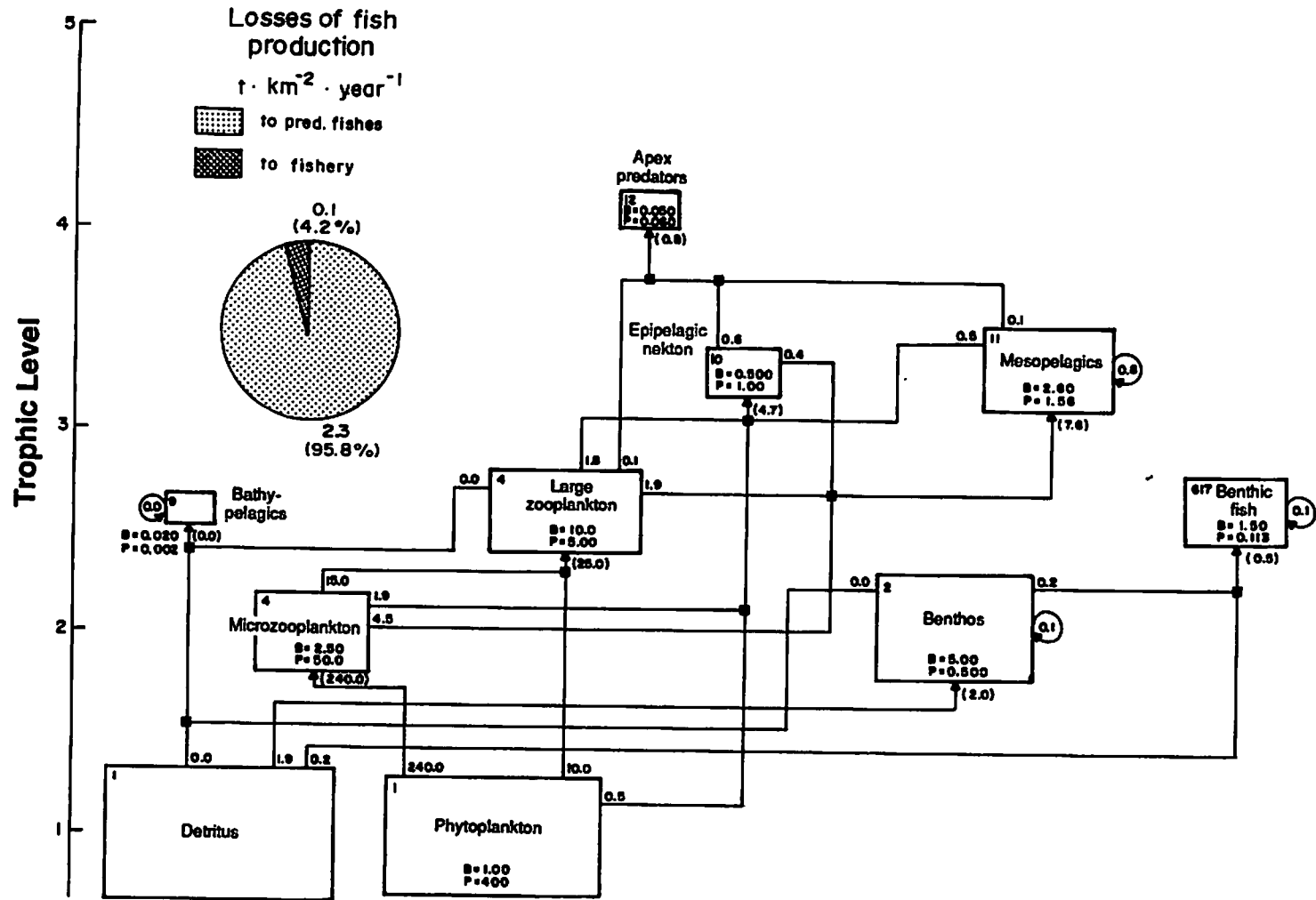


Figure 12. Model (J) of the 200–4,000 m SCS open-ocean community. (The surface area of the boxes is proportional to the log of the biomasses; all flows are in tonnes · km<sup>2</sup> · year<sup>-1</sup>; catches, respiration, and detrital backflows are omitted; see text and Figs. 3–11 for details on construction.)

