Analyzing pelagic food webs leading to top predators in the Pacific Ocean: A graph-theoretic approach

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ABSTRACT

This work examined diet data from studies of top pelagic predators from three large regions of the equatorial and South Pacific Ocean. Food webs of each of these three systems were found to have relatively high species diversity, but in contrast to other marine systems, relatively low connectance. Food webs were examined using graph-theoretic methods, which included aggregating species based on food-web relationships and identification of potentially influential species. Species aggregations were used to construct simplified qualitative models from each region's food web. Models from each region were then analyzed to make predictions of response to climate change for six commercially important species: mahi mahi, skipjack tuna, albacore tuna, yellowfin tuna, bigeye tuna, and swordfish. We found little commonality in the structure of the three food webs, although the two regions in the equatorial Pacific had food webs composed of four predation tiers, as defined by network levels of predation, whereas the southwestern region had only three predation tiers. We also found no consistent pattern in the predicted outcomes of the perturbations, which underlines the need for detailed trophic databases to adequately describe regional pelagic ecosystems. This work demonstrates that food-web structure will be central to understanding and predicting how top pelagic predators, and the ecosystems in which they are embedded, will respond to climate change.

1. Introduction

Open waters of the Pacific Ocean support major fisheries for tunas and billfishes, the impacts of which have been an important and ongoing focus of research (Sibert et al., 2006). However, given the IPCC (2007) projections for future ocean warming, environmental change may become equally important in determining the status of these and other top pelagic predators. Ocean warming could impact top pelagic predators in a number of ways. One is through direct physiological responses of predators to increasing water temperature (Sharp and Dizon, 1978; Boyce et al., 2008). Tuna species (see common names in Table 1) that are more tolerant of warmer temperatures (e.g., *Katsuwonus pelamis* and *Thunnus albacares*) could expand their range, whereas the ranges of tunas that prefer colder temperature (e.g., *T. thynnus* and *T. maccoyii*) would likely contract (Hobday, this issue). Also, an increase in

ocean temperature will likely have an important impact on the growth and reproduction of prey species that have rapid rates of turnover. In particular, cephalopods are projected to increase in population abundance in warmer ocean environments (Jackson, 2004; Jackson and Domeier, 2004). Alternatively, shifts in the distribution of prey and predator species in response to ocean warming (Pearcy and Schoener, 1987; Pearcy, 2002) can change the basic structure of the food web itself.

Considering the indirect effects of fishing mediated through the food web is a key component of ecosystem-based fisheries management (Link, 1999, 2002a). Ecosystem models based on trophic flows can be a powerful tool to assess and predict the consequences of impacts, such as fishery harvest or climate change (Walters et al., 1997; Christensen and Walters, 2004; Ulanowicz, 2004), and to identify species that are highly influential to the system's dynamics (Libralato et al., 2006). Construction of such models, however, requires the measurement (or estimation) of scores of model parameters and variables, a task which is especially difficult for pelagic ecosystems. Additionally, constructing models of

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Table 1
Common and scientific names referenced in the text.

Common name	Scientific name
Albacore tuna	*Thunnus alalunga*
Bigeye tuna	*Thunnus obesus*
Black marlin	*Istiompax indica*
Blue marlin	*Makaira nigricans*
Bullet tuna	*Auxis rochei rochei*
Frigate tuna	*Auxis thazard thazard*
Great barracuda	*Sphyraena barracuda*
Jack mackerel	*Trachurus declivis*
Longnose lancetfish	*Alepisaurus ferox*
Mahi mahi	*Coryphaena hippurus*
Northern bluefin tuna	*Thunnus thynnus*
Opah	*Lampris guttatus*
Pomfrets	*Brama* spp.
Rainbow runner	*Elagatis bipinnulata*
Scalloped hammerhead shark	*Sphyrna lewini*
Shortbill spearfish	*Tetrapturus angustirostris*
Shortfin mako shark	*Isurus oxyrinchus*
Silky shark	*Carcharhinus falciformis*
Skipjack tuna	*Katsuwonus pelamis*
Snake mackerel	*Gempylus serpens*
Spotted dolphin	*Stenella attenuata*
Striped marlin	*Tetrapturus audax*
Southern bluefin tuna	*Thunnus maccoyii*
Swordfish	*Xiphias gladius*
Tripletail	*Lobotes pacificus*
Wahoo	*Acanthocybium solandri*
Yellowfin tuna	*Thunnus albacares*

communities with many species requires that the system be simplified, so that a representative model has a smaller, more manageable, number of variables. The consequences of this simplification are far reaching. For instance, alternative models of the same system, based on different species aggregations, can result in opposing model dynamics (Metcalf et al., 2008).

In this work, we address these challenges through a graph-theoretic approach to analyze the structure of pelagic marine food webs, to aggregate species for the purpose of building simplified models of these systems, and to assess and make predictions about the qualitative dynamics of the models. Central to our approach is the concept of community (or network) structure, which, within the context of a food web, can be defined graphically as the predator and prey species (nodes) and their interactions (links). The network properties of a food web provide the essential means to address a number of graph-theory problems common to disciplines other than ecology. For instance, identifying highly influential nodes in a social network (Borgatti, 2006) has relevance to ecological systems through the concept of keystone species (Paine, 1966, 1969; Mills et al., 1993; Power et al., 1996; Jordán et al., 2006) or wasp–waist species (Rice, 1995). Furthermore, while the problem of identifying equivalent roles of species in a food web was first elucidated in ecology (Elton, 1927), it has been addressed most rigorously through social-network theory (Merton, 1949; Boyd, 2002; Everett and Borgatti, 2002; Luczkovich et al., 2003). Finally, the problem of predicting how an ecosystem will respond to a perturbation was first posed in control theory through the analysis of signal-flow graphs (Mason, 1953, 1956). Levins (1974) built upon and extended this work in developing qualitative modelling as a means to explore the role of network structure in determining ecosystem dynamics.

Qualitative modelling allows one to address how a model's structure affects its dynamics. Quantitative models, in contrast, tend to focus on obtaining precise estimates of model parameters (Levins, 1998), and typically do not consider parametric uncertainty separate from model-structure uncertainty (Ferson, 1996; Regan et al., 2002). Nevertheless, model structure can exert an over-riding effect on modelling results (Dambacher et al., 2002),

exceeding even the influence of parameter values (Pascual et al., 1997). There is, however, much relevant information that can be gained from a qualitative analysis of system structure, and such analyses can provide an important basis for understanding system dynamics, and act as a complement to quantitative models (Levins, 1966).

Working from diet studies of top pelagic predators from three regions of the Pacific Ocean, we use tools from social-network theory to identify influential species in each food web, and to aggregate species with equivalent roles. These species aggregations are then used to develop qualitative models for each region. By perturbing an influential species that could be directly affected by ocean warming, we trace the effects to commercially important species, and examine commonalities and differences in predictions of how each of these systems will respond.

2. Materials and methods

2.1. Diet data

Datasets of predator diets were collected from the south-western Pacific Ocean (Young et al., 2009), and two equatorial regions, which we identify as the central-western (Allain, 2005) and central-eastern (IATTC, 2008) Pacific Ocean (Fig. 1). These regions totaled roughly 40 million km^2 (Table 2). Collection methods are outlined in Young et al. (2006), Allain (2003) and Olson and Galván-Magaña (2002). The datasets were combined in a unified format within a Microsoft® Office Access database, which is housed at the CSIRO Marine Laboratories, Hobart, Tasmania. Stomachs collected from long-line fisheries dominated the samples in the south- and central-western regions, while collections in the central-eastern region were entirely from purse-seine fishing (Table 2). In the central-western Pacific, there was complete overlap in prey types identified in stomachs of predators common to both long-line and purse-seine fisheries, with the exception that some prey fishes from the Carangidae and Engraulidae families were not found in long-line-caught predators. There was also a small amount of data collected from hand-line and troll fishing, but it too appeared similar to the data from stomachs collected in the long-line and purse-seine fisheries. Thus, diet data from all fishing methods were combined in the central-western region.

Next, raw data in each region were reduced by eliminating prey species that occurred only rarely (e.g., species noted only once); prey species were removed if they did not constitute at least 1% wet weight to the diet of at least one predator from that region. The resulting "reduced diet data" were taken to represent the more common, or not rare, species and were the starting point of our analyses. In this study, percent wet weight was defined as the weight of a particular taxon divided by the total weight of all prey taxa for a given predator multiplied by 100.

