Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific

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ABSTRACT: We updated and expanded a model of the pelagic ecosystem for the area of the central North Pacific occupied by the Hawaii-based longline fishery. Specifically, results from the most recent diet studies were used to expand the representation of the lesser-known non-target fish species (e.g. lancetfish, opah, snake mackerel) and 9 mid-trophic micronekton functional groups. The model framework Ecopath with Ecosim was used to construct an ecosystem energy budget and to examine how changes in the various micronekton groups impact apex predator biomass. Model results indicate that while micronekton fishes represented approximately 54% of micronekton biomass, they accounted for only 28% of the micronekton production. By contrast, crustaceans represented 24% of the biomass and accounted for 44% of production. Simulated ecosystem changes resulting from changes to micronekton groups demonstrated that crustaceans and mollusks are the most important direct trophic pathways to the top of the food web. Other groups appear to comprise relatively inefficient pathways or 'trophic dead-ends' that are loosely coupled to the top of the food web (e.g. gelatinous animals), such that biomass declines in these functional groups resulted in increased biomass at the highest trophic levels by increasing energy flow through more efficient pathways. Overall, simulated declines in the micronekton groups resulted in small changes in biomass at the very top of the food web, suggesting that this ecosystem is relatively ecologically resilient with diverse food web pathways. However, further understanding of how sensitive micronekton are to changes in ocean chemistry and temperature resulting from climate change is needed to fully evaluate and predict potential ecosystem changes.

KEY WORDS: Forage species · Hawaii longline fishery · North Pacific Subtropical Gyre · Ecopath with Ecosim · Ecosystem modeling · Climate change · Marine food webs

INTRODUCTION

The pelagic ecosystem of the central North Pacific (CNP) encompasses a substantial portion of the North Pacific Subtropical Gyre, which is Earth's single largest circulation feature and most expansive living space (Roemmich & McCallister 1989, Karl 1999). In addition to performing critical ecosystem services such as global climate regulation, the CNP pelagic ecosystem houses large-scale commercial fisheries that target high-value tuna and billfish species (He et al. 1997, Bigelow et al. 2002, Sibert et al. 2006).

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Persistent harvest of predatory fish biomass has imparted measurable changes to CNP pelagic eco-system structure, while environmental variability has also been reported to affect predatory fish popula-tions and fishery removal patterns in recent decades (Doney et al. 2012). At the top of the food web, for example, decadal shifts in both target and non-target fish species and size composition have been docu-mented from the Hawaii-based longline fishery (Polovina et al. 2009, Polovina & Woodworth-Jefcoats 2013). Long-term changes at the base of the CNP pelagic food web have also been reported, namely decreasing levels of surface chlorophyll in oceanic subtropical gyres (Polovina et al. 2008, Gregg & Rousseaux 2014) accompanied by changes in phyto-plankton community composition (Karl et al. 2001, Corno et al. 2007, Sherwood et al. 2014).

Comprehensive understanding of overall ecosys-tem impacts and potential fishery management implications due to widespread fishery and environ-mental changes is still incomplete. Increasing calls have been made for ecosystem-based fishery man-agement, a holistic approach that aims to maintain the ecological integrity of a system by accounting for cumulative natural and anthropogenic impacts to all ecosystem components in management decisions (Brodziak & Link 2002). Forage or mid-trophic spe-cies (hereafter referred to as micronekton), which form critical trophic links transferring production from primary and secondary producers up to large apex species, are perhaps one of the most critically understudied components of pelagic food webs.

Micronekton communities are generally highly diverse, consisting of small but mobile crustaceans, cephalopods, fishes, and gelatinous animals ~2 to 20 cm in size (Seki & Polovina 2001, Brodeur & Yama-mura 2005). Many micronekton animals are primary prey of marine mammals, seabirds, and commer-cially important tunas and billfishes (e.g. Harrison & Seki 1987, Pauly et al. 1998, Watanabe et al. 2009). Trophic modes employed by micronekton can range widely from zooplanktivory to piscivory, including omnivory, cannibalism, and opportunistic feeding on variable prey bases (e.g. Clarke 1973, 1974, Mauch-line & Gordon 1986, Passarella & Hopkins 1991). Bio-logical production generated by phytoplankton in surface waters can thus be partitioned through multi-ple, complex pathways as energy flows through diverse micronekton groups up to apex predators. Recent studies suggest that mesopelagic micronek-ton fishes dominate global fish biomass, and together with crustacean, mollusk, and gelatinous micronek-ton species perform critical roles in the marine bio-

geochemical cycling of carbon (Davison et al. 2013, Irigoien et al. 2014).

Micronekton are particularly difficult to study as their primary habitat generally extends from beneath epipelagic waters (>200 m) to depths throughout the mesopelagic and bathypelagic (~200 to 4000 m). Dif-ferent micronekton species have varying degrees of mobility, but most are agile enough to detect and avoid traditional mid-water sampling gear (Gjosaeter & Kawaguchi 1980, Koslow et al. 1997, Kaartvedt et al. 2012). Thus, studies examining micronekton have customarily been descriptive in nature, focusing on various aspects of community composition (e.g. species distribution, behavior, abundance, and bio-mass) or examining the diets of some of the most commonly captured species (e.g. Clarke 1973, 1974, Maynard et al. 1975). However, predicted environ-mental changes to oceanic ecosystems (e.g. ocean acidification, expanding oxygen minimum zones, ocean warming, increased stratification) may dispro-portionately affect certain types of micronekton, thereby shunting or rerouting previously available flows of biological production available to apex species. For example, calcifying organisms such as pelagic crustaceans or the early life stages of cepha-lopods and other mollusks may be particularly sen-sitive to changes in oceanic carbonate chemistry (Fabry et al. 2008, Whiteley 2011, Kaplan et al. 2013a). Thus, focused studies examining the specific food web relationships of mid-trophic micronekton to economically valued apex species are needed amidst a changing marine environment.

Sampling difficulties associated with accessing re-mote mid-water environments inhibit our ability to fully characterize the ecosystem dynamics of mid-trophic communities, let alone anticipate potential ecosystem impacts given known environmental vari-ability and fishing pressures. Ecosystem modeling is an important and widely used approach for exploring system dynamics and the possible responses of those dynamics to specific environmental and anthropo-genic perturbations (Plagányi & Butterworth 2004, Colléter et al. 2015). This method is particularly im-portant for vast, ecologically complex pelagic sys-tems for which empirically based synthesis studies are especially challenging. Thus, the primary objec-tive of this study was to examine the ecological roles of mid-trophic micronekton functional groups in transferring energy to the top of the CNP pelagic food web. We compiled best available biological information to update and expand the representation of mid-trophic groups and their primary predators for a CNP model previously developed by Howell et al.

(2013), itself built based on previous iterations (Kitchell et al. 1999, Cox et al. 2002a,b). Model results provide a better understanding of the main throughways for energy flow within the CNP pelagic ecosystem and of how these trophic pathways may be altered given anticipated future climate variability and change.

