



# Biodiversity loss leads to reductions in community-wide trophic complexity

SCOTT S. GABARA <sup>1,2,†</sup> BRENDA H. KONAR,<sup>3</sup> AND MATTHEW S. EDWARDS <sup>1</sup>

<sup>1</sup>Department of Biology & Coastal Marine Institute Laboratory, San Diego State University, San Diego, California 92182 USA

<sup>2</sup>Department of Environmental Science and Policy, University of California, Davis, California 95616 USA

<sup>3</sup>College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA

**Citation:** Gabara, S. S., B. H. Konar, and M. S. Edwards. 2021. Biodiversity loss leads to reductions in community-wide trophic complexity. *Ecosphere* 12(2):e03361. 10.1002/ecs2.3361

**Abstract.** With increasing biodiversity loss occurring worldwide, there is a need to understand how these losses will affect ecosystem structure and function. Biodiversity loss leads to changes in species interactions and alters the trophic complexity of food webs. These alterations to trophic complexity can be described by changes to the diversity of food resources and the diversity of trophic levels. To understand how biodiversity affects trophic complexity of food webs, we used 10 islands across the Aleutian Archipelago to compare the alternate state communities found in kelp forest ecosystems (kelp forest and urchin barren communities) and then compared these to natural reference communities without local benthic production (their associated offshore communities). We constructed food webs for each community across the Aleutian Archipelago using primary producer and consumer carbon ( $\delta^{13}\text{C}$ , a proxy for food sources to a consumer) and nitrogen ( $\delta^{15}\text{N}$ , a proxy for consumer trophic level) stable isotope values. Our findings suggest that biodiversity loss (i.e., phase change from kelp forest to urchin barren) leads to reductions in trophic complexity, which was similar to naturally occurring communities with low local resource biodiversity. This was expressed by lower consumer isotopic dietary niche areas, especially omnivores and herbivores, and lower omnivore and carnivore trophic levels within the urchin barren communities. We clarify how biodiversity promotes food resources and increases trophic levels and complexity through critical trophic conduits.

**Key words:** Aleutian Archipelago; biodiversity loss; food webs; isotopic dietary niche breadth; keystone species; stable isotope ecology; trophic ecology.

**Received** 1 May 2020; revised 21 August 2020; accepted 3 September 2020; final version received 10 December 2020. Corresponding Editor: Hunter S. Lenihan.

**Copyright:** © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** scottgabara@gmail.com

## INTRODUCTION

A conspicuous effect of habitat loss in terrestrial, aquatic, and marine ecosystems is that a decrease in biodiversity often leads to a subsequent reduction in the function of ecological communities (O'Connor and Byrnes 2014, Tilman et al. 2014). Less studied are the changes in species interactions with reductions in

biodiversity, specifically food web interactions and trophic ecology (Barnes et al. 2018). Reductions in biodiversity may alter trophic pathways and affect food web structure and function in different ways. One perspective is to consider how the loss of horizontal biodiversity (i.e., diversity in food sources) and vertical biodiversity (i.e., diversity in trophic levels) affects food web structure. Distinguishing between changes in these

dimensions is important as biodiversity loss may affect them separately or simultaneously (Duffy et al. 2007). For example, coral reef habitat loss leads to shifts in the base of the food web (horizontal biodiversity) from turf algae and epiphytes to particulate organic matter. However, this occurred with no change to food chain length (vertical biodiversity) or consumer isotopic dietary niche breadth, which incorporates both vertical and horizontal biodiversity (Morillo-Velarde et al. 2018). This contrasts consumer responses to mangrove habitat loss where the base of the food web shifts from seagrass and macroalgae to benthic microalgae, with concurrent reductions in overall food chain length (vertical biodiversity) and reduced consumer isotopic dietary niche breadth (both horizontal and vertical biodiversity; Layman et al. 2007b). There is insufficient evidence for how biodiversity loss, and in particular functional consumer group diversity, scales-up to whole ecosystems (Cardinale et al. 2011). For kelp forests, the use of survey data to infer community-wide changes with biodiversity loss suggests shifts in the base of the food web supporting consumers from phytodetritus and attached perennial macroalgae to phytoplankton, microalgae, and macroalgae (Graham 2004). Predictions for the impacts of kelp forest biodiversity loss do not quantify energy flow, or trophic connections, and are largely based on ephemeral urchin barrens in Southern California (Ebeling et al. 1985, Graham 2004). Therefore, the effects of kelp forest biodiversity loss on community trophic ecology remain unquantified.

Sea otters, once distributed across the Pacific from Japan to Baja California, were hunted to near extinction during the Pacific maritime fur trade of the 18th and 19th centuries (Lensink 1960, Estes and Duggins 1995). Differential recovery of sea otters across the Aleutian Archipelago caused spatial variation in abundance among islands in the mid to late 1900s (Lensink 1960, Kenyon 1969, Reisewitz et al. 2006). In the late 1990s, sea otter abundance declined rapidly and synchronously across much of the archipelago (Doroff et al. 2003), potentially due to predation by killer whales (Estes et al. 1998). Reductions in sea otters across the Aleutian Archipelago, first due to harvest by the indigenous Aleut (Simenstad et al. 1978), then due to

harvest during the Pacific maritime fur trade, and more recently due to predation by killer whales, have led to reductions in sea otter densities and a top-down release on sea urchin foraging and behavior (Estes et al. 1998, 2004, Konar and Estes 2003, Konar et al. 2014). The release of predation pressure on sea urchins has resulted in widespread kelp deforestation through the formation of urchin barrens (areas with abundant sea urchins and devoid of most fleshy macroalgae). These urchin barrens can occur, and be maintained, in close proximity to kelp forests (Konar and Estes 2003, Konar et al. 2014) and have persisted for decades in some locations (Filbee-Dexter and Scheibling 2014, Konar et al. 2014). Some consequences of reduced sea otter abundances and the phase shift from kelp forests to urchin barrens are a reduction in the abundance and biodiversity of macroalgae (Metzger et al. 2019), reductions in ecosystem productivity and respiration (Edwards et al. 2020), decreases in spatial variability in community structure (Edwards and Konar 2020), reductions in kelp particulate organic matter and bivalve growth (Duggins et al. 1989), increases in sea star predation on invertebrates (Vicknair and Estes 2012), declines in fish abundance like rock greenling *Hexagrammos lagocephalus* (Reisewitz et al. 2006), and shifts in the diets of eagles from fish to birds (Anthony et al. 2008).

Consequently, widespread and long-term kelp deforestation due to urchin barren formation presents an opportunity to test how reductions in horizontal and vertical biodiversity affect consumer isotopic dietary niche breadth and trophic complexity that lead to changes in ecosystem function. Ultimately, we also have a system to estimate the importance of macroalgal biodiversity to nearshore food web structure. Specifically, we hypothesized that reductions in primary producer biodiversity (horizontal biodiversity) will lead to reductions in trophic levels (vertical biodiversity), community-wide isotopic dietary niche breadth, and therefore trophic complexity.