While rarely observed species were removed from the reduced diet data, there was also the need to exclude weak links, as subsequent network analyses and qualitative models treat all links in the network equally. We examined the effect on the food-web network of constraining food-web links to either ⩾1% or ⩾5% wet weight and subsequently removed any taxa that were isolated or not connected to the main network (isolates). We also examined the effect of removing prey whose taxonomic identification was poorly resolved (i.e., unidentified teleosts, cephalopods, and crustaceans). In all, four different representations of the diet data were considered. In deciding which representation of the food-web data to carry forward into subsequent network analyses and models, we sought to minimize the number of species removed from the food web.
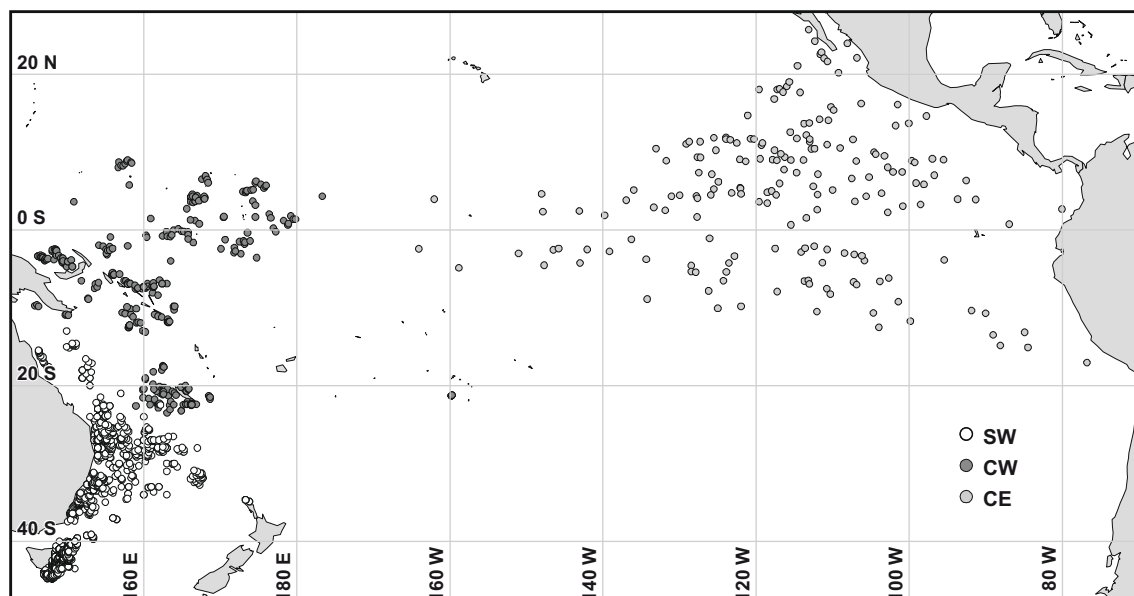
Fig. 1. Collection locations for diet studies in the south-western (SW) Pacific Ocean, and two equatorial regions that are identified as the central-western (CW) and central-eastern (CE) region.

Table 2
Numbers of stomachs collected from fisheries in diet studies of top pelagic predators in three regions of the Pacific Ocean (Fig. 1), with collection years and the area of each region sampled; listed are numbers of only the stomachs that contained prey.

	South-western	Central-western	Central-eastern
Fishery type			
Long-line	3102	1354	0
Purse-seine	0	322	3882
Hand-line or troll	0	15	0
Total	3102	1691	3882
Collection years	1999–2006	2001–2005	2003–2005
Sampled area (10^6 km^2)	3.7	8.2	27

Because data collections in each of the three regions of the Pacific Ocean were drawn primarily from stomachs of upper trophic-level pelagic predators, there was little or no detail of species from lower trophic levels, thus we emphasize that these data can only be considered as partial representations of the trophic relationships in each ecosystem. We hereafter refer to these as food webs, while recognizing that they contain only subsets of the components of the complete food webs.

2.2. Food-web graphs

The reduced diet data were used to construct predator–prey matrices for each region based on percent wet weight of prey. For each of the four representations of the data, predator–prey matrices were converted to 0, +1 matrices, from which were drawn food-web graphs, where each +1 matrix entry constituted a prey-to-predator link between graph nodes.

The food webs of each region were described by the number of species or taxa (S), interspecific links (L); link density ($D = LS^{-1}$), connectance ($C = LS^{-2}$), and percent apex predators (A)—i.e., species with no identified predator. A trophic level (TL) for individual predator species was calculated using the approach of Brodeur and Pearcy (1992), which follows Mearns et al. (1981), such that $TL = 1 + \sum_{i=1}^{s} TL_i P_i$, where TL_i is an assigned or previously calculated trophic level of prey taxon i, P_i is the proportion of that prey taxon in the predator's diet, and s is the number of prey species consumed by a predator. The calculated values of trophic level were continuous, while the assigned trophic levels for prey were discrete, and designated as 1 = primary producer, 2 = herbivore, 3 = primary carnivores (small fish and squid), and 4 = secondary carnivores (larger fish).

2.3. Key players

Defining influential nodes in a network graph can be theoretically approached by key player analyses (Borgatti, 2006) in two ways: fragmentation and reach. The fragmentation approach defines the extent to which an individual node or set of nodes maintains network cohesiveness. For example, if removal of one particular node fragments the network or produces isolates, and removal of any other node does not, then the first node would be defined as a key player for the system. The reach approach asks to what extent a node or set of nodes is connected to surrounding nodes in the network, and proceeds by determining which node or combination of nodes can reach the greatest number of other nodes in the network through a specified number of links. These two methods of identifying key players have been shown to capture a wide array of indices that describe the positional importance of nodes in food-web topologies (Jordán et al., 2006). Key player analyses are available in Analytic Technologies' KeyPlayer software at http://www.analytictech.com/.

A range of criteria can be applied to the above key player definitions. For the fragmentation method, the criteria can be adjusted to consider what subset of n number of nodes, when removed, maximizes network fragmentation. Here, we chose to consider identification of key players by the fragmentation method through removal of a single node. The reach method also considers a subset of n nodes that can reach the greatest number of other nodes, but additionally it considers the number of links allowed in the reach length. Key players were identified by the reach method through three different combinations of criteria: through either one or two nodes with a link length of one, or through two nodes with a link length of two. These criteria were applied to each of the three regional network graphs created with a constraint of $\geqslant 1\%$ wet weight, and also to a separate set of graphs that were produced from a $\geqslant 5\%$ wet-weight constraint. This latter set of analyses addresses the sensitivity of the key player results to removal of weak links, which have been found to be an important factor in studies of critical nodes in food-web networks (Allesina et al., 2006).

Species that were identified as key players were considered as candidates for perturbation scenarios. For these scenarios, we were interested in finding key players that were common to the three regions, and which were likely to be directly affected by ocean warming scenarios (e.g., Hobday, this issue).

2.4. Network aggregation

Simplifying food webs with many species to a small number of groups can proceed by various aggregation algorithms. Here, we employed the regular equivalence (REGE) algorithm developed in social-network theory (Boyd, 2002; Everett and Borgatti, 2002) to define the trophic-role similarity (Luczkovich et al., 2003) of species within each regional food web. We used the REGE algorithm in Analytic Technologies' UCINET software (available at http://www.analytictech.com/). The REGE algorithm differs from traditional diet-only based measures of similarity (e.g., Euclidean distance, Bray-Curtis) through its consideration of a whole-of-network topology, such that an organism's role in the wider community is defined not only by its prey but also by its predators—sensu Elton's (1927) niche. Metcalf et al. (2008) compared the performance of ecosystem models constructed through use of the REGE algorithm with models of the same system based on aggregations using Euclidean distance and Bray–Curtis measures of trophic similarity. Errors in predictions were minimized in models based on aggregations from the REGE algorithm.

For each food web, a level of aggregation was chosen that did not increase intraspecific (cannibalistic) or intragroup predation links beyond the number already present in the reduced diet data. In displaying the network structure of the aggregated systems, we wanted to emphasize the structural hierarchy of upper-level predators independently of their trophic level, and thus allocated a predation-tier designation, T_n, to each group, such that a group in predation tier n was a predator of at least one group in level $n + 1$, and groups in the lowest level (i.e., n = maximum) were not predators of any other group in the system.

2.5. Qualitative models and predictions of perturbation response

The aggregated food-web networks provided the basis for the development of qualitative models for the pelagic ecosystem of each region. Qualitative models are constructed from the sign of direct effects between model variables (Dambacher et al., 2002). Working from the aggregated food-web networks for each region, qualitative models were developed by converting the 0, +1 matrices associated with each food web into a community matrix $°\mathbf{A}$ with 0, +1, −1 entries. This was done by transferring all +1 elements of the predator prey matrix to $°\mathbf{A}$, setting each $°a_{ii} = -1$ (self-regulation), and for each $°a_{ij}$ = +1 (prey-to-predator link) in $°\mathbf{A}$ setting $°a_{ji} = -1$ (predator-to-prey link). Next, we derived qualitative predictions of the change in abundance due to a press perturbation (Dambacher et al., 2002, 2005). A press perturbation occurs where there is a sustained change in circumstance that causes a species to have a change in its rate of birth or death. Positive press perturbations involve an increase in a rate of birth, or a decrease in a rate of death for one of the species or variables in a model system while negative press perturbations reflect the opposite (a decreased birth rate or an increased death rate). Predictions of the response of other species in the model system depend on the sign structure of $°\mathbf{A}$, and are mediated by the summation of all direct and indirect effects that occur via interaction pathways that emanate from the perturbed variable. Predictions of the direction of a change in abundance are calculated through the adjoint of the negative community matrix, $\text{adj}(-°\mathbf{A})$. An ambiguous prediction occurs where there is a mix of both positive- and negative-signed pathways (or effects) leading from an input variable to a

response variable. These predictions can be afforded a degree of sign determinacy if there is a numerical dominance of effects with one sign over the other (Dambacher et al., 2003; Hosack et al., 2008). Software and computer programs for qualitative analysis of the community matrix are available from *Ecological Archives* at http://esapubs.org/archive/ecol/E083/022/.

