

# **Indirect effects of sea otter recovery on temperate reef fish**

**by**

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B.Sc., University of Victoria, 2010

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## Abstract

The loss or recovery of apex predators can have profound positive or negative ecological and socio-economic impacts. Effects of predator depletion or recovery are frequently accompanied by time lags, which are often context-dependent. In temperate rocky reef ecosystems, sea otters (*Enhydra lutris*) trigger a cascade of direct and indirect effects driving transitions between kelp-depleted and kelp-dominated states. We quantified the indirect effects of sea otter recovery on copper rockfish (*Sebastes caurinus*) and kelp greenling (*Hexagrammos decagrammos*) along a gradient in sea otter occupation time on the central coast of British Columbia. We used hook-and-line surveys and underwater visual transects at shallow depths (2-25 m) across 20 rocky reef sites and a space-for-time substitution representing variation in sea otter occupation time. Overall, we found higher fishable biomass of copper rockfish at sites where sea otter occupation was greatest, and evidence that copper rockfish catch rates were higher in relatively larger kelp beds. However, copper rockfish fishable biomass was negatively correlated with canopy kelp stipe density, likely due to the successional transition as sea otters return to an area from the disturbance-tolerant annual kelp *Nereocystis* to the perennial kelp *Macrocystis*. Contrary to expectations, we found no evidence for an effect of sea otter occupation time or kelp metrics on the fishable biomass of kelp greenling. We found no evidence that sea otter occupation time or any other factor tested affected rockfish or greenling density observed on underwater visual surveys. Contrary to our hypothesis, we found no appreciable enrichment of the  $\delta^{13}\text{C}$  signature across the gradient of sea otter occupation time associated with an increase in the amount of kelp-derived carbon within fish. These data allow us to evaluate trade-offs elicited by sea otter recovery and devise management plans for temperate reef systems that incorporate realistic timelines for changes to kelp forest communities.

**Keywords:** Temperate reef fish; Rockfish; indirect effects; sea otter; temporal scale; trophic cascade

*This work is dedicated to my Savta, who fostered my  
love of critters and beasts.*

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# Table of Contents

Approval.....	ii
Partial Copyright Licence .....	iii
Ethics Statement.....	iv
Abstract.....	v
Dedication .....	vi
Acknowledgements .....	vii
Table of Contents.....	viii
List of Tables.....	ix
List of Figures.....	x
List of Acronyms.....	xii
<b>Introduction .....</b>	<b>1</b>
Direct and indirect drivers of kelp forest dynamics.....	1
Kelp forest fish habitat associations .....	3
Research objectives and hypotheses .....	4
<b>Methods .....</b>	<b>6</b>
Fish density, length & biomass.....	7
Fish Diet.....	10
Statistical Analysis .....	11
<b>Results .....</b>	<b>14</b>
Fish density & biomass .....	14
Fish diet .....	15
<b>Discussion .....</b>	<b>27</b>
Indirect effects of sea otters on rocky reef fish.....	28
Comparing fish assessment methods.....	29
Importance of natural history .....	30
Policy and management implications .....	31
<b>References .....</b>	<b>34</b>
Appendix A. Site characteristics.....	46
Appendix B. Additional fish CPUE and density figures and tables.....	49
Appendix C. Additional stable isotope figures and tables .....	53

## List of Tables

Table 1.	Strength of evidence for generalized linear models (GLMs) of copper rockfish ( <i>S. caurinus</i> ) and kelp greenling ( <i>H. decagrammos</i> ) biomass (kg caught/hr) from hook-and-line fishing surveys across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AICc$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models. ....	20
Table 2.	Strength of evidence for generalized linear mixed effects models (GLMMs) of copper rockfish ( <i>S. caurinus</i> ) and kelp greenling ( <i>H. decagrammos</i> ) density (# of fish/120m <sup>2</sup> ) from underwater visual transects across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AICc$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models. ....	23
Table 3.	Strength of evidence for generalized linear mixed effects models (GLMMs) of copper rockfish ( <i>S. caurinus</i> ) and kelp greenling ( <i>H. decagrammos</i> ) $\delta^{13}C$ and $\delta^{15}N$ from 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AICc$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models. The random effect of fish length within site was nested within the fixed effects. ....	25

## List of Figures

- Figure 1. Hypothesized changes to kelp forest ecosystems with increasing time that sea otters (*Enhydra lutris*) occupy a temperate reef site. Where sea otters have been extirpated (0 years), sea urchins (in this case mostly *Mesocentrotus franciscanus*) heavily graze the canopy kelp, which leads to an urchin barrens below a few metres depth. Fast-growing annual kelps (e.g. *Nereocystis luetkeana*) still persist in the shallows. After sea otter have occupied a site and predated on most of the urchins, we hypothesize a successional shift to deeper kelp forests, characterized by perennials such as *Macrocystis pyrifera* and *Pterygophora californica*. We predict that these perennial kelps will offer additional 3-dimensional habitat for temperate reef fish including copper rockfish (*Sebastes caurinus*) and kelp greenling (*Hexagrammos decagrammos*) through the provision of shelter and a magnification of secondary production. We also predict that the extent of these canopy kelp beds will increase with longer sea otter occupation time. .... 3
- Figure 2. This research was conducted on the central coast of British Columbia, Canada. Fish and macroalgae surveys were conducted at 20 rocky subtidal sites in a space-for-time substitution where sites ranged from 0-33 years in sea otter occupation time. See Appendix for list of site names and characteristics. .... 7
- Figure 3. Example of the methods used to estimate the proportion of available rocky reef covered in canopy kelp over a standardized 300 m diameter circle centered on each dive site. The extent of canopy kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*) was measured using surface boat surveys. .... 9
- Figure 4. Biomass fished per hour of bottom time of A) copper rockfish (*Sebastes caurinus*) and B) kelp greenling (*Hexagrammos decagrammos*) caught using hook-and-line across 20 sites on the central coast of British Columbia. Sites were grouped by estimated sea otter occupation time categories of 0-2 years, 3-8 years, and 17-33 years. Solid horizontal line represents the median kg fished per hour of fishing bottom time. The coloured boxes represent the 25% and 75% quartiles. The upper whisker extends to the highest value within 1.5 \* the inter-quartile range. The lower whisker extends to the lowest value within 1.5 \* the inter-quartile range. Outliers beyond the whiskers are plotted as points. .... 17

Figure 5.	Scaled parameter estimates (circles) with 95% confidence intervals (lines) for variables in averaged mixed effects models of copper rockfish catch rates using A) Model set 1 and B) Model set 2. Predictor variables and their associated parameters are ranked in decreasing order of relative importance on a scale of 0 to 1. Relative variable importance values (RVI), were calculated by summing the Akaike weights ( $W_i$ ) over the subset of models for in which the variable was found. ....	18
Figure 6.	Relative frequency of fish lengths across 20 sites on the central coast of British Columbia from hook-and-line fishing (A & C) and underwater fish transects (B & D). The two most common fish species encountered were copper rockfish ( <i>Sebastes caurinus</i> , A & B) and kelp greenling ( <i>Hexagrammos decagrammos</i> , C & D). Copper rockfish <10 cm in underwater surveys were excluded from analysis because juveniles at this size cannot be distinguished from quillback rockfish ( <i>S. maliger</i> ). Sites were groups by estimated sea otter occupation time categories of 0-2 years, 3-8 years, and 17-33 years. Dashed line represents the mean fish length in cm. Lengths were binned every 2 cm. ....	19
Figure 7.	Mean fish density per 30 x 4 m underwater transect $\pm$ standard error (SE) (n=6 transects per site) of A) copper rockfish ( <i>Sebastes caurinus</i> ) and B) kelp greenling ( <i>Hexagrammos decagrammos</i> ) across 20 sites varying in sea otter occupation time on the central coast of British Columbia, Canada. Copper rockfish <10 cm in underwater surveys were excluded from analysis because juveniles at this size cannot be distinguished from quillback rockfish ( <i>S. maliger</i> ). ....	20
Figure 8.	Isotopic signatures of copper rockfish ( <i>Sebastes caurinus</i> ) (A & B) and kelp greenling ( <i>Hexagrammos decagrammos</i> ) (C & D) captured across 20 sites on the central coast of British Columbia varying in sea otter occupation time. Each dot represents the $\delta^{13}\text{C}$ (‰) (A & C) and $\delta^{15}\text{N}$ (‰) of an individual fish muscle sample. Fish were obtained through hook-and-line fishing. Samples were analyzed at UC Davis Stable Isotope Facility in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ration mass spectrometer. ....	24
Figure 9.	Fish stomach contents by percent of total stomach volume for A) copper rockfish ( <i>Sebastes caurinus</i> ) (n=80) and B) kelp greenling ( <i>Hexagrammos decagrammos</i> ) (n=56) across three categories of sea otter occupation time on the central coast of British Columbia, Canada. Empty stomachs were excluded from the analysis. Contents were identified to lowest possible taxon. Unknown category represented stomach contents that were too degraded to identify. ....	26

## List of Acronyms

AIC <sub>c</sub>	Akaike information criterion (small sample size corrected)
CPUE	Catch per unit effort
DFO	Department of Fisheries and Oceans Canada
RVI	Relative variable importance
SFU	Simon Fraser University

# Introduction

Investigating the complex temporal dynamics of species interactions and ecological processes is a fundamental problem in ecology and can have profound repercussions for conservation and management (Levin 1992, Menge 1997, Schneider 2001). The importance of accounting for temporal scale in studies of marine ecosystems is well-established (Dayton & Tegner 1984a, Pauly 1995, Dayton et al. 1998). Marine ecosystems are products of their temporal history, which are characterized by stochastic recruitment pulses, successional dynamics, and natural or human-induced changes to community assemblages (Vitousek et al. 1997, Dayton et al. 1998, Siegel et al. 2008, Estes et al. 2011). Here, we ask how sea otter recovery in a high latitude kelp forest ecosystem, and the ensuing biotic-driven changes to kelp forest communities, affect temperate reef fish catch rates, density, and diet over time.

## Direct and indirect drivers of kelp forest dynamics

Kelp forests are one of the most productive systems on our planet (Mann 1973, Reed et al. 2009), and their dynamics are driven by multiple abiotic and biotic interactions (Steneck et al. 2002). Regional-scale abiotic factors affecting kelp forests include wave height, storms, sedimentation, and long-term ocean climate (Dayton & Tegner 1984b, Foster & Schiel 1985, Dayton et al. 1998, Foster et al. 2006, Schiel et al. 2010, Cavanaugh et al. 2011, Reed et al. 2011). At higher latitudes, herbivory in the form of sea urchin grazing is one of the primary biotic controls of kelp forests (Steneck et al. 2002, Filbee-Dexter & Scheibling 2014). Globally, in regions where urchin abundance is high due to a lack of higher-order predators or sea urchin disease, widespread deforestation of rocky reefs (i.e. urchin barrens) is observed (Estes & Palmisano 1974, Pearse & Hines 1979, Harrold & Reed 1985, Estes & Duggins 1995, Stewart & Konar 2012).

Sea otters are well-known to consume herbivorous sea urchins, releasing macroalgae from grazing pressure and allowing kelp beds to flourish (Paine & Vadas 1969, Estes & Duggins 1995, Watson & Estes 2011). Sea otter predation on sea urchins can generate successional changes in kelp forests. By reducing urchin grazing pressure,

sea otters can indirectly induce a shift over time from annual kelps to 'old growth' perennial kelps. For example, when urchin grazing intensity is high, annual disturbance-resistant algal species such as *Nereocystis luetkeana* or *Desmarestia* spp. tend to be more abundant than perennial species (Vadas 1968, Paine & Vadas 1969, Watson & Estes 2011). The reverse occurs in the presence of sea otters—canopy (*Macrocystis pyrifera*) and understory (*Pterygophora californica* and *Ecklonia arborea*) perennials become the dominant kelp species (Watson & Estes 2011). Perennials can shade out understory kelps providing more space for sessile invertebrates (Arkema et al. 2009), and can offer substantially more 3-dimensional habitat structure for certain species of fish (Bodkin 1986, DeMartini & Roberts 1990, Holbrook et al. 1990, Anderson 1994, Levin & Hay 1996, Dean et al. 2000, Anderson & Millar 2004, Pérez-Matus et al. 2007, Pérez-Matus & Shima 2010). As such, sea otters presence may indirectly benefit fish populations by facilitating a shift to perennial kelp species (Figure 1).

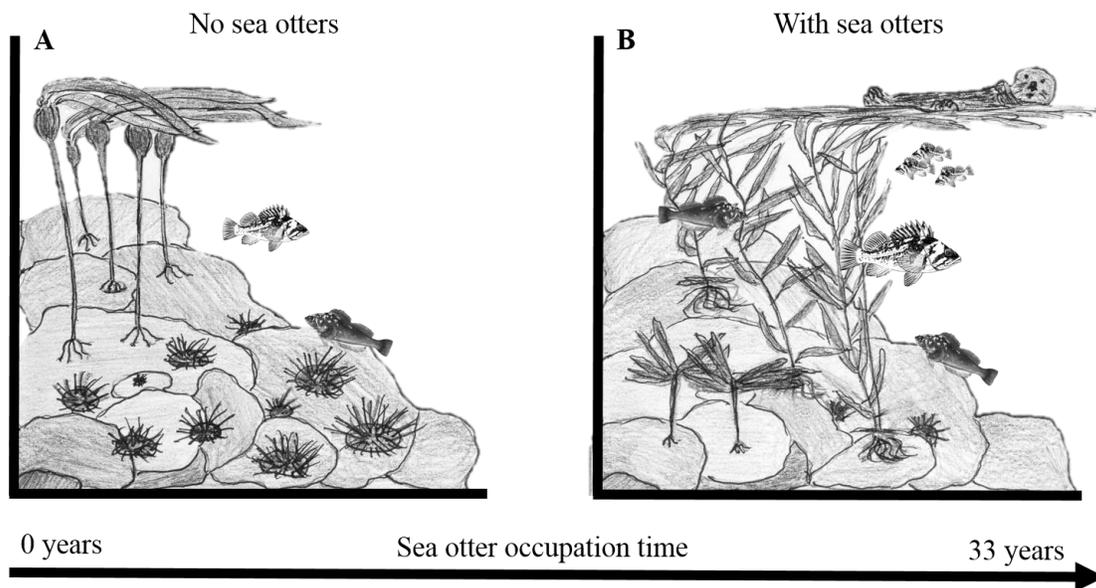


Figure 1. Hypothesized changes to kelp forest ecosystems with increasing time that sea otters (*Enhydra lutris*) occupy a temperate reef site. (A) Where sea otters have been extirpated (0 years), sea urchins (in this case mostly *Mesocentrotus franciscanus*) heavily graze the canopy kelp, which leads to an urchin barrens below a few metres depth. Fast-growing annual kelps (e.g. *Nereocystis luetkeana*) still persist in the shallows. (B) After sea otter have occupied a site and preyed on most of the urchins, we hypothesize a successional shift to deeper kelp forests, characterized by perennials such as *Macrocystis pyrifera* and *Pterygophora californica*. We predict that these perennial kelps will offer additional 3-dimensional habitat for temperate reef fish including copper rockfish (*Sebastes caurinus*) and kelp greenling (*Hexagrammos decagrammos*) through the provision of shelter and an increase in secondary production. We also predict that the extent of these canopy kelp beds will increase with longer sea otter occupation time.

