INTER-AMERICAN TROPICAL TUNA COMMISSION
COMISION INTERAMERICANA DEL ATUN TROPICAL

3RD MEETING OF THE SCIENTIFIC WORKING GROUP

LA JOLLA, CALIFORNIA, USA

MAY 6-10, 2002

BACKGROUND PAPER A22

(DRAFT OF BACKGROUND PAPER TO BE SUBMITTED AT THE 69TH MEETING OF THE IATTC)

ECOSYSTEM MODELING OF THE PELAGIC EASTERN PACIFIC TROPICAL PACIFIC OCEAN

PREPARED APRIL 2002

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INTRODUCTION

An ecosystem approach to fisheries management is important for maintaining sustainable fisheries and healthy ecosystems (FAO 1995, NRC 1999). Although the objectives of ecosystem-based management are difficult to define, a general awareness exists that modeling is an important tool for exploring the ecological consequences of fishing and to improve our knowledge of how ecosystems function. Multispecies mass-balance models endeavor to 1) represent the life histories of the principal elements of the ecosystem, 2) describe how biomass flows among them based on diet studies, and 3) represent the size and species composition of the catches of the various fisheries.

At its 58th meeting, in June 1997, the IATTC established the Purse-Seine Bycatch Working Group (BWG) to examine the issue of bycatches and discards of all species taken in the purse-seine fishery for tunas in the eastern Pacific Ocean. One of the terms of reference for the Working Group was "to define the relationships among bycatch and target species with special reference to the sustainability of the catches of all such species." This was the initial impetus for developing an ecosystem model for the eastern tropical Pacific (ETP). The purpose was to develop an hypothesis describing the pelagic ecosystem in the ETP and to investigate the relative ecological implications of alternative fishing strategies on the system.

ECOPATH WITH ECOSIM

The ecosystem model for the pelagic ETP was developed using Ecopath with Ecosim (EwE) (Walters *et al.* 1997, Christensen *et al.* 2000, Walters *et al.* 2000). EwE has been used to develop many ecosystem models in the Pacific Ocean and elsewhere (*e.g.* Christensen and Pauly 1993). Ecopath provides a framework for the construction of mass-balance models of ecosystems. The mass balance is generated from estimates of how abundant the resources are (biomasses), the productivity or mortality rates of the resources, how they interact (diet compositions and food consumption rates), and how efficiently the resources are utilized in the ecosystem. In Ecopath, the energy input and output of all model components must balance. That is,

$$\text{consumption} = \text{production} + \text{respiration} + \text{unassimilated food.} \qquad (1)$$

Given the description of the ecosystem in Ecopath, its dynamic, time-series behavior is examined with Ecosim.

THE ETP MODEL

Scope

The model of the pelagic ecosystem in the ETP covers the area circumscribed by 20ºN, 20ºS, 150ºW, and the approximate boundary of the shelf break along the coast of the Americas, approximately 32.8 million km^2. The parameter estimates for the 1993-1997 period are averaged whenever possible. The model components (Table 1) were chosen to include the principal exploited species (*e.g.* tunas and marlins), functional groups (*e.g.* sharks and cephalopods), sensitive species (*e.g.* sea turtles and dolphins), and a species that resides in the system for only part of the year (Pacific bluefin tuna). Aggregation and disaggregation of model groups depended not only upon perceived importance of the animals in the system, but also upon the availability of information about the various taxa, differences and similarities in their biology, and their life history in the ocean (*e.g.* epipelagic *versus* mesopelagic distribution). Taxa that undergo considerable trophic ontogeny, and those that are caught by different fishing gears at different sizes, were separated into two ontogenetic groups according to the size ranges in Table 1. The current version of the model has 36 components.

Parameters

Estimates of the Ecopath input parameters, *B*, *P/B*, *Q/B*, *EE*, for each model component were based on a variety of sources. Olson and Watters (submitted) summarized the sources, justifications, and assumptions for the initial and revised estimates of these parameters, and diet composition.

Fishery landings and discards, averaged over 1993-1997, were estimated for each model component by fishing gear (purse seine, longline, and pole-and-line) and fishing mode (dolphin, floating-object, and unassociated school sets by purse seiners). The catch data were obtained from IATTC tuna, bycatch, and discards databases. Small, localized coastal and artisanal fisheries are not included in the model due to a shortage of data. The biomass of exports (animals that move out of the ecosystem) is assumed to equal the biomass of imports.

Ontogenetic transition parameters are required for the taxa that are separated into two ontogenetic groups, or split pools (Olson and Watters submitted Table 7). These include life-history information from growth functions, weight-length relationships, reproductive parameters, and recruitment parameters.

Model review

The ETP ecosystem model was reviewed extensively. Two working groups were formed specifically for developing and evaluating the model. First, the participants of the Purse-Seine Bycatch Working Group (BWG) established a subgroup, Ecological Studies and Modeling (ESM), to oversee and review the model. The BWG members had agreed, during their first meeting in July 1998, that Ecopath with Ecosim provides a useful starting point for modeling ecosystem dynamics in the ETP (IATTC 1998). The ESM subgroup met in April 1999 (IATTC 1999b). The participants discussed numerous aspects of the pelagic ecosystem in the ETP, and the information required to construct steady-state and dynamic models of the ecosystem. The model was reviewed at this meeting, and eight priorities for revising and calibrating the model were made. Seven of the eight recommendations were acted upon during the subsequent year. These included adding more model groups, redefining the model arena, conducting a particle-size spectrum analysis, evaluating the relative importance of top-down and bottom-up environmental forcing, comparing the ecosystem model predictions with IATTC stock-assessments, evaluating the sensitivity of the biomass trajectories estimated by Ecosim, and incorporating recent bycatch data for the longline fishery.

Second, a working group entitled "Ecological Implications of Alternative Fishing Strategies for Apex Predators," was funded by the National Center for Ecological Analysis and Synthesis (NCEAS) in Santa Barbara, California (www.nceas.ucsb.edu), to develop and evaluate the ecosystem model of the ETP. The working group revised and balanced the first draft of the model, and ultimately used it for analyses of the ecosystem.

Sensitivity analysis

The model is one of several possible hypotheses describing the pelagic ecosystem in the ETP. Much of the information synthesized in this model is uncertain (described by Olson and Watters submitted). The sensitivity of the model, both for the Ecopath mass-balance and the dynamic trajectories predicted by Ecosim, were analyzed. First, the basic input parameters *B*, *P/B*, *Q/B*, and *EE* were varied by -50% and +50% (in steps of 10%) for each group and the resulting percent change in each of the input parameters that are computed by Ecopath were calculated for all other groups. The results of this analysis were summarized with a sensitivity index (Figure 1). The index is the count of the parameters affected by ±30% or more for each group.

The Ecopath mass-balance was relatively insensitive to parameter values for most groups (Figure 1). Varying the parameters for four groups occupying top trophic levels and three groups near the bottom of the food web indicated low-medium model sensitivity. Model sensitivity was zero for the baleen whales. However, the analysis showed that changes in the parameters of two groups, cephalopods and *Auxis* spp., exert the greatest influence on the system (Figure 1). These groups occupy middle trophic levels, and many of the upper-level predators prey on these groups. Little is known about *Auxis* spp. and the many species of cephalopods in the ETP, and studies of these two groups might represent the best use of research funds for increasing our knowledge of the ETP ecosystem.