3. Results

3.1. Diet studies

For the three diet studies of pelagic predators, a total of 651 taxa were distinguished in the raw data among the three regions of the Pacific Ocean. Removal of prey taxa that occurred only rarely in samples resulted in a major reduction in the diet data (Table 3, representation B), with a reduction of 62% of prey taxa in the south-western region, 56% in the central-western region, and 32% in the central-eastern region. After removal of rarely occurring prey species, we also removed links with less than 1% wet weight and isolates (Table 3, representation C), which left a total of 248 taxa for all three regions; Appendix A provides a complete listing of these taxa. Of the 248 taxa, there were 180 genus-level identifications and 133 species-level identifications. There were 23 taxa that were common to all three datasets, of which 14 were identified to species-level. All of these 14 species were upper trophic-level pelagic predators, and included: albacore tuna, bigeye tuna, skipjack tuna, yellowfin tuna, black marlin, blue marlin, shortbill spearfish, striped marlin, shortfin mako shark, silky shark, scalloped hammerhead shark, mahi mahi, snake mackerel, and wahoo; Table 1 gives a listing of the common and scientific names or organisms referenced in the text.

Identifications resolved at the species level ranged from 45% to 66% of the total number within each food web (Table 4). Identifications resolved at the genus or species levels ranged between 69% and 75%. Teleosts were the most commonly identified taxon in all three food webs, followed by either molluscs or chondrichthians.

All three food webs were dominated by species with trophic-level designations between 3.5 and 4.5 (Fig. 2). In each food web, the maximum trophic level of a species was 4.6 (i.e., striped marlin and swordfish), while the mean trophic level was nearly the same in all three regions—3.6 in the south-western region and 3.5 in both the central regions.

3.2. Food-web structure and link strength

Constraining food-web links to ⩾1% or ⩾5% wet weight and then omitting isolated species or unidentified taxa reduced the number of nodes and links in all three networks. These reductions, however, had only a small effect on the connectance within any of the networks, and connectance generally remained ⩽3% (Table 3). The link density was generally low and similar among the regions, and ranged between 1.2 and 2.9 across all food-web representations (Table 3). The percentage of apex predators was relatively high in all three food webs and was greatly affected by the removal of weak links, isolates, and unidentified species. For the different food-web representations presented, the proportion of apex predators in the three regions ranged from a low of 9.8% to 20% in the raw diet data, to a high of 50% to 67% where links were constrained to ⩾5% wet weight and unidentified taxa were removed.

3.3. Aggregation

When links were constrained to ⩾5% wet weight or when unidentified taxa were removed, the food webs were substantially reduced in size. We therefore chose to create aggregated food webs

Table 3
Descriptors of different representations (A–G) of the food webs from three regions of the Pacific Ocean, including number of species or nodes (S), interspecific (predation) links (L), link density ($D = LS^{-1}$), percent connectance ($C = LS^{-2}$) and percent apex predators (A) (i.e., species or groups that lack predators); in parentheses are the number of intraspecific (cannibalistic) predation links. Food webs were defined by varying the constraint on link strength and inclusion of unidentified cephalopods, teleosts, and crustaceans. The reduced diet data set was created by omitting prey that did not constitute at least 1% wet weight to the diet of at least one predator species in a region. In representation C–F, species not linked to the main food web (isolates) were deleted; representation C and G respectively correspond to the food webs of Figs. 2 and 3, and G was formed from aggregating taxa with similar predator–prey relationships.

Food web representation		South-western	Central-western	Central-eastern
A. Raw diet data	S	320	389	143
	L	690 (3)	1110 (6)	345 (4)
	D	2.2	2.9	2.4
	C	0.67%	0.73%	1.7%
	A	10%	9.8%	20%
B. Reduced diet data	S	122	165	97
	L	225 (2)	335 (2)	227 (3)
	D	1.8	2.0	2.3
	C	1.5%	1.2%	2.4%
	A	27%	23%	29%
C. Links ⩾1% wet weight	S	109	142	91
	L	202 (2)	303 (2)	215 (3)
	D	1.9	2.1	2.4
	C	1.7%	1.5%	2.6%
	A	30%	27%	31%
D. Links ⩾1% wet weight Without unidentified taxa	S	101	126	79
	L	164 (2)	231 (2)	154 (3)
	D	1.6	1.8	1.9
	C	1.6%	1.5%	2.5%
	A	33%	30%	35%
E. Links ⩾5% wet weight	S	61	96	72
	L	86 (2)	151 (2)	124 (3)
	D	1.4	1.6	1.7
	C	2.3%	1.6%	2.4%
	A	54%	40%	39%
F. Links ⩾5% wet weight Without unidentified taxa	S	49	75	56
	L	57 (2)	92 (2)	81 (3)
	D	1.2	1.2	1.4
	C	2.4%	1.6%	2.6%
	A	67%	51%	50%
G. Aggregated from C	S	24	24	23
	L	31 (2)	40 (2)	51 (3)
	D	1.3	1.7	2.2
	C	5.4%	7.1%	9.6%
	A	42%	29%	35%

Table 4
Number (percentage) of taxa identified in the pelagic food webs from three regions of the Pacific Ocean by taxonomic resolution and major categories; based on the food web representation C in Table 3.

	South-western		Central-western		Central-eastern	
Taxonomic resolution						
Species	62	(57)	64	(45)	60	(66)
Genus	20	(18)	34	(24)	7	(8)
Family (or supra-family)	27	(25)	44	(31)	24	(26)
Taxonomic category						
Algae	0	(0)	0	(0)	1	(1)
Gelatinous zooplankton	1	(1)	3	(2)	2	(2)
Mollusca	25	(23)	24	(17)	9	(10)
Crustacea	7	(6)	11	(8)	7	(8)
Other invertebrates	0	(0)	0	(0)	3	(3)
Chondrichthyes	9	(8)	11	(8)	9	(10)
Teleostei	66	(61)	93	(65)	59	(65)
Mammalia	1	(1)	0	(0)	1	(1)
Total identified	109		142		91	