## Kelp forest fish habitat associations

On temperate reefs, kelp offers architectural complexity that provides critical 3-dimensional habitat for a variety of fish species and life-history stages (Ebeling & Laur 1985, Bodkin 1986, 1988, Holbrook et al. 1990, Dean et al. 2000). Empirical evidence suggests that kelp is especially important for early life stages of many temperate reef fish such as rockfish (genus *Sebastes*), surfperch (family Embiotocidae), and sea basses (family Serranidae) (Carr 1989, 1991, 1994, Holbrook et al. 1990, Love et al. 1991, Hayden-Spear & Gunderson 2007, Markel 2011). Both juvenile and adult fish use kelp forests as shelter from predation, and to feed on prey that inhabit the kelp. For example, rockfish, surfperch, sea basses, greenling (family Hexagrammidae), and wrasses (family Labridae) have shown to preferentially inhabit kelp forests compared to less structurally

diverse surrounding habitat (Moulton 1977, Leaman 1980, Bodkin 1986, 1988, Richards 1987, Jones 1988, Demartini & Roberts 1990, Holbrook et al. 1990, Dean et al. 2000, Norderhaug et al. 2005, Pérez-Matus et al. 2007, Springer et al. 2007, Siddon et al. 2008, Pérez-Matus & Shima 2010, O'Connor & Anderson 2010). Consequently, factors that affect the local complexity and regional spatial extent of kelp forest habitat are hypothesized to influence reef-associated fish abundance, size and diet. Since many temperate rocky reef fish species have relatively small home ranges as adults (10-1000 m<sup>2</sup>) (Matthews 1990, Tolimieri et al. 2009, Reynolds et al. 2010), localized changes to habitat structure and organization (such as those induced indirectly by apex predators) can have considerable effects.

Previous studies have investigated the indirect effects of the sea otter-induced trophic cascade on rocky reef fish in the Aleutian Islands (Simenstad et al. 1978, Reisewitz et al. 2006) and British Columbia (Markel 2011, Szpak et al. 2013). In the Aleutians, Reisewitz et al. (2006) reported a >50% reduction in rock greenling (*Hexagrammos lagocephalus*) catch-per-unit-effort (CPUE) between 1986 and 2000 at islands that had shifted from high-density kelp forests with sea otters to urchin barrens in the absence of sea otters. Additional nutrient production associated with kelp forests also has the potential to alter food webs by supplementing food webs with kelp-derived carbon, which would yield an enriched  $\delta^{13}\text{C}$  signature in fish (Duggins et al. 1989, Simenstad et al. 1993, Duggins & Eckman 1997, Graham 2004, Szpak et al. 2013 but see Salomon et al. 2008, Singh 2010). In addition, the availability of invertebrate and juvenile fish prey for adult fish may vary as a result of the sea otter-induced trophic cascade (Reisewitz et al. 2006, Markel 2011). In British Columbia, Markel (2011) found that reef fish fed at a higher trophic level in areas with sea otters compared to areas where sea otters are absent, which he hypothesized was due to the increased availability of juvenile fish as prey in kelp forests. However, it remains unclear if these phenomenon are general, both across species of reef fish and among other areas in the northeastern Pacific where sea otters are recovering.

## **Research objectives and hypotheses**

We quantified the indirect effects of multiple biotic and abiotic factors driving nearshore temperate rocky reef fish density, length and diet, while incorporating how

physical and biological processes interrelate and vary over time (Menge & Olson 1990, Agrawal et al. 2007). Previous research has documented the shift from annual *Nereocystis* kelp beds to more structurally complex perennial *Macrocystis* kelp beds with sea otter occupation (Vadas 1968, Paine & Vadas 1969, Watson & Estes 2011), and the positive association between canopy kelps and adult rockfish and greenlings (Bodkin 1986, 1988, Holbrook et al. 1990, Dean et al. 2000, Reisewitz et al. 2006). Therefore, we hypothesized that as sea otter occupation time increases, overall kelp habitat complexity will be augmented by a reduction in disturbance by herbivorous grazers and subsequent algal succession towards more structurally complex perennial kelps. Consequently, we theorized that local reef fish density and size would increase the longer sea otters have occupied a site. Furthermore, if sea otter presence increases the depth and thus spatial extent of kelp forest habitat at the reef scale, we hypothesized that the overall abundance of reef fish will increase the longer sea otters have occupied a region.

We compared these effects using two species with different natural history traits—copper rockfish (*Sebastes caurinus*) and kelp greenling (*Hexagrammos decagrammos*). Copper rockfish, like many *Sebastes* spp, are late-to-mature (age at 50% maturity is 6-7 years in BC), have slow growth rates, and have lifespans of up to 50 years (Love et al. 2002). Kelp greenling, on the other hand, only live to 12 or 13 years and reach maturity in 3-5 years (Shanks & Eckert 2005). The life history traits of these fishes can affect both the behaviour and population dynamics of these fish (Love et al. 2002, Frid et al. 2012), and long-lived species may be less affected by periodic changes to kelp habitats over time (Holbrook et al. 1990).

In addition to sea otter-induced changes to kelp habitat complexity and extent, we predicted an increase in the proportion of kelp-derived carbon within reef fish diet, as kelp forests provide a source of organic material fuelling prey communities that fish feed upon. We expected that reef fish will feed trophically higher in areas of longer sea otter occupancy, as juvenile fish—which are a trophic level higher than invertebrate prey species—are more available to be eaten in kelp forests. Finally, we discuss how the indirect effects of sea otter recovery affect coastal resource management, as well as on what timescale we might expect these changes to occur.

## Methods

We investigated the relative effects of multiple biotic and abiotic factors driving nearshore (<20 m depth) rocky reef fish density, length, biomass and diet at 20 sites along the central coast of British Columbia (BC), Canada (Figure 2) in July, 2013. The central coast of BC is characterized by a complex coastline where sea otters are gradually expanding their range. Semi-exposed rocky reef sites were specifically chosen across a spatial gradient in sea otter re-establishment using a space-for-time substitution (Pickett 1989) to represent the length in time that sea otters had occupied a site—hereafter ‘sea otter occupation time’ (Figure 2). A site was considered occupied when the presence of a raft (>3 individuals) was sighted within a 3 nautical mile radius of each site (L. Nichol, personal communication). We estimated sea otter occupation time at each of our sites, based on boat-based sea otter surveys conducted from 1990 to 2013 (Nichol et al. 2009, L. Nichol, personal communication). Thus, we imposed a ‘natural experiment’ randomly on the landscape.

*History of Sea Otter Occupation* — Sea otters were ecologically extirpated from BC by the mid-1800s due to the maritime fur trade (Kenyon 1969, Sloan & Dick 2012). Along the central coast of BC, sea otter recovery was first recorded in 1989 (BC Parks 1995), although observations by local First Nations places their establishment in the area in 1979 (E. White, personal communication). Sea otters annual growth rate between 1990 and 2008 was 11% (Nichol et al. 2009), and their range has expanded both northward and southward from the original sighting location. The central coast population of sea otters is currently estimated at 1,000 individuals (COSEWIC 2007, Nichol et al. 2009, L. Nichol, personal communication).

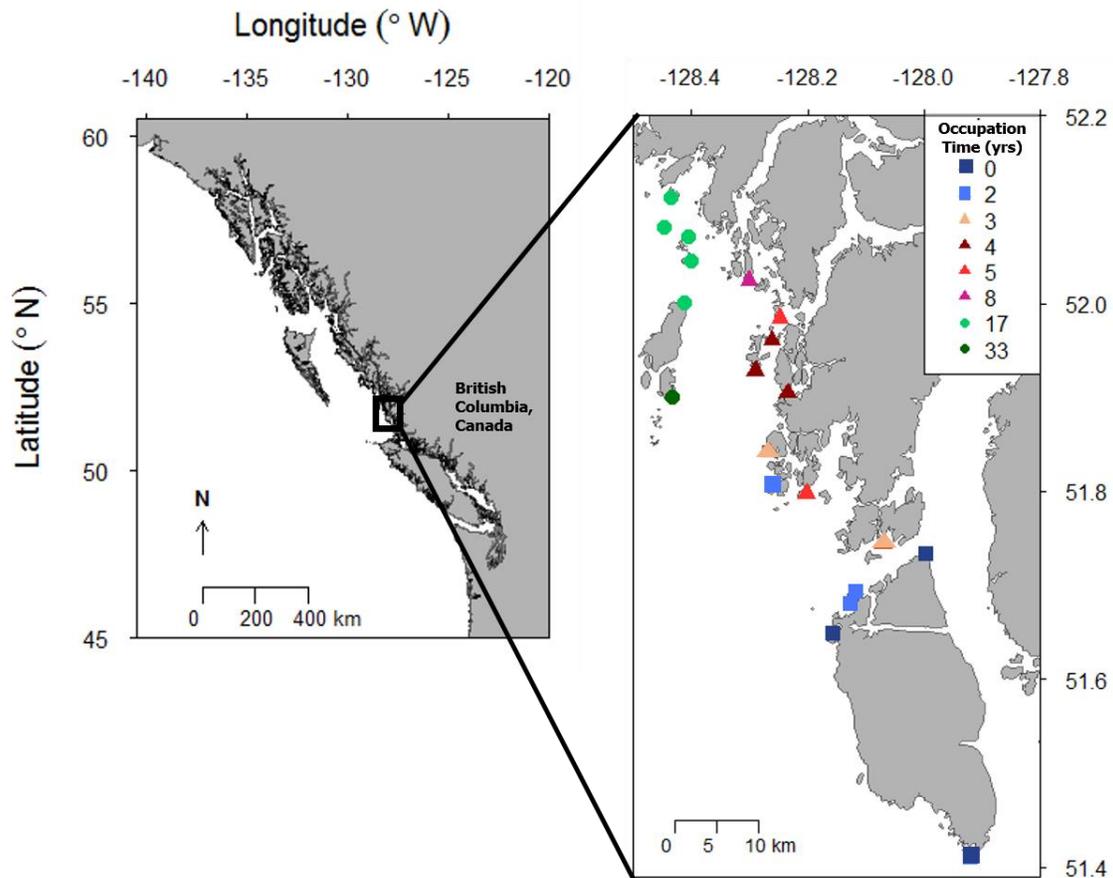


Figure 2. This research was conducted on the central coast of British Columbia, Canada. Fish and macroalgae surveys were conducted at 20 rocky subtidal sites in a space-for-time substitution where sites ranged from 0-33 years in sea otter occupation time. See Appendix for list of site names and characteristics.

## Fish density, length & biomass

*Catch-per-unit-effort (CPUE)*— We sampled adult reef-associated fish at each site using hook-and-line jigging. We fished for approximately 1 hour of total bottom time using medium Mac Deep lures with no bait. Bottom time was defined as the time an individual fisher was engaged in fishing with a lure jigging just off the sea floor. Consequently, timing was stopped every time a fish was caught or the lure was unavailable for fish (e.g. snagged on kelp). Fishing occurred between 0 and 22 m depth. Subsequently, recorded depths were tide-corrected to chart datum—based on the lowest low water large tide (LLWLT).

For each fish caught, we recorded the species, length, weight, and gape size. We calculated CPUE based on the number of fish caught for a given bottom time and

standardized the response variable to kg of fish caught per hour of bottom time. A subsample of fish were retained for diet analysis based on stomach contents and stable isotope analysis. Muscle, bone, and otolith samples were collected from all retained fish. For fish that were not retained, we descended them back to depth using a descension device to counteract possible barotrauma and reduce mortality.

*Underwater visual surveys* — We quantified reef-associated fish communities via SCUBA at each site using six 30 x 4 m belt-transects run parallel to shore at two depth ranges; n=3 shallow (3-5 m below chart datum) and n=3 deep (10-12 m below chart datum). For each transect, SCUBA divers swam each transect at an approximately constant speed. A diver identified, counted and estimated the size of all reef-associated fish to the nearest cm including; rockfish (genus *Sebastes*), kelp greenling (*Hexagrammos decagrammus*), lingcod (*Ophiodon elongatus*) and other large (>3 cm) fish. We focused our analysis on copper rockfish (*Sebastes caurinus*) and kelp greenling, as these were the most common species we encountered. Observers were trained by estimating the size of known-length objects underwater (Bell et al. 1985, Polunin & Roberts 1993). Individual fish weights were calculated from species-specific length-weight conversions (Love et al. 2002).

*Kelp stipe density* — At each site, we counted the number of canopy kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*) stipes taller than 1 m in height within a 15 m x 1 m swath of each of the fish transects (n=6 per site). To estimate the density of understory kelps (order Laminariales), we haphazardly placed 18 quadrats (1 m<sup>2</sup>) stratified within shallow and deep areas within the study site. In each quadrat, we counted and identified every adult kelp stipe (>15 cm) to species and counted the number of juvenile kelps (<15 cm).

*Kelp bed area* — To estimate the spatial extent of kelp canopy covering each rocky reef site, we measured canopy kelp bed area at the ocean surface surrounding each site using small boat surveys at as low of a tide as possible. We took GPS waypoints along the seaward edge of each kelp bed every 3 seconds. We recorded the depth at each waypoint using a depth sounder and later corrected the depths for tidal height. We demarcated the edge of the kelp bed when there was a ≥10 m gap between surface canopy kelp blades.

*Standardized kelp bed area* — We estimated the proportion of rocky reef area shallower than 10 m depth within a standardized 300 m diameter circle around each site. Based on our field observations and the geomorphology of this region, we assumed that subtidal habitat shallower than 10 m in this area was rocky reef where canopy kelp could grow. To calculate this proportion of shallow rocky reef, we used vectorized nautical charts in ArcGIS 10.2 (ESRI, 2015) (Figure 3). We then estimated the proportion of this available rocky reef covered in canopy kelp derived from the kelp bed extent measured on the boat survey. The size of the standardized circle was chosen to reflect the small home range size (~30 m<sup>2</sup>) of the fish tested (Matthews 1990) with an appropriate buffer from the end of each transect.

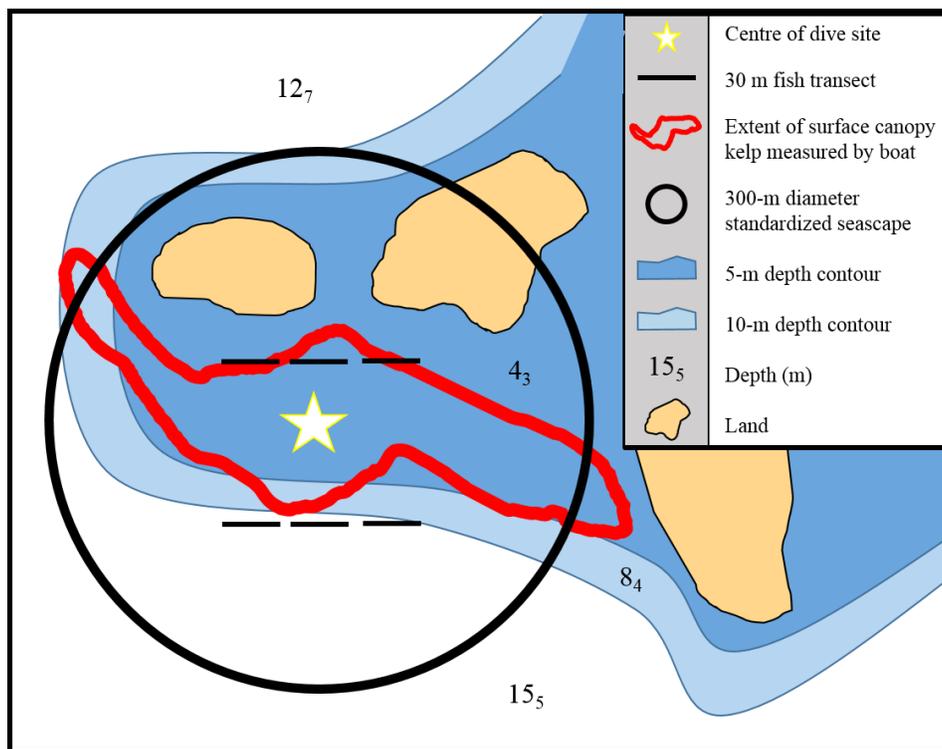


Figure 3. Example of the methods used to estimate the proportion of available rocky reef covered in canopy kelp over a standardized 300 m diameter circle centered on each dive site. The extent of canopy kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*) was measured using surface boat surveys.

