# Recovery of keystone predation magnifies community niche space by expanding trophic level diversity and shifting basal resources

**by**

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# Ethics Statement

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# Abstract

While predators can drive abrupt and profound changes in food web components, what is less well known and more difficult to quantify is how predators influence entire ecosystem organization and function. Sea otter (*Enhydra lutris*) recovery on temperate reefs is known to trigger regime shifts, converting urchin-dominated reefs to kelp-dominated reefs, yet the impacts of this keystone species on entire ecosystem dynamics remain less understood. We used stable isotope analysis and a Bayesian modeling approach to study the effects of sea otter recovery on the trophic niche space of a rocky reef species assemblage. Examination of community-wide niche metrics revealed an increase in the overall community niche space with increasing otter occupation time, driven by an increased number of trophic levels and greater uncertainty in basal resource diversity. At the species-level, the trophic positions of several reef associated fish increased with sea otter occupation time, suggesting that these species are feeding on higher trophic level prey. Concurrently, decreased trophic positions and distinct shifts in dietary carbon signatures of sea urchins suggest that sea otter recovery also drove an expansion at the base of the food web. These results contribute to our understanding of the broad, far-reaching role of keystone predation in reshaping entire ecosystems.

**Keywords**: regime shifts; keystone predator recovery; sea otter; food web dynamics; stable isotope analysis; community niche space

# Dedication

To my kind and generous mother – who braved the sticky heat of Malaysia every weekend to take us to visit the zoo when we were small. My love and appreciation for botany and animals comes from experiencing your delight whenever you see something wondrous and beautiful.

To Phillip Pullman’s *His Dark Materials* – for inspiring me to chase the *aurora borealis* and to look for worlds beyond open windows.

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Beyond the scope of my research on marine nearshore food web dynamics, I was granted opportunities to go to the traditional territory of the Heiltsuk Nation to take courses and conduct research on the herring social-ecological system. To say that this experience was life-changing is an understatement; learning from the Heiltsuk Nation altered how I perceive the world and shifted my life trajectory. I am grateful to the Heiltsuk Integrated Resource Management Department, especially Mike Reid and Kelly Brown, for being so welcoming and collaborative. I am also grateful to the elders and local experts for talking to me and trusting me with their stories. w̓álas ǧiáxsix̌a

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爸爸 – 感恩你的教育和關心. 엄마 – 난 아주 많이 당신을 사랑합니다.

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# Introduction

Emerging evidence points to the existence of regime shifts across a variety of ecosystems worldwide; from lakes, to deserts, to coral reefs, to kelp forests (Hughes 2000, Folke et al. 2004). Moreover, the loss of large apex consumers across our planet has revealed the widespread occurrence of trophic cascades as a mechanism by which these abrupt re-organizations in ecological structure and function are triggered (Estes et al. 2011). While most analyses of regime shifts measure rapid changes in the abundance of dominant system players, rarely do they examine the entire community assemblage simultaneously nor the changes in trophic characteristics and flows of energy that created those shifts. Here, we used stable isotopes and Bayesian niche modeling to reveal community-wide regime shifts and transformation in trophic diversity triggered by the recovery of a keystone predator.

Temperate rocky reefs are quintessential examples of ecosystems prone to regime shifts (Ling et al. 2015). Around the world, overgrazing by sea urchins has triggered profound changes on rocky reefs, from Chile, South Africa, New Zealand and Australia in the southern hemisphere, to Japan, Canada, Mediterranean Europe and the United States of America in the northern hemisphere (Steneck et al. 2002, Filbee-Dexter and Scheibling 2014, Ling et al. 2015). In the northeastern Pacific Ocean, the decline and subsequent recovery of sea otters (*Enhydra lutris*) and their top-down regulation of sea urchin grazing is well known to trigger a cascade of interactions driving regime shifts on subtidal rocky reefs (Estes and Palmisano 1974, Estes and Duggins 1995, Konar and Estes 2003, Watson and Estes 2011, Burt et al. 2018). With the recovery of sea otters, urchin-dominated systems devoid of adult kelps can flip into kelp-forested systems, the timing and magnitude of which varying along the northeastern Pacific coast (Steneck et al. 2002, Estes 2016). Although the knock-on effects of this trophic cascade on seagulls (Irons et al. 1986), bald eagles (Anthony et al. 2008), and reef-associated fish (Reisewitz et al. 2006, Markel and Shurin 2015) have been explored, community-wide shifts in entire rocky reef assemblages and trophic diversity have yet to be quantified.

Understanding the manifestation of community-wide regime shifts on temperate rocky reefs can be illuminated using the niche concept (Elton 1927, Hutchinson 1957). The concept of the ecological niche has undergone numerous treatments through time, yet the overall definition still retains the formalization of the niche as a multidimensional space capturing interspecific competition and patterns of resource and habitat use (Leibold 1995). Recent advances in stable isotope analysis have provided an increasingly powerful approach for describing these multiple niche dimensions (Newsome et al. 2007). Stable isotopes can be used to quantitatively characterize community-wide aspects of trophic structure and diversity at the level of an entire food web (Layman et al. 2007a, Newsome et al. 2012). Species and community isotopic niches are an emergent outcome of the species interactions and energy flows that underlie ecosystem structure and function, thus alteration to these niches may signal system-wide effects of predator decline or recovery.

We used niche theory, stable isotopes and Bayesian inference to determine how species interactions and the trophic flow of energy within an assemblage of rocky reef species have changed with the recovery of a keystone predator. We calculated four unique niche metrics from nitrogen and carbon isotopes, to ask; how have rocky reef assemblages changed with the recovery of sea otters, a well-known keystone predator. Based on previous literature exploring the role of top-down regulation on food webs (Estes and Palmisano 1974, Breen et al. 1982, Estes and Duggins 1995, Watson and Estes 2011), we hypothesized that the recovery of sea otters would prompt a greater range in $\delta^{15}$N values of reef consumers reflecting more complex food webs and greater trophic level diversity. Furthermore, we surmised that the cascading effects of sea otters enhancing the spatial extent and abundance of perennial kelp in this region (Stevenson et al. 2016, Lee et al. 2016) would prompt a shift in consumer $\delta^{13}$C values towards more $^{13}$C-enriched values reflecting an increase in system-wide primary production.

# Methods

## Study Area

This research was conducted at 28 rocky reef sites on the central coast of British Columbia (BC), Canada, where sea otter populations have been recovering since at least 1989 (Nichol et al. 2009, 2015, Figure 1, Table A1) triggering a newly documented rocky reef regime shift (Stevenson et al. 2016, Lee et al. 2016, 2018, Burt et al. 2018). The re-establishment and range expansion of sea otter populations in BC provides a spatial gradient in sea otter occupation time, recovery in keystone predation and thus associated changes in rocky reef communities that we exploited in a space-for-time substitution (Pickett 1989).

Sea otter-induced regime shifts along BC's central coast can be broadly characterized by the transition between three unique ecosystem states. Initially, the recovery of keystone predation by sea otters is associated with rapid, large decreases in sea urchin density, size and thus biomass within 1-5 years, during which time urchin density is reduced by greater than 75% and kelp densities, predominantly of the annual species *Nereocystis luetkeana*, tend to increase (Stevenson et al. 2016, Lee et al. 2016, 2018, Burt et al. 2018). After approximately 10 years of sea otter occupation, kelp densities tend to moderately decline as high densities of the dominant kelp *Nereocystis luetkeana* get partly replaced by a diversity of longer-lived perennial kelp species (i.e., *Pterygophora californica, Macrocystis pyrifera, Cymathere triplicata, Eisenia arborea*) which stabilize at densities higher than those on reefs without sea otters (Lee et al. 2018). Consequently, this sea otter-induced regime shift involves an initial swift transition from an urchin-dominated system to a variable and transient annual kelp-dominated system, which then gradually transitions towards a more consistently forested 'old-growth' kelp forest system (Lee et al. 2018, Burt et al. 2018). While these dynamics are broadly consistent along BC's central coast, the exact timing of these transitions and resulting assemblage of kelp species is variable among sites, likely due to differences in the season when sea otters first occupy a site and reduce urchin densities, and the variability in the seasonal recruitment of different kelp species (Watson and Estes 2011). Similar rocky reef regime shift dynamics have been documented elsewhere along BC's coast south of this study area (Watson and Estes 2011).

## Experimental Design

To examine the trophic diversity and isotopic niche space of rocky reef communities that exist before, during and after a sea-otter induced regime shift, we grouped our sites into three sea otter occupation categories; None (0 years), Short (2-8 years), and Long (16-33 years), representing the ‘urchin-dominated’, ‘transition’ and ‘kelp-dominated’ states respectively. These categories were based on 1) estimated sea otter occupation time (Stevenson et al. 2016, Lee et al. 2016), 2) site-specific sea urchin biomass (Stevenson et al 2016, Burt et al. 2018), and 3) the known timing of sea otter-induced regime-shifts in this area (Lee et al. 2018, Burt et al. 2018, Table A1). Sea otter occupation time was estimated from long-term boat-based sea otter surveys and the first year of sighting of an otter raft (≥ 3 individuals together) within a 3 nautical mile radius of the site (Nichol et al. 2009, 2015). Sea urchin biomass was estimated from the density and size of urchins (*Mesocentrotus franciscanus, Strongylocentrotus droebachiensis, Strongylocentrotus purpuratus*) counted and measured in 1 $m^2$ quadrats (n=18) randomly stratified between 4 and 15 m below chart datum at each site and a pre-established length-to-biomass relationship (For details see Stevenson et al. 2016). Timing of the sea otter-induced regime shift was documented by a time series of urchin biomass and kelp densities at a subset of our sites (n=11) which varied in sea otter re-establishment over 4 years (Burt et al. 2018). All 28 sites were chosen specifically for their similarity in physical characteristics (i.e., depth range, aspect, slope, wave exposure, and topography) and differences in sea otter occupation time. Reconnaissance dives were used to ensure that each reef encompassed at least 100 m of continuous rocky substrate.

## Stable Isotope Analysis

To quantify the variation in consumer isotopic signatures among reef states, we sampled representative reef fish, macroinvertebrates, and primary producers at each site in May and July of 2011 and July of 2013. An assemblage of 12 rocky reef associated species that exist on both urchin-dominated and kelp-dominated reefs, albeit at differing densities, was specifically chosen to represent the community and food web that exists among all three alternative reef states. Species-specific sample sizes ranged from n=3 to max n=63 due to the minimum sample size (n=3) required for statistical analysis and the maximum number of individuals that could be sampled at each site given logistical time constraints on field sampling and research permits (Table B2).