Table 2. ISSCAAP numbers and common names of fish and invertebrates caught in the SCS and their corresponding "boxes" in ECOPATH II models in Figs. 3 to 12.

ISSCAAP numbers*	Common names†	"Box" number‡	ISSCAAP numbers*	Common names†	"Box" number‡
921	sea weeds	1	3403	mulletts	6
941	misc. plants	1	391/392	misc. fishes (+ 3320/3412)	6
831	sponges	2	3301/2	catfishes & eels	7
751	sea urchins	2	3303	lizardfish	7
752	sea cucumbers	2	3305	groupers	7
761	jellyfish	2	3307/8	misc. snappers	7
581	misc. mollusks	2	3313	drums & croakers	7
541	mussels	2	3316	bigeyes	7
531/2	oysters	2	3404	threadfins	7
551	scallops	2	381	sharks	8
561	cockles	2	3304	pike & conger eels	8
562	misc. bivalves	2	3402	barracuda	8
421	swimming crabs	3	351/2/3/4	clupeids	9
422	mangrove crabs	3	373	Indian mackerels	9
431	spiny lobsters	3	3309	fusilier	9
432	slipper lobsters	3	3405	round scads	9
451/2	penaeid shrimps	3	3408	hardtail scads	9
471	misc. crustaceans	3	571/2	cuttlefish/squids	10
—	sergestids/zooplankton	4	3410	black pomfret	11
382	rays	5	375	hairtail	11
311/3/4	flounders, soles	6	374	Indopacific mackerel	11
312	Indian halibut	6	371/2	king mackerel	11
3306	sillago whiting	6	3406/7	misc. jacks	11
3311	pony fishes	6	3411	white pomfret	11
3312	grunters/sweetlips	6	355	wolfherring	11
3314	goatfishes	6	368	sailfish & billfish	12
3317	breams	6	361-367	tuna & frigate mackerels	12
3319	rabbitfishes	6			

\* These numbers refer to a coding system developed by FAO, the "International Standard Statistical Classification of Aquatic Animals and Plants."

† Some common names were adjusted to account for the pooling of ISSCAAP groups.

‡ Number-specific definition of the "boxes" (see text and Figs. 3-12, 14) are:

- 1: benthic producers
- 2: misc. invertebrates
- 3: crustaceans (excl. plankton)
- 4: sergestids/zooplankton
- 5: large zoobenthos feeders
- 6: small demersal prey fishes
- 7: intermediate predators
- 8: large predators
- 9: small pelagics
- 10: squids and cuttlefish
- 11: medium pelagics
- 12: large pelagics