from diet data based on a constraint of ⩾1% wet weight and inclusion of unidentified taxa. In choosing a level of aggregation that avoided additional intragroup predation, we arrived at food webs for the three regions with either 23 or 24 nodes (G in Table 3, Fig. 3). The process of aggregation resulted in a relatively large increase in connectance, as much as 4.7 times greater for the central-eastern food web. This increase was not uniform across the food webs of the three regions, and the rank order of their connectance
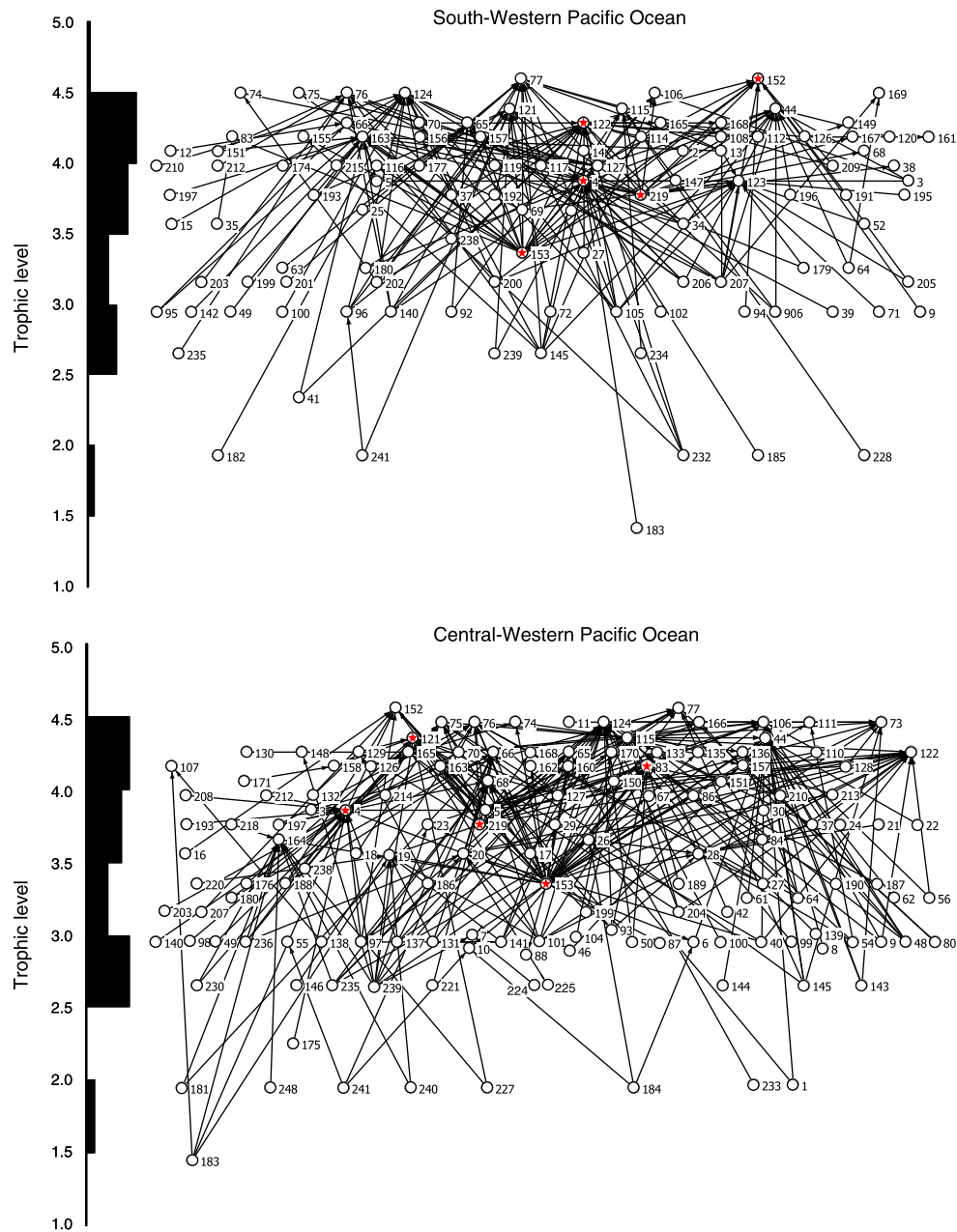
Fig. 2. Pelagic food webs leading to top predators in three regions of the Pacific Ocean (Fig. 1, based on C of Table 3). Arrows lead from prey-to-predators and represent a level of consumption that is ⩾1% wet weight for a given predator. Histograms denote relative frequency and position of trophic levels in food web. Numbers refer to sequence number of taxa listed in Appendix A. Graph nodes with a star (★) are taxa identified as key players in analyses summarized in Tables 5–4: longnose lancetfish, 44: mahi mahi, 83: opah, 85: tripletail, 115: skipjack tuna, 121: albacore tuna, 122: yellowfin tuna, 219: unidentified cephalopods, 152: swordfish, and 153: unidentified teleosts.

changed, with the central-western food web assuming an intermediate level of connectance, whereas it had the lowest level prior to being aggregated.

There was a general increase in the mean trophic level of the predation tiers within the aggregated food webs; however, there was little if any distinction between the trophic level of the top two tiers. While there was a difference of 0.4 between the top two tiers in the central-western region, this difference was matched by a standard deviation in the second predation tier that overlapped the mean of the first.

The aggregated food web of the south-western Pacific had a network structure composed of three predation tiers, while the food webs of the central-western and central-eastern regions were four tiered (Fig. 3). The lowest predation tier in all regions was com-

posed of groups containing a range of squid, crustacea, and small-sized fishes, while the highest predation tiers were generally dominated by large predatory fishes and sharks.

The aggregated food web of the south-western Pacific (Fig. 3) had a single group at its highest tier (group 2 in Appendix A), which contained shortfin mako and hammerhead sharks. The second predation tier was composed of suite of mid-sized predators. Of note is group 1, which is the prey of group 2 and was composed of snake mackerel, yellowfin tuna, and skipjack tuna; the latter two species being identified as key players (Table 5).

The food web of the central-western Pacific is topped by three groups, which generally include large predators, such as billfish, swordfish, and sharks, but also mid-sized predators such as wahoo, mahi mahi, and the great barracuda. The second predation tier had
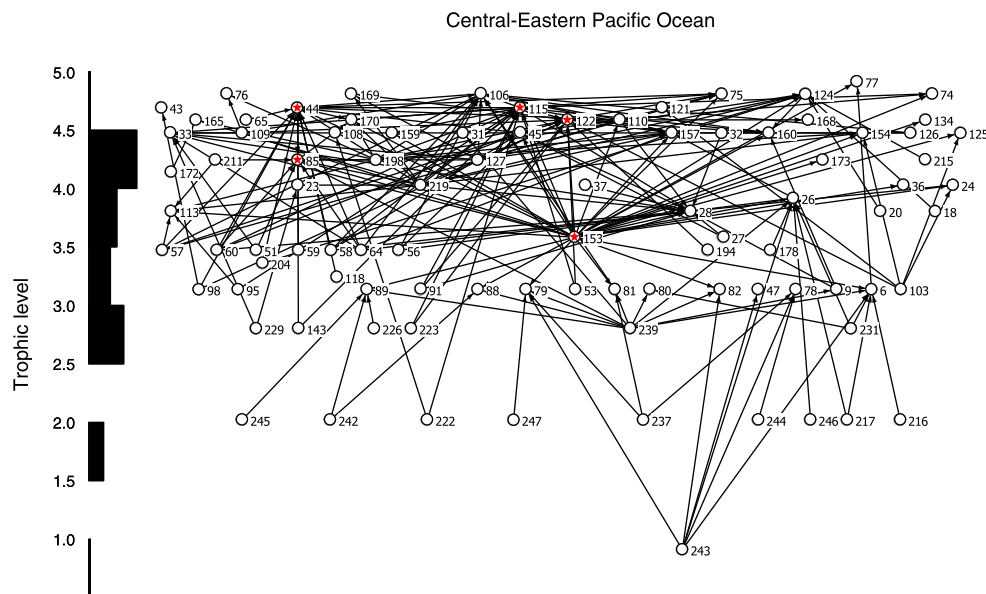
Central-Eastern Pacific Ocean

Fig. 2 (*continued*)

four groups that contained tunas, opah, and longnose lancetfish. In tier 3 were a mix of sharks and medium-size fishes that included pomfrets and skipjack tuna.

The aggregated food web of the central-eastern region was visibly more complex than those of the other two regions (Fig. 3) and had the highest level of connectance (G in Table 3). It also had three groups at the highest predation tier, two of which feed at tiers 2, 3 and 4. The groups in the first tier are generally composed of billfish and sharks. The next predation tier had three groups that contained various mid-sized predators, and included the rainbow runner and the key players tripletail, mahi mahi and yellowfin tuna. Tier 3 includes bullet, frigate, bigeye and skipjack tunas, and a range of other medium-sized predators.

3.4. Key players

Ten taxa were identified as key players through the reach and fragmentation methods (Table 5, Fig. 2). Unidentified teleosts were classified as key players in all three food webs, while unidentified cephalopods and longnose lancetfish were key players in the south- and central-western food webs, and yellowfin tuna were key players in the south-western and central-eastern food webs. Key players were distributed through the middle and lower predation tiers, but were lacking from the highest predation tier of the food webs (Fig. 3). Key players were sometimes, but not always, aggregated within the same groups; unidentified teleosts and cephalopods, however, were always aggregated within the same group.

3.5. Qualitative predictions

We selected yellowfin tuna to perturb in the qualitative models because it was identified as a key player in two of the three regions and is projected to increase its range or abundance in ocean warming scenarios (Hobday, this issue). A positive press perturbation to yellowfin tuna produced varied responses in the abundance of commercially important fishes for each model system (Table 6), though predictions generally had a high degree of sign determinacy–i.e., >95% probability of sign being correct. A perturbation to yellowfin tuna in the south-western region and the central-eastern region was predicted to lead to a decrease in the abundance of

commercial species that were not within the same group as yellowfin tuna (i.e., in the south-western region, decreases were predicted for mahi mahi, albacore and bigeye tunas, and swordfish; in the central-eastern region decreases were predicted for skipjack, albacore, and bigeye tunas). Within the central-western region, however, commercial species not sharing group membership with yellowfin tuna were predicted to increase for two species (mahi mahi and swordfish), and decrease for two others (skipjack and albacore tunas).

