

Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator

L. C. LEE,^{1,2,†} J. C. WATSON,³ R. TREBILCO,^{4,5} AND A. K. SALOMON^{1,2}

¹School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada

²Hakai Institute, Heriot Bay, British Columbia V0P 1H0 Canada

³Biology Department, Vancouver Island University, Nanaimo, British Columbia V9R 5S5 Canada

⁴Biology Department, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada

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Abstract. Managing for simultaneous recovery of interacting species, particularly top predators and their prey, is a longstanding challenge in applied ecology and conservation. The effects of sea otters (*Enhydra lutris kenyoni*) on abalone (*Haliotis* spp.) is a salient example along North America's west coast where sea otters are recovering from 18th- and 19th-century fur trade while efforts are being made to recover abalone from more recent overfishing. To understand the direct and indirect effects of sea otters on northern abalone (*H. kamtschaticana*) and the relative influence of biotic and abiotic conditions, we surveyed subtidal rocky reef sites varying in otter occupation time in three regions of British Columbia, Canada. Sites occupied by sea otters for over 30 years had 16 times lower densities of exposed abalone than sites where otters have yet to recover ($0.46 \pm 0.08/20 \text{ m}^2$ vs. $7.56 \pm 0.98/20 \text{ m}^2$), but they also had higher densities of cryptic abalone ($2.17 \pm 1.31/20 \text{ m}^2$ vs. $1.31 \pm 0.20/20 \text{ m}^2$). Abalone densities were greater in deeper vs. shallower habitats at sites with sea otters compared to sites without otters. Sea otter effects on exposed abalone density were three times greater in magnitude than those of any other factor, whereas substrate and wave exposure effects on cryptic abalone were six times greater than those of sea otters. While higher substrate complexity may benefit abalone by providing refugia from sea otter predation, laboratory experiments revealed that it may also lead to higher capture efficiency by sunflower stars (*Pycnopodia helianthoides*), a ubiquitous mesopredator, compared to habitat with lower complexity. Sea otter recovery indirectly benefited abalone by decreasing biomass of predatory sunflower stars and competitive grazing sea urchins, while increasing stipe density and depth of kelp that provides food and protective habitat. Importantly, abalone persisted in the face of sea otter recovery, albeit at lower densities of smaller and more cryptic individuals. We provide empirical evidence of how complex ecological interactions influence the effects of recovering predators on their recovering prey. This ecosystem-based understanding can inform conservation trade-offs when balancing multifaceted ecological, cultural, and socio-economic objectives for species at risk.

Key words: biotic and abiotic factors; British Columbia; conservation trade-offs; ecosystem-based management; *Enhydra lutris kenyoni*; *Haliotis kamtschaticana*; kelp forests; northern abalone; *Pycnopodia helianthoides*; risk-averse behavior; sea otter; species interactions.

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⁵ Present address: Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Hobart, Tasmania 7001 Australia.

† **E-mail:** lynn_chi_lee@sfu.ca

INTRODUCTION

Disentangling the direct and indirect effects of predators on their prey, and how these effects are mediated by environmental conditions, is a long-standing challenge in ecology. This understanding is particularly important in the context of predator recovery from overexploitation, and even more so when both predator and prey are of conservation concern (Soulé et al. 2005, Marshall et al. 2016). While re-establishing populations of strongly interacting top predators can trigger a cascade of indirect effects that may restore ecological functions, it can also put already vulnerable prey in further peril (Estes 1996, Soulé et al. 2003, 2005, Estes et al. 2011, Ripple et al. 2014). Fortunately, a clear understanding of the factors that mediate predator–prey interactions and alter their effects on prey density, size, and behavior can inform trade-offs in conservation objectives elicited by food web interactions. Here, we examined the ecological factors that mediate the interaction between endangered northern abalone (*Haliotis kamtschaticana*) and recovering sea otter (*Enhydra lutris kenyoni*) populations along the west coast of British Columbia (BC).

Predators induce changes in both prey abundance and behavior. Consequently, as predator populations recover, prey depletion through time varies as a function of predator per capita attack rates including search time and handling time (Holling 1959), and prey behavioral response to changes in predation risk. Prey can reduce their risk of predation by becoming increasingly cryptic (hiding in refugia), reducing the proportion of time they spend out in the open (exposed) to acquire food (Sih 1980, Lima 1998, Preisser et al. 2005). Risk-averse behavior may also entail selection of lower-risk but lower-quality habitat, or reduced activity levels to minimize predator detection (Sih 1982, Lima 1998). Importantly, the strength of these anti-predator behaviors can differ depending on temporal and spatial variation in predation risk and the availability of refugia (Orrock et al. 2013). Predators themselves can also mediate outcomes of predator–prey interactions when they affect the abundance of alternate predators and/or indirectly increase food availability, habitat quality, and/or refugia for their prey.

Determining the relative influence of direct and indirect effects of predators on their prey, and context-dependent effects, remains a challenge. Multiple top-down (consumer-driven) and bottom-up (resource-driven) factors can drive complex ecological interactions across different spatial and temporal scales, varying in magnitude with biotic and abiotic conditions to affect prey recovery in multiple ways (Polis and Strong 1996, Thrush and Dayton 2010). Furthermore, these forces are affected by historical and contemporary food web alterations (Simenstad et al. 1978, Salomon et al. 2007) and linked social–ecological systems (Liu et al. 2007, Salomon et al. 2015). Consequently, understanding the effects of predators on prey within their ecological and social context is particularly important for informing the conservation trade-offs involved in the recovery of interacting species at risk (Sloan 2004).

Sea otters are keystone predators (Paine 1969, Power et al. 1996) whose re-introduction and range expansion on the Pacific Coast of North America exemplify how successful recovery of one species at risk can have important ecological consequences for another (Sloan 2004). By the early 20th century, ecological extirpation of sea otters released their macroinvertebrate prey from high predation pressure, allowing prey populations including abalone to flourish (Tegner and Dayton 2000, Watson 2000, Sloan and Dick 2012). Northern abalone, a gastropod mollusk that grazes primarily on drift kelp, became a ubiquitous and abundant species on intertidal and shallow subtidal temperate rocky reefs in BC (Watson 2000, Sloan 2004). An intensive commercial dive fishery from the 1960s to 1980s dramatically reduced mature abalone abundance, leading to closure of all BC abalone fisheries in 1990 (Farlinger 1990, Fisheries and Oceans Canada 2012). Abalone surveys continued to show little evidence of recovery 20 years later (COSEWIC 2009), a conservation challenge reflected in abalone species worldwide (Hobday et al. 2001, Micheli et al. 2008). Meanwhile, sea otters re-introduced to BC between 1969 and 1972 (Bigg and MacAskie 1978) were successfully re-establishing and expanding their range. By 2009, sea otters had been legally down-listed from their original status of endangered to special concern under Canada's *Species at Risk Act* (Fisheries and Oceans Canada 2014),

whereas northern abalone had been up-listed from threatened to endangered status by 2011 (Fisheries and Oceans Canada 2012).

In spite of strong interactions, abalone and sea otters are both currently managed using a single-species approach (Fisheries and Oceans Canada 2007, Sea Otter Recovery Team 2007), leading to conservation objectives and recovery targets that are unlikely to be simultaneously achieved (Chadès et al. 2012). Previous empirical studies of abalone have considered a subset of the key biotic and abiotic factors known to affect abalone abundance and distribution, but only in the absence of sea otters (Sloan and Breen 1988, Campbell and Cripps 1998, Tomascik and Holmes 2003, Lessard and Campbell 2007). Only one study in BC has explicitly considered the effects of sea otters on abalone but without accounting for other biotic and abiotic factors (Watson 2000), limiting our empirical understanding of sea otter–abalone interactions under varying environmental conditions (for interactions between sea otters and other abalone species in California, see Fanshawe et al. 2003, Raimondi et al. 2015).

Here, we took advantage of spatial gradients of sea otter recovery along the west coast of Canada to investigate the direct and indirect effects of predator recovery on abalone density, size, biomass, and behavior. We concurrently evaluated the effect of other key biotic and abiotic factors known to affect abalone: substrate, depth, wave exposure, kelp density, sea urchin biomass, and sunflower star (*Pycnopodia helianthoides*) biomass. To explore the possible role of mesopredator release on abalone mortality in areas that remain otter-free, we conducted laboratory experiments to test how substrate complexity (spatial refugia) and the presence of alternative prey (red sea urchins; *Mesocentrotus franciscanus*) may mediate predation outcomes between a ubiquitous mesopredator, the sunflower star, and abalone. Finally, we discuss the conservation trade-offs that occur when predator recovery has both negative direct and positive indirect effects on an endangered prey.

METHODS

Study site context and field survey design

Our study was conducted in three regions across British Columbia, Canada, varying in

broad-scale patterns of sea otter recovery and abundance, latitude, oceanographic context, and human influence (Fig. 1). During the spring and summer of 2010 and 2011, we surveyed subtidal rocky reef sites on Haida Gwaii (HG; $n = 23$), BC's Central Coast (CC; $n = 19$), and West Coast Vancouver Island (WCVI; $n = 18$). Within each region, we selected sites based on the following: (1) presence of suitable abalone habitat (semi-wave-exposed to highly wave-exposed rocky reefs), (2) previously reported abalone occurrence (summarized in Sloan and Breen 1988), and (3) local expert knowledge. Sites were selected across gradients of sea otter occupation time spanning from 0 to 38 yr in a space-for-time substitution (Pickett 1989, Hargrove and Pickering 1992) in the two regions where sea otters are recovering (CC and WCVI). Across all three regions, sites also varied in a suite of biotic and abiotic factors known to influence abalone abundance, size, and distribution: Wave exposure and transects within sites varied in depth, kelp stipe density, substrate complexity, sea urchin biomass, and sunflower star biomass (Sloan and

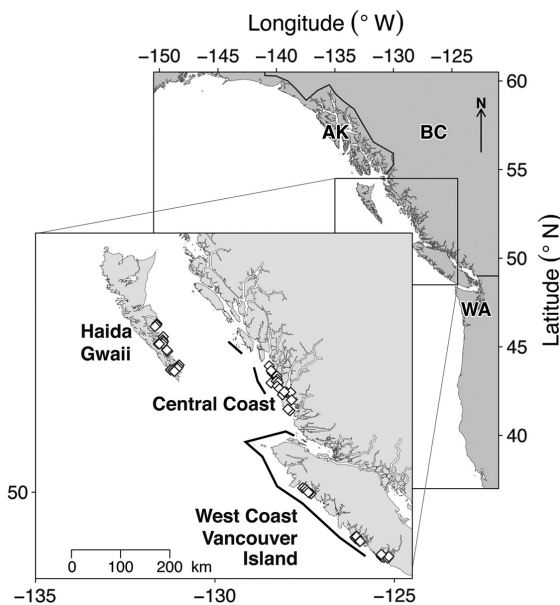


Fig. 1. Subtidal rocky reef study sites (open diamonds) along the coast of British Columbia, Canada, in three regions: Haida Gwaii ($n = 23$), Central Coast ($n = 19$), and West Coast Vancouver Island ($n = 18$), with the range of sea otter occupation at the time of surveys highlighted in bold black lines.