*Rugosity* — To quantify site rugosity, we contoured a 3 m length of fine-link chain (<1 cm links) to the rock parallel to the transect tape at 3 randomly stratified points along the transect. We then calculated the ratio between the length of the chain (3 m) and the distance along the transect line between the start and end point (Risk 1972, Alvarez-Filip

et al. 2011). We used the mean of these three measurements to calculate transect-level rugosity.

*Wave Exposure* — For each site, we calculated the relative July wave exposure where:

$$\text{Relative Exposure Index} = \sum_{i=1}^3 (V_i \times W_i \times F_i)$$

$V_i$  is average wind speed from the  $i$ th direction (Bella Bella wind station downloaded from <http://climate.weather.gc.ca/>),  $W_i$  is the frequency of observations when the wind blew from the  $i$ th direction, and  $F_i$  is the fetch from the  $i$ th direction. We calculated fetch at 10° compass bearings and capped the maximum single fetch length at 200 km (based on Ekebom et al. 2002). July wind data were chosen, as this month is representative of the prevailing northwesterly wind direction in the region during the spring and summer when fish sampling took place (Thomson 1981).

## Fish Diet

A sub-sample of fish was retained for diet analysis using stomach contents and stable isotopes as indicators of kelp-derived carbon in fish diet and their prey sources. To address short-term food sources in all retained fish, we identified stomach contents to the lowest possible taxon and estimated the relative volume of each taxon. Total stomach contents were plotted as a percentage of the stomach volume for each fish species.

To determine long-term sources of carbon and nitrogen, we quantified the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic signatures from fish muscle samples. Thawed dorsal muscle was rinsed with 10% HCl followed by de-ionized water before oven drying for 48 hours at 60°C. We manually ground samples to a fine powder and packaged 0.8-1.2 mg portions into 5x3.5 mm tin capsules. Samples were analyzed at UC Davis Stable Isotope Facility in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer.

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures are calculated relative to international standards, V-PBD

for carbon and air for nitrogen:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \right]$$

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

## Statistical Analysis

*Copper rockfish and kelp greenling catch rates* — To assess the strength of evidence for alternative biotic and abiotic factors driving differences in copper rockfish and kelp greenling CPUE among sites, we fit generalized linear models (GLM) and took an information-theoretic approach (Burnham & Anderson 2002). To explore our hypothesized mechanisms driving differences in fish biomass and increase interpretability of our model output with minimized multicollinearity (O'Brien 2007), we sequentially tested two model sets with different groups of factors (Appendix B). In model set 1, we treated sea otter occupation time, rugosity, and relative site exposure as fixed effects. In model set 2, we replaced sea otter occupation time with kelp habitat metrics—canopy kelp stipe density, subcanopy kelp density, and proportion of available rocky reef covered by canopy kelp—while rugosity and relative exposure remained. To achieve model convergence, we added a constant of 0.1 to all biomass values prior to log transformation. Analysis were conducted using the *lm* function in R version 3.0.3 (R Core Team 2013).

*Copper rockfish and kelp greenling density and biomass* — To assess the strength of evidence for potential effects of biotic and abiotic factors on copper rockfish and kelp greenling fish density estimated from underwater visual transects, we fit generalized linear mixed-effects models (GLMM) and took an information-theoretic approach (Burnham & Anderson 2002). All rockfish <10 cm in total length were removed from the analysis, because it is difficult to reliably differentiate copper from quillback rockfish in this size range. In both model sets, transect depth nested within site was treated as a random effect. We sequentially tested two model sets in the same manner as the CPUE models. Models of copper rockfish and kelp greenling density were fit with a Poisson likelihood and

log link function. We tested for overdispersion on the global model by dividing the sum of squares Pearson residuals by the residual degrees of freedom (Venables & Ripley 2003), and compared zero-inflated Poisson models with non-zero inflated models using AIC calculated in the *glmmADMB* package in R (Fournier et al. 2012). We found no evidence for overdispersion or zero-inflation. All GLMM Poisson models were run in R version 3.0.3 (R Core Team 2013) using the *lme4* package (Bates et al. 2014). Given the large number of zeros in the data resulting in a lack of model convergence, we also tested models of fish biomass using a Hurdle framework (Zeileis et al. 2008) to assess only transects where fish were seen. In the first step of the Hurdle framework, we tested a binomial distribution of transects where fish were seen and transects where fish were not seen. In the second step of the Hurdle framework, we tested the effect of the chosen factors only on transects where fish were seen. Since these Hurdle models yielded comparable results, we based our results predominantly on the parsimonious Poisson count models.

*Fish diet and isotopic signatures* — We used generalized linear mixed-effects models (GLMM) and an information-theoretic approach (Burnham & Anderson 2002) to assess the strength of evidence for potential effects of sea otter occupation time, canopy kelp stipe density, subcanopy kelp density, and the proportion of available rocky reef covered in canopy kelp on the isotopic signature of copper rockfish and kelp greenling muscle tissue. Fish length nested within site were treated as a random effect nested within the fixed effects. Models of copper rockfish (n=80) and kelp greenling (n=56)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were fit with a Gaussian likelihood and an identity link function. Models were run using the *lmer* function within the *lme4* package (Bates et al. 2014).

*Model selection* — We assessed the relative strength of evidence for alternative candidate models with small-sample bias-corrected Akaike's Information Criterion (AIC<sub>c</sub>), standardized to the most parsimonious model to produce ( $\Delta\text{AIC}_c$ ) values (Burnham & Anderson 2002, Grueber et al. 2011). We normalized the model likelihoods to a set of positive Akaike weights ( $w_i$ ), representing the strength of evidence in favour of a given model relative to the set of candidate models (Burnham & Anderson 2002). We calculated multi-model averaged parameter estimates and relative variable importance (RVI) using the MuMIn package (Barton 2012). The RVI for each factor was calculated by summing Akaike weights across all models where the factor occurs (Burnham & Anderson 2002). To facilitate interpretation among factors, we standardized each factor to a common scale

by subtracting their mean and dividing by 2 standard deviations (Gelman 2008). The marginal  $R^2$  (proportion of variance explained by the fixed factors) and the conditional  $R^2$  (proportion of variance explained by both the fixed and random factors) (Nakagawa & Schielzeth 2013) were calculated using the `r.squaredGLMM` function within the `MuMIn` package (Barton 2012).

# Results

## Fish density & biomass

*Adult copper rockfish catch rates* — We found relatively strong evidence that sea otter occupation time had a positive effect on adult copper rockfish catch rates (Model set 1: Figure 4A, Figure 5A, Table 1A, RVI=0.83, scaled parameter estimate=1.36, 0.26-2.46 95% CI). Furthermore, the positive effect of sea otter occupation time on adult copper rockfish catch rates was 1.8 times greater than the effect of reef rugosity (Figure 5A, RVI = 0.46). Models of sea otter occupation time only, and sea otter occupation time + rugosity were equivalent (within 2  $\Delta$ AICc, Table 1). We found relatively little evidence for an effect of wave exposure on adult copper rockfish catch rates among sites (Figure 5).

We detected strong evidence that the proportion of available rocky reef covered with canopy kelp had a positive effect on adult copper rockfish catch rates (Model set 2: Figure 5B, Table 1B, RVI=0.97, scaled parameter estimate=1.55, 0.58 - 2.52 95% CI). We also detected a strong negative effect of canopy kelp stipe density on adult copper rockfish catch rates (Figure 5B, RVI=0.94, scaled parameter estimate = -1.40, -2.36 to -0.42 95% CI). We found the effects of reef rugosity, wave exposure, and subcanopy kelp stipe density on copper rockfish catch rates were relatively less important (Figure 5B, RVI= 0.28, 0.27, 0.17, respectively). On average, adult copper rockfish tended to be slightly larger at older sea otter occupation sites, based on both our hook-and-line surveys (Figure 6A) and underwater visual transects surveys (Figure 6B).

*Adult kelp greenling catch rates* — We found no evidence for an effect of sea otter occupation time, reef rugosity, or wave exposure on adult kelp greenling catch rates (Figure 4B, Table 1C). Our intercept-only model of no effect had the lowest AICc relative to all other candidate models of adult kelp greenling catch rates. Furthermore, all other candidate models were  $\geq 2.55$   $\Delta$ AICc values away from this null model. Subsequently, in model set 2, we did not detect evidence for an effect of the proportion of available rocky reef covered with canopy kelp, canopy kelp stipe density, subcanopy kelp stipe density, reef rugosity, or relative wave exposure on adult greenling catch rates (Table 1D). Lastly, we observed no consistent trend in adult greenling size frequency distributions across sites varying in sea otter occupation time category (Figure 6C & D).

*Reef fish density from underwater visual transects* — We found no evidence of an effect of any of the factors estimated from our underwater visual transects on copper rockfish or kelp greenling density (Figure 7, Table 4). Specifically, our intercept-only null models for both species of reef fish were indistinguishable from all other candidate models (within 0-2  $\Delta$ AICc). Consequently, we did not detect any evidence at the underwater transect scale for an effect of sea otter occupation time, reef rugosity, wave exposure, canopy kelp stipe density, subcanopy kelp stipe density, or proportion of available rocky reef covered with canopy kelp in driving the spatial variation in these two fish species across our 20 sites. Rockfish (*Sebastes* spp) recruits were only recorded on 11 out of 120 underwater transects, and >3 total recruits were recorded at only 4 of 20 sites (Appendix B).

## Fish diet

$\delta^{13}\text{C}$  — When we controlled for fish length, we found no evidence that the  $\delta^{13}\text{C}$  of either fish species became increasingly enriched as sea otter occupation time increased (Figure 8A & B). Contrary to our hypotheses, we found that as the proportion of reef covered with canopy kelp increased, the  $\delta^{13}\text{C}$  of copper rockfish became more depleted ( Table 5A, Appendix C, RVI=0.83, scaled parameter estimate = -0.31, -0.57 to -0.05 95% CI). Consistent with the hypothesis, we found evidence of an effect of canopy kelp stipe density yielding a more enriched signature ( Table 5A, Appendix C, RVI=0.68), but the magnitude of this effect was negligible (average 0.01% enrichment per 1 unit increase in canopy stipe density). Despite determining a top model, given the factors tested, this model only explained 10% of the variation across sites, as determined by the marginal  $R^2$ . We found no evidence that any of the factors tested had an effect on the  $\delta^{13}\text{C}$  of kelp greenling, as our intercept-only null model was indistinguishable from all other candidate models (within 0-2  $\Delta$ AICc) ( Table 5B).

$\delta^{15}\text{N}$  — We found evidence that the wave exposure at a site had a marginal effect on the  $\delta^{15}\text{N}$  of copper rockfish ( Table 5C, Appendix C, RVI=1, scaled parameter estimate = 0.43, 0.24 to 0.61 95% CI). However, the magnitude of the effect of wave exposure on copper rockfish  $\delta^{15}\text{N}$  was a negligible 0.19‰ enrichment per 100 point increase in the relative exposure index (range at sites tested was 2-400). This top model only explained 21% of the variation across sites, as determined by the marginal  $R^2$ . We found evidence

that the proportion of reef covered by canopy kelp (RVI=0.69) and wave exposure (RVI=0.68) explained the most variation in kelp greenling  $\delta^{15}\text{N}$  ( Table 5D, Appendix C). Similar to copper rockfish, the magnitude of the effect of wave exposure on copper rockfish  $\delta^{15}\text{N}$  was a negligible 0.20‰ enrichment per 100 point increase in the relative exposure index. The magnitude of the effect of proportion reef covered by canopy kelp was an enrichment of 0.90‰ per percentage increase in proportion covered, but the top model containing both metrics only explained 22% of the variation across sites, as determined by the marginal  $R^2$ .

*Stomach contents* — We found some trends in the stomach contents of kelp greenling, across sites varying in sea otter occupation time (Figure 9). Kelp greenling stomachs contents tended to have a higher proportion of small crabs (mostly *Lophopanopeus bellus*, *Glebocarcinus oregonensis*, juvenile *Metacarcinus magister*, and juvenile *Cancer productus*) and amphipods (suborder Gammaridea and family Caprellidae), but with fewer fish at longer sea otter occupation sites. We found an increase in the proportion of sessile or mostly sessile invertebrates (e.g. hydroids, bryozoans, sea cucumbers) in kelp greenling stomachs at shorter sea otter occupation sites. Overall, kelp greenling had a much high proportion of unidentifiable prey (~25% total stomach volume) than copper rockfish (<5% total stomach volume). In contrast, we found no clear trends in copper rockfish stomach contents across sites of different sea otter occupation time. Approximately 75% of the total volume of copper rockfish stomachs was comprised of unidentifiable fish, and crabs (same species as kelp greenling) across all three categories of sea otter occupation (Figure 9). The proportion of fish within stomach contents did not vary predictably between sites for either species (Appendix C). Kelp greenling had the most diverse diet of any species with an average of  $5.4 \pm 4.9$  SD prey taxa per stomach, while copper rockfish had an average of  $2.6 \pm 1.9$  SD prey per stomach.

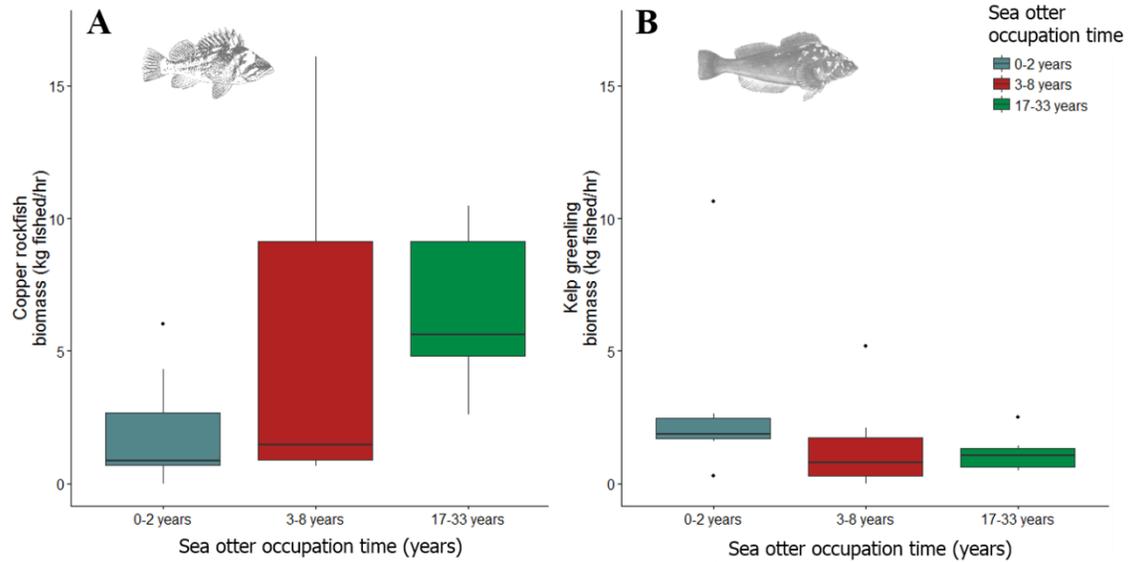


Figure 4. Biomass fished per hour of bottom time of A) copper rockfish (*Sebastes caurinus*) and B) kelp greenling (*Hexagrammos decagrammos*) caught using hook-and-line across 20 sites on the central coast of British Columbia. Sites were grouped by estimated sea otter occupation time categories of 0-2 years, 3-8 years, and 17-33 years. Solid horizontal line represents the median kg fished per hour of fishing bottom time. The colored boxes represent the 25% and 75% quartiles. The upper whisker extends to the highest value within 1.5 \* the inter-quartile range. The lower whisker extends to the lowest value within 1.5 \* the inter-quartile range. Outliers beyond the whiskers are plotted as points.

