

Research

Testing the generality of sea otter-mediated trophic cascades in seagrass meadows

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The presence and strength of trophic cascades can be a function of the local abiotic environment and relative abundance of key species. The reintroduction and expansion of sea otters *Enhydra lutris*, a known keystone species in kelp ecosystems, in southeast Alaska provides a rare natural experiment to test the generality of a apex-predator – seagrass trophic cascades across a broad spatial scale. We conducted an in-depth seagrass community survey at 21 sites spanning ~100 km with variable sea otter presence to test for patterns of alternating abundance and direct relationships between species indicative of trophic cascades. Our analysis revealed some of the trophic relationships predicted by the apex predator–seagrass trophic cascades theory, including a strong negative relationship between sea otters and crabs and many of the expected relationships between nitrate, seagrass, epiphytes and epifauna. Other expected relationships within a trophic cascade, however, were not supported – including no relationship between crabs and epifauna, a critical link in the trophic cascade. Given the lack of evidence for all hypothesized direct relationships, we conclude that a sea otter mediated trophic cascade may not be present in southeast Alaska and could be due to local scale factors including the spatial heterogeneity, low resource availability and non-linear food chains in southeast Alaska seagrass communities. However, correlation analyses suggest further interactions among biological and environmental variables in southeast Alaska seagrass communities, including a positive correlation between sea otters and seagrass biomass. These results suggest that the effects of recovering apex-predator populations may not be generalizable across regions and spatial scales, highlighting a need for local assessment on the ecology and management of these populations.

Keywords: estuary, food web, southeast Alaska, *Zostera marina*

Introduction

The loss of apex predators is one of humankind's greatest impacts on Earth (Estes et al. 2011, Ripple et al. 2014). Known as trophic downgrading (Estes et al. 2011), the functional decline of top predator populations can lead to drastic changes in many ecosystems including lakes, temperate and tropical reefs, terrestrial forests and tundra (Terborgh and Estes 2010). Predators like sharks, fishes, sea otters and alligators are linked to the health of vegetated coastal habitats by modulating the behavior or abundance of herbivores. Overfishing of predatory fishes and crabs, for example, resulted in an increase in herbivorous crabs that decimated salt marshes in the northwestern Atlantic Ocean (Altieri et al. 2012). The loss of seagrass meadows in the Bermuda, Indonesia and Indian Oceans has been attributed to overgrazing by an abundance of sea turtles that resulted from a lack of shark predation (Fourqurean et al. 2010, Lal et al. 2010, Christianen et al. 2014). In the northeast Atlantic, the decline of commercially valuable Atlantic cod *Gadus morhua* increased mesopredatory fish abundance, leading to decreased epifauna abundance and subsequent increased seagrass epiphyte load and decreased seagrass abundance (Moksnes et al. 2008, Baden et al. 2010, 2012).

Examples of predator recovery suggest declines in vegetated or foundational habitats are reversible through top-down forces sometimes resulting in trophic cascades. For example, the recovery of wolf *Canis lupus* populations in Yellowstone National Park, USA led to increased riparian habitat by reducing elk *Cervus elaphus* foraging pressure (Ripple and Beschta 2003). In the northeast Pacific Ocean, the recovery of sea otters *Enhydra lutris* to nearshore rocky habitats initiated a three-level trophic cascade. Sea otters greatly reduced sea urchin abundance which in turn reduced grazing on kelp resulting in increased kelp abundance, and leading to enhanced primary productivity, greater fish abundance and an overall increase in ecosystem diversity (Estes et al. 1978, Duggins 1980, Duggins et al. 1989, Estes and Duggins 1995, Reisewitz et al. 2006). Using time series, observations and experiments the recovery of sea otters to seagrass *Zostera marina* meadows in Elkhorn Slough California (CA) USA initiated a five-level trophic cascade ultimately leading to increased seagrass biomass by releasing invertebrate epifauna from predation by crabs. In turn these epifauna reduced epiphytic algal loads, preventing them from smothering the seagrass (Hughes et al. 2013). These cascading effects were strong enough to ameliorate eutrophication in the region, which provides a strong bottom-up force that favors the production of epiphytes (Burkholder et al. 2007, Waycott et al. 2009). While dramatic, Elkhorn Slough is noted for its unique physical features and abiotic environment including high nutrient loading, an abundance of effective epifauna grazers including the sea hare *Phyllaplysia taylori*, and the relatively enclosed geography of the slough itself. Therefore whether or not this beneficial effect of sea otters to seagrass occurs independent of this unique setting or in other regions was a motivating factor for this study.

Sea otters inhabit an expansive and remote stretch of seagrass habitats in southeast Alaska (Fig. 1), which provides a unique opportunity to assess the generality of apex predator mediated effects, including trophic cascades, across a large spatial scale and without the bottom-up stress of nutrient over-enrichment. Southeast Alaska supports over 10 000 km of seagrass-dominated shoreline (Harper and Morris 2004, NOAA 2019), nearly as much shoreline (of any type) as the entire west coast of the contiguous United States. Seagrass meadows provide a wealth of ecosystem services, with benefits to the regional economy and social-ecological system, including habitat for fishes and invertebrates, many of which are commercially and traditionally harvested (Johnson et al. 2012, Hughes et al. 2014, Lefcheck et al. 2019). Despite the well-known ecological role of sea otters in kelp forests (Estes et al. 1978, Duggins 1980, Estes and Duggins 1995), little is known about their role in seagrass habitats (Hughes et al. 2019), other than the dramatic patterns seen in Elkhorn Slough, CA (Hughes et al. 2013). More generally, the top-down effects of invertebrate grazers or 'epifauna' in seagrass communities have been well described around the world (reviewed by Heck and Valentine 2007) and indicate that on average top-down forces are stronger than bottom-up forces (Hughes et al. 2004). This pattern appears relatively generalizable across large spatial scales, however, community composition and environmental conditions can differ greatly at the local scale, which can modulate the importance of top-down versus bottom-up (Duffy et al. 2015).

The presence of certain species alone does not guarantee that a trophic cascade will form in a given ecosystem or community. Whether or not a trophic cascade may occur can depend on the spatial heterogeneity of the ecosystem, resource availability, linearity of food chains (Borer et al. 2005), the abundance of key taxa (Ling et al. 2015, Dunn and Hovel 2019) and the intensity of primary productivity in the system (Oksanen et al. 1981, Pace et al. 1999, Sieben et al. 2011). To date, all documented apex predator – seagrass trophic cascades have occurred in eutrophic systems with high dissolved nitrate concentrations. For example, dissolved nitrate in Elkhorn Slough ranges from 10.0 μmol to 600 μmol (Hughes et al. 2013). The trophic cascade patterns described in Elkhorn Slough are a major catalyst for the present study; however they may be the product of a unique combination of biological and environmental factors. In addition to very high nutrient loading, Elkhorn slough has an abundant sea otter population with densities ranging from approximately 0.25 to nearly 400 sea otters km^{-2} . Recent analysis of sea otter population status in southeast Alaska estimate the current maximum densities of sea otters in southeast Alaska at 10.5 sea otters km^{-2} and a range of 0.16–3.66 sea otters km^{-2} around Prince of Wales Island (Tinker et al. 2019). Finally, Elkhorn Slough is a small (~11 km) protected estuary immediately adjacent to an exposed coastline that may constrain the movement of otherwise mobile predators including sea otters, crabs and fishes. This enclosed setting may exacerbate ecological interactions leading to the strong trophic relationships observed.