MATERIALS AND METHODS

Study area and ecosystem description

The study area encompasses offshore waters of the central North Pacific Ocean used by the Hawaii-based pelagic longline fishery, from approximately 170° E to 150° W and 10° N to 40° N, with the northern boundary defined by the 17°C sea surface temperature isotherm (Fig. 1). The study area directly follows that of Howell et al. (2013), covering a surface area of roughly 13 275 700 km² in which the vast majority of Hawaii longline fishery sets are made (Fig. 1). These open ocean waters are seaward of any continental shelves and surround the Hawaiian Archipelago, forming a substantial portion of the North Pacific Subtropical Gyre biome. This biome is characterized by oligotrophy (low levels of bioavailable nutrients), generally low surface-chlorophyll levels (<0.1 mg m^{-3}), mesoscale oceanographic variability, seasonally variable surface mixed layers, strong water column stratification, and complex microbial loop dynamics (reviewed in Karl 1999). Despite generally low productivity, these waters house a diverse pelagic community of typically 5 or more trophic levels, with micronekton fishes, cephalopods, crustaceans, and
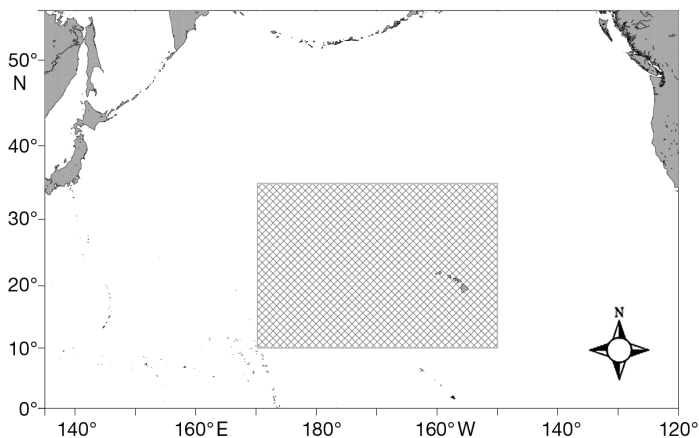

Fig. 1. The central North Pacific, showing the core area of the Hawaii-based longline fishing grounds and model study region (cross-hatched area)
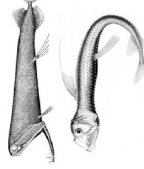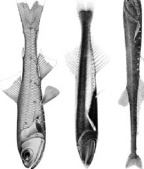
gelatinous animals occupying intermediate trophic levels (Maynard et al. 1975), and sharks, tuna, and billfishes occupying the highest trophic levels (Seki & Polovina 2001).

Ecosystem modeling approach

All trophic and temporal model explorations were conducted with the Ecopath with Ecosim software package (EwE, version 6.4.10486.0), a well documented and widely used ecosystem modeling platform (Polovina 1984, Pauly et al. 2000, Christensen & Walters 2004). Ecopath models the static state of an ecosystem, balancing mortality sources (e.g. migration, predation, fishery removals) with net production for food web functional groups defined and parameterized by the user. Ecosim is the dynamic expression of Ecopath, allowing for temporal explorations of biomass and system changes in relation to growth, ecological efficiency, and consumption, relative to the same sources of mortality (see Christensen et al. 2008 for underlying master equations). For each defined functional group, in addition to diet (relative to the other defined food web groups), EwE models require 3 of the 4 following biological input parameters: biomass (B), production to biomass ratio (P:B), consumption to biomass ratio (Q:B), and ecotrophic efficiency (EE).

We directly expanded and modified the Ecopath component of the Hawaii Longline Fishing Grounds EwE model (HLFG1) built by Howell et al. (2013), which originally contained 28 functional groups and 3 fishing fleets (international longline, international purse seine, and US albacore troll fisheries). Thirteen functional groups were added to improve Ecopath model parameterization of the CNP pelagic ecosystem and work undertaken included literature synthesis of the feeding and trophic ecology of these additional groups and adjustments based on updated biological data for the other 28 functional groups. Specifically, our Ecopath model was expanded to include a total of 41 functional groups, increasing the representation of micronekton groups (from 5 groups to 9 total), and intermediate mesopredator groups (e.g. adding 'opah' and 'snake mackerel and escolar' as separate individual groups) for which updated diet information from the CNP exists (Table 1). Comprehensive fisheries catch, effort, and species length and weight data were preserved intact from Howell et al. (2013).

Functional groups were assigned by aggregating species that are ecologically and functionally similar in terms of behavior, diet, preferred habitat, and gen-
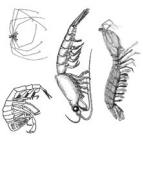
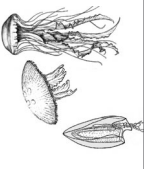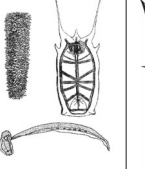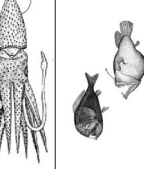Table 1. Biological input and output parameters for the ecosystem components in the central North Pacific Ecopath with Ecosim ecosystem model. Parameters in **bold** represent model-estimated output. B: biomass (tons km^{-2}); P:B: production: biomass ratio (yr^{-1}); Q:B: consumption:biomass ratio (yr^{-1}); P: production (t km^{-2} yr^{-1}); EE: ecotrophic efficiency; TL: trophic level. Functional groups with italicized names are groups additional to the last model iteration (Howell et al. 2013)

	Functional group	B	P:B	Q:B	P	EE	TL
1	Blue sharks	0.0019	0.42	1.50	0.0008	**0.476**	**4.95**
2	Other sharks	0.0020	0.32	2.82	0.0006	**0.264**	**5.14**
3	Broadbill swordfish	0.0018	0.35	3.30	0.0006	**0.759**	**4.52**
4	Blue marlin	0.0005	0.47	3.80	0.0002	**0.683**	**4.95**
5	Striped marlin	0.0006	0.47	3.80	0.0003	**0.553**	**4.84**
6	Other billfishes	**0.0005**	0.81	6.07	0.0004	0.400	**4.77**
7	Small billfishes	**0.0700**	1.00	10.00	0.0700	0.600	**4.61**
8	*Baleen whales*	0.0780	0.08	7.40	0.0061	**0.000**	**3.77**
9	*Toothed whales*	0.0349	0.03	13.00	0.0010	**0.154**	**4.70**
10	Bigeye tuna	0.0041	0.50	8.20	0.0020	**0.305**	**4.81**
11	Juvenile bigeye tuna	0.0030	0.60	14.70	0.0018	**0.786**	**4.37**
12	Yellowfin tuna	0.0196	0.40	10.60	0.0079	**0.309**	**4.62**
13	Juvenile yellowfin tuna	0.0011	0.50	26.33	0.0006	**0.840**	**4.13**
14	Albacore tuna	0.0152	0.40	9.60	0.0061	**0.430**	**4.68**
15	Juvenile albacore tuna	0.0182	0.35	14.92	0.0064	**0.750**	**4.09**
16	Skipjack tuna	0.0208	1.90	14.09	0.0395	**0.194**	**4.32**
17	Juvenile skipjack tuna	0.0643	5.50	30.00	0.3535	**0.110**	**3.92**
18	Mahi-mahi	**0.0761**	1.00	8.48	0.0761	0.800	**4.67**
19	Lancetfish	**0.9031**	0.47	4.00	0.4244	0.600	**4.34**
20	*Opah*	**0.0535**	0.22	3.50	0.0118	0.600	**4.72**
21	*Snake mackerel and escolars*	**1.1579**	0.28	3.88	0.3199	0.600	**4.46**
22	Other large pelagic fishes	**2.8368**	0.60	4.13	1.7021	0.900	**4.02**
23	*Sea birds*	0.0003	1.00	80.00	0.0003	**0.230**	**4.66**
24	*Sea turtles*	0.0029	0.12	19.80	0.0004	**0.156**	**3.66**
25	Small epipelagic fishes	2.0000	2.40	9.00	4.8000	**0.830**	**3.53**
26	*Zooplanktivorous micronekton fishes*	5.8000	2.10	8.00	12.1800	**0.964**	**3.20**
27	*Carnivorous micronekton fishes*	3.9000	1.70	6.00	6.6300	**0.994**	**4.07**
28	*Decapod crustaceans*	2.4951	4.80	25.00	11.9765	**0.910**	**2.92**
29	*Other crustaceans*	**3.0427**	8.00	25.00	24.3414	0.950	**2.93**
30	*Predatory gelatinous*	1.8644	5.01	25.05	9.3408	**0.702**	**3.44**
31	*Filter-feeding gelatinous*	0.9120	5.40	20.00	4.9249	**0.934**	**2.11**
32	Epipelagic mollusks	0.9000	3.50	10.00	3.1500	**0.965**	**4.07**
33	Mesopelagic mollusks	1.6000	4.00	10.00	6.4000	**0.995**	**3.26**
34	Bathypelagic fishes	2.9000	1.50	2.45	4.3500	**0.897**	**3.59**
35	Mesozooplankton	**8.4927**	20.00	30.00	169.854	0.980	**2.44**
36	Microzooplankton	11.1300	25.00	60.00	278.250	**0.447**	**2.00**
37	*Diatoms*	0.2300	120.00	–	27.600	**0.602**	**1.00**
38	*Diazotrophs*	0.4100	120.00	–	49.200	**0.338**	**1.00**
39	*Other large phytoplankton*	0.4900	120.00	–	58.800	**0.451**	**1.00**
40	*Small phytoplankton*	10.9400	180.00	–	1969.200	**0.342**	**1.00**
41	Detritus	100	–	–	0.0000	**0.092**	**1.00**

