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Running head: *Sea otters affect rockfish trophic dynamics*

Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests

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Abstract: Sea otters are a classic example of a predator controlling ecosystem productivity through cascading effects on basal, habitat forming kelp species. However, their indirect effects on other kelp associated taxa like fishes are poorly understood. We examined the effects of sea otter (*Enhydra lutris*) reintroduction along the west coast of Vancouver Island, Canada on giant kelp (*Macrocystis pyrifera*) distributions and the trophic niches and growth of two common kelp forest fishes- black (*Sebastes melanops*) and copper (*S. caurinus*) rockfishes. We sampled 47 kelp forests, and found that red sea urchins (*Strongylocentrous franciscanus*) were eliminated in the presence of otters, and that kelp forests were 3.7 times deeper and 18.8 times larger. Despite order-of-magnitude differences in kelp forest size, adult black and copper rockfishes contained less kelp-derived carbon in their tissues (as measured by stable isotopes of C and N) in regions with otters. Adults of both species had higher mean trophic positions in the presence of otters, indicating more frequent consumption of higher trophic level prey such as fishes. Smaller trophic niche space of rockfishes in the presence of otters indicated a higher degree of trophic specialization. Juvenile black rockfishes rapidly shifted to higher kelp-carbon contents, trophic positions and body condition factors after settling in kelp forests. The relationships of growth to length, % kelp carbon and trophic position varied between the two regions, indicating that potential effects of kelp forest size on trophic ontogeny may also affect individual performance. Our results provide evidence that the indirect effects of otters on rockfishes arise largely through the creation of habitat for fishes and other prey rather than a direct trophic connection through invertebrates or other consumers of kelp productivity.

Keywords: Enhydra lutris; *sea otter;* Strongylocentrotus franciscanus; *sea urchin*; Macrocystis pyrifera (=integrifolia); *kelp forest size*; Sebastes *spp*.; *rockfish; trophic niche space*

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INTRODUCTION

The loss of apex consumers can have widespread indirect effects on ecosystems (Duffy 2003, Estes et al. 2011). Since Hairston et al. (1960) proposed that regulation of herbivores by predators maintains plant populations and primary productivity, trophic cascades have become a central theme in ecology (Shurin et al. 2002, Terborgh and Estes 2010). The collateral effects of trophic cascades on biodiversity and ecosystem properties remain poorly understood and difficult to predict (Pringle et al. 2007, Anthony et al. 2008, Beschta and Ripple 2009). The 'otter-urchin-kelp' trophic cascade is a classic example of an apex predator with strong indirect effects on habitat-forming primary producers (Estes and Palmisano 1974, Simenstad et al. 1978, Duggins et al. 1989b, Estes et al. 1998, Reisewitz et al. 2006, Anthony et al. 2008, Hughes et al. 2013). Although factors such as wave disturbance and nutrient availability certainly affect kelp productivity (Dayton 1985, Reed et al. 2011), otters exert strong top-down control over kelps *via* urchins at high latitudes (Watson and Estes 2011).

Kelp forests provide both nutrition and habitat structure to associated consumers and epifauna. Kelp-derived primary productivity and detritus supports consumer populations and microbial productivity (Duggins et al. 1989b, Bustamante et al. 1995, Clasen and Shurin 2015), and kelps provide three-dimensional structural habitat that mediates predator-prey interactions and current velocity (Gaylord et al. 2007, Johnson 2007). For example, filter-feeding mussels and barnacles in the Aleutian Islands are enriched in kelp-derived carbon and grow 2-3 times faster at islands with otters present than in their absence (Duggins et al. 1989). The diets and foraging behaviours of Glaucous-winged gulls (*Larus glaucescens*) and bald eagles (*Haliaeetus leucocephalus*) also vary between food webs with and without sea otters (Irons et al. 1986,

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Anthony et al. 2008). Otters therefore alter the nearshore environment by providing both production that supports consumers and shelter from predators, waves and currents.

Many fishes are sustained by kelp productivity and habitat structure to different degrees at various life stages (Holbrook et al. 1990). Primary consumers of living and decaying kelp provide a critical prey base for rocky reef and kelp forest fishes (Stephens et al. 2006, Davenport and Anderson 2007). Sea otters may therefore have indirect effects on reef fishes by increasing the productivity of kelp forest habitats and the quantity and quality of the prey resources they provide. Alternatively, kelps may provide habitat for forage fishes and planktonic invertebrates that do not consume kelps directly or indirectly, but are prey for larger predatory fishes. Although fish abundance is higher in the presence of abundant kelp populations (Reisewitz et al. 2006), the mechanisms by which kelp forests support fish communities are poorly understood.

This paper addresses several questions concerning the effects of sea otter recovery on the trophic ecology of two species of rockfish. First, we examined kelp forest sizes and depth distributions in regions with and without sea otters along the west coast of Vancouver Island to establish that the availability of kelp forest habitat varied with otter presence. Second, we asked how the diets and growth of kelp-associated reef fishes vary between regions with vs. without sea otters. We used stable isotopes of C and N to estimate (1) trophic position (the number of trophic links separating a species from the base of production, Post 2002), (2) the proportion of carbon in the tissues derived from kelp vs. phytoplankton productivity (Duggins et al. 1989a, Miller et al. 2011), and (3) the trophic niche width of the population, or variation among individuals in C and N isotopic signatures (Bearhop et al. 2004). If kelps influence fish populations primarily by supporting invertebrate prey, then we expect to see a greater contribution of kelp-derived carbon in fish tissues in areas with sea otters and larger kelp forests. Alternatively, if kelps primarily provide habitat for pelagic forage fishes that are consumed by rockfishes, then we may see

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differences in growth or trophic position reflective of greater piscivory, but not a more benthic carbon isotopic signature.

Kelp forest size may also affect individual specialization among rockfishes or the range of prey items consumed. As prey availability increases, consumers can become more selective in order to maximize their energy intake (Krebs et al. 1977, Thompson and Colgan 1990), reducing trophic niche space or individual variability in diet (Bolnick et al. 2003, Tinker et al. 2008). We therefore predicted that the trophic niche space of kelp-associated reef fishes should decrease in the presence of sea otters and large kelp forests. Alternatively, if large kelp forests support more diverse assemblages of potential prey, then opportunities for greater niche width in the presence of otters may lead to more individual dietary variation. We measure population trophic niche space as the range of variation in $\delta^{15}N$ and $\delta^{13}C$ signatures among individual fish.

Finally, we evaluated the demographic consequences of altered food web structure in the presence of otters by examining individual growth histories through otolith and body condition analyses (e.g. Vander Zanden et al. 1999, Post 2003). We tested for associations between growth rates of black rockfish, their kelp-carbon content, trophic position, and body condition. If higher kelp productivity leads to greater secondary productivity and enhanced prey availability for rockfishes, then we expect individual condition and growth rates to increase in the presence of otters. We evaluated all of these predictions by examining kelp forest habitat, fish isotopic signatures, otolith growth records and body condition for black and copper rockfishes in contrasting regions west coast of Vancouver Island, Canada with and without sea otters.

METHODS

Study system

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This research was conducted on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1), a complex coastline that spans approximately 470 km between 48^{o} 18' N / 123^{o} 32 W and 50^{o} 48'N / 128 29' W, characterized by reef and island-studded sounds, inlets, and deep fjords. Historical records (Busch and Gough 1997) and modern estimates of habitat carrying capacity (Gregr et al. 2008), indicate that as many as 55,000 sea otters may have been harvested from British Columbia during the maritime fur trade. The last record of a sea otter being killed in British Columbia is from 1929 (Cowan and Guiguet 1960), after which otters were extirpated until 89 Alaskan animals were introduced between 1969 and 1972 (Bigg and Macaskie 1978). This population grew at approximately 15% year^{-1} and by 2008 had increased to an estimated 4110 animals (Nichol et al. 2009). As in Alaska (Estes and Duggins 1995), range expansion of sea otters was followed by rapid transformation to kelp-dominated rocky reef ecosystems (Morris et al. 1981, Breen et al. 1982). Where sea otters remain absent, abundant sea urchin populations maintain extensive 'barrens' devoid of fleshy macroalgae (Watson and Estes 2011).

