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Evaluating the role of large jellyfish and forage fishes as energy pathways, and their interplay with fisheries, in the Northern Humboldt Current System

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ABSTRACT

Large jellyfish are important consumers of plankton, fish eggs and fish larvae in heavily fished ecosystems worldwide; yet they are seldom included in fisheries production models. Here we developed a trophic network model with 41 functional groups using ECOPATH re-expressed in a donor-driven, end-to-end format to directly evaluate the efficiency of large jellyfish and forage fish at transferring energy to higher trophic levels, as well as the ecosystem-wide effects of varying jellyfish and forage fish consumption rates and fishing rates, in the Northern Humboldt Current system (NHCS) off of Peru. Large jellyfish were an energy-loss pathway for high trophic-level consumers, while forage fish channelized the production of lower trophic levels directly into production of top-level consumers. A simulated jellyfish bloom resulted in a decline in productivity of all functional groups, including forage fish (12%), with the exception of sea turtles. A modeled increase in forage fish consumption rate by 50% resulted in a decrease in large jellyfish productivity (29%). A simulated increase of 40% in forage fish harvest enhanced jellyfish productivity (24%), while closure of all fisheries caused a decline in large jellyfish productivity (26%) and productivity increases in upper level consumers. These outcomes not only suggest that jellyfish blooms and fisheries have important effects on the structure of the NHCS, but they also support the hypothesis that forage fishing provides a competitive release for large jellyfish. We recommend including jellyfish as a functional group in future ecosystem modeling efforts, including ecosystem-based approaches to fishery management of coastal ecosystems worldwide.

1. Introduction

Forage fishes, defined here as small pelagic planktivorous fishes, not only represent the main food source of piscivorous fishes, seabirds, and marine mammals in marine ecosystems worldwide, but also comprise ~30% of global marine fisheries catch (Pikitch et al., 2014). Because of their importance as prey to broad diversity of predators, they are a crucial conduit for energy transfer between lower and higher trophic levels within marine foodwebs. This is particularly true in eastern boundary current ecosystems where fluctuations in forage fish abundance can alter the dynamics, structure and function of ecosystems (Smith et al., 2011). Forage fish production is highly susceptible to variations in environment and harvest rates (Chavez et al., 2003), with subsequent changes cascading upwards and downwards through the foodweb (Pauly et al., 1998; Daskalov et al., 2007). Such susceptibility has encouraged policy-makers and managers to implement ecosystem-based fishery modeling efforts to conserve and manage forage fish populations (Alder et al., 2008; Pikitch et al., 2012).

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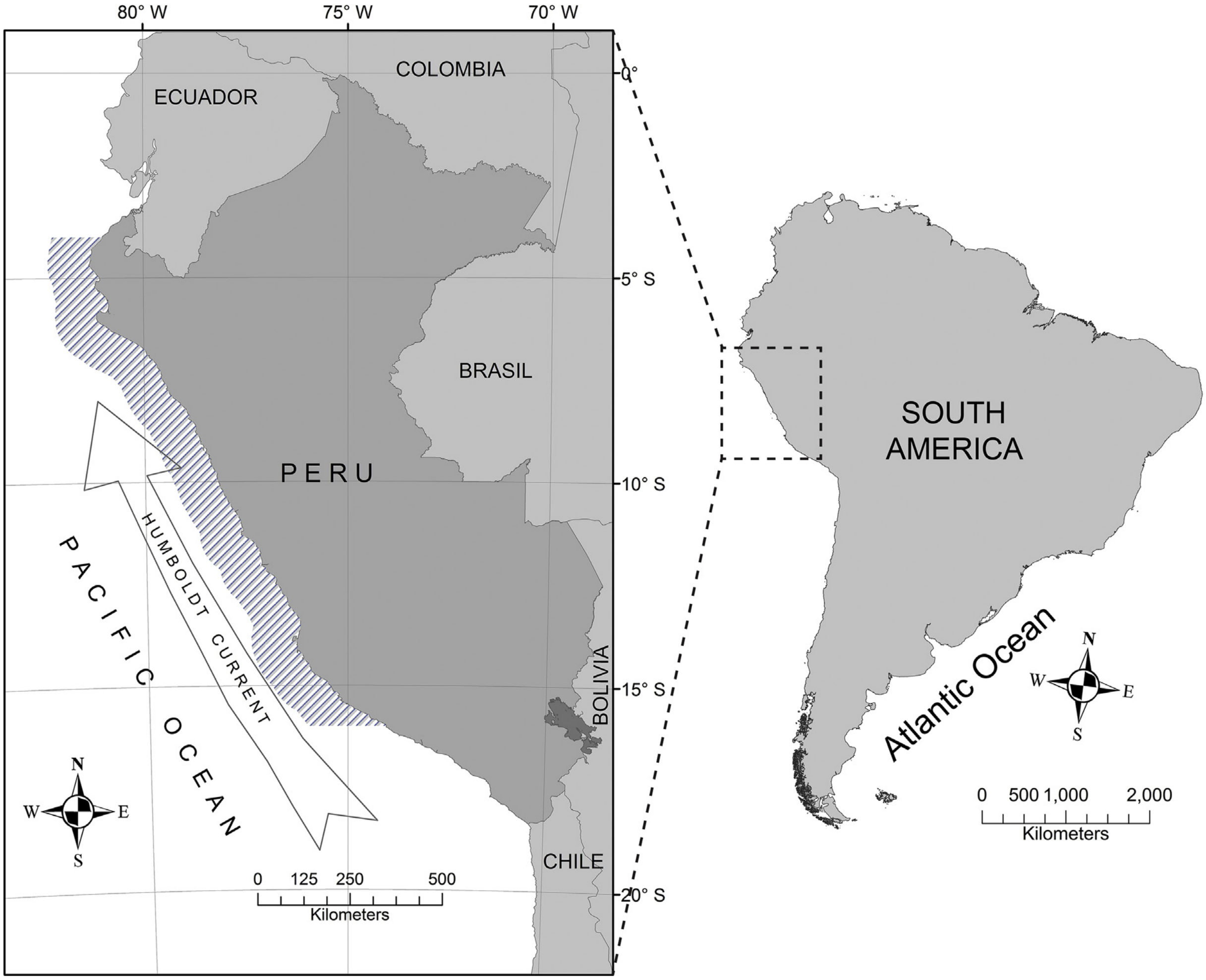

Fig. 1. Map of the study area (shaded area) covering from 4°S to 16°S, and up to 111 km (60 nm) from the coastline, in the Northern Humboldt Current Ecosystem.