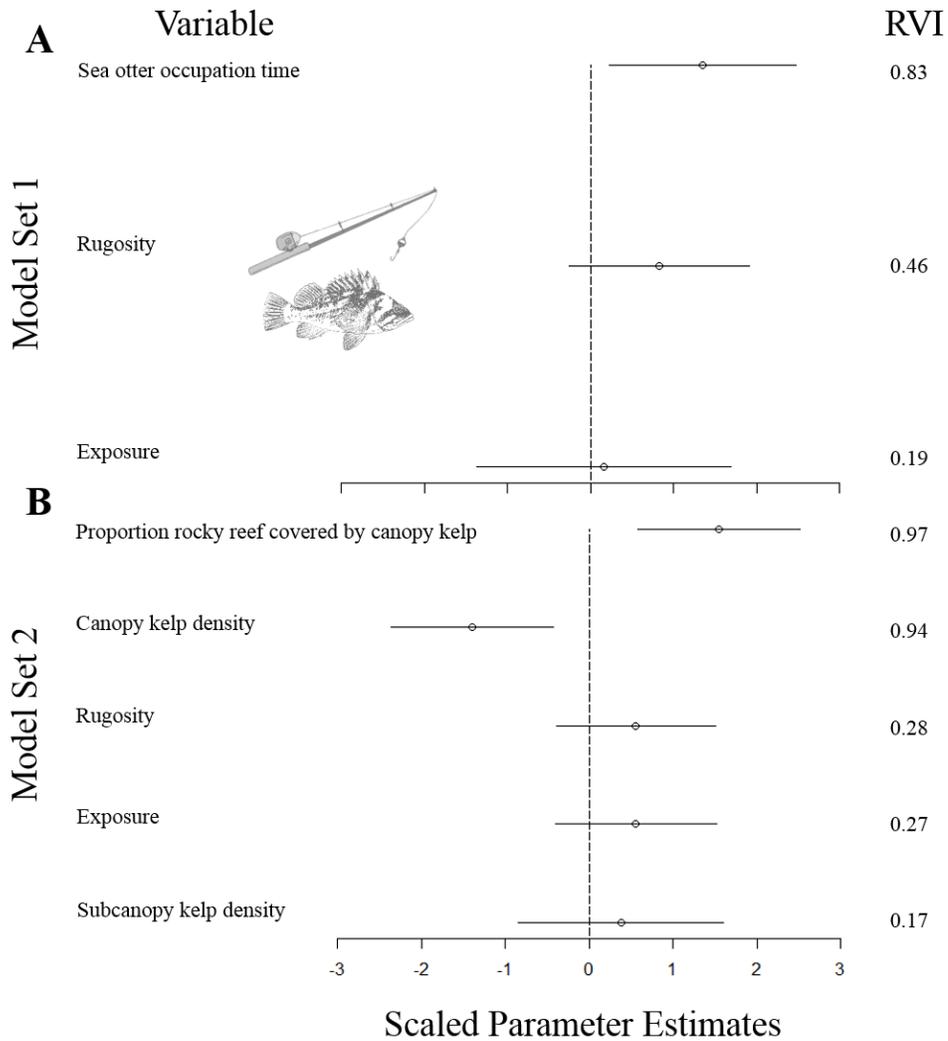


Figure 5. Scaled parameter estimates (circles) with 95% confidence intervals (lines) for variables in averaged mixed effects models of copper rockfish catch rates using A) Model set 1 and B) Model set 2. Predictor variables and their associated parameters are ranked in decreasing order of relative importance on a scale of 0 to 1. Relative variable importance values (RVI), were calculated by summing the Akaike weights ( $W_i$ ) over the subset of models for in which the variable was found.

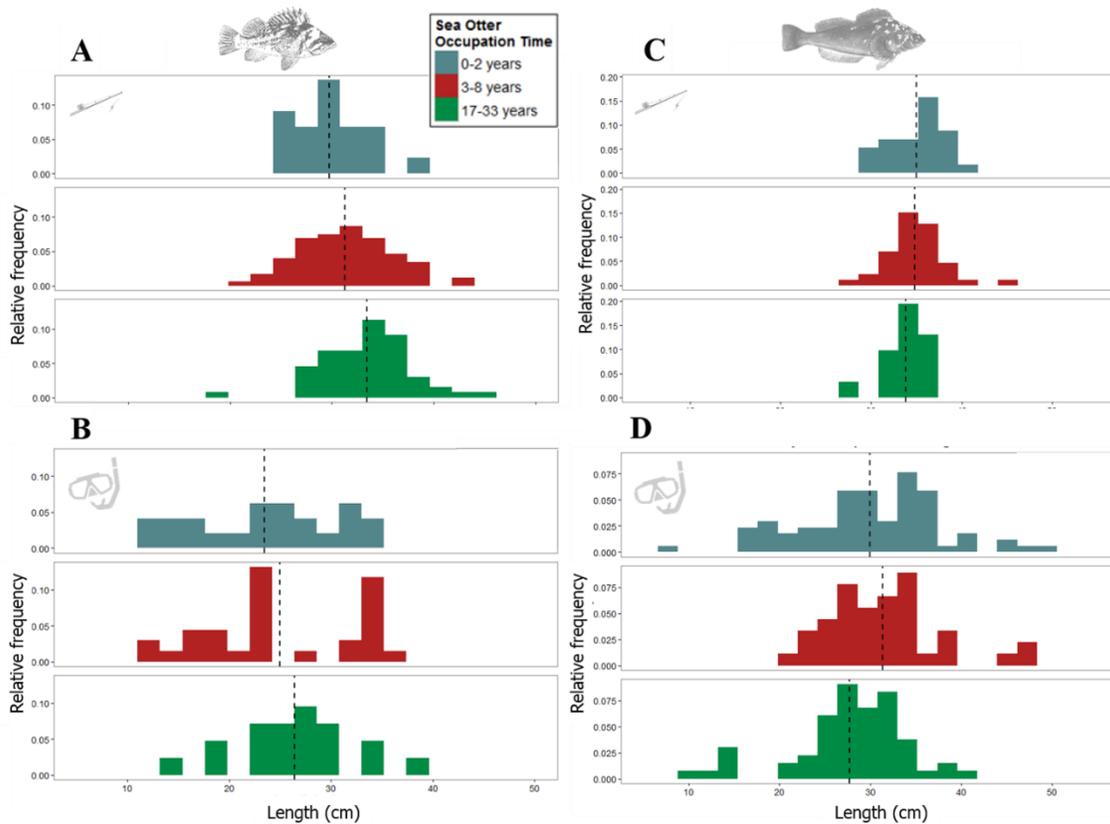


Figure 6. Relative frequency of fish lengths across 20 sites on the central coast of British Columbia from hook-and-line fishing (A & C) and underwater fish transects (B & D). The two most common fish species encountered were copper rockfish (*Sebastes caurinus*, A & B) and kelp greenling (*Hexagrammos decagrammos*, C & D). Copper rockfish <10 cm in underwater surveys were excluded from analysis because juveniles at this size cannot be distinguished from quillback rockfish (*S. maliger*). Sites were grouped by estimated sea otter occupation time categories of 0-2 years, 3-8 years, and 17-33 years. Dashed line represents the mean fish length in cm. Lengths were binned every 2 cm.

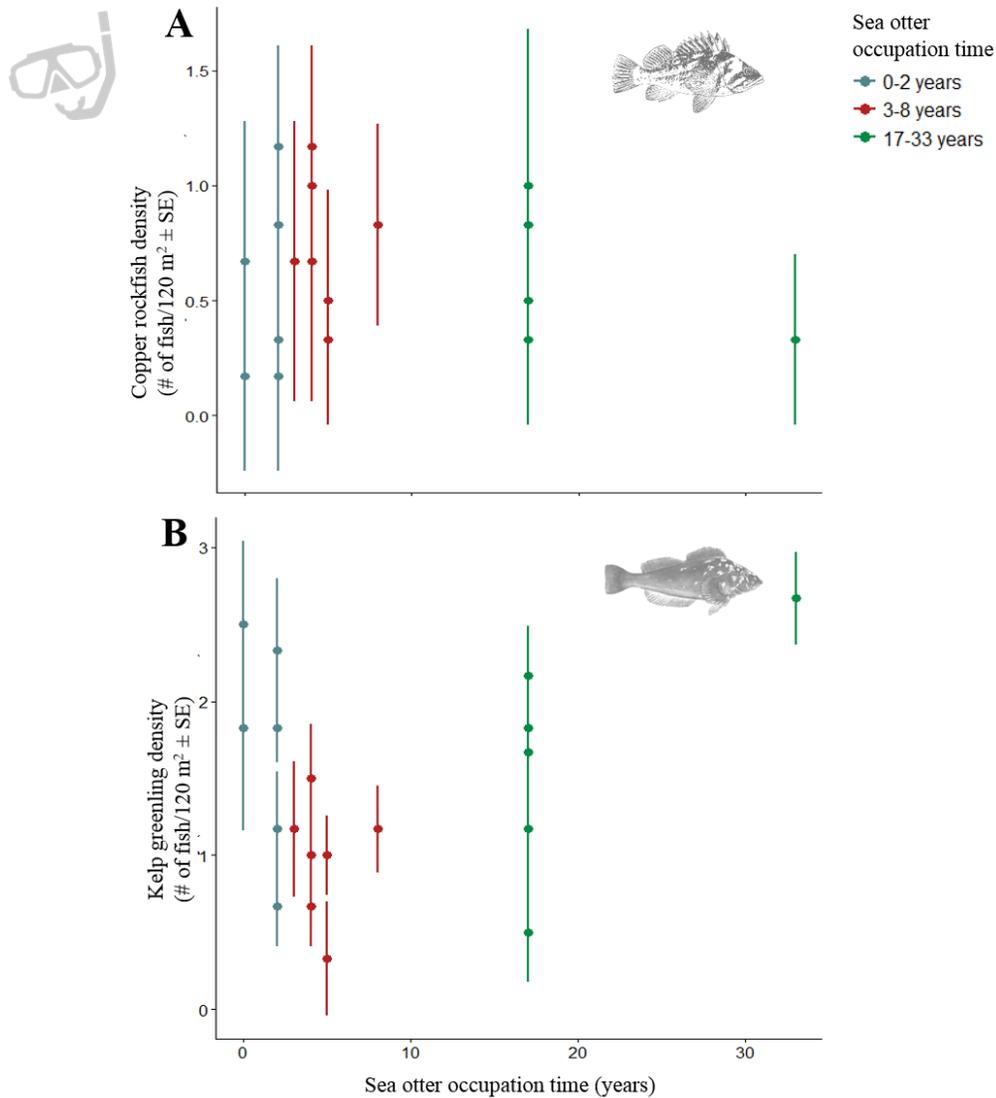


Figure 7. Mean fish density per 30 x 4 m underwater transect  $\pm$  standard error (SE) (n=6 transects per site) of A) copper rockfish (*Sebastes caurinus*) and B) kelp greenling (*Hexagrammos decagrammos*) across 20 sites varying in sea otter occupation time on the central coast of British Columbia, Canada. Copper rockfish <10 cm in underwater surveys were excluded from analysis because juveniles at this size cannot be distinguished from quillback rockfish (*S. maliger*). Table 1. Strength of evidence for generalized linear models (GLMs) of copper rockfish and kelp greenling biomass (kg caught/hr) from hook-and-line fishing surveys across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AIC_c$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models.

Table 2. Strength of evidence for generalized linear models (GLMs) of copper rockfish and kelp greenling biomass (kg caught/hr) from hook-and-line fishing surveys across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AIC_c$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models.

<b>Response &amp; Model</b>	<b>LogLL</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><math>W_i</math></b>	<b><math>R^2_{Marg}</math></b>
<b>A Copper rockfish catch rates – Model Set 1</b>					
Sea otter occupation time	-29.90	67.31	0.00	0.36	0.26
Sea otter occupation time + Rugosity	-28.39	67.44	0.14	0.34	0.34
Sea otter occupation time + Exposure	-29.90	70.46	3.16	0.07	0.25
Intercept	-33.01	70.72	3.42	0.07	N/A
Sea otter occupation time + Rugosity + Exposure	-28.29	70.86	3.56	0.06	0.34
<b>B Copper rockfish catch rates – Model Set 2</b>					
Canopy kelp density + Proportion reef covered by canopy kelp	-24.89	64.08	0.00	0.30	0.51
Canopy kelp density + Proportion reef covered by canopy kelp + Rugosity	-23.53	65.52	1.44	0.14	0.52
Proportion reef covered by canopy kelp + Rugosity	-26.06	66.41	2.32	0.09	0.56
Proportion reef covered by canopy kelp	-27.92	66.50	2.42	0.09	0.37
Canopy kelp density + Proportion reef covered by canopy kelp + Exposure	-24.36	67.18	3.10	0.06	0.52
<b>C Kelp greenling catch rates – Model Set 1</b>					
Intercept	-30.50	65.70	0.00	0.51	N/A
Rugosity	-30.37	68.25	2.55	0.14	
Sea otter occupation time	-30.47	68.44	2.74	0.13	
Exposure	-30.47	68.44	2.74	0.13	
Rugosity + Exposure	-30.31	71.29	5.59	0.03	
<b>D Kelp greenling catch rates – Model Set 2</b>					
Intercept	-30.50	65.70	0.00	0.29	N/A
Proportion reef covered by canopy kelp	-29.92	67.34	1.64	0.13	
Canopy kelp density	-30.31	68.12	2.42	0.09	
Rugosity	-30.37	68.25	2.55	0.08	
Subcanopy kelp density	-30.44	68.37	2.68	0.08	

Table 3. Strength of evidence for generalized linear models (GLMs) of copper rockfish and kelp greenling biomass (kg caught/hr) from hook-and-line fishing surveys across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AIC_c$ ), and normalized Akaike weights ( $W_i$ ). We report top 5 alternative models.