Because the Ecopath mass-balance was most sensitive to parameters for cephalopods and *Auxis* spp., the second part of the sensitivity analysis was concentrated on these two groups. The sensitivity of the biomass trajectories estimated by Ecosim to changes in the basic parameters was evaluated for these groups. The *P/B*, *Q/B*, and *EE* for cephalopods and *Auxis* spp. were changed by 20%, 30%, and 50%, and the fit of the predicted biomasses to CPUE data for yellowfin tuna (Figure 31 from IATTC 1999a) was evaluated. This sensitivity analysis (Table 2) showed that reductions in the sum of squares (SS) of the fits, indicating an improvement over the initial values, occurred in only a few cases. SS improvements were slight, and in most cases the fits were worse. For the cephalopods, 5 of the 14 determinations showed negative changes in SS relative to the fit using the initial values, but the maximum change was only –3.3%. Positive changes in SS values, indicating a worse fit, ranged up to 69.7%. For *Auxis* spp., none of the parameter variations produced a better fit to the CPUE data for yellowfin (Table 2).

Fitting the model to historical data

The ETP ecosystem model was fitted to historical time series for yellowfin and bigeye tunas. Initial conditions for the fit were set up by simulating a 51-year period with no fishing effort, and then incorporating an historical series of fishing effort for each of the five gears and fishing modes in the model from 1961 to 1998. Running the simulation for 51 years without fishing allowed the biomasses of the model groups to return to equilibrium at higher levels, possibly approaching unexploited or "early-exploited" conditions. Estimates of fishing effort (days fishing for three purse-seine set types and for baitboats; numbers of hooks for longline) from 1961-1998 were standardized to the effort in 1993 (Figure 2). The empirical climate driver, described in the ***Environmental forcing*** section, for 1910 to 1998 was used to include the effect of climate variation on the food web in the simulation.

The ecosystem model was fitted to independent estimates of biomass and average total mortality rates for large and small yellowfin (Figure 2) and large and small bigeye (Figure 3) for 1975-1998. These independent estimates were taken from stock assessments done during 1999 (Maunder and Watters 2001, Watters and Maunder 2001). For large yellowfin, the biomass estimate at the start of each year for fish in the seventh quarter or more after recruitment to the fisheries was used. For large bigeye, the biomass estimate at the start of each year for fish in the ninth quarter or more after recruitment to the fisheries was used. For small yellowfin and bigeye, the biomass estimates for the large fish were subtracted from the total biomass estimates. All biomass estimates were scaled to biomasses in 1993 and treated as CPUEs. Fitting entailed iteratively adjusting the vulnerability rate (v, equation (5) Olson and Watters submitted) for the predator-prey links to minimize the sum of square errors (SS). When estimating vulnerability rates, similar model components were grouped in several ways to explore the hypothesis that animals performing comparable roles in the ecosystem would be vulnerable to predation in comparable ways. For example, *v*'s were estimated separately for apex predators (defined here as groups at trophic levels ≥ 5.0), predators (defined here as groups at trophic levels 4.0-5.0), and prey (defined here as groups at trophic levels <4.0). None of the alternative vulnerability scenarios were better (lower SS and a more parsimonious parameterization) than estimating a single common *v*. The best estimate of *v* was 0.2429. Fits to the yellowfin and bigeye CPUEs are displayed in Figures 2 and 3, respectively. The fits for yellowfin were considerably better than those for bigeye. The fits for yellowfin captured the apparent higher recruitment regime of 1985-1998 (Maunder and Watters 2002) (Figure 2). The fits for bigeye, however, miss the increase in CPUEs observed for 1984-1987 (Figure 3).

RESULTS

Food web diagrams are useful for representing the structure and flows of ecosystems. A simplified food-web diagram, with approximate trophic levels (TLs), of the pelagic ETP is illustrated in Figure 4. Sharks (average TL 5.25) and billfishes (average TL 5.08) are top-level predators. Tunas and other pelagic fishes (*e.g.* dolphinfishes) occupy slightly lower TLs. Smaller pelagic fishes (*e.g. Auxis* spp.) and cephalopods are the principal forage of many of the upper-level predators in the ecosystem. Small fishes and crustaceans prey on two zooplankton groups, and the herbivorous zooplankton feed on the producers, phytoplankton and bacteria (Figure 4).

Trophic levels of the fisheries

In exploited pelagic ecosystems, the fisheries often act as apex predators. The primary flows, accounting for 80% of total trophic flows to each model group, to the purse-seine and longline fisheries in the ETP averaged over 1993-1997 are represented in food-web diagrams in Figure 5. Purse-seine sets on dolphins draw from the simplest food web among the various tuna fisheries. The catch (*i.e.* landings and discards) of dolphin sets has a weighted-average TL estimate of 4.78, which is the highest TL among all the fisheries except the longline fishery (Figure 6). Purse-seine sets on unassociated fish draw from a more-diverse food web than dolphin sets, and catch smaller tunas (Figure 5). The weighted-average TL of that fishery is, therefore, slightly lower, 4.72 (Figure 6). Purse-seine sets on floating objects draw from a more-diverse food web than either dolphin sets or sets on unassociated fish (Figure 5). Because of the bycatch of floating-object sets (not shown because of its small contribution to the total catch) is greater than that of the other three set types, the average TL (4.77) is slightly higher than that of sets on unassociated fish. The longline fishery also utilizes a diverse food web (Figure 5) and catches large fishes. Its weighted-average TL (5.19) is estimated to be considerably higher than those of the other fisheries (Figure 6). The baitboat fishery (not shown in Figure 5) catches mostly small tunas and an occasional shark. Like purse-seine sets on unassociated fish, the average TL is estimated at 4.72. Overall, the weighted-average TL of the catch of all fisheries during 1993-1997 was estimated by the ecosystem model to be 4.83 (Figure 6).

Trophic levels were also estimated for the time series of total catches by year for the surface fisheries from 1993 to 2001. Current landings and discard data for the longline fishery were not yet available to the Commission, so the TLs for the longline fishery are not shown. The TL estimates were made by applying the TLs estimated with the base model (*i.e.* for catches averaged over 1993-1997) weighted by the catch data by fishery and year for all model groups from the IATTC tuna, bycatch, and discard databases. The TLs of the summed catches of all fisheries varied slightly from year to year (Figure 7). The lowest average TLs of the catch were estimated for 1998 and 1999, followed by the largest increase in TL in 2000. The average TL dropped again slightly in 2001, to nearly the same level as in 1994-1996. The TL of the floating-object sets varied more than that of the other fisheries. This was due to the interannual variability in the sizes of the tunas caught and the species composition of the bycatch in sets on floating objects. The trend in TL of the floating-object sets seemed to influence the TL trend of the total catches more so than for the other fisheries (Figure 7).

Trophic levels were also estimated separately for the time series of landings and discards by year for the surface fisheries from 1993 to 2001. The TLs of the landings were quite stable from year to year. Again, the size distribution of the landed and discarded tunas influenced the trend in landings. This was especially important for the floating-object sets. The TLs of the discarded catches varied considerably. The largest variation occurred for sets on unassociated fish. The greatest change in TL of the discards in unassociated sets from one year to the next (0.63) took place from 1997 to 1998. In 1997 the discards were dominated by large sharks (274 mt, TL 5.1), followed by 82 tons of rays (TL 3.9), 60 tons of large bigeye (TL 5.3), and 60 tons of small sharks (TL 5.4). In 1998, however, the discards were dominated by 385 tons of rays (TL 3.9), followed by 121 tons of large sharks (TL 5.1) and low quantities (25 mt) of small dolphinfishes (TL 4.8).