Ecosystem production models, however, focus only on parameters with a direct link to fish, such as those associated with fish food and fish predators and prey (Walters et al., 2008; Pauly et al., 2009). Less consideration is given to other ecologically important components with indirect links to fish, such as large jellyfish. These gelatinous zooplanktivorous predators can not only compete with forage fish for food and prey on their eggs and larvae (Hansson et al., 2005; Zeman et al., 2016), but they also often form large, seasonal blooms that can dominate the coastal pelagic biomass. The lack of adequate parameterization of jellyfish in ecosystem production models may be due to the paucity of system-specific data (Condon et al., 2012), to an under appreciation of their role in marine foodwebs (Pauly et al., 2009), or to the perception that they are "trophic dead ends" (Robinson et al., 2014). However, recent studies have synthesized biomass data for multiple gelatinous taxa (Lucas et al., 2014) and demonstrated that gelatinous plankton are frequently consumed by fish (Mianzan et al., 1996; Cardona et al., 2012; Milisenda et al., 2014), deep sea scavengers (Sweetman et al., 2014), and sea turtles (Heaslip et al., 2012; Heithaus, 2013).

The absence of jellyfish in ecological foodweb models in heavily-fished ecosystems like those in eastern boundary currents is concerning because evidence suggests that jellyfish populations can go through extended periods of high abundance (Condon et al., 2013). Size and frequency of jellyfish blooms are affected by climate (Lynam et al., 2011; Chiaverano et al., 2013; Robinson and Graham, 2014), habitat modification (Lo et al., 2008), eutrophication (Oguz, 2005), hypoxia (Purcell et al., 2001; Graham, 2001), and overfishing (Roux et al., 2013). Previous studies on ecosystem-wide effects of jellyfish blooms in intensively fished ecosystems like the Northern California Current (Ruzicka et al., 2012), Gulf of Alaska (Ruzicka et al., 2013), the Black Sea (Kideys et al., 2005), and the northern Gulf of Mexico (Robinson et al., 2015) indicate an inverse relationship between jellyfish production and forage fish production. Because jellyfish and forage fish overlap in space and time (Brodeur et al., 2008; Decker et al., 2018) and diets (Brodeur et al., 2008; Purcell and Sturdevant, 2001), the removal of forage fish through harvest may indirectly enhance jellyfish production by increasing prey availability (Robinson et al., 2014).

Eastern boundary currents, like the northern part of the Humboldt Current System (NHCS) off of the Peruvian coast, are among the most productive in the world (Pennington et al., 2006; Bakun and Weeks, 2008). The NHCS experiences year-round upwelling (Carr, 2001) and supports large forage fish fisheries, including sardines *Sardinops sagax* (Chavez et al., 2008; Cardenas-Quintana et al., 2015) and the world's largest fishery by weight for anchovy *Engraulis ringens* (Pennington et al., 2006; Chavez et al., 2008). These forage fishes overlap spatially and temporally in the NHCS with scyphomedusae of *Chrysaora plocamia* (Quiñones et al., 2015). These large (~50 cm bell diameter) jellyfish can dominate the pelagic biomass in this system, comprising as much as 70% (wet weight) of the total pelagic catch during periods of high abundance (Quiñones et al., 2013). Previous studies revealed that *C. plocamia* diets include anchovy eggs (Riascos et al., 2014) and forage fish prey (see Espinoza and Bertrand, 2008; Espinoza et al., 2009), thus, spatio-temporal overlap between forage fish and large jellyfish in the NHCS may result in predatory and competitive interactions. These trophic interactions are expected to affect forage fish harvests, which averages ~6.5 million tons year^{-1} (1950–2001; FAO, 2011). Although the NHCS has been modeled extensively using carbon and nitrogen budget models (Walsh, 1981), mass balance models (Jarre and Pauly, 1993), carbon flow models (Carr, 2001), and steady-state models (Tam et al., 2008), none of these models have included large jellyfish and their interactions with forage fish.

In this study, we adopted a steady-state trophic model for the NHCS previously developed by Tam et al. (2008) and added data on large jellyfish (*C. plocamia*), marine turtles, anchovy eggs, and fishery discards in order to quantify for the NHCS: (1) the efficiency of large jellyfish and forage fish at transferring energy to upper trophic levels through the foodweb, and (2) the ecosystem-wide effects of changes in large jellyfish and forage fish consumption rates, and fishery harvests.

2. Data and models

A steady-state foodweb model for the NHCS was constructed based on the models previously developed by Tam et al. (2008). The model domain covers an area of 165,000 km^2, extending from 4°S to 16°S and out to 111 km (60 nm) from the shoreline (Fig. 1). The model was constructed using ECOPATH (Christensen and Pauly, 1992), which uses a mass-balance approach to estimate energy flows between pre-defined functional groups. Net production of a given group equals energy losses via predation, fishery catch rates, senescence, and net migration according the following Eq. (1).

$$b_p \times \left(\frac{p}{b}\right)_p \times ee_p = y_P + \sum b_c \left(\frac{q}{b}\right)_p \times D_{pc} + ba_p + nm_p \tag{1}$$

where b_p is the biomass of a producer or prey group (p), b_c is the biomass of a consumer group (c), $(p/b)_p$ is the production rate per unit of biomass, ee_p is the fraction of total group production utilized within the ecosystem (i.e., ecotrophic efficiency), y_p is the fisheries catch rate per unit area and time, $(q/b)_p$ is the food consumption rate per unit of biomass of consumer (c), D_{pc} is the contribution of producer (p) to the diet of consumer (c), ba_p is the biomass accumulation rate, and nm_p is the net migration rate of the producer. Using linear equations that represent each functional group (Eq. (1)) and wet weight biomass, ECOPATH constructs a matrix Q_{pc} describing the energy demand for each consumer through each trophic linkage of the foodweb.

The fully resolved NHCS model developed for this study includes 41 groups, including 36 living groups (-phytoplankton (2), zooplankton (3), jellyfish (2), macro invertebrates (3), bony fish (18), cartilaginous fish (2), fish eggs (1), seabirds (1), sea turtles (2), marine mammals (2)-), fisheries (2), and detritus pools (3) (Supplementary Table A). The 41 groups included in the fully resolved model were aggregated into 25 functional groups (Table 1) following the criteria described in Robinson et al. (2015).