Tissue samples for stable isotope analysis were dissected from reef fish (dorsal muscle), sea stars (tube feet), sea urchins (connective tissue around Aristotle's lantern) and California mussels (gill). Frozen tissue samples were thawed and rinsed with 10% HCl and de-ionized water to remove carbonates (Levin and Currin 2012). Cleaned samples were dried at 60°C for 48 hours, finely ground, placed in tin capsules, and sent for analysis at the UC Davis Stable Isotope Facility. $\delta^{13}C$ and $\delta^{15}N$ values are calculated relative to international standards, Vienna Pee Dee Belemnite for carbon and Air for nitrogen:

$$\delta X = \left[\left(\frac{\text{Rsample}}{\text{Rstandard}} - 1\right) \text{x } 1000\right] \qquad (1)$$

where X = $^{13}C$ or $^{15}N$ and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. $\delta$ units are in parts per thousand (‰), representing the relative enrichment of heavy to light isotope.

## Trophic Niche Calculations

Stable isotope ratios were used to calculate community niche metrics representing various aspects of trophic diversity for each sea otter occupation category. Individual niches were first estimated for each species in the rocky reef assemblage plotted in $\delta^{13}C$-$\delta^{15}N$ bi-plot space using standard ellipse areas. Convex hulls were then created from the mean $\delta^{13}C$ and $\delta^{15}N$ of the species niche widths in each category to represent the community niche widths. Four community isotopic niche metrics were calculated from the convex hulls for each sea otter occupation category.

Bayesian multivariate standard ellipse areas ($SEA_B$) were estimated for each species plotted in $\delta^{13}C$-$\delta^{15}N$ bi-plot space using 'SIBER' (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011), within the R package 'SIAR' (Stable Isotopic Analysis in R) to represent isotopic niche widths at the species level (Parnell and Jackson, 2013). The standard ellipse is the bivariate equivalent to the univariate standard error. The Bayesian estimates of $SEA_B$ was constructed using $\delta^{13}C$ and $\delta^{15}N$ means, variance and covariance. $SEA_B$ is robust to variation in sample size, allowing better comparison of niche areas than if species niche areas were based on convex hulls (Jackson et al.

2011). To prevent bias from small sample sizes and to allow for isotopic niche overlap to be calculated, a correction factor was applied to the bivariate data to produce a final estimate of species niche width: $\mathrm{SEA_C}$ (corrected standard ellipse area, Table B3).

Convex hulls were then created from the mean $\delta^{13}$C and $\delta^{15}$N of all the species niche widths ($\mathrm{SEA_B}$) in each community to calculate the community niche metrics. For each category, the total area (TA), nitrogen range (NR), carbon range (CR), and mean distance to centroid (CD), were calculated based on convex hulls in community niche space (for details see Layman et al. 2007a, Jackson et al. 2011) using 'SIAR' (Parnell and Jackson, 2013). The total area of the convex hull provides an estimate of the total niche space occupied by the community assemblage along the $\delta^{13}$C and $\delta^{15}$N axes. Nitrogen and carbon ranges are calculated as the difference between the maximum and minimum $\delta^{15}$N and $\delta^{13}$C values of the convex hull, respectively. The nitrogen range represents the vertical structure of the community food web and thus provides a metric of trophic level diversity, while the carbon range reflects the diversity of basal energy resources. Centroid distance is the distance between a species and the community centroid, providing a measure of species spacing which reflects the average degree of trophic diversity within the community.

## Data analysis

To determine the probability that community and species niche metrics differed among urchin-dominated, transition and kelp-dominated reef states, we compared community and species-specific niche metrics among sea otter occupation category. We calculated the probability of a community's niche metric (area *a*) being smaller than another's (area *b*) as the number of estimates in the metric's posterior distribution for that area that are smaller than the one it is being compared to, divided by the total number of estimates:

$$\mathrm{P}(a < b) = \frac{(\mathrm{X}a \, < \, \mathrm{X}b)}{\mathrm{n}} \qquad (2)$$

where, *a* and *b* represent the posterior distributions of the niche metric being compared. X is a single estimate in the posterior distribution of *a* and *b*, and n is the total number of estimates in each posterior distribution ($\mathrm{n} = 10^5$). The proportion of estimates smaller than the niche metric of area *b* provides a direct probability of the niche metric of area *a* being smaller than the niche metric of area *b* (Table 1). This methodology was used to determine the probability that each species niche metrics differ among species within each area (Table B4).

## Assumptions and Limitations

Although space-for-time-substitutions are valuable in the absence of long-term data, they have their limitations (Pickett 1989, Vitousek et al. 1997). Importantly, substituting space for time assumes that the variable of interest, in this case the recovery of keystone predation and the associated regime shift, is imposed randomly on the landscape and that sites differ only due to this variable. In reality, variables other than sea otter occupation such as wave energy, water temperature and sea urchin and kelp recruitment rates likely differed among our sites and may have also affected the trophic interactions and thus isotopic signatures and community niche metrics we calculated for each occupation category. Nonetheless, strong evidence suggests that sea otter occupation time is the dominant driver of community configuration across our sites (Stevenson et al. 2016, Lee et al. 2016, 2018, Burt et al. 2018).

The selection of the species for the rocky reef species assemblage was solely based on their presence in all three communities and a minimum sample size to run our analysis (n=3). While all 12 species were provided with the same weight for consideration between communities, it is important to note that while these species are able to exist in all three communities (i.e., does not require a specific habitat state), their function within the ecosystem is unlikely to remain static with changes to the kelp forest dynamics. Changes in the number of species individuals and their biomass were not accounted for in our analysis and might have some effect on the community niche metrics. As well, the use of small sample sizes also typically results in a bias and underestimation of the population and thus community niche metrics (Jackson et al. 2011).

The use of community isotopic niche metrics also comes with assumptions. Here we describe differences in the pattern of isotopic data and their derived metrics from which we infer the ecological mechanisms driving them. Moreover, isotopic data reflect ‘ghosts of interactions past’, consequently, the lens by which we are characterizing these alternative rocky reef community states and the mechanisms driving them, is both opaque and myopic.

# Results

## Community Niche Metrics

*Total Niche Space (Total Area – TA).* – Total temperate reef community-wide niche space increased with sea otter occupation (Figures 2 & 3A). Specifically, we found that reef communities exposed to keystone predation for short periods of time (2-8 years) had an 89% probability of being larger than those with no exposure to sea otters (Table 1). Moreover, where top-down regulation by sea otters had been imposed for long periods (16-33 years), reef assemblages had a 76% probability of being larger than those assemblages with no exposure to keystone predation (Table 1; Figure 3A). The variability in total niche space however, was greatest among the long sea otter occupation sites. Lastly, the overall shape of the isotopic community convex hull changed with increasing sea otter occupation, expanding in the $\delta^{15}$N range (y-axis) and narrowing at the base along the $\delta^{13}$C range (x-axis) (Figure 2).

*Trophic Level Diversity (Nitrogen Range – NR).* – Total community niche expansion with increasing otter occupation time was largely due to an expansion in nitrogen range reflecting greater trophic level diversity (Figure 3B). Specifically, we found that the nitrogen range of reef communities at short occupation time sites had an 89% probability of being greater than those assemblages with no exposure to keystone predation (Table 1). Similarly, sites subject to keystone predation for the longest periods of time had a 93% probability of being greater than those with no exposure to sea otters (Table 1).

*Basal Resource Diversity (Carbon Range – CR).* – The mode of the posterior estimates of the carbon range for the communities among all three sea otter occupation categories were similar. Consequently, we detected low probabilities (41%, 51%, 60%) that basal resource diversity differed among reef communities varying in sea otter occupation (Table 1; Figure 3C). However, basal resources became distinctly more uncertain among reef communities exposed to keystone predation by sea otters for the longest period of time (Figure 3C).

*Species Spacing (Centroid Distance – CD).* – Species spacing increased consistently with increasing sea otter occupation (Figure 3D). We found, with 100%

probability, that species spacing in reef communities exposed to short and long sea otter occupation was greater than those not exposed to keystone predation (Table 1).

## Species Specific Isotope Signatures and Niche Metrics

*Reef Associated Fish.* – Reef-associated fish tended to more enriched in nitrogen at longer sea otter occupation sites dominated by kelp compared to urchin-dominated sites that had not been exposed to sea otter predation. Specifically, mean $\delta^{15}N$ values of lingcod (*Ophiodon elongatus*), kelp greenling (*Hexagrammos decagrammus*), and copper rockfish (*Sebastes caurinus*) were higher in short and long sea otter occupation sites compared to sites not yet exposed to sea otter predation (Figures 4A-C). This pattern was less clear among black rockfish (*Sebastes melanops*) and quillback rockfish (*Sebastes maliger*) whose mean $\delta^{15}N$ values were highest at long sea otter occupation sites but intermediate and highly variable among urchin-dominated reefs unoccupied by sea otters (Figure B1A & B1B). We found no clear pattern in the carbon signatures of reef fish among sea otter occupation categories (Figures 5A, 5B, B2A & B2B) and no striking difference in species-specific niche size based on standard ellipse area ($SEA_C$ ; Table B3).

*Grazers.* – Red and green sea urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus droebachiensis*) tended to be depleted in $^{15}N$ and have smaller isotopic niches at kelp-dominated reefs exposed to long sea otter occupation relative to urchin-dominated sites unexposed to sea otter predation. (Figure 4D&E, Table B3). This was not the case for purple urchins (*Strongylocentrotus purpuratus*) (Figure B1C). The carbon isotope composition of red and purple sea urchins were the most depleted at long sea otter occupations sites compared to unoccupied and recently occupied sites (Figures 5D & B2C). Both red and green sea urchins displayed the greatest variability in their $\delta^{13}C$ values at short sea otter occupation time periods (Figures 5D&E).

*Filter-feeders.* – We did not detect much change in the isotopic composition or overall size and positioning of the California mussel (*Mytilus californianus*) niche space, among the three categories of sea otter occupation (Figures 4F & 5F, Table B3).