Our research focuses on the habitat and productivity formed by the giant kelp *Macrocystis pyrifera* (Phaeophyceae, Laminariales). Perennial sporophytes consist of multiple stipes that originate from a common holdfast and extend vertically to form extensive surface canopies (Graham et al. 2007). In comparison to southern California, giant kelp forests on the west coast of Vancouver Island are found in semi-wave-protected outer coast habitats, and are generally shallower, have higher densities, and experience higher mortality rates resulting from more seasonally variable environments (Druehl 1978, Druehl and Wheeler 1986). The bull kelp *Nereocystis luetkeana* also seasonally forms extensive forests in this region, generally in areas of higher wave exposure and less stable substrata (Springer et al. 2007). Understory kelps include *Pterygophora californica, Eisenia aborea*, and *Laminaria setchellii.*

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We studied two of the most abundant species of kelp-associated nearshore Pacific rockfishes found in British Columbia: black rockfish (*Sebastes melanops)* and copper rockfish (*S. caurinus*). Black rockfish range from southern California to the western Aleutian Islands, and are most common to depths less than 55 m (Love et al. 2002). After a pelagic duration of approximately 80 days (Markel 2011), juveniles settle into shallow vegetated habitats; macroalgae on rocky reefs and seagrasses in shallow embayments (Love et al. 1991). Both juveniles and adults form aggregations in the water column above rocky reefs and frequent the perimeter of kelp forests. Copper rockfish range from central California to the northern Gulf of Alaska, and are most commonly found to depths of 90 m (Love et al. 2002). After an average pelagic duration of 55 days (Markel 2011), pelagic juveniles settle into shallow macroalgal habitats on rocky reefs (Love et al. 1991).

Study design

We took advantage of the natural experiment created by sea otter reintroduction and range expansion along the west coast of Vancouver Island to investigate the indirect effects of sea otters on rockfish trophic dynamics via changes to giant kelp forest habitat size. We delineated 'otter-present' (Kyuquot Sound to Nuchatlitz Inlet) and 'otter-absent' (Barkley Sound) regions separated by approximately 145 km (Fig. 1). We randomly selected four outer coast sites in each region with typical giant kelp forests. Sites were separated by approximately 2-15 km and each covered approximately 2 km of coastline. Within each site we established six sampling locations by selecting the largest giant kelp forests present that were separated from adjacent forests by at least 250 m. All fieldwork was conducted between May and August 2006.

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Our study represents a regional comparison, an approach which has been used to reveal ecological impacts of large and wide-ranging species and systems where experimental manipulations are impractical (Hargrove and Pickering 1992, Menge 2000, Terborgh and Estes 2010). This approach is powerful for revealing ecological interactions over broad spatial scales in the presence of natural environmental variation; however, it is subject to potentially unknown confounding sources of variation (Hurlbert 1984). A number of considerations give us confidence that the contrasts we observe are related to the presence or absence of sea otters. First, the spatial extent of rocky habitat is similar or greater in the otter-absent region, and unlikely to constrain kelp forest depth or size. Second, exposure to ocean swell is equivalent or slightly lower in the otter-absent region, and also unlikely to drive differences in kelp forest depth of size. Third, we randomly selected six locations at each of four sites in each of the two regions; therefore our spatial replication within each region was extensive. Finally, a 23-year study by Watson and Estes (2011) in the same regions documented the persistent transition from urchin-dominated to kelp-dominated rocky reef habitats following sea otter range expansion. Although other environmental gradients may contribute to the differences between our regions, several independent lines of evidence suggest that the presence of sea otters transforms shallow rocky reef ecosystems by increasing the extent of kelp forest habitat.

Urchin density and kelp forest size

At each location we measured red sea urchin (*Strongylocentrotus franciscanus*) densities, and giant kelp forest depth (m) and surface area (ha). Urchin densities were determined by counting all urchins within 50 x 50 cm quadrats placed at 10 random points along the seaward edge of each giant kelp forest. We measured the depths to which kelp extend into the subtidal

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(hereafter 'perimeter depth') using a digital depth sounder while maneuvering a small boat around the perimeter of the surface canopy of each forest. Depths were recorded approximately every three meters and converted to values below Canadian chart datum (mean lowest low tide). We measured giant kelp forest surface areas using a hand-held GPS unit with an area calculator function, or in the case of very small forests where GPS-based estimates became unreliable, a 100 m tape. We tested for effects of sea otters on urchin density, giant kelp forest depth and surface area using REML-based linear mixed effects models ('lme' in R package 'nlme'), using Otters (presence/absence) as a fixed effect nested within Site, and Site as a random effect.

Adult and juvenile rockfish kelp-carbon content and trophic position

We collected approximately 25 adult black and copper rockfishes at the periphery of giant kelp forests throughout each region by hook-and-line angling. All fish were weighed (kg) and measured (total length, cm), and dorsal muscle tissue samples were collected for stable isotope analysis. We collected juvenile black and copper rockfish from SMURFs (Ammann 2004) deployed at the seaward edge of each kelp forest location using a BINCKE net (Anderson and Carr 1998) every four weeks between May and August. Because black rockfish recruitment and collections were exceptionally high in 2006 (Markel 2011), we sub-sampled individuals for isotopic analysis. We ensured replication across all body sizes by pooling collections within region and randomly selecting approximately 30 individuals from within each of the following size classes: <40, 40-50, 50-60, 60-70, 70-80, >80 mm. We inspected the stomach contents of selected individuals in the lab for evidence (present/absent) of piscivory (i.e. scales, vertebrae, fresh or decaying fish).

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We used naturally occurring carbon and nitrogen stable isotope ratios to compare population mean and variance of kelp-derived carbon contents and trophic positions of adult and juvenile rockfishes from our two regions. Carbon stable isotope ratios ($^{13}C/^{12}C$) vary between macro-algae and phytoplankton, but change little during trophic transfers, and therefore can be used to determine ultimate sources of dietary carbon (Peterson and Fry 1987). In contrast, nitrogen stable isotope ratios ($^{15}N/^{14}N$) exhibit predictable rates of enrichment with trophic transfers, and therefore can be used to estimate consumer trophic positions (Post 2002).

Stable isotope ratios are reported in the standard delta (δ) notation, where $\delta^{13}C$ or $\delta^{15}N$ = ($[R_{sample}/ R_{standard}] - 1$) x 1000, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ (Peterson and Fry 1987). We used the following simple two-source mixing model (Eq. 1) to estimate the relative contributions of phytoplankton- vs. kelp-derived carbon (Mcconnaughey and Mcroy 1979, Bustamante and Branch 1996):

$$\%C_{kelp-derived} = \frac{(\delta^{13}C_{consumer} = \delta^{13}C_{phytoplankton} - I)}{(\delta^{13}C_{kelp} - \delta^{13}C_{phytoplankton})} \times 100 \quad \text{(Eq. 1)}$$

where I is the average post-photosynthetic fractionation of $\delta^{13}C$ per trophic level. Based on the review of Post (2002), we used $I = 0.5$ and mean giant kelp $\delta^{13}C$ and $\delta^{15}N$ values for each region. We tested for potential differences in the isotopic values of fresh and decaying giant kelp tissues by collecting two tissue types at each location: 'fresh' (blades dark in colour, firm and not decaying) and 'decaying' (tattered, pale, and senescent in appearance; collected from the distal ends of blades).