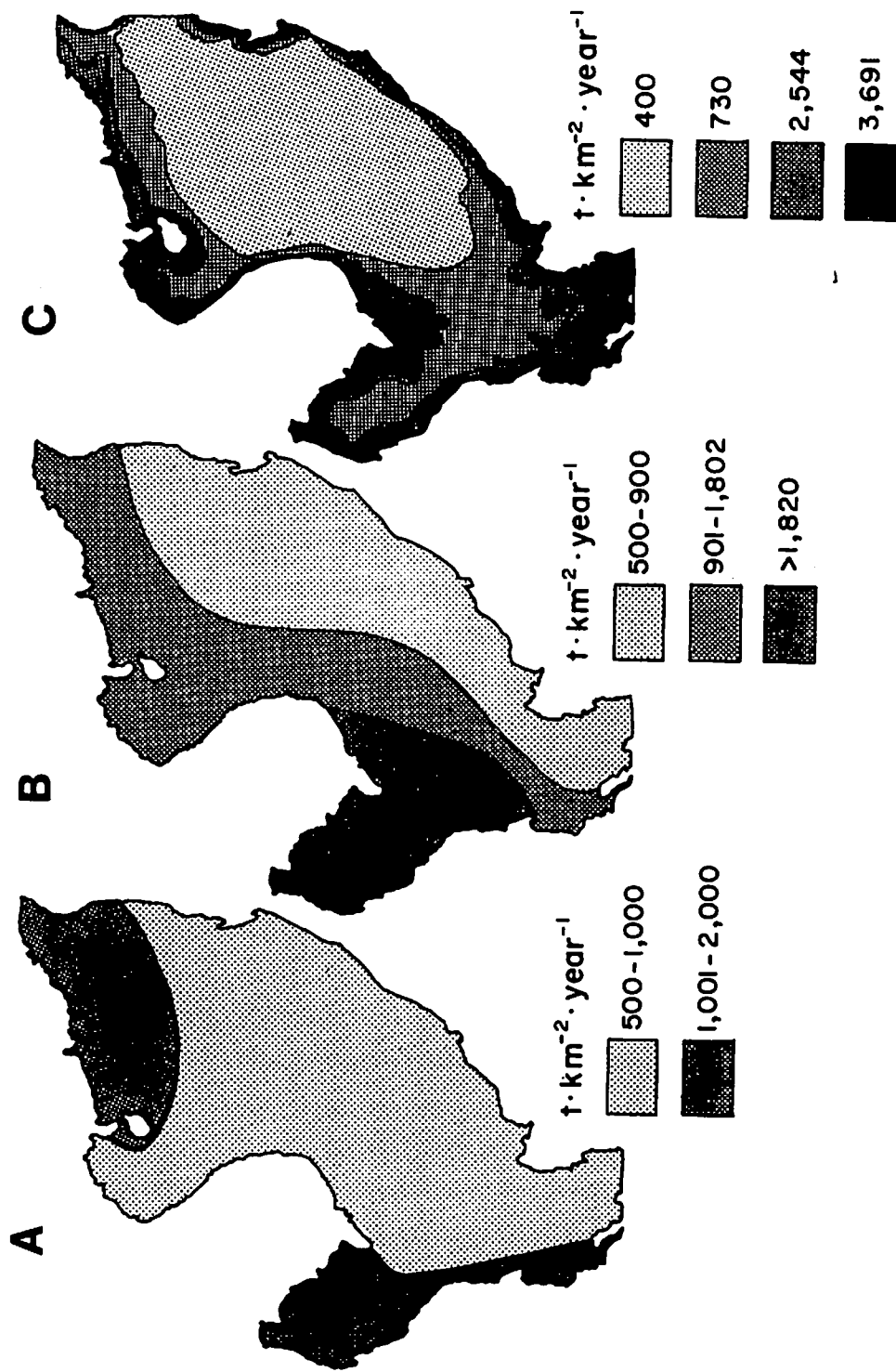


Figure 13. Mean annual distribution of primary production in the SCS. Map A, adapted from Lieth (1975), suggests a primary production of  $3.36 \cdot 10^8$  tonnes per year for the entire SCS. Map B, adapted from FAO (1961), suggests a total primary production of  $4.2 \cdot 10^8$  tonnes per year if one assumes, as in Lieth (1975), an upper limit of  $2,000$  tonnes  $\cdot km^{-2} \cdot year^{-1}$  for the Gulf of Thailand and adjacent areas. Map C presents our depth-based stratification; the corresponding estimate of total production is  $4.0 \cdot 10^8$  tonnes, within the range of the other two estimates.

depth. This does not match the distribution patterns given by FAO (1981) or by Lieth (1975), both of whom reported a northwest/southeast gradient in the primary production of the SCS (Fig. 13a, b, and c). Based on our 10 submodels, we estimated a mean primary production of the whole SCS ecosystem of 1,143 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>, corresponding to  $4.0 \times 10^9$  tonnes wet weight  $\cdot$  year<sup>-1</sup>. From planimetry of the primary production maps given by Lieth (1975) and FAO (1981) (Figs. 13a and b), total primary production for the SCS system ranges from 336 to 418 million tonnes carbon  $\cdot$  year<sup>-1</sup>, which neatly brackets our estimate (if a carbon-to-weight conversion factor of 10 is used, as we have done throughout).