<b>Response &amp; Model</b>	<b>LogLL</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><math>W_i</math></b>	<b><math>R^2_{Marg}</math></b>
<b>A Copper rockfish catch rates – Model Set 1</b>					
Sea otter occupation time	-29.90	67.31	0.00	0.36	0.26
Sea otter occupation time + Rugosity	-28.39	67.44	0.14	0.34	0.34
Sea otter occupation time + Exposure	-29.90	70.46	3.16	0.07	0.25
Intercept	-33.01	70.72	3.42	0.07	N/A
Sea otter occupation time + Rugosity + Exposure	-28.29	70.86	3.56	0.06	0.34
<b>B Copper rockfish catch rates – Model Set 2</b>					
Canopy kelp density + Proportion reef covered by canopy kelp	-24.89	64.08	0.00	0.30	0.51
Canopy kelp density + Proportion reef covered by canopy kelp + Rugosity	-23.53	65.52	1.44	0.14	0.52
Proportion reef covered by canopy kelp + Rugosity	-26.06	66.41	2.32	0.09	0.56
Proportion reef covered by canopy kelp	-27.92	66.50	2.42	0.09	0.37
Canopy kelp density + Proportion reef covered by canopy kelp + Exposure	-24.36	67.18	3.10	0.06	0.52
<b>C Kelp greenling catch rates – Model Set 1</b>					
Intercept	-30.50	65.70	0.00	0.51	N/A
Rugosity	-30.37	68.25	2.55	0.14	
Sea otter occupation time	-30.47	68.44	2.74	0.13	
Exposure	-30.47	68.44	2.74	0.13	
Rugosity + Exposure	-30.31	71.29	5.59	0.03	
<b>D Kelp greenling catch rates – Model Set 2</b>					
Intercept	-30.50	65.70	0.00	0.29	N/A
Proportion reef covered by canopy kelp	-29.92	67.34	1.64	0.13	
Canopy kelp density	-30.31	68.12	2.42	0.09	
Rugosity	-30.37	68.25	2.55	0.08	
Subcanopy kelp density	-30.44	68.37	2.68	0.08	

Table 4. Strength of evidence for generalized linear mixed effects models (GLMMs) of copper rockfish and kelp greenling density (# of fish/120m<sup>2</sup>) from underwater visual transects across 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta AIC_c$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models.

<b>Response &amp; Model</b>	<b>LogLL</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><math>W_i</math></b>
<b>A Copper rockfish density – Model Set 1</b>				
Intercept	-132.02	270.26	0.00	0.48
Rugosity	-131.92	272.20	1.94	0.18
Sea otter occupation time + Rugosity	-131.69	273.91	3.66	0.08
Sea otter occupation time	-131.69	273.91	3.66	0.08
Rugosity + Exposure	-131.92	274.37	4.11	0.06
<b>B Copper rockfish density – Model Set 2</b>				
Intercept	-132.02	270.26	0.00	0.13
Canopy kelp density	-131.09	270.52	0.27	0.12
Proportion reef covered by canopy kelp	-131.40	271.24	0.99	0.08
Canopy kelp density + Proportion reef covered by canopy kelp	-130.70	271.93	1.67	0.06
Rugosity	-131.92	272.20	1.94	0.05
<b>C Kelp greenling density – Model Set 1</b>				
Intercept	-186.53	379.26	0.00	0.36
Rugosity + Exposure	-185.31	381.15	1.89	0.14
Exposure	-185.31	381.15	1.89	0.14
Rugosity	-186.45	381.25	1.99	0.13
Sea otter occupation time + Rugosity	-186.06	382.64	3.38	0.07
<b>D Kelp greenling density – Model Set 2</b>				
Exposure	-185.45	379.24	0.00	0.14
Intercept	-186.53	379.26	0.02	0.13
Proportion reef covered by canopy kelp	-186.06	380.46	1.22	0.07
Proportion reef covered by canopy kelp + Exposure	-184.98	380.49	1.25	0.07
Rugosity + Exposure	-185.31	381.15	1.91	0.05

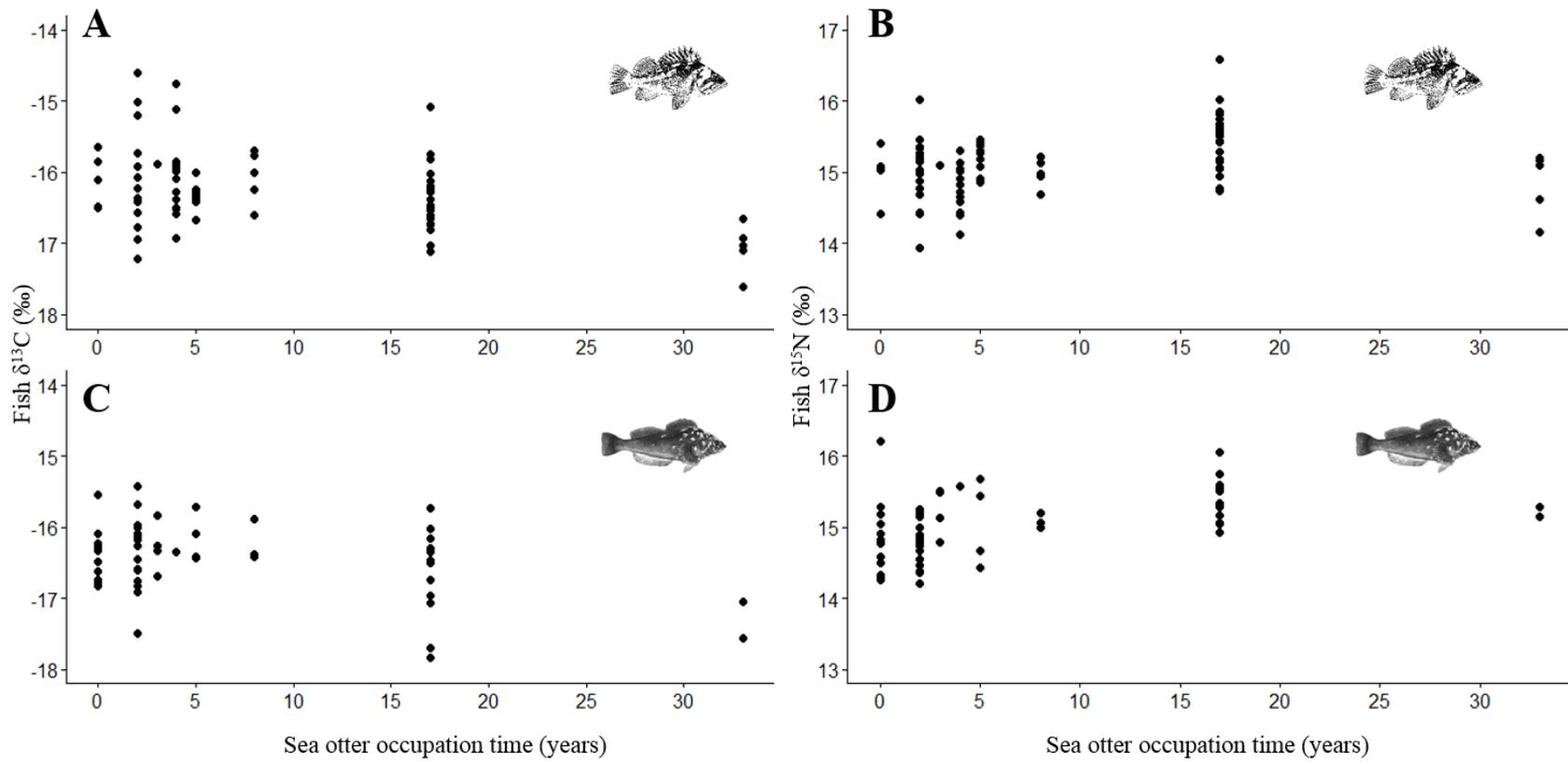


Figure 8. Isotopic signatures of copper rockfish (*Sebastes caurinus*) (A & B) and kelp greenling (*Hexagrammos decagrammos*) (C & D) captured across 20 sites on the central coast of British Columbia varying in sea otter occupation time. Each dot represents the  $\delta^{13}\text{C}$  (‰) (A & C) and  $\delta^{15}\text{N}$  (‰) of an individual fish muscle sample. Fish were obtained through hook-and-line fishing. Samples were analyzed at UC Davis Stable Isotope Facility in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer.

Table 5. Strength of evidence for generalized linear mixed effects models (GLMMs) of copper rockfish (*S. caurinus*) and kelp greenling (*H. decagrammos*)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from 20 sites on the central coast of British Columbia, Canada. Models with varying numbers of parameters (K) were compared using differences in small-sample bias-corrected Akaike Information Criterion ( $\Delta\text{AIC}_c$ ), and normalized Akaike weights ( $W_i$ ). We report the top 5 alternative models. The random effect of fish length within site was nested within the fixed effects.

<b>Response &amp; Model</b>	<b>LogLL</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta\text{AIC}_c</math></b>	<b><math>W_i</math></b>	<b><math>R^2_{\text{Marg}}</math></b>
<b>A Copper rockfish <math>\delta^{13}\text{C}</math></b>					
Proportion reef covered by canopy kelp + Canopy kelp stipe density	-56.73	126.60	0.00	0.25	0.10
Proportion reef covered by canopy kelp + Canopy kelp stipe density + Exposure	-55.66	126.87	0.27	0.22	0.13
Proportion reef covered by canopy kelp	-59.04	128.89	2.28	0.08	0.05
Proportion reef covered by canopy kelp + Canopy kelp stipe density + Subcanopy kelp stipe density + Exposure	-55.47	128.97	2.36	0.08	0.13
Proportion reef covered by canopy kelp + Exposure	-57.92	129.00	2.39	0.07	0.08
<b>B Kelp greenling <math>\delta^{13}\text{C}</math></b>					
Intercept	-39.76	88.30	0.00	0.22	N/A
Canopy kelp stipe density	-38.99	89.17	0.87	0.14	0.03
Proportion reef covered by canopy kelp	-39.33	89.85	1.55	0.10	0.02
Canopy kelp stipe density + Subcanopy kelp stipe density	-38.14	89.99	1.68	0.09	0.06
Proportion reef covered by canopy kelp + Canopy kelp stipe density	-38.24	90.19	1.89	0.09	0.06
<b>C Copper rockfish <math>\delta^{15}\text{N}</math></b>					
Exposure	-41.78	94.38	0.00	0.30	0.21
Proportion reef covered by canopy kelp + Exposure	-40.84	94.84	0.46	0.24	0.23
Proportion reef covered by canopy kelp + Exposure + Subcanopy kelp stipe density	-40.40	96.36	1.98	0.11	0.24
Exposure + Subcanopy kelp stipe density	-41.73	96.61	2.23	0.10	0.21
Exposure + Canopy kelp stipe density	-41.78	96.71	2.33	0.09	0.21
<b>D Kelp greenling <math>\delta^{15}\text{N}</math></b>					
Proportion reef covered by canopy kelp + Exposure	-27.80	69.32	0.00	0.20	0.22
Exposure + Subcanopy kelp stipe density	-27.99	69.69	0.37	0.17	0.21
Subcanopy kelp stipe density	-29.35	69.91	0.59	0.15	0.17
Proportion reef covered by canopy kelp + Exposure + Subcanopy kelp stipe density	-26.91	70.16	0.84	0.13	0.24
Canopy kelp stipe density + Subcanopy kelp stipe density	-28.95	71.62	2.30	0.06	0.18

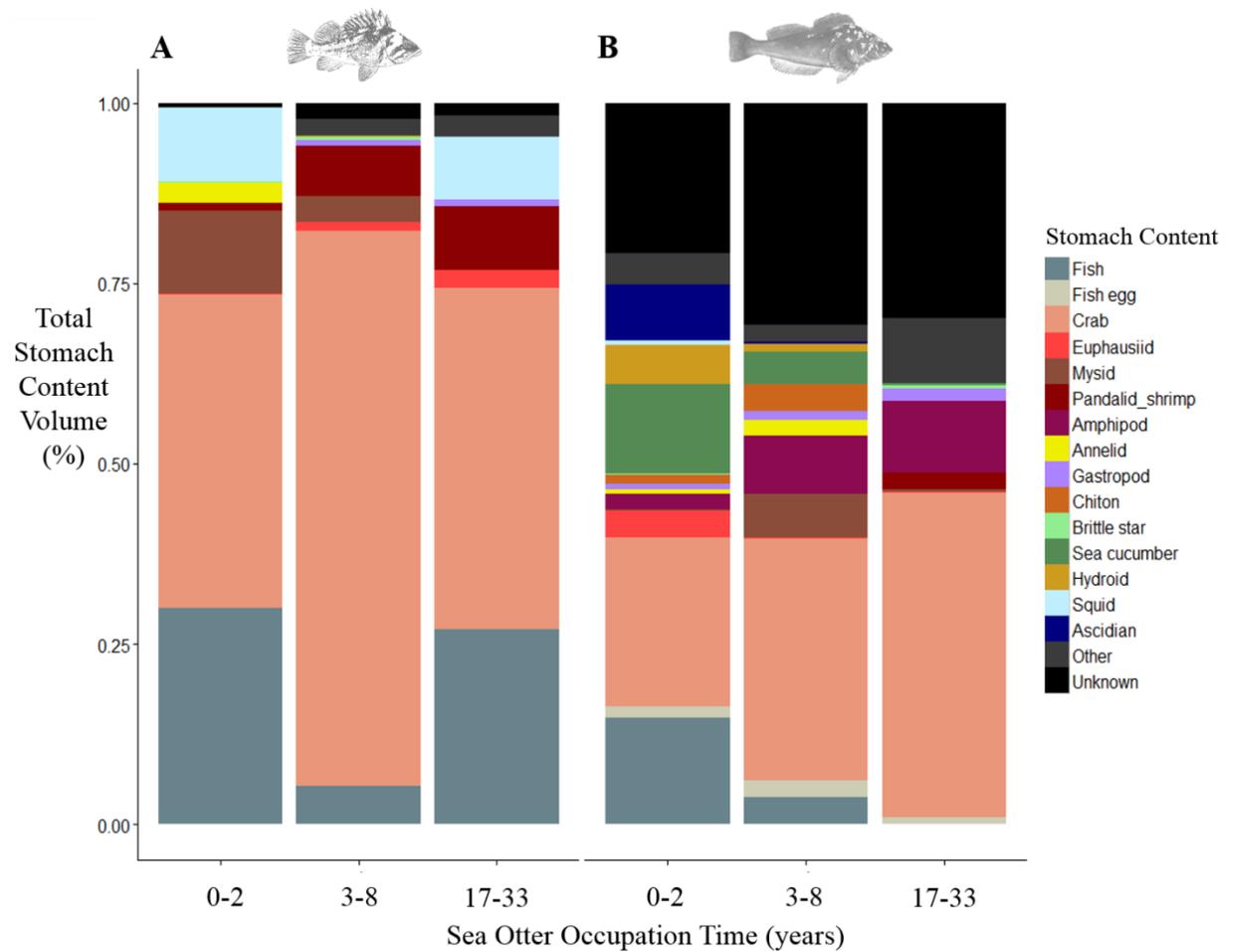


Figure 9. Fish stomach contents by percent of total stomach volume for A) copper rockfish (*Sebastes caurinus*) (n=80) and B) kelp greenling (*Hexagrammos decagrammos*) (n=56) across three categories of sea otter occupation time on the central coast of British Columbia, Canada. Empty stomachs were excluded from the analysis. Contents were identified to lowest possible taxon. Unknown category represented stomach contents that were too degraded to identify.

## Discussion

We found some evidence for indirect effects of sea otter recovery on temperate reef fish, but not for all species. Overall, as predicted, we found higher catch rates of copper rockfish biomass at sites where sea otter occupation was greatest (Figure 4A, Table 1, RVI=0.83). Furthermore, the effect of sea otter occupation time on copper rockfish catch rates was 1.8 times greater than the effect of reef rugosity and 4.4 times greater than the effect of wave exposure, which was negligible and highly imprecise. Mechanistically, strong evidence suggests that copper rockfish catch rates increased with an increase in the proportion of rocky reef covered in canopy kelp (Figure 4B, RVI=0.97) and a corresponding decrease in the stipe density of canopy kelps (Figure 4B, RVI=0.94). We hypothesize that the negative relationship between copper rockfish and canopy kelp stipe density was a result of a successional shift from the annual kelp *Nereocystis* to the perennial kelp *Macrocystis* as sea otters reduced destructive sea urchin grazing over time. *Macrocystis* grows at lower stipe densities, but provides more 3-dimensional habitat for fish with blades throughout the water column (compared to *Nereocystis*, which only has blades at the surface when fully grown).