Breen 1988, Campbell and Cripps 1998, Tomascik and Holmes 2003, Lessard and Campbell 2007). Abalone, other macroinvertebrates, and transect-level abiotic factors were quantified using 10 × 2 m belt transects placed parallel to shore, with the ends of each transect at least 5 m apart. Replicate transects were surveyed at each site (n = 6–9) with three transects in each of two or three depth ranges (0–2, 2–5, 5–10 m below chart datum) to capture the subtidal range for the majority of abalone (Sloan and Breen 1988).

Sea otter occupation time.—Sea otter occupation time on the CC was determined from the first year of sighting of an otter raft (≥ 3 individuals together) within a 3 nautical mile radius of the site (Nichol et al. 2009, 2015). For WCVI sites, sea otter survey data and published records were used to determine occupation time (Watson 1993, Nichol et al. 2009, 2015, Watson and Estes 2011). Sea otters, which were re-introduced to northern WCVI, included approximately 5000 individuals along the WCVI at the time of our survey with a regional growth rate of about 7%/yr (Nichol et al. 2015). Along the CC, groups of sea otters were first recorded in 1989 and at the time of our survey included approximately 800 individuals with a regional growth rate of about 13%/yr (Nichol et al. 2015). Both CC and WCVI have sea otter-free areas (no observations of three or more individuals in a group or raft, following Nichol et al. 2009) and HG has remained sea otter-free since otters were extirpated, although 17 confirmed sightings of individual sea otters were recorded between 1970 and 2012 (Sloan and Dick 2012).

Abalone.—All abalone visible to the observer without turning over rocks and removing algae were counted and their length measured to the nearest millimeter. We classified observed abalone sheltering behavior (i.e., behavioral class) as exposed (visible out in the open; Fig. 2A), covered (under kelp, other algae, seagrass, and urchin spine canopies; Fig. 2B), or cryptic (in a crevice or between boulders; Fig. 2C, G). Abalone biomass was calculated from an established length–mass regression (Zhang et al. 2007; Appendix S1: Table S1).

Sea urchin and sunflower star biomass.—Sea urchins were counted and test diameters measured to the nearest centimeter, including red urchin, *Strongylocentrotus purpuratus* (purple urchin), and

S. droebachiensis (green urchin). For transects with >10 urchins/m², we measured a random sample of at least 50 urchins per species per transect and counted the remainder. For a subset of 25 transects on the CC in 2010, some red urchins were classified and counted in three test diameter size classes: small <5 cm, medium 5–9 cm, and large >9 cm. Urchin biomass was estimated from established length–mass regressions for each species (Appendix S1: Table S1). For red urchins counted in size classes, we used the median value of each size class for length-to-biomass conversions (small = 4 cm, medium = 7 cm, large = 10 cm). For urchins that were counted but not measured, missing lengths were randomly sampled from measured urchins of the same species along each transect. We counted and measured the diameter of sunflower stars to the nearest centimeter and estimated biomass from an established length–mass regression (Appendix S1: Table S1).

Kelp stipe density.—We quantified kelp stipe density of individuals >0.15 m in height within five randomly placed 1 × 1 m quadrats along each transect (see Appendix S1: Table S2 for kelp species list). At seven sites on the CC, we sampled five random quadrats in 2011 within the same depth range as each transect with quadrats missing from 2010 surveys.

Substrate complexity.—We classified substrate types using a modified Wentworth scale: sand, shell, pea gravel (2–16 mm diameter (D)), gravel (16–64 mm D), cobble (64–256 mm D), small boulder (256–500 mm D), medium boulder (500–1000 mm D), large boulder (>1000 mm D), smooth bedrock, lumpy bedrock, or creviced bedrock. Substrate type was recorded at two spatial scales: (1) transect-level—primary and secondary substrates determined by percent cover over the entire transect; and (2) abalone-level—substrate the abalone was using. To account for substrate suitability (stable rock) and availability of cryptic habitat, each substrate type was assigned a score for substrate complexity. We determined complexity by summing scores accounting for three criteria: stability (0–3), presence/absence of cryptic habitat (1/0), and relative amount of cryptic habitat (0–3), for a maximum score of 7 (Appendix S1: Table S3). To account for differences in the contribution of secondary substrate to overall complexity, transect-level complexity values were determined by weighting the

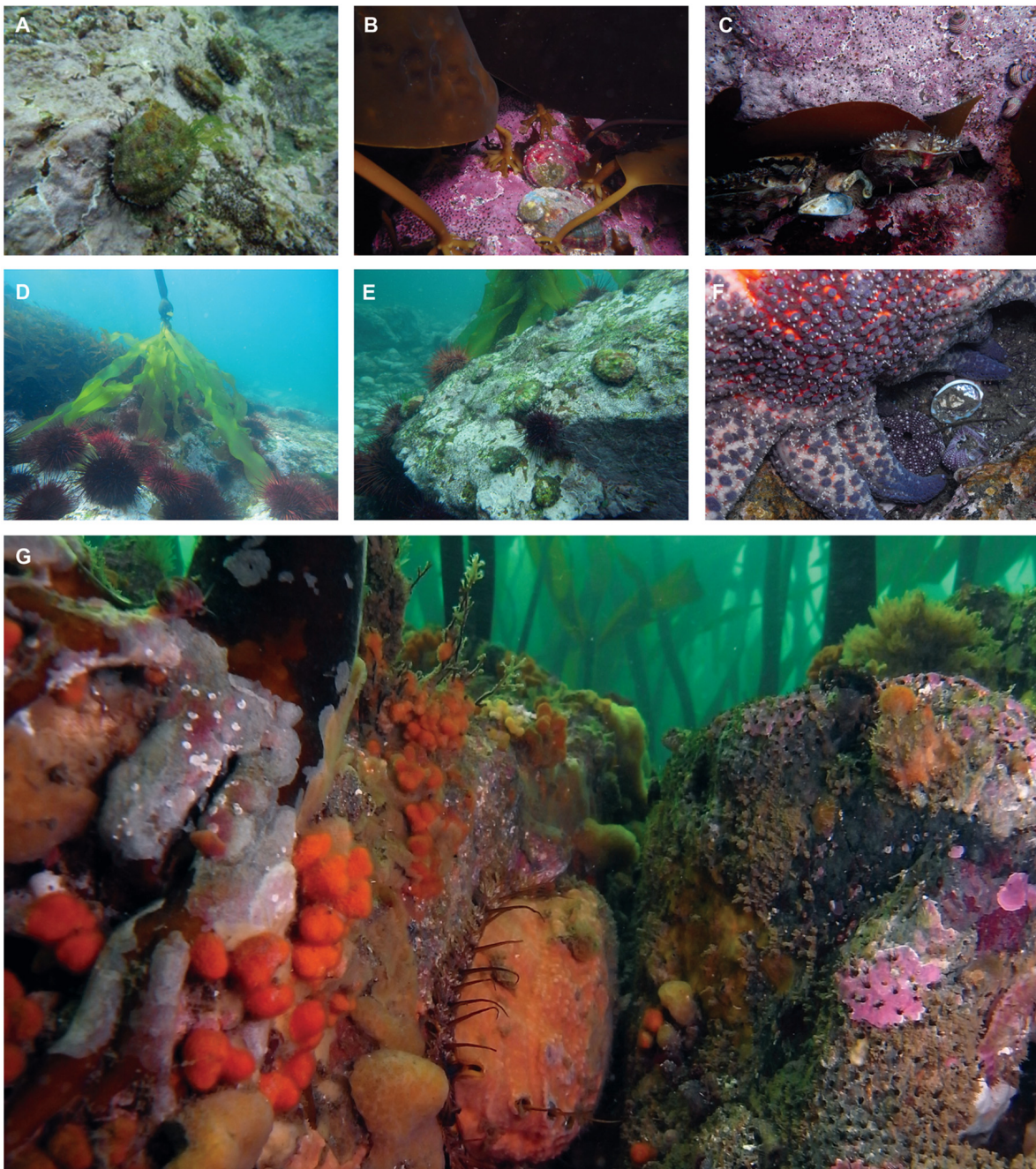


Fig. 2. Abalone in different behavioral classes: (A) three exposed abalone in urchin barrens habitat, (B) two covered abalone under Laminarian kelp in an area occupied by sea otters for 3 yr, and (C) two cryptic abalone capturing drift kelp in an area occupied by sea otters for 6 yr. Natural history observations: (D) red urchins capturing bull kelp in an urchin barrens, (E) nine abalone moving in to feed on kelp captured by red urchins, (F) abalone shell and urchin test expelled following digestion by a sunflower star in habitat with high complexity substrate, and (G) cryptic abalone in a kelp forest occupied by sea otters. Images by Lynn Lee.

primary substrate score by 70% and secondary substrate score by 30% (based on mean percent cover of primary and secondary substrate from previous surveys in abalone habitat; L. Lee, unpublished data).

Wave exposure and depth.—We represented wave exposure as average fetch for 5° compass bearing intervals measured in ArcGIS 9.3 to a maximum single fetch length of 200 km (following Ekeboom et al. 2003). We used average fetch from combined southeast (90–180°) and northwest (270–360°) bearings to represent prevailing southeast winter storms and northwest summer winds (Thomson 1981). Depths were tide-corrected to chart datum based on the time of survey and closest tidal station with NobelTec Lite version 2.1.

Laboratory predation experimental design

We tested the extent to which crevice habitat and alternate prey affect sunflower star predation rates on abalone. We placed hatchery-raised second-generation northern abalone in $1.24 \times 0.90 \times 0.30$ m fiberglass tanks under three treatments: + crevice (addition of crevice habitat using four 9-cm-high concrete blocks 20×19 cm in area, with 6-cm-high \times 13-cm-long archways); + urchins (addition of three 65–70 mm diameter red sea urchins); and control (no crevice habitat or alternate prey). We conducted three-hour-long experimental trials randomly replicated in four separate tanks over 3 days. At the start of each trial, we placed one wild-caught sunflower star (45–70 cm diameter) held without food for 5–7 days into a trial tank with six abalone (55–75 mm length; mimicking aggregative behavior and high abalone transect densities up to 7.5 abalone/m²) acclimatized in tanks overnight. Sunflower star and abalone behavior were continuously observed over the entire trial. Sunflower star behavior was noted as stationary, cruising (moving at slow speed without tracking abalone), hunting (tracking abalone), attacking (contact with abalone being hunted), and consuming (ingesting captured abalone). Each attack was classified as successful (abalone consumed) or unsuccessful (abalone escaped). Two trials could not be used because the sunflower stars did not move over the entire trial and these were not considered representative of hunting behavior (+ crevice, $n = 3$; + urchins, $n = 3$; control, $n = 4$).