Our base model was constructed using data on fisheries catch (y, t km^{-2} y^{-1}), as well as biomass (b, t km^{-2} y^{-1}), production/biomass ratio (p/b y^{-1}), consumption/biomass ratio (q/b), and diet composition for phytoplankton, zooplankton (including small gelatinous zooplankton), fish (except sardine and anchovy), seabird, and marine mammals from Tam et al. (2008) and averaged over the period 1995–1998. The ecotrophic efficiency (ee) data for other small and large pelagic fish, hake, small and medium demersal fish, benthic elasmobranchs, chondrichthyans, and seabirds were borrowed from Guénette et al. (2008). Large jellyfish (*C. plocamia*) biomass data were obtained from Quiñones et al. (2015). Because the distribution of *C. plocamia* medusae is not homogeneous within the model domain (see Quiñones et al., 2018), annual (from 1975 to 2014) mean biomasses were estimated by using a delta-distribution following the method described by Pennington (1996). Large jellyfish biomass was expressed in kg wet weight (WW) 1000 m^{-3} and converted to tons (t) WW km^{-2} y^{-1} by integrating the top 7.5 m of the water column, which represents the layer in which *C. plocamia* medusae typically occur (Quiñones, pers. obs.). Diet composition of *C. plocamia* was obtained from previous studies (Ceh et al., 2015; Aller, 2017). Values of p/b and q/b for *C. plocamia* medusae were borrowed from the Northern California Current models of Ruzicka et al. (2012). Diets of forage fishes (anchovy and sardine) were updated from Tam et al. (2008) by adding data from Espinoza and Bertrand (2008) and Espinoza et al. (2009). Abundances of green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) turtles in the NHCS were derived from fisheries by-catch (Alfaro-Shigueto et al., 2011) and survey data (2010–2015, Quiñones, unpub. data). Sea turtle biomass estimates were obtained from growth equations (Jones et al., 2011) using a mean curved carapace length (CCL) of 58.7 cm and 139.6 cm for green and leatherback turtles, respectively (Alfaro-Shigueto et al., 2011). Diets of sea turtles were compiled from IMARPE (2011), Paredes (2015) and Quiñones et al. (2010). Both p/b and q/b values for sea turtles were borrowed from Robinson et al. (2015). Anchovy egg biomass was estimated using mean density of anchovy eggs in the NHCS from Lett et al. (2007) and egg volume/mass (Castro et al. 2009). Production rates of anchovy eggs were assumed to be 25% (Ruzicka et al. 2012; Robinson et al. 2015). Fishery discards were obtained by reconstructing catches using gear-specific discard rates (%) described in Kelleher (2005). A discard rate of 10% was assumed for all artisanal fisheries. In order to achieve a balanced model, we only reduced sardine landings from 5.65 t km^{-2} year^{-1} (1995–1998 average; Tam et al., 2008) to 1.4 t km^{-2} year^{-1}.

In order to estimate ecosystem-wide consequences of changes in forage fish and large jellyfish abundances, or changes in fishery harvest rates (e.g., Robinson et al., 2015), the steady-state ECOPATH solution for the foodweb as a "top-down" network of consumer demands (Q_{pc}) was re-expressed as a "bottom-up" map of production fate (A_{cp}) using the ECOTRAN technique described in Steele and Ruzicka (2011).

$$A_{cp} = \frac{D_{pc} Q_c}{\sum_c Q_c D_{pc}} \tag{2}$$

where A_{cp} is the production matrix, the fraction of the total production of each producer (p) consumed by each consumer (c), and Q_c is the total consumption rate of consumer (c). Senescence and egestion flows to detritus and bacterial metabolism of detritus into recycled nutrient pools were added to the production matrix A_{cp} as separate functional groups. Thus, the model is an end-to-end model in the strict sense of the term, tracking production flowing upwards through the foodweb from nutrient inputs to the production of top consumers and fisheries, and downwards via the recycling of detritus and nutrients. Metabolic rates were estimated from the defined ECOPATH physiological parameters as described in Ruzicka et al. (2012) and distributed between pelagic and benthic pools according to life histories and behaviors of each functional group. The efficiency of large jellyfish and forage fish to transfer energy to upper trophic levels in the foodweb was evaluated by using the "footprint" and "reach" metrics (Ruzicka et al., 2012). The ecosystem level "footprint" of a particular group of interest is the fraction of total production in the ecosystem required to support that group. The ecosystem level "reach" is the fractional contribution of a particular group of interest to total consumer production in the ecosystem via all direct and indirect trophic pathways.

Structural scenarios were performed to evaluate the ecosystem-wide effects of changes in biomass and consumption rates of large jellyfish and forage fish, as well as changes in fishery catch rates (see Ruzicka et al., 2012; Robinson et al. 2015). A structural scenario is generated by changing the consumption demands or production rates of one or more groups and re-calculating the energy flow rates through a steady state representation of the foodweb (matrix Acp, Eq. (2)). Structural scenarios represent linear, asymptotic solutions of time-dynamic simulations (Collie et al., 2009; Steele et al., 2007). Four scenarios were run: (I) jellyfish boom (jellyfish consumption increased by 50%), (II) forage fish dominance (forage fish consumption increased by 50%), (III) increased fishing pressure (40% increase in forage fish harvest by fisheries, considering a mean harvest rate of 29 t km^{-2} y^{-1}, corresponding

Table 1
Aggregated ECOPATH model parameterization for the Northern Humboldt Current System (NHCS).