In contrast to kelp tissue, samples of naturally occurring phytoplankton are difficult to isolate because seawater samples contain mixtures of micro-organisms and suspended particulate detritus in addition to phytoplankton. Particulate organic matter (POM) samples collected offshore (i.e., with low probability of containing particulate marine benthic or terrestrial detritus)

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233 are typically used to represent phytoplankton isotopic signatures (Kaehler et al. 2000, Fredriksen
234 2003, Hill et al. 2006). The utility of this approach may be limited if phytoplankton species
235 compositions differ between nearshore and offshore waters (Page et al. 2008). To represent
236 phytoplankton isotopic signatures in mixing models to estimate kelp-carbon content and trophic
237 position, we used isotopic data provided by Ramshaw (2012) from 0.7 – 20 μm and 20 – 63 μm
238 filtered POM samples along two transects in each of three regions along the west coast of
239 Vancouver Island, including Barkley Sound (otters-absent), Clayoquot Sound (otters present for
240 less than 5 years), and Kyuquot Sound (otter present for more than 15 years). Each transect began
241 in kelp forests and extended up to 30 km offshore. Sampling occurred during both summer and
242 winter, and during oceanographic conditions corresponding to both "blooming" and "non-
243 blooming" phytoplankton communities. Pooled samples collected ≥ 4 km from kelp forests were
244 classified as offshore samples and used to represent baseline values of phytoplankton $\delta^{13}C$ and
245 $\delta^{15}N$. We also compare the POM isotopic ratios reported in Ramshaw (2012) with those reported
246 in Perry et al. (1999) for the slope waters off Vancouver Island.

247 We tested for effects of kelp State ('fresh' vs. 'decaying' kelp), POM Location ('in-kelp'
248 vs. 'out-kelp' POM) and Region (otters present/absent) on the $\delta^{13}C$ and $\delta^{15}N$ values of giant kelp
249 and POM, respectively, using State, Location, Otters, and their interaction as fixed effects nested
250 within Site as a random effect.

251 We estimated the trophic positions of adult and juvenile rockfishes using the model (Eq. 2)
252 developed by Post (2002):

$$TL = 1 + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} \text{ x } \alpha + \delta^{15}N_{base2} \text{x } (1-\alpha)]/\Delta_n \quad \text{(Eq. 2)}$$

253 where TL is the trophic position of the consumer, $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer
254 (i.e. rockfish), $\delta^{15}N_{base\ 1}$ is the average $\delta^{15}N$ of POM (i.e. as a proxy for phytoplankton

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255 signatures), $\delta^{15}N_{base\ 2}$ is the average $\delta^{15}N$ value of giant kelp (i.e. as proxy for kelp signatures),
256 and Δ_n is the enrichment value of $\delta^{15}N$ per trophic level. We used Δ_n = 3.4 ‰ based on Post
257 (2002). The parameter α is the proportion of nitrogen in the consumer derived from the primary
258 producers at the base of each food web (Post 2002). This value is estimated based on carbon
259 isotopes as:

$$\alpha = \frac{(\delta^{13}C_{consumer} - \delta^{13}C_{base2})}{(\delta^{13}C_{base1} - \delta^{13}C_{base2})} \quad \text{(Eq. 3)}$$

260 Finally, to assess the trophic pathways by which kelp production reaches rockfishes, we
261 opportunistically collected common kelp-associated crustaceans (decapod crabs, amphipods,
262 isopods, and shrimp) as well as a common gastropod (*Tegula pulligo*) and California mussels
263 (*Mytilus californianus*). All tissue samples collected for isotope analyses were rinsed with de-
264 ionized water and dried at 50°C for 48 hrs before being ground into a fine powder using a digital
265 Touchpad Amalgamator (Henry Schien Inc). We conducted an experiment to test for the effects
266 of lipid extraction on juvenile and adult rockfish muscle tissue $\delta^{13}C$ and $\delta^{15}N$ (refer to Ingram et
267 al. 2007). We found no effect of lipid extraction on isotope ratios; therefore we report values
268 from non-extracted samples. All stable isotope analyses were performed at the University of
269 California-Davis Stable Isotope Facility using an elemental analyzer and a continuous flow
270 isotope ratio mass spectrometer (IRMS).
271
272 *Analysis of effects of kelp-carbon and trophic position*
273
274 We performed all statistical and graphical analyses using R (R Core Development Team
275 2011). We tested for an effect of Region (otters-present or absent) on kelp-carbon content and
276 trophic position of adult rockfishes using Welch's two-sample *t*-test. We used *F* tests to test for

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277 homogeneity of variances and quantile-quantile plots to check for normal distribution of residual
278 errors and transformed when appropriate to meet the assumptions of ANOVA. We tested for
279 regional differences in ontogenetic relationships (i.e. slope) between rockfish body size (total
280 length), kelp-carbon content, trophic position, and condition factor (juvenile only) using analysis
281 of covariance (ANCOVA).

282 We refer to variation among individuals in $\delta^{13}C$ - $\delta^{15}N$ as 'niche space' (Bearhop et al.
283 2004) and used convex hulls (i.e. the minimum adequate polygon) to quantify the trophic niche
284 space occupied by all individuals for comparison among regions and species (Cornwell et al.
285 2006). Niche space serves as proxy for the total range of trophic diversity among individuals in a
286 population (Layman et al. 2007). We compared adult rockfish trophic niche space using
287 augmented convex hull plots (Vidmar and Pohar 2005) with marginal density distributions
288 ('chplot' and 'chadd' in R package 'chplot'). We tested for regional differences in convex hull
289 volume ('convhulln' in R package 'geometry') by jackknifing trophic position~kelp-carbon
290 matrices and comparing the resulting distributions using Welch's two-sample *t*-tests.
291
292 *Analysis of effects of kelp-carbon content and trophic position on juvenile rockfish growth*
293
294 We analyzed otolith microstructure to estimate daily growth rates of individual juvenile
295 black rockfishes and to examine relationships between kelp-carbon content, trophic position,
296 body condition, and growth. Deposition of otolith daily increments by juvenile rockfishes has
297 been validated previously for numerous early post-settlement rockfishes (Yoklavich and Boehlert
298 1987, Laidig et al. 1991, Woodbury and Ralston 1991, Kokita and Omori 1999, Plaza et al.
299 2001). Methodological details of otolith microstructure analyses are provided in Appendix A of
300 *Ecological Archives* xxxx. We defined individual growth rates as the mean width of daily growth

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increments (μm /day) between parturition and collection. We used Fulton's condition factor, K (Blackwell et al. 2000) to represent individual body condition as:

$$K = (W/L^3) \times 100{,}000 \quad \text{(Eq. 4)}$$

where W is fish weight (grams) and L is fish length (mm). We used linear models (lm in R package 'stats') and ANCOVA to test for the fixed effects of length, % kelp-carbon, trophic position, and their interactions on juvenile black rockfish growth rates factor. Second order terms for each independent variable were included to test for non-linear patterns of association.

RESULTS

Urchin density and kelp forest depth and surface area

Red sea urchins (*Strongylocentrotus franciscanus*) were abundant at the periphery of giant kelp forests in the absence of sea otters, (16.2 ± 1.72 / m^2 [mean ± SE], $n = 22$), but absent in the presence of otters (Fig. 2*a*). Perimeters of kelp forests were on average 3.7 times deeper in the otter present region (5.58 ± 0.35 m, $n = 21$) than in the region without otters (1.51 ± 0.15 m, $n = 22$, $F_{1,6} = 17.77$, $P = 0.0056$, Fig. 2b). Giant kelp forest surface areas on average were 18.8 times larger in the presence of otters (11,290.72 ± 1701.46 m^2) than in their absence (599.44 ± 100.23 m, $F_{1,6} = 101.61$, $P < 0.0001$, Fig. 2*c*).