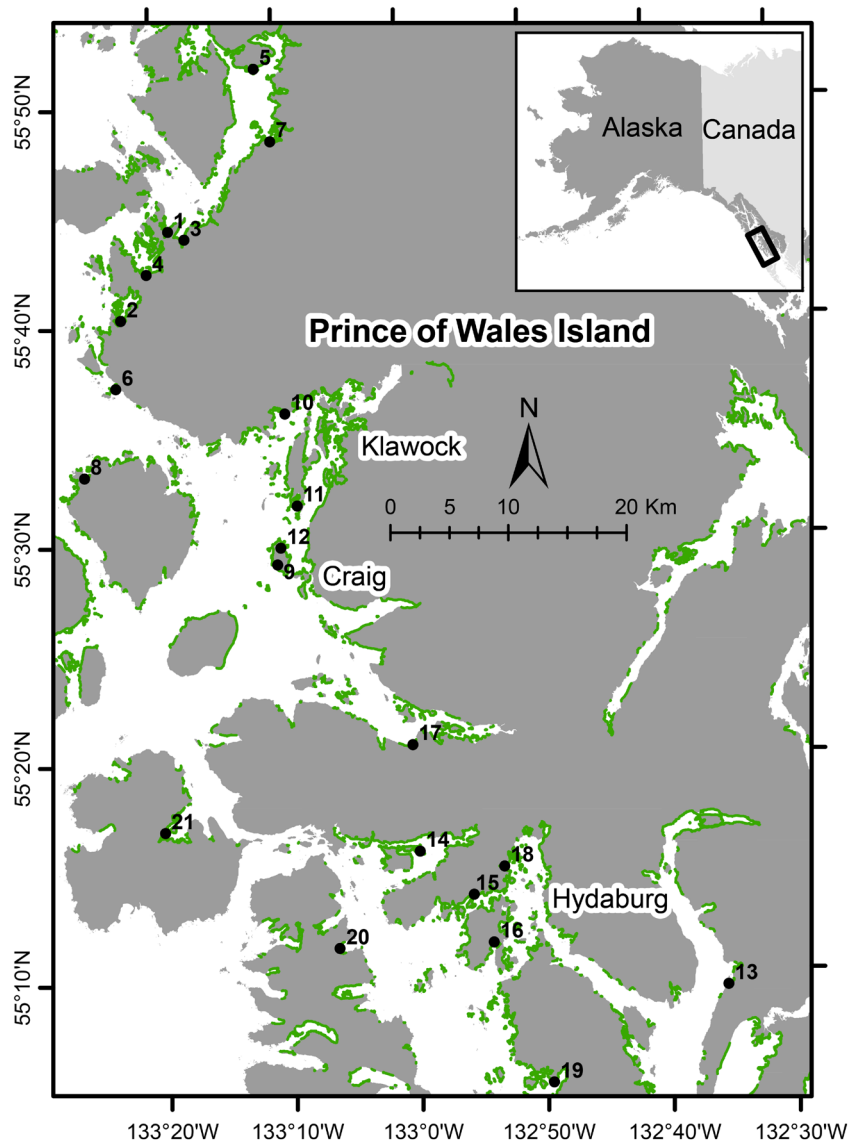


Figure 1. Study are on Prince of Wales Island, Alaska. Green shoreline indicates presence of seagrass (Harper and Morris 2004, NOAA 2019). Points indicate sites of seagrass community surveys, ordered from high (1) to low (21) in terms of the sea otter index.

We examined the ecological relationships between apex-predators, sea otters and seagrass communities to test for the presence of a trophic cascade similar to the patterns described in Elkhorn Slough (Hughes et al. 2013) and the northeast Atlantic (Moksnes et al. 2008, Baden et al. 2010, 2012) in southeast Alaska. While vast, the seagrass communities of southeast Alaska are not well understood, and therefore we developed our hypotheses based on literature from other regions, including the trophic cascade and top-down literature described above, basic ecological theory and sea otter foraging studies from southeast Alaska (Hoyt 2015). We hypothesized that if a sea otter-mediated trophic cascade is present in southeast Alaska, we would find patterns of alternating abundance moving down the trophic hierarchy from sea otters to seagrass, and therefore negative direct biomass

relationships between each successive pair of taxa in the trophic hierarchy. Following trophic cascade theory, these direct negative relationships would lead to positive indirect relationships between sea otters and epifauna, and sea otters and seagrass, as well as between crabs and epiphytes, and epifauna and seagrass. Beyond the ecological relationships described in sea otter–seagrass trophic cascade, we also examined our data for other biotic and abiotic relationships known to influence seagrass communities in other regions. These included the role of mesopredatory fishes which can exert top-down pressure on epifauna (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012, Lewis and Anderson 2012), benthic macroalgae and diatoms (Heck et al. 2000, Valentine and Duffy 2006), sediment grain size (De Boer 2007) and light availability (Lee et al. 2007).

Methods

Study area

The present study was conducted in southeast Alaska on the western coast of Prince of Wales Island (Fig. 1). The region is composed of numerous small and large mountainous islands, glacial fjords, inlets and bays (O'Clair et al. 1997). This varied geography creates a complex nearshore marine environment that includes canopy and understory kelp forests, sand and mud flats, cobble and boulder fields, alluvial fans and seagrass meadows (NOAA 2019). Southeast Alaska's sea otter population is recovering from local extinction during the commercial fur trade (Bodkin 2015) and is concentrated on the outer coast (Tinker et al. 2019). After reintroduction in the late 1960s, the southeast Alaska sea otter population was estimated at 25 000 animals in 2011 (Burris and McKnight 1973, USFWS 2014, Tinker et al. 2019).