#### Transfer efficiencies

Table 2 also gives transfer efficiencies between trophic levels. For this analysis, the consumption of each group in each system has been split in discrete trophic levels (Christensen and Pauly, 1991). These transfer efficiencies depend on the structure of the food webs (and thus on a multitude of assumptions, many of which may not have been met), yet a general pattern emerged with an overall mean transfer efficiency of around 9%. This is in line with values generally assumed—but often not estimated. Table 2 also suggests that there is no correlation between the mean transfer efficiencies of various models, which vary from 4% to 15%,

and primary productivity in the areas represented. Thus, even the least productive offshore systems pass their energy up the food chain as efficiently as the more productive coastal systems.

Transfer efficiencies from primary producers to fishery catches can be viewed as measures of the efficiency of the various fisheries and are found to vary by two orders of magnitude between systems (Table 2). This indicates that the systems are harvested at different trophic levels. A difference of one trophic level between fisheries implies a difference of at least one order of magnitude in their catches—even if the systems these fisheries exploited are otherwise similar.

#### Catch estimates (Table 3)

The highest catches come from the coastal areas, the Gulf of Thailand, and the southwestern SCS. The estimated catches add up to nearly 5 million tonnes  $\cdot$  year<sup>-1</sup>. Small demersal fishes, small pelagics, and intermediate predators are the most important groups caught (Fig. 14a). In order to compare the annual catch data with those from SEAFDEC (1981) for the year 1979, the latter had to be adjusted to fit our definition of the SCS. Thus, we included 33% of the overall catch of Taiwan, the catches from eastern peninsular Malaysia (from Sarawak and Sabah), and from the Gulf of Thailand (totaling 1.96 million tonnes).

Table 3. Summary statistics for 10 models, representing different subareas of the SCS.

Model	Fig.	Primary production (t $\cdot$ km <sup>-2</sup> $\cdot$ year <sup>-1</sup> )	Transfer efficiency (%) by trophic level*			Geometric mean	Transfer efficiency from primary production to fishery (%)
			II	III	IV		
A. Shallow waters	3	3,650	6.2	3.1	9.6	5.7	0.17
B. Reef-flats/seagrass	4	4,023	8.6	11.0	6.6	8.6	0.33
C. Gulf of Thailand	5	3,650	7.2	13.8	7.0	8.9	0.26
D. Vietnam/China	6	3,003	3.5	10.7	6.9	6.4	0.05
E. NW Philippines	7	913	9.3	8.9	9.3	9.2	1.23
F. Borneo	8	913	15.9	18.4	11.7	15.1	0.08
G. SW SCS	9	2,433	11.7	15.1	8.7	11.5	0.35
H. Coral reef	10	2,766	10.0	1.4	—	3.7	0.14
I. Deep shelf	11	730	8.0	13.0	8.1	9.4	0.03
J. Open Ocean	12	400	9.3	12.3	7.4	9.5	0.01
SCS Weighted means	2	1,143	8.3	10.4	7.0	9.2	0.12

\* II refers to first consumer level, III to second, etc.; transfer efficiencies computed after removal of cycles.

We added Vietnamese catches (approximately 700,000 tonnes) (Nguyen, 1989), Chinese catches (e.g., 400,000 tonnes) (Shindo, 1973), and catches from Hong Kong, northwest Philippines, Cambodia, Brunel, northwest Indonesia, and Singapore. The total catch is about 4 million tonnes annually—a figure similar to our estimate and to the figure of 4.6 million tonnes derived by Marr (1976) for the SCS as defined here. We conclude that our models incorporate and/or lead to a reasonable estimate of total catches.