*Primary Producers.* – Carbon signatures for all brown macroalgal species and particulate organic matter (POM), used to represent pelagic oceanic signatures, exhibited considerable overlap in $\delta^{13}C$ values (Tables C1 & C2, Figures C1 & C2). The carbon isotopic compositions of annual species *Nereocystis luetkeana* and old-growth kelp *Pterygophora californica* overlapped significantly with POM values (Tables C1 & C2, Figures C1 & C2). Seagrasses (*Phyllospadix* spp.) exhibited comparatively $^{13}C$-enriched values compared to many of the kelp species but did not show distinctly different stable isotopic compositions from perennial kelp *Macrocystis pyrifera* (Table C1). Only *Opuntiella californica*, a red macroalgae, displayed distinctly $^{13}C$-depleted values (Table C1, Figures C1 & C2).

# Discussion

Regime shifts are well known to trigger wholesale community re-organization, yet rarely are these system-wide changes quantified, nor are the changes in trophic characteristics and energy flows that created them. Here, we found that total temperate reef community niche space increased and shifted with the recovery of keystone predation by sea otters on the central coast of British Columbia, Canada. This was due to an increase in both trophic level diversity and species spacing among reef consumers, and greater uncertainty in basal resource diversity. Specifically, as sea otter occupation time increased, we detected an expansion in the nitrogen range of the community assemblage driven by an increase in the $\delta^{15}N$ values of high trophic level predators (lingcod, kelp greenling and copper rockfish) and a decrease in the $\delta^{15}N$ values of benthic grazers (green and red sea urchins). Moreover, the distance between species' isotopic niches increased suggesting that species became more trophically distinct with the recovery of keystone predation. Multiple, non-mutually exclusive ecological mechanisms can be invoked to explain these patterns.

## Predator Recovery Expands Food Chain Length via Multiple Pathways

Recent evidence, from a diversity of ecosystems, points to a mosaic of interacting determinants of food chain length (Post 2002, Vander Zanden and Fetzer 2007, McHugh et al. 2010, McIntosh et al. 2018), that is the number of transfers of energy or nutrients from the base to the top of a food web (Yodzis 1984). Multiple ecological processes, such as predation and disturbance, and their resulting effects on resource availability, habitat stability, ecosystem size and the history of community organization have all been shown to affect food chain length (Post 2002, Layman et al. 2007, Doi et al. 2008, Takimoto and Post 2013). Therefore, counter to conventional wisdom, no singular determinant of food chain length exists, rather, a dynamic interplay among a mosaic of processes are often at work. The expansion in community niche space (Figures 2 & 3A) and food chain length (Figure 3B) with the recovery of keystone predation that we report here is in line with this notion given that sea otter range expansion on high latitude temperate reefs is associated with greater resource availability, ecosystem size, and predator-prey size structure.

On temperate rocky reefs from Alaska through to California, the recovery of keystone predation can trigger a cascade of interactions, increasing both resource availability and ecosystem size, and thus secondary production. By reducing the density, size and grazing rates of sea urchins, a dominant reef herbivore, the recovery of reef predators, be they sea otters, sheephead wrasse, lobster or predatory sea stars, can lead to both an increase in primary production per unit area and an overall expansion in the spatial extent and structural complexity of kelp forests (Estes and Palmisano 1974, Duggins 1980, Lafferty 2004, Watson et al 2011). Energetic theory suggests that food chain length should increase as the amount of energy (or limiting resources) available to top predators' increases because energetic efficiencies are typically low (~10%), thus, there is a diminishing amount of energy available to support each subsequent trophic level. The 'productive space hypothesis' (Schoner 1989) suggests that food chain length should increase as a function of total ecosystem productivity - the product of both ecosystem size (area or volume) and some measure of productivity per unit area. Unlike previous energetic hypotheses based on per-unit-area estimates of productivity alone, this recent formalization explicitly includes a spatial component to estimate more accurately the total availability of resources for upper trophic levels. In our study area, an increase in the density of kelp (Stevenson et al. 2016, Lee et al. 2016, Burt et al. 2018) and the proportion of rocky reef covered in kelp increased with sea otter occupation time and was positively associated with increased copper rockfish biomass (Silberg 2015). Just south of our study area structural kelp forest habitat supporting kelp-associated food webs was 20 times higher in the presence of keystone predation by sea otters and black and copper rockfish had higher mean trophic positions compared to urchin-dominated reefs and the absence of keystone predation by sea otters (Markel and Shurin 2015). Moreover, previous research on California rocky reefs documented a positive association between canopy kelps and secondary productivity through the provision of physical habitat supporting resources for consumers (Carr 1989, Holbrook et al. 1990, Steneck et al. 2002). And yet, observations from lakes, islands and kelp forests suggest that a combination of total ecosystem productivity and associated changes in the size structure of predator-prey interactions and degree of trophic omnivory all contribute to longer food chains (Schoener 1989, Post et al. 2000).

In food webs dominated by size-structured predator-prey interactions, food chain length is a function of both the ratio between predator and prey body size and the range of body sizes across the food chain. These two variables are influenced by a combination of resource availability, ecosystem size, and disturbance (Post 2002). On temperate rocky reefs around the world, kelp abundance has been shown to be an important positive predictor of fish body size (Babcock et al. 1999, Davis and Wing 2012, Koenigs et al. 2015) thereby influencing predator-prey interactions and ultimately food chain length. Larger fish typically feed on larger prey at higher trophic levels due to the positive relationship between fish length and gape size (Jennings et al. 2002, Davis and Wing 2012, Frid et al. 2012, Trebilco et al. 2015). Our results show that reef fish, specifically lingcod, kelp greenling and copper rockfish, exhibited more $^{15}$N-enriched values and thus higher trophic levels on reefs dominated by kelp due to keystone predation compared to reefs dominated by urchins in the absence of keystone predation by otters (Figures 4A-C). These results suggest that in the presence of keystone predation, reef fish are more frequently consuming and assimilating higher trophic level prey compared to reef fish inhabiting urchin-dominated reefs. Given that reef fish did exhibit higher $\delta^{15}$N values on kelp-dominated reefs but no difference in their isotopic carbon compositions, the expansion of food-chain length with the recovery of keystone predation by otters likely arises through the creation of habitat for mid trophic level fishes rather than a direct trophic connection through invertebrates or other consumers of kelp productivity. Similar results and inferences were made south of this study region (Markel and Shurin 2015).

Food chain length can also be expanded at the base of a food web when lower trophic level consumers exhibit less omnivory and feed lower on the food chain. As primary consumers in rocky reef food webs, sea urchins can exhibit a high degree of food selectivity and will preferentially consume macroalgae given the opportunity (Larson et al. 1980, Scheilbling and Anthony 2001). On reefs dominated by urchins however, sea urchins are known to be omnivorous and will feed on whatever is available (Lawrence et al. 2013), including their own species and prey that occupy higher trophic levels such as hydroids, bryozoans and even jelly fish (LeGault and Hunt 2016). Our results indicate that sea urchins occupy lower trophic levels on forested reefs in the presence of keystone predation by sea otters compared to reefs devoid of kelp that have not been exposed to sea otter predation (Figures 4D&E). In addition to increasing the availability of primary producers for urchins to consume, our results suggest that keystone predation can expand community-level isotopic niche space by increasing the variability in basal resources.

The greater dispersion of individual isotopic signatures from the mean of the community niche with keystone predator recovery further supports the increase in the degree of trophic diversity within the community (Figure 3D). However, caution is required in the interpretation of this diversity metric. We focused on a set species assemblage in this study; our results do not account for changes in species diversity which would impact the results of this metric. For example, the immigration of a redundant species such as mid-trophic level forage fish would result in a decrease in the distance between individuals and the mean of the community niche (Layman et al. 2007a).

## Basal Resources Shifted with the Recovery of Keystone Predation

The recovery and decline of keystone predation have been shown to play an important role in shifting and diversifying basal resources, particularly in aquatic systems (Shurin et al. 2002). For example, phytoplankton communities exhibited measurable shifts as a result of recovering populations of largemouth bass in North America (Carpenter 1987) and overfishing of Atlantic cod (Frank et al. 2005). We did not detect an effect of keystone predation on the community-wide basal resources (Figure 3C); the carbon range of the community did not suggest source differentiation and appeared to become more uncertain among the reef assemblages exposed to keystone predation for the longest period of time (Figure 3C). As sea otter occupation time increases on rocky reefs, kelp forests tend to encompass a greater diversity of kelp species and a higher proportion of perennial, longer-lived species such as giant kelp (*Macrocystis pyrifera*) and palm kelp (*Pterygophora californica*) relative to reefs newly occupied by sea otters which are dominated by the weedy annual bull kelp (*Nereocystis luetkeana*) (Watson et al 2011, Lee et al 2016). Our results suggest that different source groups have similar carbon isotope ratios (e.g., particulate organic matter representing pelagic signatures, annual species *Nereocystis luetkeana*, and old-growth species *Pterygophora califonica*; Figures C1 & C2). Consequently, it is possible that the uncertainty in basal resources we detected among reef communities at longer occupation sites reflects the diversity of attached and detrital kelp-carbon sources on those reefs, the variability and overlap in their isotopic signatures (Figures C1 & C2).

Paradoxically, both primary and secondary consumers on kelp-dominated reefs were not more enriched in kelp carbon (Figures 5 & B2). Filter feeders in kelp forests have been shown to be more enriched in $^{13}$C than those in urchin barrens, reflecting a greater assimilation of kelp derived organic carbon (Duggins et al. 1989, Salomon et al. 2008). Contrary to our expectations, we did not find evidence for an effect of otter occupation period on California mussel (*Mytilus californianus*) or reef fish carbon signatures suggesting that both consumers did not measurably assimilate greater concentrations of kelp at kelp-dominated sites with longer sea otter occupation history (Figure 5F). Similar results have been found elsewhere on BC's coast (Singh 2010, Markel and Shurin 2015) suggesting that, kelp forest recovery in BC may not be reflected in consumer carbon values as they have been in Alaska, New Zealand and the Arctic (Kaehler et al. 2006, Ramshaw 2012, vonBiela et al. 2016, Olson 2017). This may be due to pelagic primary production not being limited, high movement rates of detrital kelp among reefs and across habitats (von Biela et al. 2016, Docmac et al. 2017, Smith et al. 2018), highly variable and overlapping isotopic signatures between pelagic and benthic end members, or a combination of factors.