Sea otter index

Infrequent population assessments (7–10 years) and variable population growth (Tinker et al. 2019) make annual and local estimates of the southeast Alaska sea otter population difficult. To overcome this, we developed a 'sea otter index' from various sea otter related measures as an overall measure of sea otter occupation and use to apply to each seagrass survey site. The index combined four measures: 1) average sea otter density from two boat-based sea otter surveys conducted for this study, 2) sea otter density estimated from historical population surveys (Tinker et al. 2019), 3) sea otter pits and 4) shell-litter predation assays. 1) Two replicate boat-based sea otter abundance surveys were conducted by driving a small boat at 14 km h⁻¹ and counting all sea otters within a 3.8 km distance (over water) from each seagrass site. Sea otter counts were converted to density based on the total surveyed area and averaged. Given the complex shoreline of the region, the exact survey area differed for each site. 2) The estimated sea otter population density was drawn from a population modeling analysis which fitted all available Southeast Alaska sea otter survey data to a spatially-explicit density dependent population model (Tinker et al. 2019). 3) We counted pits generated by sea otters foraging for clams at each site across three shore parallel 100 × 2 m transects located inside the seagrass bed, on the upper edge and above the upper edge of the seagrass bed. Sea otter pits were defined as depressions greater than ~30 cm in diameter. 4) Along the same 100 m transects, but within a 1-m swath, we collected all clam shell litter that had a complete valve hinge, had no evidence of fouling, and were resting on top of the substrate. We calculated the proportion of shells that showed break patterns consistent with sea otter predation, as opposed to crabs, predatory snails and sea stars/natural death (Boulding 1984, Ambrose et al. 1988, Kvitek et al. 1991, 1992). The combination of sea otter dug pits and the proportion of sea otter cracked bivalve shells helped account for ambiguity surrounding whether or not a pit was actually created by a

sea otter (Traiger et al. 2016). The sea otter index is defined as the first principal component of the four sea otter variables that were transformed via natural log (for counts) or arcsine-square root (for proportions) and standardized to the maximum value across all sites. Principal component analysis was performed using the 'princomp' function in R ver. 3.5.1 (<www.r-project.org>).

Seagrass community surveys

We sampled seagrass *Zostera marina* communities at 21 sites on the west coast of Prince of Wales Island from April through August 2017 (Fig. 1). Sites were randomly selected using the shoreline characterization data in publicly available ShoreZone database (<www.fisheries.noaa.gov/alaska/habitat-conservation/alaska-shorezone>; Harper and Morris 2004, NOAA 2019). This was accomplished by identifying shoreline segments defined as continuous seagrass, without overlap with canopy kelps, with either semi-protected, protected or very protected wave exposure, and with no upland development such as roads or buildings. Along these segments we generated 100 random points. These random points were assessed for logistical feasibility, known sea otter density based on population surveys (Tinker et al. 2019), and compared to prior on-the-ground knowledge of the area. Candidate sites we scouted in person and exact site locations were refined to identify meadows with at least 100 m of continuous seagrass.

At each site, we characterized the composition of the seagrass community including aboveground seagrass biomass, seagrass shoot density, epiphytes on seagrass, macroalgal and benthic diatom percent cover, seagrass associated invertebrate epifauna (hereafter 'epifauna'), crabs (excluding hermit crabs; superfamily Paguroidea) and fishes. We sampled seagrass, epiphytes and epifauna in eight 0.5 × 0.5 m quadrats evenly spaced along a 100 m transect placed at least 5 m linear distance below the upper intertidal edge of the continuous seagrass bed. Given these criteria this transect was placed at approximately -0.5 m relative to mean lower low water (MLLW) across all sites. In each quadrat we measured percent cover of living attached macroalgae, benthic diatoms mats and seagrass shoot density. From each quadrat we randomly collected five seagrass shoots in a 400 µm mesh bag, which was kept cool and transported back to the laboratory for analysis. In the lab, each shoot was floated in freshwater to collect epifauna and then scraped to collect epiphytes. Epifauna primarily consisted (by mass) of isopods (*Pentidotea resicata* = *Idotea resicata*) and limpets *Lottia pelta* and also included gammarid amphipods (suborder Gammaridea), caprellid amphipods (family Caprellidae) and other gastropods (primarily *Littorina* spp. and *Lacuna* spp.). For analysis all taxa were pooled together. Seagrass leaves, epiphytes and epifauna were dried for at least 24 h at 60°C and weighed to the nearest 0.0001 g. For analysis, aboveground seagrass leaf mass was converted to mass per square meter using the shoot density estimates per quadrat. Epiphyte and epifauna load were calculated as mass per gram of total seagrass biomass of the five shoots collected from each quadrat. All seagrass,

epiphyte and epifauna data were then averaged across the eight quadrats at each site.

Crabs were sampled by setting three strings of three pots at each site for 24 h within the seagrass bed. Each string consisted of one 61 × 61 × 33 cm rectangular pot with 10 × 10 cm wire mesh and four 20 cm openings, one 71 cm diameter × 33 cm circular pot with 2.5 × 2.5 cm fabric mesh and two 7.5 cm diameter openings, and one ‘fukui’ pot measuring 60 × 45 × 20 cm with 1 × 1 cm fabric mesh and two 20 cm openings. All pots were baited with ~500 g chopped frozen herring. When pots were collected, all crabs were identified to species and carapace width measured. Carapace widths were converted to biomass using species-specific conversion factors (Supporting information) using Eq. 1. Crab catches were dominated (by mass) by *Cancer productus* and *Metacarcinus* sp. and also included *Telmessus cheiragonus* and *Oregonia* sp. Crab biomass was summed for each string and then averaged across the three strings at each site.

$$\text{mass(g)} = a \times \text{length(cm)}^b \quad (1)$$

Fish abundance, biomass and species composition were quantified following methods described in Johnson et al. (2012). Briefly, fish were captured using a 37 m beach seine designed to capture a wide range of fish with variable-mesh (10 m sections of 32 mm mesh, 4 m sections of 6 mm mesh, 9 m section of 3.2 mm mesh). The seine tapered from 5 m tall at the center to 1 m tall at the ends and was set as a round haul by holding one end on the beach while backing around the other end in a small boat to the beach. All hauls were conducted within ± 1 h of the lowest tide of a given day between 06:30 and 11:00 h. The catch was sorted, identified to species, counted and a subsample (up to 30 fish) of each species was measured to the nearest mm (fork or total length). Unmeasured fish were assigned lengths based on the distribution of lengths from measured fish of that species at a given site. Fish lengths were converted to biomass using species specific length–weight conversion factors (Supporting information) using Eq. 1 and summed for each site. Species composition varied among hauls but were often dominated (by mass) by *Cymatogaster aggregata*, *Gasterosteus aculeatus* and Cottidae and Stichaeidae.