### Potential catches

The notable differences in the efficiency of the fishery discussed above raise the question whether the catches can be increased by directing the fishery toward the lower parts of the food web. One way to consider this is to look at the fate of the fish production within the system. To facilitate this, pie charts were added to each submodel (Figs. 3–12) showing the fate of fish production. For all submodels, the bulk of the fish production is consumed by fish predators, while the fisheries and invertebrate predators take the rest.

Total fish production in the SCS area is estimated at about 30 million tonnes annually. About 13% is harvested by the fisheries and the rest is eaten by predators (Fig. 14 a, b).

If we assume that it is possible to harvest all systems as efficiently as the fully exploited coastal systems (i.e., models A, B, C, and G, but disregarding E, the northwest Philippines system, whose transfer efficiency may be biased upward because of a low estimate of primary production), we obtain a mean potential fishery efficiency of 0.275% of primary production. If the less-exploited systems could be harvested with this efficiency, the additional catches from the SCS would be about 5.8 million tonnes annually, more than doubling the catch; however, this potential may not be feasible in practice. The Vietnam/China system was only lightly exploited in the period covered here, the mid-1970s to mid-1980s. The potential for the area is estimated to be 1.86 million tonnes per year, corresponding to an increased catch rate of 1.6 to 8.2 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>, which is extremely high and probably unrealistic.

The Bornean coast, beyond 10 m deep, was not exploited intensively in the late 1970s, and this is reflected in the potential for increases in catch of some 260 thousand tonnes  $\cdot$  year<sup>-1</sup>. This corresponds to an increase in catch rate of 0.7–2.5 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>. Much of this potential has probably been realized, since the fishery in Sarawak and Sabah has increased considerably in the last decade.

The potential for the deeper coralline areas is estimated at about 300,000 tonnes  $\cdot$  year<sup>-1</sup>, doubling the catch and bringing the total catch rate to about 7.5 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>. There are large coralline areas in the central part of the SCS that are only lightly exploited. Because catch rates for intensively exploited coral areas can exceed 20 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup> (Alcala, 1981; White, 1989), we conclude that there may be a basis for some increase. However, because the model is based on data from outside the region, we stress that one should consider these estimates with care.

The bulk of the additional potential 5.8 million tonnes  $\cdot$  year<sup>-1</sup> comes from the deeper areas of the SCS. This potential may not be realized because it is difficult to fish the deeper areas in a way that is economically viable.

The same problems also occur with regard to the abundant offshore resources of mesopelagic fish such as myctophids. It may well be that the only realistic way to harvest these resources is by catching their predators, the large pelagics and cephalopods.