## METHODS

Primary producers and consumers were collected from 10 islands that span the Aleutian Archipelago (Attu, Nizki, Kiska, Amchitka, Adak, Atka, Yunaska, Chuginadak, Umnak,

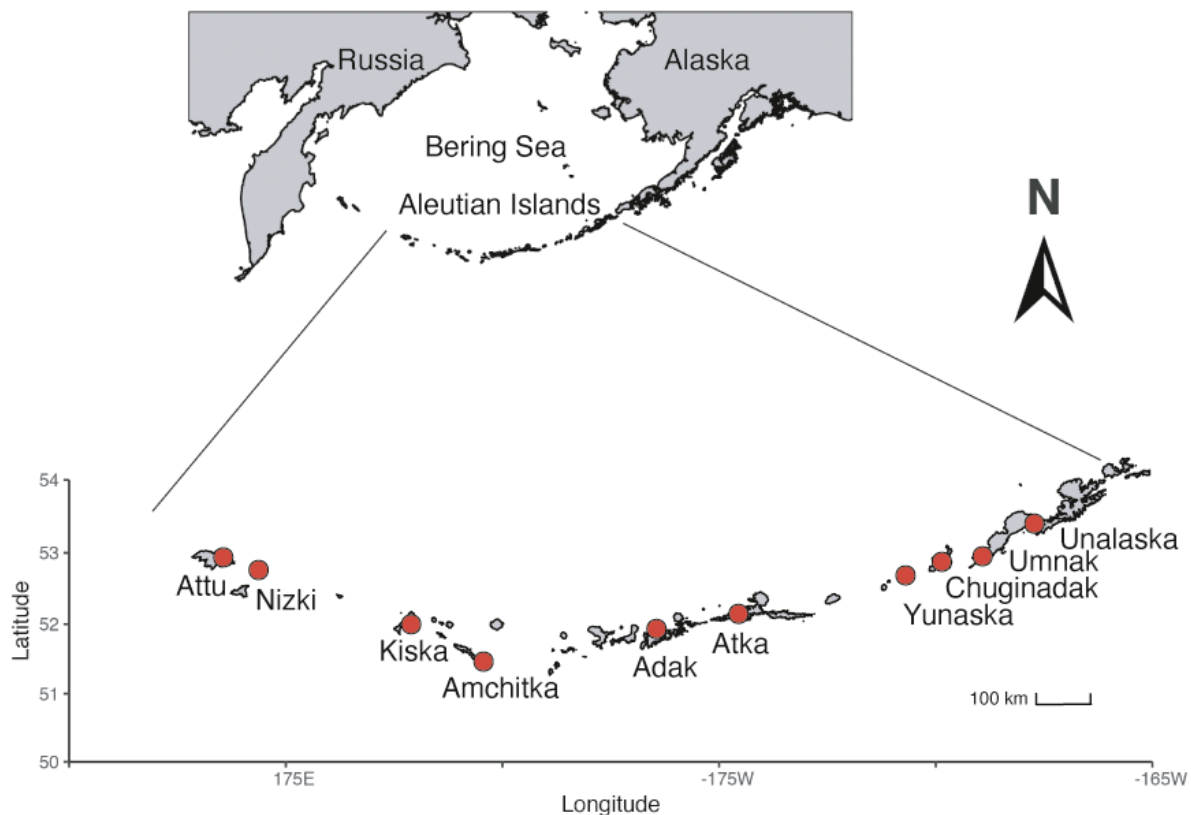


Fig. 1. Map of 2016/2017 primary producer and consumer collection sites off of 10 Aleutian Islands. Collections were made within kelp forests, urchin barrens, and offshore areas.

Unalaska; Fig. 1) during the summers of 2016 and 2017. At each island, producers and consumers were collected on SCUBA in shallow (5–10 m) nearshore habitats that were dominated by either kelp forests or urchin barrens, and in adjacent deeper offshore (>100 m) habitats using ship-based trawls. Without local benthic production below the photic zone, offshore consumers are likely reliant on subsidies from the photic zone including phytoplankton near the surface or drifting macroalgae originating from shallow nearshore areas (Vetter 1995, Kelly et al. 2012, Duggins et al. 2016). We compared nearshore kelp forest and urchin barren consumers to offshore consumers to determine whether non-local subsidies (drifting detached macroalgae from kelp forests) were important for consumers within urchin barren and offshore habitats. Specifically, filtered seawater, macroalgae, sessile and mobile invertebrates, and fishes were collected from kelp forests, urchin barrens, and

offshore areas. To estimate the isotopic signatures of phytoplankton and suspended particulate organic matter (SPOM) in both nearshore and offshore areas, three water collections ( $n = 3$ ) were made within each habitat (kelp forest, urchin barren, offshore) at each of the 10 islands. The samples in the nearshore were collected while on SCUBA at ~7 m water depth using a 5-L custom-made water sampler. Due to timing restraints, offshore water samples were collected at ~7 m depth using the intake seawater lines on the research ship *R/V Oceanus*. Water samples (5 L) were filtered through pre-combusted (500°C for 4 h) 47 mm glass microfiber filters (grade GF/F, Whatman Arbor Technologies, Ann Arbor, MI, USA) under low pressure (~5–7 mmHg) using a custom system utilizing SCUBA cylinder pressure to push seawater through the filters.

Collections of macroalgae and invertebrates were made within two kelp forest and two

urchin barren sites at each island using randomly placed 0.25-m<sup>2</sup> quadrats ( $n = 10$  per site, per habitat, per island, see Metzger et al. 2019 for details). Kelp and urchin barren communities were typically paired within a few km from each other. All macroalgae and invertebrates within the quadrats were cleared/scraped from the benthos and collected in mesh bags (0.05 mm mesh size). Three dragon kelp *Eualaria fistulosa* individuals were haphazardly selected at a kelp forest site at an island within 30 m of each other. Individuals were taken back to the *R/V Oceanus* and laid out on deck in order to sample tissues. Samples were made of the sporophyll and blade tissue (excluding the midrib) taken at every meter until the end of the individual or until tissues became too frail and senescent. Opportunistic sampling for fish muscle tissues was made using hook and line and by pole spear (Valladares and Planas 2012). Offshore benthic trawls were conducted in 100–200 m of water ~2–6 km offshore of the kelp forest and urchin barren habitats at each island (see Bland et al. 2019 for details). Organisms were sorted on the research vessel and identified to the lowest taxonomic resolution possible. The most common taxa available, 1–21 individuals per habitat per island, were selected for analysis. To make comparisons of consumer stable isotope values among habitats, consumers were combined into trophic groups within similar feeding guilds (Appendix S1: Table S1). Differences among consumers within habitats were then more likely due to differences in resource availability rather than how consumers feed. Consumers were assigned as either tertiary consumers, secondary or primary consumers, and urchin muscle or urchin gonad tissue groups (for names of taxa, see Appendix S1: Table S1). Samples of urchin muscle and gonad tissues were taken and separated due to differences in tissue turnover time and lipid content (DeNiro and Epstein 1977, Post et al. 2007). Collections of sponges, bivalves, brittle stars, chiton, and shrimp were combined to represent primary consumers (Duggins et al. 1989). Collections of crabs, sea stars, anemones, and gastropods were combined to represent herbivorous, omnivorous, and carnivorous secondary consumers (Brewer and Konar 2005, Vicknair and Estes 2012). Collections of greenling, rockfish, cod and other fishes were combined to represent tertiary

consumers (Konar et al. 2015). Within each consumer group, there is likely variation in consumer diet. For example, within the tertiary consumer group, rockfish incorporate more sources from pelagic production, while greenling and cod incorporate more sources from benthic production (von Biela et al. 2016, Cyr et al. 2019). These trophic groups are coarse divisions as most taxa, and therefore, these groupings likely exist along a trophic continuum rather than discrete levels within food chains or webs (McTigue and Dunton 2014). Lipid extraction was not performed with most consumer [C]/[N] values <4.0 (Newsome and Bentall 2010, Hamilton et al. 2014).