Examining the variability of the trophic levels of the landings and discards may hold promise as a metric for evaluating the effect of the fisheries on the ecosystem. The ETP model predicts that fishing on animals at high trophic levels has the greatest top-down effect on the ecosystem. However, it has not been established whether or not the variability in the TLs observed in Figures 6 and 7 are important.

Environmental forcing

The members of the NCEAS working group explored how climate variation at the scale of El Niño-Southern Oscillation (ENSO) might affect the animals at middle and upper trophic levels in the ETP. They used the ETP model to simulate the bottom-up effects of single climate-anomaly pulses, regular climate cycles, and greenhouse warming. First, they established an empirical relationship between sea surface temperature (SST) anomalies in the NIÑO3 region[1] of the ETP and surface chlorophyll concentrations to simulate the effect, on the food web, of physically forcing the biomass of the producers. They also developed an alternative hypothesis that, in addition to affecting producer biomass, physical forcing also simultaneously affects egg production by predators and the degree to which recruiting predators are themselves vulnerable to predation. Watters *et al.* (manuscript) summarize the results and conclusions of that work.

The interaction between bottom-up and top-down forces is partly modulated by the physical environment, but, in exploited systems, it is also complicated by the addition of fisheries. In other ecosystems, fishing is known to have imparted profound changes in food-web structure (*e.g.* Caddy and Rodhouse 1998, Fogarty and Murawski 1998). The modeling results described by Watters *et al.* (manuscript) suggest that pelagic fisheries that operate in the ETP impart control on both target species (*e.g.* yellowfin tuna) and non-target species (*e.g.* sharks) (high variance ratios, Table 3). Other non-target species taken by the fisheries (*e.g.* small mahimahi) appear to be controlled from the bottom up (low variance ratios, Table 3). An important prediction from the ETP model is that the top-down effects from fishing did not propagate down the food web to the middle trophic levels. In contrast, bottom-up effects, particularly a long-term reduction in producer biomass, appeared to be strong all the way to the top of the food web (Figure 8) (see Watters *et al.* manuscript). Thus, the modeling results support the concept that bottom-up forces define a template on which top-down forces may act (Power 1992).

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[1] The NIÑO3 region of the eastern equatorial Pacific is defined by the U.S. National Weather Service's Climate Prediction Center (CPC) as 5ºN-5ºS, 150º-90ºW. Monthly mean SST anomalies are provided by the CPC on its website, http://www.cpc.noaa.gov.

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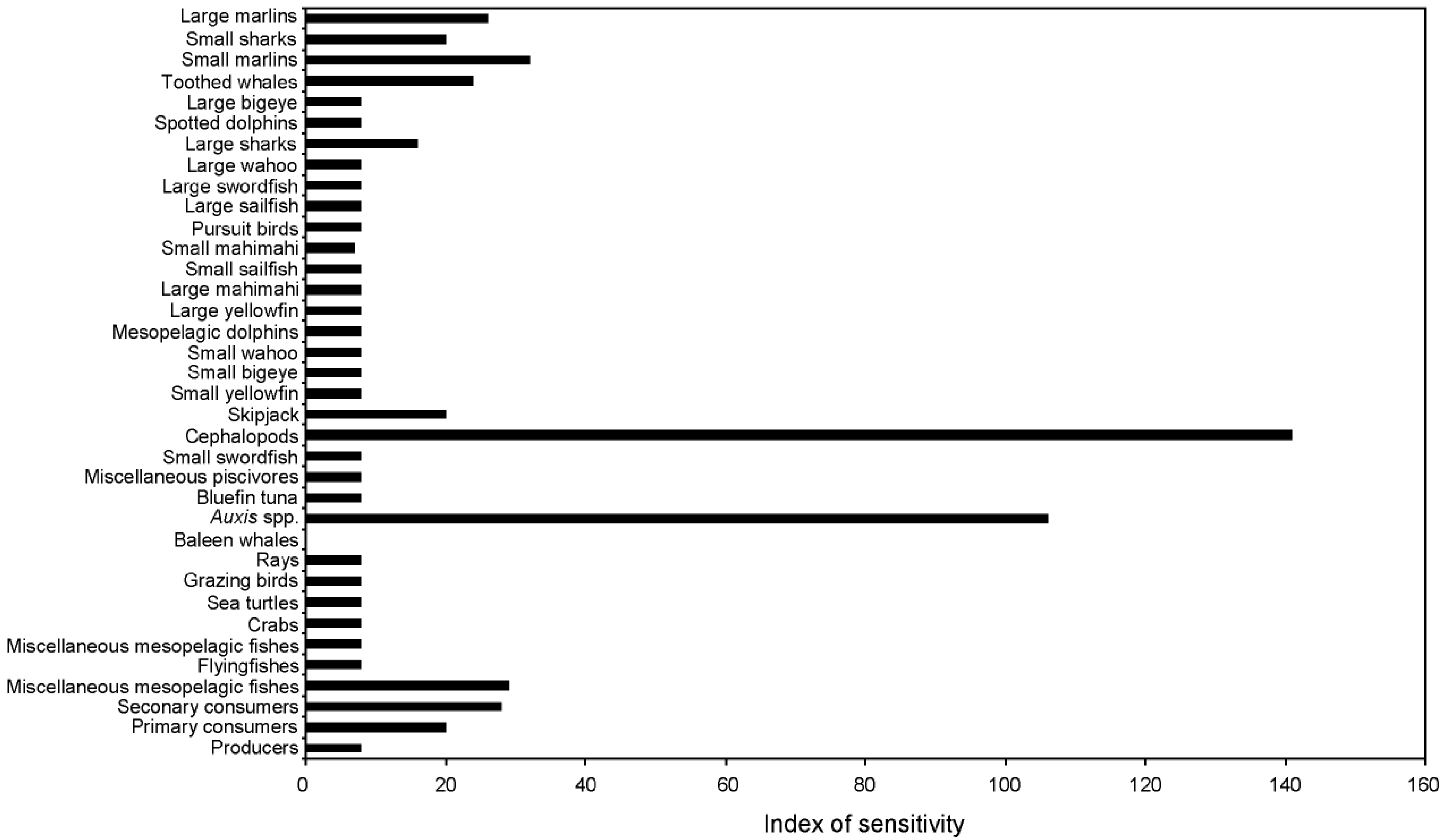

FIGURE 1. Sensitivity analysis results for the ETP ecosystem model, using an index of sensitivity (the count of parameters for other groups affected by ±30% or more for each group). The model groups are sorted by trophic level.