4. Results

We have used a graph-theoretic approach to examine the structure of complex pelagic food webs derived from samples of fisheries catches from across the Pacific Ocean (Table 2). We identified potentially influential species, and simplified the food-web data for the purpose of developing qualitative models of regional pelagic ecosystems. Ten key players were identified from the three regions, but none were common to all three regions except unidentified teleosts (Table 5). We found that in the south-western and central-eastern Pacific Ocean, a positive press perturbation to the key player yellowfin tuna can be predicted to negatively impact the abundance of a number of commercially important fishes in the region. In the central-western region, however, there was both a positive and a negative change in abundance predicted for the other commercial fishes. In contrast to our expectations, sharks, which have been considered as keystone predators in some studies (Hinman, 1998; Stevens et al., 2000 as discussed in Kitchell et al., 2002), do not appear to play a key role in the Central Pacific, as also demonstrated by Kitchell et al. (2002). In their study of the pelagic food webs of the Central Pacific, Kitchell et al. (1999), using a compartment-flow type model, could not identify any keystone species. Complementary to our key player results for the central-eastern region (Table 5), however, Kitchell et al. (1999) singled out yellowfin and skipjack tunas as the most important components of the system in terms of diet diversity, but also in terms of biomass and rates of turnover.

The food web of the south-western region had only three predation tiers topped by a group with only shortfin mako and hammerhead sharks. In contrast, the other two regions had four tiers in which these sharks occupied either the first or the third predation
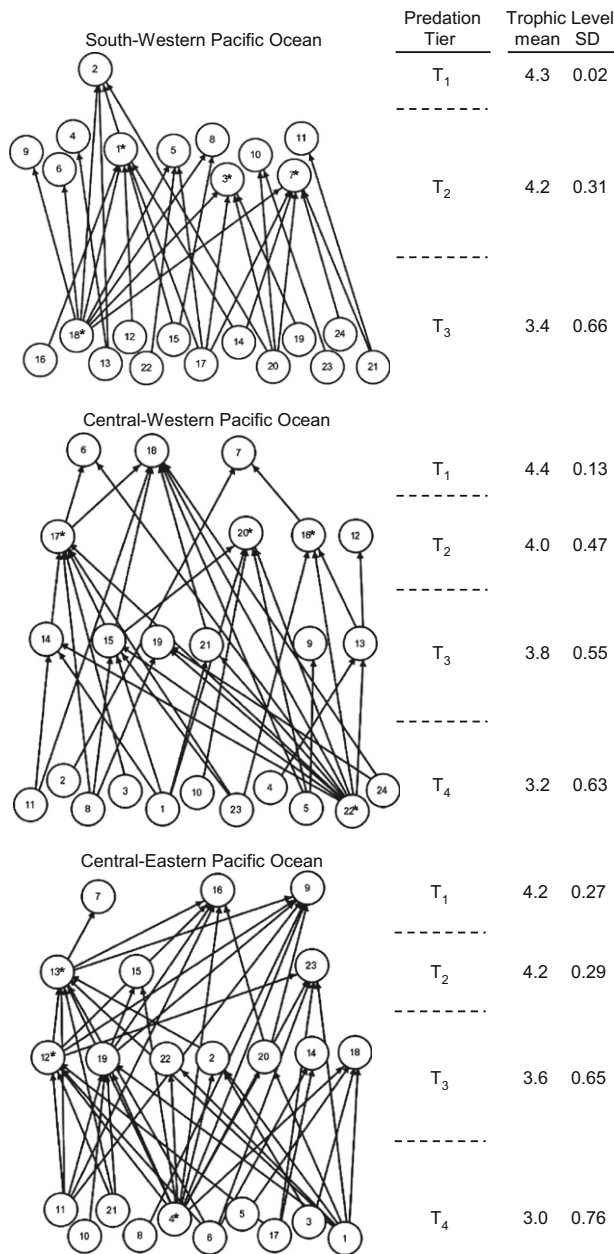
Fig. 3. Aggregated food webs of three regions of the Pacific Ocean (based on G of Table 3). Nodes represent groups of taxa with similar predator–prey relationships (Fig. 2; Appendix A) and are arranged in predation tiers (T_n) such that a group at level n is predator of at least one group at level $n + 1$, and a group at the lowest level (i.e., $T_{maximum}$) is not predator of any other group in the system. Groups with asterisks contain key players identified in Table 5. Shown for each tier are mean and standard deviation of trophic levels of taxa in each group. These network structures were used to create qualitative models of each pelagic ecosystem, which were used for perturbation analyses detailed in Table 6.

knowledge of food-web structure will thus be central to understanding and predicting how top pelagic predators and the open-ocean ecosystems in which they are embedded, will respond.

4.1. Comparisons with other marine food webs

The three pelagic food webs analyzed in this study show marked differences compared to the food webs described for four other marine ecosystems, which include an upwelling (Benguela) and a continental-shelf ecosystem (Northeast US shelf), both of which include pelagic and demersal species, and two Caribbean reef ecosystems (Table 7). In the pelagic food webs that we analyzed, the number of species falls within the range of these other ecosystems, but values of link density, and connectance are considerably less. This pattern is not a consequence of excluding rare species or weak links, as values of link density and connectance in the raw diet data are similarly low. The mean trophic level of the food webs analyzed in this study were roughly half a level higher than those reported from other marine systems, which likely reflects the aforementioned top-predator bias, and a resulting lack of resolution in lower trophic levels. Also, these differences in connectance could be driven by differences in taxonomic resolution. The representation of the food webs from our study that are compared in Table 7 lacked aggregations of trophically or functionally similar species, though they did include groupings defined by poorly resolved taxa (Table 4). Food webs composed of aggregated species groups are a common feature in other food webs, and have the potential to greatly affect link density (Martinez, 1991), but the effect of aggregation is expected to lower link density (Martinez, 1993). Hence, if the food webs in this study are relatively disaggregated, then they could be expected to have had comparatively higher, not lower, link densities. And while connectance can also be affected by the overall number of species in the web (Dunne, 2006), the three food webs analyzed in this study are of an intermediate size yet represent the lowest levels of connectance of any marine system compared. Thus, the relatively low levels of connectance reported here may reflect real characteristics of pelagic ecosystems; clearly, this is an area for future research.

4.2. Utility and limitations of the approach

This work was purely data-driven, in that we have only considered species and predator–prey interactions represented by data directly available from the catches of tuna and billfish fisheries in the three regions, and thus we did not, as is commonly done, include supplementary information from other studies and other regions. Also, we have adhered to constructing qualitative models from an aggregation algorithm based only on the structure of food-web graphs and have avoided a priori classifications based on size or functional attributes, such as whether a species inhabits the epi- or meso-pelagic habitats.

The food webs analyzed here are not meant to represent the entire pelagic ecosystem, rather they are only partial food webs defined by the diet of the ecosystem's upper trophic-level predators, as sampled from various fisheries. While the stomachs were collected from different fisheries, sometimes by different types of fishing gear, using different sampling schemes, and also processed in different laboratories, the three sets of diet data appear to generally have a similar level of taxonomic resolution (i.e., at genus level), and a similar distribution of major taxonomic categories (Table 4) and trophic levels (Fig. 2). Nevertheless, there is the likelihood that some of the differences noted in the comparisons can be attributed to different fishing methods that can impact the catch composition in terms of species (e.g., Alepisaurus are caught only by long-lines, rainbow runner only by purse-seines) and fish size (e.g., long-line caught tuna are usually larger

tier. Examination of the database revealed that in the south-western Pacific the diets of these sharks were dominated by tuna species, whereas in the other regions their diets were dominated by lower trophic-level species such as ommastrephid squid. Stable-isotope analysis of predator white-muscle tissues supports this lack of distinction between top- and mid-order predators in the south-western region (Revill et al., 2009).

The qualitative predictions from the three models generally illustrate the point that the response that a species might have to a change in ocean conditions depends on food-web structure. Given the high likelihood of ocean warming (IPCC, 2007), detailed

Table 5
Key players in the pelagic food webs of three regions of the Pacific Ocean. Key players were identified, through an array of criteria[a–h], by their role in fragmenting the food web if removed, or by how many other species can be reached through them in a specified number of links. Sequence numbers (Seq. no.) reference taxa in Appendix A and graph nodes of Fig. 2.

Kay player	Seq. no.	South-western	Central-western	Central-eastern
Longnose lancetfish	4	Reach[d]	Fragment[a] Reach[c]	[A]
Mahi mahi	44			reach[c]
Opah	83		Reach[g]	[A]
Tripletail	85	[A]	[A]	Reach[d]
Skipjack tuna	115			Fragment[e] Reach[g]
Albacore tuna	121		Reach[d]	
Yellowfin tuna	122	Fragment[a] Reach[b, c]		Reach[h]
Swordfish	152	Fragment[e] Reach[h]		[A]
Unidentified teleosts	153	Reach[c, d, f–h]	Fragment[e] Reach[b–d, f–h]	Fragment[a] Reach[b–d, f–h]
Unidentified cephalopods	219	Reach[g]	Reach[h]	

[a–h] Criteria applied in key player analyses: criteria a–d: food web links ⩾1% wet weight in diet of predator; criteria e–h food web links ⩾5% wet weight; criteria a and e: single species that if removed creates maximal fragmentation of food web; criteria b and f: single species reaching highest number of other species within one link; criteria c and g: two species reaching highest number of other species in one link; and criteria d and h: two species reaching highest number of other species in two links.
[A] Does not occur in food web.