We calculated capture efficiency (α ; number of prey eaten as a function of search time and number of prey; Eq. 1), handling time per abalone (h ; Eq. 2), and feeding rate assuming a type II prey-dependent functional response where the rate at which a predator captures and consumes prey is constrained by search and handling time (Eq. 3; Holling 1959, Gotelli 2008):

$$\alpha = \frac{n}{t_s V} \quad (1)$$

where n = number of prey items captured in total trial time t , t_s = search time, and V = abundance of prey;

$$h = \frac{t_h}{n} \quad (2)$$

where t_h = handling time, and n = number of prey items captured in total trial time t ; and

$$\frac{n}{t} = \frac{\alpha V}{1 + \alpha V h} \quad (3)$$

where α , h , and V are defined in Eqs. 1 and 2, and t = total trial time (180 min). Search time, t_s , was defined as the sum of cruising, hunting and unsuccessful attack times. Handling time, t_h , was defined as the sum of successful attack and consumption time. All attacks were unsuccessful in one + urchins trial, resulting in $n = 2$ for feeding rate and handling time for this treatment. The number of trials was constrained due to limited access to captive-bred endangered abalone and laboratory facilities. Lastly, we measured the speed of abalone fleeing from sunflower stars in the laboratory and field, and the speed of hunting sunflower stars and fleeing urchins in the laboratory.

Statistical analysis

Field surveys.—To test which biotic and abiotic factors drove abalone density and biomass, we fit generalized linear mixed-effects models (GLMMs) of total abalone and three behavioral classes: exposed, covered, and cryptic. In these models, the three-level categorical variable of region, seven continuous predictor variables—sea otter occupation time, depth, substrate complexity, wave exposure, kelp stipe density, urchin biomass, and sunflower star biomass—and an interaction between depth and sea otter occupation time were treated as fixed effects, while site was treated as a random effect (see Appendix S2:

1. What affects abalone density?
What effects abalone biomass?

Table S1 for saturated models). We checked for multi-collinearity among all response variables using correlation coefficients and variance inflation factors (VIF; Zuur et al. 2010, 2013). Correlation coefficients >0.6 and VIF scores >3.5 indicate variables considered to have a high degree of collinearity that may be problematic if collinear variables are included in the same model (Zuur et al. 2009). Correlation coefficients in this analysis ranged from 0.01 to 0.41, and all VIF scores were <3 , indicating that multi-collinearity is unlikely to be a problem in this analysis (Appendix S2: Fig. S1). To facilitate direct comparison of parameter coefficients among continuous variables on different scales and between continuous and categorical variables, we standardized all continuous variables by subtracting their mean and dividing by two standard deviations (Gelman 2008). Models of abalone density were fit with a negative binomial likelihood and exponential link function, accounting for zero-inflation as needed. Abalone biomass was modeled as a two-stage Hurdle model. First, we determined factors that best predicted abalone presence/absence; then, we modeled factors that best predict abalone biomass with the non-zero subset of these data (Barry and Welsh 2002). Models of abalone presence/absence were analyzed with a binomial likelihood and logit link function, while models of abalone biomass were analyzed with a gamma likelihood and exponential link function. All models were run in R version 3.1.0 using the glmmADMB package (R Development Core Team 2008, Fournier et al. 2012, Skaug et al. 2013).

2. What affects abalone size?

To test for the effect of these biotic and abiotic predictor variables on abalone length, we fit linear mixed-effects models with Gaussian likelihoods and identity link functions (see Appendix S2: Table S1 for saturated models) using the lme4 package in R (Bates et al. 2014). Abalone lengths from all transects within a site were pooled and individual lengths were centered about zero by subtracting the global mean length within each data set (i.e., grouped for total, exposed, covered, and cryptic abalone lengths separately) prior to model fitting to facilitate use of Gaussian likelihoods. To evaluate whether transect-level or abalone-level substrate was a better predictor of abalone length, we fit abalone length models to substrate complexity at both spatial scales. Model results were similar in

explaining variation in the length of total, exposed, and covered abalone, but abalone-level substrate explained more of the variation for cryptic abalone; therefore, we used abalone-level substrate for length models.

We fit GLMMs to test the effect of sea otters and other biotic and abiotic factors on sunflower star presence and biomass, urchin presence and biomass, and kelp stipe density. In all models, standardized continuous factors of sea otter occupation time, depth, substrate, wave exposure, and an interaction between depth and sea otter occupation time were treated as fixed effects, while site was treated as a random effect. In addition, urchin biomass was treated as a fixed effect in the kelp and sunflower star models, and both kelp stipe density and sunflower star biomass were treated as fixed effects in the urchin models (Appendix S2: Table S2). Models of sunflower star and urchin presence were fit with a binomial likelihood and logit link function, while those for biomass were fit with a gamma likelihood and exponential link function. Models of kelp stipe density were fit with a negative binomial likelihood and exponential link function. Kelp, sunflower star, and urchin models were run in R version 3.1.0 using the glmmADMB package (R Development Core Team 2008, Fournier et al. 2012, Skaug et al. 2013).

We evaluated relative support for models with all possible combinations of fixed factors using Akaike's information criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2004). Models were standardized to the best-fit and most parsimonious model to determine ΔAIC_c values. Using the dredge function in the R package MuMIn (Bartoń 2013), we generated an initial set of candidate models based on their cumulative Akaike weights (W_i), indicating the relative strength of evidence in favor of a given model. The dredge function did not include the random effect of site in model evaluation using glmmADMB, and also did not determine the degrees of freedom in model sets that included both models with and without the categorical factor of region. We therefore ran each model within the 95% cumulative W_i model set individually using glmmADMB to determine AIC_c values for each model. The final model set included models within $\Delta AIC_c < 2$. We evaluated the effect of biotic and abiotic factors on abalone based on three

3. What affects sunflower star presence & biomass?

What affects urchin presence & biomass?

What affects kelp density?

attributes: (1) the magnitude and direction of parameter coefficients, (2) 95% confidence intervals (CIs) around coefficient estimates, and (3) relative variable importance (RVIs) of each parameter, calculated by summing the W_i of candidate models in which the parameter was found (Burnham and Anderson 2002). Effects were considered weak and imprecise if the parameter coefficients were close to zero and their confidence intervals were widely overlapping zero.

To examine the effect of sea otter occupation time on the proportion of abalone in different behavioral classes, we fit and compared three alternative models: (1) non-linear, (2) linear, and (3) null (intercept only). We fit a non-linear exponential decay curve for exposed and covered abalone, based on the premise that exposed abalone would be most susceptible to sea otter predation, followed by covered abalone, such that proportions of both should decline over time: $y = a \times (1 - b)^x$. Conversely, we fit a saturation curve for cryptic abalone, under the hypothesis that the proportion of cryptic abalone should increase with sea otter occupation time: $y = a \times x/(b + x)$. We compared model AIC_c values to determine the strength of evidence supporting each of the three alternative relationships for exposed, covered, and cryptic abalone.

Predictive models for Haida Gwaii region.—We generated model predictions for the effect of sea otter occupation on abalone density using coefficients, in their original units, from the model with the lowest AIC_c . To illustrate the interaction effect between depth and otter occupation time for HG, we predicted abalone density as a function of otter occupation time for two depths (0 m and the average surveyed depth of 4.3 m chart datum), with all other continuous factors set to their average values, the categorical HG region coefficient set to 1, and the CC and WCVI coefficients set to 0.

Laboratory experiments.—We used linear models to compare capture efficiency, feeding rate, and handling time of sunflower stars between treatments, where each response variable was modeled as a function of treatment and compared to a null model (intercept only). We also constructed GLMMs of the probability of each of six abalone being consumed per trial with treatment as a fixed effect and trial as a random effect, using a binomial likelihood and logit link

function (Appendix S2: Table S3). Abalone seemed to tire, moving more slowly as each trial progressed, particularly in tanks where sunflower stars were very active. To test for the effect of abalone fatigue, we constructed GLMMs of sunflower star attack success with treatment and trial run time as fixed effects and trial as a random effect, using a binomial likelihood and logit link function (Appendix S2: Table S3).

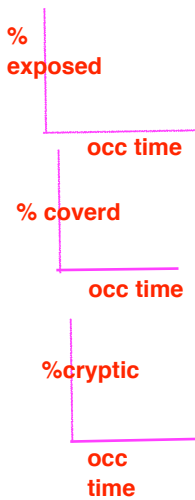
RESULTS

Biotic and abiotic factors influence abalone distribution and abundance

The magnitude, direction, and identity of key factors affecting abalone abundance, size, and distribution differed for each behavioral class (Figs. 3–5; Appendix S3: Figs. S1–S4; Appendix S4: Tables S1–S4). Consequently, we report the relative strength of evidence for each factor on abalone density, length, and biomass; factor by factor; and by behavioral class (Fig. 5). We also show the best model for each abalone population metric by behavioral class (Table 1).

Sea otter occupation time.—Sea otter occupation time had a strong negative effect on exposed abalone density, length, and thus overall biomass (RVI = 1, 1, 1, respectively; Figs. 3B, 5B), with an effect on density that was three times greater than the magnitude of any other local-scale biotic or abiotic factor. In contrast, sea otter occupation time had a weakly positive but imprecise effect on covered and cryptic abalone density (RVI = 0.85, 0.66, respectively; Figs. 3C, D, 5C, D). Specifically, the strong negative effect of sea otter occupation time on exposed abalone density was 18 times greater than its weakly positive effect on cryptic and covered abalone densities, for which other local-scale biotic and abiotic factors had greater relative importance and magnitudes of effect (Fig. 5B–D). Consequently, the effect of sea otter occupation time on total abalone density was negative (RVI = 1; Fig. 5A). Abalone biomass declined with increasing sea otter occupation time due to decreasing size across all behavioral classes, with the largest effect on exposed abalone and the smallest effect on cryptic abalone (Fig. 5B–D).

Substrate complexity.—Increasing substrate complexity was positively associated with abalone density across all behavioral classes (Fig. 5).