## Implications for Management

Our study builds on and integrates concepts of keystone predator recovery and community niche space, as inferred by stable isotopes. Our results suggest that sea otter recovery has expanded the overall community niche space, primarily due to greater trophic level diversity stemming from increased primary productivity and shifts in basal resource use. While the main caveat of using stable isotopes in a food web context is that the data are only indirect indicators of feeding pathways and require additional analyses (e.g., stomach content analyses) to further illuminate results, this study demonstrates the usefulness of stable isotopes as a means to take snapshot overviews of entire ecosystem niches and measure changes to trophic dynamics due to regime shifts. Understanding the important role sea otter recovery plays in reshaping nearshore food web organization and function can provide information about the mechanisms driving those changes and thus give insight on which features to focus on when making conservation decisions.

# Tables

**Table 1** **Differences in community niche widths between three sea otter occupation categories: None (0 years), Short (2-8 years), and Long (16-33 years) based on isotopic niche width metrics. Probability (%) of difference in niche widths were calculated as the proportion of estimates smaller in area a vs. b which gives a direct probability of area b being greater than area a.**

| Comparison | | Probability of difference of a < b | | | |
|---|---|---|---|---|---|
| a | b | Total Niche Space Occupied (Total Area) | Trophic Level Diversity (N Range) | Basal Resource Diversity (C range) | Species Spacing (Centroid Distance) |
| None | Long | 76 | 93 | 51 | 100 |
| None | Short | 89 | 89 | 41 | 100 |
| Short | Long | 45 | 69 | 60 | 84 |

# Figures

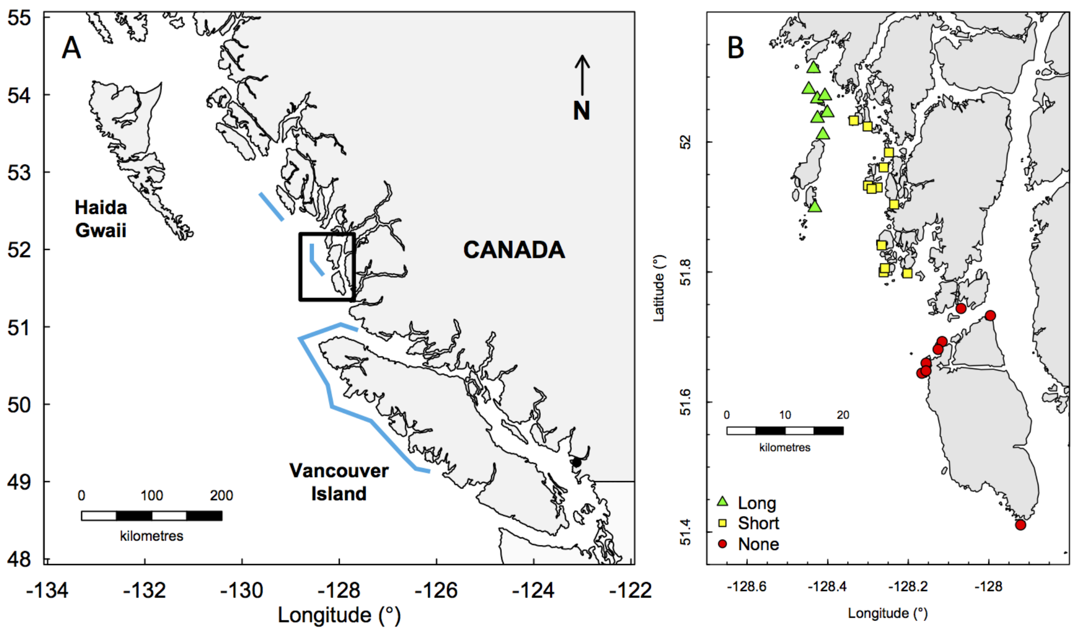

**Figure 1** On the A) central coast of British Columbia, Canada (black rectangle inset) sea otters (Enhydra lutris) have been expanding their range (blue lines) north and southwards creating sites that differ in sea otter occupation time. We surveyed (B) subtidal rocky reef communities at 28 sites varying in sea otter occupation category: None (0 years; red circles), Short (2-8 years; yellow squares), and Long (16-33 years; green triangles).

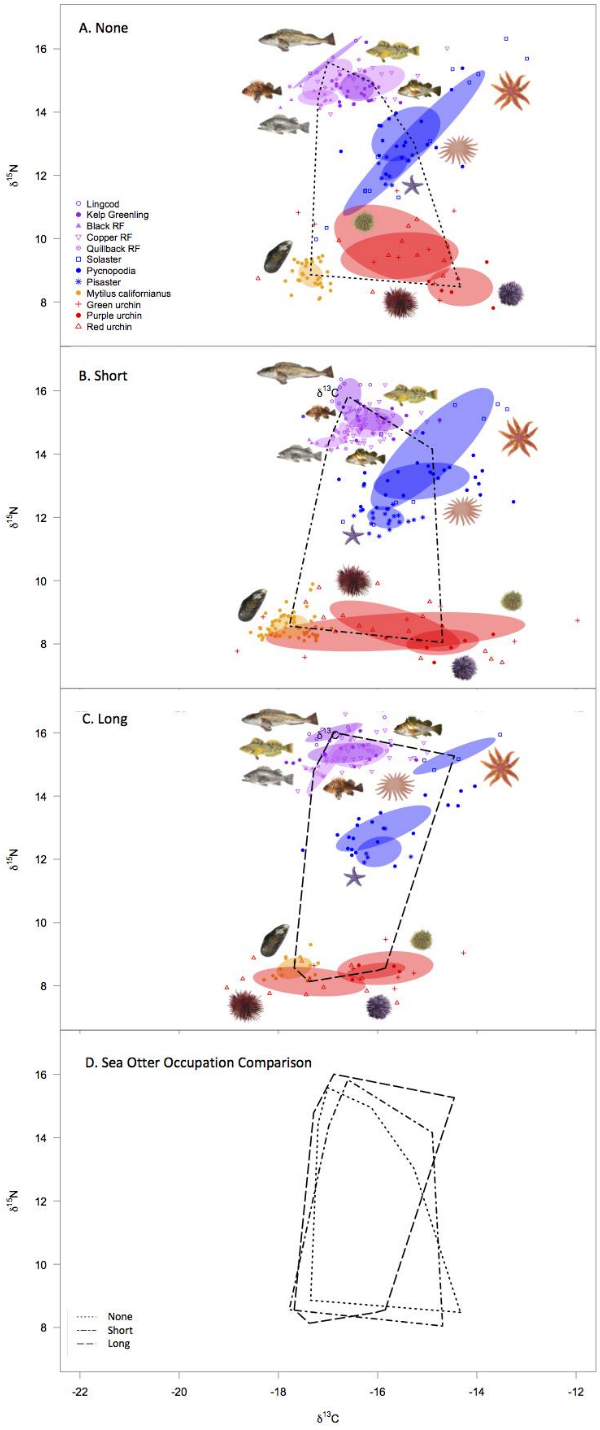

**Figure 2** Community isotopic niche widths based on standard ellipse areas (SEA$_C$) for three sea otter occupation categories: (A) None (0 years), (B) Short (2-8 years), and (C) Long (16-33 years). (D) Comparison of community isotopic niche widths for all three sea otter occupation periods. Unique symbols indicate different species in the community assemblage. Different colours represent different functional groups.

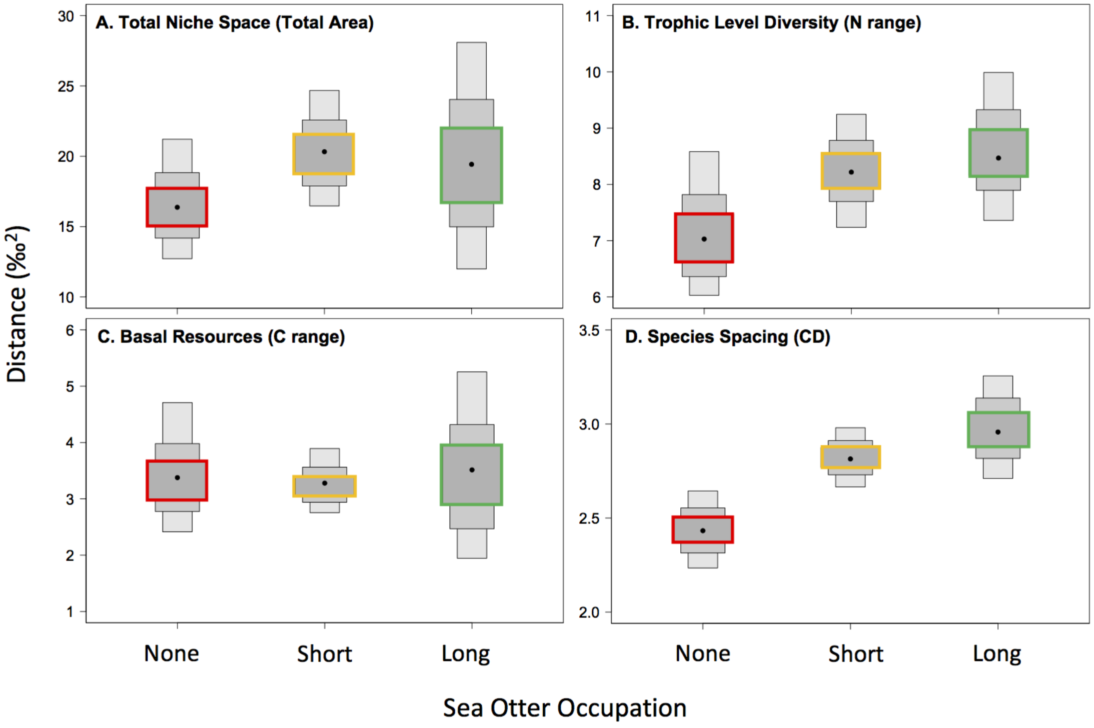

**Figure 3** Community-level isotopic niche metrics for the three sea otter occupation categories: None (0 years; red box), Short (2-8 years; yellow box), and Long (16-33 years; green box), calculated using Bayesian inferences; median estimate (black dot) and 50%, 75% and 95% credible intervals (increasing dark shades of grey). Each metric is shown separately comparing all three occupation categories, with y-axis values representing the relative comparison: (A) total niche space (total area), (B) trophic level diversity (nitrogen range), (C) basal resource diversity (carbon range), and (D) species spacing (centroid distance).