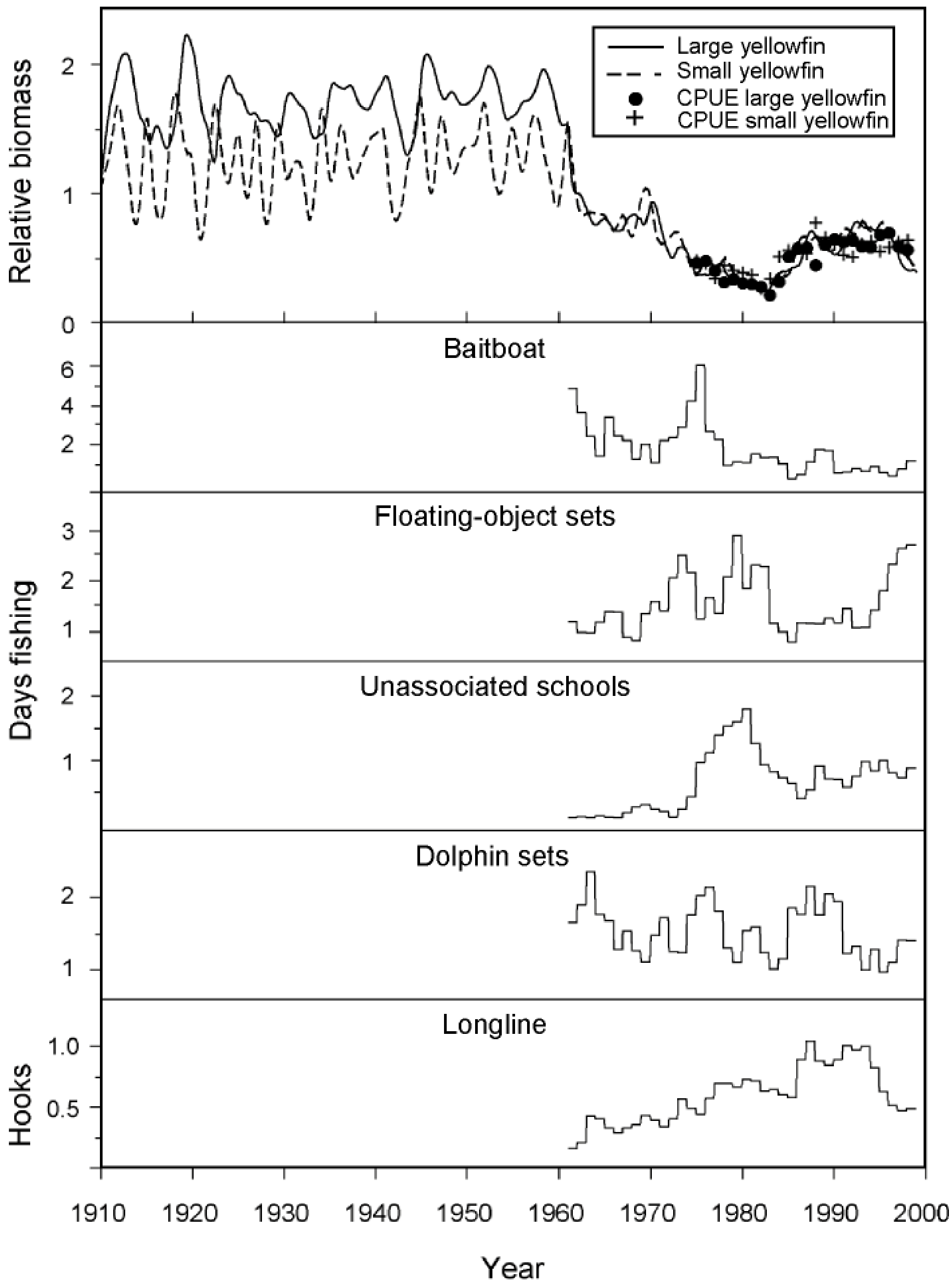

FIGURE 2. Simulation results (top panel) of fitting the ETP ecosystem model to historical time series of fishing effort for yellowfin tuna in the eastern Pacific Ocean. The effort time series (days fishing for three purse-seine fishing modes and for baitboats; numbers of hooks for longline gear) are standardized to the effort in 1993 for each gear (bottom five panels). In the simulation, there was no fishing effort, only climate forcing, between 1910 and 1961. The climate driver is shown in Figure 3. Note the y-axes of the panels are drawn at different scales.

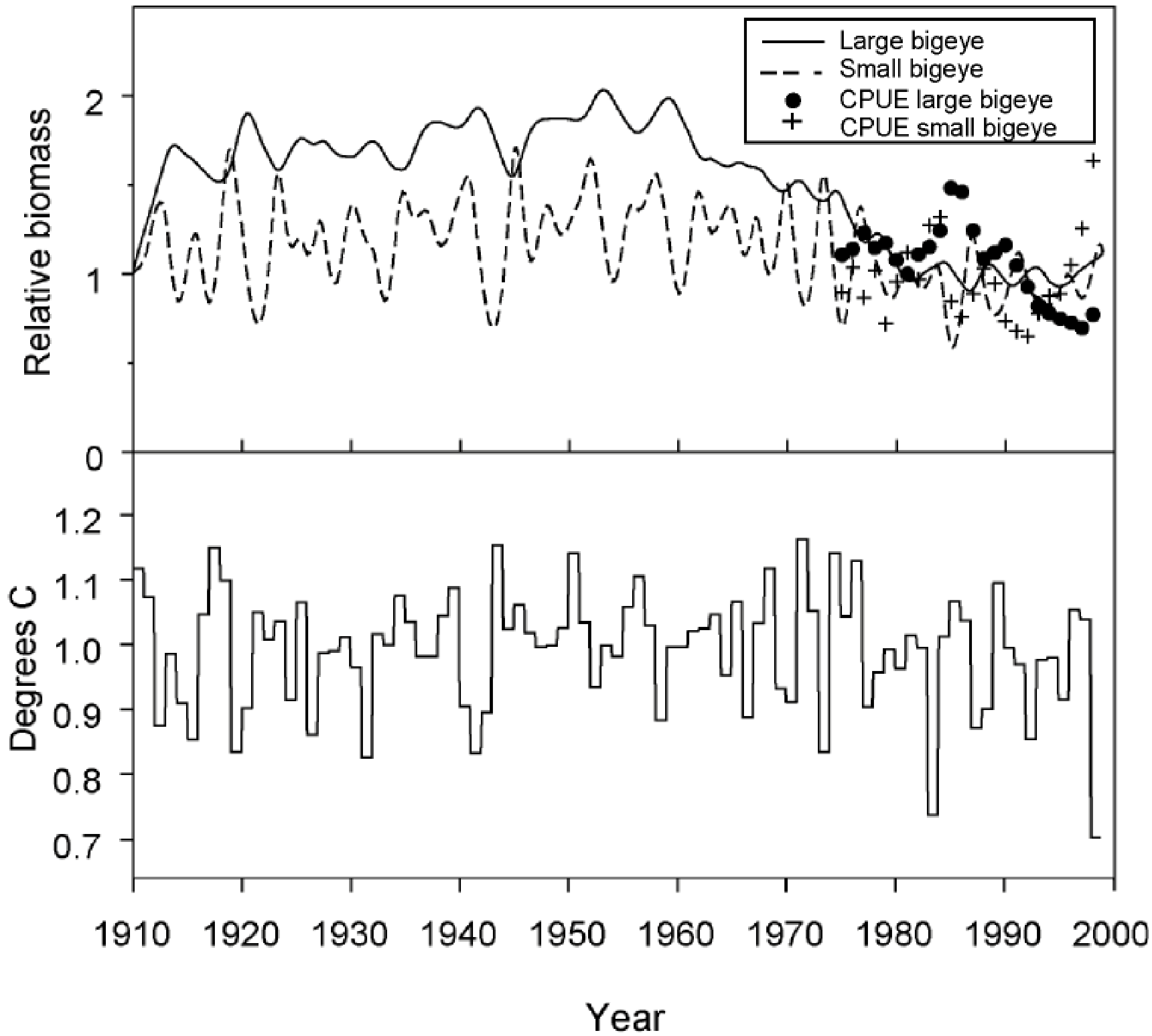

FIGURE 3. Simulation results (top panel) of fitting the ETP ecosystem model to historical time series of fishing effort (shown in Figure 2) for bigeye tuna in the eastern Pacific Ocean. The bottom panel displays the SST anomalies for the NIÑO3 region during 1910 to 1998, which was used as a climate driver for the simulation.