Contrary to expectations, we found no evidence for an effect of sea otter occupation time, canopy kelp density, or subcanopy kelp density on the catch rates of kelp greenling (Figure 4B, Table 1). We also found no evidence that sea otter occupation time or any other factor tested affected copper rockfish or greenling density observed on underwater visual surveys (Figure 7, Table 1). Although we tended to catch and observe larger copper rockfish at sites with longer sea otter occupation times (Figure 6A), this was not the case for kelp greenling (Figure 6B). Although model selection showed some effects of kelp metrics and exposure on variation in the isotopic signatures of copper rockfish and kelp greenling across sites, the model fits were poor and the magnitude of these effects were negligible. Contrary to our hypothesis, we found no appreciable enrichment of the  $\delta^{13}\text{C}$  signature across the gradient of sea otter occupation time associated with an increase in the amount of kelp-derived carbon within fish (Figure 8).

## Indirect effects of sea otters on rocky reef fish

Sea otters have been shown to have indirect effects on bald eagles (Palmisano & Estes 1977, Anthony et al. 2008), gulls (Irons et al. 1986), sea stars (Vicknair & Estes 2012), mussels (Singh et al. 2013), and some temperate rocky reef fish (Simenstad et al. 1978, Reisewitz et al. 2006, Markel 2011). There is consistency across studies with regard to the positive association between canopy kelp and juvenile rockfish (Carr 1989, 1991, 1994, Holbrook et al. 1990, Love et al. 1991, Hayden-Spear & Gunderson 2007, Markel 2011), but the paradigm that more canopy kelp yields a higher density of adult fish is both context- and species-dependent (Bodkin 1986, 1988, Richards 1987, DeMartini & Roberts 1990, Holbrook et al. 1990, Dean et al. 2000, Siddon et al. 2008, Efird & Konar 2014, Edwards et al. 2015). In Prince William Sound (AK), Dean et al. (2000) found that fish-habitat associations were greatly dependent on fish demographic and life-history traits such as age-to-maturity, lifespan, and preferred prey. Greenlings (family Hexagrammidae) were numerically dominant in *Nereocystis* beds, while rockfish (mostly <15 cm copper rockfish) showed only weak associations with canopy kelp. In BC, some have found evidence of increased reef-associated fish associated with canopy kelp (Leaman 1980, Trebilco et al, in press), but Richards (1987) found that copper rockfish densities were related to high-relief sites, and not to measured kelp metrics. We found that copper rockfish catch rates did increase with sea otter occupation time and the relative kelp bed size; however, this relationship was not apparent from the underwater visual surveys. Consistent with our study, underwater visual transects in California also found no considerable variation in adult kelp greenling densities across sites varying in habitat characteristics (Holbrook et al. 1990).

Contrary to our expectations, stable isotope analysis of adult fish diet showed no consistent patterns in the fish  $\delta^{13}\text{C}$  across sites (Figure 8). Consistent with Markel (2011), we found no difference in the amount of kelp-derived carbon in fish diet related to the sea otter-induced trophic cascade. This contrasts with Szpak et al (2013), who found an increase in the amount of kelp-derived carbon in ancient fish bones found at historical First Nations midden sites associated with the presence of sea otters on Haida Gwaii. However, rockfish bones could not be differentiated to species, so all *Sebastes* spp bones were lumped together for analysis (Szpak et al. 2013). Two-source mixing models, which

attempt to parse out the influence of kelp-derived versus offshore planktonic carbon, have traditionally used a pelagic phytoplankton  $\delta^{13}\text{C}$  signature closer to  $-23\text{‰}$  compared to a kelp signature of approximately  $-14\text{‰}$ . The pelagic phytoplankton value corresponds to an offshore phytoplankton signature measured off Vancouver Island (Perry et al 1999), and is comparable with signatures of cultured phytoplankton from the northeast Pacific (Duggins et al. 1989). But kelp and phytoplankton isotopic signatures (Appendix C) can be highly variable (Ramshaw 2012), and it is difficult to determine a true pelagic signature for use in two-source mixing models (Miller & Page 2012, Miller et al. 2013). In addition, in geographic areas where considerable amounts of kelp detritus are perpetually circulated throughout the coastal ecosystem (Krumhansl & Scheibling 2012), kelp-derived carbon may not be a limiting factor (Salomon et al. 2008, Singh 2010). At sites with low sea otter occupation time, we still found appreciable amounts of *Nereocystis*, which is tolerant to grazing disturbance (Appendix A).

We also found no enrichment in reef fish  $\delta^{15}\text{N}$  isotopic signatures with increasing sea otter occupation time. On the west coast of Vancouver Island, where sea otters are also recovering, Markel (2011) reported an increase in the trophic position of adult copper rockfish in areas with sea otters, which he hypothesized was caused by the increased availability of small fish as prey in these areas with larger kelp forests. However, in addition to consistency in fish  $\delta^{15}\text{N}$  across sites, we also did not find a consistent increase in the presence of fish in adult copper rockfish stomachs (Figure 9, Appendix C). In fact, for kelp greenling, we found a decrease in the amount of fish in their diet as sea otter occupation time increased (Figure 9, Appendix C).

## **Comparing fish assessment methods**

The detection of ecological associations between fish and adjacent habitats is dependent on the scale of observation (Dean et al. 2000, Kendall et al. 2011). In theory, fish density estimates derived from catch-per-unit-effort and underwater visual census should yield comparable measures for a site, but results from these two methods can be highly variable over space and time (Karnauskas & Babcock 2012). Due to inherent biases, some have suggested that both methods be used simultaneously (Bennett et al. 2009). Nevertheless, certain species or ages of fish may be more accurately assessed by

one method over another, especially if the fish are strongly diver positive or averse (Bennett et al. 2009, Bozec et al. 2011, Karnauskas & Babcock 2012) or have differing detection probabilities (MacNeil et al. 2008, Green et al. 2013). We found no discernable trends when comparing our fishable biomass estimates and underwater biomass estimates from dive surveys (Appendix B). In the Aleutians, Reisewitz et al. (2006) chose to omit diver estimates of rock greenling abundance in relation to kelp forest habitat due to their 'extreme diver averse' behavioural tendencies. Poor water visibility, which occur regularly in kelp forests, could also affect fish estimates underwater.

One alternative hypothesis to explain the variation we observed in fishable copper rockfish biomass is the presence of conservation areas that restrict certain fishing activities at some of the sites that we sampled. Five of the six high otter occupancy sites were situated within Rockfish Conservation Areas (established in 2005). However, these conservation areas are not no-take marine reserves and fishing activity by coastal First Nations is still permitted within these zones. Studies that have investigated the effectiveness of these conservation areas to increase the number of rockfish only a few years after their establishment have yielded mixed results (Marliave & Challenger 2009, Yamanaka & Logan 2010, Cloutier 2011), which is unsurprising given that many of these rockfish species live for decades (Love et al. 2002). The design effectiveness of existing marine protected areas on the central coast of BC has been called into question (Ban et al. 2014), although encouraging marine planning processes are in progress (e.g. MaPP, <http://mappocean.org/>).

## **Importance of natural history**

The natural history of species—what they are, the prey they eat, where they live, and the biotic and abiotic interactions linking them to ecosystems—is critical to our understanding of ecosystems, and should be incorporated into modeling exercises (Tewksbury et al. 2014). Holbrook et al. (1990) hypothesized that the presence of canopy kelp may not be as critical to fish species that live multiple decades compared to short-lived species. Species can be subdivided by their life-history traits to predict the impacts of environmental or anthropogenic stressors on certain taxa (Darling et al. 2012). Stomach content analysis revealed that kelp greenling had a more diverse diet than other fish

species collected (Figure 9). The diversity in kelp greenling diet may be a result of their faster life history (estimated lifespan 12-13 years), which leads to bolder foraging strategies in the presence of predators compared to longer-lived mesopredators like copper rockfish (lifespan up to 50 years with 50% age-at-maturity after 6-7 years) (Love et al. 2002, Shanks & Eckert 2005, Frid et al. 2012). The generalist life-history traits of kelp greenling may explain why we found no difference in kelp greenling catch rates or density across different kelp communities because they can readily adapt and switch prey given changing conditions. However, we did find some positive effect of sea otter occupation time on copper rockfish catch rates.

Through a meta-analysis of multi-decadal studies in the marine intertidal, Menge (1997) found little evidence to support the notion in community ecology that indirect effects take longer to appear than direct effects (Bender et al. 1984, Yodzis 1988). However, in some ecosystems (e.g. desert communities), indirect effects may only be revealed long after the consequences of direct interactions are noted (Brown et al. 1986, 2001). Time lags in indirect effects have also been noted in marine ecosystems with fishery-induced trophic cascades (Salomon et al. 2010). It is possible that time lags between direct and indirect effects were not observed in the marine intertidal because interspecific interactions in this ecosystem tend to be apparent on relatively short timescales (Connell 1972, Menge 1997). In contrast, we might expect indirect effects to take longer to accrue with long-lived species such as rockfish.

## **Policy and management implications**

Responsive conservation strategies and ecosystem-based management should consider the expected time lags in ecosystem dynamics based on the demographics of the species in the system. Understanding the mechanisms that affect ecosystem processes, and the time scales on which these mechanisms operate, can contribute to making effective management decisions (Folke et al. 2005, McClanahan et al. 2011, Levin & Möllmann 2015). The ability to predict how dramatic ecosystem changes affect tightly linked social-ecological systems is dependent on identifying potential trade-offs between ecosystems and human well-being (Levin & Lubchenco 2008, Cinner et al. 2009, Ostrom 2009). It will be essential to anticipate when these changes are expected to occur given

the unique species life-history traits of species that communities are interested in, so that management plans are designed with realistic expectations on appropriate time scales. Sound resource management is vital to coastal communities whose livelihoods and culture are founded on the diversity of goods and services that these ecosystems provide (Carpenter et al. 2009, Lester et al. 2010, Poe et al. 2014, Rocha et al. 2015).

As sea otters recover over parts of their range, it will be critical to understand the implications on the entire kelp forest food web in order to predict trade-offs for both nearshore marine ecosystems and the social systems that depend on them (Sloan & Dick 2012, Chadès et al. 2012, Salomon et al. 2015). Coastal First Nations have a long history and cultural connection to nearshore reef marine resources associated with sea otters and kelp forests (Erlandson et al. 2007, 2008, Brown & Brown 2009, Erlandson & Rick 2010, Lyman 2011, McKechnie & Wigen 2011, Moss & Losey 2011, Sloan & Dick 2012, Szpak et al. 2013, 2012, Salomon et al. 2015). Increasing invertebrate populations in the absence of otters subsequently led to the establishment of valuable invertebrate fisheries (Watson & Smith 1996, Watson 2000). Conversely, sea otter recovery has created conflicts with fishers who compete with the sea otters for invertebrates such as sea urchins, abalone, sea cucumbers, clams and crabs (Breen et al. 1982, Watson & Smith 1996, Watson 2000, Sloan 2004, Reidy 2011, Chadès et al. 2012, Larson et al. 2013). The sea otter-induced reduction in shellfish can threaten livelihoods and food security in communities that rely on shellfish abundance (Stewart 2005, Levine 2014), but other changes to the kelp forest ecosystems can produce positive trade-offs.

Sea otter recovery can yield benefits for coastal communities by increasing the extent of kelp forests that can provide additional provisioning, supporting, regulating and cultural services to these communities (Stewart 2005, Wilmers et al. 2012). One proposed positive trade-off of sea-otter induced kelp forest recovery is an increase in kelp-associated fish. However, the species that benefit from additional kelp habitat are not necessarily the species that coastal communities are interested in for commercial, recreational, and cultural purposes (Levine 2014). While certain taxa and life-history stages may increase as kelp forests grow in extent (e.g. juvenile rockfish, surfperches, tubesnouts), the indirect effects of sea otter occupation on adult fish is species-dependent (Holbrook et al. 1990, Dean et al. 2000). In the case of rockfish, an increase in juvenile

fish abundance (e.g. Carr 1989, 1991) will not necessarily translate into more abundant adult fish, as recruitment strength is often poorly correlated to adult fish biomass (Houde 2009). We did find evidence for an indirect positive effects of sea otter occupation time on adult copper rockfish catch rates, but these effects were not detected using underwater visual transects. Surprisingly, we found no evidence of the indirect effects of sea otter occupation time on kelp greenling associated with nearshore rocky reef habitat.

Coastal communities neighbouring areas of sea otter recovery—and the associated cascade of direct and indirect effects to adjacent nearshore marine ecosystems—must navigate the ensuing complex socio-ecological trade-offs (Sloan & Dick 2012, Salomon et al. 2015). By investigating how these effects manifest over space and time, communities can carefully evaluate the trade-offs elicited by sea otter recovery. These resource assessments can then be incorporated into ecosystem-based marine use planning initiatives already taking place in the region (Ban et al. 2014). The unique, ecosystem-altering nature of sea otter recovery necessitates management solutions that require cooperative interdisciplinary creativity. Ultimately, sea otters could act as a catalyst towards improved ecosystem-based management, but evaluations of the trade-offs of sea otter recovery should assess the potential indirect effects on species based on their life history traits at appropriate temporal scales.

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## Appendix A.

### Site characteristics

Table A1. Sites sampled for fish and kelp metrics along a gradient of sea otter occupation time on the central coast of British Columbia, Canada (alphabetical order).

Site	Site Code	Latitude	Longitude	Sea otter occupation time (years)	Relative Exposure Index
Athabaskan	AT	52.02431	-128.301	8	60.18
Fingal	FL	52.08066	-128.448	17	408.96
Goose	GE	52.00072	-128.413	17	25.49
Gosling	GG	51.8998	-128.433	33	152.02
Houghton	HG	52.11253	-128.435	17	253.62
Kelpie	KE	51.73361	-127.996	0	19.09
Manley	MA	51.7978	-128.202	5	12.47
McMullin S	MC	52.04512	-128.4	17	112.75
McMullin N	MM	52.0711	-128.407	17	243.28
Mercury	MR	51.74406	-128.07	3	12.25
McNaughton	MT	51.9043	-128.235	4	1.58
Odlum	OM	51.69311	-128.117	2	3.94
Robert	RT	51.98397	-128.248	5	19.39
Simonds N	SM	51.96072	-128.262	4	20.7
Spider	SP	51.8412	-128.265	3	46.97
Simonds S	SS	51.92828	-128.291	4	84.25
Starfish	ST	51.68042	-128.126	2	199.69
Thrasher	TH	51.80589	-128.259	0	87.49
Triquet	TR	51.41061	-127.92	2	55.88
West Beach	WB	51.64869	-128.156	0	20.4

Table A2. Available rocky habitat and kelp forest within a standardized seascape (300 m diameter circle centred on each dive site). Sites are ordered from low to high proportion of rocky reef covered with canopy kelp (*Nereocystis* and *Macrocystis*). All area shallower than 10 m depth was assumed to be available rocky habitat.