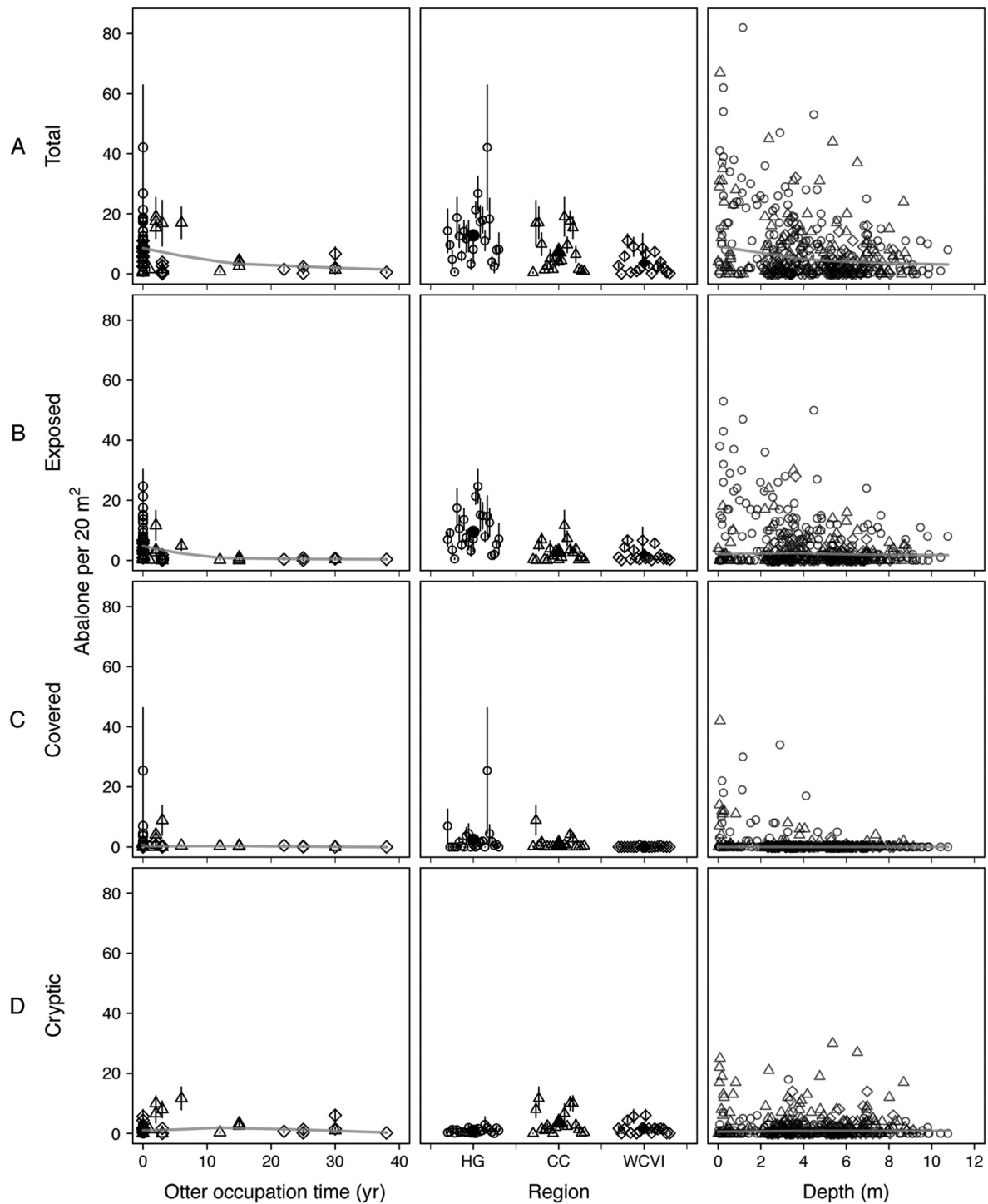


Fig. 3. Bivariate relationships between density of (A) total, (B) exposed, (C) covered, and (D) cryptic abalone and three factors: sea otter occupation time, region, and depth. Symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles), and West Coast Vancouver Island (WCVI; open diamonds). Error bars are site means \pm SE. Closed symbols (region panel) are the mean of site means by region. Lines are LOWESS smoothers (otter occupation time and depth panels).

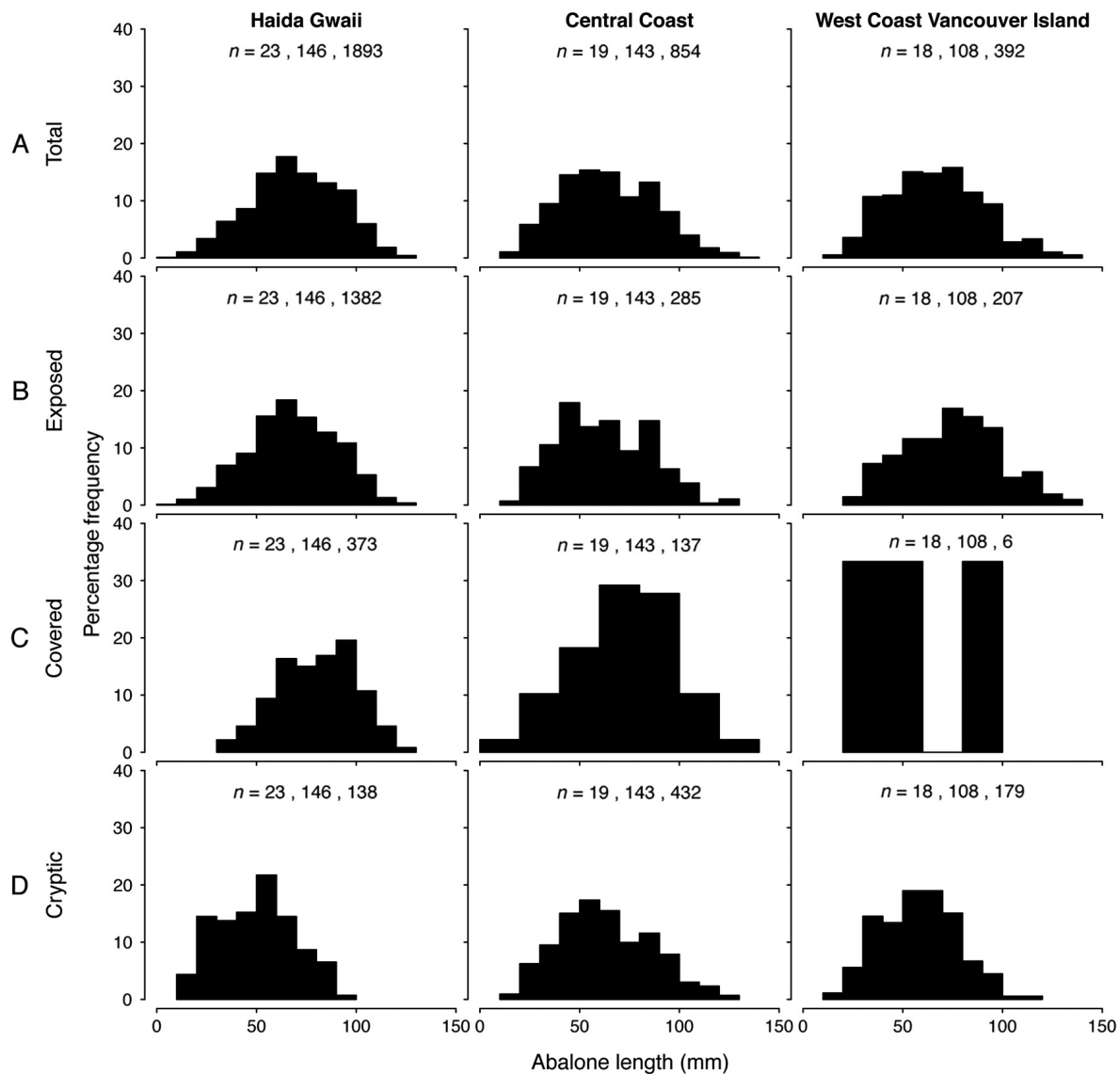


Fig. 4. Size frequency histograms of shell length for (A) total, (B) exposed, (C) covered, and (D) cryptic abalone for each of three surveyed regions of BC. Sample sizes (n) are given in sequence: sites, transects, abalone. Numbers of sample sites and transects are the same within regions, but differ across regions. Bin sizes are 10 mm except for covered abalone in Central Coast and West Coast Vancouver Island that are 20 mm.

Substrate complexity had the strongest effect on density of cryptic abalone (RVI = 1; Fig. 5D), a moderately important and certain effect on exposed abalone (RVI = 0.80; Fig. 5B), and an imprecise effect of low importance on covered abalone (RVI = 0.18; Fig. 5C). Substrate complexity was also an important positive driver for cryptic abalone biomass and length (RVIs = 1; Fig. 5D), yet had low to no importance for

exposed and covered abalone length (RVIs < 0.25; Fig. 5B, C).

Wave exposure.—Increasing wave exposure to prevailing NW-SE winds was associated with lower exposed and cryptic abalone densities, but was not important for covered abalone (Fig. 5B–D). Wave exposure was the strongest local-scale driver for cryptic abalone density (RVI = 1; Fig. 5D), less important for exposed abalone

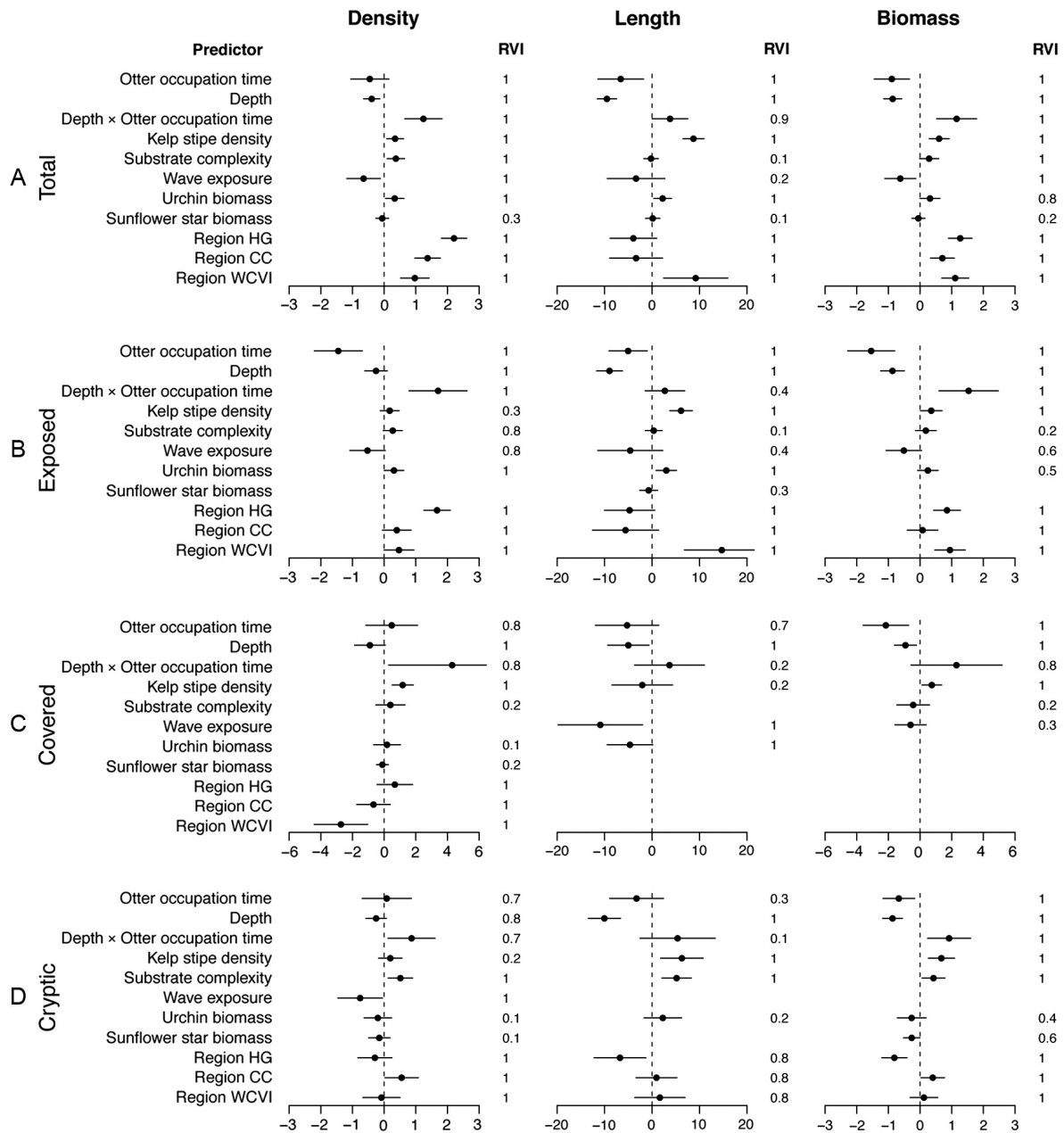


Fig. 5. Standardized coefficients and 95% confidence intervals for relationships of biotic and abiotic factors with the density, length, and biomass of (A) total, (B) exposed, (C) covered, and (D) cryptic abalone from averaged models within $\Delta AIC_c < 2$. Factors without coefficient and relative variable importance (RVI) values were absent from final model sets. CC, Central Coast; HG, Haida Gwaii; WCVI, West Coast Vancouver Island.