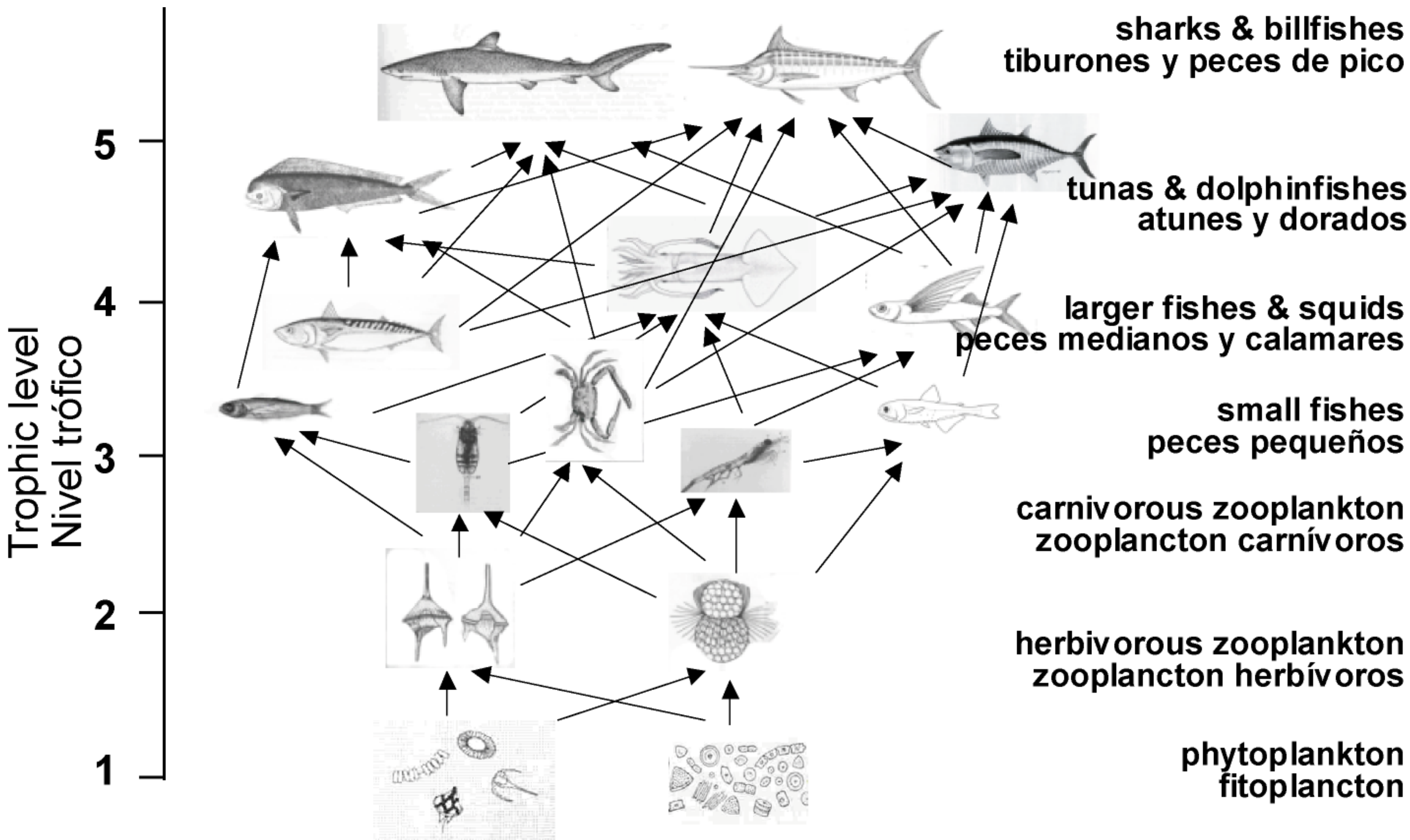

FIGURE 4. A simplified food-web diagram for the pelagic ecosystem in the eastern tropical Pacific Ocean.