Group code	Functional group (Aggregated)	Biomass $t\ km^{-2}\ y^{-1}$	p/b y^{-1}	q/b	p/q	ae	ee	Landings $t\ km^{-2}\ y^{-1}$	Discards $t\ km^{-2}\ y^{-1}$
4	Large phytoplankton	34.09	237.50				0.82	0.00	0.00
5	Small phytoplankton	13.38	237.50				0.97	0.00	0.00
6	Microzooplankton	13.54	256.00	1024.00	0.25	0.80	0.96	0.00	0.00
7	Mesozooplakton	24.08	40.00	125.00	0.32	0.65	0.92	0.00	0.00
8	Macrozooplankton	37.42	19.09	46.55	0.41	0.80	0.95	0.00	0.00
9	Small jellyfish	0.01	0.58	2.92	0.20	0.65	0.95	0.00	0.00
10	Large jellyfish	8.46	15.00	56.00	0.27	0.65	0.00	0.00	0.00
11	Macrobenthos	23.17	1.20	10.00	0.12	0.80	0.79	0.00	0.00
12	Forage fish	69.05	1.91	14.51	0.13	0.65	0.82	28.13	0.87
13	Mesopelagics	14.63	1.40	14.00	0.10	0.65	0.26	0.00	0.00
14	Cephalopods	2.19	5.11	12.59	0.41	0.80	0.89	0.13	0.01
15	Pelagic planktivorous fish	11.01	1.00	9.98	0.10	0.65	0.89	1.52	0.17
16	Pelagic piscivorous fish	16.16	0.99	9.46	0.10	0.70	0.21	2.72	0.11
17	Demersal piscivorous fish	2.37	1.20	7.97	0.15	0.68	0.62	1.06	0.21
18	Demersal planktivorous fish	5.78	2.40	15.30	0.16	0.80	0.68	0.02	0.00
19	Demersal benthivorous fish	1.17	1.08	7.23	0.15	0.80	0.79	0.53	0.06
20	Apex predatory fish	0.05	0.49	3.24	0.15	0.80	0.56	0.01	0.00
21	Seabirds	0.04	0.04	61.00	0.00	0.80	0.00	0.00	0.00
22	Marine mammals	0.13	0.10	25.83	0.00	0.77	0.00	0.00	0.00
23	Sea turtles	0.00	0.19	3.50	0.05	0.80	0.00	0.00	0.00
24	Fish eggs	0.44					0.87	0.00	0.00
25	Detritus offal	0.05					0.00	0.00	0.00
26	Pelagic detritus	20.00					0.00	0.00	0.00
27	Benthic detritus	60.00					0.89	0.00	0.00
28	Fisheries								

to forage fish landings and discards; see Table 1), and IV) fishery moratorium (the closing of all fisheries). Total predation pressure on each prey type was left unchanged. Changes in predation pressure upon a prey group by a modified consumer were balanced by proportional changes to the predation pressure exerted by all other consumers of the shared prey (Robinson et al., 2015). Scenario results are reported as the fractional change in production of each functional group caused by the scenario modifications (fractional change = ($P_{\text{scenario model}} - P_{\text{base model}}$)/$P_{\text{base model}}$). Indices of confidence for all model-derived metrics and scenarios were estimated via Monte Carlo analysis. One thousand alternate models were randomly generated by drawing from a normal distribution about each trophic connection defined within production matrix A_{cp}. The level of uncertainty about each element of the production matrix was calculated from the defined levels of uncertainty for each model parameter (biomass, P/B, P/Q, AE, diet, landings, and discards; see Supplementary Table I). Scenarios were repeated using each randomly generated model. Scenarios I and II were also run under alternate levels of uncertainty about biomass, growth efficiency (P/Q), and diet (see Supplementary Material).

3. Results

The input data for the aggregated base model of the NHCS is summarized in Table 1. Additional details on the fully resolved and aggregated model parameters can be found in the Supplementary Material section.

3.1. Foodwebs

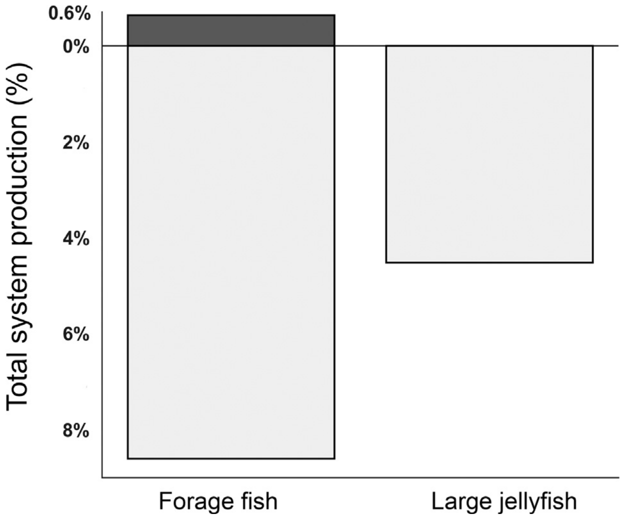

Fig. 2. System-wide reach (dark grey) and footprint (light grey) metrics for forage fish and large jellyfish in the northern Humboldt Current System. Reach is the percent of total system production produced by, or passing through, each target group, while footprint is the total system production consumed by the target group. The reach of large jellyfish does not show up in the graph because of a comparatively much lower value than that of forage fish (see Results).

Forage fish and large jellyfish exhibited similar system footprint values (7.3×10^{-2} and 4×10^{-2}, respectively). However, the system reach of forage fish (7×10^{-3}) was four orders of magnitude larger than that of large jellyfish (*C. plocamia*) (2×10^{-7}), suggesting that in the NHCS forage fish are considerably more important as an energy transfer nexus to top consumers than jellyfish (Fig. 2). Foodweb network diagrams of flow patterns to (footprint) and from (reach) forage fish and large jellyfish illustrate how forage fish are a more efficient, direct energy pathway from phytoplankton to top-level consumers than are large jellyfish which act as an energy-loss pathway by diverting energy away from higher trophic-level consumers (Fig. 3). The greater energy transfer efficiency of forage fish is highlighted by the large fraction of energy (i.e., thicker lines) flowing from phytoplankton and zooplankton groups to forage fish, and from there to upper trophic levels, including apex pelagic fish predators, piscivorous demersal fish, seabirds, marine mammals, and fisheries (Fig. 3A). In contrast, large jellyfish diverted zooplankton and phytoplankton production away from top consumers, which is highlighted by the smaller fraction of energy (i.e., thinner lines) transferred upwards to higher trophic levels (Fig. 3B). Instead, large jellyfish in this system directly supported production of only small planktivorous fishes and marine turtles (Fig. 3B).