(RVI = 0.82; Fig. 5B), and of no importance to covered abalone density (RVI = 0; Fig. 5C). Wave exposure had a strong negative effect on covered abalone length (RVI = 1; Fig. 5C), but an imprecise and less important effect on exposed abalone

(RVI = 0.39; Fig. 5B), and was of no importance to cryptic abalone length (RVI = 0; Fig. 5D).

Depth.—We detected a strong negative effect of depth on the density, length, and thus biomass of abalone across all behavioral classes (RVI = 1 for

Table 1. Best models of the effects of biotic and abiotic factors on density, presence, length, and biomass of total, exposed, covered, and cryptic abalone from field surveys.

Response	Model
Abalone density	
Total	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth × Otter occupation time + (1 Site)
Exposed	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Urchin biomass + Depth × Otter occupation time + (1 Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + Depth × Otter occupation time + (1 Site)
Cryptic	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Depth × Otter occupation time + (1 Site)
Abalone presence	
Total	Region + Wave exposure + Substrate complexity + (1 Site)
Exposed	Region + Depth + Wave exposure + Urchin biomass + (1 Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + Depth × Otter occupation time + (1 Site)
Cryptic	Wave exposure + Otter occupation time + (1 Site)
Abalone length	
Total	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth × Otter occupation time + (1 Site)
Exposed	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + (1 Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + (1 Site)
Cryptic	Region + Depth + Wave exposure + Sunflower star biomass + (1 Site)
Abalone biomass	
Total	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth × Otter occupation time + (1 Site)
Exposed	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass + Depth × Otter occupation time + (1 Site)
Covered	Depth + Kelp stipe density + Otter occupation time + Depth × Otter occupation time + (1 Site)
Cryptic	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Depth × Otter occupation time + (1 Site)

Note: See Appendix S4: Tables S1–S4 for strength of evidence for alternative candidate models.

all except cryptic abalone density where RVI = 0.78; Figs. 3, 5). Depth was the strongest driver of exposed and cryptic abalone length compared to all other factors. We found that the negative effect of depth on abalone density and biomass was mediated by sea otter occupation time where increasing otter time strongly reduced the negative effect of depth. This mediating effect was strongest for exposed abalone density (RVI = 1; Fig. 5B), greatest but most imprecise for covered abalone density (RVI = 0.85; Fig. 5C), and least important to cryptic abalone density (RVI = 0.66; Fig. 5D). Comparing predictive models of abalone density on Haida Gwaii as a function of sea otter occupation time at two depths illustrated this mediating effect (Fig. 6). As sea otter occupation time increased, a predicted distributional change occurred where abalone densities at 4.3 m exceeded those at 0 m after approximately 10 yr.

Kelp stipe density.—Kelp stipe density had a positive effect on total and covered abalone

densities (RVI = 1, 1, respectively; Fig. 5A, C), yet a weak and imprecise effect on exposed and cryptic abalone densities (RVI = 0.25, 0.24, respectively; Fig. 5B, D). More kelp was strongly associated with larger abalone and thus higher abalone biomass across all behavioral classes (RVI = 1 for all except for covered abalone length where RVI = 0.16; Fig. 5).

Urchin biomass.—Higher urchin biomass was associated with higher exposed abalone density, length, and biomass (RVIs = 1, 1, 0.49, respectively; Fig. 5B); this was also the case for total abalone (RVIs = 1, 1, 0.79, respectively; Fig. 5A). In contrast, increasing urchin biomass was associated with decreasing covered abalone length (RVI = 1; Fig. 5C). Urchin biomass was otherwise unimportant to covered abalone density or biomass (RVIs < 0.15; Fig. 5C) and of little importance to cryptic abalone density, length, or biomass (RVIs < 0.40; Fig. 5D).

Of the 3814 abalone surveyed where behavior was recorded, 46 (1.2%) were found under the

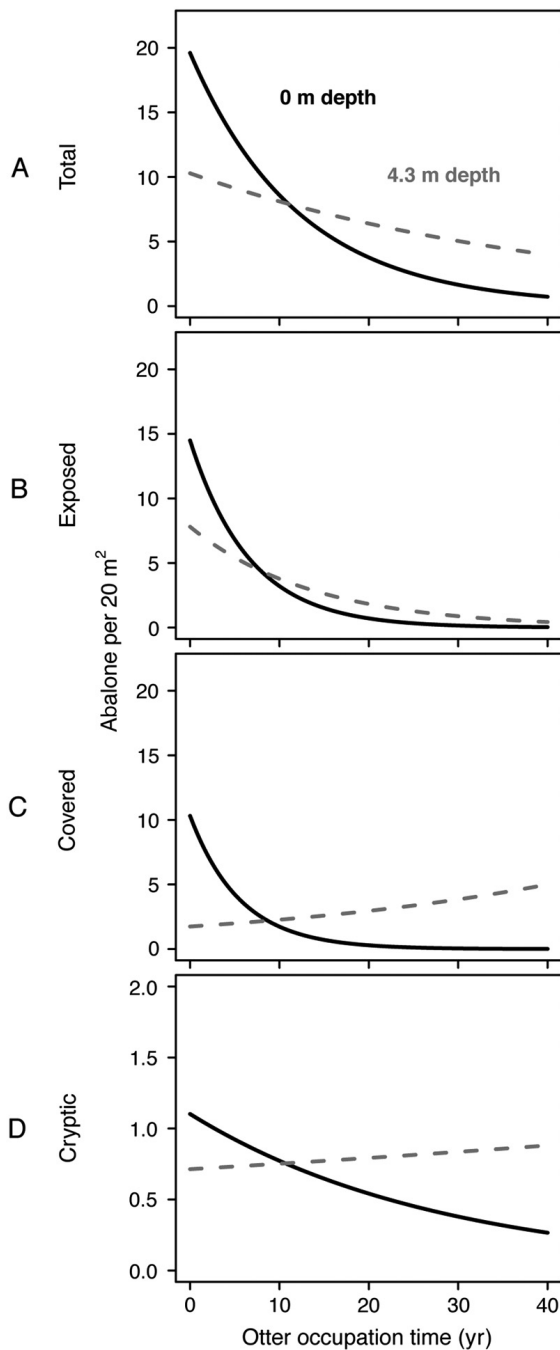


Fig. 6. Predicted abalone densities from best model parameters for (A) total, (B) exposed, (C) covered, and (D) cryptic (note different scale bar) abalone on Haida Gwaii as a function of sea otter occupation time at two depths, 0 m and the average survey depth of 4.3 m, when other biotic and abiotic factors are held at their mean surveyed values.

spine canopy of sea urchins (majority under red urchins). Abalone under urchin spine canopies ranged from 18 to 107 mm, averaging 60.9 ± 3.0 mm. Of the 634 juvenile abalone ≤ 45 mm surveyed, nine (1.4%) were sheltered under urchin spine canopies (mean length = 31.3 ± 2.6 mm).

Sunflower star biomass.—Sunflower star biomass was not an important driver of abalone density, length, or biomass across all behavioral classes (RVIs < 0.30 ; Fig. 5). The exception was a potential negative association with cryptic abalone biomass (RVI = 0.63; Fig. 5D).

Region.—We found strong regional differences in total abalone density with HG (sea otters absent) having higher densities than the CC and WCVI (0–38 years of sea otter occupation; Figs. 3A, 5A). The effect of region on total abalone density was primarily driven by variation in the number of exposed abalone (Figs. 3B, 5B). Specifically, total abalone densities on HG were 1.6 and 2.3 times greater than on the CC and WCVI (Fig. 5A), respectively; exposed abalone densities on HG were 4.2 and 3.6 times greater, respectively (Fig. 5B). Covered abalone density was slightly higher on HG than on the CC, which was slightly higher than that on the WCVI (Figs. 3C, 5C). Cryptic abalone density was less variable between regions, slightly higher on the CC (~800 sea otters) than on the WCVI (~5000 sea otters), and lowest for HG (no sea otters; Figs. 3D, 5D).

Regional differences in length of exposed and cryptic abalone resulted in different trends in abalone biomass compared to density: Total abalone length patterns were driven by variation in exposed abalone length. The average length of exposed abalone was larger on the WCVI than on HG and the CC (Figs. 4B, 5B), whereas the average length of cryptic abalone was lower for HG compared to the CC and WCVI (Figs. 4D, 5D). Thus, we detected similar total and exposed abalone biomass on HG and the WCVI in spite of lower densities on the WCVI. The effect of region was not important to covered abalone biomass or length, which were more strongly influenced by local-scale biotic and abiotic factors (Figs. 4C, 5C).

Abalone behavioral class shifts with sea otter occupation

The proportion of abalone in each behavioral class shifted as a function of sea otter occupation

time (Fig. 7). Increasing sea otter occupation time was associated with decreased proportions of exposed abalone and increased proportions of cryptic abalone (Fig. 7A, C). By 6 years of sea otter occupation, the majority of abalone were cryptic (Fig. 7C). The relatively flat trend line for covered abalone proportion suggested little relationship with sea otter occupation time (Fig. 7B). We found strong evidence that the non-linear decay curve best fit the effect of sea otter occupation time on proportion of exposed abalone, while the linear model best described the proportion of cryptic abalone; for covered abalone, all models were within $\Delta AIC_c < 2$ indicating no best model (Table 2).

