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Contribution to the Theme Section 'Drivers of dynamics of small pelagic fish resources: biology, management and human factors'

Ecosystem modeling in the western North Pacific using Ecopath, with a focus on small pelagic fishes

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ABSTRACT: Small pelagic fishes like sardine, anchovy, and mackerel play important commercial and ecological roles in the western North Pacific. We present a static, mass-balance 'Ecopath' model for this region, focusing on small pelagic fish species, as an initial step to evaluate the role of these fishes in this ecosystem. Our quasi sub-model structure has 3 blocks (coastal Oyashio, coastal Kuroshio, and offshore) that were established to take sub-regional differences of bottom topography and oceanography into consideration. This model consists of 41 functional groups and assumes that some species are endemic to a single block, while some migrating species occur in 2 or 3 blocks. We evaluated the quality of our model using pedigree and pre-balance diagnostics. The impact of fisheries on the marine ecosystem assessed by both the *L*-index, i.e. the index of loss in secondary production due to fisheries exploitation, and the impact of fisheries targeting small pelagic fishes on the total production of small pelagic fishes, are compared with other ecosystems. Both ecological indices indicate that the western North Pacific ecosystem is not overexploited. Our static mass-balanced Ecopath model will contribute to expanding ecological knowledge of the western North Pacific.

KEY WORDS: Ecosystem model · Ecopath · Quasi sub-model structure · Western North Pacific · Small pelagic fishes · Forage fish · Fishing impact

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1. INTRODUCTION

Small pelagic fishes (also called forage fishes), such as Japanese sardine *Sardinops melanostictus*, Japanese anchovy *Engraulis japonicus*, rounded herring *Etrumeus teres*, Pacific saury *Cololabis saira*, Japanese jack mackerel *Trachurus japonicus*, chub mackerel *Scomber japonicus*, and spotted mackerel *S. australasicus*, are economically important to Japan. Production quantities and monetary values in 2013 constituted 45% and 32% of the total marine fish production of Japan (MAFF 2015). Since 1996, stocks have been assessed by the Fisheries Agency of Japan and Japan Fisheries Research and Education Agency using single-species models, such as virtual population analysis (Ichinokawa et al. 2017).

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Commercial catch histories of small pelagic fishes in the western North Pacific off Japan have fluctuated drastically since the 1900s, with quasi-decadal alterations in species composition (so-called species replacement) in response to oceanographic changes (Yatsu et al. 2001, Takasuka et al. 2008). Development of multispecies ecosystem models, such as 'Ecopath' (Christensen & Walters 2004), have been widely used to address structure and function of marine ecosystems and to evaluate the effects of fisheries. Ecopath provides a static, mass-balanced snapshot of an ecosystem that can deal with multispecies and multifleet data. Although Pikitch et al. (2014) reviewed 72 international, published Ecopath models, and assessed the global contribution of forage fish to marine fisheries and ecosystems, they did not include models for the western North Pacific, as none was then available.

The Oyashio Current (a subarctic current with cold, low-salinity water) influences the northern part of the western North Pacific off Japan, while the Kuroshio Current (the subtropical western boundary current with warm high-salinity water) and the Kuroshio extension influence the southern part. The area between the Oyashio and the Kuroshio extension is called the Kuroshio–Oyashio transition (inter-frontal) zone (area) (Fig. 1). This zone is also referred to as the subarctic–subtropical transition zone.

Among small pelagic fishes in the western North Pacific, round herring and Japanese jack mackerel occur only in coastal areas. Although Japanese sardine and anchovy generally occur in coastal areas, when they are abundant, their distribution can also extend from the coast to 180° E offshore (Giannoulaki et al. 2014). The western North Pacific spawning area for Japanese sardine and anchovy is located in coastal waters of southern Japan where the influence of the Kuroshio is strong. Eggs, larvae, and juveniles of Japanese sardine and anchovy are transported from the spawning area to the Kuroshio–Oyashio transition zone by the Kuroshio and its extension, with the transition zone serving as a feeding ground. Pacific saury, chub, and spotted mackerel all have similar migration patterns. Spatial heterogeneity must be considered when constructing ecosystem models for small pelagic fishes in the western North Pacific because their geographical distribution is large.

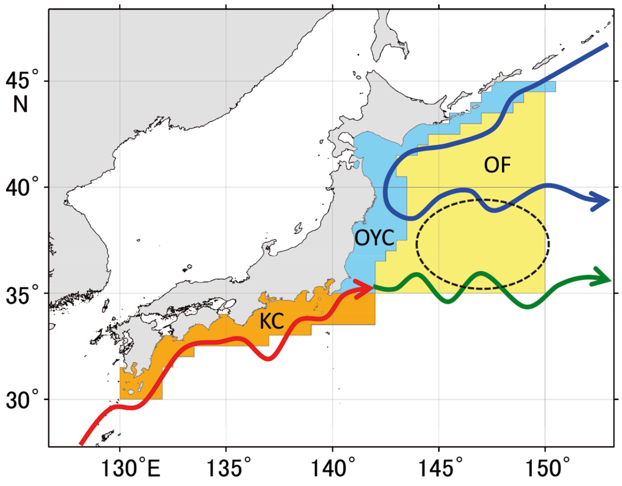

Fig. 1. Western North Pacific Ecopath modeling area with schematic oceanographic structures: OYC: coastal Oyashio (186 128 km^2); KC: coastal Kuroshio (186 220 km^2); OF: offshore (540 754 km^2). Arrows in red, blue, and green indicate the Kuroshio Current, Oyashio Current, and Kuroshio extension, respectively. The dashed oval between the Oyashio and Kuroshio extension indicates the Kuroshio–Oyashio transition zone

The primary objective of this study was to construct an Ecopath model for waters of the western North Pacific off Japan, focusing on small pelagic fishes, using data from 2013. To construct such a model, we followed guidelines outlined by Heymans et al. (2016); notably, quality of input data was assessed by pedigree (sensu Gaichas et al. 2015), while a series of pre-balance diagnostics, 'PREBAL' (Link 2010), were conducted to evaluate the initial static energy budget. Various ecosystem network analysis indicators were used, such as mixed trophic impact (MTI), to assess the role of small pelagic fishes in the ecosystem. We also compared the role of small pelagic fishes in waters off the western North Pacific of Japan with other ecosystems.