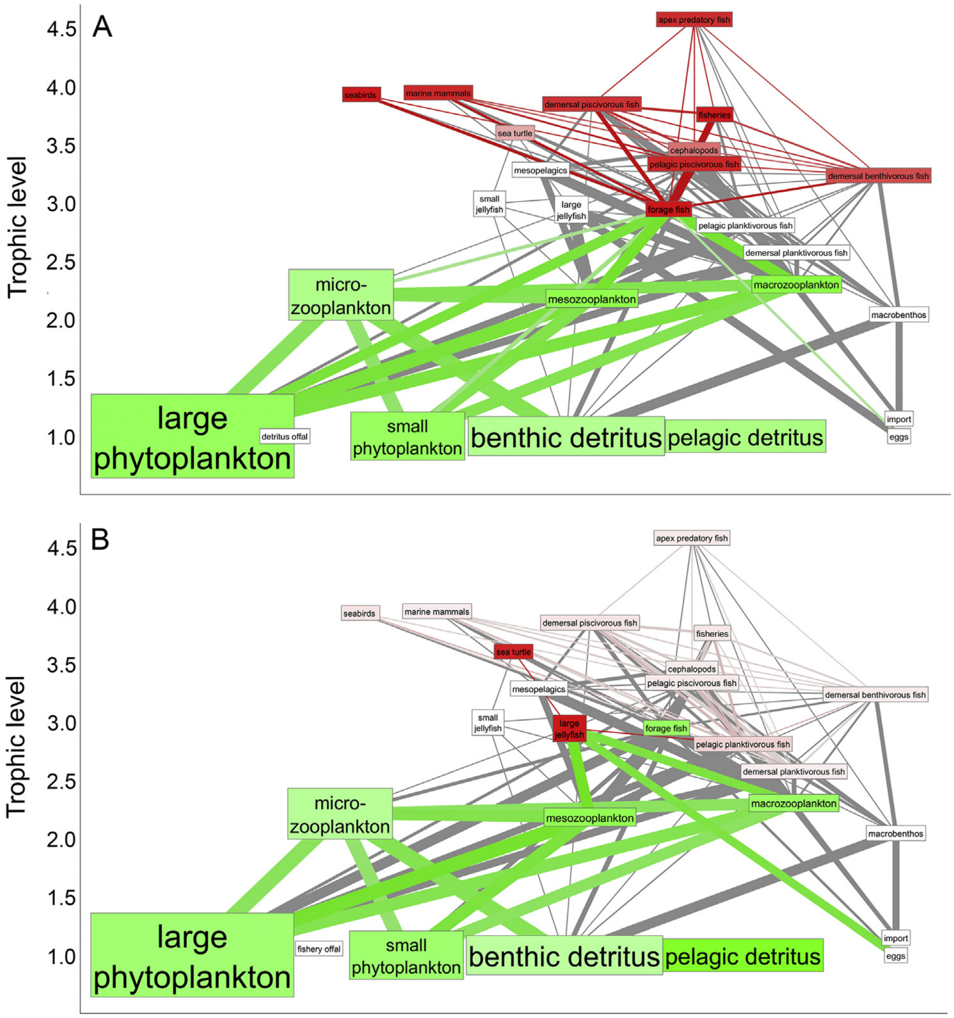

Fig. 3. Comparative food web diagrams highlighting energy flow patterns to (footprint, green) and from (reach, red) forage fish (A) and large jellyfish (B) in the Northern Humboldt Current system. Box size is proportional to functional group biomass. Color intensity and width of lines are scaled to the amount of energy flow between forage fish and large jellyfish and the rest of the functional groups.

3.2. Structural scenarios

In our jellyfish bloom scenario (Scenario I), we found that the modeled NCHS could only support only a 39% increase in large jellyfish consumption, limited by the production of jellyfish prey. A 39% increase in jellyfish biomass and consumption demands resulted in declines in productivity among most mid-trophic level and upper-trophic level groups (Fig. 4A, Table 2). By contrast, sea turtles were the only group that exhibited an increase in production (Fig. 4A, Table 2). Interestingly, a 39% increase in large jellyfish consumption yielded a 13% decline in productivity of fisheries (Fig. 4A, Table 2).

The impacts of increasing forage fish consumption by 50% (Scenario II) had a considerable negative impact upon the production of large jellyfish, mesopelagic fish cephalopods, pelagic planktivorous fish, and sea turtles (Fig. 4B, Table 2). Production of seabirds, anchovy eggs and fisheries however, increased under this scenario (Fig. 4B, Table 2). Relatively small negative effects on the production of zooplankton, all piscivorous fish, and top predatory fish were observed under this scenario (Fig. 4B, Table 2).

The increased fishing pressure scenario (Scenario III, 40% increase in removal of forage fish by fisheries) resulted in large productivity increases of mid-trophic groups (demersal and pelagic planktivorous fish and large jellyfish) and upper level consumers (mesopelagic fish, cephalopods, and sea turtles (Fig. 4C, Table 2). Seabird and anchovy egg production exhibited the largest decline in productivity (−30% and −44%, respectively) (Fig. 4C, Table 2).

The closure of all fisheries (Scenario IV) resulted in large productivity increases of forage fish and demersal benthivorous fish, as well as in most upper-level consumers, including demersal piscivorous and apex predatory fish, seabirds, and marine mammals (Fig. 4D, Table 2). By contrast, relatively large productivity declines were observed in most mid-trophic level groups, including large jellyfish, mesopelagic fish, and pelagic and demersal planktonic fish (Fig. 4D, Table 2). Productivity of upper-level consumers, such as cephalopods and sea turtles also declined (Fig. 4D and Table 2).