Environmental data

Concurrent with seagrass sampling, we measured water temperature, salinity, light transmittance, primary surface sediment type, and collected a 50 ml water sample for dissolved nitrate concentration analysis at approximately 1 m water depth in the eelgrass bed on the outgoing tide. We also sampled each of these parameters, except light transmittance, at 1 and 4 m water depths at all 21 sites within a single 8 h period on 14 August 2017 to better understand if these parameters varied across space while controlling for seasonal variation. We measured seawater temperature and salinity using a YSI Pro2030 meter. Light transmittance was calculated as the

proportion of light measured at 1 m to light measured at the surface. Light was measured as $\mu\text{mol s}^{-1} \text{m}^{-2}$ using a spherical quantum sensor. Water samples were immediately filtered through a 0.4 μm Whatman GF/F filter into sample vials and then frozen at -20°C until analysis on 11 October 2017 using a flow injection analyzer. We characterized primary surface sediment type along the same transect used for eelgrass collections using a qualitative score (1 = mud, 2 = sandy mud, 3 = muddy sand, 4 = sand, 5 = coarse sand, 6 = pebble, 7 = gravel, 8 = cobble, 9 = boulder, 10 = bedrock) characterized at ten 10 m intervals that were averaged per site.

Statistical analyses

Our analyses focused on identifying the direct ecological relationships between successive pairs of species in the seagrass trophic hierarchy. Our hypotheses were based on trophic cascade theory, documented trophic cascades in the northeast Atlantic and Elkhorn Slough, CA, and sea otter foraging ecology in southeast Alaska and focused on direct relationships between variables. Specifically we hypothesized that sea otters would have a negative relationship with crab biomass (Hoyt 2015), crab and fish biomass would have a negative relationship with epifauna load (Moksnes et al. 2008, Baden et al. 2010, 2012, Lewis and Anderson 2012, Hughes et al. 2013), epifauna load would have a negative relationship with macroalgae cover, diatom cover and epiphyte load, and epiphyte load would have a negative relationship with seagrass biomass (Hughes et al. 2004, Heck and Valentine 2007, Jephson et al. 2008, Duffy et al. 2015). We also hypothesized that the bottom–up forces of light and water nitrate concentration would have a positive relationship with both seagrass biomass and epiphyte load. We included sediment grain size as a possible covariate as it varied somewhat across our study sites and may affect seagrass biomass (Short 1987, Holmer et al. 2006). Finally, we hypothesized that sea otter pits, resulting from foraging for clams, may have a negative direct effect on seagrass biomass. We did not explicitly test for indirect relationships which may arise in communities structured by trophic cascades. Rather, indirect effects can be inferred through series of negative direct relationships between successive trophic levels and alternating patterns of abundance.

We fit linear models for the responses of aboveground seagrass biomass, epiphyte load, epifauna load, crab biomass and fish biomass with predictor variables determined from our hypotheses above. In order to identify which predictors had the greatest weight of evidence for a given response, we fit all possible combinations of predictor variables for a given response and ranked the resulting models with AICc using the ‘dredge’ function in the MuMIn package in R (<www.r-project.org>, Barton 2019). Since our study was aimed at describing the direct ecological relationships among different components of the seagrass community, and we wanted to balance the number of parameters in a given model with our overall replication, we did not include interaction terms in linear models. Full models passed to the ‘dredge’ function are as shown in Eq. 2–6:

$$\text{Seagrass biomass} = \text{epiphyte load} + \text{nitrate} + \text{light} + \text{sediment} + \text{sea otter pits} \quad (2)$$

$$\text{Epiphyte load} = \text{epifauna load} + \text{nitrate} + \text{light} \quad (3)$$

$$\text{Epifauna load} = \text{crab biomass} + \text{fish biomass} + \text{epiphyte load} + \text{macroalgae} + \text{diatom} \quad (4)$$

$$\text{Crab biomass} = \text{sea otter index} + \text{epifauna load} \quad (5)$$

$$\text{Fish biomass} = \text{epifauna load} \quad (6)$$

We averaged model coefficients from all models with $\Delta\text{AICc} < 2$ (hereafter ‘top models’) (Burnham and Anderson 2002) using only models where a given factor was included, as is recommended when factors may have weak interactions with the response (Grueber et al. 2011) with the ‘model.avg’ function in the MuMIn package (Barton 2019). We did not follow the above ‘dredge’ and model averaging procedure for fish biomass because we only hypothesized that epifauna load to have a direct relationship with fish biomass (Eq. 6). To account for different units and magnitudes of measurement among response and predictor variables in a given model, and to allow easy comparison of a coefficient’s magnitude across linear models, we standardized model coefficients in the model averaging procedure to the standard deviation of the response of interest (Barton 2019). We interpret model coefficients based on both the coefficient weight calculated from the model averaging procedure and the p-value from the averaged model. We interpret the coefficient weight as a measure of the relative importance of that factor in explaining a response and the p-value as a measure of the amount of support of the direction and magnitude of the coefficient. Together these values provide an overall measure of the relationship between a given response and a given factor.

All response variables were examined for normality; epifauna load was natural log transformed, crab biomass was square-root transformed, and macroalgae and benthic diatom cover were arcsine square-root transformed for analysis. Furthermore, we were unable to obtain an estimate of benthic diatom cover at one seagrass site. Rather than exclude this site from analysis we replaced this missing value with the overall mean benthic diatom cover from all sites. Given that seagrass community sampling spanned the summer growing season, we first evaluated the effect of time by fitting a linear model for the effect of Julian day on each response variable. We found strong evidence of a positive relationship between Julian day and seagrass biomass ($p < 0.001$) and negative relationship with epiphyte load ($p = 0.005$) and hereafter used the residuals of these linear models as a detrended form of seagrass biomass and epiphyte load.

To further investigate the ecological relationships among the seagrass community, including indirect effects, possible

environmental covariates and alternative ecological relationships in southeast Alaska seagrass communities we preformed correlation analysis on all variables above. Correlation analysis was performed on untransformed data; however we used the detrended forms of seagrass biomass and epifauna load. Analysis was performed with the ‘cor’ function and visualized with ‘corrplot’ function in the corrplot package in R (Wei et al. 2017).

All statistical analyses were performed using the R ver. 3.5.1 statistical environment (www.r-project.org). Data and analysis code can be accessed at doi: 10.5063/V986FN.

Results

Sea otter index

The sea otter index provided a robust measure of sea otter presence at our seagrass survey sites (Supporting information). The first principal component of the principal components analysis accounted for 67.5% of the variation in sea otter measures, with the highest loading on boat-based sea otter surveys (0.575), followed by the population model of sea otter density (0.530), number of sea otter pits (0.527) and the proportion of sea otter cracked clam shells (0.337).