Table 6
Qualitative change in abundances of commercially important species due to a positive perturbation to yellowfin tuna, as predicted by models of pelagic ecosystems for three regions of the Pacific Ocean (Fig. 3). Numbers denote membership in aggregated food web groups, as listed in Appendix A; those in parentheses are of species in groups that include yellowfin tuna.

Region	Predicted direction of change in abundance of commercial spp.					
	Mahi mahi	Skipjack tuna	Albacore tuna	Yellowfin tuna	Bigeye tuna	Sword-fish
South-western	– 7	+ (1)	– 7	+ (1)	– 3	– 7
Central-western	+ 18	– 15	– 16	+ (17)	+ (17)	+ 18
Central-eastern	+ (13)	– 2	– 20	+ (13)	– 19	[a]

[a] Swordfish not in central-eastern model.

Table 7
Descriptors of seven marine food-web networks, including number of species or graph nodes (S), link (L) density ($D = LS^{-1}$), percent connectance ($C = LS^{-2}$), mean trophic level ($\overline{TL}$), and percent apex predators (A), i.e., species or groups that lack predators. Food webs are arranged in ascending order of number of species. Food web descriptors of this study refer to representation C in Table 3.

	S	D	C (%)	$\overline{TL}$	A (%)	Source
Benguela	29	7.0	24	3.2	0	Yodzis (1998)[a]
Small Caribbean reef	50	11	22	2.9	0	Opitz (1996)[a]
North-east US shelf	79	18	22	3.1	4	Link (2002b)[a]
Central-eastern Pacific	91	2.4	2.6	3.5	31	This study
South-western Pacific	109	1.9	1.7	3.6	30	This study
Central-western Pacific	142	2.1	1.5	3.5	27	This study
Large Caribbean reef	245	14	5	3.1	0	Opitz (1996)[a]

[a] As reported by Dunne et al. (2004).

than 90 cm while purse-seine caught tuna can be as small as 40 cm). Data collections from the long-line fishery in the central-eastern region would help to resolve this question.

By limiting ourselves to a qualitative assessment of the diet data, we have nevertheless sought a general understanding of how pelagic ecosystems of these three regions are structured, and to develop hypotheses that can be explored and tested in quantitative models and other studies of these systems. The qualitative techniques employed here can be viewed as complementary to quantitative modelling approaches, such as compartment-flow type models, that account for the magnitude of trophic flows be-

tween species or species groups (Ulanowicz and Puccia, 1990; Christensen and Walters, 2004; Ulanowicz, 2004). The use of trophic-role similarity (Everett and Borgatti, 2002; Luczkovich et al., 2003) is an objective means of describing simplified aggregations of large complex food webs, and provides a basis for comparing the underlying structure of different ecosystems. A chief benefit of these qualitative approaches explored here is that they require less data, and while they lack precision in model parameters and predictions, they are nonetheless rigorous in describing the structure of an ecosystem and providing a basis for understanding its dynamics.

4.3. Future research

The scope of this study has been broad and rarely attempted in comparative studies of marine ecosystems. One of the challenges of this study was incorporating data from different fisheries with different sampling regimes, which has the potential to bias the representation of the predator and prey species in a food web. Nevertheless, our results suggest potentially important differences between three pelagic ecosystems of the equatorial and South Pacific Oceans, and these results can be used to inform the construction of quantitative ecosystem models for the three regions.

Perturbation scenarios for qualitative modelling, such as those involving ENSO and decadal regimes shifts, can be based on any context that directly affects the survival, growth or reproduction of a population. Such scenarios, however, require understanding

of the biology of the species concerned. The perturbation scenario with yellowfin tuna applied here was based on a projection of change in its distribution due to ocean warming (Hobday, this issue). Yellowfin tuna are generally considered to be a tropical species limited by cooler temperate waters (Block et al., 1997), and in the south-western region of the Pacific Ocean they are at or near the southern limit of their range (Young et al., 2001). Presumably ocean warming will be beneficial for this species such that its competitive advantage could increase. Our modelling results for the south-western region suggest that a positive press perturbation to yellowfin tuna could conceivably lead to a decline in the abundance of mahi mahi, albacore and bigeye tunas, and swordfish, and these effects are mediated indirectly through resource competition.

Finally, a conspicuous omission from all three food webs was fisheries exploitation, which has been identified as the keystone predator for at least the central Pacific Ocean (Kitchell et al., 1999). Incorporating fisheries into these qualitative analyses requires consideration of the main feedbacks that drive and regulate the fishing fleet, the market, and the ecosystem (Dambacher et al., 2009).

Acknowledgements

Appendix A

Table A1.

Table A1

Listing of 248 taxa identified in diet studies of top pelagic predators in the south-western (SW), central-western (CW) and central-eastern (CE) regions of the Pacific Ocean (Fig. 1), with calculated or assigned trophic level (TL). Based on representation C in Table 3. Sequence numbers (Seq. No.) correspond to graph nodes in Fig. 2 and group numbers refer to nodes in aggregated foodwebs of Fig. 3.

Seq. no.	Parent taxa	Family (or supra-family group)	Genus	Species	TL	Group no.		
						SW	CW	CE
1	Teleostei	Acanthuridae			2.00		11	
2	Teleostei	Acropomatidae	Apogonops	anomalus	4.10	12		
3	Teleostei	Alepisauridae	Alepisaurus	brevirostris	3.89	20	22	
4	Teleostei	Alepisauridae	Alepisaurus	ferox[‡]	3.89	3	17	
5	Teleostei	Alepisauridae	Alepisaurus	spp.	3.89	20	22	
6	Teleostei	Balistidae	Canthidermis	maculatus	3.00		21	19
7	Teleostei	Balistidae	Melichthys	niger	3.00		20	
8	Teleostei	Balistidae	Xenobalistes	spp.	3.00		24	
9	Teleostei	Balistidae			3.00	24	22	20
10	Teleostei	Balistidae, Monacanthidae[a]			3.00		20	
11	Teleostei	Belonidae	Tylosurus	spp.	4.50		24	
12	Teleostei	Belonidae			4.10	24		
13	Teleostei	Bramidae	Brama	brama	4.14	20		
14	Teleostei	Bramidae	Brama	orcini	4.14	19		
15	Teleostei	Bramidae	Brama	spp.	3.60	19		
16	Teleostei	Bramidae	Eumegistus	illustris	3.60		24	
17	Teleostei	Bramidae	Pteraclis	spp.	3.60		22	
18	Teleostei	Bramidae	Pterycombus	petersii	3.60		24	10
19	Teleostei	Bramidae	Taractichthys	longipinnis	3.60		20	
20	Teleostei	Bramidae			3.60		15	10
21	Teleostei	Carangidae	Alepes	spp.	3.80		3	
22	Teleostei	Carangidae	Atropus	atropos	3.80		24	
23	Teleostei	Carangidae	Caranx	sexfasciatus	3.80		21	23
24	Teleostei	Carangidae	Caranx	spp.	3.80		3	20
25	Teleostei	Carangidae	Decapterus	koheru	3.69	19		
26	Teleostei	Carangidae	Decapterus	macarellus	3.69		14	19
27	Teleostei	Carangidae	Decapterus	spp.	3.40	12	22	11
28	Teleostei	Carangidae	Elagatis	bipinnulata	3.59		17	9
29	Teleostei	Carangidae	Gnathanodon	speciosus	3.80		19	
30	Teleostei	Carangidae	Selar	spp.	3.89		3	
31	Teleostei	Carangidae	Seriola	lalandi	4.20			22
32	Teleostei	Carangidae	Seriola	peruana	4.20			8

Table A1 (*continued*)