eral production and consumption. The 9 micronekton groups were defined based on classic size fractions of oceanic plankton and nekton (2–20 cm) from Sieburth et al. (1978) and general trophic guilds from known diet information. Descriptions of the micronekton groups with representative members are provided in Table 2. Modeled phytoplankton biomass for 4 primary producer groups ('diatoms', 'diazotrophs', 'other large phytoplankton' 5–200 µm, and 'small

phytoplankton' 0.2–5 µm) were obtained from the NOAA GFDL prototype Earth System Model (ESM2.1). ESM2.1 links a climate model (CM2.1; Delworth et al. 2006, Gnanadesikan et al. 2006) to a biogeochemical model, Tracers of Phytoplankton with Allometric Zooplankton (TOPAZ; Dunne et al. 2005), and data used represent the IPCC Special Report on Emissions Scenario A2 (for details, see Polovina et al. 2011, Howell et al. 2013).

Table 2. Description of 9 micronekton functional groups. Key references are given, where more ecological information on each group can be found. Images are from Wikimedia Commons. See Table S1 in the Supplement for additional information on micronekton group parameterization for Ecopath

	Micronekton group	Description and representative species	Sample key reference(s)
	Carnivorous micronekton fishes	Mesopelagic fishes from the families Stomiidae, Melamphaeidae, and Paralepididae that are dominant upper-trophic level predators of the mesopelagial and inflict the highest predation on mycotophids and gonostomatids. E.g. *Chauliodus sloani, Idiacanthus fasciola.*	Clarke (1973), Maynard et al. (1975), Childress et al. (1980), Hopkins & Gartner (1992), Sutton & Hopkins (1996)
	Zooplanktivorous micronekton fishes	Mesopelagic fishes from the families Myctophidae, Gonostomatidae, Phosichthyidae, Bregmacerotidae, and Sternoptychidae inhabiting waters ~200–1000 m. Many are vertical migrators and feed on zooplankton. E.g. *Ceratoscopelus warmingii, Cyclothone pallida, Sternoptyx diaphana.*	Maynard et al. (1975), Clarke & Wagner (1976), Clarke (1978), Childress et al. (1980), Mundy (2005)
	Decapod crustaceans	Sergestid, oplophorid, penaeid, pasiphaeid, and pandalid shrimps. Mostly mesopelagic, with some extending into the bathypelagic zone. Mostly zooplanktivorous and often red or half-red in color with stalked eyes. E.g. *Gennadas sp., Oplophorus gracilirostris, Janicella spinicauda, Sergestes similis.*	Maynard et al. (1975), Walters (1976), Hopkins et al. (1994)
	Other crustaceans	Crustaceans outside of the order Decapoda, including pelagic mysids, hyperiid amphipods, isopods, lobster phyllosoma, crab megalopae, stomatopods, and scyllarids. Can occur in high abundances and occupy diverse trophic niches ranging from zooplanktivory to detritivory to omnivory. E.g. *Phronima sedentaria, Gnathophausia ingens.*	Brodeur and Yamamura (2005), Hopkins et al. (1994), Maynard et al. (1975)
	Predatory gelatinous	Typically larger, soft-bodied gelatinous organisms that are active predators utilizing tentacles and/or stinging cells to capture prey. Distributed across epipelagic, mesopelagic, and bathypelagic habitats, with some vertically migrating taxa. E.g. *Aurelia sp., Chrysaora sp., Periphylla periphylla, Atolla vanhoeffeni.*	Purcell (1991), Robison (2004), Haddock (2004)
	Filter-feeding gelatinous	Primarily tunicates, including salps, pyrosomes, and appendicularians that filter small organic particles from the water for food. Can occur in high numbers and some are extensive vertical migrators. E.g. *Salpa sp., Bathochordaeus sp., Pyrosoma atlantica.*	Alldredge & Madin (1982), Robison (2004), Lucas et al. (2014)
	Epipelagic mollusks	Typically larger, more muscular and fast-moving predatory squids inhabiting the upper 200 m of the water column at night or during the day. E.g. *Ommastrephes bartramii, Sthenoteuthis oualaniensis, Hyaloteuthis pelagica.*	Young (1978), Watanabe et al. (2004), Parry (2006)
	Mesopelagic mollusks	Deeper-living cephalopod families with night or daytime depths in the mesopelagic zone. Encompass a wide range of body sizes and feeding strategies, with some species vertically migrating. E.g. *Gonatus sp., Taonius pavo, Cranchia scabra, Histioteuthis sp.*	Young (1978), Passarella & Hopkins (1991), Hoving et al. (2014)
	Bathypelagic fishes	Deeper-water fishes from an array of families with daytime depths typically below 1000 m. Many are black or darkly-colored and are carnivorous or feed opportunistically. E.g. *Anoplogaster cornuta, Melanocetus murrayi, Chiasmodon niger.*	Torres et al. (1979), Childress et al. (1980), Mundy (2005), Drazen et al. (2011), Sutton (2013)

Biological input parameters for the 41 functional groups were taken, where possible, from Howell et al. (2013) and data that informed the development of the HLFG1 model. Otherwise, best-available biological information for the region was derived and synthesized from field studies, stock assessments, fishery reports, communications with physiological and ecological experts, related EwE pelagic ecosystem models (Cox et al. 2002b, Kitchell et al. 2002, Essington 2006, Griffiths et al. 2010), and FishBase (Froese & Pauly 2015). Functional groups, including representative species and the source(s) of biological input parameters are detailed in Table S1 in the Supplement (at www. int-res.com/articles/suppl/m549p009_supp.pdf). The diet matrix is provided in Table S2 in the Supplement and was populated using best available stomach content data from the CNP (see Table S1 for sources). Whenever possible, diet contributions for groups containing multiple species were scaled according to the relative biomass contributions of individual species to the overall group.

Ecosim perturbation scenarios

We used Ecosim to evaluate and quantify the relative trophic importance of the 9 distinct micronekton functional groups by independently reducing the biomass of each of the 9 groups by 30% of initial biomass levels over a 50 yr period. A 50 yr time period was chosen after observing that food web responses stabilized over this time frame. Biomass reductions of 30% of initial model biomass levels were chosen in line with a number of common fishery management targets for non-forage stocks (Clark 2002, Kaplan et al. 2013b). Reduction of micronekton biomass for the perturbation scenarios was achieved using constant fishing mortality levels. During the Ecosim scenarios, phytoplankton biomass was kept constant (simulating no bottom-up control), as were fishery removals for commercially harvested fish species (simulating constant top-down mortalities). To further reduce top-down and bottom-up influences, as well as potentially confounding species-specific interactions, all vulnerability values were set to the default value of 2 (Mackinson et al. 2009). Once it was determined which 2 micronekton groups elicited the strongest responses to species at the top of the food web, those 2 micronekton groups were simultaneously reduced by 30% of their initial biomass levels for a 50 yr period using Ecosim ('crustaceans and mollusks' scenario).