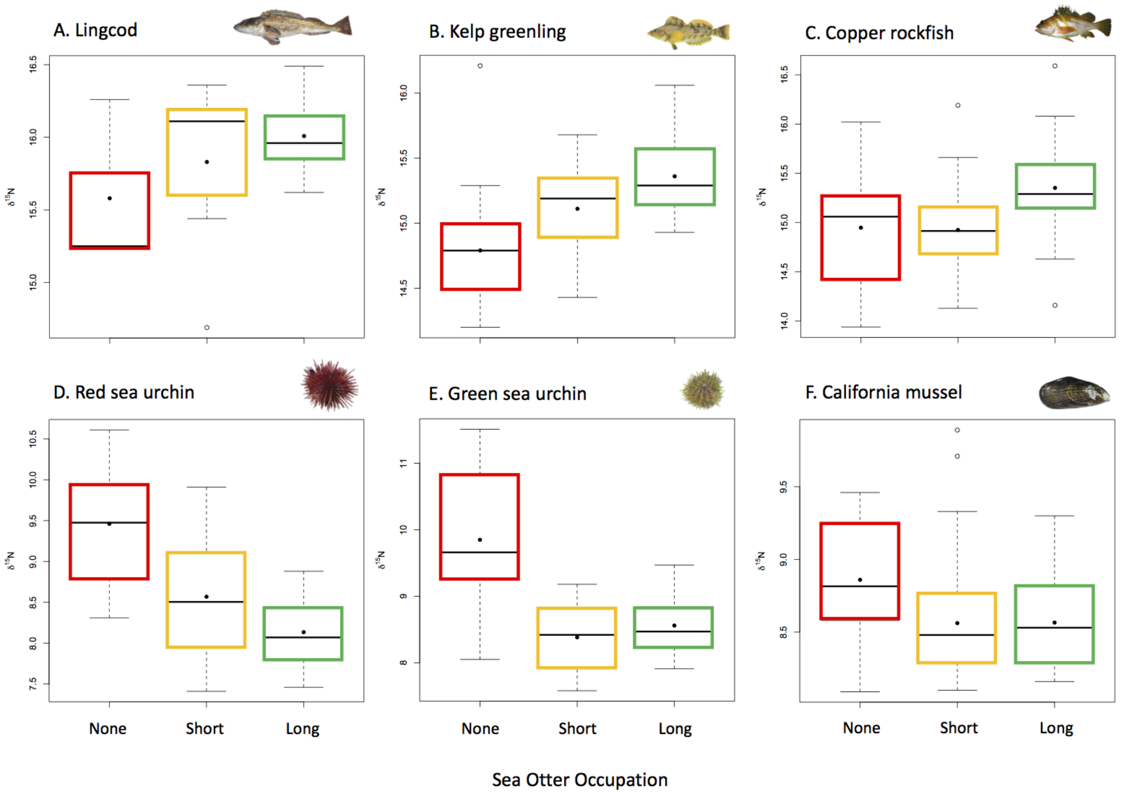

**Figure 4** Nitrogen signatures ($\delta^{15}N$) of six reef associated species at sites varying in sea otter occupation category: None (0 years; red box), Short (2-8 years; yellow box), and Long (16-33 years; green box) for (A) lingcod, (B) kelp greenling, (C) copper rockfish, (D) red sea urchin, (E) green sea urchin, and (F) California mussel. Boxplots depict the mean (black dot), median (horizontal black bar), the 1st and 3rd quantiles (box edges), and 95% confidence intervals of the median (error bars).

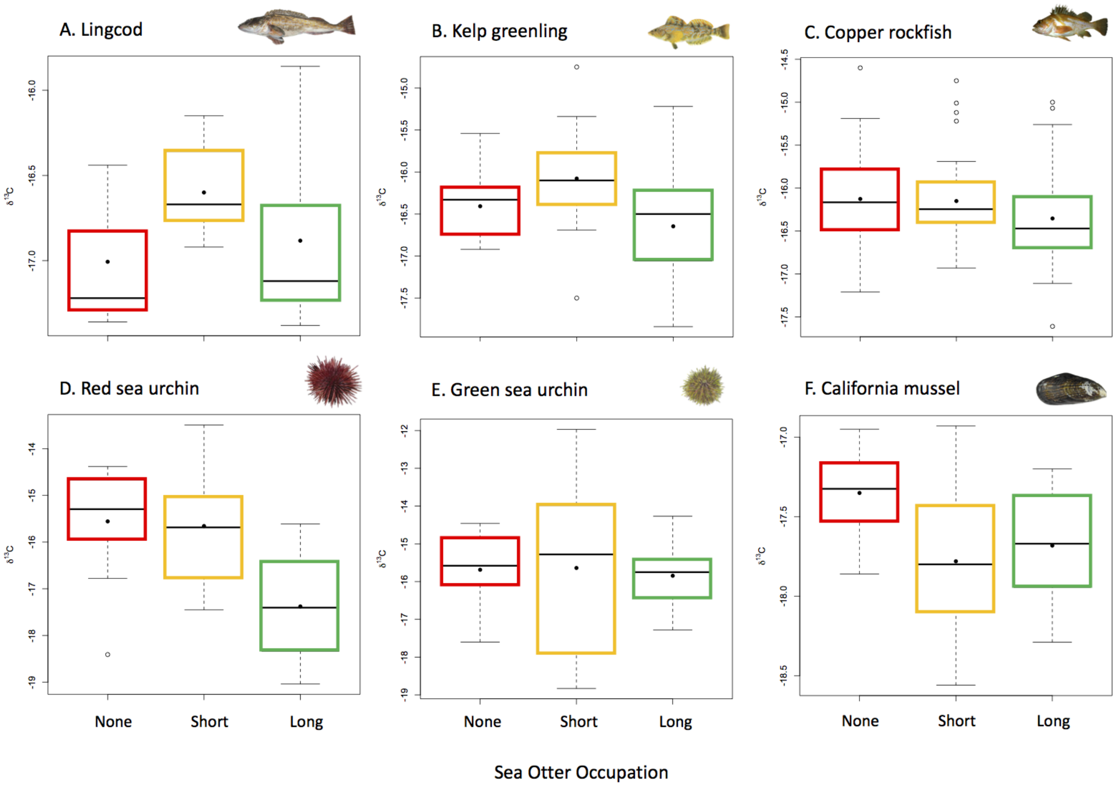

**Figure 5** Carbon signatures ($\delta^{13}C$) of six reef associated species at sites varying in sea otter occupation category: None (0 years; red box), Short (2-8 years; yellow box), and Long (16-33 years; green box) for (A) lingcod, (B) kelp greenling, (C) copper rockfish, (D) red sea urchin, (E) green sea urchin, and (F) California mussel. Boxplots are comprised of the mean (black dot), median (horizontal black bar), the 1st and 3rd quantiles (box edges), and 95% confidence intervals of the median (error bars).

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# Appendix A. Site characteristics

**Table A1.** **Sites surveyed in 2011 and 2013 in kelp forest monitoring surveys on the central coast of British Columbia (n=28). Categorization of sea otter occupation time was based on strong evidence that sea otter recovery is associated with dramatic decreases in sea urchin density and biomass across their distribution within the study region (mean ± standard error). We surveyed subtidal rocky reef sites varying in sea otter occupation category: None (0 years), Short (2-8 years), and Long (16-33 years).**

| Sea Otter Occupation Category | Sample Site | Lat | Long | Sample Year | Otter Occ. Time (Years) | Urchin Density (mean ± s.e.) | Urchin Biomass (mean ± s.e.) | Kelp Stipes (mean ± s.e.) |
|---|---|---|---|---|---|---|---|---|
| None | Fifth Beach Rocks | 51.64436 | -128.166 | 2011 | 0 | N/A | N/A | N/A |
| None | Kelpie Pt | 51.73361 | -127.996 | 2013 | 0 | 5.17 ± 1.96 | 1576.72 ± 398.71 | 4.17 + 1.44 |
| None | Mercury | 51.74406 | -128.070 | 2013 | 0 | 4.44 ± 0.73 | 1073.57 ± 223.71 | 0.11 ± 0.11 |
| None | Odlum | 51.69311 | -128.117 | 2013 | 0 | 7.11 ± 1.07 | 1611.51 ± 247.62 | 0.00 ± 0.00 |
| None | Starfish | 51.68042 | -128.126 | 2013 | 0 | 5.17 ± 1.97 | 1124.18 ± 401.78 | 9.94 ± 2.61 |
| None | Thrasher | 51.80589 | -128.259 | 2013 | 0 | 9.28 ± 1.74 | 2687.59 ± 484.15 | 0.00 ± 0.00 |
| None | West Beach North | 51.65989 | -128.156 | 2011 | 0 | N/A | N/A | N/A |
| None | West /2nd Beach | 51.64869 | -128.156 | 2013 | 0 | 15.39 ± 3.75 | 2052.83 ± 567.66 | 0.056 ± 0.056 |
| Short | Athabaskan | 52.02431 | -128.301 | 2013 | 8 | 1.89 ± 0.84 | 62.86 ± 34.04 | 6.61 ± 1.44 |
| Short | Granville | 51.93008 | -128.276 | 2011 | 3 | N/A | N/A | N/A |
| Short | Iroquois | 52.03306 | -128.335 | 2011 | 3 | N/A | N/A | N/A |
| Short | Manley | 51.7978 | -128.202 | 2013 | 5 | 1.00 ± 0.48 | 215.16 ± 112.50 | 3.56 ± 1.38 |
| Short | McNaughton | 51.9043 | -128.235 | 2013 | 4 | 3.06 ± 1.41 | 393.52 ± 184.24 | 6.25 ± 1.80 |
| Short | Purple Bluff | 51.93306 | -128.300 | 2011 | 3 | N/A | N/A | N/A |
| Short | Robert | 51.98397 | -128.248 | 2013 | 5 | 0.78 ± 0.29 | 17.28 ± 9.27 | 9.33 ± 0.96 |
| Short | Simonds NE | 51.96072 | -128.262 | 2013 | 4 | 0.67 ± 0.30 | 85.79 ± 53.08 | 7.94 ± 1.24 |
| Short | Simonds SE | 51.92828 | -128.291 | 2013 | 4 | 1.22 ± 0.61 | 23.06 ± 10.72 | 16.06 ± 2.26 |
| Short | Spider | 51.8412 | -128.265 | 2013 | 3 | 0.056 ± 0.056 | 0.72 ± 0.72 | 14.94 ± 1.16 |
| Short | Triquet | 51.79972 | -128.261 | 2011 | 2 | N/A | N/A | N/A |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Short | Triquet | 51.41061 | -127.92 | 2013 | 2 | 2.1 ± 0.91 | 281.47 ± 147.83 | 11.06 ± 1.87 |
| Long | Fingal | 52.08066 | -128.448 | 2013 | 17 | 0 | 0 | 11.17 ± 1.06 |
| Long | Goose | 52.00072 | -128.413 | 2013 | 17 | 2.06 ± 0.92 | 141.76 ± 61.28 | 9.61 ± 1.03 |
| Long | Gosling | 51.8998 | -128.433 | 2013 | 33 | 1.72 ± 0.99 | 69.91 ± 48.20 | 7.72 ± 1.35 |
| Long | Houghton | 52.11253 | -128.435 | 2013 | 17 | 0.39 ± 0.24 | 18.84 ± 10.93 | 5.06 ± 1.03 |
| Long | McMullin | 52.06639 | -128.426 | 2011 | 16 | N/A | N/A | N/A |
| Long | MidEast McMullin | 52.03654 | -128.425 | 2011 | 16 | N/A | N/A | N/A |
| Long | McMullin N | 52.0711 | -128.407 | 2013 | 17 | 0.83 ± 0.43 | 36.27 ± 19.08 | 7.39 ± 1.05 |
| Long | McMullin S | 52.04512 | -128.4 | 2013 | 17 | 0.56 ± 0.33 | 23.06 ± 18.69 | 5.50 ± 0.60 |