Producer isotopic baselines and consumer kelp-carbon content and trophic positions

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Giant kelp showed distinct $\delta^{13}C$ values from offshore POM in both the otter-present and otter-absent region (Fig. 3), enabling us to use these as endpoints in two-source mixing models to estimate kelp-derived carbon contents and trophic positions of benthic invertebrates and fishes. There was no effect of Region (with vs. without otters, $F_{1,6} = 0.567$, $P = 0.48$) or State (fresh vs. decaying, $F_{1,6} = 0.02$, $P = 0.892$) on *Macrocystis* $\delta^{13}C$ values, therefore we pooled data from both types and regions in the mixing models: $\delta^{13}C$ (-14.61 ± 0.2, $n = 89$) and $\delta^{15}N$ (6.39 ± 0.2, $n = 89$). The isotopic values of offshore POM samples collected by Ramshaw (2012) used to represent phytoplankton end-members were: $\delta^{13}C$ (-22.12 ± 0.3, $n = 60$) and $\delta^{15}N$ (6.41 ± 0.2, $n = 60$) (Fig. 3). The carbon isotopic values are also comparable to those reported by Perry et al. (1999) of -22.2 to -23.6 for POM from the Pacific slope waters of British Columbia.

Mass ratios of C/N of adults of both rockfish species were consistently low (ranges of 2.7-3.6 and 2.7-3.5 for black and copper rockfish, respectively), while C/N was higher for juvenile black rockfishes (3.4-3.9, Appendix D). These ratios are indicative of low lipid contents for adult fish. While the lipid content of juveniles was likely higher, the variation among individuals was small (a range of only 0.5). Post et al. (2007) suggest extracting or correcting isotopic values for lipid content when C/N ratio is >3.5 for aquatic animals or when the variation among animals is high. Based on the low C/N of adult fish and the low variation among juveniles, we did not apply a correction to our isotopic values for lipid content.

Kelp carbon contents of benthic invertebrates were high (approximately 60-100%), while those of juvenile Pacific herring and early post-settlement black rockfish were low (approximately 35-45%), and similar between regions (Fig. 3). Kelp-carbon contents of both adult black rockfish (otter-absent: [mean ± SE] 57.48% ± 0.90, $n = 25$; otters-present: 52.66% ± 0.85, $n = 24$; $T = 3.82$, $P = 0.0004$) and copper rockfish (otter-absent: 64.13 ± 0.78, $n = 23$; otters-

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present 58.41 ± 0.80, $n = 26$; $T = 5.08$, $P < 0.0001$) were higher in the regions without otters. In contrast, trophic positions of both adult black rockfish (otter-absent: 3.14 ± 0.03, $n = 25$; otters-present 3.51 ± 0.03, $n = 24$; $T = 8.47$, $P < 0.0001$) and adult copper rockfish (otter-absent: 3.40 ± 0.03, n =23; otters-present 3.80 ± 0.05, $n = 26$; $T = 7.44$, $P < 0.0001$) were higher in the presence of sea otters and large kelp forests (Figs. 3 and 4).

Adult rockfish niche space and niche shifts

The trophic niche space of adult black rockfish was greater ($t = 2.65$, $P = 0.01$) in the otter-absent region (otter-present, mean ±SE, 6.37 ± 0.07, $n = 24$ and otter-absent 6.73 ± 0.10, $n = 24$, Fig. 4*a*). Similarly, adult copper rockfish occupied less trophic niche space ($t = 42.67$, $P < 0.0001$) in the otter-present region (5.56 ± 0.05, $n = 26$) than in the otter-absent region (11.03 ± 0.14, $n = 24$) (Fig. 4*b*). Trophic position of copper rockfish differed more between regions than kelp carbon content (Fig. 4*b*).

We found ontogenetic increases in trophic position of adult black (Length: $F_{1,44} = 4.02$, $P = 0.051$) and adult copper (Length: $F_{1,46} = 26.0$, $P < 0.0001$) rockfishes (Fig. 5). Both black (Region: $F_{1,44} = 32.06$, $P < 0.0001$) and copper rockfish (Region: $F_{1,46} = 28.14$, $P < 0.0001$) had higher trophic positions in the otter present region (Fig. 5). Ontogenetic increases in trophic position of copper rockfish were steeper in the absence of otters than in their presence (Region*Length: $F_{1,46} = 12.49$, $P < 0.0009$). The relationship between body length and trophic position for black rockfish was equivalent between the two regions (Region*Length: $F_{1,44} = 0.35$, $P = 0.56$).

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Juvenile rockfish ontogenetic niche shifts

A model including region (with vs. without otters) and first and second order terms for body size best predicted juvenile black rockfish % kelp carbon and body condition (Fig. 6, Table B1). Trophic position was a linear function of fish size and was higher in the otter-present region. Trophic position (Fig. 6*a*), % kelp-derived carbon content (Fig. 6*b*) and body condition (Fig. 6*c*) all increased with fish size. Kelp carbon content and body condition were both higher in the region without otters (Table B1). The allometric relations varied between regions for condition and % kelp-derived carbon (the region*size interactions were significant, Table B1), but not for trophic position. After settling in giant kelp forests in early June, juvenile black rockfish in both regions moved rapidly from low trophic position diets dominated by phytoplankton-derived carbon to high trophic position diets dominated by kelp-derived carbon.

The relationship between juvenile black rockfish body size and kelp-carbon content was non-linear, with the largest individuals in the otter-absent region demonstrating a decrease in kelp-carbon that corresponded to onset of consumption of juvenile Pacific herring (*Clupea pallisi,* Fig. 6*b*). Consumption of juvenile herring was rarely detected in the otter-present region, but occurred frequently in the otter-absent region by individuals greater than ~65 cm, which also had higher body condition factor values (Fig. 6c).

Juvenile rockfish growth

Juvenile black rockfish individual growth rates increased with body size (total length), kelp-derived carbon content and trophic position (Fig. 7, Table B2). We fit second order polynomial models and found that growth rates depended strongly on body size and increased

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394 more steeply in the otter-absent region. Growth rates increased linearly with both kelp carbon
395 content and trophic position, and the increase in growth with both kelp carbon and trophic
396 position was steeper in the absence of otters than in their presence (Table B2).
397
398 ## DISCUSSION
399 Our study indicates that the transformation of rocky reef ecosystems that accompanies
400 recovery of sea otter populations has important indirect effects on nearshore rockfish populations.
401 Repatriation of sea otters enables giant kelp beds to expand and dramatically increase their depth
402 range and aerial extent by regulating sea urchin populations (in agreement with results from the
403 Aleutians and Vancouver Island; Estes and Duggins 1995, Watson and Estes 2011). Because total
404 primary productivity of giant kelp forests varies directly with kelp forest size (e.g. area of
405 seafloor occupied, Druehl and Wheeler 1986), the benthic primary productivity available to
406 support higher trophic levels following sea otter reintroduction is approximately 20-times higher.
407 The adults of two kelp-associated rockfishes occupy higher mean trophic positions in the
408 presence of otters, suggesting that larger giant kelp forests support more consumers at higher
409 trophic positions. Surprisingly, neither rockfish species showed more kelp-derived carbon in their
410 tissues in the presence of otters and larger kelp forests. Although the growth rates and condition
411 of larger (> 65 mm) juvenile black rockfish were greater in the absence of otters, the adults show
412 lower trophic positions and broader niche space. Our results indicate substantial indirect impacts
413 of sea otters and kelp forests on rockfish reliance on benthic vs. pelagic production pathways,
414 trophic positions and growth.

Effects of sea otters on giant kelp forest depth and surface area

415 We found clear relationships between sea otters, sea urchin abundance, and giant kelp
417 forest depth distributions and surface areas. In the absence of sea otters, sea urchins were

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418 abundant and kelp forests comprised small, shallow sub-littoral fringes surrounded by urchin
419 barrens. This result agrees with Watson and Estes (2011) who studied the same regions on the
420 west coast of Vancouver Island and showed that sea otters maintained persistent rocky reef
421 ecosystems in which urchins were rare and kelp populations were abundant over 23 years. Our
422 data indicate that otters increase kelp forest area largely by expanding their borders at the seaward
423 edge, thereby increasing their depth limits. At locations where sea otters were present and sea
424 urchins rare, the lower limits of giant kelp forests extended 3.7 times deeper than they did at
425 locations without sea otters. Similarly, Pace (1981) experimentally removed sea urchins in
426 Barkley Sound (otter-absent region, this study) and found higher kelp population densities and
427 lower depth distributions after just one year. The deeper lower limits and larger giant kelp surface
428 canopies result from reduced urchin grazing and lower wave-induced mortality following tissue
429 damage due to grazing (Tegner et al. 1995, Markel and DeWreede 1998).