Seagrass communities

We found a range of evidence for the direct relationships we hypothesized to be present in a sea otter–seagrass trophic cascade. (Table 1, Fig. 2, Supporting information). As predicted, the best fit model for crab biomass indicated a strong negative relationship with only sea otter index, and therefore negated the need for model averaging ($p = 0.002$; Table 1, Fig. 2A, Supporting information). We found no evidence of a negative relationship between crab biomass and epifauna load (Fig. 2D). We also found no evidence for a relationship between fish biomass and epifauna load ($p = 0.782$; Table 1, Supporting information). As predicted we found a positive relationship between benthic diatom cover and epifauna load (weight = 0.79, $p = 0.034$; Table 1, Fig. 2B, Supporting information). Contrary to our prediction we found evidence for a negative relationship between epiphyte load and epifauna load (weight = 1.00, $p = 0.028$; Table 1, Fig. 2E, Supporting information). We found weak evidence for a positive relationship between nitrate and epiphyte load (weight = 0.55, $p = 0.097$; Table 1, Fig. 2E, Supporting information). The average model for seagrass biomass did not indicate that any factors had a strong effect or strength of evidence on seagrass biomass. Epiphyte load showed weak evidence of a negative relationship with seagrass biomass (weight = 0.12, $p = 0.092$; Table 1, Fig. 2C, Supporting information). Contrary to our prediction that sea otter pits would have a negative effect on seagrass biomass we found no evidence of this relationship, but sea otter pits were included in the averaged model (Table 1).

Correlation analyses highlighted ecological relationships relating to trophic cascade theory and alternative processes

Table 1. Statistical results for averaged linear models testing the trophic cascade hypothesis. The number of top models ($\leq \Delta 2$ AICc) is reported along with the sum of the Akaike weights from top models, the number of top models containing a given factor and the sum of weights across top models for each factor. Model averaged coefficients were standardized to the standard deviation of a given response. Variables that end in (*) were detrended for the effect of Julian day. Since only one factor, epifauna, was tested against fish biomass, model averaging was not preformed. Detailed model fit provided in the Supporting information.

| Response | N top models | Sum Akaike weights of top models | Factor | N containing models | Sum of weights | Est. | SE | p-value |
|------------|--------------|----------------------------------|------------|---------------------|----------------|--------|-------|---------|
| Fish | — | — | Epifauna | — | — | 0.064 | 0.229 | 0.782 |
| Crabs | 1 | 0.77 | SOI | 1 | — | -0.632 | 0.178 | 0.002 |
| Epifauna | 3 | 0.43 | Epiphytes* | 3 | 1.00 | -0.482 | 0.205 | 0.028 |
| | | | Diatoms | 2 | 0.79 | 0.456 | 0.201 | 0.034 |
| | | | Crabs | 1 | 0.26 | 0.269 | 0.202 | 0.215 |
| Epiphytes* | 5 | 0.83 | Nitrate | 2 | 0.55 | 0.371 | 0.209 | 0.097 |
| | | | Epifauna | 2 | 0.45 | -0.325 | 0.211 | 0.149 |
| | | | Light | 1 | 0.11 | 0.243 | 0.223 | 0.309 |
| Seagrass* | 5 | 0.47 | Sediment | 2 | 0.32 | -0.333 | 0.225 | 0.165 |
| | | | Nitrate | 2 | 0.27 | 0.332 | 0.268 | 0.207 |
| | | | Pits | 1 | 0.21 | 0.297 | 0.234 | 0.204 |
| | | | Epiphytes | 1 | 0.12 | -0.409 | 0.225 | 0.092 |

which may be present in southeast Alaska seagrass communities (Fig. 3A). Notably, we found a positive correlation between sea otter index and seagrass biomass ($R^2=0.43$; Fig. 3B) which was also the greatest correlation between

seagrass biomass and all other untransformed variables. We did not find strong correlation between sea otter index and indicators of primary production including light availability ($R^2=-0.07$) and nitrate concentration ($R^2=-0.08$). Beyond

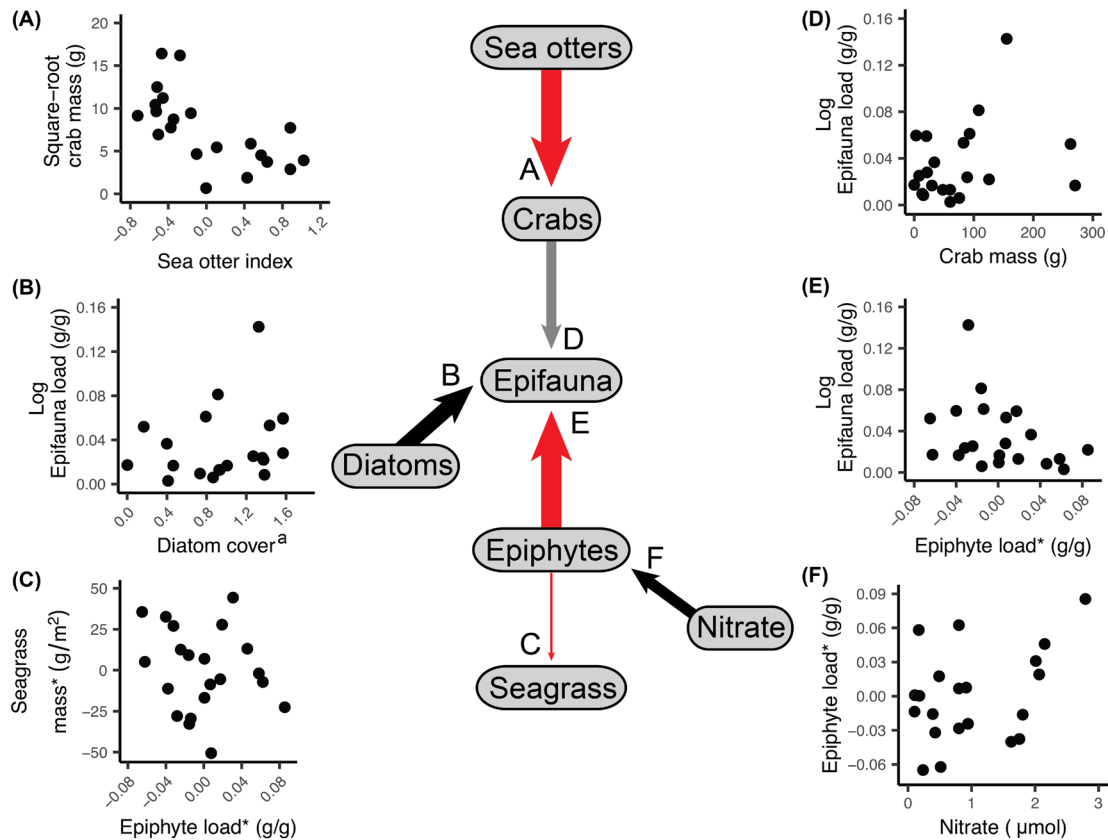


Figure 2. Summary of results of linear models testing for trophic cascade relationships. Arrows point from a factor to a response and indicate positive (black), negative (red) and non-significant (grey) based on coefficients from averaged linear model where p-values ≤ 0.1 . Arrow width is proportional to coefficient weight for a given response. Arrow letters correspond to plots (A-F). Full averaged linear model results are presented in Table 1. Variables that end in (*) were de-trended for the effect of Julian day, and variables that end in (A) were arcsine square-root transformed.

expected trophic cascade relationships we did identify other ecological relationships which may indicate alternative processes which may contribute to the structure of southeast Alaska seagrass communities. These include a strong negative correlation between sea otter index and sediment grain size ($R^2 = -0.66$; Fig. 3C), a negative correlation between sediment grain size and benthic diatom cover ($R^2 = -0.39$; Fig. 3D), and a positive correlation between sediment grain size and crab biomass ($R^2 = 0.46$; Fig. 3E).