# Appendix B. Rocky Reef Consumer Stable Isotopes

**Table B1. Twelve species sampled at British Columbian central coast rocky reef sites representing the rocky reef food web species assemblage used in stable isotope analysis from surveys conducted in 2011 and 2013.**

| Common name | Scientific name | Functional group |
|---|---|---|
| Lingcod | *Ophiodon elongatus* | Mesopredator fish |
| Kelp greenling | *Hexagrammos decagrammus* | Mesopredator fish |
| Copper rockfish | *Sebastes caurinus* | Mesopredator fish |
| Black rockfish | *Sebastes melanops* | Mesopredator fish |
| Quillback rockfish | *Sebastes maliger* | Mesopredator fish |
| Sunflower star | *Pycnopodia helianthoides* | Seastar |
| Sunstar | *Solaster* spp. | Seastar |
| Ochre star | *Pisaster ochraceus* | Seastar |
| Green sea urchin | *Strongylocentrotus droebachiensis* | Benthic grazer |
| Red sea urchin | *Mesocentrotus franciscanus* | Benthic grazer |
| Purple sea urchin | *Strongylocentotus purpuratus* | Benthic grazer |
| California mussel | *Mytilus californianus* | Filter feeder |

**Table B2.** **Twelve species sampled at British Columbian central coast rocky reef sites representing the rocky reef food web species assemblage used in stable isotope analysis from surveys conducted in 2011 and 2013 (mean ± standard error).**

| | None (0 yr) | | | Short (2-8 yr) | | | Long (16-33 yr) | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species Name** | **n** | **$\delta^{13}$C** | **$\delta^{15}$N** | **n** | **$\delta^{13}$C** | **$\delta^{15}$N** | **n** | **$\delta^{13}$C** | **$\delta^{15}$N** |
| Lingcod (*Ophiodon elongatus*) | 3 | -17.01 ± 0.29 | 15.58 ± 0.34 | 9 | -16.60 ± 0.084 | 15.83 ± 0.18 | 7 | -16.88 ± 0.20 | 16.01 ± 0.11 |
| Kelp greenling (*Hexagrammos decagrammus*) | 25 | -16.41 ± 0.067 | 14.79 ± 0.087 | 19 | -16.08 ± 0.13 | 15.11 ± 0.083 | 15 | -16.65 ± 0.19 | 15.36 ± 0.080 |
| Copper rockfish (*Sebastes caurinus*) | 16 | -16.13 ± 0.16 | 14.95 ± 0.13 | 56 | -16.15 ± 0.058 | 14.93 ± 0.053 | 39 | -16.35 ± 0.092 | 15.35 ± 0.070 |
| Black rockfish (*Sebastes melanops*) | 12 | -17.20 ± 0.11 | 14.46 ± 0.069 | 9 | -16.99 ± 0.094 | 14.37 ± 0.053 | 3 | -17.29 ± 0.099 | 14.78 ± 0.082 |
| Quillback rockfish (*Sebastes maliger*) | 6 | -17.01 ± 0.19 | 15.04 ± 0.24 | 6 | -16.70 ± 0.039 | 14.66 ± 0.13 | 4 | -16.92 ± 0.21 | 15.20 ± 0.46 |
| Sunflower star (*Pycnopodia helianthoides*) | 17 | -15.43 ± 0.16 | 13.31± 0.20 | 26 | -15.11 ± 0.19 | 13.14 ± 0.11 | 21 | -15.88 ± 0.20 | 12.97 ± 0.16 |
| Sunstar (*Solaster* spp.) | 13 | -15.27 ± 0.38 | 13.02 ± 0.61 | 10 | -14.90 ± 0.37 | 14.16 ± 0.58 | 4 | -14.46 ± 0.34 | 15.27 ± 0.24 |
| Ochre star (*Pisaster ochraceus*) | 10 | -15.66 ± 0.078 | 12.24 ± 0.12 | 20 | -15.84 ± 0.081 | 12.00 ± 0.077 | 5 | -15.98 ± 0.18 | 12.24 ± 0.19 |
| Green urchin (*Strongylocentrotus droebachiensis*) | 9 | -15.69 ± 0.37 | 9.85 ± 0.38 | 8 | -15.64 ± 0.86 | 8.38 ± 0.20 | 8 | -15.85 ± 0.32 | 8.56 ± 0.18 |
| Red urchin (*Mesocentrotus franciscanus*) | 12 | -15.56 ± 0.33 | 9.46 ± 0.21 | 16 | -15.66 ± 0.32 | 8.57 ± 0.19 | 12 | -17.38 ± 0.31 | 8.13 ± 0.13 |
| Purple urchin (*Strongylocentotus purpuratus*) | 5 | -14.33 ± 0.26 | 8.48 ± 0.24 | 7 | -14.69 ± 0.25 | 8.05 ± 0.14 | 4 | -16.03 ± 0.24 | 8.48 ± 0.11 |
| California mussel (*Mytilus californianus*) | 30 | -17.35 ± 0.045 | 8.86 ± 0.073 | 63 | -17.78 ± 0.049 | 8.56 ± 0.046 | 15 | -17.68 ± 0.090 | 8.57 ± 0.088 |

**Table B3.** **Species-specific niches represented by standard ellipse areas corrected for small sample sizes ($SEA_C$) of the 12 species representing the rocky reef food web species assemblage used in stable isotope analysis from surveys conducted in 2011 and 2013.**

| Species | None | Short | Long |
|---|---|---|---|
| Lingcod (*Ophiodon elongatus*) | 0.23 | 0.48 | 0.33 |
| Kelp greenling (*Hexagrammos decagrammus*) | 0.47 | 0.69 | 0.74 |
| Copper rockfish (*Sebastes caurinus*) | 1.03 | 0.54 | 0.77 |
| Black rockfish (*Sebastes melanops*) | 0.33 | 0.16 | 0.067 |
| Quillback rockfish (*Sebastes maliger*) | 0.85 | 0.12 | 0.55 |
| Sunflower star (*Pycnopodia helianthoides*) | 1.76 | 1.74 | 1.44 |
| Sunstar (*Solaster* spp.) | 2.88 | 4.26 | 0.66 |
| Ochre star (*Pisaster ochraceus*) | 0.27 | 0.41 | 0.69 |
| Green sea urchin (*Strongylocentrotus droebachiensis*) | 4.20 | 4.78 | 1.61 |
| Red sea urchin (*Mesocentrotus franciscanus*) | 2.75 | 2.41 | 1.60 |
| Purple sea urchin (*Strongylocentotus purpuratus*) | 1.27 | 0.92 | 0.45 |
| California mussel (*Mytilus californianus*) | 0.32 | 0.45 | 0.38 |

**Table B4.** **Differences in individual species-level niche widths between three otter occupation categories: None (0 years), Short (2-8 years), and Long (16-33 years) based on Bayesian standard ellipse area niches ($SEA_B$). $SEA_B$ is a measure of isotopic niche with estimated by Bayesian multivariate standardized ellipse areas and is insensitive to biases of small sample sizes. Probability (%) of difference in species niche width were calculated as the proportion of estimates smaller in area *a* versus area *b* which gives a direct probability of area *b* being greater than area *a*. Niche overlap was calculated for each species $SEA_C$ The extent of the overlap will range from 0 to 1, with values closer to 0 representing less overlap.**

| Species | Comparison | | Probability (%) of difference of *a* < *b* | Calculated overlap of niches between *a* and *b* |
|---|---|---|---|---|
| | *a* | *b* | | |
| Lingcod (*Ophiodon elongatus*) | None | Long | 36 | 0.05 |
| | None | Short | 10 | 0.08 |
| | Short | Long | 87 | 0.13 |
| Kelp greenling (*Hexagrammus decagrammus*) | None | Long | 95 | 0.05 |
| | None | Short | 85 | 0.18 |
| | Short | Long | 76 | 0.23 |
| Copper rockfish (*Sebastes caurinus*) | None | Long | 84 | 0.30 |
| | None | Short | 1 | 0.54 |
| | Short | Long | 100 | 0.17 |
| Black rockfish (*Sebastes melanops*) | None | Long | 92 | 0.02 |
| | None | Short | 54 | 0.12 |
| | Short | Long | 90 | 0 |
| Quillback rockfish (*Sebastes maliger*) | None | Long | 4 | 0.37 |
| | None | Short | 19 | 0.02 |
| | Short | Long | 24 | 0 |
| Sunflower star (*Pycnopodia helianthoides*) | None | Long | 51 | 0.90 |
| | None | Short | 42 | 1.11 |
| | Short | Long | 55 | 0.78 |
| Sunstar (*Solaster* spp.) | None | Long | 0 | 0 |
| | None | Short | 69 | 1.89 |
| | Short | Long | 0 | 0.64 |
| Ochre star (*Pisaster ochraceus*) | None | Long | 79 | 0.20 |
| | None | Short | 23 | 0.14 |
| | Short | Long | 95 | 0.28 |
| Green sea urchin (*Strongylocentrotus droebachiensis*) | None | Long | 21 | 0.39 |
| | None | Short | 97 | 0.38 |
| | Short | Long | 2 | 1.47 |
| Red sea urchin (*Mesocentrotus franciscanus*) | None | Long | 10 | 0 |
| | None | Short | 66 | 0.66 |
| | Short | Long | 3 | 0 |
| Purple sea urchin (*Stongylocentrotus purpuratus*) | None | Long | 41 | 0 |
| | None | Short | 38 | 0.44 |
| | Short | Long | 52 | 0 |
| California mussel (*Mytilus californianus*) | None | Long | 100 | 0.08 |
| | None | Short | 53 | 0.05 |
| | Short | Long | 100 | 0.34 |