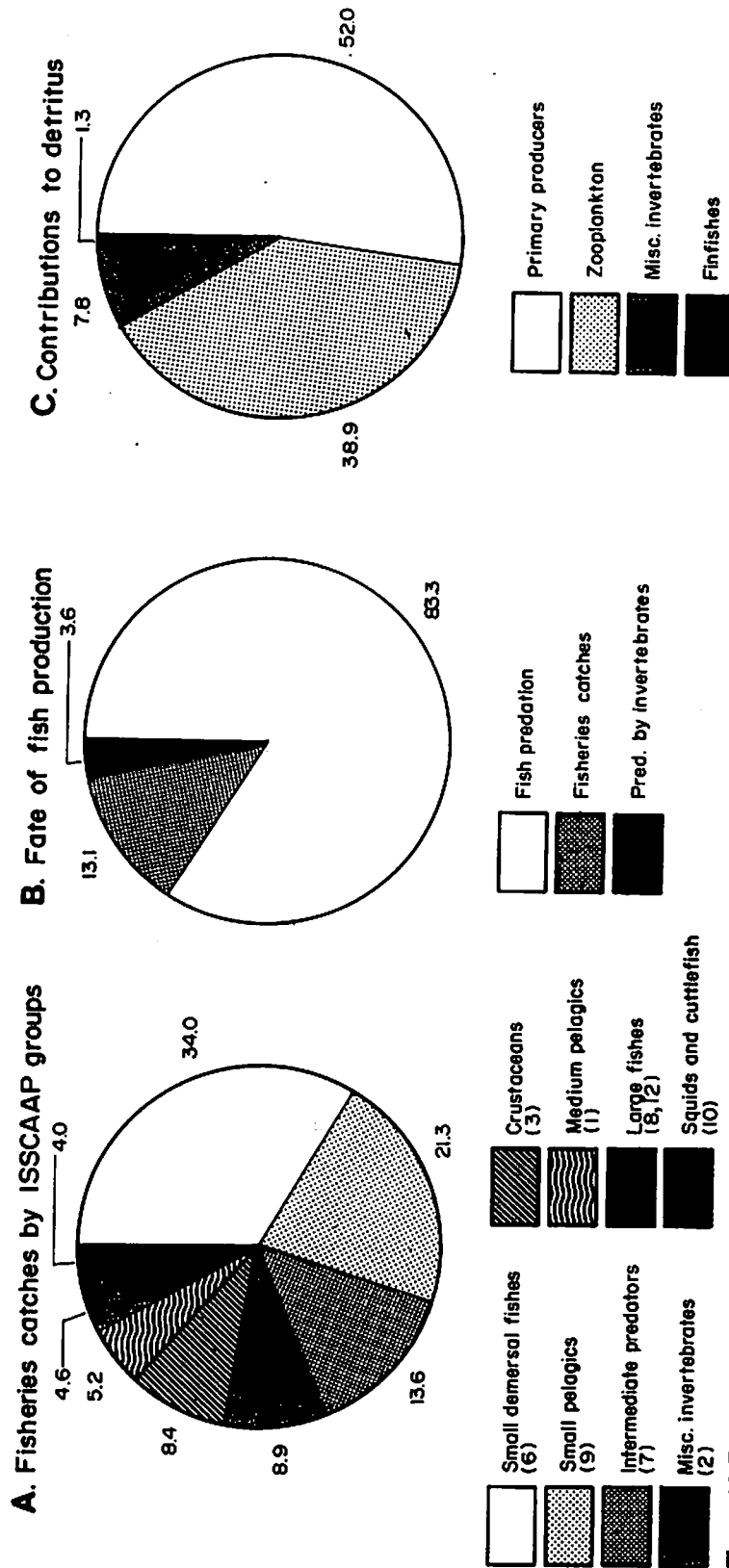
FAO (1981) estimated the potential of the SCS at 3.3 and 2.8 million tonnes  $\cdot$  year<sup>-1</sup> for demersal and pelagic fishes, respectively. Our corresponding estimates are 2.6 and 1.5 million tonnes  $\cdot$  year<sup>-1</sup>.

The potential catches presented here are tentative, as were those of FAO (1981); however, this does not mean that the method we employed is not useful. Indeed, the problems associated with estimating potential catches in data-sparse areas make even indicative approaches worthwhile.

Many fisheries in the region suffer from high fishing pressure, use of small-meshed nets, and sometimes from destructive fishing methods (Pauly and Chua, 1988). Carefully designed, new fishing regimes could therefore, even in these cases, be expected to lead to increased catches.

### Detritus flows within the South China Sea

The models we have presented here can be linked to show the flow of detritus within the SCS system (Table 5, Fig. 14c). Total sedimentation is estimated at 10<sup>9</sup> tonnes  $\cdot$  year<sup>-1</sup> or 25% of primary production. Assuming all of this to be deposited at depths in excess of 200 m, the total input to the bottom is about 650 tonnes  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>. This estimate is one order of magnitude higher than the estimate of Rowe and Gardner (1979) for the deep North Atlantic. Expecting a higher estimate for the SCS, and bearing in mind our assumption that all detritus is deposited in the deepest stratum (which makes up only 50% of the SCS) and that we



**Figure 14.** Fate of biological production for the entire SCS (especially finfishes), mid-1970s to the mid-1980s. (see Figs. 3-12 for details; for International Standard Statistical Classification of Aquatic Animals and Plants [ISSCAAP] groupings, see Table 2).  
**A-** Percent composition of fisheries catches by ISSCAAP groups.  
**B-** Percent of fish production consumed by fish predators, harvested as fisheries catches, and consumed by invertebrate predators.  
**C-** Percent contribution to detritus of primary producers, zooplankton, miscellaneous invertebrates, and finfishes.