Consumer tissues were removed from their tests, shells, or tubes, and their tissues, which were primarily muscle, were isolated and placed in 20 mL glass scintillation vials and dried at 60°C for 48 h (Grall et al. 2006, Schaal et al. 2012). Samples of coralline algae were decalcified with 1 mol/L HCl to remove inorganic carbonate and dried to isolate protein for stable isotope analyses (MacArthur et al. 2011). Macroalgal samples were sorted, rinsed of epiphytes using DI water, and placed into 20 mL glass scintillation vials and dried at 60°C for 48 h (Grall et al. 2006, Schaal et al. 2012). In total, 479 producer and 659 consumer samples were collected for this study. All dried macroalgal and invertebrate samples were ground to a fine powder using an agate mortar and pestle, weighed into tin capsules (Costech Analytical Technologies, Valencia, California, USA), and sent to University of New Mexico for isotopic analysis.

### Statistical analysis

To examine consumer stable isotope variation among communities, we first tested for differences in their Standard Ellipse Areas (SEA<sub>B</sub>) using Stable Isotope Bayesian Ellipses in R (SIBER) and for differences in the average  $\delta^{13}\text{C}$  (source  $\delta^{13}\text{C}$  supporting consumers) and  $\delta^{15}\text{N}$  (trophic level of consumers) values of consumers within each community using separate ANOVAs. Next, we used SIBER to test for differences in various isotopic niche metrics among communities using centroids of our consumer trophic groups (Jackson et al. 2011). These trophic group metrics describe the extent of isotopic dietary niche spacing, including biodiversity for basal resources assimilated by

consumers (i.e., the range of  $\delta^{13}\text{C}$  among trophic groups) and estimates of trophic level biodiversity (i.e., the  $\delta^{15}\text{N}$  range among trophic groups). By combining both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , we can estimate the occupied isotopic dietary niche space of consumers (i.e., total area [TA]) for each trophic group. We can also compare how similar trophic groups are by comparing the Euclidean distance of each trophic group to the centroid of all groups within a habitat (centroid distance, CD). The last two metrics describe the isotopic position of taxa from one another. These included the overall trophic similarity or the mean nearest neighbor Euclidean distance (NND) for consumers within a trophic group. Lastly, we compared trophic evenness or the standard deviation of mean nearest neighbor Euclidean distance (SDNND) among communities (Layman et al. 2007a, b). Additionally, we compared Standard Ellipse Area ( $\text{SEA}_B$ ) for each of the trophic groups separately among communities to understand changes to the isotopic dietary niche space of each trophic group relative to the entire community within a habitat. SIBER analyses were conducted using RStudio v 1.3.1073 (RStudio Team 2020).

## RESULTS

### Impacts of kelp loss on consumer communities

Overall isotopic dietary niche breadth of consumers was higher in kelp forests ( $\text{SEA}_B$   $21.8\text{‰}^2$ ) and 19.7% lower in urchin barrens ( $\text{SEA}_B$   $17.5\text{‰}^2$ ,  $P = 0.024$ ) and 32.1% lower in offshore communities ( $\text{SEA}_B$   $14.8\text{‰}^2$ ,  $P < 0.001$ ; Fig. 2a). Consumers within urchin barren habitats had greater average  $\delta^{13}\text{C}$  values, which suggested carbon sources supporting these consumers were different than sources supporting consumers within kelp forests (Fig. 2b). Average  $\delta^{15}\text{N}$  values for all consumers within kelp forest and urchin barren communities were similar suggesting equivalent trophic levels with all consumers pooled, while offshore consumers had higher  $\delta^{15}\text{N}$  values (Fig. 2c). The shift toward more positive carbon isotope values (less negative  $\delta^{13}\text{C}$  values) suggests decreasing contributions from macroalgae to all consumers (Fig. 3; Appendix S1: Fig. S1) and increasing contribution from coralline algae assimilated by urchins (Fig. 3; Appendix S1: Figs. S1–S3). Isotopic variability for green urchins within kelp forests mirrored the variability of

dragon kelp *E. fistulosa* within kelp forests and variability for green urchins within urchin barrens mirrored the variability of coralline algae within urchin barrens (Appendix S1: Fig. S2). The similarity in isotopic variability for these primary consumers with the dominant primary producers within their habitats suggests that with the loss of kelp and other macroalgae within urchin barrens, fewer macroalgae are available

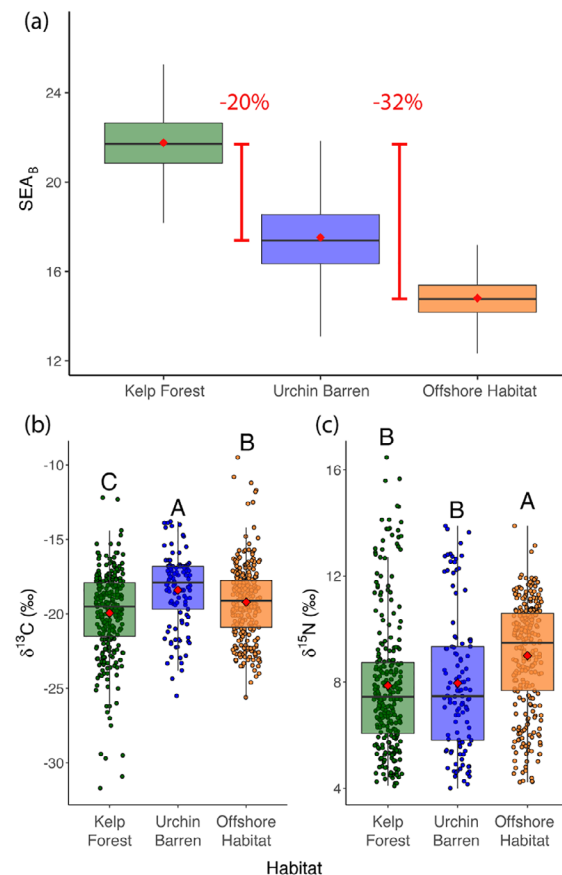


Fig. 2. Box plots showing (a) Standard Ellipse Area ( $\text{SEA}_B$ ) estimates for consumers within each habitat calculated using SIBER. Percent change of  $\text{SEA}_B$  from kelp forest consumers to consumers within other habitats shown in red. Consumer isotope values for (b) basal resources ( $\delta^{13}\text{C}$ ) and (c) trophic levels ( $\delta^{15}\text{N}$ ) using all consumer stable isotope values within each habitat. Sample sizes for consumer isotope values within each habitat are kelp forest ( $n = 274$ ), urchin barren ( $n = 113$ ), and offshore habitat ( $n = 272$ ). Means are indicated by the red diamond, medians are black lines, and error is standard error.



and the trophic pathways supporting primary consumers may have shifted from fleshy macroalgal-derived to coralline algal-derived (Appendix S1: Figs. S1–S3); however, microalgae isotope values were not quantified. Offshore consumers had intermediate  $\delta^{13}\text{C}$  values relative to consumers within the nearshore habitats, suggesting that a mixture of broad sources from the nearshore and offshore supported consumers in offshore habitats (Figs. 2b, 3; Appendix S1: Fig. S1).

#### *Impacts of kelp loss across consumer trophic groups within communities*

By comparing consumer isotopic dietary niche metrics between kelp forests and urchin barrens, we can estimate the trophic impacts of losing horizontal biodiversity within kelp forests. All community-wide niche metrics were lower for consumer groups within urchin barrens relative to kelp forests with the exception of the standard deviation of nearest neighbor distance (SDNND, Fig. 4f; Appendix S1: Tables S2, S3). Isotopic differences between consumers within kelp forests and urchin barrens suggest that the loss of kelp forest horizontal biodiversity leads to reduced basal resources to consumers (range of  $\delta^{13}\text{C}$ , decreased by 8.4%,  $P = 0.205$ , Fig. 4a) and reduced consumer trophic levels ( $\delta^{15}\text{N}$  range, decreased by 12.8%,  $P = 0.004$ , Fig. 4b). Reductions of both basal resources and trophic levels result in reductions in the isotopic variation and biodiversity of resources assimilated by urchin barren consumers (TA, decreased by 30%,  $P = 0.048$ , Fig. 4c), causing consumer groups to become more isotopically similar (distance of consumer groups to centroid, decreased by 20.8%,  $P = 0.007$ , Fig. 4d) and overall isotope values of consumers to become more similar (mean nearest neighbor distance, decrease by 16.7%,  $P = 0.011$ , Fig. 4e). However, consumer trophic evenness was similar between kelp forest and urchin barren habitats (Fig. 4f, 7.2% increase within urchin barrens,  $P = 0.541$ ).