**Table B5.** **Maximum likelihood community-level Layman metrics for each community. Community-level metrics for each of the three communities. The maximum area calculated from the convex hull is represented by TA, which provides an estimate of the total niche space occupied by the community assemblage along the $\delta^{13}C$ and $\delta^{15}N$ axes. NR and CR are calculated as the difference between the maximum and minimum $\delta^{15}N$ and $\delta^{13}C$ values of the convex hull, respectively. NR represents the vertical structure of the community food web and reflects trophic level diversity, while CR reflects the diversity of basal energy resources. CD is calculated by the distance between an individual and the $\delta^{13}C$-$\delta^{15}N$ centroid in the community convex hull, providing a measure of species spacing or measure of the average degree of trophic diversity.**

| Sea Otter Occupation Period | Total Niche Space Occupied (Total Area - TA) | Trophic Level Diversity (Nitrogen Range – NR) | Basal Resource Diversity (Carbon Range - CR) | Species Spacing (Centroid Distance - CD) |
|---|---|---|---|---|
| None | 14.00 | 7.10 | 3.02 | 2.45 |
| Short | 17.10 | 7.78 | 3.09 | 2.81 |
| Long | 16.94 | 7.87 | 3.23 | 2.97 |

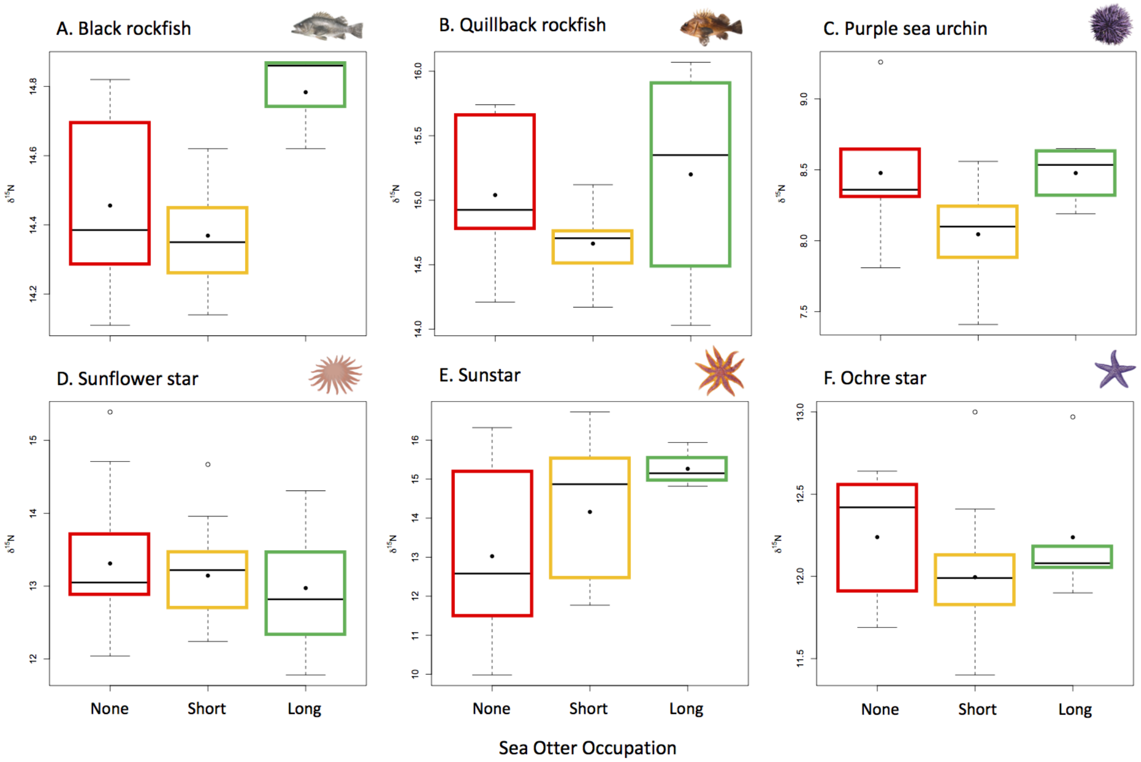

**Figure B1.** Nitrogen signatures ($\delta^{15}N$) of six reef associated species at sites varying in sea otter occupation categories: None (0 years; red box), Short (2-8 years; yellow box), and Long (16-33 years; green box) for (A) black rockfish (*Sebastes melanops*), (B) quillback rockfish (*Sebastes maliger*), (C) purple sea urchin (*Strongylocentrotus purpuratus*), (D) sunflower star (*Pycnopodia helianthoides*), (E) sunstar (*Solaster* spp.), and (F) ochre star (*Pisaster ochraceus*). Boxplots depict the mean (black dot), median (horizontal black bar), the 1st and 3rd quantiles (box edges), and 95% confidence intervals of the median (error bars).

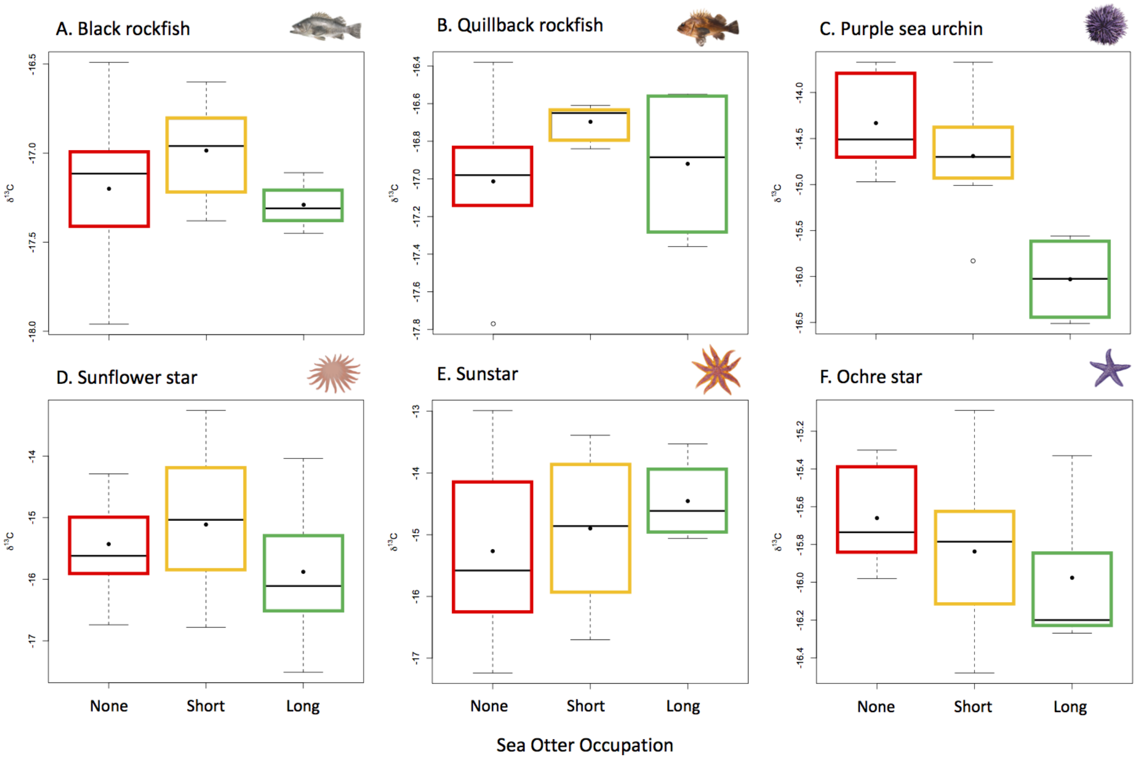

**Figure B2.** **Carbon signatures ($\delta^{13}$C) of six reef associated species at sites varying in sea otter occupation categories: None (0 years; red box), Short (2-8 years; yellow box), and Long (16-33 years; green box) for (A) black rockfish (*Sebastes melanops*), (B) quillback rockfish (*Sebastes maliger*), (C) purple sea urchin (*Strongylocentrotus purpuratus*), (D) sunflower star (*Pycnopodia helianthoides*), (E) sunstar (*Solaster* spp.), and (F) ochre star (*Pisaster ochraceus*). Boxplots depict the mean (black dot), median (horizontal black bar), the 1st and 3rd quantiles (box edges), and 95% confidence intervals of the median (error bars).**

# Appendix C. Primary Producer Stable Isotopes

**Table C1.** **Mean $\delta^{13}C$ and $\delta^{15}N$ values (± standard deviation) of macroalgal species sampled on BC's central coast rocky reef sites from surveys conducted in 2011 and 2013. Numbers of individuals sampled from three sea otter occupation categories are provided: None (0 years), Short (2-8 years), and Long (16-33 years).**

| Name | Group | $\delta^{13}C$ | $\delta^{15}N$ | None (n) | Short (n) | Long (n) |
|---|---|---|---|---|---|---|
| *Agarum fimbriatum* | Brown algae | -24.08 ± 1.95 | 7.44 ± 0.89 | 1 | 10 | 14 |
| *Alaria marginata* | Brown algae | -16.65 ± 2.54 | 6.90 ± 0.65 | 23 | 36 | 15 |
| *Costaria costata* | Brown algae | -21.54 ± 2.40 | 6.64 ± 0.81 | 15 | 13 | 17 |
| *Cymathaere triplicata* | Brown algae | -17.76 ± 2.03 | 6.65 ± 0.57 | 1 | 12 | 7 |
| *Eisenia arborea* | Brown algae | -21.63 ± 2.81 | 6.92 ± 0.91 | 0 | 5 | 8 |
| *Hedophyllum sessile* | Brown algae | -17.81 ± 0.90 | 8.25 ± 0.36 | 10 | 20 | 6 |
| *Laminaria bongardiana* | Brown algae | -15.89 ± 1.01 | 5.73 ± 1.03 | 0 | 5 | 3 |
| *Macrocystis pyrifera* | Brown algae | -15.65 ± 2.34 | 7.01 ± 1.47 | 5 | 23 | 25 |
| *Nereocystis luetkeana* | Brown algae | -19.97 ± 2.36 | 7.23 ± 0.92 | 24 | 47 | 24 |
| *Opuntiella californica* | Red algae | -33.56 ± 0.91 | 6.73 ± 0.52 | 14 | 16 | 14 |
| *Phyllospadix spp.* | Seagrass | -14.24 ± 1.29 | 6.09 ± 1.07 | 3 | 8 | 5 |
| *Pleurophycus gardneri* | Brown algae | -19.74 ± 1.75 | 7.37 ± 0.54 | 5 | 9 | 13 |
| *Pterygophora californica* | Brown algae | -21.09 ± 2.10 | 6.97 ± 1.06 | 0 | 10 | 18 |
| *Saccharina groenlandica* | Brown algae | -19.20 ± 2.52 | 6.54 ± 0.87 | 13 | 19 | 10 |
| *Saccharina latissima* | Brown algae | -21.72 ± 2.13 | 5.74 ± 1.07 | 13 | 17 | 14 |