Environmental data

Environmental data varied among sites but was within expected ranges for intertidal ecosystems in southeast Alaska and are summarized in the Supporting information. Light transmittance did not vary across the sampling season (linear regression against sample date 29 April–22 August; $p = 0.166$, adjusted $r^2 = 0.051$). As expected, water temperature increased through the sampling season and ranged from 8.0° to 16.6°C (linear regression against sample date 29 April–22 August; $p < 0.001$, adjusted $r^2 = 0.495$). Nitrate measured throughout the sampling season did not show a relationship with sampling date (linear regression against sample date 29 April–22 August; $p = 0.239$, adjusted $r^2 = 0.023$). Salinity showed little variation through the sampling season (linear regression against sample date 29 April–22 August; $p = 0.164$, adjusted $r^2 = 0.052$).

Discussion

We found evidence for some of the hypothesized ecological relationships indicative of a trophic cascade but they varied in their strength of evidence. This included many of the direct relationships among environmental variables–seagrass–epiphyte–epifauna portion of the community, consistent with numerous trophic seagrass studies (reviewed by Hughes et al. 2004) and to other large scale studies (Duffy et al. 2015). However, the strength of evidence for these relationships varied. Notably we found weak evidence for a negative relationship between epiphytes and seagrass biomass, contrary to examples of apex-predator – seagrass trophic cascades. We did not find the expected negative relationship between crabs or fish and epifauna, a critical link in the hypothesized apex-predatory – seagrass trophic cascades. Furthermore, we found no evidence of a relationship between sea otter pits, light availability or nitrate with seagrass biomass. Our correlation analysis supported results from our trophic cascade focused linear models and suggested additional ecological relationships in southeast Alaska seagrass communities including those of sediment grain size, benthic diatoms and possible positive indirect effects between sea otter and seagrass. Given the lack of evidence for all direct relationships necessitating a trophic cascade, our results suggest that sea otters do not initiate a trophic cascade similar to those described in Elkhorn Slough (Hughes et al. 2013) and the northeast Atlantic (Moksnes et al. 2008, Baden et al. 2010, 2012). This may

indicate that sea otter initiated trophic cascades in seagrass ecosystems may depend on the biotic and abiotic context of the system itself (Borer et al. 2005) and that other unique community features may modulate the importance of top-down and bottom-up forces in southeast Alaska seagrass communities compared to other regions (Duffy et al. 2015).

The weak evidence for a trophic cascade in the present study may be a function of the different biotic contexts at all trophic levels and abiotic forces in Prince of Wales Island and southeast Alaska compared to eutrophic ecosystems such as Elkhorn Slough (Hughes et al. 2013) and the northeast Atlantic (Moksnes et al. 2008, Baden et al. 2010, 2012). Strong species interactions can depend on certain species meeting biomass thresholds and can vary across space (Filbee-Dexter and Scheibling 2014, Ling et al. 2015, Dunn and Hovel 2019). Considering the crucial link between crabs and epifauna, we measured drastically lower epifauna loads and crab biomass (= ‘grazer load’) in our system compared to Elkhorn Slough (Hughes et al. 2013). It may be that epifauna in southeast Alaska seagrass communities do not occur in sufficient biomass to provide a reliable and consistent prey resource for crabs; therefore decreasing the interaction strength between these two groups, therefore precluding cascading effects. Furthermore, the isopod *Pentidotea resicata*, which dominated epifauna biomass in our study, is an effective consumer of seagrass associated microalgae, however may experience low predation compared to other epifauna (Best and Stachowicz 2012) further weakening the relationship between mesopredators and epifauna. The unexpected negative relationship of epiphytes on epifauna may be the product of our epifauna and epiphyte loads existing in one of two states: sites that had high epifauna loads with very little epiphytes, or the opposite, similar to patterns described in the northeast Atlantic (Jephson et al. 2008). This pattern may be a function a miss-match between resource (nitrate) availability fueling epiphyte production and the recruitment timing of epifauna at each survey site. Relatively low sea otter densities at our study sites compared to Elkhorn Slough (Hughes et al. 2013) may also have contributed to a lack of evidence for a trophic cascade. While sea otters clearly had a strong negative effect on crab biomass, their predation pressure may not have been sufficient to hold epifauna in check to a similar degree in Elkhorn Slough (Hughes et al. 2013). Finally, while our observed weak negative relationship between epiphytes and seagrass was not in-line with our trophic cascade hypothesis, a similar pattern has been observed in other seagrass systems where microalgae are the predominant epiphyte (Ruesink 2016), suggesting that the patterns described here may be more of a description of the average state of seagrass epiphytes in southeast Alaska than the product of a trophic cascade.

The lack of a relationship between crabs and fish and epifauna load may be the greatest indicator for the absence of a sea otter mediated trophic cascade in southeast Alaska. This result could be due to resource availability described above, and spatial scale induced uncoupling between mesopredators and epifauna. Trophic relationships among species may uncouple when each species functions at a fundamentally