4. Discussion

4.1. Foodwebs

Footprint and reach metrics calculated from the NHCS foodweb model indicate that increases in large jellyfish (*C. plocamia*) could make the foodweb considerably less efficient at transferring energy to upper trophic levels than when forage fish are abundant. Forage fish in this system had a larger footprint (0.07) than jellyfish (0.04), indicating that forage fish are using more of the total system production relative to jellyfish. Large jellyfish however, had a reach (2×10^{-7}) four orders of magnitude smaller than forage fish (7.3×10^{-3}), resulting in a much smaller contribution by jellyfish to the production of upper-level consumers. Large jellyfish in the NHCS directly contributed to the

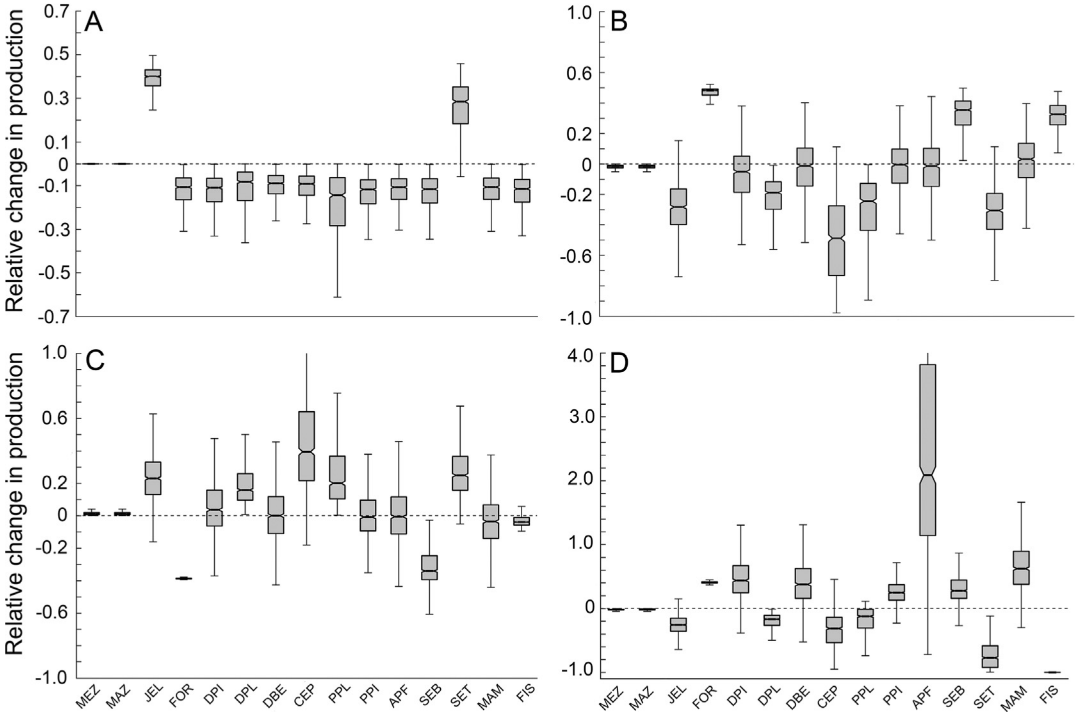

Fig. 4. System responses to a modeled (A) jellyfish bloom (Scenario I), (B) forage fish dominance (scenario II), (C) overfishing of forage fish (scenario II), and (D) fisheries moratorium (Scenario IV). MES: mesozooplankton, MAC: macrozooplankton, JEL: large jellyfish, FOF: forage fish, DPI: demersal piscivorous fish, DPL: demersal planktivorous fish, DBE: demersal benthivorous fish, CEP: cephalopods, PPL: pelagic planktivorous fish, PPI: pelagic piscivorous fish, APE: apex predatory fish, SEB: seabirds, TUR: sea turtles, MAM: marine mammals, FIS: fisheries. Box: 25–75% quartile, whiskers: min–max. Notice different scale in Y-axis.

production of only planktivorous fish (mostly butterfishes) and sea turtles (mainly leatherbacks). However, considering all direct and indirect pathways of energy flow in the NHCS, large jellyfish indirectly supported several higher-order consumers in the system (Fig. 3). Therefore, large jellyfish cannot be considered as trophic dead-ends in the NHCS. This is in line with previous studies showing that large jellyfish can support the production of several taxa, such as parasitic cnidarians (Chiaverano et al., 2015), crustaceans (Fleming et al., 2014),

Table 2
Mean (standard deviation) fractional changes (%) in the production of aggregated functional groups in response modeled scenarios. Scenario I: jellyfish bloom. Scenario II: forage fish dominance. Scenario III: increased fishing pressure. Scenario IV: fisheries moratorium. Fractional change = (scenario model − base model)/ base model) × 100. Values lower than 0.01% are indicated by dash symbols.

Code	Aggregated functional group	Scenario I	Scenario II	Scenario III	Scenario IV
1	NO3	–	–	–	–
2	Pelagic NH4	−1.1 (0.7)	0.9 (0.9)	−0.8 (0.8)	1.2 (0.9)
3	Benthic NH4	3.0 (1.6)	−4.5 (1.9)	3.7 (1.6)	−3.7 (1.7)
4	Large phytoplankton	–	–	–	–
5	Small phytoplankton	–	–	–	–
6	Microzooplankton	0.1 (0.05)	−1.8 (1.2)	1.4 (1.0)	−1.6 (1.1)
7	Mesozooplankton	–	−1.9 (1.5)	1.5 (1.2)	−1.7 (1.3)
8	Macrozooplankton	0.01 (0.01)	−1.9 (1.7)	1.5 (1.2)	−1.8 (1.5)
9	Small jellyfish	−28.9 (22.5)	−49.9 (26.7)	47.1 (34.9)	−45.7 (24.9)
10	Large jellyfish	38.5 (6.7)	−28.9 (16.5)	24.0 (15.3)	−26.2 (14.8)
11	Macrobenthos	0.9 (0.6)	−0.4 (1.0)	0.3 (0.8)	−0.1 (0.9)
12	Forage fish	−12.4 (7.8)	46.3 (4.5)	−38.7 (0.4)	40.0 (3.1)
13	Mesopelagic fish	−14.1 (11.1)	−56.3 (26.9)	52.3 (32.3)	−51.5 (24.9)
14	Cephalopods	−11.4 (8.6)	−49.8 (26.4)	47.1 (34.7)	−34.1 (28.3)
15	Pelagic planktivorous fish	−20.2 (18.9)	−30.5 (22.4)	27.9 (25.4)	−18.9 (23.2)
16	Pelagic piscivorous fish	−14.0 (9.5)	−2.6 (17.4)	1.7 (17.3)	−24.4 (20.1)
17	Demersal piscivorous fish	−12.9 (8.7)	−6.9 (18.1)	5.2 (18.5)	48.1 (36.2)
18	Demersal planktivorous fish	−12.8 (13.0)	−22.5 (14.6)	20.9 (18.4)	−20.6 (13.6)
19	Demersal benthivorous fish	−10.4 (6.8)	−2.7 (18.8)	1.8 (20.8)	41.7 (40.7)
20	Apex predatory fish	−12.4 (7.9)	−3.3 (20.1)	2.1 (21.8)	297 (300)
21	Seabirds	−13.7 (9.2)	30.9 (15.2)	−30.3 (15.1)	31.6 (30.1)
22	Marine mammals	−12.4 (8.2)	1.7 (16.4)	−2.8 (17.1)	66.3 (43.1)
23	Sea turtles	25.2 (14.5)	−31.8 (16.5)	27.7 (17.9)	−73.4 (21.4)
24	Eggs	−12.4 (7.8)	46.3 (4.5)	−44.4 (4.5)	41.8 (23.2)
25	Detritus offal	−13.1 (8.0)	30.7 (10.2)	−.7 (4.6)	−100 (0)
26	Fisheries	−3.1 (8.0)	30.7 (10.2)	−2.7 (4.6)	−100 (0)
27	Pelagic detritus	0.05 (0.05)	−1.7 (1.2)	1.3 (0.9)	−1.5 (1.1)
28	Benthic detritus	0.9 (0.6)	−0.4 (1.0)	0.3 (0.8)	−0.01 (0.9)