#### *Offshore comparison using consumer trophic groups*

Community-wide niche metrics differed between kelp forest consumers and their offshore consumer communities that have low local production and are reliant on subsidies. Relative to

kelp forest consumer groups, most metrics were lower for offshore consumers, suggesting natural communities with lower benthic production and therefore lower local horizontal biodiversity have lower trophic complexity and more consumer group overlap (Figs. 3, 4b–e). When comparing consumer metrics in kelp forests to offshore habitats, horizontal biodiversity assimilated by consumers increased within offshore habitats (range of  $\delta^{13}\text{C}$ , increased by 40.2%,  $P < 0.001$ , Fig. 4a); however, trophic levels decreased ( $\delta^{15}\text{N}$  range, decreased by 62.4%,  $P < 0.001$ , Fig. 4b). Despite high horizontal biodiversity, the decrease in trophic levels resulted in lower isotopic dietary niche space (TA, decreased by 63.3%,  $P < 0.001$ , Fig. 4c), lower consumer trophic group dissimilarity (distance to centroid, decreased by 40.9%,  $P < 0.001$ , Fig. 4d), lower overall trophic dissimilarity (mean nearest neighbor distance, decreased by 48.3%,  $P < 0.001$ , Fig. 4e), and lower trophic evenness (SDNND values increased by 47.0% suggesting evenness decreased by 47.0%,  $P = 0.018$ , Fig. 4f).

#### *Impacts of kelp loss on individual trophic groups*

Isotopic dietary niche breadth of consumer trophic groups differed among kelp forests, urchin barrens, and offshore communities (Figs. 3, 5). Isotopic dietary niche breadth of all consumer trophic groups, except for the tertiary consumer fishes group, decreased within urchin barrens relative to kelp forests (Fig. 5). Offshore consumer groups had wide isotopic dietary niche breadths, often similar to nearshore kelp forest consumers (Fig. 5). With similar isotopic dietary niche estimates to kelp forest trophic groups, offshore consumers may receive a wide variety of subsidies similar to the biodiversity of basal resources available to trophic groups within kelp forests (Fig. 5). Offshore consumer trophic groups had wider isotopic dietary niche breadths relative to urchin barren consumers (Fig. 5) likely resulting from higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranges (Appendix S1: Table S3).

## DISCUSSION

Our findings suggest that the loss of biodiversity of basal resources within kelp forests leads to reductions in herbivore and omnivore isotopic dietary niche breadth, leading to overall reduced

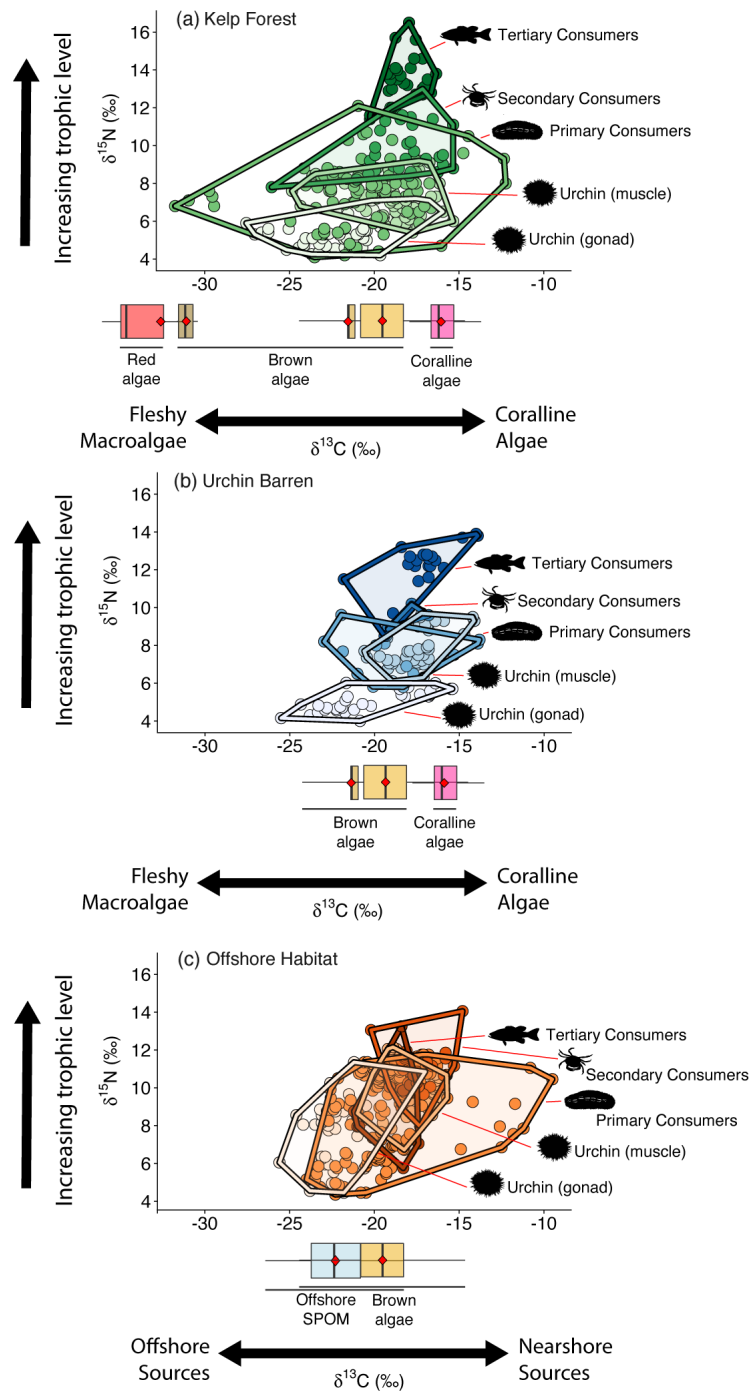


Fig. 3. Carbon and nitrogen isotope values with convex hull areas for each trophic group within a habitat including (a) kelp forest (green), (b) urchin barren (blue), and (c) offshore habitat (orange). Consumer graphics and lines indicate trophic groups which are distinguished by the amount of shading of each color. Decreasing convex hull areas of primary and secondary consumers within urchin barren habitat led to the lowering of tertiary consumer trophic levels relative to consumers in kelp habitat. Sample sizes for consumer isotope values within each habitat are kelp forest ( $n = 274$ ), urchin barren ( $n = 113$ ), and offshore habitat ( $n = 272$ ).

isotopic dietary niche breadth for consumer communities and the lowering of overall food web length within urchin barren habitat (Fig. 3). Although stable isotopes have been used to estimate changes to isotopic dietary niche breadth of consumers (Layman et al. 2007a, b, Yurkowski et al. 2018), here we show novel evidence for community-wide changes to isotopic dietary niche breadth with kelp forest biodiversity loss and identify which trophic groups caused changes to food web structure. With reductions in biodiversity of kelp and other macroalgae within the urchin barren phase state, we found herbivore and omnivore diets were most affected, and through the loss of these conduits, this impacted community-wide dietary niche metrics.