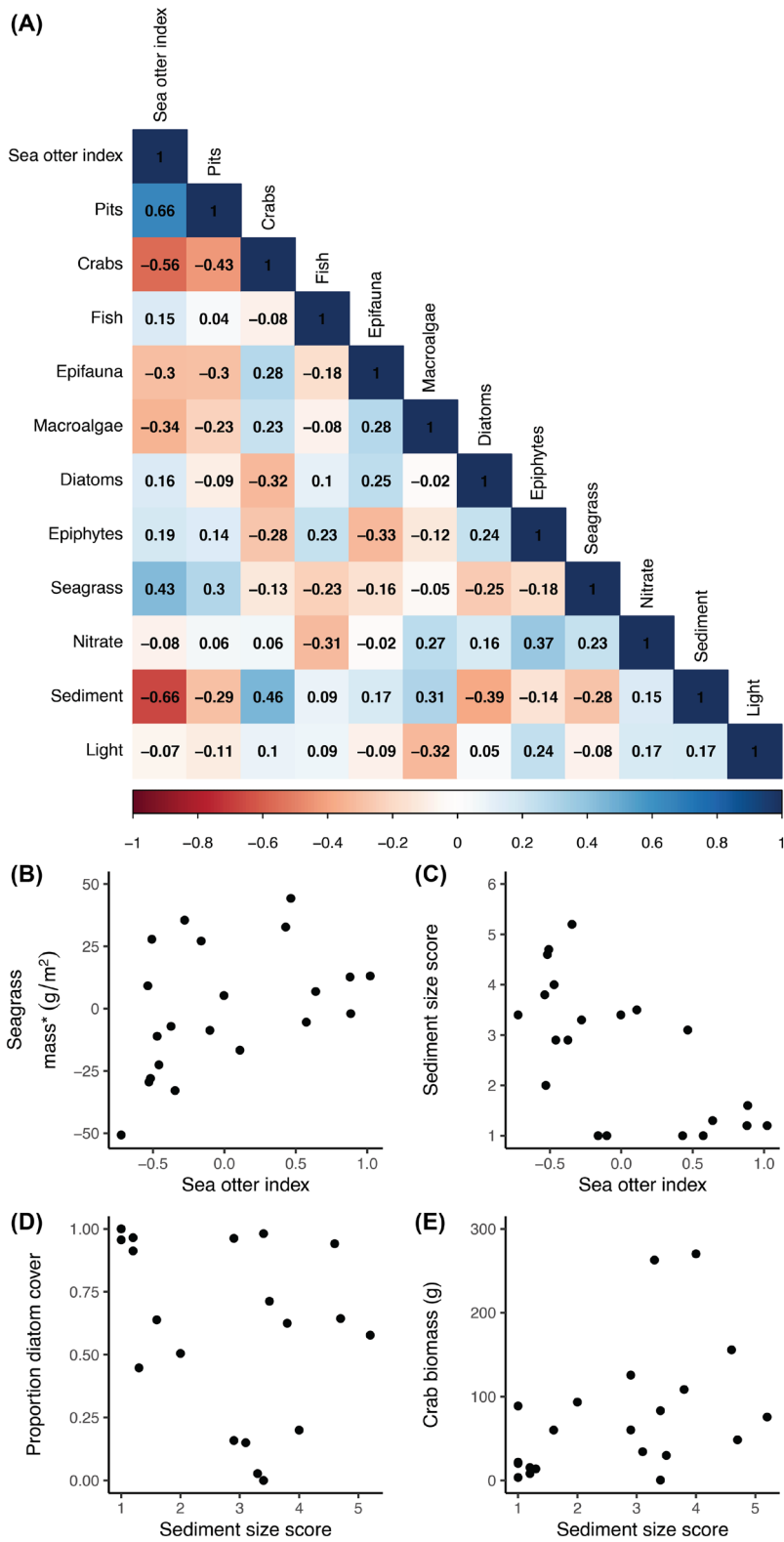


Figure 3. (A) Pearson correlation coefficients among variables used in linear models. Subplots highlighting strong correlations between sea otter index and seagrass biomass (B), sea otter index and sediment size score (C), sediment size score and proportion benthic diatom cover (D) and sediment size score and crab biomass (E).

different spatial scale (van de Koppel et al. 2005). Southeast Alaska and our study area on Prince of Wales Island are composed of a large mosaic of nearshore habitats. Given the mobility and generalist feeding strategy of crabs (*Cancer productus* and *Metacarcinus* sp.) and fishes, it is possible that they consume a variety of prey inside and outside of seagrass meadows which could weaken their direct relationship with seagrass associated epifauna. These potentially weak interactions and complex food webs could further hinder the presence of a trophic cascade (reviewed by Borer et al. 2005). Together, the potential that epifauna are not a reliable food source for crabs and fishes and the likelihood that these species life history operate on different spatial scales may indicate that our assumption that crabs and fishes consume seagrass epifauna was flawed. Field and laboratory studies have tightly linked these mesopredators and seagrass epifauna (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010, 2012, Lewis and Anderson 2012, Hughes et al. 2013), however our results suggest that this may not be the case in southeast Alaska; yet another example of local abiotic and biotic conditions potentially influencing the importance of top-down forces (Duffy et al. 2015). It is also possible that our metric of epifauna biomass is not a good indication of grazing pressure. For example, large bodied and effective sea hares in Elkhorn Slough dominate epifauna biomass in that system (Hughes et al. 2013), whereas sea hares are not present in southeast Alaska. Therefore, future studies may need to focus on certain epifauna taxa with known consumption rates, rather than bulk biomass which may mask strong epifauna–epiphyte interactions.

Our results may highlight how spatial heterogeneity, low resource availability and non-linear food chains can weaken or limit trophic cascades from occurring (Borer et al. 2005). First, our study system is an open, heterogonous seascape consisting of a mosaic of habitat types which may allow species to move among habitats for food and shelter. Second, low resource availability via primary production may have lowered the probability of the formation of trophic cascades and highlights how the intensity of primary production is linked to trophic cascades (Oksanen et al. 1981, Borer et al. 2005, Sieben et al. 2011). For example, the relatively low dissolved nitrate concentrations measured across all our study sites may limit epiphyte production compared to eutrophic systems, therefore limiting the resources available to primary consumers including epifauna. Finally, as a function of both spatial heterogeneity and low resource availability, the seagrass communities in southeast Alaska may not operate as linear food chains. Many trophic cascades have been documented in relatively simple (e.g. three trophic level) food chains with relatively low diversity and/or food chains with strong bottom-up forcing (Borer et al. 2005). To date, data on the food chain complexity of southeast Alaska seagrass communities is limited. However, multiple studies from other regions indicate that seagrass communities are characterized by diverse sources of primary production and diverse consumer diets indicating multiple and potential trophic pathways (Kharlamenko et al. 2001, Jaschinski et al. 2008,

Douglass et al. 2011, Jankowska et al. 2018). Our study provides the best picture to date of southeast Alaska seagrass ecosystems. Further investigations on the community and trophic dynamics of southeast Alaska seagrass communities in light of sea otters, and in general will be needed to fully tease apart the patterns described here.

The lack of evidence for all ecological relationships indicative of a trophic cascade could also be due to spurious correlations which we are unable to resolve in the natural experiment approach of our study. Notably, all sea otter reintroduction sites are along the outer coast of southeast Alaska (Fig. 1), precluding a comparison of sea otter population dynamics and ecosystem effects in inside waters across the same time period. Since the sea otter population is still expected to grow (Tinker et al. 2019) it remains to be seen if sea otters will remain on the outer coast because it is their preferred habitat or if they are only present there because that is where they were reintroduced. Furthermore, our substrate and exposure criteria for selecting suitable seagrasses may not account for other physical and biological factors that influence the presence, absence or density of seagrasses. Temperature and sedimentation, for example, may affect the ability of seagrass to thrive (Zimmerman et al. 2015) and could be influenced by glaciated watersheds which are common in the inside waters in southeast Alaska. We also observed that nearly all the seagrass beds we surveyed existed as relatively narrow (10–20 m) fringing ‘bands’ and other seagrass beds we scouted in our study area were < 100 m patches, rather than expansive ‘meadows’ present in other regions. The high edge-to-area ratio may contribute to many of the results described here, as edge effects can influence predation, survival and growth of multiple seagrass associated species (Boström et al. 2006). To date, how these factors influence seagrasses in southeast Alaska are not well understood.