430 The increase in kelp forest size due to otter recovery may affect fish communities both by
431 fueling productivity of invertebrate consumers of kelps and by providing habitat and refuge for
432 invertebrate and forage fish prey. The large differences we found in kelp forest depth and size in
433 the two regions imply that the structural habitat and benthic primary productivity available to
434 support kelp-associated food webs is approximately 20-times higher in presence of sea otters. In
435 addition to giant kelp, several understory kelp species (notably *Pterygophora california,* Watson
436 and Estes 2011), also respond positively to sea otter reintroduction, and may contribute as much
437 or more to ecosystem net primary productivity (NPP) as giant kelp (Miller et al. 2011). Thus,
438 increases in kelp-derived habitat and productivity following sea otter reintroduction are likely
439 substantially higher than our estimate for giant kelp alone.

440 *Effects of sea otters on adult rockfish*

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Despite order-of-magnitude smaller areas of giant kelp forest habitat, adult rockfish of both species contained a greater proportion of kelp derived carbon in the otter absent region. Rockfish therefore rely less on prey that consume kelp production even though kelp forests are much larger with otters. However, adult black and copper rockfishes both occupied higher trophic positions in the otter-present region, indicating that the food webs leading to rockfish contained more links. A likely explanation is that large kelp forests support a greater abundance of prey fishes that feed on pelagic invertebrates. The trophic niche spaces of both rockfish species were smaller in the otter-present region, indicating lower dietary diversity among individuals. The difference was driven more by variation in trophic position among individuals rather than differences in the range of kelp-derived carbon. This pattern supports both theory and empirical evidence that high resource availability enables consumers to specialize on the most energetically profitable prey, resulting in reduced trophic niche space (Bolnick et al. 2003, Newsome et al. 2009).

Invertebrate consumers (including snails, shrimp, crabs, amphipods, mussels and isopods) also did not show a consistently higher contribution of kelp carbon to their diets in the region with otters. This result contrasts with Duggins et al. (1989) who found a greater proportion of kelp carbon in invertebrate consumers at islands in the Aleutians with otter populations. Many invertebrates, especially isopods, amphipods and snails, were consistently high in kelp carbon in both regions in our study. The region with otters and large kelp forests may have supported a greater density of these invertebrates; however, their reliance on kelp derived carbon was equivalent between regions. Thus, the lower contribution of kelp carbon to rockfishes in the region with otters likely reflects a decreased reliance on these benthic feeding invertebrates as prey rather than a shift in the diets of the prey away from kelps.

Although not quantified in this study, the larger kelp forests in the presence of sea otters may support higher abundances of benthic and pelagic kelp-associated fishes that prey on primary

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consumers of fresh and decaying kelp (e.g. crustacean mesograzers, Davenport and Anderson 2007). Opportunistic piscivorous adult black and copper rockfishes focus their diets on these high trophic position prey items rather than invertebrate prey. Kelps support abundant invertebrate consumers as well as small carnivorous reef fishes and their predators (Horn and Ferry-Graham 2006). Fish prey are generally more energetically and nutritionally profitable than invertebrates as rockfish prey (Love and Ebeling 1978, Hobson et al. 2001, Love et al. 2002). Black rockfish feed more on pelagic prey than copper rockfish, including more macro-zooplankton than benthic crustaceans such as crabs, shrimps, and isopods. However, both species are opportunistic piscivores and consume fish prey when available. The higher trophic position of adults of both rockfish species in the otter-present region may indicate a greater availability of fish prey with higher trophic positions and lower fractions of kelp derived carbon than invertebrates (Vander Zanden et al. 1999).

The contrasting relationships between adult rockfish body size and trophic position between the two regions also indicate that otters indirectly shape the food webs supporting rockfishes in ways that favor longer food chains. Trophic positions of adult black rockfish in both regions increased with body size but were consistently higher for all body sizes in the presence of otters. In contrast, trophic positions of adult copper rockfish in the otter-absent region increased with body size, but only at the largest body sizes did these individuals attain trophic positions comparable to conspecifics in the otter-present region. These results suggest that the availability of high-trophic position prey for adult rockfishes may be lower in the absence of otters. Longer food chains in the presence of otters may occur either due to the higher overall benthic productivity, or because larger kelp forests attract and support more high trophic level prey.

Effects of kelp-carbon and trophic position on juvenile rockfish performance

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Although studies have documented shifts in carbon supply and/or trophic positions of consumers in response to altered food web structure (e.g. Vander Zanden et al. 1999), few have investigated their consequences for growth or demographics of consumers (but see Post 2003). We found that juvenile black rockfish showed higher growth and body condition in the otter-absent region, possibly as a consequence of more frequent piscivory. We frequently collected juvenile black rockfish larger than 65 mm in late July and August in the otter-absent region with juvenile herring in their stomachs or with herring tails protruding from their mouths (Appendix C of *Ecological Archives* xxxx). Consumption of juvenile herring in the otter-absent region corresponded to abrupt increases in Fulton's condition factor, and slowly decreasing kelp-carbon contents may reflect the depleted $\delta^{13}C$ values of juvenile Pacific herring. The otter-absent region (Barkley Sound) includes a major Pacific herring (*Clupea pallisi*) spawning site, therefore the regional difference in juvenile black rockfish piscivory rates may be unrelated to sea otters and kelp forest size. The lack of individual fish larger than ~75 mm from the otter-present region constrains this interpretation. Alternatively, juvenile fish density may have been greater in the otter present region, resulting in more intense competition for prey.

The growth rates of juvenile black rockfish, their trophic position and kelp carbon content all varied with body size as well as between the regions. Growth rate, trophic position, kelp carbon and body condition of juvenile black rockfishes all increased after recruiting into kelp forests, indicating that kelp forests offer a more favorable foraging environment than the plankton. Growth rates increased with increasing body size with a decelerating rate of increase around 70 mm. In the otter-present region where juvenile rockfish were rarely piscivorous, we found that growth increased with trophic position and kelp carbon more slowly than in the otter-absent region in the presence of piscivory (otters-absent region). These results suggest that access to energy-rich high-trophic level prey has strong positive effects on body condition and growth

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512 rates of juvenile black rockfish. Other differences between the regions such as temperature or
513 oceanographic conditions may also have contributed to the differences in growth rate we
514 observed.

515 One caveat to our estimates of the proportion of kelp derived carbon in the bodies of
516 consumers based on stable C isotopes is that the isotopic signature of the pelagic base is more
517 difficult to determine than that of kelps. We used offshore POM (>4km) isotopic values as our
518 measure of the pelagic producer base; however POM contains a mixture of benthic detritus and
519 phytoplankton that cannot be easily separated (Lowe et al. 2014), and phytoplankton C isotopic
520 ratios may vary seasonally and with distance to shore (Kaehler et al. 2006, Miller and Page 2012).
521 Although the isotopic signatures of pelagic producers can be difficult to assign, two studies found
522 very consistent values for POM off of Vancouver Island around -22 (Perry et al. 1999, Ramshaw
523 2012). Thus, while our estimates of the proportion of kelp derived carbon in fish and
524 invertebrates has some uncertainty associated with it due to spatial or temporal variability in the
525 POM isotopic ratio, the comparison between the two regions is robust as the POM and kelp
526 isotopic signatures did not vary by region.