Model balancing and sensitivity analysis

Before balancing the updated model, we performed a pre-balance check of all input parameters (Link 2010, Heymans et al. 2016). Each of the input parameters was plotted against the species trophic level ranked from lowest to highest (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m549p009_supp.pdf). Where biomass (B), production to biomass ratio (P:B), or consumption to biomass ratio (Q:B) diverged from the slope line, values were double-checked for data integrity and adjusted if necessary. Additionally, we diagnosed model input parameters by examining the P:Q ratio, or the gross food conversion efficiency, which should fall between approximately 0.1 and 0.3 (Darwall et al. 2010). If necessary, and based entirely upon available reference materials and/or informed expert opinion, P:B or Q:B values were adjusted to reach P:Q values between 0.1 and 0.3. Changes resulting from the pre-balance checks are noted in Fig. S1.

To test the sensitivity of the model output to the vulnerability (v) value (2) used in our simulations, we compared this output to that with stronger bottom-up forcing ($v = 1$) and stronger top-down forcing ($v = 10$). For each perturbation scenario in Ecosim, additional simulations were run with the vulnerability of the relevant micronekton functional group (or 2 groups in the case of the 'crustaceans and mollusks' scenario) changed to 1 and to 10.

Trophic guild analysis

To aid in interpreting responses of food web components to micronekton perturbation scenarios, a principal components analysis (PCA) was conducted using the balanced model diet matrix, which parameterizes the exchange of biomass among food web components through feeding interactions. PCA was performed on non-transformed percent composition (by weight) diet data, and the principal components were used to determine the prey items (as functional groups) contributing most to separation between observed predator groups. PCA results conducted on the diet matrix are presented to guide interpretation of model perturbation results. Hierarchical cluster analyses performed on Bray-Curtis similarity matrices were used to augment PCA results by overlaying clusters on principal component plots using 60% similarity cut-offs (Clarke & Gorley 2006). PCA and cluster analyses were performed using Primer 6 (Primer-E).

RESULTS

Ecopath model

The model comprises 41 functional groups, organized into approximately 5 trophic levels, with sharks and billfishes occupying the top of the CNP pelagic food web. Selected biological model parameters for all functional groups are shown in detail in Table 1 (see also Table S1 in the Supplement for referenced literature sources and full group descriptions). We balanced the Ecopath model through small adjustments to the model diet matrix (generally <5% adjustment per predator–prey group) (Fig. S1 in the Supplement). Changes to the model diet matrix are the typical first step in obtaining a balanced model because diet studies of diverse pelagic animals have cited flexibility in feeding habits due to changes in prey and environmental variability, among other factors (e.g. Young et al. 2010, Choy et al. 2013, Olson et al. 2014). Based on results of our pre-balance check, we made additional changes to the biomasses and Q:B values of 2 groups (changes detailed in Fig. S1). Biomass estimates from fishery-dependent stock assessments and midwater trawling studies commonly acknowledge potential sources of error that may lead to inaccurate biomass estimations. Biomass underestimates are frequently reported for many micronekton groups sampled with oceanic trawling equipment, the primary literature source for our original biomass estimates. Within the final balanced Ecopath model, the 4 primary producer groups accounted for 19% of the total system biomass, while apex predator groups (trophic levels > 4.0) accounted for 8% of total system biomass. Detailed information on the 9 micronekton functional groups, the key focus of our study, is presented in Table 2, including their primary species composition and the key literature references utilized to parameterize each group.

Model sensitivity analyses

Sensitivity analyses revealed that the simulated responses to ecosystem change were not an artifact of chosen vulnerability values. As expected, lowering vulnerability values of the micronekton groups reduced their consumption by predators and vice versa, but in general, biomass changes using different vulnerabilities were less than 5% (Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m549p009_supp.pdf). In all cases, changes in predator and prey biomasses were in the direction expected given the change in vulnerability and scaled with percent diet composition of the impacted groups. Thus, simulation results are not expected to drastically change given different vulnerability values.

Feeding similarities

The backbone of an Ecopath model consists primarily of the predator–prey interactions between functional groups as parameterized by the diet matrix. For this reason, we compared the diets of each of the functional groups using PCA. For more detailed interpretation, 2 separate PCA analyses were conducted: one targeting the top of the food web (i.e. functional groups with computed trophic levels greater than 3.5), and one targeting only the 9 micronekton functional groups that are the primary focus of this study. For the micronekton, principal component 1 (PC1) explained most of the variance in diet (51.2%), with PC2 explaining 18.9% of the variance. For the top of the food web, PC1 explained only 31.9% of the variance, while PC2 explained 23% of the variance.

The micronekton functional groups have distinct diets according to their consumption of mesopelagic zooplankton (along the PC1 axis) and micronekton crustaceans, as well as detritus and some phytoplankton groups (along the PC2 axis) (Fig. 2A). 'Zooplanktivorous micronekton fishes' and 'other crustaceans', along with the 'decapod crustaceans' and 'predatory gelatinous' groups, clustered most closely together based on their heavy consumption of mesopelagic zooplankton. As expected, the 'filter-feeding gelatinous' group (e.g. salps, doliolids, larvaceans) was the most different in PCA space, with unique consumption of detritus and phytoplankton. Though not significantly clustered together at the 60% similarity level, 'epipelagic mollusks' and 'mesopelagic mollusks' had diets similar to that of the 'bathypelagic fish' group, with all 3 groups feeding heavily on combinations of different micronekton crustaceans (e.g. amphipods) and fishes (e.g. myctophids and gonostomatids).