2. METHODS

2.1. Basic model

The program Ecopath with Ecosim (EwE, version 6.5.0) was used to construct an ecosystem model for the western North Pacific. Ecopath was used to represent mass-balanced trophic structure (Christensen et al. 2005). Ecopath estimates trophic mass-balance linkages using data for biomass, production ratio, consumption ratio, diet composition, and landings. This relationship can be expressed as:

$$B_i(P/B)_i EE_i - Y_i - \sum_{j=1}^{n} B_j(Q/B)_j DC_{ji} = 0 \qquad (1)$$

where B_i and B_j are the biomass of functional group i and j, respectively; $(P/B)_i$ is the production per biomass ratio of i, which is equivalent to the total mortality coefficient Z by Allen (1971); EE_i is ecotrophic efficiency of i, which is described as the proportion of the production that is utilized in the system; Y_i is landing of i; $(Q/B)_i$ is consumption per biomass of i; and DC_{ji} is diet composition for predator j feeding on prey i. Ecopath requires DC_{ji} and Y_i for all functional groups. Three of the 4 parameters of B_i, $(P/B)_i$, $(Q/B)_i$, and EE_i must be known for each functional group, while the fourth parameter can be estimated using a system of equations. The mass-balance was taken following guidelines of Heymans et al. (2016).

2.2. Modeled area

A quasi sub-model structure with 3 geographical areas (blocks), namely coastal Oyashio (OYC), coastal Kuroshio (KC), and offshore (OF), was established that took sub-regional differences of bottom topography and oceanography throughout the modeled area into consideration (Fig. 1). We adopted an approach similar to that attempted in the Mediterranean Sea (Piroddi et al. 2015). To separate each western North Pacific area within the full single model, we assigned a habitat area which corresponded to the fraction of the total area where the functional groups occurred. KC and OYC (186 220 and 186 128 km^2, respectively) were set around continental shelf areas where offshore bottom trawl fisheries operated. OF (540 754 km^2) was bound by the easternmost line of the OYC, 30° N, 50° N and 150° E, and serves as a feeding ground for small pelagic fishes. It was assumed that some species were endemic to a single block (e.g. demersal fishes), while highly migratory species (e.g. tunas, whales) occurred in 2 or 3 blocks. Blocks are connected by some small pelagic fishes (Japanese sardine, Japanese anchovy, Pacific saury, chub mackerel, and spotted mackerel) which migrate among the blocks. The modeled year (2013) was chosen for being data rich relative to other years.

2.3. Functional groups

We defined 41 functional groups, including living animals and detritus. Eleven commercially important species were classified into single-species functional groups: skipjack *Katsuwonus pelamis*, yellowtail *Seriola quinqueradiata*, Japanese sardine, Japanese anchovy, Pacific saury, chub mackerel, spotted mackerel, round herring, jack mackerel, walleye pollock *Gadus chalcogrammus* (also known as Alaska pollock), and Pacific cod *Gadus macrocephalus*. Other species were classified into functional groups that included several species (based on ecological similarities, such as niche overlap): baleen whales, toothed whales, seabirds, sharks, tunas, miscellaneous piscivores, righteye flounders, flatfishes, miscellaneous bottom fishes, seabreams, demersal piscivores, mesopelagic fishes, epipelagic cephalopods, mesopelagic cephalopods, benthos, zooplankton, phytoplankton, and detritus. Krill was considered a single functional group as *in situ* biomass estimates were available for the study area, but other zooplankters were aggregated as 'zooplankton' because species-specific biomass was not available for the study area. For each of the 3 geographical areas, the block to which each functional group belonged was based on available biological habitat. Some species, such as small pelagic fishes, occurred in more than 1 block. Details of functional groups are presented in Table 1 and in Supplement 1 at www.int-res.com/articles/suppl/m617p295_supp.pdf.

2.4. Input parameters

Basic input parameters, i.e. biomass (B), production per biomass (P/B), consumption per biomass (Q/B), diet composition (DC), and landings (Y), of each functional group were obtained from the literature (Table 2; detailed information is provided in Supplement 1). Even though the modeled area was divided into 3 blocks, Ecopath required biomass of species i in the total area (B_i) rather than for the habitat area (B'_i). To obtain B_i, B'_i was multiplied by fraction of habitat area relative to the total area (H'_i):

$$B_i = B'_i \times H'_i \tag{2}$$

Fractions for OYC, KC, and OF were assigned 0.2, 0.2, and 0.6, respectively.

In principle, these basic input parameters were obtained from each habitat area. Where data for species/functional groups were collected at scales coarser than the size of our 3 blocks, we allocated data in proportions to the area of the blocks, although such an approach was not ideal. Either B_i or EE_i was estimated for each functional group.