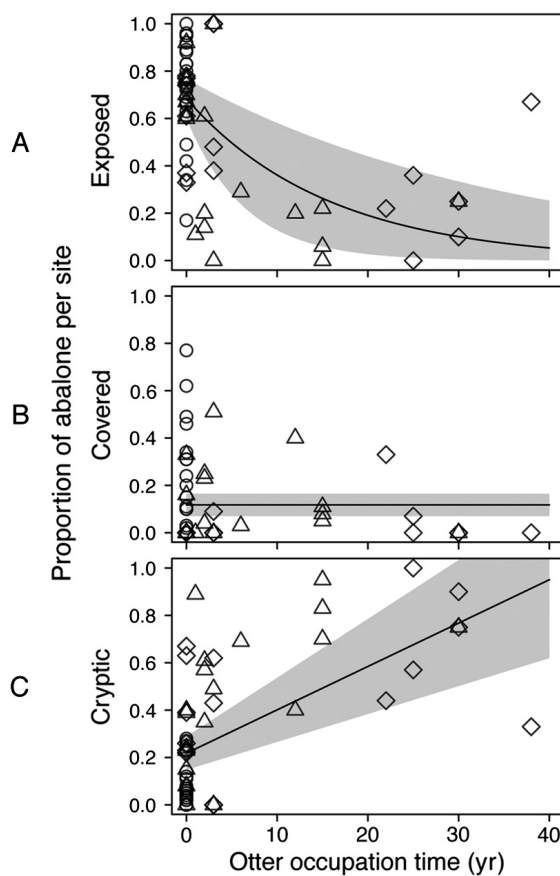


Fig. 7. Proportion of (A) exposed, (B) covered, and (C) cryptic abalone in each behavioral class by site. Symbols are as in Fig. 3. Shaded areas represent confidence intervals about best-fit relationships: (A) non-linear exponential decay, (B) intercept, and (C) linear.

Biotic and abiotic factors may mediate predation outcomes

In laboratory experiments, we detected higher capture efficiency (α) and feeding rate of sunflower stars on abalone in trials with higher substrate complexity (+ crevice; Fig. 8C, E), along with lower handling time in trials with alternate urchin prey (+ urchins; Fig. 8D). Sunflower stars used their tube feet to chase and capture fleeing abalone. When chased by sunflower stars, abalone could initially move at at least twice the speed of the sea star both in the laboratory and in the wild (Fig. 8B; Video S1; Video S1 legend); however, we observed that the speed of each fleeing abalone decreased over time. If held by a sunflower star, abalone would attempt to escape by wildly twisting their shells to break the suction of the star's tube feet, then flee away. Some abalone moved out of the water onto the tank edge to escape. Successfully captured abalone were engulfed whole into the sunflower star's stomach (Video S2; Video S2 legend). Most stars ingested only one abalone, but some ingested up to three during a trial. Handling time per abalone varied (range = 4–65 min), as a function of time needed to capture and ingest the abalone. Ingested abalone were digested over the following 24 h, after which clean abalone shells were expelled. Although model summaries indicated that treatment effects explained much of the variation in the data ($R^2 = 0.86$ for α ; $R^2 = 0.93$ for feeding rate), strength of evidence for a treatment effect was weak, in part due to low sample size. Specifically, null models (intercept only) of capture efficiency, handling time, feeding rate, and abalone survival were $\Delta AIC_c > 2$ from models including treatment effects (Appendix S7: Table S1). Irrespective of treatment, trial run time best explained variation in sunflower star attack success (Fig. 8A; Appendix S7: Table S1).

Indirect benefits of sea otters for abalone

We found strong evidence that sea otter recovery was associated with an increase in kelp stipe density and decrease in the biomass of predatory sunflower stars and sea urchin competitors (Fig. 9; Appendix S5: Tables S1–S3; also see Figs. S1, S2 for effects on presence of sunflower stars and urchins). Compared to other biotic and abiotic factors, sea otter occupation time had the greatest magnitude of effect on sunflower star

Table 2. Strength of evidence for alternative candidate models of the effects of sea otter occupation time on the proportion of exposed, covered, and cryptic abalone by site.

Response and model	df	log(L)	AIC _c	ΔAIC _c	W _i
Exposed abalone proportion					
Non-linear decay	3	-2.726	11.889	0.000	0.937
Linear	3	-5.434	17.305	5.417	0.062
Intercept	2	-13.695	31.604	19.715	0.000
Covered abalone proportion					
Intercept	2	17.764	-31.314	0.000	0.475
Linear	3	18.318	-30.200	1.114	0.272
Non-linear decay	3	18.247	-30.057	1.257	0.253
Cryptic abalone proportion					
Linear	3	1.803	2.830	0.000	0.993
Non-linear saturation	3	-3.124	12.684	9.854	0.007
Intercept	2	-11.213	26.641	23.811	0.000

Notes: Models with varying degrees of freedom (df) were compared using likelihood of the model given the data (log(L)), differences in Akaike's information criterion corrected for small sample size (ΔAIC_c), and normalized Akaike weights (W_i). Bold typeface indicates a model that has substantial empirical support relative to alternate candidate models (ΔAIC_c > 2 from the next best model).

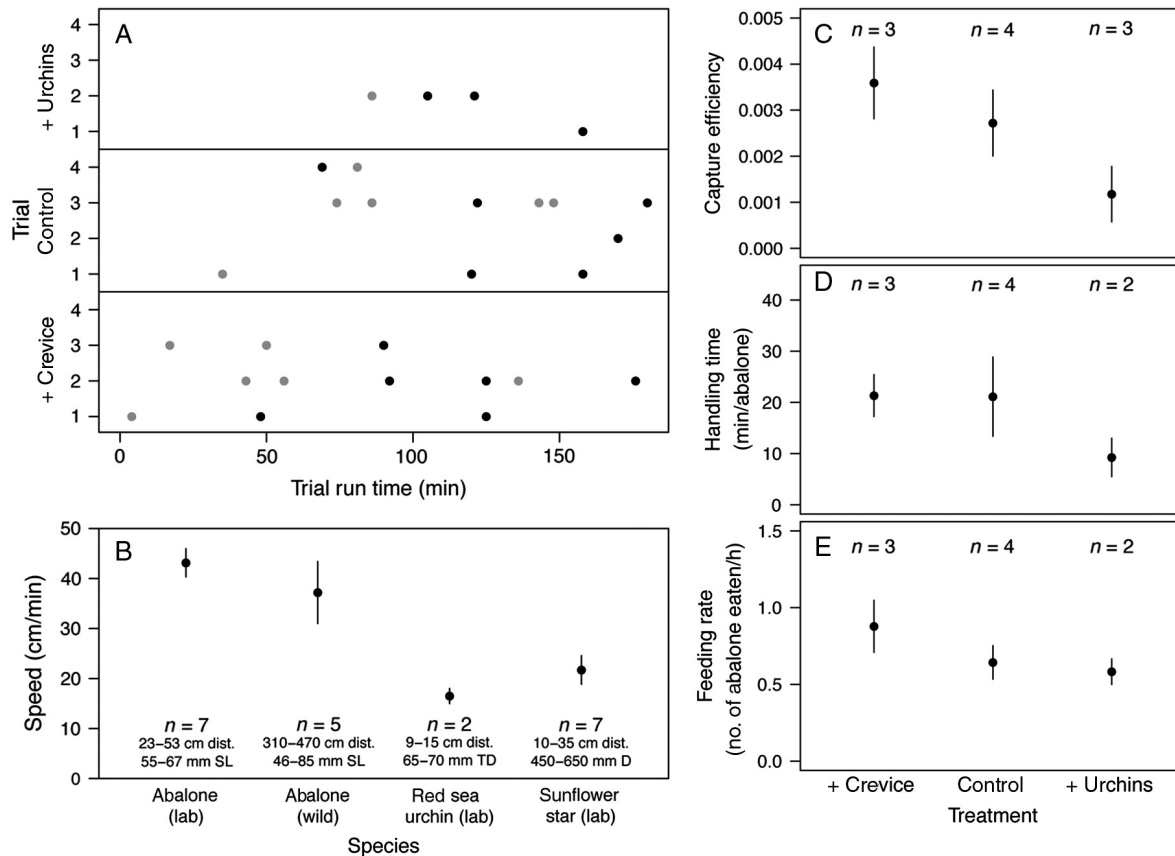


Fig. 8. (A) Successful (black) and unsuccessful (gray) attacks by sunflower stars on hatchery-raised abalone in laboratory predation trials ($n = 4$ per treatment). Trials with no circles indicate no attacks. (B) Escape speeds of abalone and red urchins, and attack speed of sunflower stars, measured in the laboratory and field. (C) Capture efficiency, (D) handling time, and (E) feeding rate of sunflower stars by treatment (mean \pm SE).

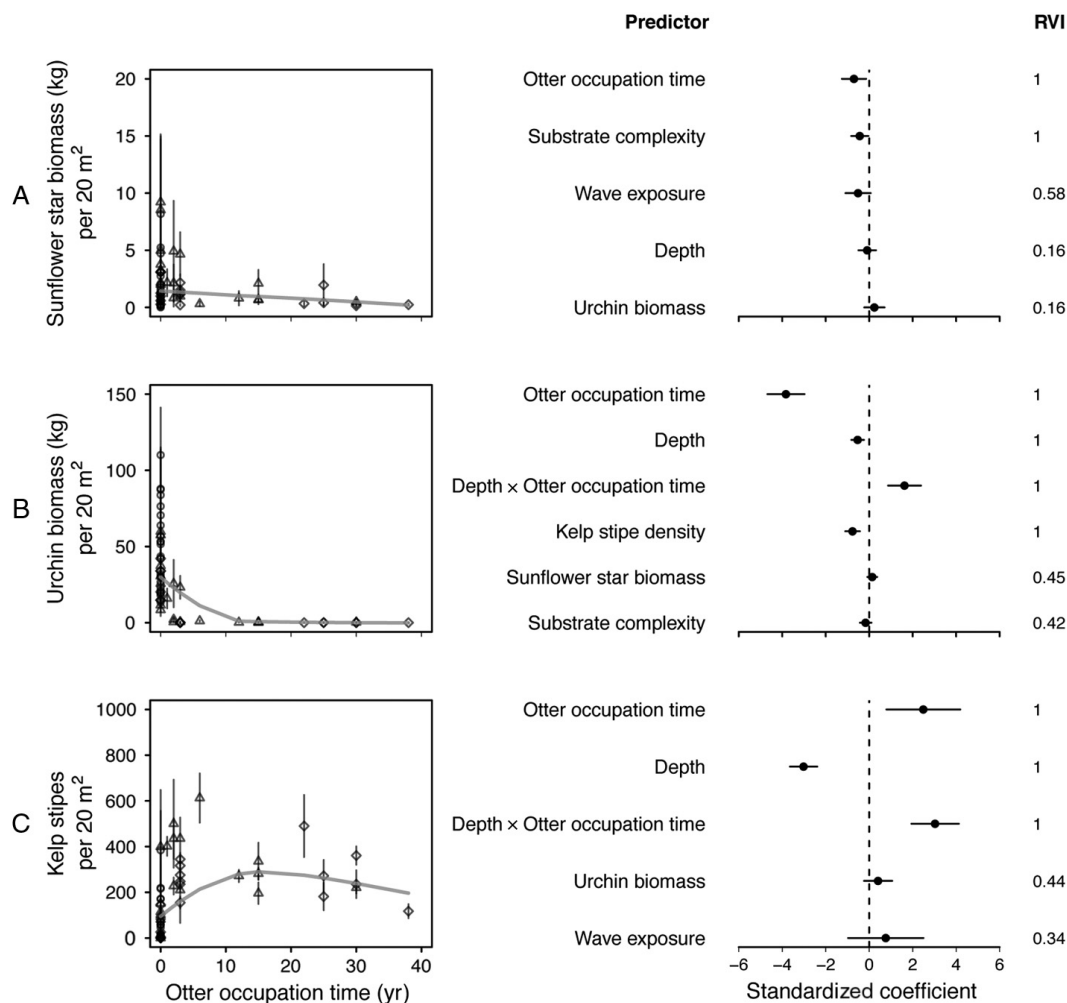


Fig. 9. Bivariate relationships (left) and standardized coefficients and 95% confidence intervals from averaged models within $\Delta AIC_c < 2$ (right) for relationships between (A) sunflower star biomass, (B) urchin biomass, and (C) kelp stipe density, and sea otter occupation time. For bivariate plots, symbols are as in Fig. 3. Error bars are site means \pm SE. Lines are LOWESS smoothers.

biomass, urchin biomass, and kelp stipe density, and it was one of the most important factors along with depth. We also found a strong positive interaction between depth and sea otter occupation time, where increasing otter occupation time strongly reduced the negative effect of depth on urchin biomass and kelp stipe density (Fig. 9B, C). At sites increasing in sea otter occupation time, these interactive effects were observed as an increase in the depth and areal extent of kelp forests, and a dramatic reduction in the high density of urchins concentrated along the sublittoral fringe.