The main prey groups contributing most to the separation of the predator functional groups along PC1 are 'epipelagic mollusks' and 'mesopelagic mollusks' (Fig. 2B, see overlain vectors). Separation in predator feeding along PC2 can be attributed to consumption of 'other crustaceans' (positive PC2 scores) as well as 'other large pelagic fishes' and 'mesopelagic mollusks' (negative PC2 scores). Selected functional
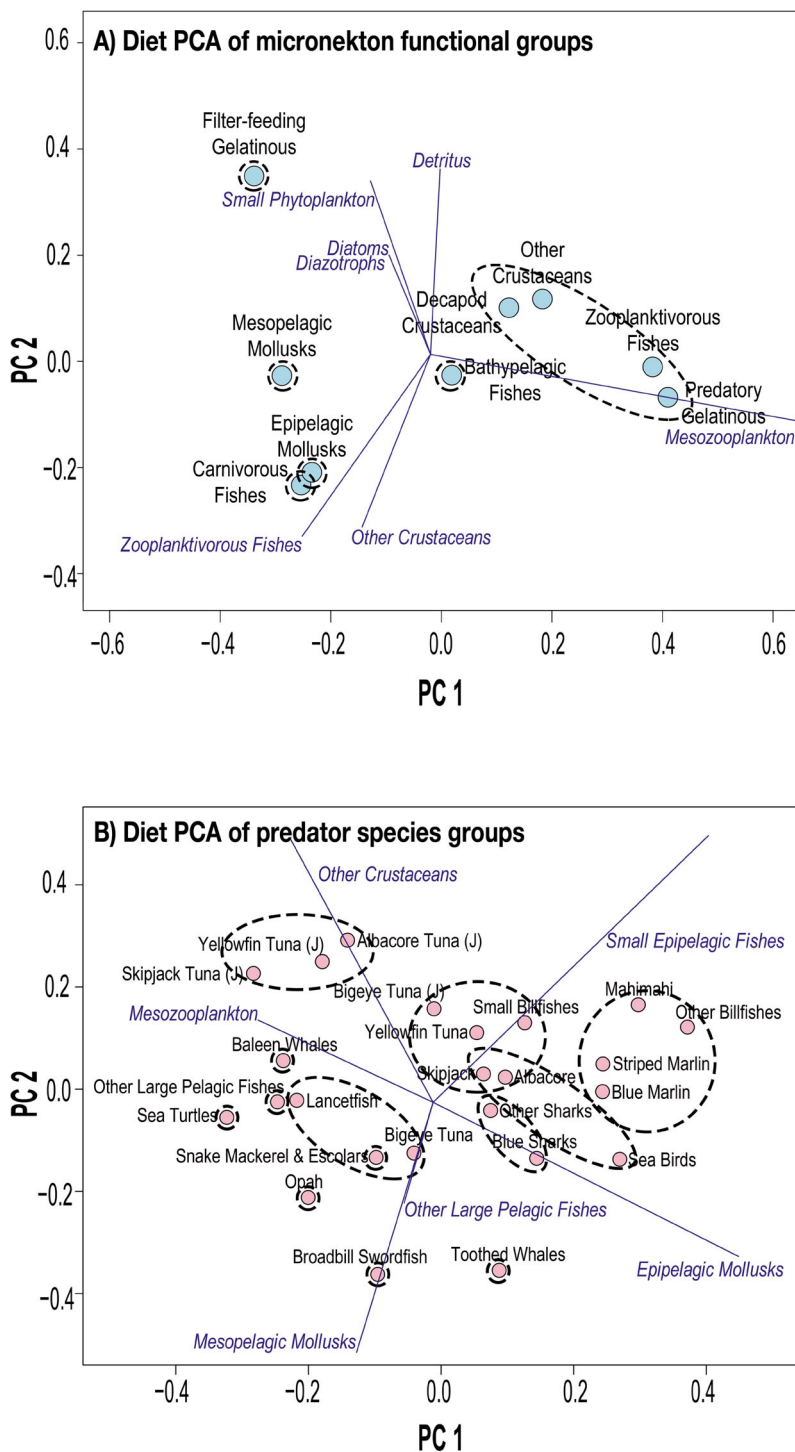
Fig. 2. Biplot of the first and second principal components (PC) derived from the percent diet composition of pelagic food web functional groups. Trophic guilds of food web groups with similar diets are shown for (A) 9 micronekton functional groups (blue circles) alongside zooplankton and phytoplankton functional groups, and (B) predator groups (pink circles) at trophic level 3.5 and greater. Dashed ellipses indicate hierarchical clustering results at 60% similarity. Overlain vectors indicate the most important prey items leading to trophic guild separation, and prey item names are shown in blue, italic text. (J) indicates juvenile tuna species groups

groups representing the top of the CNP pelagic ecosystem are nicely clustered according to relative depths of forage, as well as by average diet composition. For example, large bill-fishes ('striped marlin', 'blue marlin', 'other billfishes') cluster with 'mahi-mahi' *Coryphaena hippurus* with increasingly positive PC2 scores, denoted by high consumption of 'small epipelagic fishes' (e.g. molids, flying fish). Commercially important bill-fishes and mahi-mahi have broadly known feeding habits focused on smaller epipelagic fishes, mollusks, and crustaceans (e.g. Gibbs & Collette 1959, Brock 1984, Moteki et al. 2001, Olson & Galvan-Magana 2002). Another shallow-foraging cluster of fishes are the juvenile tunas (albacore, yellowfin, and skipjack), which have high PC2 and low PC1 scores to indicate the dietary importance of 'other crustaceans' such as stomatopods and amphipods, and 'mesopelagic zooplankton' such as euphausiids. In contrast, spread across PC1, but all with negative PC2 scores, are deep-diving and presumably deep-foraging pelagic fishes (e.g. 'broadbill swordfish', 'snake mackerel & escolars', 'opah' *Lampris guttatus*, 'bigeye tuna' *Thunnus obesus*) along with 'toothed whales' (Fig. 2B). These deep-foraging predators all consume substantial amounts of large, vertically migrating onychoteuthid and ommastrephid squids (indicated by negative PC2 scores), but also feed on varying amounts of other mollusks and large pelagic fishes, as well as micronekton crustaceans such as amphipods (King & Ikehara 1956, Moteki et al. 2001, Barlow et al. 2008, Watanabe et al. 2009, Choy et al. 2013). At the 60% similarity level, 'sea birds' cluster with 'albacore tuna' and 'skipjack tuna', all of which are known to form subsurface feeding aggregations (Hebshi et al. 2008). The anomalously feeding planktivorous animals are the 'sea turtle' and 'baleen whale' groups, which cluster

near to one another in PCA space, but do not cluster closely with other predators. Thus, the PCA results from both the micronekton and top predator functional groups align well with known dietary expectations reported in the literature, and directly guide interpretation of ecosystem model perturbation scenarios according to parameterized diet.

Micronekton functional group contributions to biomass and energy flow

The trophic levels of the 9 micronekton functional groups were estimated from the Ecopath model based on their diets. The micronekton groups encompassed 2 trophic levels, ranging from 2.11 for 'filter-feeding gelatinous' organisms to 4.07 for 'epipelagic mollusks' and 'carnivorous micronekton fishes', with most groups estimated at approximately trophic level 3 (Table 1). Relative productivity, measured as the ratio of production to biomass (P:B), ranged from 1.5 for 'bathypelagic fishes' to 8 for the 'other crustaceans' group. The P:B for 'other crustaceans' is well above values of all other micronekton groups and explains why that group accounts for 29% of the micronekton production, more than double that of any other micronekton group, even though it represents only 13% of total micronekton biomass (Table 3). The 3 fish groups together represent approximately 54% of micronekton biomass but only 28% of micronekton production. The pattern is opposite for the 2 crustacean groups that together represent only 24% of biomass but 44% of production (Table 3). The 2 remaining micronekton categories, gelatinous organisms and mollusks, account for 12 and 11%, respectively, of total micronekton biomass and 17 and 11% of total micronekton production. Three functional micronekton groups, 'other crus-

taceans', 'epipelagic mollusks', and 'mesopelagic mollusks' figure prominently in the diets of higher trophic organisms. 'Other crustaceans' account for 20 to 40% of the diet of juvenile tuna while the 2 mollusks groups account for 10 to 60% of the diets of apex species including marlins, swordfish, and toothed whales.

Micronekton perturbation scenarios in Ecosim

Food-web-wide responses (measured as percent change in biomass per group from initialized model biomass) are visualized as heat maps in Fig. 3. We focus separately on visualizing the responses to the micronekton perturbation scenarios within the middle of the food web (Fig. 3A) and at the top of the food web (Fig. 3B) to provide individual group-level context to the pooled trophic level biomass results shown in Fig. 4. Biomass impacts to the top of the food web were highly variable in response to independently reducing the biomass of each of the 9 micronekton groups. The most direct negative changes in the species groups with the highest trophic levels (>4.5) occurred in response to 30% reductions in 'other crustaceans' followed by 'epipelagic mollusks' (Fig. 4). Predator groups with a trophic level between 4.0 and 4.5 appeared to be the least affected by reductions in micronekton biomass (Fig. 4). The micronekton groups with an overall positive effect on the high-level trophic species groups were 'predatory gelatinous' and 'zooplanktivorous micronekton fishes', with the latter just barely resulting in positive increases in apex species biomass.