2.5. Input data quality and pre-balance diagnostics

Input data quality was ranked based on pedigree (Gaichas et al. 2015) into 1 of 8 categories, from high (1) to low (8) (Table S2-1 in Supplement 2). Our model's initial static energy budget was checked based on pre-balance diagnostics (PREBAL) comprising 17 criteria,

Table 1. Western North Pacific Ecopath model functional groups in coastal Oyashio (OYC), coastal Kuroshio (KC), and offshore (OF) regions. Parentheses indicate distributions of each functional group

No.	Group name (distribution)	Category
1	Baleen whales (OYC & OF)	Cetaceans
2	Toothed whales (all)	
3	Seabirds (all)	Seabirds
4	Sharks (all)	Elasmobranchs
5	Tunas (all)	Tunas
6	Skipjack (all)	
7	Miscellaneous piscivores (all)	Miscellaneous piscivores
8	Yellowtail (OYC & KC)	
9	Japanese sardine (all)	Small pelagic fishes
10	Japanese anchovy (all)	
11	Pacific saury (all)	
12	Chub mackerel (all)	
13	Spotted mackerel (all)	
14	Round herring (KC)	
15	Jack mackerel (OYC & KC)	
16	Righteye flounders (OYC)	Demersal fishes
17	Walleye pollock (OYC)	
18	Pacific cod (OYC)	
19	Miscellaneous bottom fishes (OYC)	
20	Flatfishes (KC)	
21	Seabreams (KC)	
22	Demersal piscivores (KC)	
23	Miscellaneous bottom fishes (KC)	
24	Mesopelagic fishes (OYC)	Mesopelagic fishes
25	Mesopelagic fishes (KC)	
26	Mesopelagic fishes (OF)	
27	Epipelagic cephalopods (all)	Cephalopods
28	Mesopelagic cephalopods (all)	
29	Benthos (OYC)	Benthos
30	Benthos (KC)	
31	Krill (OYC)	Krill
32	Krill (OF)	
33	Zooplankton (OYC)	Zooplankton
34	Zooplankton (KC)	
35	Zooplankton (OF)	
36	Phytoplankton (OYC)	Phytoplankton
37	Phytoplankton (KC)	
38	Phytoplankton (OF)	
39	Detritus (OYC)	Detritus
40	Detritus (KC)	
41	Detritus (OF)	

and the results were ranked into 1 of 3 categories: 'good,' 'acceptable,' and 'caution' (Link 2010).

2.6. Ecosystem characteristics

Summary statistics of the constructed model were extracted from Ecopath. MTI was used to assess the positive or negative effect of changes in biomass of a group on the biomass of other groups in the steady state ecosystem (Christensen et al. 2005). MTI is calculated by constructing an $n \times n$ matrix, where j and i represent the interaction between impacting group j and impacted group i:

$$\mathrm{MTI}_{ji} = DC_{ji} - FC_{ij} \tag{3}$$

where DC_{ji} is the diet composition term which expresses how much species i contributes to the diet of j, while FC_{ij} is a host composition term giving the proportion of the predation on i that is due to j as predator. MTI allows the quantification of impacts that change in the biomass of a group (including fisheries) has on the biomass of other groups in the ecosystem. System biomass and total commercial catches fractionated by trophic level were also calculated. Trophic levels were calculated for each consumer functional group as the length of the different consumption pathways, and expressed in roman numerals (Lindeman 1942).

Characteristics of the ecosystem and the impact of fisheries were evaluated by using the L-index (L, Libralato et al. 2008), which expresses loss in secondary production due to fisheries exploitation; it is calculated as:

$$L = -\frac{\mathrm{PPR} \cdot \mathrm{TE}^{\mathrm{TL}_c - 1}}{P_1 \cdot \ln \mathrm{TE}} \tag{4}$$

where PPR is primary production required excluding detritus groups in the sense of Libralato et al. (2008) and represents primary production needed to support the production of a fishery; TE is transfer efficiency, TL_c is mean trophic level of landing, and P_1 is primary production. Mean trophic level in this calculation indicates the weighted average of the preys' trophic levels (Odum & Heald 1975). Sustainability of fishing in our modeled area was assessed based on P_{sust} (the probability of an ecosystem being sustainably fished) as described by Libralato et al. (2008), wherein 51 ecosystems divided into 2 groups were analyzed, namely overexploited (Group 1) and sustainably fished (Group 2) ecosystems. P_{sust} is expressed as:

$$P_{\mathrm{sust}} = \frac{P(L_2 > L)}{P(L_2 > L) + P(L_1 < \mathrm{L})} \tag{5}$$

Table 2. Basic input and output parameters for the western North Pacific Ecopath model. Functional groups were defined in coastal Oyashio (OYC), coastal Kuroshio (KC), and offshore (OF) regions. Values in **bold** are model estimates