Site	Site code	Sea otter occupation time (years)	Available rocky habitat (m <sup>2</sup> )	Proportion rocky habitat	Kelp forest area (m <sup>2</sup> )	Proportion rocky reef covered by kelp
Athabaskan	AT	8	43,429	0.61	12,602	0.29
Fingal	FL	17	47,006	0.67	19,886	0.42
Goose	GE	17	26,847	0.38	15,188	0.57
Gosling	GG	33	41,326	0.59	23,207	0.56
Houghton	HG	17	21,248	0.3	8,536	0.4
Kelpie	KE	0	30,583	0.43	9,621	0.31
Manley	MA	5	27,684	0.39	10,554	0.38
McMullin N	MM	17	43,642	0.62	18,626	0.43
McMullin S	MC	17	47,565	0.67	11,857	0.25
McNaughton	MT	4	25,870	0.37	1,687	0.07
Mercury	MR	3	38,596	0.55	4,912	0.13
Odlum	OM	2	28,371	0.4	14,540	0.51
Robert	RT	5	23,845	0.34	15,958	0.67
Simonds N	SM	4	40,913	0.58	20,259	0.5
Simonds S	SS	4	20,841	0.3	9,191	0.44
Spider	SP	3	63,700	0.9	31,583	0.5
Starfish	ST	2	51,406	0.73	13,324	0.26
Thrasher	TH	0	34,306	0.49	6,338	0.18
Triquet	TR	2	30,034	0.43	19,295	0.64
West Beach	WB	0	43,167	0.61	14,591	0.34

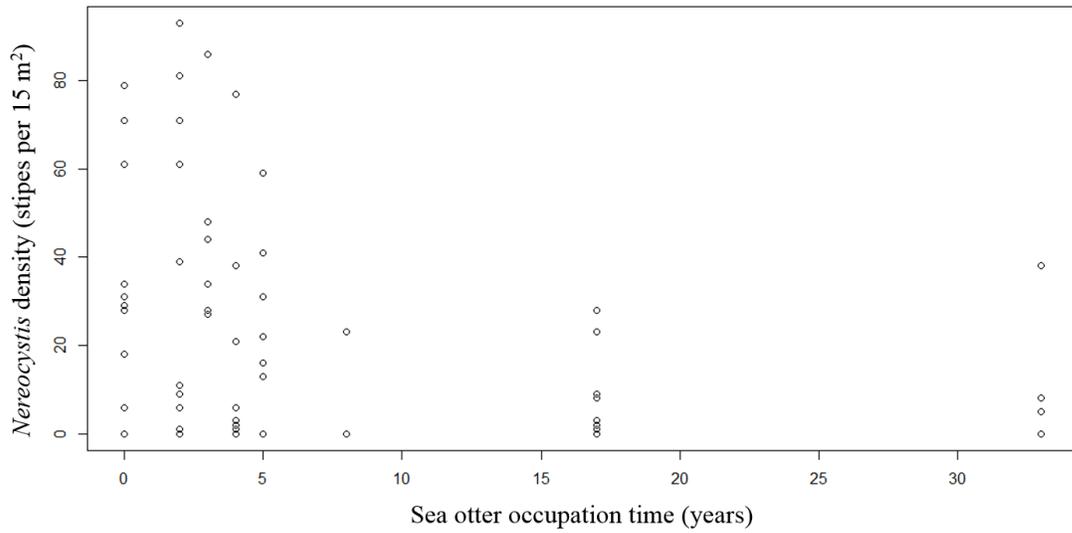


Figure A1. *Nereocystis luetkeana* stipe density across 20 sites on the central coast of British Columbia, Canada varying in sea otter occupation time. Each dot represents a 15 x 1 m transect (n=6 per site).

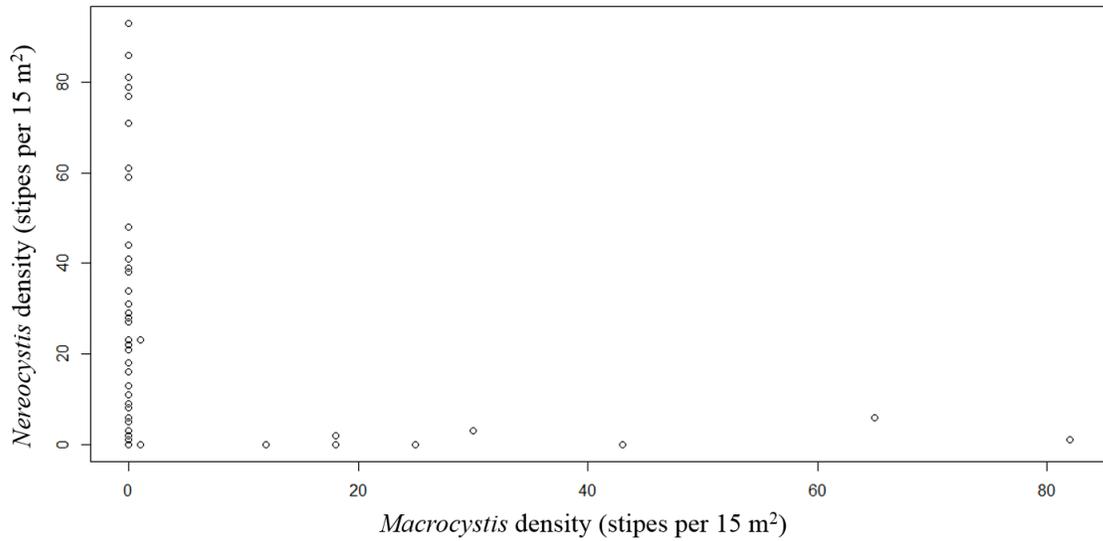


Figure A2. *Nereocystis luetkeana* stipe density compared to *Macrocystis pyrifera* stipe density at 20 sites on the central coast of British Columbia, Canada. Each dot represents a 15 x 1 m transect (n=6 per site).

## Appendix B.

### Additional fish CPUE and density figures and tables

Table B1. Variance inflation factors (VIF) calculated for model set 2, which tested the evidence of an effect of biotic and abiotic factors on copper rockfish and kelp greenling catch rates and densities. VIFs are included for models with and without the factor of sea otter occupation time to demonstrate how VIFs increased with sea otter occupation time included due to multicollinearity between factors. We therefore chose to separate the factor of sea otter occupation time and model it separately (model set 1).

Factor	VIF model set 2	VIF if sea otter occupation time included in model set
Proportion of reef covered by canopy kelp	1.25	1.45
Canopy kelp stipe density	1.36	1.95
Subcanopy kelp stipe density	1.76	1.82
Rugosity	1.15	1.31
Wave exposure	1.24	1.81
Sea otter occupation time	N/A	2.34

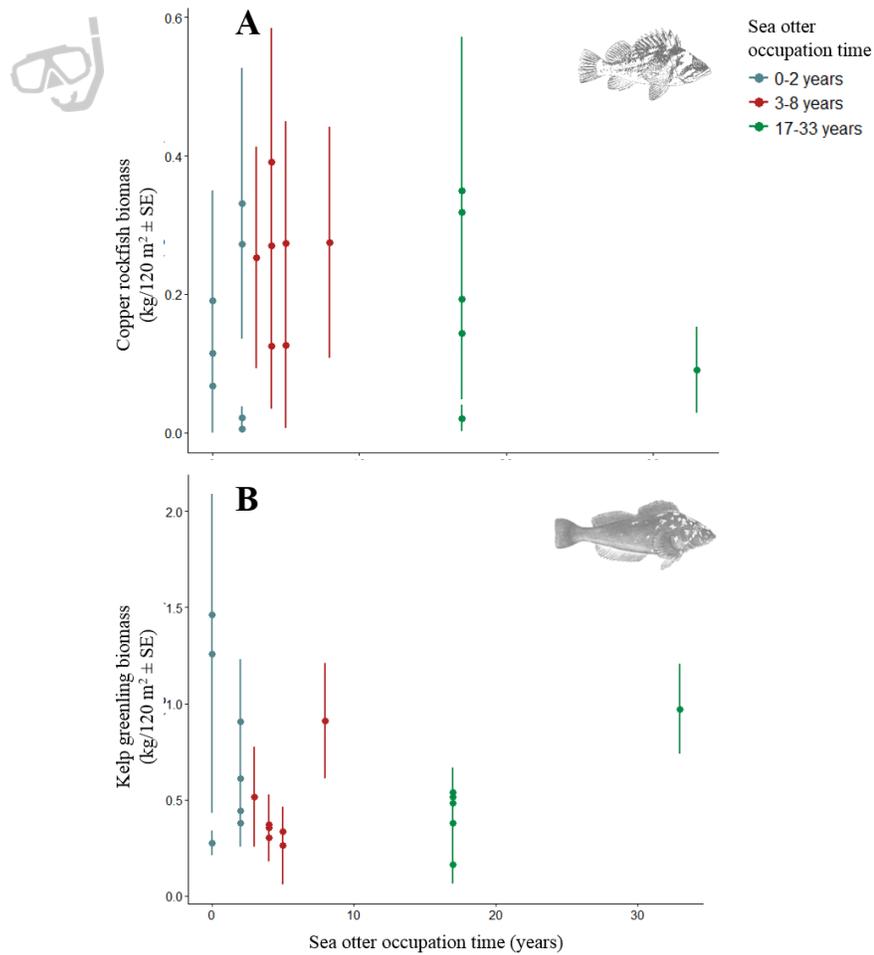


Figure B1. Mean fish biomass per 30 x 4 m underwater transect  $\pm$  standard error (SE) (n=6 transects per site) of A) copper rockfish (*Sebastes caurinus*) and B) kelp greenling (*Hexagrammos decagrammos*) across 20 sites varying in sea otter occupation time on the central coast of British Columbia, Canada. Copper rockfish <10 cm in underwater surveys were excluded from analysis because juveniles at this size cannot be distinguished from quillback rockfish (*S. maliger*).

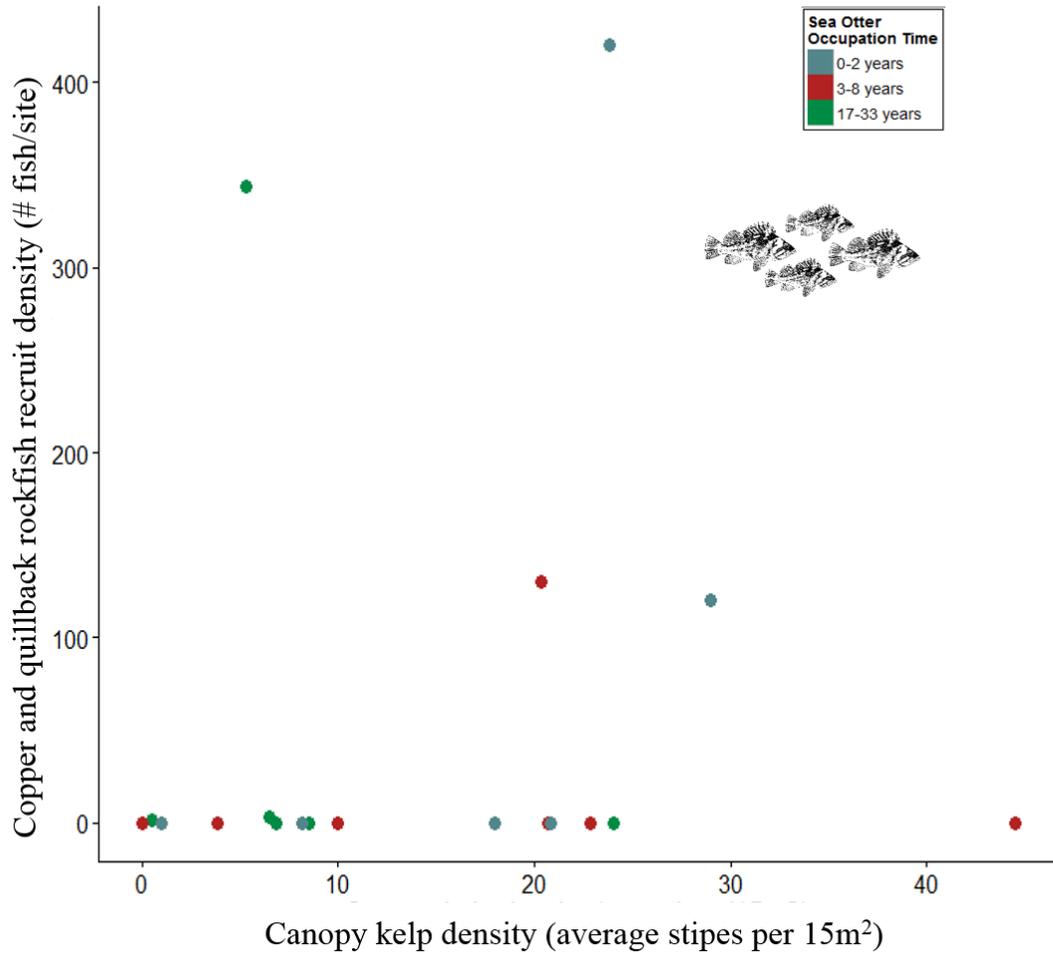


Figure B2. Copper rockfish (*Sebastes caurinus*) and quillback rockfish (*S. maliger*) recruit and juvenile (<10 cm total length) density at varying canopy kelp stipe densities at 20 sites on the central coast of British Columbia, Canada. Fish densities were measured using 30 x 4 m underwater SCUBA transects (n=3 per site at 3-5 m depth; n=3 per site at 10-12 m depth).

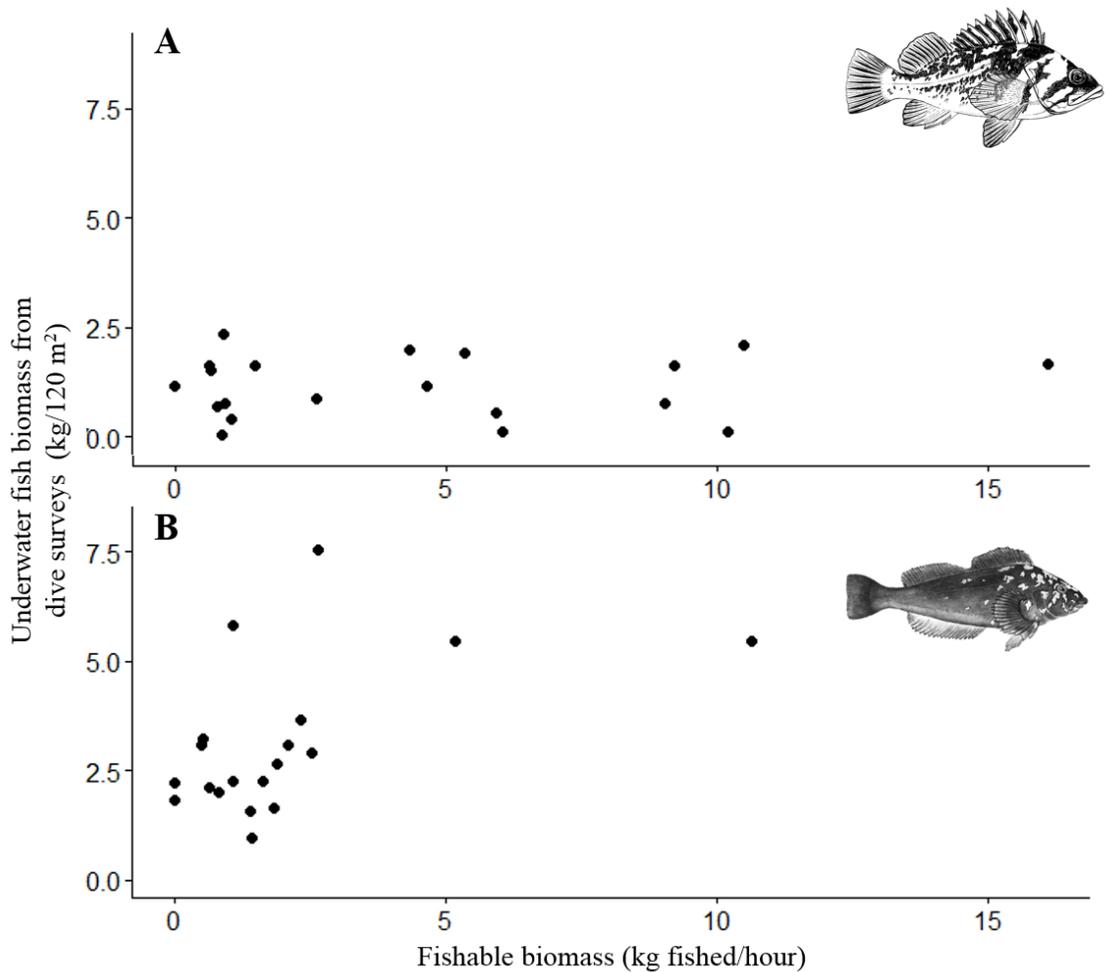


Figure B3. Comparison of (A) copper rockfish (*S. caurinus*) and (B) kelp greenling (*H. decagrammos*) biomass estimates from hook-and-line fishing and underwater visual transects at 20 sites on the central coast of British Columbia, Canada. Individuals caught by hook-and-line were weighed with an electronic scale. The lengths of individual fish underwater were estimated by divers, and biomass was calculated using known length-weight regression curves.