DISCUSSION

Here, we show how the complex interplay between direct negative effects, indirect positive effects, and prey behavior promotes the coexistence of a keystone predator and its endangered prey. Sea otter recovery had direct negative effects on abalone via predation, but positive indirect effects via food and habitat provisioning, and reduced abundance of mesopredators and competitive herbivores (Figs. 3, 5, 9; also see Fig. 2D, E for natural history observations of positive interactions between abalone and

urchins). As has been observed elsewhere, sea otter recovery reduced average abalone size and abundance to low densities (Fig. 5) and likely triggered a change in behavior from exposed to cryptic (Fig. 7; Watson 2000, Micheli et al. 2008, Raimondi et al. 2015). Changes in abalone behavior may then dampen negative predation effects, suggested by sea otter recovery having a strong negative effect on the density of exposed abalone compared to a weak positive effect on covered and cryptic abalone (Figs. 5B–D, 6). At the same time, by dramatically reducing the abundance and size of one of the most important temperate reef grazers, sea urchins (Fig. 9B; Stevenson et al. 2016), sea otters also transformed two-dimensional urchin barrens into structurally complex three-dimensional kelp forest habitat (Fig. 9C; Estes and Palmisano 1974, Watson and Estes 2011, Markel and Shurin 2015). This indirect magnification of kelp forest habitat and associated drift kelp increases the availability of food and shelter for abalone, promoting the persistence of abalone as sea otters recover.

Abalone behavior may reduce predation effects

We propose alternative yet not mutually exclusive mechanisms that may have led to the exponential decline in the proportion of exposed abalone (Fig. 2A) with sea otter recovery. Our data suggest that the majority of abalone were cryptic (Fig. 2C, G) by 6 years of sea otter occupation (Fig. 7A, C). This observation could be due to a change in abalone behavior from exposed to cryptic triggered by the presence of sea otters and/or increasing extent and depth of kelp forests, higher sea otter-induced mortality rates on exposed vs. cryptic abalone, or some combination of these.

We expect that abalone mortality caused by sea otters would be highest for exposed individuals. Exposed abalone are likely easiest to detect and capture, resulting in a more rapid decline in their density compared to covered or cryptic abalone which are harder to detect and/or in refugia inaccessible to sea otters. Our finding that sea otter occupation time had a strong negative effect on exposed abalone density vs. a weak positive effect on covered and cryptic abalone density (Fig. 5B–D) supports this hypothesis. Sites with sea otters had lower densities of exposed abalone

than those without otters ($1.38 \pm 0.51/20 \text{ m}^2$ vs. $7.56 \pm 0.98/20 \text{ m}^2$), but higher densities of cryptic abalone ($2.96 \pm 0.75/20 \text{ m}^2$ vs. $1.31 \pm 0.20/20 \text{ m}^2$). In the initial years of sea otter occupation, site-specific predation rates on abalone may also be lower due to high availability of easily accessible alternate prey such as urchins, crustaceans, and other mollusks (Honka 2014). This situation would afford the opportunity for surviving exposed and covered abalone to change behavior and move into cryptic habitats.

Alternatively, abalone behavioral changes may be triggered by sea otter predation pressure and/or increased extent of kelp habitat and food. Once exposed abalone experience the threat of sea otter predation, they may restrict their foraging behavior to spend more time in crevices and become increasingly cryptic. Increased extent of kelp forests with sea otter recovery may also assist abalone with obtaining food while they remain in crevices. The latter two hypotheses are suggested by the weak positive effect of sea otters on cryptic abalone (Fig. 5D), and predicted increase in densities of cryptic abalone with increasing sea otter occupation time (Fig. 6D). The positive effect of sea otters on cryptic abalone may in fact be greater than our estimate because some cryptic abalone would have gone undetected given our non-intrusive field survey protocol (Campbell and Cripps 1998, Cripps and Campbell 1998).

Foraging theory predicts that animals will alter their behavior to maximize energetic gain and minimize predation risk (Lima and Dill 1990, Brown and Kotler 2004), and diverse empirical evidence exists to support this trade-off in marine ecosystems (Heithaus et al. 2008). Drift kelp is scarce in deforested urchin barrens. We expect this scarcity of food to result in abalone spending more time foraging in the open and less time in refugia, leading to a higher proportion of exposed abalone. In contrast, drift kelp is abundant in kelp forests and abalone can obtain food while remaining in refugia with reduced predation risk. Other grazers such as urchins make a similar shift from active grazing to passive detritivory as drift kelp supply increases (Harrold and Reed 1985, Day and Branch 2002). In barrens habitat in areas without sea otters, urchins appear to react to predation risk by maintaining minimum distances from sunflower

stars, creating a “halo” effect, while staying close to the edge of shallow fringing kelp forests that provide food (Appendix S6: Figs. S1, S2; also see Duggins 1981, Schultz et al. 2016).

While data from our study cannot tease apart the relative contribution of these alternative mechanisms, future field studies and experiments may help elucidate causal mechanisms. For example, experimental arenas in areas with similar crevice habitat availability and varying in levels of mock sea otter predation pressure (divers disturbing abalone by trying to pry them off the substrate) and kelp stipe density would provide evidence for whether exposed abalone will actively change their behavior in response to predation risk and/or food availability. Field studies observing a cohort of tagged abalone through time with sea otter recovery would help distinguish between abalone behavioral changes vs. higher sea otter predation rates on exposed abalone compared to cryptic ones.

The importance of habitat characteristics

Habitat features important for abalone include substrate complexity, kelp abundance, wave exposure, depth, and sea urchin spine canopy cover (Sloan and Breen 1988, Campbell and Cripps 1998, Cripps and Campbell 1998, Tomasik and Holmes 2003, Lessard and Campbell 2007, Rogers-Bennett et al. 2011). Although evidence from temperate reefs elsewhere suggests that urchin spine canopies are important to the survival of juvenile abalone of other species (Rogers-Bennett and Pearse 2001, Day and Branch 2002), we did not detect such an effect for northern abalone in BC. The importance of habitat features can also vary depending on abalone life history stage (Griffiths and Gosselin 2008, Aguirre and McNaught 2012). For example, complex substrate is important to juvenile abalone because it provides refuge from large, mobile predators including sea stars, larger crabs, and piscivorous fish (Aguirre and McNaught 2013, Read et al. 2013).

Predator recovery can cause dramatic changes in habitat conditions (Ripple et al. 2014), which can indirectly benefit prey species. Longer sea otter occupation time was associated with greater abalone densities at deeper depth (Figs. 5, 6), likely due to habitat change from urchin barrens to deeper and larger kelp forests created via the

otter–urchin–kelp trophic cascade (Figs. 9B, C, 10; Estes and Palmisano 1974, Breen et al. 1982, Estes and Duggins 1995, Watson and Estes 2011, Markel and Shurin 2015). In addition to providing food in the form of algal drift, kelp forests provide shelter for abalone by attenuating wave energy and reducing water flow through understory kelps (Duggins 1987, Eckman and Duggins 1991). Accordingly, higher wave exposure was associated with lower abalone densities within the semi- to highly wave-exposed range of our study sites (Fig. 5).

Recovery of predators after a prolonged absence may also alter the habitat needs of their prey (e.g., Ripple and Beschta 2012). In otter-occupied areas, higher densities and larger abalone were associated with complex substrate, with the size of cryptic abalone likely dictated by refuge size. We generally found smaller abalone persisting as sea otters recovered (Fig. 5) potentially because larger abalone must emerge as they outgrow crevice refugia, placing them at risk of predation by sea otters. Although larger abalone have higher fecundity, many abalone mature at approximately 50 mm length (2–4 years of age; Sloan and Breen 1988), which allows reproductive individuals to persist in crevices within sea otter-occupied areas. Most abalone are cryptic in areas occupied by sea otter for over 6 years, so we expect that semi-wave-exposed kelp forests with complex substrate will become increasingly important habitat for northern abalone as sea otters expand their range.

Mesopredator effects

The loss of top predators can result in “mesopredator release,” a situation in which lower trophic-level predators become more abundant because higher trophic-level predators no longer control their abundance through predation and/or competition (Crooks and Soulé 1999, Roemer et al. 2009, Hughes et al. 2013, Ripple et al. 2014). Sea otters compete with and may also consume many invertebrate mesopredators including sunflower stars, giant Pacific octopus (*Enteroctopus dofleini*), and crabs (Garshelis and Garshelis 1984, Tinker et al. 2008, Honka 2014). Sea otter recovery is expected to result in smaller and fewer mesopredators including sunflower stars (Fig. 9A), which could have direct and indirect consequences for abalone. For example,