No.	Group name (distribution)	Trophic level	Habitat area (fraction)	Biomass in habitat area (t km^{-2})	Biomass (t km^{-2})	Production per biomass (yr^{-1})	Consumption per biomass (yr^{-1})	Ecotrophic efficiency	Landings (t km^{-2})
1	Baleen whales (OYC & OF)	**3.19**	0.80	0.16	0.13	0.07	5.10	**0.08**	<0.01
2	Toothed whales (all)	**4.08**	1.00	0.25	0.25	0.08	8.16	**0.01**	<0.01
3	Seabirds (all)	**4.13**	1.00	<0.01	<0.01	0.12	36.67	**0.00**	–
4	Sharks (all)	**4.27**	1.00	0.20	0.20	0.39	2.19	**0.09**	0.01
5	Tunas (all)	**4.21**	1.00	0.04	0.04	0.33	6.75	**0.75**	0.01
6	Skipjack (all)	**4.22**	1.00	**0.09**	**0.09**	0.46	16.20	0.77	0.03
7	Miscellaneous piscivores (all)	**4.00**	1.00	**0.53**	**0.53**	0.52	5.00	0.62	0.02
8	Yellowtail (OYC & KC)	**3.99**	0.40	0.27	0.11	0.93	3.10	**0.56**	0.06
9	Japanese sardine (all)	**2.88**	1.00	0.78	0.78	0.69	2.30	**0.98**	0.14
10	Japanese anchovy (all)	**3.02**	1.00	0.68	0.68	2.96	9.87	**0.96**	0.20
11	Pacific saury (all)	**3.02**	1.00	0.94	0.94	1.25	4.17	**0.79**	0.46
12	Chub mackerel (all)	**3.31**	1.00	1.49	1.49	0.66	2.20	**0.74**	0.25
13	Spotted mackerel (all)	**3.31**	1.00	0.86	0.86	0.64	2.13	**0.97**	0.11
14	Round herring (KC)	**3.00**	0.20	0.35	0.07	3.60	12.00	**0.45**	0.04
15	Jack mackerel (OYC & KC)	**3.49**	0.40	0.16	0.07	1.52	5.07	**0.96**	0.04
16	Righteye flounders (OYC)	**3.66**	0.20	0.82	0.16	0.42	1.40	**0.97**	0.02
17	Walleye pollock (OYC)	**3.34**	0.20	4.89	0.98	0.44	1.47	**0.26**	0.08
18	Pacific cod (OYC)	**3.91**	0.20	1.50	0.30	0.45	1.51	**0.79**	0.03
19	Miscellaneous bottom fishes (OYC)	**3.10**	0.20	3.03	0.61	0.45	1.51	**0.87**	0.03
20	Flatfishes (KC)	**3.66**	0.20	**0.06**	**0.01**	0.56	1.87	0.95	<0.01
21	Seabreams (KC)	**3.78**	0.20	0.08	0.02	0.41	1.36	**0.45**	<0.01
22	Demersal piscivores (KC)	**3.80**	0.20	**0.28**	**0.06**	0.70	2.32	0.95	0.01
23	Miscellaneous bottom fishes (KC)	**3.11**	0.20	2.08	0.42	0.70	2.32	**0.97**	0.02
24	Mesopelagic fishes (OYC)	**3.11**	0.20	**5.94**	1.19	1.50	6.00	0.90	–
25	Mesopelagic fishes (KC)	**3.06**	0.20	**4.99**	1.00	1.50	6.00	0.90	<0.01
26	Mesopelagic fishes (OF)	**3.02**	0.60	**1.44**	0.87	1.50	6.00	0.90	–
27	Epipelagic cephalopods (all)	**3.32**	1.00	**0.68**	0.68	2.56	7.30	0.95	0.11
28	Mesopelagic cephalopods (all)	**3.33**	1.00	**0.52**	0.52	3.50	13.64	0.95	–
29	Benthos (OYC)	**2.22**	0.20	**7.72**	1.54	3.44	11.47	0.90	0.01
30	Benthos (KC)	**2.22**	0.20	13.70	2.74	3.22	10.73	**0.61**	0.01
31	Krill (OYC)	**2.10**	0.20	19.31	3.86	2.56	12.05	**0.88**	0.03
32	Krill (OF)	**2.10**	0.60	8.05	4.83	2.56	12.05	**0.50**	–
33	Zooplankton (OYC)	**2.00**	0.20	35.65	7.13	5.80	19.33	**0.31**	–
34	Zooplankton (KC)	**2.00**	0.20	29.02	5.80	5.80	19.33	**0.36**	–
35	Zooplankton (OF)	**2.00**	0.60	41.88	25.13	5.80	19.33	**0.13**	–
36	Phytoplankton (OYC)	**1.00**	0.20	13.56	2.71	153.78	–	**0.41**	–
37	Phytoplankton (KC)	**1.00**	0.20	10.01	2.00	128.27	–	**0.45**	–
38	Phytoplankton (OF)	**1.00**	0.60	9.04	5.42	153.78	–	**0.63**	–
39	Detritus (OYC)	**1.00**	0.20	47.91	9.58	–	–	–	–
40	Detritus (KC)	**1.00**	0.20	30.18	6.04	–	–	–	–
41	Detritus (OF)	**1.00**	0.60	47.50	28.50	–	–	–	–

where $P(L_1 < L)$ is the number of cases within Group 1 that have index values lower than a chosen value L. $P(L_2 > L)$ is the number of cases within Group 2 that have index values larger than a chosen value of L. An L value corresponding to P_{sust} level of 0.5 ($L_{50\%}$) indicates an intermediate state between an overexploited and sustainably fished ecosystem; the estimated $L_{50\%}$ was 0.054. Accordingly, L corresponding to P_{sust} levels of 0.75 ($L_{75\%}$) and 0.95 ($L_{95\%}$) were defined as reference values for moderate and low risks of ecosystem overfishing, with corresponding L of 0.021 and 0.007, respectively.

2.7. Assessing roles of small pelagic fishes in the static ecosystem

Proportions of catches of small pelagic fishes, the total support service contribution of small pelagic fishes to ecosystem predator production (S_z), and the support service contribution of small pelagic fishes to the catch of other commercially targeted species (S_c), were used to investigate the importance and contribution of forage fish to the ecosystem (Pikitch et al. 2014). The values of S_z and S_c were calculated as follows:

$$S_z = \sum_j \sum_i D_{ji} P_j \tag{6}$$

$$S_c = \sum_j \sum_i D_{ji} Y_j \tag{7}$$

where D_{ji} is predator group j's respective diet dependence on small pelagic fishes, P_j is total annual production of predator j that preys on small pelagic fishes, and Y_j is landing of j. In an evaluation of global trends in S_z and S_c, Pikitch et al. (2014) included krill in their definition of forage fish; we calculated both S_z and S_c including and excluding krill, to enable comparison with Pikitch et al. (2014), and to assess the role of fish species, respectively.