## Appendix C.

### Additional stable isotope figures and tables

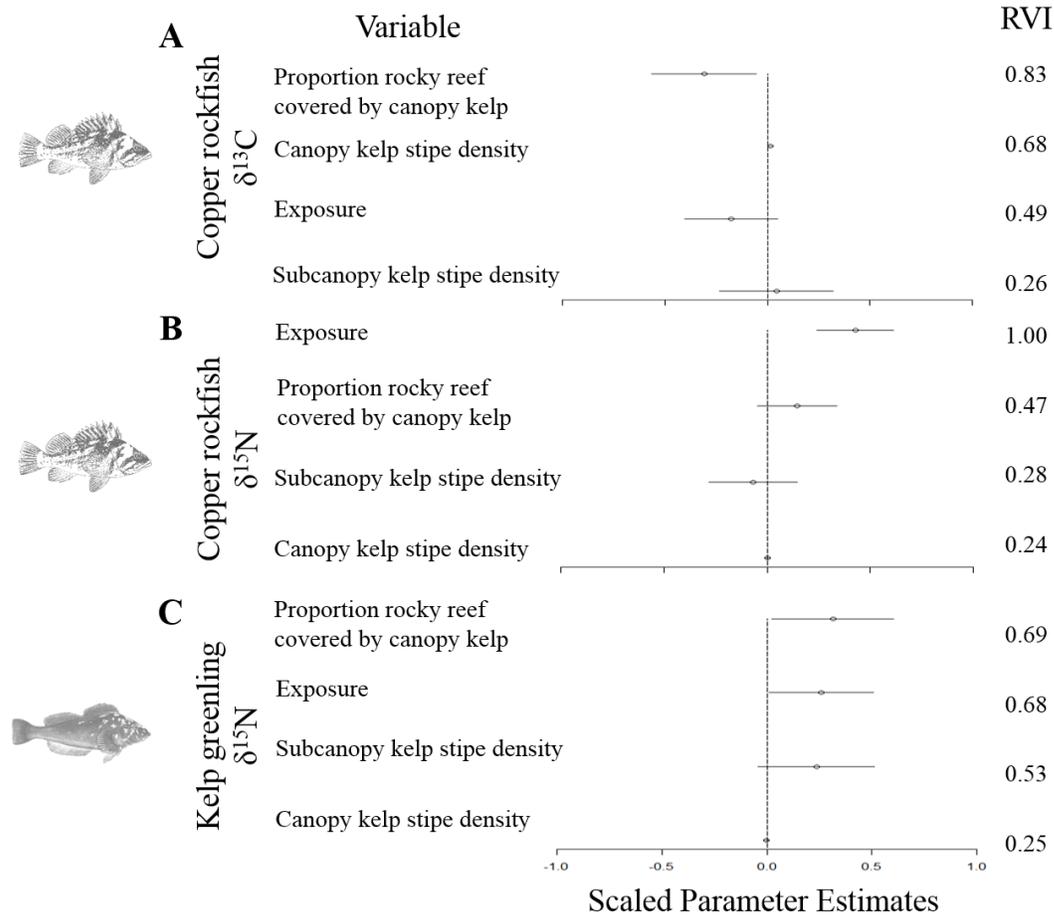


Figure C1. Scaled parameter estimates (circles) with 95% confidence intervals (lines) for variables in averaged mixed effects models of A) copper rockfish  $\delta^{13}\text{C}$  B) copper rockfish  $\delta^{15}\text{N}$ , and C) kelp greenling  $\delta^{15}\text{N}$ . Note there is no RVI plot for kelp greenling  $\delta^{13}\text{C}$  because the intercept-only null model was the top model. Predictor variables and their associated parameters are ranked in decreasing order of relative importance on a scale of 0 to 1. Relative variable importance values (RVI), were calculated by summing the Akaike weights ( $W_i$ ) over the subset of models for in which the variable was found.

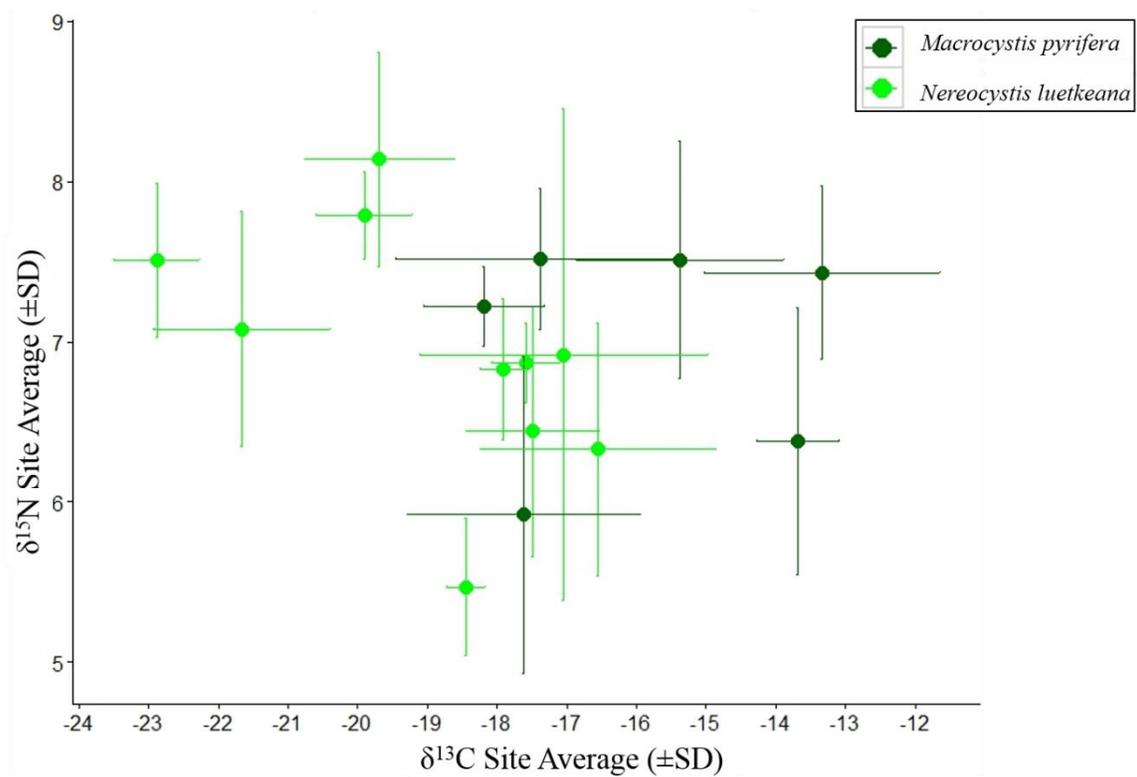


Figure C2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of *Macrocystis pyrifera* and *Nereocystis luetkeana* collected on the central coast of British Columbia, Canada. Each dot represents one site where kelp were collected (n=5 per site where that species occurred).

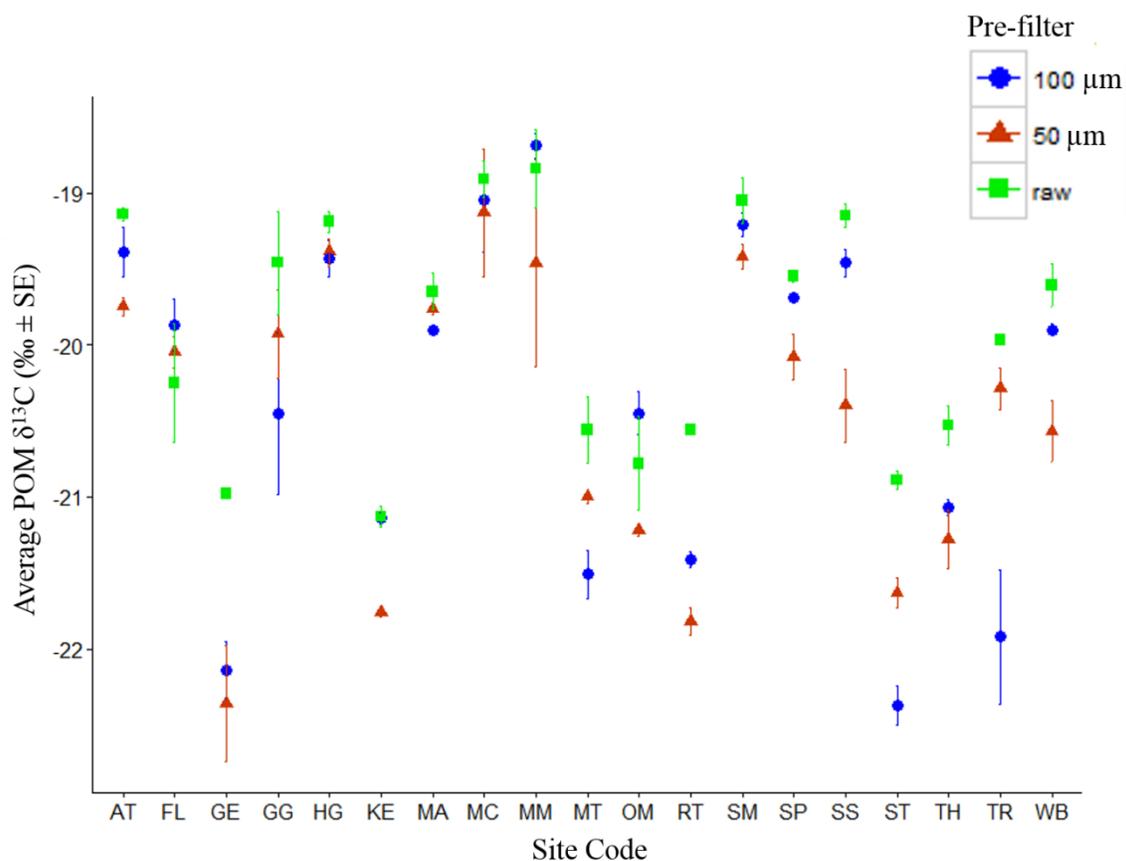


Figure C3.  $\delta^{13}\text{C}$  of particulate organic matter (POM) collected on the central coast of British Columbia, Canada. Each dot represents the mean of samples using different pre-filter sizes ( $n=3$  per filter). Water for POM analysis was collected at the surface adjacent to the kelp bed at each site.

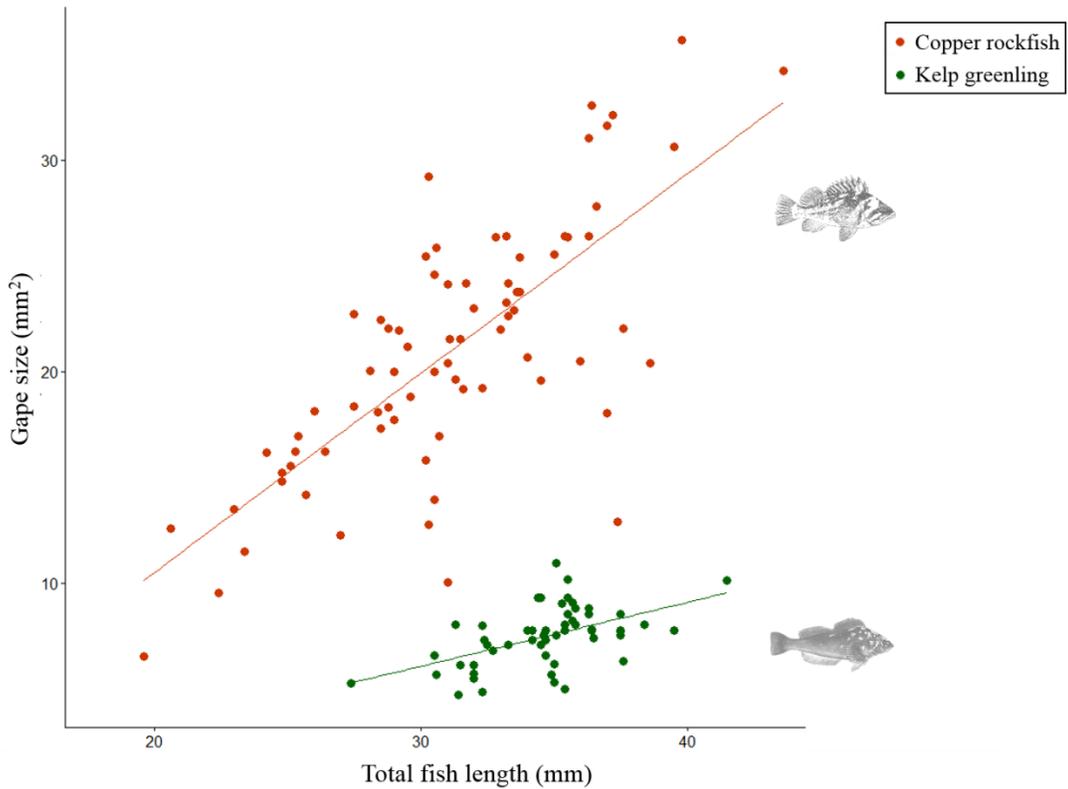


Figure C4. Relationship between gape size and total fish length of copper rockfish (n=80) and kelp greenling (n=56) caught on the central coast of British Columbia, Canada. Each point represents one fish captured by hook-and-line jigging. Gape size was measured to the nearest 0.1 mm using calipers to estimate maximum gape width and gape height. Total fish length was measured from nose to the end of the caudal fin to the nearest 0.1 cm. Solid lines represent simple linear regression.

Table C1. Percentage of copper rockfish and kelp greenling stomachs that contained fish prey. Fish were captured by hook-and-line jigging at sites varying in sea otter occupation time on the central coast of British Columbia, Canada.

Species	Sea otter occupation category	# of stomachs containing fish as prey	N	%
Copper rockfish	0-2 years	5	20	0.25
	3-8 years	4	9	0.14
	17-33 years	11	27	0.41
Kelp greenling	0-2 years	10	27	0.37
	3-8 years	1	13	0.08
	17-33 years	0	14	0.00