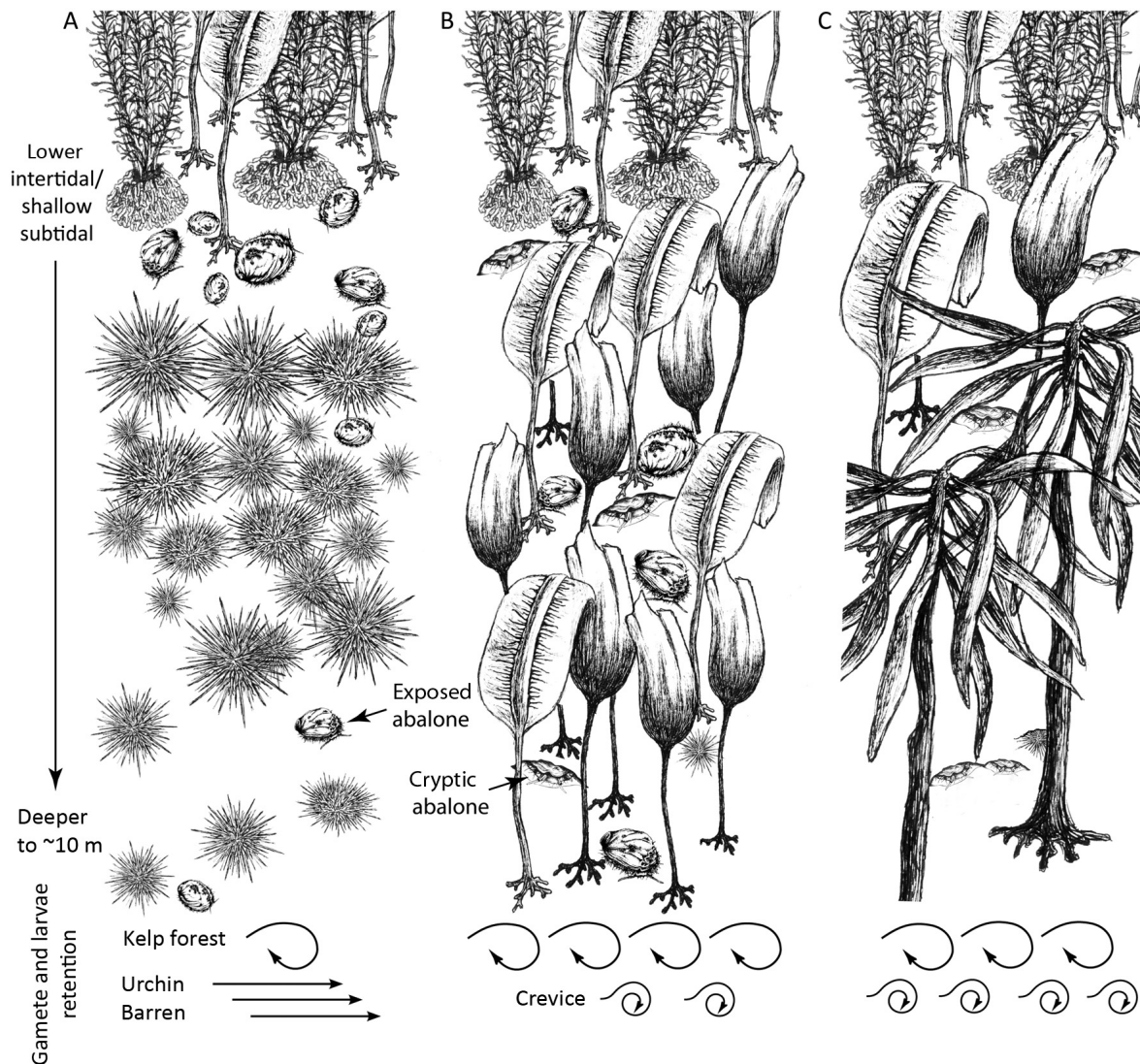


Fig. 10. Conceptual models of habitat and abalone conditions with (A) no sea otters, (B) short sea otter occupation time (≤ 6 yr), and (C) long sea otter occupation time (≥ 10 yr), illustrating multiple mechanisms by which sea otter recovery may facilitate abalone persistence at low densities. Moving from panel A to C demonstrates: (1) increased extent and depth of kelp cover, including growth of longer-lived kelp species, providing abalone with increased access to food and protection from predators that visually detect prey; (2) shift to higher proportions of cryptic abalone due to behavioral change, increased predation risk, and/or increased drift kelp food supply; (3) distributional shift in abalone from concentration at the low intertidal/shallow subtidal kelp line to dispersion across deeper depths with increased depth of kelp forests; (4) increased abalone fertilization success due to gamete retention within kelp forests and crevices, potentially reducing Allee effects at low overall abalone densities; and (5) increased retention of short-lived abalone larva (3–12 d; Sloan and Breen 1988) to facilitate settlement within kelp forests (also see Watson 2000). Potential lower abundance and smaller size of mesopredators (e.g., sunflower stars, octopus, crabs) due to decreased prey availability and/or direct predation by sea otters, and higher abalone growth rates within kelp forests, may also indirectly benefit abalone. Arrows at the bottom of each panel illustrate expected retention of gametes and larva in urchin barrens, kelp forest, and crevice habitats, with increasing spirals indicating higher retention. Drawings by Lynn Lee.

fewer predatory crabs may reduce mortality particularly for juvenile abalone (Griffiths and Gosselein 2008), and fewer and smaller sunflower stars may also reduce predation rates on abalone.

Our laboratory investigation of mesopredator effects additionally highlights that predation rates can vary with habitat characteristics. Counter to simple expectations, we found that complex substrate actually increased the risk of abalone predation by sunflower stars (Figs. 2F, 8C), similar to interactions between a molluscan prey and predatory sea star in Chile (Dayton et al. 1977). When sunflower stars moved to hunt, nearby abalone fled, often releasing a cloudy substance that appeared to trigger adjacent abalone to flee. Abalone can move at twice the speed of sunflower stars (Fig. 8B), and we observed three events in the field in which abalone escaped sea stars chasing them on locally low-relief substrate (e.g., Video S1; Video S1 legend). However, our laboratory experiments showed that high complexity substrate can reduce the abalone's horizontal speed relative to that of the sunflower star (which can travel in the horizontal plane across high-relief substrate) and compromise the abalone's ability to evade capture.

Ocean conditions and human influence

The three study regions differed in overall sea otter abundance, oceanographic conditions, abalone fishing history, and accessibility to poachers. These differences limit our ability to pinpoint a unique causal factor behind our detected effects of region. Nonetheless, the absence of sea otters likely best explains higher abalone density on Haida Gwaii, while the number and occupation time of sea otters likely explain lower abalone density on West Coast Vancouver Island compared to the Central Coast (Fig. 5A). However, different oceanographic conditions over the latitudinal range of our study may also have an influence, with declining densities and failing recruitment of northern abalone at lower latitudes possibly due to warming sea water temperatures (Washington, USA; Rogers-Bennett 2007, Rogers-Bennett et al. 2011). Warmer water in southern BC may also foster larger average abalone size on the WCVI compared to CC and HG due to higher growth rates, larger maximum size, and/or lower juvenile recruitment rates.

The history of abalone exploitation also varies between regions. Abalone catch-per-unit-effort statistics show that HG and CC were more productive commercial abalone fishing areas than the WCVI (Farlinger 1990, Harbo and Hobbs 1997), reflecting our observed regional differences in total abalone density. However, the magnitude of abalone poaching within each region is not known (Fisheries and Oceans Canada 2012). For example, on southern Vancouver Island where the coastline is more accessible, abalone abundance was found to be highest only at well-enforced sites (Wallace 1999). Yet the remoteness of HG and the CC may enable more poaching given that the majority of poaching and suspected poaching reports come from northern BC (Provincial Court of British Columbia 2002, 2007, Lessard et al. 2007).

Implications for interacting species of conservation concern

The dynamic nature of interacting species over space and time challenges the efficacy of single-species-based approaches to conservation. Recovery targets for endangered prey species based on their abundance and conservation status in an ecosystem bereft of their top predator can lead to conservation conundrums as their predators recover. For example, local-scale recovery of endangered wolves (*Canis lupus*) may be increasing the vulnerability of threatened European wild-forest reindeer (*Rangifer tarandus fennicus*) in Finland (Kojola et al. 2009). Here, northern abalone and sea otters co-evolved on the Northeast Pacific coast (Estes et al. 2005) and co-existed with people for thousands of years. Prior to the 18th century, traditional hunting of sea otters by coastal indigenous people (self-referred to as First Nations in Canada) likely maintained a mosaic of macroinvertebrate abundances along the BC coast (Corbett et al. 2008, McKechnie and Wigen 2011, Szpak et al. 2012, Salomon et al. 2015). In California, archaeological, historical, and ecological evidences show persistence of red abalone over millennia and suggest how both human hunting of sea otters and changing environmental conditions caused dramatic shifts in red abalone abundance over 8000 years (Tegner and Dayton 2000, Braje et al. 2009).

Sea otters are currently identified as a threat to northern abalone recovery where they co-occur

(COSEWIC 2009, Fisheries and Oceans Canada 2012, Busch et al. 2014). Yet here, we found evidence that abalone persist in the face of sea otter recovery, albeit at reduced densities and sizes, and thus overall biomass (Fig. 5). Abalone densities from our study were consistent with low yet persistent densities of <0.05 northern abalone/m² on West Coast Vancouver Island (Watson 1993) and 0.03 red abalone (*H. rufescens*)/m² in California (Micheli et al. 2008), at sites with decades of sea otter occupation. Although abalone recovery targets have not been established for areas with sea otters, abalone densities here were also consistent with predicted densities from simulation modeling for areas where sea otters have re-established (Chadès et al. 2012). Our data also support several mechanisms—increased kelp abundance and depth, decreased sunflower star predators, and decreased urchin competitors—by which the indirect effects of sea otters could support the persistence of abalone (Figs. 9, 10). Similar cascading predator effects have been shown in other systems where re-introduction of a top predator controlled densities of a hyperabundant herbivore to indirectly benefit other competing herbivorous prey species. For example, gray wolf predation directly decreased elk density and indirectly increased the abundance of other prey including bison and beavers, likely by fostering growth and recruitment of woody browse tree species and reducing competition for herbaceous forage species (Ripple and Beschta 2012). In a perverse case of shifting baselines (Pauly 1995, Dayton et al. 1998), the extirpation of sea otters facilitated a hyperabundance of abalone and other macroinvertebrate prey in the mid-1900s (Tegner and Dayton 2000) that many fishers, resource managers, policy makers, and scientists perceive as “normal” today. Such perceptions can bias expectations of recovery and highlight the urgent need to move toward ecosystem-based approaches to management of interacting species of conservation concern, one that acknowledges linked social and ecological drivers of change from the present, the deep past, and into the future.

Holistic approaches could be used to address some of the complex and often conflicting social and ecological objectives that surround predator recovery (Brown and Trebilco 2014). For example in Canada, BC coastal First Nations, including the

Haida on HG, Heiltsuk on the CC, and Nuu-chah-nulth on the WCVI, hunted sea otters and fished abalone for millennia (McKechnie and Wigen 2011, Menzies 2015). The loss of abalone as a traditional food deeply affected coastal indigenous communities who now aim to restore abalone to self-sustaining levels that can support food fisheries (Sloan 2004, Menzies 2010, 2015). In this case, incorporating indigenous values into management plans (Plagányi et al. 2013) can help facilitate the constitutional rights of indigenous peoples to access and manage resources within their traditional territories (Sloan 2004, Trosper 2009, Menzies 2010, Salomon et al. 2015).

Our results highlight the need to develop multi-species and ecosystem-based models and conservation plans that consider the direct and indirect effects of predator recovery on their recovering prey. Although the call for marine ecosystem-based management is by no means new (Norse 1993, Larkin 1996), implementation has been hampered by difficulty in finding a set of tools and approaches that can be broadly applied (Arkema et al. 2006, Thrush and Dayton 2010, Long et al. 2015). Our case study of northern abalone and sea otters in BC reveals how species interactions, environmental conditions, and historical change are all critical considerations in developing conservation policy and ecosystem-based management strategies for interacting species. For sea otters and northern abalone, spatially and temporally explicit objectives could range from abalone enhancement areas where higher abalone densities are fostered, to sea otter protection areas where abalone will remain in cryptic habitats at lower densities. Such alternative strategies co-crafted with local communities and informed by ecosystem-based knowledge have the potential to deliver conservation plans that promote resilience in both ecological and human (social) communities.

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