3. RESULTS

3.1. Basic input parameters

Basic input and estimated parameters are summarized in Table 2. When we estimated parameters with Ecopath at earlier stages of thermodynamic balancing, the ecotrophic efficiency (EE_i) of several functional groups (including miscellaneous piscivores, Japanese sardine, Pacific cod and krill [OF]) exceeded 1.0, indicating predation and landings exceeded production. To achieve thermodynamic balance in the model, some adjustment of predator group *DC* values (sharks, tunas, skipjack, miscellaneous piscivores, yellowtail, Pacific cod, demersal piscivores, mesopelagic fishes, and cephalopods) was performed to achieve mass-balance through the system (Table 3). *DC* values were adjusted as pedigree scores were generally high (i.e. low reliability) when compared with other parameters, such as *B* or *P/B*. Mean trophic levels by species/functional group ranged from 1.0 to 4.3; predators at mean trophic levels greater than 4.0 included toothed whales, seabirds, sharks, tunas, skipjack, and miscellaneous piscivores (Fig. 2, Table 2).

3.2. Quality of Ecopath model

Pedigree indices *B* and *P/B* for small pelagic species and demersal fish species, commercially important and targeted for stock assessment, ranked lower (i.e. high reliability) than mesopelagic fishes and cephalopods, for which data were scarce. Pedigree indices for *Q/B* and *DC* were generally imprecise (i.e. high scores) across functional groups. Pedigree indices for each species/functional group are shown in Supplement 2 (see Supplement 1 for reasoning for assignment). PREBAL diagnostics resulted in either 'good' or 'acceptable' outcomes for the energy budget parameter. Results of PREBAL are presented in Supplement 3.

3.3. Ecosystem characteristics

Values of MTI revealed that changes in small pelagic fish biomass impacted most functional groups, including top predators and the small pelagic fishes themselves (Table S4-1 in Supplement 4). The MTI indicated a positive impact of small pelagic fishes on fisheries (range 0.014 to 0.199, average 0.066). This impact is 3 times larger than the impact of all functional groups on fisheries (range –0.074 to 0.199, average 0.019). Changes in zooplankton and krill biomass had a positive impact on most fish functional groups, including small pelagic and top-predator fishes (range –0.081 to 0.400, average 0.022); more positive impacts were shown for small pelagic fishes (range –0.067 to 0.400, average 0.043). Fisheries had a negative impact on most groups (range –0.828 to 0.454, average –0.126), except functional groups subject to low fishing pressure, such as mesopelagic fishes and miscellaneous piscivores (range 0.053 to 0.454, average 0.211).

Fractions of biomass and commercial catch for trophic levels I–VIII are shown in Fig. 3; the highest total catch and biomass were reported for trophic levels III and II, respectively. It should be noted that most small pelagic fishes would be included in trophic level III.

The western North Pacific Ecopath summary statistics are presented in Table 4. *L* of the western North Pacific ecosystem was 0.0548, which was comparable with the $L_{50\%}$ (0.054) reported by Libralato et al. (2008).

3.4. Assessing roles of small pelagic fishes in the static ecosystem

Values of small pelagic fish contribution to supported production (S_z), supported catch (S_c), and catch of small pelagic fishes including krill (as in the case of Pikitch et al. 2014) were 4.77, 0.51, and 1.33 (t km^{-2}), respectively, whereas the values of S_z, S_c, and catch of small pelagic fishes excluding krill were 0.67, 0.14, and 1.22 (t km^{-2}), respectively. Values of S_z and S_c including krill were 7.1 times and 3.6 times greater than those values excluding them. The proportions of catch of small pelagic fishes to the sum of S_z, S_c, and catch of small pelagic fishes excluding, and then including krill, were 0.21 and 0.60, respectively.

Table 3. Proportions of diet composition for the western North Pacific Ecopath model. Functional groups (numbered) were defined in coastal Oyashio (OYC), coastal Kuroshio (KC), and offshore (OF) regions (in parentheses). Values in **bold** indicate adjusted diet composition to achieve thermodynamic balancing