527 *Summary*

528 The ecological consequences of the near extinction and recovery of sea otters have figured
529 prominently in our understanding of the role of trophic cascades in structuring ecosystems
530 (Watson and Estes 2011). We found that the presence of otters was associated with the virtual
531 disappearance urchins and large increases in the depth range and surface area of giant kelp forests
532 on the west coast of Vancouver Island. The contrast in the amount of kelp forest habitat and
533 productivity between regions is very likely a consequence of the presence or absence of otters as
534 Watson and Estes (2011) documented very similar shifts over time with otter recovery in the
535 same study areas. Kelp forests provide critical habitat and a likely source of prey for many

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nearshore fishes, including rockfish that use kelps as refuges during their juvenile stages. We found differences between the two regions in trophic positions and niche space of adult and juvenile rockfish, and growth rates of juveniles. Surprisingly, isotopes provided no evidence that the greater area of kelp habitat resulted in a higher fraction of kelp derived carbon in the tissues of either of two rockfish species. A direct trophic link between rockfish and kelps may be less important than the effects of kelp providing habitat for rockfish and their prey. Higher trophic positions of adults of both species in the region with otters may indicate that larger kelp forests where sea otters have recovered support a greater availability of fish prey relative to invertebrates. Although potential positive indirect effects of sea otters on rocky reef and kelp forest fish communities have long been suspected (Ebeling and Laur 1988), few studies have tested the mechanisms by which they may occur (but see Reisewitz et al. 2006). Our results indicate the surprising result that higher benthic production in the presence of sea otters does not contribute more kelp-derived carbon to fish tissues. Rather, the larger kelp forests where otters are present affect food webs and therefore the trophic position and performance of individual fish.

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FIGURE LEGENDS

Figure 1. Otters-present and otters-absent regions along the west coast of Vancouver Island. Green shading indicates current distribution of sea otter population (Nichol et al. 2009). Boxes indicate sites nested within each region.

Figure 2. Box plots comparing (A) urchin densities, (B) giant kelp forest perimeter depth, and (C) giant kelp forest surface area, between sites within regions with and without sea otters. Giant kelp forests were 3.7 times deeper ($F_{1,6} = 17.77$, $P = 0.0056$) and 18.8 times larger ($F_{1,6} = 101.61$, $P < 0.0001$) in the otter-present region.

Figure 3. Comparison of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SE) of primary producers (shaded lower plot) and % kelp-derived carbon and trophic levels (mean ± SE) of benthic invertebrates and fishes (upper plot) between regions with and without sea otters. Offshore POM refers to the POM values used to calculate % kelp-derived carbon and trophic position.

Figure 4. Comparison of trophic niche space (convex hull area) of (A) adult black rockfish and (B) adult copper rockfish between regions with and without sea otters. Error bars represent means ± 1 standard deviation and marginal distribution plots are density plots.

Figure 5. Comparison of the relationship between body size and trophic level of (A) adult black rockfish and (B) adult copper rockfish between regions with and without sea otters. Fitted lines indicate significant ($p \leq 0.05$; solid) and non-significant (dashed) linear regressions.

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Figure 6. Comparison of the relationships between juvenile black rockfish body size and (A) % kelp-derived carbon and (B) trophic position in regions with and without sea otters. Fitted lines indicate significant ($p \leq 0.05$) linear and polynomial regressions, and the regression statistics are shown in Table B1.

Figure 7. Comparison of the association between daily growth rates of juvenile black rockfish and (A) body size (A), (B) % kelp-derived carbon, and (C) trophic position between regions with and without sea otters. Regression statistics are shown in Table B2.

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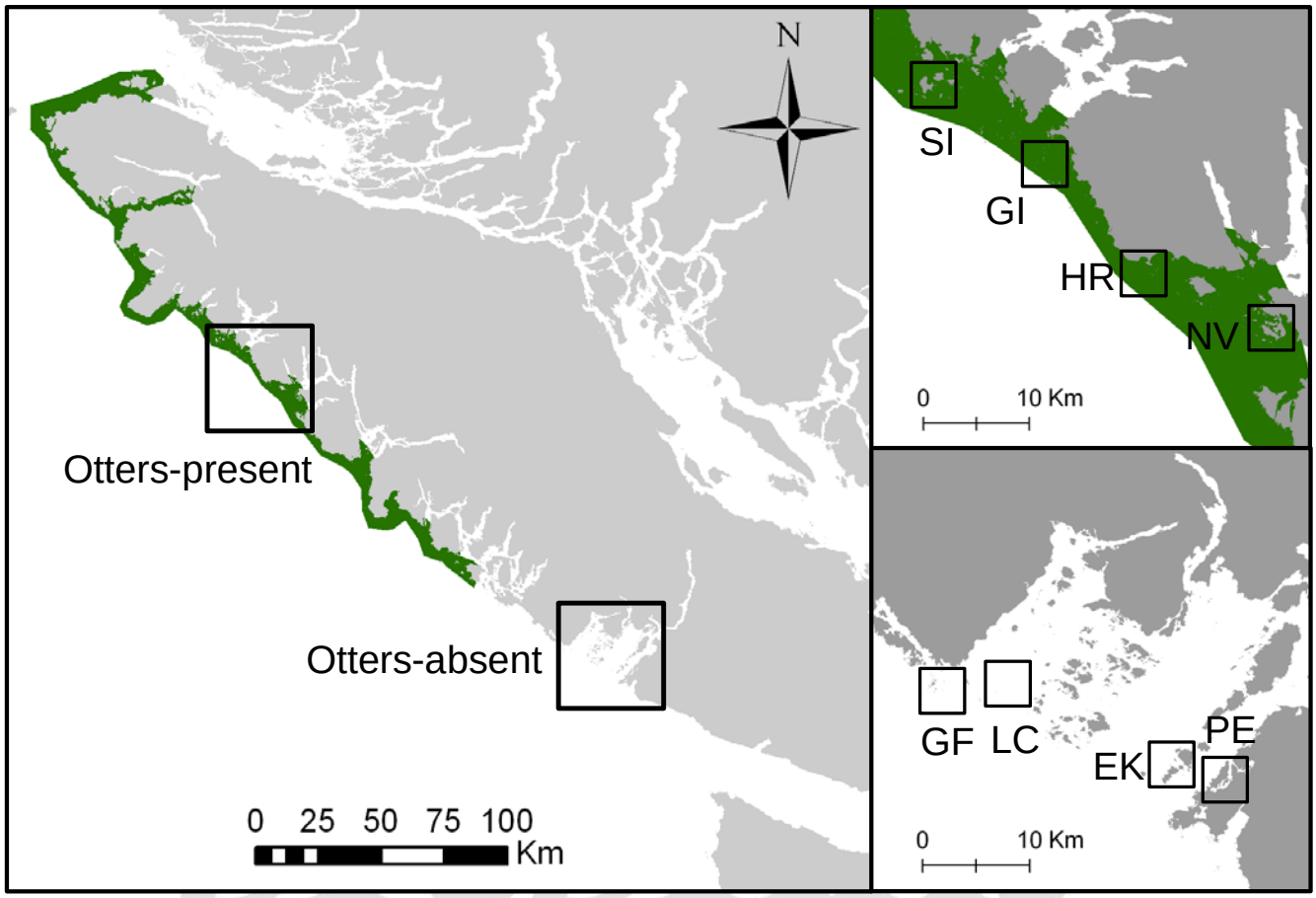