#### *The importance of omnivores and herbivores to isotopic dietary niche breadth*

The loss of kelp, other macroalgae, and consumer biodiversity within urchin barrens leads to a reduction in the biodiversity of basal resources assimilated by all consumers (Figs. 2b, 3, 4a) and by most consumer groups revealed by reductions in Standard Ellipse Areas (Fig. 5b–e; Appendix S1: Fig. S4) and convex hull areas (Appendix S1: Fig. S3, Table S3). The reduction in biodiversity of basal resources corresponded with a decrease in trophic level biodiversity among consumer groups ( $\delta^{15}\text{N}$  range, Fig. 4b) and a shift in the mean  $\delta^{13}\text{C}$  value for consumers away from kelp and other macroalgae and toward isotopic values for coralline algae (Appendix S1: Figs. S1, S2). These findings

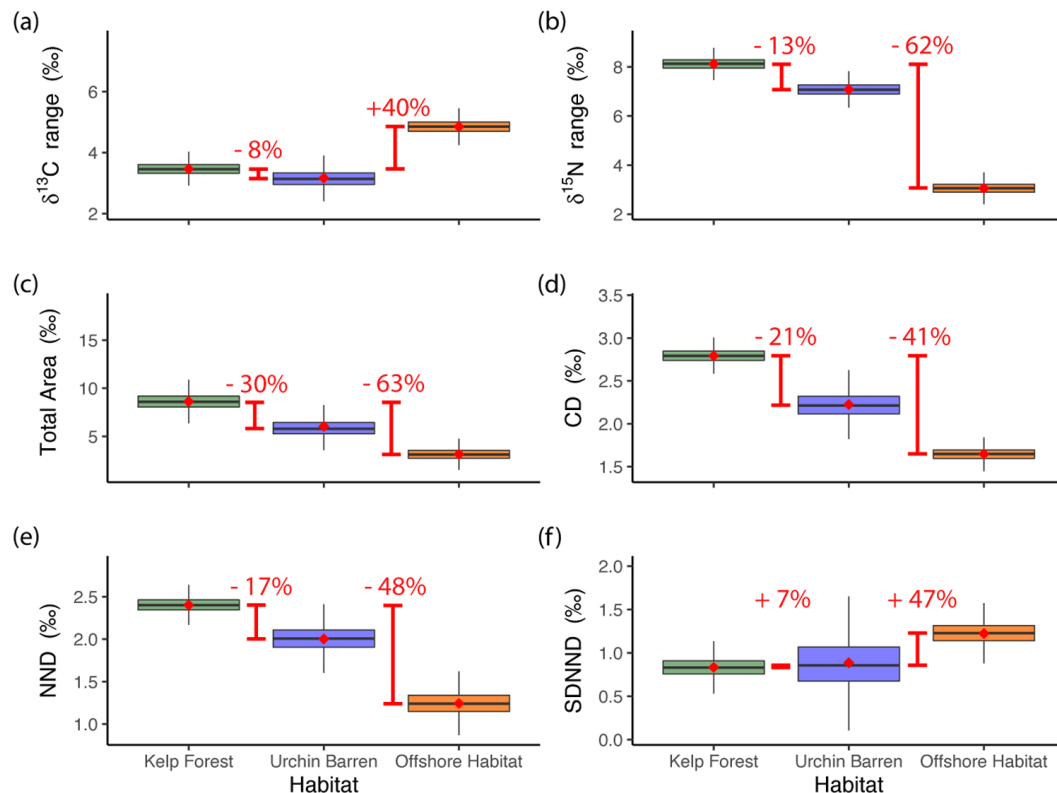


Fig. 4. Box plots for community-wide isotope niche metric estimates from SIBER including basal resources ( $\delta^{13}\text{C}$  range, a), trophic levels ( $\delta^{15}\text{N}$  range, b), isotopic dietary niche breadth (total area, c), trophic group similarity (distance to centroid—CD, d), trophic similarity (nearest neighbor distance—NND, e), and trophic evenness (standard deviation of nearest neighbor distance—SDNND, f). Sample sizes for consumer isotope values within each habitat are kelp forest ( $n = 274$ ), urchin barren ( $n = 113$ ), and offshore habitat ( $n = 272$ ). Means are indicated by the red diamond, medians are black lines, and error is standard error.



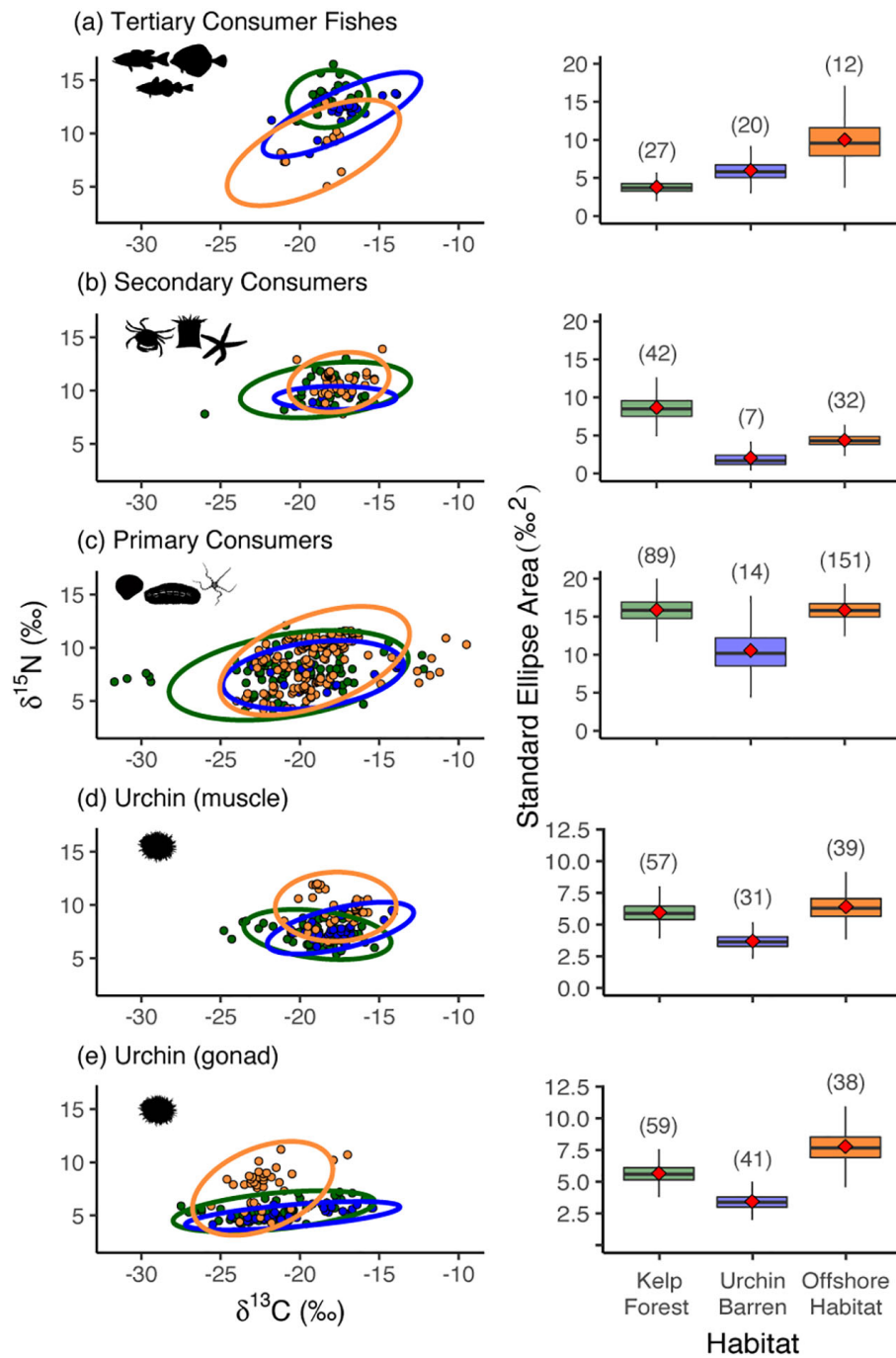


Fig. 5. Carbon and nitrogen isotope values with Standard Ellipse Area (SEA) ellipses (on left) and SEA estimates (on right) for consumer trophic groups including tertiary consumer fishes (a), secondary consumers (b), primary consumers (c), urchin muscle (d), and urchin gonad (e). Colors of ellipses denote consumer habitat; kelp forest in green, urchin barren in blue, and offshore habitat in orange. Means are indicated by the red diamond, medians are black lines, and error is standard error.