No	Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	Baleen whales (OYC & OF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Toothed whales (all)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Seabirds (all)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Sharks (all)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Tunas (all)	0	0	0	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	Skipjack (all)	0	0	0	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	Miscellaneous piscivores (all)	0	0	0	0	**0.09**	**0.09**	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	Yellowtail (OYC & KC)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	Japanese sardine (all)	0.01	0.01	0.10	**0.06**	**0.09**	**0.05**	**0.04**	0.05	0	0	0	0.01	0.01	0	0.01	0	0	0	0	0	0	**0.06**	0	0	0	0	0.01	0	0	0	0	0	0	0	0
10	Japanese anchovy (all)	0.05	0.05	0.10	**0.06**	**0.09**	**0.05**	**0.04**	**0.11**	0	0	0	0.24	0.24	0	0.19	0	0	0	0	0	0	**0.06**	0	0	0	0	0.01	0	0	0	0	0	0	0	0
11	Pacific saury (all)	0.02	0.02	0.10	**0.06**	**0.09**	**0.089**	**0.07**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0
12	Chub mackerel (all)	0.01	0.011	0.10	**0.06**	**0.09**	**0.089**	**0.08**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0
13	Spotted mackerel (all)	0.01	0.011	0.10	**0.06**	**0.09**	**0.089**	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0
14	Round herring (KC)	0	0	0.004	**0.005**	**0.005**	**0.005**	**0.005**	**0.005**	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.005**	0	0	0	0	0.01	0	0	0	0	0	0	0	0
15	Jack mackerel (OYC & KC)	0.01	0.001	0.003	**0.005**	0.001	0.001	**0.005**	**0.005**	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.005**	0	0	0	0	0.005	0	0	0	0	0	0	0	0
16	Righteye flounders (OYC)	0	0	0	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.05**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	Walleye pollock (OYC)	0	0	0	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	Pacific cod (OYC)	0	0	0	**0.058**	0	0	**0.01**	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0
19	Miscellaneous bottom fishes (OYC)	0	0	0	**0.06**	0	0	**0.02**	**0.09**	0	0	0	0	0	0	0	0.20	0	**0.10**	0	0	0	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0
20	Flatfishes (KC)	0	0	0	**0.01**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	Seabreams (KC)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	Demersal piscivores (KC)	0	0	0	**0.06**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	Miscellaneous bottom fishes (KC)	0	0	0	**0.06**	0	0	**0.069**	**0.08**	0	0	0	0	0	0	0	0	0	0	0	0.20	0.20	**0.11**	0	0	0	0	0	0	0	0	0	0	0	0	0
24	Mesopelagic fishes (OYC)	0	0.10	0.10	**0.064**	**0.091**	**0.12**	**0.12**	**0.10**	0	0	0	0	0	0	0	0.10	0.10	**0.21**	0	0	0	0	0	0	0	0	0.04	0.05	0	0	0	0	0	0	0
25	Mesopelagic fishes (KC)	0	0.10	0.10	**0.064**	**0.085**	**0.11**	**0.12**	**0.10**	0	0	0	0	0	0	0	0	0	0	0	0.10	0.10	**0.11**	0	0	0	0	0.04	0.05	0	0	0	0	0	0	0
26	Mesopelagic fishes (OF)	0	0.19	0.10	**0.064**	**0.091**	**0.12**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0.05	0	0	0	0	0	0	0
27	Epipelagic cephalopods (all)	0.01	0.20	0.10	**0.064**	**0.091**	**0.091**	**0.09**	**0.105**	0	0	0	0.01	0.01	0	0.10	0.10	0	**0.11**	0	0.10	0.10	**0.06**	0	0	0	0	0.03	0.05	0	0	0	0	0	0	0
28	Mesopelagic cephalopods (all)	0	0.20	0.10	**0.064**	**0.091**	**0.091**	**0.09**	**0.11**	0	0	0	0.01	0.01	0	0.10	0.10	0.10	**0.21**	0	0.10	0.10	**0.06**	0	0	0	0	0.03	0.05	0	0	0	0	0	0	0
29	Benthos (OYC)	0	0.051	0	0	0	0	**0.09**	**0.10**	0	0	0	0	0	0	0	0.20	0.30	**0.21**	0.30	0	0	0	0	0.25	0	0	0	0	0.10	0	0	0	0	0	0
30	Benthos (KC)	0	0.051	0	0	0	0	**0.09**	**0.10**	0	0	0	0	0	0	0	0	0	0	0	0.30	0.45	**0.41**	0.50	0	0.25	0	0	0	0	0.10	0	0	0	0	0
31	Krill (OYC)	0.10	0	0.001	0.001	0.001	0.001	0	0	0.10	0.10	0.10	0.10	0.10	0	0.20	0.20	0.30	**0.11**	0.30	0	0	0	0	0.50	0	0	**0.20**	**0.20**	0	0	0	0	0	0	0
32	Krill (OF)	0.50	0	0.001	0.001	0.001	0.001	0	0	0.20	0.10	0.10	0.20	0.20	0	0	0	0	0	0	0	0	0	0	0	0	**0.19**	**0.20**	**0.20**	0	0	0	0	0	0	0
33	Zooplankton (OYC)	0.14	0	0.001	0	0.001	0.001	0	0	0.10	0.15	0.15	0.10	0.10	0	0.20	0.10	0.20	0	0.40	0	0	0	0	0.25	0	0	**0.12**	**0.15**	0.10	0	0.10	0	0	0	0
34	Zooplankton (KC)	0	0	0.001	0	0.001	0.001	0	0	0.10	0.15	0.15	0.10	0.10	1.00	0.20	0	0	0	0	0.20	0	0	0.50	0	0.75	0	**0.115**	**0.05**	0	0.10	0	0	0	0	0
35	Zooplankton (OF)	0.14	0	0.001	0	0.001	0.001	0	0	0.35	0.50	0.50	0.23	0.23	0	0	0	0	0	0	0	0	0	0	0	0	**0.81**	**0.12**	**0.15**	0	0	0	0.10	0	0	0
36	Phytoplankton (OYC)	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0	0.70	0	1.00	0	0
37	Phytoplankton (KC)	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.10	0	0	0	1.00	0
38	Phytoplankton (OF)	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.70	0	0	1.00
39	Detritus (OYC)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.70	0	0.20	0	0	0	0
40	Detritus (KC)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.70	0	0	0	0	0
41	Detritus (OF)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.20	0	0	0