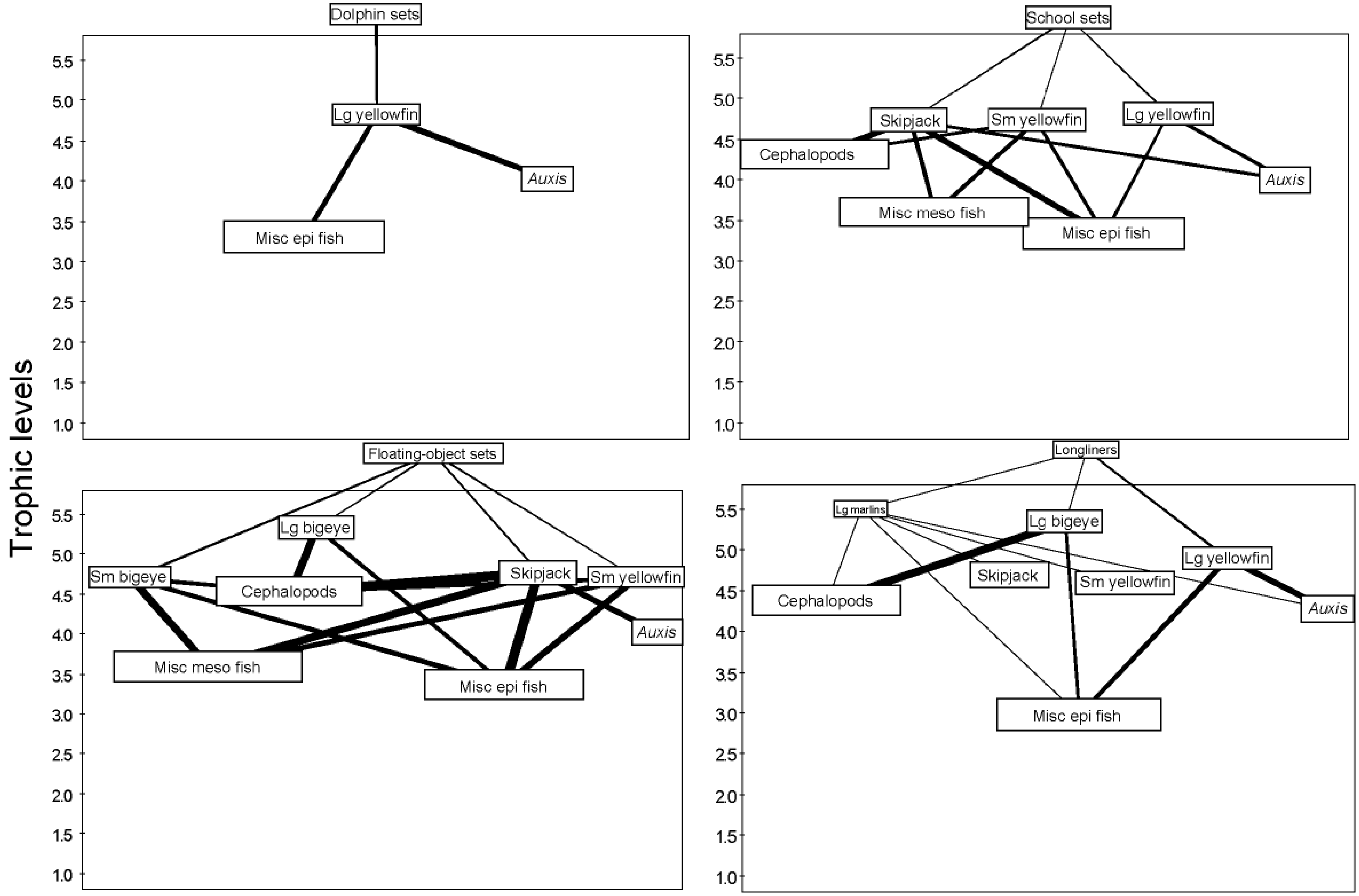

FIGURE 5. Food web diagrams representing the primary flows (accounting for 80% of the total trophic flows) to the principal groups caught by the purse-seine and longline fisheries in the ETP averaged over 1993-1997 and their principal prey.

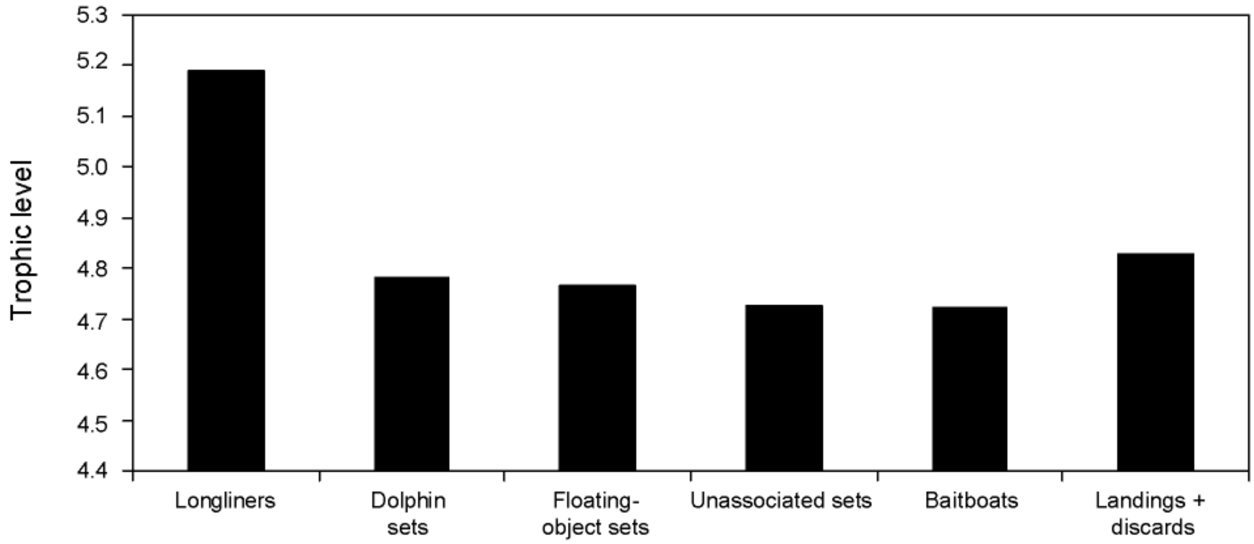

FIGURE 6. Average trophic levels of the catch (landings and discards) by the surface and longline fisheries in the eastern tropical Pacific Ocean during 1993-1997.

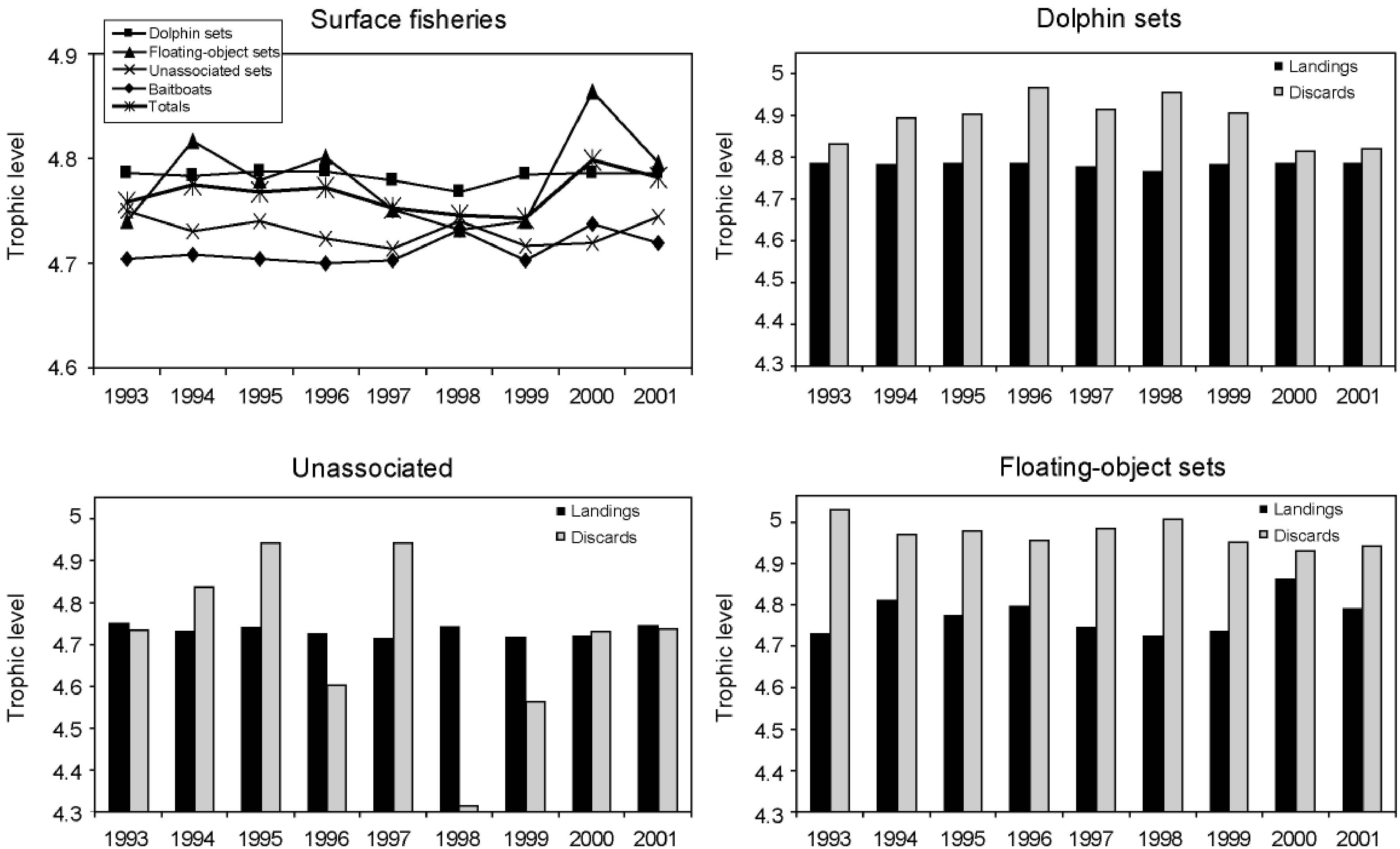

FIGURE 7. Trophic-level estimates of the total catches (panel labeled "Surface Fisheries"), and landings and discards by the various purse-seine set types in the ETP.