Seq. no.	Parent taxa	Family (or supra-family group)	Genus	Species	TL	Group no.		
						SW	CW	CE
33	Teleostei	Carangidae	*Seriola*	*rivoliana*	4.20			13
34	Teleostei	Carangidae	*Trachurus*	*declivis*	3.61	17		
35	Teleostei	Carangidae	*Trachurus*	spp.	3.61	17		
36	Teleostei	Carangidae	*Uraspis*	*helvola*	3.80			23
37	Teleostei	Carangidae			3.80	15	22	8
38	Teleostei	Centrolophidae	*Centrolophus*	*niger*	3.95	9		
39	Teleostei	Chiasmodontidae	*Pseudoscopelus*	spp.	3.00	19		
40	Teleostei	Chiasmodontidae			3.00		22	
41	Teleostei	Clupeidae	*Sardinops*	*neopilchardus*	2.43	14		
42	Teleostei	(Clupeiformes)			3.20		24	
43	Teleostei	Coryphaenidae	*Coryphaena*	*equiselis*	4.37			14
44	Teleostei	Coryphaenidae	*Coryphaena*	*hippurus*[b]	4.37	7	18	13
45	Teleostei	Coryphaenidae			4.20			13
46	Teleostei	Diodontidae	*Cyclichthys*	*spilostylus*	3.00		24	
47	Teleostei	Diodontidae	*Diodon*	*holocanthus*	3.00			22
48	Teleostei	Diodontidae	*Diodon*	spp.	3.00		24	
49	Teleostei	Diodontidae			3.00	24	24	
50	Teleostei	Diretmidae			3.00		22	
51	Teleostei	Echeneidae	*Remora*	*remora*	3.30			21
52	Teleostei	Emmelichthyidae	*Emmelichthys*	*nitidus nitidus*	3.61	24		
53	Teleostei	Engraulidae	*Cetengraulis*	*mysticetus*	3.00			21
54	Teleostei	Engraulidae			3.00		8	
55	Teleostei	Ephippidae, Drepaneidae[a]			3.00		9	
56	Teleostei	Exocoetidae	*Cheilopogon*	spp.	3.30		22	11
57	Teleostei	Exocoetidae	*Exocoetus*	spp.	3.30			6
58	Teleostei	Exocoetidae	*Exocoetus*	*volitans*	3.30			11
59	Teleostei	Exocoetidae	*Hirundichthys*	*marginatus*	3.30			21
60	Teleostei	Exocoetidae	*Oxyporhamphus*	*micropterus*	3.30			11
61	Teleostei	Exocoetidae	*Oxyporhamphus*	spp.	3.30		24	
62	Teleostei	Exocoetidae	*Parexocoetus*	*brachypterus*	3.30		24	
63	Teleostei	Exocoetidae	*Parexocoetus*	spp.	3.30	12		
64	Teleostei	Exocoetidae			3.30	23	22	11
65	Teleostei	Gempylidae	*Gempylus*	*serpens*	4.25	1	20	21
66	Teleostei	Gempylidae	*Lepidocybium*	*flavobrunneum*	4.34	7	18	
67	Teleostei	Gempylidae	*Promethichthys*	*prometheus*	4.00		19	
68	Teleostei	Gempylidae	*Ruvettus*	*pretiosus*	4.08	9	20	
69	Teleostei	Gempylidae	*Thyrsites*	*atun*	3.74	24		
70	Teleostei	Gempylidae			4.25	17	20	
71	Teleostei	Gonostomatidae	*Gonostoma*	*elongatum*	3.00	24		
72	Teleostei	Hemiramphidae			3.00	24		
73	Teleostei	Istiophoridae	*Istiophorus*	*platypterus*	4.50		18	
74	Teleostei	Istiophoridae	*Istiompax*	*indica*	4.46	6	18	16
75	Teleostei	Istiophoridae	*Makaira*	*nigricans*	4.46	9	18	16
76	Teleostei	Istiophoridae	*Tetrapturus*	*angustirostris*	4.50	7	18	23
77	Teleostei	Istiophoridae	*Kajijia*	*audax*	4.58	3	18	15
78	Teleostei	Kyphosidae	*Kyphosus*	*analogus*	3.00			18
79	Teleostei	Kyphosidae	*Kyphosus*	*elegans*	3.00			18
80	Teleostei	Kyphosidae	*Kyphosus*	spp.	3.00		24	22
81	Teleostei	Kyphosidae	*Sector*	*ocyurus*	3.00			2
82	Teleostei	Kyphosidae			3.00			22
83	Teleostei	Lamprididae	*Lampris*	*guttatus*[b]	4.22	5	20	
84	Teleostei	Lethrinidae	*Gymnocranius*	spp.	3.70		24	
85	Teleostei	Lobotidae	*Lobotes*	*pacificus*[b]	4.00			13
86	Teleostei	Lobotidae	*Lobotes*	*surinamensis*	4.00		19	
87	Teleostei	Lophotidae	*Lophotus*	*capellei*	3.00		19	
88	Teleostei	Monacanthidae	*Aluterus*	*monoceros*	3.00		19	18
89	Teleostei	Monacanthidae	*Aluterus*	*scriptus*	3.00			18
90	Teleostei	Monacanthidae			3.00	20		
91	Teleostei	Myctophidae	*Benthosema*	*panamense*	3.00			11
92	Teleostei	Myctophidae	*Diaphus*	spp.	3.00	12		
93	Teleostei	Myctophidae			3.00	17	22	
94	Teleostei	Nomeidae	*Cubiceps*	*baxteri*	3.00	24		
95	Teleostei	Nomeidae	*Cubiceps*	*pauciradiatus*	3.00	20		17
96	Teleostei	Nomeidae	*Psenes*	*pellucidus*	3.00	11		
97	Teleostei	Omosudidae	*Omosudis*	*lowii*	3.00		15	
98	Teleostei	Ostraciidae	*Lactoria*	*diaphana*	3.00		23	6
99	Teleostei	Paralepididae	*Magnisudis*	*indica*	3.00		23	
100	Teleostei	Paralepididae	*Sudis*	*atrox*	3.00	19	23	
101	Teleostei	Paralepididae			3.00		22	
102	Teleostei	Phosichthyidae	*Phosichthys*	*argenteus*	3.00	19		
103	Teleostei	Phosichthyidae	*Vinciguerria*	*lucetia*	3.00			1
104	Teleostei	Scaridae	*Cetoscarus*	*bicolor*	3.00		10	
105	Teleostei	Scomberesocidae	*Scomberesox*	*saurus scomberoides*	3.00	17		
106	Teleostei	Scombridae	*Acanthocybium*	*solandri*	4.50	6	18	13

Table A1 (*continued*)

Seq. no.	Parent taxa	Family (or supra-family group)	Genus	Species	TL	Group no.		
						SW	CW	CE
107	Teleostei	Scombridae	*Allothunnus*	*fallai*	4.20		20	
108	Teleostei	Scombridae	*Auxis*	*rochei rochei*	4.20	12		14
109	Teleostei	Scombridae	*Auxis*	spp.	4.20			12
110	Teleostei	Scombridae	*Auxis*	*thazard*	4.34		24	12
111	Teleostei	Scombridae	*Euthynnus*	*affinis*	4.47		19	
112	Teleostei	Scombridae	*Euthynnus*	*alletteratus*	4.20	12		
113	Teleostei	Scombridae	*Euthynnus*	*lineatus*	3.57			23
114	Teleostei	Scombridae	*Euthynnus*	spp.	4.20	12		
115	Teleostei	Scombridae	*Katsuwonus*	*pelamis*[b]	4.35	1	15	12
116	Teleostei	Scombridae	*Sarda*	*australis*	4.00	5		
117	Teleostei	Scombridae	*Scomber*	*australasicus*	4.03	16		
118	Teleostei	Scombridae	*Scomber*	*japonicus*	3.09			21
119	Teleostei	Scombridae	*Scomber*	spp.	4.00	12		
120	Teleostei	Scombridae	*Scomberomorus*	spp.	4.20	24		
121	Teleostei	Scombridae	*Thunnus*	*alalunga*[b]	4.44	7	16	20
122	Teleostei	Scombridae	*Thunnus*	*albacares*[b]	4.30	1	17	13
123	Teleostei	Scombridae	*Thunnus*	*maccoyii*	3.87	7		
124	Teleostei	Scombridae	*Thunnus*	*obesus*	4.50	3	17	19
125	Teleostei	Scombridae	*Thunnus*	*orientalis*	4.21			23
126	Teleostei	Scombridae	*Thunnus*	spp.	4.18	13	24	11
127	Teleostei	Scombridae		spp.	4.00	18	22	11
128	Teleostei	(Scombroidei)			4.20		11	
129	Teleostei	Scombrolabracidae	*Scombrolabrax*	*heterolepis*	4.25		13	
130	Teleostei	Scombrolabracidae, Gempylidae[a]			4.25		12	
131	Teleostei	Scopelarchidae			3.00		15	
132	Teleostei	Serranidae			4.00		4	
133	Teleostei	Sphyraenidae	*Sphyraena*	*barracuda*	4.30		18	
134	Teleostei	Sphyraenidae	*Sphyraena*	*ensis*	4.30			23
135	Teleostei	Sphyraenidae	*Sphyraena*	*qenie*	4.30		19	
136	Teleostei	Sphyraenidae			4.30		18	
137	Teleostei	Sternoptychidae	*Argyropelecus*	*aculeatus*	3.00		22	
138	Teleostei	Sternoptychidae	*Argyropelecus*	*sladeni*	3.00		10	
139	Teleostei	Sternoptychidae	*Maurolicus*	spp.	3.00		23	
140	Teleostei	Sternoptychidae	*Sternoptyx*	spp.	3.00	22	23	
141	Teleostei	Sternoptychidae			3.00		22	
142	Teleostei	Tetragonuridae	*Tetragonurus*	spp.	3.00	24		
143	Teleostei	Tetraodontidae	*Lagocephalus*	*lagocephalus*	2.67		24	21
144	Teleostei	Tetraodontidae	*Lagocephalus*	spp.	2.67		24	
145	Teleostei	Tetraodontidae			2.67	18	24	
146	Teleostei	(Tetraodontiformes)			2.67		24	
147	Teleostei	Trachichthyidae			3.90	19		
148	Teleostei	Trachipteridae	*Desmodema*	*polystictum*	4.30		19	
149	Teleostei	Trachipteridae			4.30	9		
150	Teleostei	Trichiuridae	*Assurger*	*anzac*	4.10		14	
151	Teleostei	Trichiuridae			4.10	24	23	
152	Teleostei	Xiphiidae	*Xiphias*	*gladius*[b]	4.55	7	18	
153	Teleostei	(Unidentified teleosts[b])			3.35	18	22	4
154	Chondrichthyes	Alopiidae	*Alopias*	*pelagicus*	4.21			23
155	Chondrichthyes	Alopiidae	*Alopias*	*superciliosus*	4.21	9		
156	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*brachyurus*	4.20	8		
157	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*falciformis*	4.20	9	18	16
158	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*leucas*	4.20		7	
159	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*limbatus*	4.20			16
160	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*longimanus*	4.20		19	16
161	Chondrichthyes	Carcharhinidae	*Carcharhinus*	*obscurus*	4.20	4		
162	Chondrichthyes	Carcharhinidae	*Galeocerdo*	*cuvier*	4.20		19	
163	Chondrichthyes	Carcharhinidae	*Prionace*	*glauca*	4.24	7	6	
164	Chondrichthyes	Dasyatidae	*Pteroplatytrygon*	*violacea*	3.70		20	
165	Chondrichthyes	Lamnidae	*Isurus*	*oxyrinchus*	4.28	2	18	18
166	Chondrichthyes	Lamnidae	*Isurus*	*paucus*	4.50		18	
167	Chondrichthyes	Lamnidae	*Lamna*	*nasus*	4.21	9		
168	Chondrichthyes	Sphyrnidae	*Sphyrna*	*lewini*	4.25	2	19	7
169	Chondrichthyes	Sphyrnidae	*Sphyrna*	*zygaena*	4.50	10		16
170	Chondrichthyes	Sphyrnidae			4.30		20	16
171	Chondrichthyes	(Elasmobranchii)			4.05		2	
172	Chondrichthyes	(Rajiformes)			3.90			5
173	Mammalia	Delphinidae	*Stenella*	*attenuata*	4.00			23
174	Mammalia	Delphinidae			4.00	24		
175	Mollusca	Amphitretidae	*Amphitretus*	spp.	2.27		23	
176	Mollusca	Ancistrocheiridae	*Ancistrocheirus*	*lesueurii*	3.44		23	
177	Mollusca	Architeuthidae	*Architeuthis*	spp.	4.00	20		
178	Mollusca	Argonautidae	*Argonauta*	*cornutus*	3.25			10
179	Mollusca	Argonautidae	*Argonauta*	*nodosa*	3.25	20		