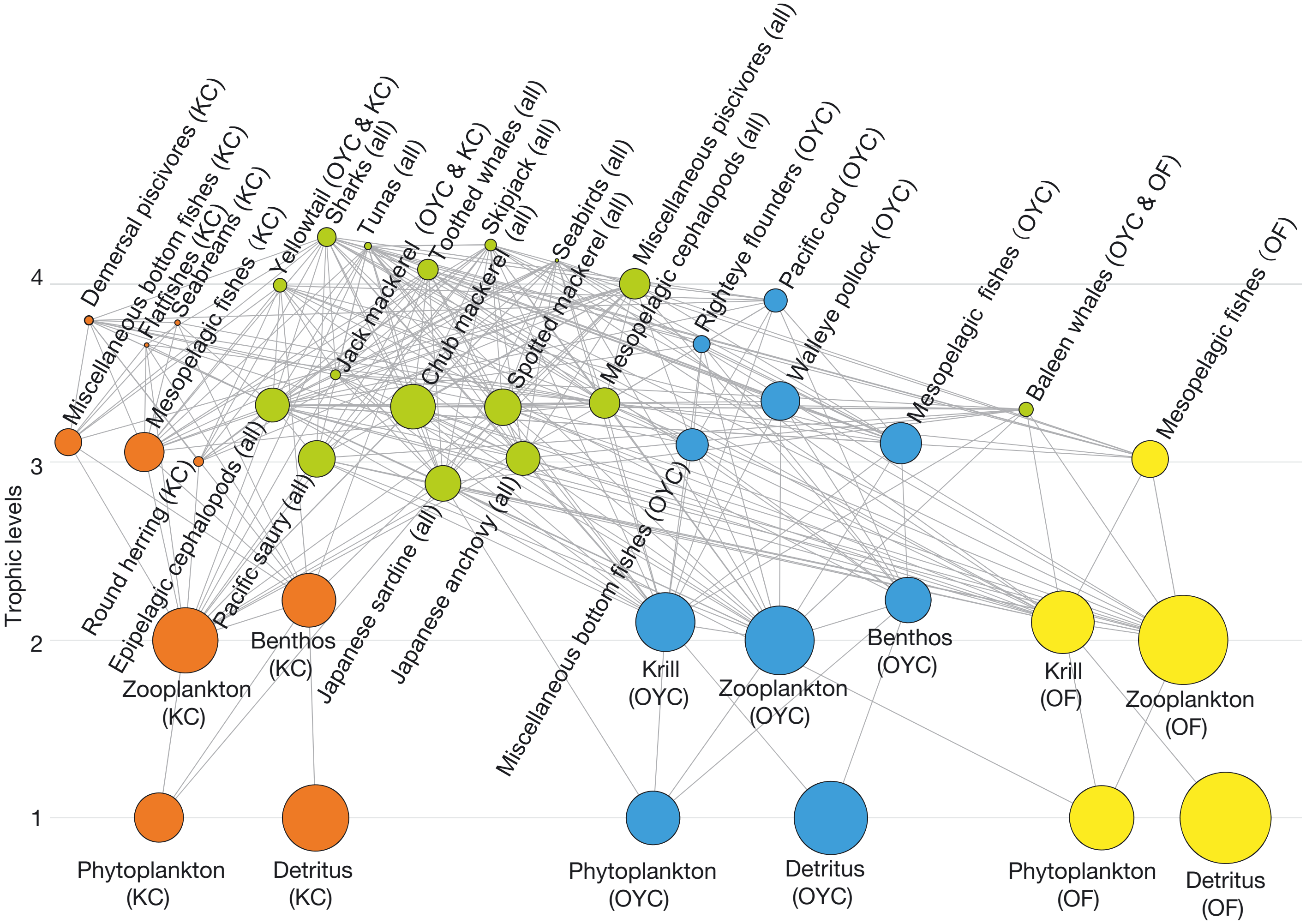

Fig. 2. Estimated food web for the western North Pacific Ecopath model. Bubble colors indicate spatial block allocation of species/groups (where OYC: coastal Oyashio, KC: coastal Kuroshio, and OF: offshore regions); bubble size indicates relative biomass

4. DISCUSSION

Our Ecopath model represents the first published account for the western North Pacific to focus on small pelagic fishes, and serves as a basis for understanding the role of these fishes in this ecosystem. The balanced model follows general ecological and fisheries principles based on the results of PREBAL. Pedigree ranking revealed that reliable *B* and *P*/*B* data were available for commercial functional groups, whereas comparably reliable data for non-commercial functional groups such as seabirds, mesopelagic fishes, and mesopelagic cephalopods, were not. Pedigree ranking also revealed *Q*/*B* and *DC* data quality to be low for most functional and poorly studied groups, except for some cetaceans. *B* and *P*/*B* are available from stock assessment data for fisheries

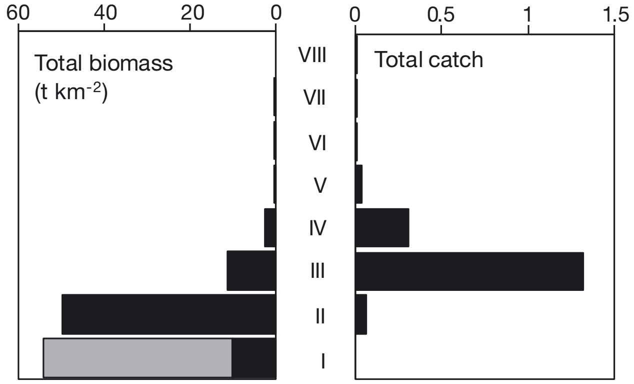

Fig. 3. System biomass (left panel) and total catch (right panel) fractionated by trophic levels I–VIII for the western North Pacific. Black and grey bars indicate living animals and detritus, respectively

Table 4. Western North Pacific Ecopath model summary statistics

	Value	Unit
Ecosystem feature		
Area (coastal Oyashio: OYC)	186.220	km^2
Area (coastal Kuroshio: KC)	186.128	km^2
Area (offshore: OF)	540.754	km^2
Functional groups	41	Number
Indicator		
Sum of all consumption	948.85	t km^{-2} yr^{-1}
Sum of all exports	1.021.03	t km^{-2} yr^{-1}
Sum of all respiratory flows	486.42	t km^{-2} yr^{-1}
Sum of all flows into detritus	1.073.24	t km^{-2} yr^{-1}
Total system throughput	3.529.54	t km^{-2} yr^{-1}
Sum of all production	1.780.12	t km^{-2} yr^{-1}
Mean trophic level of the catch	3.20	Unitless
Gross efficiency (catch/net primary production)	0.00114	Unitless
Calculated total net primary production	1.507.46	t km^{-2} yr^{-1}
Total primary production / total respiration	3.10	Unitless
Net system production	1.021.04	t km^{-2} yr^{-1}
Total primary production / total biomass	20.31	Unitless
Total biomass / total throughput	0.02	yr^{-1}
Total biomass (excluding detritus)	74.21	t km^{-2}
Total catch	1.71	t km^{-2} yr^{-1}
Connectance index	0.19	Unitless
System omnivory index	0.10	Unitless
L-index	0.0548	Unitless
Primary production required (PPR) excluding detritus	10.94	%

management. Although the constructed model could be used as a basis for strategic management considerations at the ecosystem level (e.g. broader effect of harvesting on ecosystems), it would not be suitable for tactical management considerations (e.g. setting catch quotas for a particular species) given the quality of input data. Continued data collection is important to improve data quality and the model.