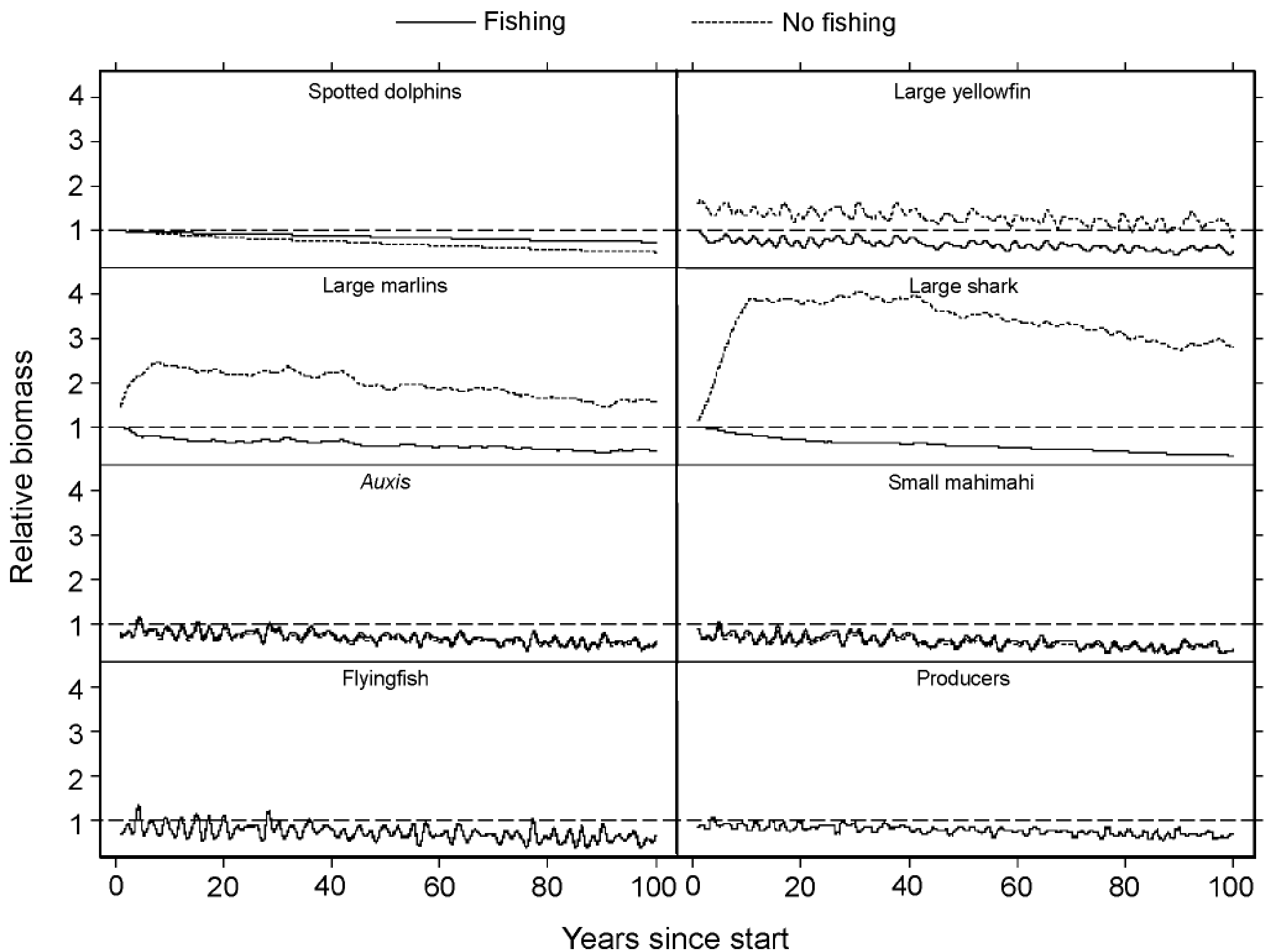

FIGURE 8. The simulated effects of global warming on components which have direct trophic connections with *Auxis* spp. The simulations were forced with mean SST anomalies predicted by the Max Planck Global Climate Model (Timmermann *et al.* 1999). Simulations with "fishing" have F = average F during 1993-1997, and simulations with "no fishing" have $F = 0$.

TABLE 1. Food-web components of the pelagic ETP ecosystem model. Size ranges are listed for taxa that are separated into small and large ontogenetic groups. The common names do not necessarily include all the species in the corresponding model group.

Group	Taxa	Common names	Size range
Pursuit birds	Fregatidae, Sulidae, Laridae, Procellariidae, Stercorariidae	Frigatebirds, Boobies, Terns, Shearwaters, Petrels, Jaegers	
Grazing birds	Oceanitidae, Phalaropodidae	Storm petrels, Phalaropes	
Baleen whales	*Balaenoptera musculus, B. edeni*[1]	Blue, Bryde's whale[1]	
Toothed whales	*Tursiops, Grampus, Steno, Globicephala, Peponocephala, Feresa, Pseudorca, Orcinus, Zyphius, Mesoplodon, Kogia, Physeter*	Dolphins: bottlenose, Risso's, rough-toothed. Whales: pilot, pygmy killer, false killer, killer, goose-beaked, beaked, pygmy sperm, sperm	
Spotted dolphins	*Stenella attenuata*	Spotted dolphin	
Mesopelagic dolphins	*Stenella longirostris, Stenella coeruleoalba, Delphinus delphis, Lagenodelphis hosei*	Spinner dolphin, striped dolphin, common dolphin , fraser's dolphin	
Sea turtles	*Lepidochelys olivacea, Chelonia mydas, Caretta caretta*	Olive Ridley, green sea, loggerhead	
Yellowfin tuna (large and small)	*Thunnus albacares*	Yellowfin tuna	Sm. <90 cm Lg. $\geq$ 90 cm
Bigeye tuna (large and small)	*Thunnus obesus*	Bigeye tuna	Sm. <80 cm Lg. $\geq$ 80 cm
Marlins (large and small)	*Makaira indica, M. mazara, Tetrapturus audax*	Black marlin, blue marlin, striped marlin	Sm. <150 cm Lg. $\geq$ 150 cm
Sailfish (large and small)	*Istiophorus platypterus*	Sailfish	Sm. <150 cm Lg. $\geq$ 150 cm
Swordfish (large and small)	*Xiphias gladius*	Swordfish	Sm. <150 cm Lg. $\geq$ 150 cm
Mahimahi (large and small)	*Coryphaena hippurus, C. equiselis*	Common dolphinfish, pompano dolphinfish (mahimahi)	Sm. <90 cm Lg. $\geq$ 90 cm
Wahoo (large and small)	*Acanthocybium solandri*	Wahoo	Sm. <90 cm Lg. $\geq$ 90 cm
Sharks (large and small)	*Sphyrna* spp., *Alopias* spp., *Isurus oxyrinchus, Carcharhinus* spp. (4 species), *Prionace glauca, Nasolamia velox*	Hammerhead, thresher, mako, blacktip, silky, oceanic whitetip, bull, blue, whitenose	Sm. <150 cm Lg. $\geq$ 150 cm
Rays	*Manta birostris*	Manta ray	
Skipjack tuna	*Katsuwonus pelamis*	Skipjack tuna	
Auxis spp.	*Auxis thazard, A. rochei*	Frigate and bullet tuna	
Bluefin tuna	*Thunnus orientalis*	Pacific bluefin tuna	
Misc. piscivores	*Euthynnus lineatus, Sarda orientalis, S. chiliensis,* various Carangidae, Gempylidae	Black skipjack, striped bonito, green jack, pilotfish, jack mackerel, rainbow runner, greater amberjack, snake mackerel	
Flyingfishes	Primarily: *Exocoetus* spp., *Hirundichthys* spp., *Prognichthys* spp., *Oxyporhamphus micropterus*	Flyingfishes	