suggest that the long-term response of the consumer community to kelp forest loss and the associated basal resource biodiversity loss occurs through a reduction in the frequency of herbivory and omnivory, and this leads to decreases in overall isotopic dietary niche breadth. Herbivores are important conduits to the rest of the food web (Amsler 2008) and therefore we suggest cascading effects of their loss to isotopic dietary niche reductions to higher trophic levels. The degree to which urchins are an important direct food source (prey), or indirectly provide important food sources (e.g., providers of macroalgal detritus through shredding or fecal pellets), or act as trophic dead ends within urchin barrens, remains unknown (Dethier et al. 2019, Yorke et al. 2019). Omnivores increase food web connectivity by traversing multiple trophic levels (Polis and Strong 1996, Strong 2014) and dampen trophic cascades (Polis and Strong 1996). With the loss of kelp and other macroalgae within urchin barrens, we observed decreased trophic levels for tertiary consumers through the reductions in isotopic dietary niche breadth of omnivores and herbivores.

#### *Potential resources supporting communities*

The wide variation in kelp forest consumer  $\delta^{13}\text{C}$  values may be due to differences in primary producer carbon uptake strategies and suggests that these consumers receive carbon from a wide variety of sources, with low  $\delta^{13}\text{C}$  values for red algae, intermediate  $\delta^{13}\text{C}$  values for various brown algae, and high  $\delta^{13}\text{C}$  values for kelps that use carbon concentrating mechanisms (Raven and Hurd 2012). Urchin barren consumer  $\delta^{13}\text{C}$  values were higher and less variable relative to kelp forest consumers and overlapped with isotope values of brown algae and coralline algae. Contrasting previous work, this suggests that the effects of kelp forest biodiversity loss on community-wide trophic ecology lead to shifts in the base of the food web supporting consumers from phytodetritus and attached annual and perennial fleshy macroalgae to fleshy macroalgae and coralline algae (Graham 2004). With reduced abundance and biomass of primary producers within urchin barrens, biomass of dragon kelp *E. fistulosa* ( $2.54 \pm 1.07 \text{ kg/m}^2$ ) and subcanopy algae ( $6.09 \pm 2.95 \text{ kg/m}^2$ ) both decreased within urchin barrens to  $<0.5 \text{ kg/m}^2$  (Metzger et al.

2019), it is surprising that consumer  $\delta^{13}\text{C}$  values would be similar to brown algae. However, macroalgal subsidies from kelp forests, the intertidal, or macroalgae in areas of refuge from urchins, such as on the tops of pinnacles, may be important sources of organic matter increasing the survival, growth, and reproduction of sea urchins within urchin barren and offshore habitats (Vanderklift and Wernberg 2008, Kelly et al. 2012). Urchins are able to convert drift algal subsidies to gonad tissue and use this tissue as a nutritive store (Hughes et al. 2006). This strategy of food conversion may be important to the survival of urchins within urchin barren and offshore areas with such ephemeral pulses in subsidies to these habitats. Green urchins from kelp forest and urchin barren habitats had similar overlapping isotope values to some degree (Fig. 5d, e; Appendix S1: Figs. S2, S3) suggesting similar food resources may support urchins within these phase states. Coralline algae are relatively unpalatable with high percent calcium carbonate and low protein content and therefore may only be accessed by consumers that scrape the benthos like urchins and chiton (Steneck 1986). With high abundances of urchins within urchin barrens, their ability to shred fleshy macroalgae and access coralline algae may provide a critical net ecosystem service providing macroalgal detritus and fecal pellets to urchin barren consumer communities (Dethier et al. 2019). Aged urchin fecal pellets can actually increase in nutritive value from fresh macroalgae and may influence consumer population growth rates (Dethier et al. 2019). This information may help explain why other urchin barren consumers that are unable to access fleshy macroalgae and coralline algae have similar isotopic values to urchins.

Some urchins from offshore habitats have similar isotope values to those from nearshore habitats, suggesting that nearshore macroalgal subsidies may reach some offshore individuals (Appendix S1: Fig. S3). Greater  $\delta^{15}\text{N}$  range for consumer trophic groups within offshore habitats relative to consumer groups within both nearshore and offshore food sources (Galloway et al. 2013). The preferential uptake of  $^{14}\text{N}$  of food sources (i.e., SPOM or drifting macroalgae) by microorganisms in the water column, or  $^{15}\text{N}$  enrichment due to recycling, will lead to  $\delta^{15}\text{N}$

increases in food resources and be reflected in consumers (Stasko et al. 2018). Relatively fresh and/or large pieces of organic material can be mixed into sediments via bioturbation and degrade more slowly (Mintenbeck et al. 2007). Potentially this variability in degradation and microbial alternation creates variability in the nitrogen isotope values of offshore organic material and this is reflected by increases in the  $\delta^{15}\text{N}$  variability for many of the consumer trophic groups in offshore habitats relative to nearshore habitats (Appendix S1: Figs. S3, S4).

Performing biodiversity experiments at a relevant ecological scale will likely never occur (Cardinale et al. 2011) as it is difficult to conduct large-scale whole ecosystem manipulations (Carpenter et al. 1985, 1995). It would be difficult to perform a large-scale removal of kelp forests; however, this was naturally accomplished when sea otters were extirpated from the system (Estes et al. 1998). This natural experiment allows us to test for the importance of kelp forest biodiversity to community trophic complexity by making a comparison between communities in kelp forest and urchin barren phase states. The impact of kelp forest biodiversity loss on consumer community diets likely varies based on the frequency, magnitude, and duration of kelp forest loss (Castorani et al. 2018). While we concentrated on a generalized pattern across islands, future work should consider a comprehensive exploration of among island differences in sea otter history which may reveal gradients in community-wide trophic responses to reductions in kelp and other macroalgae. We specifically chose to compare consumers within remnant Aleutian Island kelp forests that were adjacent to urchin barrens at each island and, due to close proximity, reduce spatial variation among communities. It is surprising that we detected such striking differences in trophic ecology of some consumer groups despite the potential for such strong spatial exchanges of energy and matter across habitats and ecosystem boundaries (Polis et al. 1997, Kelly et al. 2012). We also chose this region as these urchin barrens may be those with some of the greatest magnitudes of herbivory, highest frequencies, and longest durations of urchin barren formation in the world, and therefore represent communities that have been in an alternative stable state for a relatively long period of time and therefore have experienced long-

term kelp forest biodiversity loss (Filbee-Dexter and Scheibling 2014).