Ecopath models traditionally have been constructed as closed ecosystems. The complex oceanographic conditions in the western North Pacific, and differences in the distribution patterns of species within the region, required us to incorporate heterogeneity by using a quasi (in the sense that our 3 blocks were not entirely independent) sub-model structure. Each block in our modeled area took bottom topography, oceanography, and the distribution patterns of functional groups into consideration — an approach similar to that of Piroddi et al. (2015) for the Mediterranean Sea. The time scale of our model is 1 yr, with input parameters being average values for 1 yr. Consequently, seasonal distribution patterns of migratory species and seasonal or spatial differences in diet composition are not incorporated. Therefore, a single *DC* value is used for each prey–predator relationship, and differences in *DC* values among the different blocks are not considered. Predation pressure may be seasonally high within certain blocks where prey and predator distributions overlap, but biological features like this are not fully accounted for in our model. Although spatially explicit ecosystem models like 'Atlantis' (Fulton et al. 2011) can handle finer-scale spatiotemporal resolution, such models require fine-scale biological data that are not available for most of the species distributed in our modeled area. Given the limited nature of some of our input data, we consider a quasi sub-model structure using Ecopath with 3 geographical blocks to be a more appropriate approach. However, future efforts should be made to collect finer-scale input data.

For 2013, the total landings of all fishes from Japanese waters were 2.4 Mt, while total landings of small pelagic fishes from the western North Pacific coast of Japan were 1.1 Mt. Commercial fisheries targeting small pelagic fishes off the western North Pacific coast of Japan represent some of the most important fisheries for Japan, amounting to 45 % of total landings. The proportionally high catch of trophic level III species to other trophic levels identifies the significance of small pelagic fishes to current fisheries (Fig. 3).

Our estimated *L* (0.0548) for the western North Pacific is comparable to the $L_{50\%}$ of Libralato et al. (2008), according to which we determined the state of this ecosystem (for the year 2013) to be intermediate between overexploited and sustainably fished.

Estimated *EE* values of some commercially exploited species/functional groups, including small pelagic fishes, were higher than 0.9. Reported *EE* values for sardine and anchovy elsewhere throughout the Pacific Ocean are: 0.95 for the eastern subtropical Pacific Ocean (Olson & Watters 2003), 0.80 for the northern California Current (Field et al. 2006), and 0.14–0.85 for the northern Humboldt Current (Tam et al. 2008). With the possible exception of the northern Humboldt Current, our values are similar. High *EE* values for small pelagic fishes in these ecosystems mean that these fish are of considerable importance and are highly utilized in both food chains and fisheries.

Pikitch et al. (2014) compared the total support service contribution of small pelagic fishes (including krill) to ecosystem predator production (S_z), and the support service contribution of small pelagic fishes to the catch of other commercially targeted species (S_c), for 72 ecosystems. Values of S_z and S_c estimated by our model rank the western North Pacific among the top 10 of these ecosystems (Figs. 3 & 5 in Pikitch et al. 2014). This suggests that the contribution of small pelagic fishes (including krill) to both predator production and commercial catch of other species in the western North Pacific is high compared with many other ecosystems (for which comparable data are available).

Pikitch et al. (2014) summarized S_z by latitude into 'tropical-subtropical,' 'temperate,' and 'high latitude' groups, for which they reported S_z values of 1.18, 1.81, and 3.79 t km^{-2} yr^{-1}, respectively. At 4.77 t km^{-2} yr^{-1}, the western North Pacific supports more production than any one of these groups. Our model can be classified to the temperate group in the sense of Pikitch et al. (2014). Most ecosystems formerly classified as 'temperate' were 'non-upwelling coastal areas' or 'semi enclosed areas' (Pikitch et al. 2014), in contrast to our situation where the western North Pacific represents an open ocean ecosystem. The proportion of catch of small pelagic fishes to the sum of S_z, S_c, and catch of small pelagic fishes including krill is 0.21 in our study. Although absolute values cannot be read from Pikitch et al. (2014), all of these values appear lower than averages for 'tropical-subtropical,' 'temperate,' and 'upwelling' ecosystems reported in that paper. The total production of small pelagic fishes allocated for services exceeded the direct catch of small pelagic fishes in our modeled area, indicating that S_z is higher than for other latitude groups, and suggesting that the impact of fisheries targeting small pelagic fishes (including krill) on the total production of small pelagic fishes (including krill) is small relative to other studied ecosystems investigated by Pikitch et al. (2014). In contrast, the proportion of catch of small pelagic fishes to the sum of S_z, S_c, and catch of small pelagic fishes excluding krill is 0.60 — quite different from those including krill in the analysis. Accordingly, if concerned about the role of small pelagic fishes in ecosystems, it might be prudent to exclude krill from the analysis.

Our static, mass-balanced Ecopath model is a first step towards understanding the ecosystem of the western North Pacific. However, the ability to forecast using a time-dynamic ecosystem model (e.g. Ecosim) would be of greater value to fisheries and environmental managers and stakeholders. Development of such an EwE model requires fitting of time series data (e.g. biomass or landing data) to incorporate density dependence, which best is done by evaluating how the EwE model can reproduce historical dynamics (Heymans et al. 2016). However, we need to construct Ecopath models for past years and collect these time series data for this approach. Time series data are available for landings of each functional group by block, and phytoplankton and zooplankton biomass by block, but not for biomass or catch per unit effort by block for many fish functional groups. If these steps are complete, we think that simulation of the quasi sub-model structure by Ecosim would be possible. This approach will contribute the logical next step for expanding our ecological knowledge of the western North Pacific.

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