fish (Purcell and Arai, 2001), and sea turtles (Cardona et al., 2012).

Forage fish in the NHCS represented one of the most important mid-trophic level groups for transferring energy upwards within the foodweb, channeling plankton production directly into production of upper-level consumers (Fig. 3). Therefore, when large jellyfish become highly abundant in this system (i.e., during blooms), the fraction of total ecosystem production, and the efficiency at which it is transferred upwards in the foodweb, can be substantially reduced compared to situations when forage fish dominate (i.e., non-bloom periods). These findings are in agreement with previous studies of the northern Gulf of Mexico (Robinson et al., 2015), the Northern California Current (Ruzicka et al., 2012), and the Eastern Bering Sea (Robinson et al., 2014) ecosystems, adding support to the proposed role of forage fish and large jellyfish as energy conduits and production-loss pathways, respectively, in pelagic marine ecosystems worldwide (Robinson et al., 2014).

4.2. Structural scenarios

Ecosystem-wide responses to a simulated jellyfish bloom (39% increase in jellyfish consumption, Scenario I) resulted in a decline in the productivity of almost all NHCS mid-trophic and upper level consumers (Fig. 4A). This finding is similar to the ecosystem responses observed in other marine pelagic ecosystems, including the Northern California Current (Ruzicka et al., 2012) and the Gulf of Mexico (Robinson et al., 2015). Previous studies indicate that forage fish and large jellyfish can overlap in their diets (Brodeur et al., 2008). Therefore, an increase in consumption by jellyfish could lead to decline in forage fish productivity by reducing prey availability. Forage fish and *C. plocamia* medusae appear to share prey items in the NHCS (see Ceh et al., 2015; Espinoza and Bertrand 2008; Espinoza et al., 2009; Supplementary Table B). Thus, during a jellyfish bloom there is likely a reduced prey availability to forage fish and other pelagic planktivorous taxa can consume in this system, which could result in productivity declines of planktivorous fish (Fig. 4A). Since scenario analyses account for trophic energy flows to functional groups via all direct and indirect pathways, the productivity declines of piscivorous and benthivorous fish, apex predatory fish, seabirds, and marine mammals (mainly pinnipeds) obtained in our modeled jellyfish bloom scenario are likely due to the declines in the production of their forage fish prey (Table 2). Considering how important forage fish are at transferring energy through the NHCS foodwebs (Fig. 3A), any factors affecting forage fish production are expected to have strong subsequent effects throughout the entire ecosystem. Under the jellyfish bloom scenario, sea turtles represented the only functional group that responded positively to an increase in jellyfish consumption. This outcome can be explained by the fact that *C. plocamia* medusae appear to be an essential prey item in the diet of leatherback and green sea turtles (Paredes, 2015; Quiñones et al., 2015) in the NHCS.

Increasing forage fish consumption by 50% (Scenario II) negatively impacted production of large jellyfish (29% decrease), while increasing forage fishing pressure by 40% (Scenario III) resulted in the opposite effect (24% increase in large jellyfish production). These model outcomes may be also explained by the aforementioned dietary overlap between *C. plocamia* medusae and forage fish in the NHCS. Increased forage fish consumption would therefore re-direct zooplankton production away from large jellyfish, which would negatively affect medusa growth and production (Parsons and Lalli, 2002). By contrast, the opposite effect is likely to happen when forage fish are removed by fisheries (Robinson et al., 2014). In addition, this is likely the mechanism driving the observed changes in productivity of cephalopods (excluding jumbo squid), mesopelagic fish, and planktivorous fish obtained under scenarios II and III because these groups are primarily zooplanktivorous in this system (see Supplementary Table B).

Despite the importance of forage fish in the NHCS as energy pathways to upper trophic levels, the changes in productivity of piscivorous fish obtained under these two scenarios were unexpectedly low (Table 2). Similar results were obtained under the same modeled scenarios for the northern Gulf of Mexico (Robinson et al., 2015). Plausible explanations for these outcomes are that most piscivorous fishes may not be food limited in this highly productive system (Carr, 2001), and that a 50% increase in forage fish consumption or a 40% increase of forage fish removal by fisheries is perhaps not sufficient to cause large changes in piscivorous fish productivity. In addition, most piscivorous fish included in our model have diverse diets and do not feed exclusively on forage fish (Supplementary Table B). Therefore, they may be able to compensate for reduced forage fish availability by consuming other prey items, such other small mesopelagic fish and macrozooplankton (Table 2). Nevertheless, our increased fishing pressure scenario resulting in changes in productivity of high-level consumers, including *C. plocamia*, supports findings from previous studies on other heavily fished systems in which forage fish harvesting altered the structure and dynamics of marine ecosystems (Jackson et al., 2001; Pikitch et al., 2014), and resulted in increased jellyfish populations (Lynam et al., 2011; Roux et al., 2013). Although *C. plocamia* abundance in the NHCS has not increased during periods of high fishing pressure on forage fish (Quiñones et al., 2015), overfishing could contribute to larger jellyfish blooms if it took place during periods of favorable environmental conditions for polyp asexual propagation and medusa growth. Previous work has shown that *C. plocamia* blooms occur mostly during the warm phase of ENSO events throughout the sardine-dominated El Viejo regime (Quiñones et al., 2015). Hence, during these periods, stock managers should design appropriate adaptation methods to determine fishing quotas in the NHCS.