The community response to losing kelp forests was more dramatic relative to the response found with the loss of foundational corals that create coral reefs (Morillo-Velarde et al. 2018). The impact of kelp forest habitat loss for most consumer groups was similar to the impacts of mangrove habitat loss on a top predator fish with reductions in the biodiversity of basal resources (lower variation in  $\delta^{13}\text{C}$ ), shifts in the base of the food web (change in mean  $\delta^{13}\text{C}$ ), and reductions in trophic levels (lower variation in  $\delta^{15}\text{N}$ , Layman et al. 2007b). However, as a group, tertiary consumer fishes did not follow this pattern of decreasing isotopic dietary niche breadth with kelp forest loss suggesting that these mobile consumers may be less vulnerable to reductions in biodiversity relative to fishes in mangrove habitat (Layman et al. 2007b). Our findings are opposite to the pattern that coral reef fishes increase their isotopic dietary niche breadth with increasing productivity, although our comparison was across habitats at an island and not directed to test for differences among islands (Miller et al. 2019). Isotopic dietary niche breadth of tertiary consumer fishes was lowest in kelp forests, intermediate in urchin barrens, and highest in offshore habitats, coinciding with decreasing trophic levels. This suggests that mobile generalist predators at higher trophic levels may be able to shift and broaden their diet to compensate for biodiversity and resource loss. Predatory fishes may alter foraging to match resource availability within the different phase states and this may help to explain why fish assemblage structure is similar between kelp forests and urchin barrens across the Aleutian Archipelago (Konar et al. 2015). Our findings of increasing isotopic variation and potential variation in diet for fishes within urchin barrens matches previous work that provided evidence that the biodiversity of prey for fishes like greenling expand within urchin barrens (Reisewitz et al. 2006). The isotopic dietary niche width of mobile predatory consumers may expand when preferred high quality prey and resource biodiversity is low, however, that implies that alternative resources are available (Layman et al. 2007b). Alternatively, changes in fish diets between kelp forests and urchin barrens may also be due to kelp forests providing refuge and

altering fish foraging behavior or may be due to environmental changes due to kelp structure, such as flow and light, altering prey availability (Reisewitz et al. 2006).

Kelp forest habitat loss has been reported due to seawater warming (Rogers-Bennett and Catton 2019, Smale et al. 2019), the loss of sea urchin predators like sea otters and sea stars (Estes and Palmisano 1974, Estes et al. 1998, Burt et al. 2018), and the combined effects of warm seawater and swell over long time scales like El Niño Southern Oscillation cycles (Edwards 2004, 2019, Edwards and Estes 2006). We predict that kelp forest loss results in decreases to trophic levels of higher-level consumers and isotopic dietary niche breadth of communities through the loss of herbivores and omnivores; however, the frequency, magnitude, and duration of kelp forest loss must influence this pattern (Krumhansl et al. 2016). On the West coast of the United States kelp forest recovery and therefore persistence varies by region. Following a disturbance, kelp forests north of Point Conception recover quickly, those between Baja and this break express moderate recovery, and kelp forests south of Southern California take years to recover to pre-disturbance densities (Edwards 2004, Edwards and Hernández-Carmona 2005, Edwards and Estes 2006). While we have estimated changes to community trophic ecology with extreme kelp forest loss, we suggest future work should consider community-wide isotopic dietary niche impacts on intermediate frequencies, magnitudes, or durations of kelp forest loss. We have no way to predict if small declines in horizontal or vertical kelp forest biodiversity led to immediate declines in community trophic metrics or if they only occur with higher declines in biodiversity. With declines in kelp forests due to multiple stressors along the Eastern Pacific and restoration efforts occurring to restore kelp forests, we propose the use of stable isotopes as a tool to help determine if and when trophic interactions are restored during the process of kelp forest recovery (Rogers-Bennett and Catton 2019).

## ACKNOWLEDGMENTS

We thank S. Lamerdin, and the captain and crew of the R/V Oceanus for two safe and productive cruises. We thank M. Good, M. Spector, G. Sullaway, S. Small,

S. Traiger, T. McHugh, J. Metzger, A. Bland, A. Ravelo, and B. Weitzman for assistance with field operations and field collections. We also thank the Alaska Maritime National Wildlife Refuge for logistical support. We would like to offer recognition and respect to the many Aleut or Unanga whose land we were able to visit and learn about: Sasignan (Attu and Nizki Islands), Qaxun (Kiska, Amchitka), Niiuugis (Adak, Atka), Akuugun (Yunaska, Chuginadak), and Qawalan-gin (Umnak and Unalaska). This research was partially funded by a grant from the National Science Foundation (OCE1435194) to MSE and BHK. Collections of producers and consumers were made through the Alaskan Department of Fish and Game permit CF-17-096, and collections of fishes were made through IACUC APF# 16-05-006E permit accepted through SDSU. SSG, MSE, and BHK designed the research. SSG performed the research and collected the data. SSG analyzed the data. SSG, MSE, and BHK wrote the paper. All authors reviewed the manuscript.

## LITERATURE CITED

- Amsler, C. D. 2008. Algal chemical ecology. Springer-Verlag, Berlin, Germany.
- Anthony, R., J. A. Estes, and M. Ricca. 2008. Bald eagles and sea otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology* 89:2725–2735.
- Barnes, A. D., M. Jochum, J. S. Lefcheck, N. Eisenhauer, C. Scherber, M. I. O'Connor, P. de Ruiter, and U. Brose. 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends in Ecology & Evolution* 33:186–197.
- Bland, A., B. Konar, and M. S. Edwards. 2019. Spatial trends and environmental drivers of epibenthic shelf community structure across the Aleutian Islands. *Continental Shelf Research* 175:12–29.
- Brewer, R., and B. Konar. 2005. Chemosensory responses and foraging behavior of the seastar *Pycnopodia helianthoides*. *Marine Biology* 147:789–795.
- Burt, J. M., M. Tim Tinker, D. K. Okamoto, K. W. Demes, K. Holmes, and A. K. Salomon. 2018. Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. *Proceedings of the Royal Society B: Biological Sciences* 285:1–9.
- Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany* 98:572–592.
- Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. *Science* 269:324–327.