While our linear models do not suggest a trophic cascade, our correlation results do suggest a positive indirect relationship between sea otters and seagrass biomass and other features of the community which deserve further investigation. However, our analysis was not able to point to a potential mechanism for the positive correlation between sea otters and seagrass. Furthermore, we found an interesting three-way correlation among sea otter index, sediment grain size and seagrass biomass. Sediment grain size was negatively correlated with sea otter index and seagrass biomass ($R^2 = -0.68$, -0.28 respectively; Fig. 3), and sea otter index and seagrass biomass are positively correlated ($R^2 = 0.43$; Fig. 3). This pattern may suggest interplay between sea otter disturbance, sediment grain size and seagrass. We observed that sea otters pits sometimes appeared to remove seagrass, particularly at the upper edge of the intertidal seagrass meadow. However we did not find evidence for any relationship between sea otter pits and seagrass biomass. As our sampling occurred within seagrass beds, this study was not designed to evaluate the effect of sea otter disturbance on seagrass distribution and abundance. We also did not include benthic infauna in our analyses. Notably, burrowing clams, a key component of sea otter diets (Kvitek et al. 1992), could be a linkage between sea otters

and seagrass as benthic infauna can compete with seagrass for belowground space (Castorani et al. 2014). Sediment grain size alone may also influence seagrass biomass. Fine sediments, common at high values of our sea otter index, often have greater ammonium and phosphate concentrations in pore water which are critical to seagrass growth (Short 1987, Holmer et al. 2006). While we did not measure pore water nutrients or sediment organic matter for this study, the negative correlation between sediment grain size and seagrass biomass may reflect patterns of pore water nutrient availability. Furthermore, benthic diatoms may serve as a food source to epifauna (Lebreton et al. 2011, Jankowska et al. 2018) and were found to have a strong positive relationship with epifauna load and a potential propagule source of seagrass epiphytes. This may be especially true in intertidal portions of the seagrass meadow, as at low tide seagrass leaves lie on the substrate perhaps allowing transfer of benthic diatoms to seagrass leaves. However, we found weak correlation between diatoms and other variables.

Fishes are common in seagrass communities worldwide and can consume seagrass associated epifauna, sometimes leading to cascading effects (Moksnes et al. 2008, Baden et al. 2010, Lewis and Anderson 2012), however we did not find evidence of this relationship in southeast Alaska. This may be due to similar reasons as crabs, including mobility, generalist feeding strategy and scale-induced uncoupling described above. The lack of evidence for a relationship between fish biomass and epifauna and weak correlation with other variables may be due to sampling inefficiencies, especially in high seagrass biomass sites, where maintaining optimal beach seine technique was more challenging. Seagrass associated fish biomass was highly variable across sites with a mean of 19.6 ± 30.9 kg. This variability is common in the region (Murphy et al. 2000, Johnson et al. 2012), and may mask an effect of the fish assemblage on epifauna or other variables. Furthermore, we conducted one beach seine set at each site and all seines were conducted at the same portion of the daily tidal cycle, precluding detection of seasonal or tide dependent trends in diversity, abundance and biomass that may influence the epifaunal community and potentially hampered our ability to suggest clear mechanistic relationships. Given the support for the important role of fishes and crabs in seagrass ecosystems from other regions, further research is needed to identify the community and trophic relationships of these species in southeast Alaska.

Temporal changes in the seagrass community which we were unable to detect could have further contributed to variability in our data. Seagrass communities are subject to seasonal changes affecting the seagrass itself (Nelson and Waaland 1997, Clausen et al. 2014) and the abundance and diversity of seagrass-associated species (Heck et al. 1989, Douglass et al. 2010). We did find seasonal variation in seagrass biomass and epiphyte load and were able to account for it by detrending those variables before analysis. However, seasonal trends were not the focus of our study, but could have introduced variation in our data that we are unable to account for. Furthermore, seagrass communities can vary

at both small (< 100 m) and large spatial scales (> 10 km) (Whippo et al. 2018). Our sampling regime was designed to take advantage of the natural experiment set up by the spatial variability of sea otter presence. We designed our sampling so that we would evenly spread our effort across the sea otter gradient through time to reduce confounding the sea otter index with any seasonal effect. This approach precluded assessment of seagrass community variability within sites through time. Seagrass community phenology coupled with spatial variation may have introduced variability in our data that we are unable to account for and may influence our results. Seasonal variation in seagrass community phylogeny almost definitely occurs in southeast Alaska and deserves further study, and may modulate the ecological relationships described here.

The recovery of sea otters is a conservation success story, but has generated conflicts with commercial, recreational and subsistence shellfish harvesters (Carswell et al. 2015). To date it remains unclear if the positive effects of sea otters to seagrass, or kelp forests (Estes and Duggins 1995), outweigh their negative effects on these fisheries (Larson et al. 2013, Carswell et al. 2015, Hoyt 2015) in southeast Alaska. As predator populations continue to recover, an understanding of their effects in multiple ecosystems, and across multiple spatial scales will be essential for their successful conservation and management (Roman et al. 2015, Silliman et al. 2018). Our study directly addressed these questions and found that sea otters may not generate a trophic cascade in seagrass ecosystems characterized by low dissolved nitrate levels, and low epiphyte and epifauna biomass. However, the positive correlation found between our sea otter index and seagrass biomass may suggest an alternative ecological pathway by which sea otters benefit seagrass or vice versa. The southeast Alaska sea otter population is expected to increase (Tinker et al. 2019), further threatening shellfish fisheries. To address the present and coming wave of sea otters, continued research on the social and ecological effects of sea otter recovery will be needed to address these competing views (GREGG et al. 2020). This and other studies provide evidence for the ecological importance of apex predators and highlights the need to integrate this information into management and conservation across diverse habitats, spatial scales and community contexts such as nutrient loading and species composition.

Data availability statement

Data available from the Knowledge Network of Biocomplexity doi: 10.5063/V986FN. (Raymond et al. 2020).

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Author contributions

Wendel W. Raymond: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (equal); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Brent B. Hughes:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Tiffany A. Stephens:** Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Catherine R. Mattson:** Conceptualization (supporting); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Ashley T. Bolwerk:** Formal analysis (supporting); Investigation (equal); Methodology (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Ginny L. Eckert:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (lead); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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