Table 4. Estimated catches ( $t \cdot km^{-2} \cdot year^{-1}$ ) in 10 submodels from the SCS, representative of the late 1970s.

Group/Model*	A	B	C	D	E	F	G	H	I	J	Total ( $10^3 t \cdot year^{-1}$ )
1. Primary producers	—†	0.988	—	—	—	—	—	—	—	—	21
2. Miscellaneous invertebrates	1.840	5.210	0.053	—	0.210	0.003	—	—	—	—	439
3. Crustaceans (excl. plankton)	1.455	0.276	0.594	—	—	0.174	0.174	0.404	—	—	411
4. Sergestids/zooplankton	—	—	—	—	0.350	—	—	—	—	—	10
5. Large zoobenthos feeders	0.026	—	0.022	0.006	—	0.012	0.086	—	0.001	—	21
6. Small demersal predators	1.075	5.409	5.449	0.408	4.514	0.136	1.541	2.375	0.036	—	1,672
7. Intermediate predators	0.140	0.440	0.251	0.867	3.220	0.060	1.556	0.129	0.077	—	664
8. Large predators	0.260	—	0.058	0.033	0.130	0.058	0.110	0.006	0.003	—	49
9. Small pelagics	0.925	0.006	1.497	—	0.340	0.283	5.126	0.831	—	—	1,047
10. Squids and cuttlefish	0.152	0.750	0.440	0.255	0.176	—	—	—	0.023	—	198
11. Medium pelagics	0.402	—	0.921	—	0.320	—	—	—	—	—	257
12. Large pelagics	0.042	—	0.050	0.050	—	—	—	0.028	0.050	0.050	157
Total		6.083	13.079	9.335	1.619	11.260	0.726	8.593	3.773	0.190	0.050
Total catch ( $10^3 t \cdot year^{-1}$ )	1,046	275	1,242	453	315	105	962	291	176	80	4,945
Potential catch§ ( $10^3 t \cdot year^{-1}$ )	—	—	—	1,860	—	257	—	295	1,688	1,686	5,786

\* Refer to Table 1 for the stratification of the SCS used in this analysis.

† Dashes indicate missing information or zero catches.

‡ From SEAFDEC (1981), referring to the year 1979.

§ This "potential" may not be realizable (see text).



Table 5. Estimated flows ( $10^3\text{t} \cdot \text{year}^{-1}$ ) of excess fish and detritus production for the SCS.

Model*	Fish		Detritus	
	Import	Export	Import	Export
A	0	60	0	30,000
B	0	280	0	56,000
C	60	410	15,000	22,000
D	120	180	31,000	260,000
E	10	23	3,100	3,800
F	60	330	16,000	30,000
G	50	210	12,000	64,000
H	30	130	8,500	150,000
I	1,300	4,300	530,000	700,000
J	4,300	0	700,000	1,000,000

\* See Table 1 and text for definition and construction.

have no independent estimate of flux to the deep bottom layer from other highly productive tropical areas, we conclude that our estimate, although high, is not unrealistic.

We initiated this exercise in response to the challenge represented by the LME concept and are surprised and pleased to see that some sense has come out of our rather crude modeling approach. We view our results as an indication of the robustness of the approach incorporated in ECOPATH II and are confident that the steadily increasing number of aquatic ecosystems that are being quantified using steady-state models will help to improve our understanding of the ecology of LMEs.

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