Our modeled fishery moratorium (Scenario IV) resulted in an increase in productivity of forage fish and in a decline in productivity of large jellyfish and other planktivorous groups (mesopelagic fish and small cephalopods), most likely as a result of food competition. Competition for resources can also explain the declined productivity of pelagic piscivorous fishes, since this group is mainly represented (93%) by horse and chub mackerel, which also feed on zooplankton in this system (see Supplementary Table B). Under this scenario, productivity of most piscivorous fish, apex predatory fish, seabirds, and marine mammals increased, most likely due to the increased availability of forage fish as prey. Similar results have been obtained from "no fishing" scenarios modeled for the northern Gulf of Mexico, the Northern California Current, and the Bering Sea ecosystems, suggesting that forage fish, as well as piscivorous, apex predatory fish, and seabird production, are likely most susceptible to complete fishery closures (Robinson et al., 2014, 2015). Although a "no fishing" scenario is perhaps extreme and unrealistic, it represents a valuable exercise to examine the potential ecosystem-wide effects of fisheries, not only in the NHCS, but in heavily fished marine ecosystems worldwide.

An important result from our jellyfish bloom scenario (Scenario I) was a 13% decline in fisheries productivity overall (Table 2). In Peru, forage fish (anchovies and sardines) make up > 95% of the country's annual fishery (commercial and artisanal) landings, with the Peruvian anchoveta (*Engraulis ringens*) accounting for 99% of total forage fish landings (FAO, 2011). Thus, this model outcome suggests that when large jellyfish are abundant in this system, fisheries production can decrease mainly due to a negative effect of jellyfish increased consumption on forage fish production (Table 2), presumably through resource competition (see above). Although a 13% decrease in fisheries production may seem relatively low, consider that the Peruvian anchoveta fishery is one of the largest fisheries in the world, with an average annual landing of 6.5 million metric (FAO, 2011). Thus, a 13% decrease in productivity of this fishery would translate to a potential decline of ~845,000 tons of fish. In addition, our modeled jellyfish bloom represents a very conservative scenario (39% increase) in which the system is supporting ~12 t WW km^{-2} of jellyfish biomass. During exceptionally large bloom events in the NHCS, such as those occurred during 1976, 1982–83, 1986–87, and 2014 (Quiñones et al., 2015, 2018), *C. plocamia* biomass can reach up to 62, 37, 81 and 43 t WW km^{-2}, respectively, a biomass increase 2.9–6.4 times greater than our scenario. Hence, such events are expected to have a much higher negative impact on forage fish production, and consequently, on forage fish fisheries. During years of exceptionally large jellyfish blooms, harvest rates for forage fish and other upper-level fish may require to be adjusted so the system can support production of higher-trophic level consumers, including piscivorous fish, seabirds, and marine mammals (Cury et al., 2011; Pikitch et al., 2012). Our model scenarios did suggest that the ecosystem could support a maximum level increase in jellyfish consumption of about 39%. The structural scenarios run here estimated sustained production levels in perpetuity and were designed specifically to prevent the complete extinction of any model group. In reality, jellyfish blooms in the NHCS can greatly exceed this level for short time periods in localized regions (Quiñones et al., 2018). Future research including a seasonal, regional model will help to evaluate the potential effects of very large jellyfish blooms on forage fish and fisheries production in this upwelling region.

4.3. Limitations and caveats

As with all modeling approaches, there are certain aspects of our model that could be improved. First, additional quantitative estimates on the contribution of large jellyfish (and gelatinous zooplankton in general) to the diets of other consumers in this system are needed. Future studies should aim at evaluating the role of jellyfish as primary and alternative food sources of apex predatory fish and sea birds, as shown by recent studies in other marine systems (Cardona et al., 2012; Thiebot et al., 2017). In addition, our model may also be improved by including biomass of small jellyfish estimated from surveys using sampling gears that specifically target this group. Moreover, large jellyfish carcasses have been shown to play a critical role as energy pathways to benthic communities (Sweetman et al., 2014). In the NHCS, large aggregations of dead *C. plocamia* medusae have been observed during May-June on the seafloor of Bahía Independencia, Peru (14°14′S; 76°08′W), with various species of crabs, such as *Hepatus chilensis*, *Platymera gaudichaudii* and *Cancer plebejus* preying upon them (Quiñones, pers. obs.). Future studies on pelagic-benthic trophic links in the NHCS will also help to improve our model and to better understand the roles of large jellyfish in this ecosystem.

5. Conclusions

The present study represents the first evaluation of the role of forage fish and jellyfish as energy pathways, as well as the combined effect of fisheries, in energy pathways of the Northern Humboldt Current System. In the present study we have showed that forage fish are highly efficient at transferring energy from producers to top-level consumers, while large jellyfish are considerably less efficient as energy conduits by diverting energy from plankton producers into several low and mid-trophic level consumers. The results from all structural scenarios indicate that forage fish, large jellyfish, and forage fish fisheries are likely interrelated in the NHCS. Increases in jellyfish consumption led to reduced forage fish productivity, while increased forage fish consumption lead to a decline in jellyfish productivity. In addition the removal of forage fish by fisheries increased jellyfish production, while a fisheries moratorium resulted in a decrease in jellyfish production, presumably through competition for resources. Our findings therefore suggest a negative effect on forage fish productivity not only through fisheries harvest, but also through blooms of large jellyfish. These suggestions are in line with results from model simulations for other marine ecosystems, where removal of forage fish through fisheries yielded an increase in forage fish competitors, including large jellyfish (Robinson et al., 2014, 2015). Our findings, together with previous studies (Ruzicka et al., 2012; Robinson et al., 2014, 2015), suggest that interactions among large jellyfish, forage fish, and fisheries can have ecosystem-wide implications, particularly on upper trophic levels, since a decrease in forage fish production can result in reduced productivity of seabirds (Cury et al., 2011) and economically important pelagic fish (Smith et al., 2011; Pikitch et al., 2014). Therefore, we recommend jellyfish to be included as a functional group in future ecosystem modeling, as well as be considered as an indicator of ecosystem perturbations, in ecosystem-based approaches to fishery management of coastal ecosystems worldwide (Brodeur et al., 2016).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2018.04.009.

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