Table A1 (continued)

Seq. no.	Parent taxa	Family (or supra-family group)	Genus	Species	TL	Group no.		
						SW	CW	CE
180	Mollusca	Argonautidae	*Argonauta*	spp.	3.25	14	22	
181	Mollusca	Atlantidae	*Atlanta*	spp.	2.00		24	
182	Mollusca	Atlantidae			2.00	22		
183	Mollusca	Carinariidae	*Carinaria*	spp.	1.50	19	22	
184	Mollusca	Cavoliniidae	*Cavolinia*	spp.	2.00		1	
185	Mollusca	Cavoliniidae	*Cavolinia*	*tridentata*	2.00	19		
186	Mollusca	Chiroteuthidae			3.44		4	
187	Mollusca	Enoploteuthidae	*Abralia*	spp.	3.44		10	
188	Mollusca	Enoploteuthidae	*Enoploteuthis*	spp.	3.44		24	
189	Mollusca	Enoploteuthidae	*Pyroteuthis*	spp.	3.44		10	
190	Mollusca	Enoploteuthidae			3.44		10	
191	Mollusca	Histioteuthidae	*Histioteuthis*	*bonnellii*	3.75	24		
192	Mollusca	Histioteuthidae	*Histioteuthis*	*miranda*	3.75	19		
193	Mollusca	Histioteuthidae	*Histioteuthis*	spp.	3.75	24	23	
194	Mollusca	Loliginidae	*Loliolopsis*	*diomedeae*	3.25			21
195	Mollusca	Lycoteuthidae	*Lycoteuthis*	*lorigera*	3.75	24		
196	Mollusca	Octopodidae	*Octopus*	spp.	3.80	24		
197	Mollusca	Octopodidae			3.80	24	22	
198	Mollusca	Ommastrephidae	*Dosidicus*	*gigas*	4.00			4
199	Mollusca	Ommastrephidae	*Eucleoteuthis*	*luminosa*	3.20	19	22	
200	Mollusca	Ommastrephidae	*Nototodarus*	*gouldi*	3.20	20		
201	Mollusca	Ommastrephidae	*Nototodarus*	*sloanii*	3.20	19		
202	Mollusca	Ommastrephidae	*Ommastrephes*	*bartramii*	3.20	20		
203	Mollusca	Ommastrephidae	*Ornithoteuthis*	*volatilis*	3.20	24	23	
204	Mollusca	Ommastrephidae	*Sthenoteuthis*	*oualaniensis*	3.20		23	21
205	Mollusca	Ommastrephidae	*Todarodes*	*filippovae*	3.20	24		
206	Mollusca	Ommastrephidae	*Todaropsis*	*eblanae*	3.20	18		
207	Mollusca	Ommastrephidae			3.20	20	24	
208	Mollusca	Onychoteuthidae	*Moroteuthis*	*lonnbergi*	4.00		23	
209	Mollusca	Onychoteuthidae	*Moroteuthis*	*robsoni*	4.00	20		
210	Mollusca	Onychoteuthidae	*Moroteuthis*	spp.	4.00	19	10	
211	Mollusca	Onychoteuthidae	*Onychoteuthis*	*banksii*	4.00			6
212	Mollusca	Onychoteuthidae	*Onychoteuthis*	spp.	4.00	24	23	
213	Mollusca	Onychoteuthidae	*Walvisteuthis*	spp.	4.00		23	
214	Mollusca	Onychoteuthidae			4.00		23	
215	Mollusca	Thysanoteuthidae	*Thysanoteuthis*	*rhombus*	4.00	19		10
216	Mollusca	(Bivalvia)			2.00			10
217	Mollusca	(Gastropoda)			2.00			10
218	Mollusca	(Octopoda)			3.80		10	
219	Mollusca	(Unidentified cephalopods[b])			3.75	18	22	4
220	Crustacea	Cyphocarididae			3.44		24	
221	Crustacea	Enoplometopidae	*Enoplometopus*	spp.	2.67		24	
222	Crustacea	Euphausiidae	*Nyctiphanes*	*simplex*	2.00			17
223	Crustacea	Galatheidae	*Pleuroncodes*	*planipes*	2.67			21
224	Crustacea	Lepadidae			2.67		10	
225	Crustacea	Oplophoridae	*Acanthephyra*	spp.	2.67		23	
226	Crustacea	Penaeidae			2.67			5
227	Crustacea	Phronimidae	*Phronima*	spp.	2.00		22	
228	Crustacea	Platyscelidae	*Platyscelus*	*ovoides*	2.00	12		
229	Crustacea	Portunidae			2.67			6
230	Crustacea	Thalassocarididae	*Thalassocaris*	spp.	2.67		22	
231	Crustacea	(Cirripedia)			2.67			1
232	Crustacea	(Decapoda-megalopa)			2.00	17		
233	Crustacea	(Decapoda-phyllosoma)			2.00		10	
234	Crustacea	(Decapoda-prawn)			2.67	12		
235	Crustacea	(Decapoda-shrimp)			2.67	24	1	
236	Crustacea	(Hyperiidea)			3.00	12	22	
237	Crustacea	(Mysida)			2.00			3
238	Crustacea	(Stomatopoda)			3.50	24	23	
239	Crustacea	(Unidentified crustacea)			2.67	14	22	1
240	Gelatinous Zooplankton	Pyrosomatidae	*Pyrosoma*	spp.	2.00		10	
241	Gelatinous Zooplankton	Salpidae			2.00	21	5	
242	Gelatinous Zooplankton	(Actiniaria)			2.00			5
243	Algae	(Alga)			1.00			1
244	Other Invertebrate	(Ascidiacea)			2.00			5
245	Gelatinous Zooplankton	(Cnidaria)			2.00			5
246	Other Invertebrate	(Foraminifera)			2.00			10
247	Other Invertebrate	(Porifera)			2.00			5
248	Gelatinous Zooplankton	(Scyphozoa)			2.00		10	
Total taxa identified						109	142	91

[a] Multi-family group.
[b] Key player identified in Table 5.

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