As parameterized by the Ecopath model, the 9 micronekton groups all have finite shared prey resources (meso- and microzooplankton, some of the phytoplankton groups; see diet matrix, Table S2 in the

Table 3. Comparison of modeled bioenergetic parameters for the 9 micronekton functional groups. Percent biomass, production, and consumption are computed for the 9 mid-trophic micronekton groups only. Production:biomass ratios (P:B; yr^{-1}) are also provided

Micronekton functional group	Micronekton biomass (B, %)	Micronekton production (P, %)	Micronekton consumption (Q, %)	P:B
Zooplanktivorous micronekton fishes	24.8	14.6	15.2	2.10
Carnivorous micronekton fishes	16.7	8.0	7.7	1.70
Decapod crustaceans	10.7	14.4	20.4	4.80
Other crustaceans	13.0	29.2	24.9	8.00
Predatory gelatinous	8.0	11.2	15.3	5.01
Filter-feeding gelatinous	3.9	5.9	6.0	5.40
Epipelagic mollusks	3.8	3.8	2.9	3.50
Mesopelagic mollusks	6.8	7.7	5.2	4.00
Bathypelagic fishes	12.4	5.2	2.3	1.50

A) Micronekton functional group responses to simulated micronekton changes

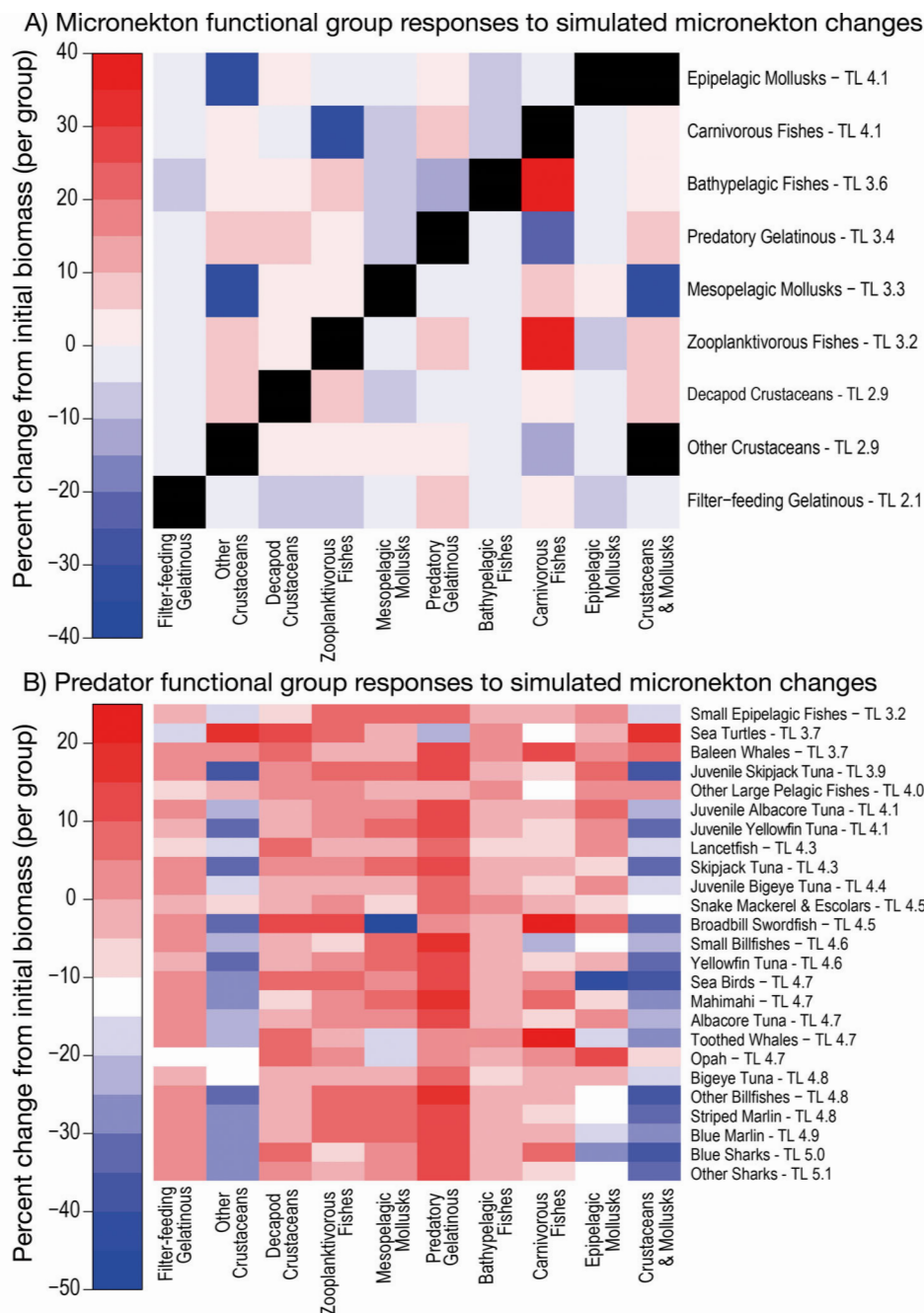## B) Predator functional group responses to simulated micronekton changes

Fig. 3. Heat map diagrams illustrating how each functional group (rows) changes in response to independent 30% reductions in the biomass of each of the 9 micronekton groups (columns), and to the 'crustaceans and mollusks' scenario (where 'other crustaceans' and 'epipelagic mollusks' are both simultaneously reduced by 30%). Separate heat maps are shown for (A) the middle of the food web (micronekton groups) and (B) the top of the food web. Warmer colors indicate positive responses, while cooler colors indicate negative responses (as percent change from initial biomass). TL: trophic level

micronekton fishes'). An understanding of between-group micronekton dynamics can explain the variable responses within the middle of the food web when the biomass of each micronekton group is independently decreased (Fig. 3A). For example, when the biomass of the 'other crustaceans' group is reduced by 30% in Ecosim there are 3 different responses within the micronekton community (Fig. 3A). First, large squids, the primary mid-trophic predators of this group, decrease (~26%) while their trophic competitors ('decapod crustaceans', 'zooplanktivorous micronekton fishes', and 'predatory gelatinous' animals) secondarily increase in response by 8 to 12%. Finally, other groups lacking prominent trophic connections to the 'other crustaceans' show little to no change in biomass (e.g. 'filter feeding gelatinous').

At the top of the food web (except for 'sea turtles', 'baleen whales', and 'other large pelagic fishes'), the largest, across-the-board negative biomass changes are seen in response to a 30% decrease in 'other crustaceans' (Fig. 3B). Aside from 'opah' and 'snake mackerel and escolars', all predator groups decline by >14% and up to 36% for 'juvenile skipjack tunas', indicating that 'other crustaceans' are the most critical pathway bridging the top and bottom of the CNP pelagic food web. This functional group comprises 20 to 40% of the diets of juvenile tunas, which are then directly and strongly linked to apex predators such as large billfish and sharks. With a P:B value of 8, a 30% reduction in biomass of this group is highly amplified across multiple food web pathways (Table 3).