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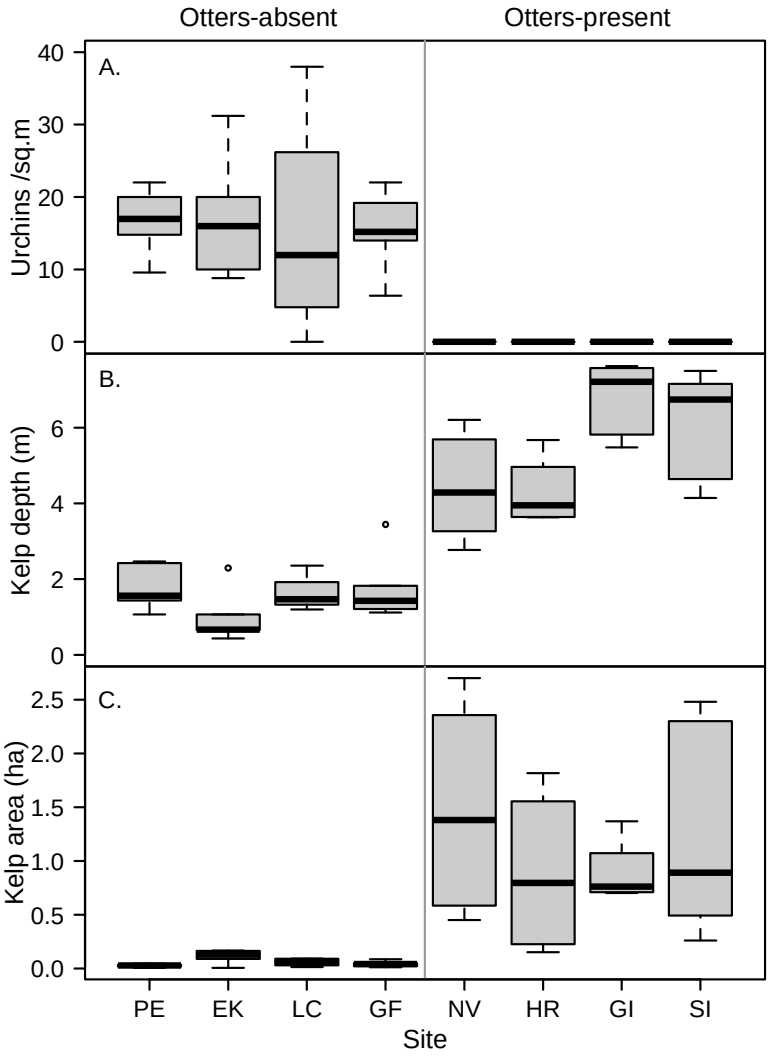

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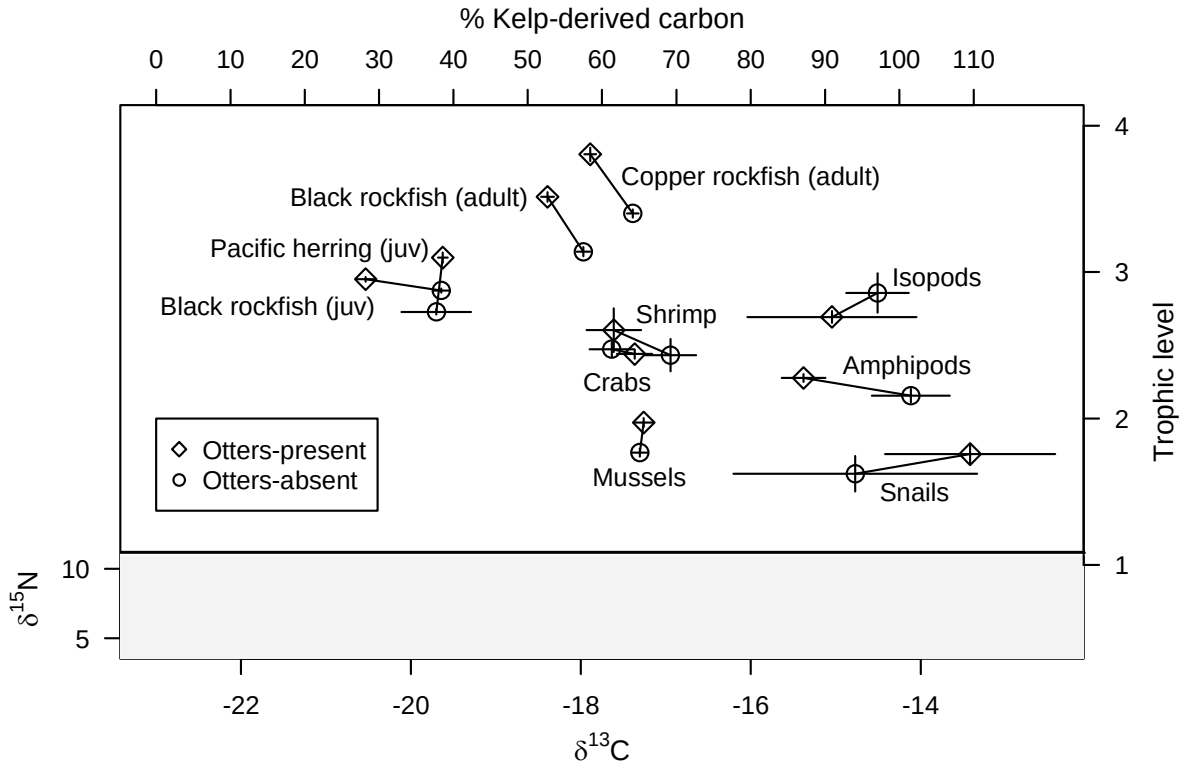

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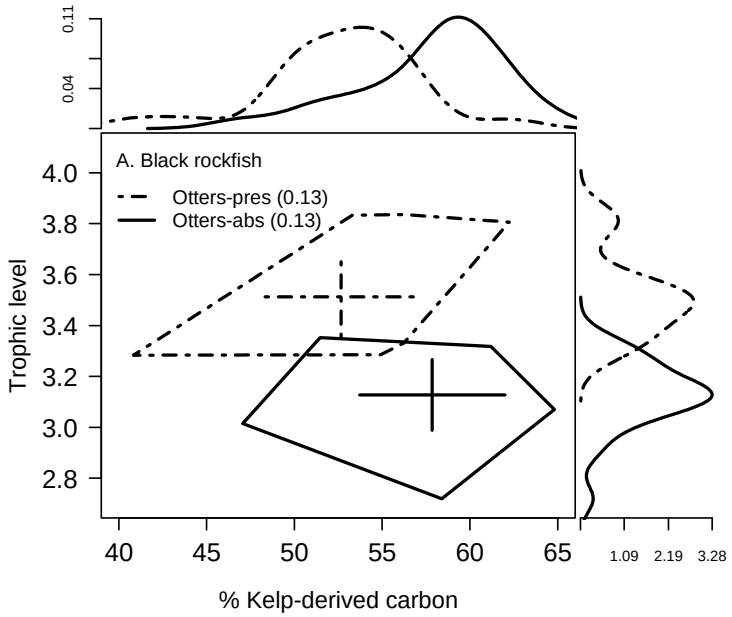

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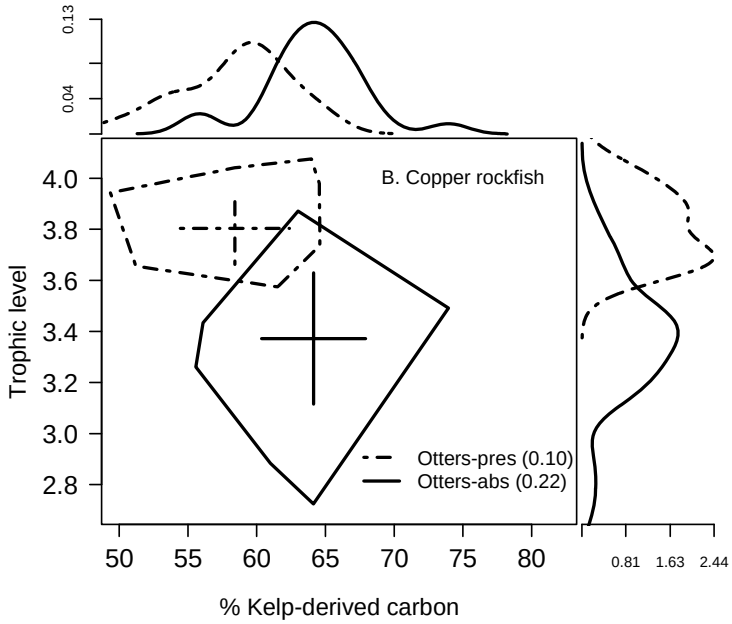