- Carpenter, S., J. Kitchell, and J. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Castorani, M. C. N., D. C. Reed, and R. J. Miller. 2018. Loss of foundation species: Disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology* 99:2442–2454.
- Cyr, A., J. A. López, L. Rea, M. J. Wooller, T. Loomis, S. Mcdermott, and T. M. O'Hara. 2019. Mercury concentrations in marine species from the Aleutian Islands: spatial and biological determinants. *Science of the Total Environment* 664:761–770.
- DeNiro, M., and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science* 197:261–263.
- Dethier, M. N., G. Hoins, J. Kobelt, A. T. Lowe, A. W. E. Galloway, J. B. Schram, M. Raymore, and D. O. Duggins. 2019. Feces as food: the nutritional value of urchin feces and implications for benthic food webs. *Journal of Experimental Marine Biology and Ecology* 514–515:95–102.
- Doroff, A. M., J. A. Estes, M. T. Tinker, D. M. Burn, and T. J. Evans. 2003. Sea otter population declines in the Aleutian Archipelago. *Journal of Mammalogy* 84:55–64.
- Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.
- Duggins, D. O., M. Gómez-buckley, A. T. Lowe, and A. W. E. Galloway. 2016. Islands in the stream: kelp detritus as faunal magnets. *Marine Biology* 163: 1–10.
- Duggins, D. O., C. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science, New Series* 245:170–173.
- Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biology* 84:287–294.
- Edwards, M. S. 2004. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. *Oecologia* 138:436–447.
- Edwards, M. S. 2019. Comparing the impacts of four ENSO events on giant kelp (*Macrocystis pyrifera*) in the northeast Pacific Ocean. *Algae* 34:141–151.
- Edwards, M. S., and J. A. Estes. 2006. Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. *Marine Ecology Progress Series* 320:79–87.
- Edwards, M. S., and G. Hernández-Carmona. 2005. Delayed recovery of giant kelp near its southern range limit in the North Pacific following El Niño. *Marine Biology* 147:273–279.
- Edwards, M. S., and B. Konar. 2020. Trophic downgrading reduces spatial variability on rocky reefs. *Scientific Reports* 10:18079.
- Edwards, M., B. Konar, J. H. Kim, S. Gabara, G. Sullaway, T. McHugh, M. Spector, and S. Small. 2020. Marine deforestation leads to widespread loss of ecosystem function. *PLOS ONE* 15:1–21.
- Estes, J. A., E. M. E. Danner, D. F. Doak, B. Konar, A. M. A. Springer, P. D. P. Steinberg, M. T. M. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Science* 74:621–638.
- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65:75–100.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Filbee-Dexter, K., and R. Scheibling. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Marine Ecology Progress Series* 495:1–25.
- Galloway, A. W. E., A. T. Lowe, E. A. Sosik, J. S. Yeung, and D. O. Duggins. 2013. Fatty acid and stable isotope biomarkers suggest microbe-induced differences in benthic food webs between depths. *Limnology and Oceanography* 58:1451–1462.
- Graham, M. H. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357.
- Grall, J., F. Le Loc'h, B. Guyonnet, and P. Riera. 2006. Community structure and food web based on stable isotopes ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analysis of a North Eastern Atlantic maerl bed. *Journal of Experimental Marine Biology and Ecology* 338:1–15.
- Hamilton, S. L., S. D. Newsome, and J. E. Caselle. 2014. Dietary niche expansion of a kelp forest predator recovering from intense commercial exploitation. *Ecology* 95:164–172.
- Hughes, A. D., M. S. Kelly, D. K. A. Barnes, A. I. Catarino, and K. D. Black. 2006. The dual functions of sea urchin gonads are reflected in the temporal variations of their biochemistry. *Marine Biology* 148:789–798.
- Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80:595–602.
- Kelly, J., K. A. Krumhansl, and R. Scheibling. 2012. Drift algal subsidies to sea urchins in low-



- productivity habitats. *Marine Ecology Progress Series* 452:145–157.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. *North American Fauna* 68:1–352.
- Konar, B., M. Edwards, and T. Efrid. 2015. Local habitat and regional oceanographic influence on fish distribution patterns in the diminishing kelp forests across the Aleutian Archipelago. *Environmental Biology of Fishes* 98:1935–1951.
- Konar, B., M. S. Edwards, and J. A. Estes. 2014. Biological interactions maintain the boundaries between kelp forests and urchin barrens in the Aleutian Archipelago. *Hydrobiologia* 724:91–107.
- Konar, B., and J. A. Estes. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84:174–185.
- Krumhansl, K. A., et al. 2016. Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences USA* 113:13785–13790.
- Layman, C. A., D. A. Arrington, C. G. Montaña, and D. M. Post. 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48.
- Layman, C. A., J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* 10:937–944.
- Lensink, C. J. 1960. Status and distribution of sea otters in Alaska. *Journal of Mammalogy* 41:172.
- MacArthur, L. D., D. L. Phillips, G. A. Hyndes, C. E. Hanson, and M. A. Vanderklift. 2011. Habitat surrounding patch reefs influences the diet and nutrition of the western rock lobster. *Marine Ecology Progress Series* 436:191–205.
- McTigue, N. D., and K. H. Dunton. 2014. Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. *Deep-Sea Research Part II: Topical Studies in Oceanography* 102:84–96.
- Metzger, J. R., B. Konar, and M. S. Edwards. 2019. Assessing a macroalgal foundation species: community variation with shifting algal assemblages. *Marine Biology* 166:1–17.
- Miller, S., B. Zgliczynski, M. Fox, L. Kaufman, R. Michener, S. Sandin, and S. Hamilton. 2019. Niche width expansion of coral reef fishes along a primary production gradient in the remote central Pacific. *Marine Ecology Progress Series* 625:127–143.
- Mintenbeck, K., U. Jacob, R. Knust, W. E. Arntz, and T. Brey. 2007. Depth-dependence in stable isotope ratio  $\delta^{15}\text{N}$  of benthic POM consumers: the role of particle dynamics and organism trophic guild. *Deep-Sea Research Part I: Oceanographic Research Papers* 54:1015–1023.
- Morillo-Velarde, P. S., P. Briones-Fourzán, L. Álvarez-Filip, S. Aguiñiga-García, A. Sánchez-González, and E. Lozano-Alvarez. 2018. Habitat degradation alters trophic pathways but not food chain length on shallow Caribbean coral reefs. *Scientific Reports* 8:4109.
- Newsome, S. D., and G. Bentall. 2010. Variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  diet-vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications* 20:1744–1752.
- O'Connor, M. I., and J. E. K. Byrnes. 2014. Biodiversity and ecosystem function: Does pattern influence process? Pages 109–130 in M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. *Marine community ecology and conservation*. Sinauer, Sunderland, Massachusetts, USA.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189.
- RStudio Team. 2020. RStudio: integrated Development Environment for R. Boston, MA: RStudio.
- Raven, J. A., and C. L. Hurd. 2012. Ecophysiology of photosynthesis in macroalgae. *Photosynthesis Research* 113:105–125.
- Reisewitz, S. E. S., J. A. Estes, and C. C. A. Simenstad. 2006. Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian Archipelago. *Oecologia* 146:623–631.
- Rogers-Bennett, L., and C. A. Catton. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports* 9:15050.
- Schaal, G., P. Riera, and C. C. Leroux. 2012. Food web structure within kelp holdfasts (*Laminaria*): a stable isotope study. *Marine Ecology* 33:370–376.
- Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* 200:403–411.
- Smale, D. A., et al. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change* 9:306–312.
- Stasko, A. D., B. A. Bluhm, J. D. Reist, H. Swanson, and M. Power. 2018. Relationships between depth and  $\delta^{15}\text{N}$  of Arctic benthos vary among regions and trophic functional groups. *Deep-Sea Research Part I: Oceanographic Research Papers* 135:56–64.

- Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. *Annual Review of Ecology and Systematics* 17:273–303.
- Strong, D. R. 2014. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754.
- Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* 45:471–493.
- Valladares, S., and M. Planas. 2012. Non-lethal dorsal fin sampling for stable isotope analysis in seahorses. *Aquatic Ecology* 46:363–370.
- Vanderklift, M. A., and T. Wernberg. 2008. Detached kelps from distant sources are a food subsidy for sea urchins. *Oecologia* 157:327–335.
- Vetter, E. W. 1995. Detritus-based patches of high secondary production in the nearshore benthos. *Marine Ecology Progress Series* 120:251–262.
- Vicknair, K., and J. A. Estes. 2012. Interactions among sea otters, sea stars, and suspension-feeding invertebrates in the western Aleutian Archipelago. *Marine Biology* 159:2641–2649.
- von Biela, V. R., S. D. Newsome, J. L. Bodkin, G. H. Kruse, and C. E. Zimmerman. 2016. Widespread kelp-derived carbon in pelagic and benthic near-shore fishes suggested by stable isotope analysis. *Estuarine, Coastal and Shelf Science* 181:364–374.
- Yorke, C. E., H. M. Page, and R. J. Miller. 2019. Sea urchins mediate the availability of kelp detritus to benthic consumers. *Proceedings of the Royal Society B: Biological Sciences* 286:20190846.
- Yurkowski, D. J., N. E. Hussey, S. H. Ferguson, and A. T. Fisk. 2018. A temporal shift in prey species availability decreases trophic diversity among predator assemblage in a changing Arctic. *Royal Society Open Science* 5:180259.

### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3361/full>