**Table C2.** **Mean $\delta^{13}C$ and $\delta^{15}N$ values (± standard deviation) of particulate organic matter (POM) sampled on BC's central coast rocky reef sites from surveys conducted in 2011 and 2013 sampled from three sea otter occupation categories: None (0 years), Short (2-8 years), and Long (16-33 years). Each group represents different filter sizes (raw, <53um and <100um).**

| Group | None | | | Short | | | Long | | |
|---|---|---|---|---|---|---|---|---|---|
| | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ | n | $\delta^{13}C$ | $\delta^{15}N$ |
| Particulate organic matter (POM) | 21 | -20.79 ± 0.60 | 4.57 ± 1.06 | 39 | -20.07 ± 0.69 | 4.60 ± 1.41 | 24 | -19.91 ± 0.93 | 5.09 ± 1.21 |
| POM (<53 um) | 15 | -21.29 ± 0.47 | 4.00 ± 1.14 | 24 | -20.32 ± 0.76 | 4.77 ± 0.70 | 18 | -20.05 ± 1.24 | 4.01 ± 1.81 |
| POM (<100 um) | 15 | -20.99 ± 0.87 | 4.29 ± 0.69 | 24 | -20.31 ± 1.09 | 4.62 ± 1.13 | 18 | -19.94 ± 1.24 | 4.68 ± 1.42 |

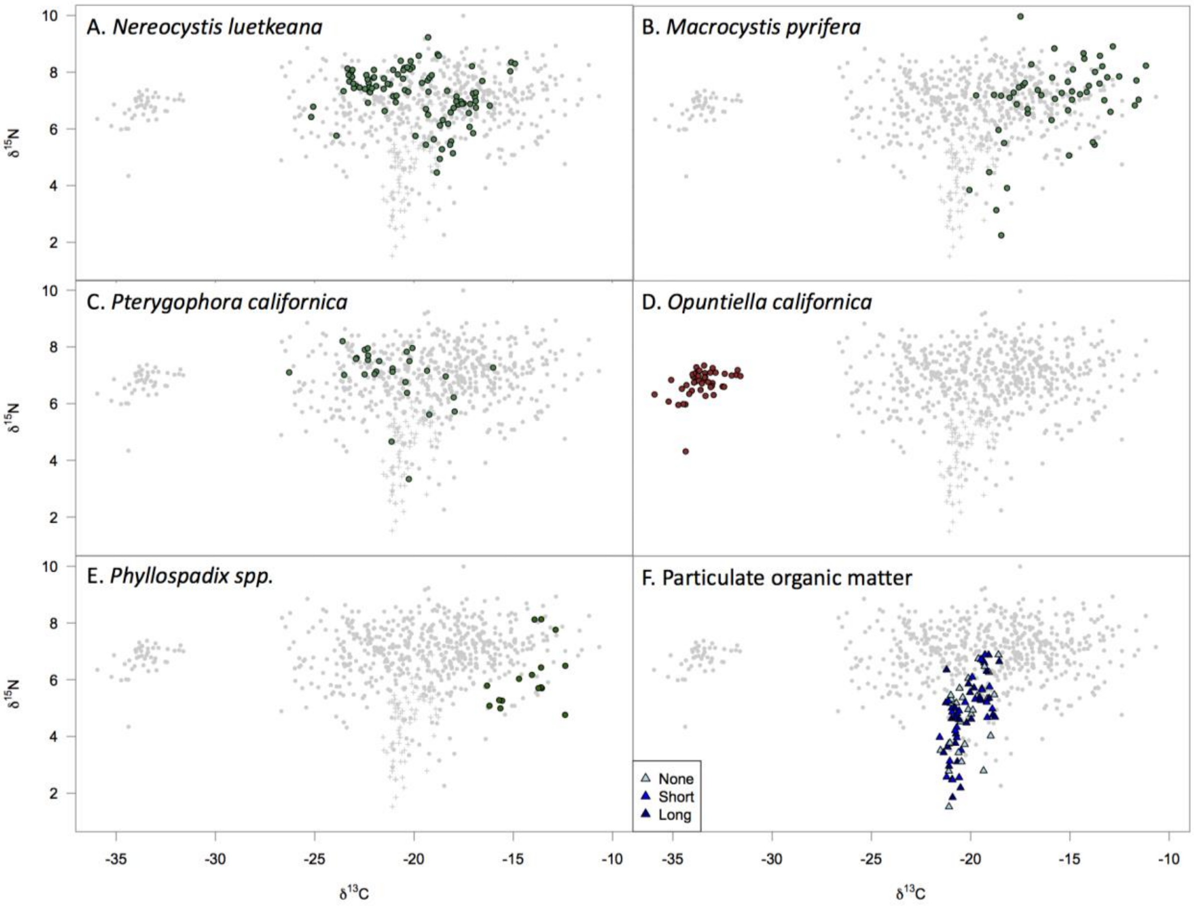

**Figure C1.** Bivariate plots of $\delta^{13}C$ and $\delta^{15}N$ values of key primary producers sampled on BC's central coast. Grey closed circles represent the raw data of all macroalgal species sampled. Grey crosses represent the raw data of all particulate organic matter (POM) samples. Coloured circles are used to identify the stable isotopic signatures of (A) annual species *Nereocystis luetkeana*, (B) perennial species *Macrocystis pyrifera*, (C) old-growth *Pterygophora californica*, (D) red algae *Opuntiella californica*, and (E) seagrass species *Phyllospadix* spp. Coloured triangles represent POM isotopic signatures from three sea otter occupation categories: None (0 years; light blue), Short (2-8 years; blue), and Long (16-33 years; dark blue).

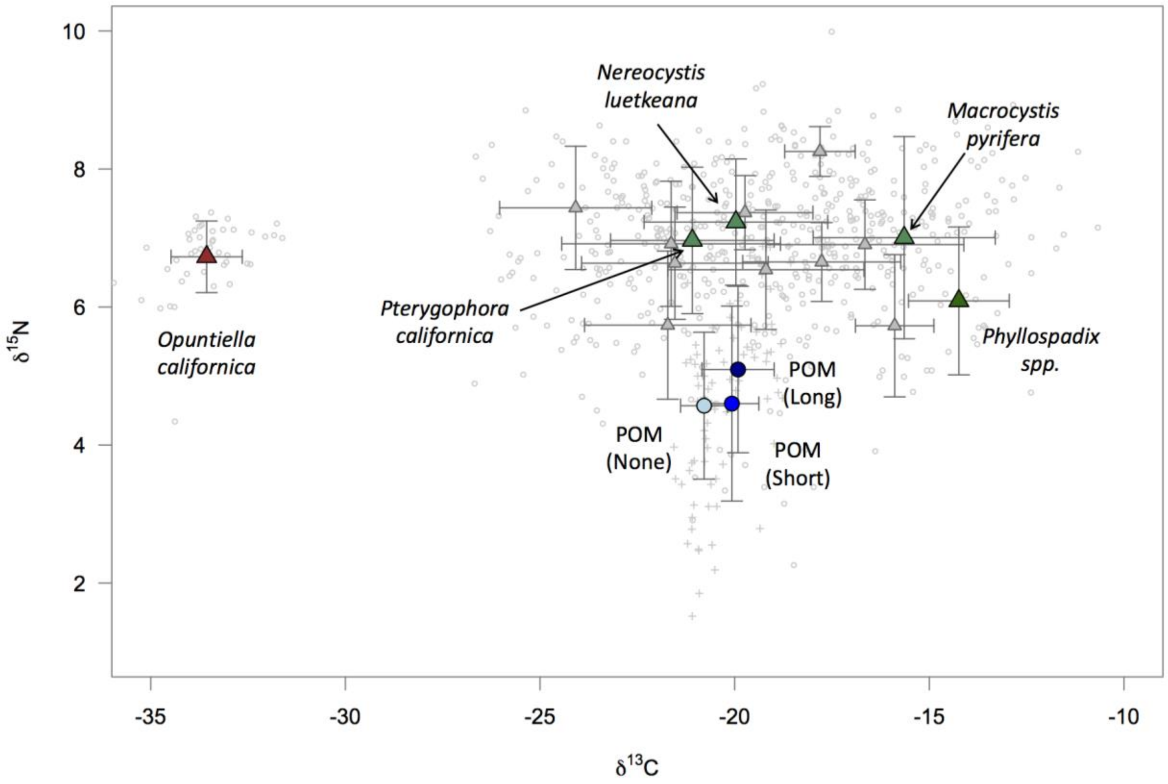

**Figure C2.** **Bivariate plot of primary producer $\delta^{13}C$ and $\delta^{15}N$ values sampled on BC's central coast. Grey open circles represent the raw data of all macroalgal species sampled. Grey crosses represent the raw data of all particulate organic matter samples. Open triangles represent the means (± standard deviation) of 15 macroalgae and seagrass species sampled. Coloured triangles represent the means (± standard deviation) of key primary producers: brown algae (*Nereocystis luetkeana, Macrocystis pyrifera,* and *Pterygophora californica*; green triangles), red algae (*Opuntiella californica*; red triangle), and seagrass (*Phyllospadix* spp.; dark green triangle). Coloured circles represent the means (± standard deviation) of particulate organic matter (POM) sampled from three sea otter occupation categories: None (0 years; light blue circle), Short (2-8 years; blue circle), and Long (16-33 years; dark blue circle).**