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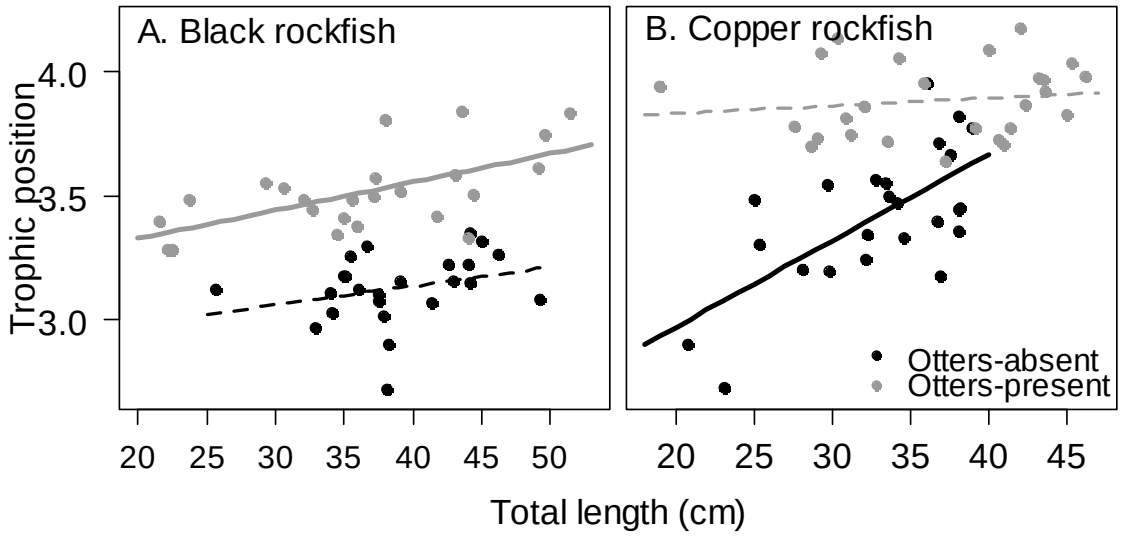

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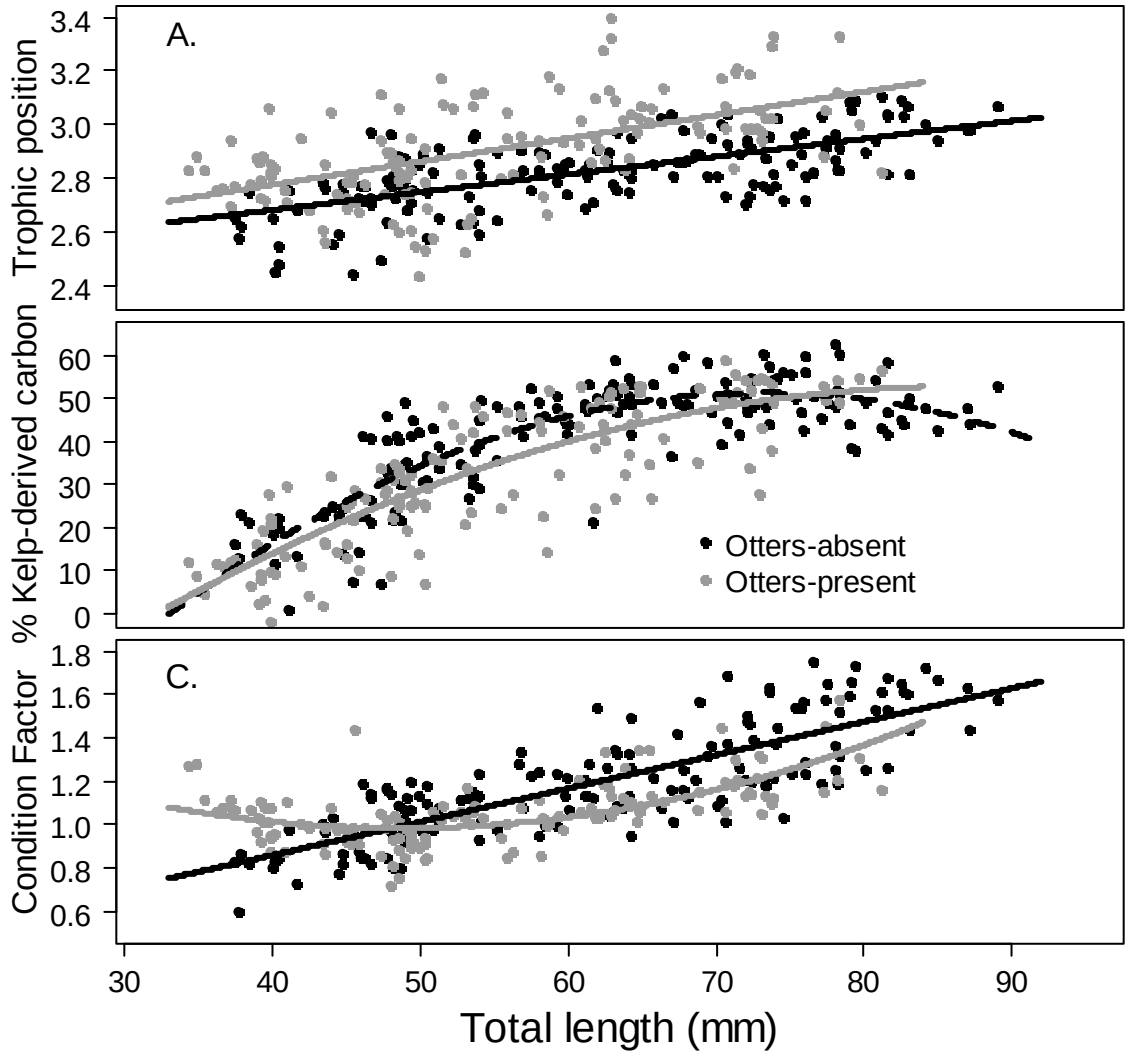

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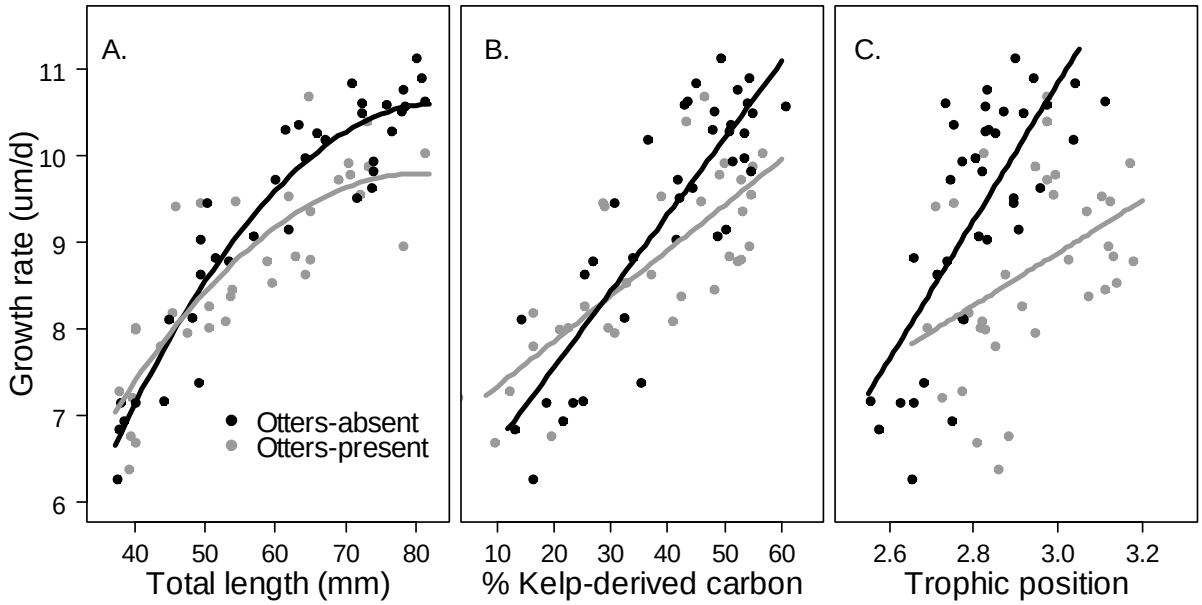

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