A 30% reduction in the biomass of 'epipelagic mollusks' and 'mesopelagic mollusks' elicited the next 2 most negative responses to the top of the
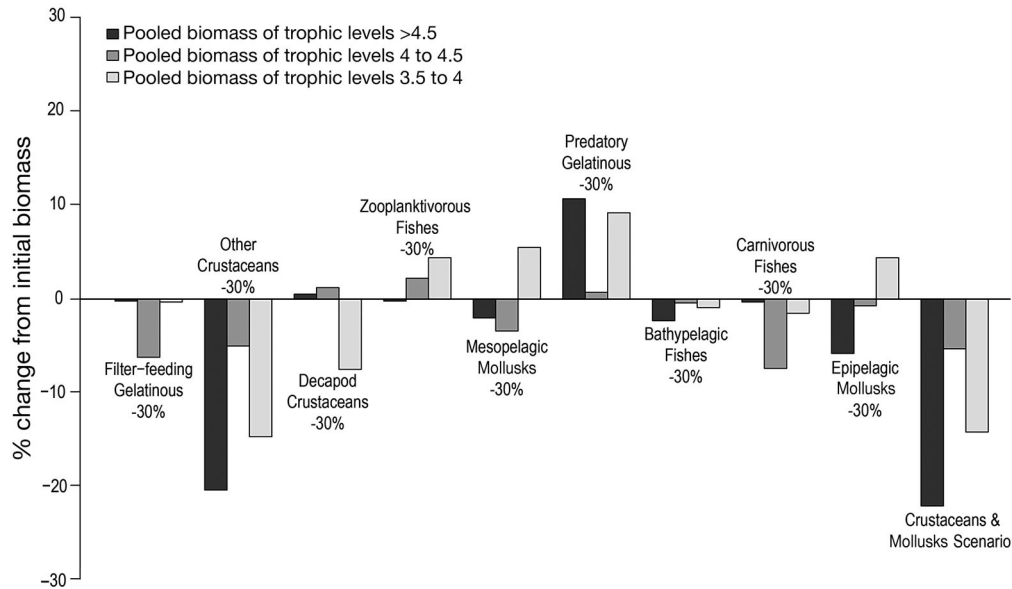
Supplement). Additionally, some of the larger, higher trophic level micronekton groups (e.g. 'epipelagic mollusks' and 'bathypelagic fishes') also prey heavily upon the smaller, lower trophic level micronekton groups (e.g. 'decapod crustaceans', 'zooplanktiverous

Fig. 4. Grouped bar plot showing the percent change for pooled fractional trophic levels from initial biomass levels, in response to independent 30% biomass reductions in each of the 9 micronekton functional groups. Biomass changes to the micronekton groups that fall within the pooled fractional trophic level ranges represented here are not included in final tabulations. At the far right are predicted changes to pooled fractional trophic levels in response to the 'crustaceans and mollusks' scenario, where the biomass of 'other crustaceans' and of 'epipelagic mollusks' are simultaneously reduced by 30% in Ecosim

food web. For the 'mesopelagic mollusks' this was especially true for the 'broadbill swordfish' *Xiphias gladius*, 'opah', and 'toothed whales'. All 3 of these predators feed heavily on 'mesopelagic mollusks' (Barlow et al. 2008, Watanabe et al. 2009, Choy et al. 2013), indicating that projected declines are direct food web responses to changes in one of their primary prey items. Additional support for this type of direct food web response occurred when biomass reductions in 'epipelagic mollusks' led to large declines in 'sea birds' (40%), 'blue sharks' (27%), 'toothed whales' (16%), and 'blue marlins' (15%). Declines in 'predatory gelatinous' organisms also elicited a strong decline (21%) in sea turtles. Reductions in biomasses of many of the other micronekton groups resulted in biomass increases at the highest trophic levels. These micronekton groups are generally not highly important prey items of top trophic level species groups, so a reduction in their biomass allows energy to flow through the more efficient pathways of 'other crustaceans' and 'mesopelagic mollusks' (Fig. 5). The specific importance of the 'other crustaceans' and 'epipelagic mollusks' micronekton groups to the top of the food web is highlighted in the 'crustaceans and mollusks' scenario, which resulted in substantial declines in almost all top predator groups (Fig. 3B).

DISCUSSION

Our Ecopath model is, to date, the most comprehensive attempt to examine energy flows within the CNP pelagic ecosystem by focusing on the relative trophic importance of key micronekton functional groups comprising the middle of the food web. We attempted to more comprehensively partition and parameterize fish, crustacean, mollusk, and gelatinous micronekton taxa into our ecosystem model, as has been done previously but sparingly with other ecosystem models (Lehodey et al. 2010). A key result was that crustaceans represented 24% of micronekton biomass but generated 44% of the overall (9 micronekton functional groups) production. In particular, 'other crustaceans' (e.g. mysids, amphipods, isopods, etc.) represented only 13% of the micronekton biomass but accounted for 29% of total micronekton production. By simulating the independent removal of each micronekton group, our results showed the direct trophic importance of micronekton crustaceans and epipelagic mollusks to predatory fishes and marine mammals at the top of the CNP pelagic food web. Simulated micronekton biomass reductions resulted in varying degrees of top predator declines. In some instances these changes were substantial, indicating that trophic flow in this ecosystem can be strongly controlled by dynamics of
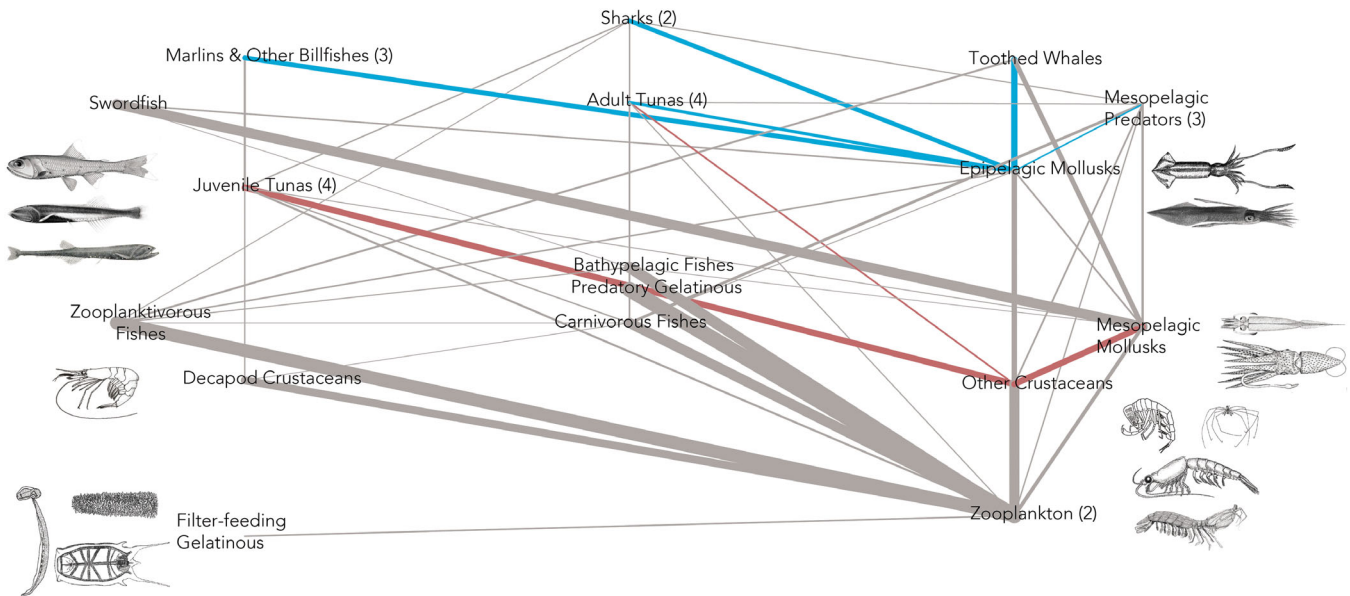
Fig. 5. Simplified food web diagram showing the energy flow through key micronekton and top predator functional groups. Diet proportions 5% or greater (from the balanced diet matrix) are shown between groups, where the thickness of the lines is scaled to parameterized diet proportions. Numbers in parentheses next to group names indicate the number of pooled functional groups within that group, and diet fractions are averaged for included groups. Colored lines highlight the energy pathways of 'other crustaceans' (red) and 'epipelagic mollusks' (blue) through the food web

select mid-trophic micronekton groups. Predicted declines in total biomass levels at the top of the food web were quite substantial in response to simulated reductions in 'other crustaceans', 'epipelagic mollusks', and 'mesopelagic mollusks' (Figs. 3 & 4B). Reductions in other micronekton groups showed little impact or, in some cases, resulted in increases in biomass at top trophic levels. These results suggest that the biomass at the top trophic levels is sensitive to the composition of micronekton functional groups, particularly the biomass proportions of mollusks and crustaceans relative to other groups. The magnitude of these top predator declines was equal to or greater than those predicted by Howell et al. (2013) in response to declines in phytoplankton biomass and increased fishing effort.