TABLE 1. (continued)

Group	Taxa	Common names	Size range
Misc. epipelagic fishes	Primarily: Clupeidae, Nomeidae, Balistidae, Ostraciidae, Tetraodontidae, Diodontidae, *Scomber japonicus, Scomberomorus sierra*, Engraulidae	Sardines, herrings, driftfishes, triggerfishes, filefishes, spiny boxfish, oceanic puffer, porcupine fish, chub mackerel, sierra, anchovies	
Misc. mesopelagic fishes	Primarily: Phosichthyidae, Myctophidae	Bristlemouths, lightfishes	
Cephalopods	Primarily: Argonautidae, Octopoteuthidae, Thysanoteuthidae, Ommastrephidae, Enoploteuthidae	Pelagic octopods, argonauts, squids	
Crabs	*Pleuroncodes planipes, Portunus xantusii, Euphylax robustus*	Red crabs, pelagic crabs	
Secondary consumers	Copepods (carnivorous), misc. micro/meso zooplankton, chaetognaths, pteropods, euphausiids, larval fishes		
Primary consumers	Copepods (herbivorous), flagellates, infusorians, ciliates, nauplii and copepodids, heterotrophic dinoflagellates, heterotrophic nanoflagellates, larval euphausiids		
Producers	Phytoplankton, bacteria		

1. Other baleen whales occur seasonally in the model area, but they do not feed there (S. Reilly, NOAA, NMFS, La Jolla, California, U.S.A., personal communication; M. Scott, IATTC, La Jolla, California, U.S.A., personal communication), so they were not included in the model.

TABLE 2. Results of the sensitivity analysis for the ETP Ecosim simulations, including the effect of 20%, 30%, and 50% changes of the *P/B*, *Q/B*, and *EE* parameters for cephalopods and *Auxis* spp. on the sum of squares (SS) of the model's fit to catch per day's fishing data for yellowfin tuna.

Parameter	Multiplier	Initial value	Modified value	SS	% change in SS
			Cephalopods		
P/B	+0.2	2.0	2.4	2.2357	-0.22
P/B	-0.2	2.0	1.6	2.4269	8.32[1]
P/B	+0.3	2.0	2.6	2.2392	-0.06
P/B	-0.3	2.0	1.4	3.8030	69.74[1]
P/B	+0.5	2.0	3.0	2.2503	0.44
P/B	-0.5	2.0	1.0	--[2]	
Q/B	+0.2	7.0	8.4	2.2136	-1.20[1]
Q/B	-0.2	7.0	5.6	2.2614	0.93
Q/B	+0.3	7.0	9.1	2.1667	-3.30[1]
Q/B	-0.3	7.0	4.9	2.2713	1.38
Q/B	+0.5	7.0	10.5	3.2558	45.31[1]
Q/B	-0.5	7.0	3.5	2.2900	2.21
EE	+0.2	0.85	1.02	2.2563	0.70[3]
EE	-0.2	0.85	0.68	2.1809	-2.66[1]
EE	-0.3	0.85	0.595	2.5578	14.16[1]
EE	-0.5	0.85	0.425	--[2]	
			Auxis spp.		
P/B	+0.2	2.5	3.0	2.3053	2.89
P/B	-0.2	2.5	2.0	2.3467	4.74[4]
P/B	+0.3	2.5	3.25	2.3586	5.27
P/B	-0.3	2.5	1.75	2.7691	23.59[1,4]
P/B	+0.5	2.5	3.8	2.4959	11.40
P/B	-0.5	2.5	1.3	--[2]	
Q/B	+0.2	25.0	30	2.3224	3.65[4]
Q/B	-0.2	25.0	20	2.3234	3.70
Q/B	+0.3	25.0	32.5	2.4556	9.60[1,4]
Q/B	-0.3	25.0	17.5	2.4272	8.33
Q/B	+0.5	25.0	37.5	3.3352	48.86[1,4]
Q/B	-0.5	25.0	12.5	2.7900	24.53
EE	+0.2	0.95	1.14	2.2453	0.21[3]
EE	-0.2	0.95	0.76	2.3444	4.64[4]
EE	-0.3	0.95	0.67	2.6630	18.85[1,4]
EE	-0.5	0.95	0.48	--[2]	

1 The *EE* for miscellaneous mesopelagic fishes is slightly greater than 1.0 for this parameterization.

2 The model could not balance with this modified parameter value.

3 Inputted *EE* of 1.0 because *EE*>1.0 cannot be inputted.

4 The *EE* for small yellowfin tuna is slightly greater than 1.0 for this parameterization.

TABLE 3. Variance ratios from the global-warming simulations by Watters *et al.* (manuscript). They treated the two levels of *F* used in these simulations (*F* = average *F* during 1993-1997, and *F* = 0) as random effects and estimated the fraction of the total variation in the two trajectories predicted for each ecosystem component that was explained by differences in *F*. These variance ratios were estimated by maximum likelihood, and ranged from 0 (for the producers) to about 0.9 (for predators like large sharks and large swordfish). Relatively low variance ratios were interpreted as indicators of bottom-up control and relatively high ratios as indicators of top-down control. In general, forage components (*e.g. Auxis* and Flyingfish) were controlled more from the bottom up, and predators (*e.g.* large sharks and large marlins) were controlled more from the top down. Marine mammals were an exception to the latter result.

Group	Hypothesis 1	Hypothesis 2
Axis of the *Auxis*		
Lg Sharks*	0.918	0.907
Lg Marlins	0.906	0.916
Lg Yellowfin	0.848	0.692
Spotted Dolphins	0.288	0.102
Sm Mahimahi	0.051	0.015
Auxis	0.053	0.025
Flyingfish	0.005	0
Producers*	0	0
Axis of the Squid		
Lg Swordfish	0.922	0.910
Lg Bigeye	0.786	0.734
Mesopelagic Dolphins	0.306	0.132
Cephalopods	0.001	0
Misc. Mesopelagic Fish	0	0

* These components are members of both axes.