Ecosystem models have previously been developed for different sectors of the Pacific Ocean, primarily to anticipate ecosystem impacts resulting from changes in commercial fishing pressure (e.g. Cox et al. 2002a, Kitchell et al. 2002, Essington 2006), and/or climate variability and change (e.g. Watters et al. 2003, Griffiths et al. 2010, Howell et al. 2013). To fully understand these ecosystems and more meaningfully inform fishery managers of activities utilizing and impacting these systems, it is important to discern energy flows through mid-trophic groups, in addition to food web impacts of fishing and climate change. Earlier ecosystem models of the Pacific Ocean para-

meterized mid-trophic forage groups as lumped cephalopod, fish (epipelagic and mesopelagic together, in some cases), and zooplankton (microzooplankton and mesozooplankton) groups. Later studies highlighted the importance of some of these mid-trophic groups in funneling energy to higher trophic levels. For example, in the eastern tropical Pacific ecosystem, Watters et al. (2003) identified the 'axis of the *Auxis*' and the 'axis of the squid' as important mid-trophic pathways for translating climate induced bottom-up changes (e.g. El Niño Southern Oscillation, ENSO) to the top of the food web. Additionally, Griffiths et al. (2010) demonstrated that mesopelagic fish such as myctophids and cephalopods with high biomass and high production and consumption rates exert strong 'wasp-waist' control within the pelagic ecosystem off eastern Australia.

The oceanographic setting of the CNP ecosystem model is distinct from those in the eastern tropical Pacific, southeastern Australia, and the California Current. The California Current, for example, is a highly productive ecosystem with wind-driven upwelling that delivers high levels of nutrients to surface waters. Kaplan et al. (2013b) demonstrated that the specific removal of key forage species such as euphausiids, sardines, and anchovies had substantial impacts on top predator biomass in the California Current. While interannual cycles of the Pacific Decadal Oscillation and ENSO have a demonstrated

influence on the dominance of different forage species in the California Current (Barber & Chavez 1983, Chavez et al. 2003, Koslow et al. 2011), the CNP pelagic ecosystem described here generally presents dynamics more similar to those reported from southeastern Australia. However, the CNP pelagic ecosystem does not appear to exhibit the 'wasp-waist' control described by Griffiths et al. (2010), with mid-trophic biomass spread across multiple species and functional groups of shared but varying trophic importance to the top of the food web. The idea of ecosystem resilience due to diverse species assemblages within the CNP is supported by earlier ecosystem modeling efforts (Kitchell et al. 1999, Cox et al. 2002a) and independent lines of study. For example, Choy et al. (2015) reported a high degree of overlap in the trophic positions of 10 species of top predator tunas, billfishes, and mesopredators included in this ecosystem model. Redundancy in trophic positions was attributed to niche partitioning in diet and vertical habitat preferences, and these ecological niches are represented here. PCA results from the present study showed important trophic differences in the way mesopredators and top predators of the CNP pelagic ecosystem would respond to changes in micronekton composition based on distinct dietary preferences (Fig. 2).

By independently simulating micronekton reductions with targeted scenarios we were able to track food web responses in primary prey resources (zooplankton) and key predator groups (e.g. mesopredators, tunas, billfishes, sharks, and toothed whales), highlighting the relative importance of diverse micronekton groups in structuring energy flow from primary and secondary producers through to apex species. The most direct negative changes in apex predator species occurred in response to declines in 'other crustaceans' (Fig. 4B), which are not necessarily primary prey items for these apex species, but function as an important food web node with strong trophic connections to other micronekton groups ('epipelagic mollusks' and 'mesopelagic mollusks') and intermediate predators (juvenile tunas) (Fig. 5). Apex predators declined in response to reductions in intermediate trophic groups who prey directly on micronekton crustaceans (Fig. 4). These important food web pathways are underlined in the 'crustaceans and mollusks' scenario, wherein the simultaneous reduction of the 'other crustaceans' and 'epipelagic mollusks' groups caused significant declines in the highest trophic levels (Fig. 3). Other micronekton, such as the 2 gelatinous groups, function more as trophic shunts in overall food web energy flow. Gelatinous

micronekton taxa are not dominant in the diets of apex predators, but can consume large amounts of zooplankton and ultimately reduce available resources for other micronekton that are preyed upon more heavily by intermediate and apex predators. The role of gelatinous taxa as trophic 'dead ends' has also been reported from the Northern California Current (Brodeur et al. 2008, Ruzicka et al. 2012). However, it is possible that their direct importance as prey based on stomach content analyses may be underestimated due to rapid digestion (Choy et al. 2013).

The application of the ecological modeling software suite Ecopath with Ecosim to gain greater understanding of the importance of mid-trophic micronekton groups to top predator production is appealing and practical, as demonstrated by a number of previous studies (Field et al. 2010, Griffiths et al. 2010, Ruzicka et al. 2012, Kaplan et al. 2013b). However, some of the approach's limitations and assumptions warrant studies focusing on ways to comprehensively evaluate and improve current findings.

Firstly, much of the foundation of an Ecopath model lies in its diet matrix describing the predator–prey interactions between different food web components. While based on empirical data, availability and sample size of studies describing feeding habits of species included within the diet matrix are likely to be disproportionally skewed toward commercially important species (e.g. tuna and billfish species), declining in scope as one moves down the food web. Inferring diet in pelagic animals from stomach content analysis is widely acknowledged as being limited by generally small sample sizes from difficult-to-obtain specimens that may miss seasonal, spatial, or even ontogenetic shifts in diet (Allain et al. 2007, Kaplan et al. 2013b). Future work should seek to evaluate this type of underlying uncertainty in the parameterized diets, including how diet might change with animal size or prey availability, and how this might influence overall energy flow within pelagic ecosystems. Secondly, through the synthesis of existing studies and data, as well as communication with relevant experts, this exercise underlined the lack of a strong empirical foundation for mid-trophic micronekton groups (Buckley & Buckley 2010, Handegard et al. 2013). Given their importance in the functioning of pelagic systems, and to better understand and manage future impacts to these very systems, targeted efforts to obtain empirical biological data for these groups should be encouraged and supported. Finally, Ecopath models do not consider differences in the energy content of prey in contributing to overall energy flow through the food web. Diverse micro-

nekton taxa can differ substantially in potential energy content (on a per gram basis). For example, lipid contents of myctophid fishes (the primary species component of our 'zooplanktivorous fishes' group) can be up to an order of magnitude greater than those of mature epipelagic fish and squid prey (Childress et al. 1990, Van Pelt et al. 1997). Thus, lower levels of consumption of high energy density prey items will contribute disproportionately more to overall energy flow and declines in these species are likely to inordinately impact the fitness of their predators. This should be considered when interpreting biomass changes based on parameterized diet compositions in this study and others utilizing Ecopath.

While all modeling approaches are accompanied by uncertainty and caveats, our results aim to augment existing ecological findings and provide a baseline quantification of the ecological significance of mid-trophic micronekton communities to overall pelagic ecosystem structure and energy flow. Future studies might consider expanding the use of our mid-trophic group reduction scenarios, building in stronger empirical bases for model parameterization, and exploring the potential impacts of climate change on altering the overall flow and partitioning of energy in pelagic systems. The continued refinement and expansion of pelagic ecosystem models ultimately increases their utility and flexibility toward future applications and improvements of ecosystem-based management efforts for finite and dynamic pelagic resources, especially in the advent of climate change.

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