**Title:** Spatial dynamics of animal-mediated nutrients in temperate waters

**Running title:**

**Authors:**  
Em G Lim1,2\*, Claire M Attridge1, Jasmin M Schuster2,3,4, Kieran D Cox1, Kiara R Kattler1§, Emily J Leedham1¶, Bridget Maher3, Andrew L Bickell1†, Francis Juanes3, Isabelle M Côté1

**Affiliations:**

1Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

2Bamfield Marine Sciences Center, Bamfield, British Columbia, Canada

3Department of Biology, University of Victoria, Victoria, British Columbia, Canada

4Hakai Institute, Campbell River, British Columbia, Canada

§Present address: Department of Biological Sciences,University of Alberta, Edmonton, Canada

¶Present address: Institute of Marine Science, Waipapa Taumata Rau The University of Auckland, New Zealand

†Present address: Department of Biology, University of Victoria, Victoria, British Columbia, Canada

\*Corresponding author: Em Lim, em.g.lim13@gmail.com

**ORCID**

Em G Lim:

Claire M Attridge: 0009-0007-8777-2781

Jasmin M Schuster:

Kieran D Cox: 0000-0001-5626-1048

Kiara R Kattler: 0009-0006-4181-5945

Emily J Leedham:

Bridget Maher: 0000-0002-8061-9932

Andrew L Bickell:

Francis Juanes: 0000-0001-7397-0014

Isabelle M Côté: 0000-0001-5368-4061

Significance Statement

Author Contribution Statement

**Abstract**

Consumer-mediated nutrient dynamics (CND), through which animals’ metabolic waste products fertilize primary producers, drives variability in nutrient availability in tropical waters. This variability influences primary productivity and community functioning. Yet, examinations of CND as a driver of variation in nutrient availability in temperate marine ecosystems are limited. Therefore, we assessed the existence and drivers of variation in CND at meso, small, and fine spatial scales within temperate marine ecosystems. To do so, we quantified the occurrence of 48 fish and 92 macroinvertebrate taxa and measured in situ ammonium at 27 northeast Pacific rocky reefs for three years and 17 kelp forests of varying density for one year. Ammonium concentrations ranged from 0.01 to 2.5 uM across rocky reefs separated by tens of km. The relationship between animal biomass and ammonium among sites was mediated by water flow, where flood tides seemed to “wash away” the effect of nutrient regeneration by animals, although enrichment was possible on ebb tides. Ammonium was significantly higher within than outside of kelp forests, a difference that increased with tide exchange, kelp biomass, and to a lesser degree animal biomass. Caging experiments revealed that fine-scale (~2 m) ammonium variability and nutrient enrichment were only possible under low-flow conditions. Our results suggest that CND drives nutrient variability at scales ranging from two meters to over 20 km, acting on a finer scale than allochthonous nitrogen sources such as upwelling. Therefore, consumer-mediated nutrient dynamics are implicated as a previously overlooked driver of spatial variation in primary productivity in temperate marine systems.

**Introduction**

Variation in resource availability across spatial and temporal scales can drive substantial heterogeneity in the growth, biomass and composition of primary producers (Dayton et al., 1999; Leibold, 1991; McInturf et al., 2019; Tilman, 1984). In many marine ecosystems, community structure is regulated through bottom-up control, i.e., it depends on factors that generate variability in the resources available to lower trophic levels (Gruner et al., 2008). Although marine ecologists have historically focused on external, abiotic sources of nutrients (e.g., upwelling) as drivers of variability in nutrient availability, there is emerging evidence that consumers also contribute to bottom-up effects (Allgeier et al., 2017). Metabolic waste products (i.e., excretion and egestion) of animals fertilize primary producers via a process termed consumer-mediated nutrient dynamics (CND; Vanni, 2002). Consumers excrete metabolic waste in the form of ammonium (NH₄⁺), which is preferentially taken up by primary producers over other forms of nitrogen like nitrate and nitrite (Lobban and Harrison, 1994; Phillips and Hurd, 2004). However, the ecological importance of consumer-regenerated nutrients at varied spatial scales remains unclear. Therefore, identifying the extent to which biologically relevant variation in nutrient availability contributes to heterogeneity in primary productivity remains an active area of research (Allgeier et al., 2017).

Heterogeneity in consumer habitat use greatly influences spatial and temporal variation in nutrients supplied by animal waste (Benkwitt et al., 2019; Roman and McCarthy, 2010; Uthicke, 2001). For example, tropical coral reefs provide habitat, shelter, and food sources that attract dense aggregations of vertebrate and invertebrate consumers which regenerate nutrients (Archer et al., 2015; Shantz et al., 2015). On a meso scale, productivity increases with proximity to reefs with high densities of fishes (Layman et al., 2016), while on a fine scale, sheltering schools of fish increase nitrogen concentrations around individual heads of corals relative to neighboring uninhabited corals (Holbrook et al., 2008). Diurnal migrations are another source of temporal and spatial variation in consumer-regenerated nutrients, as some fishes travel away from reefs to forage at night, then return to excrete waste around their hiding spots during the day (Francis and Côté, 2018; Meyer and Schultz, 1985). At an even larger-scale, variation can arise from the migration of megafauna; for instance, whales transport and deposit nutrients across thousands of kilometers as they travel from their feeding to breeding grounds (Doughty et al., 2016). However, the current understanding of animal-driven spatio-temporal variability of nitrogen is drawn substantially from tropical ecosystems (Allgeier et al., 2013; Holbrook et al., 2008; Meyer et al., 1983), often overlooking productive temperate marine ecosystems.

In temperate oceans, external sources of nutrients, such as upwelling and freshwater runoff, are generally considered the dominant drivers of nitrogen variability (Dayton et al., 1999; Lønborg et al., 2021). Due to the open nature of nearshore environments, high water flow from currents, tides, and wave action are believed to limit small-scale (1 to 100 m2) nutrient variation (Probyn and Chapman, 1983). Therefore, research on intertidal and shallow subtidal ecosystems has traditionally focused on top-down trophic interactions as the drivers of community composition at small scales, while limiting considerations of resource limitation to large regional or continental scales (Menge, 1992; Paine, 1986). However, evidence suggests meso-scale (10 to 100 km; Broitman et al., 2001) variation in allochthonous nitrogen via upwelling may contribute to bottom-up control of marine communities (Menge et al., 1997; Nielsen and Navarrete, 2004) and even weaken top-down control (Sellers et al., 2020). Consumer-mediated nutrient dynamics may also contribute to smaller scales of nutrient variability than previously assumed. For instance, abundance of intertidal mussel beds has been linked to variation in nitrogen concentrations along entire coastlines (Pfister et al., 2014), across 10s of meters (Aquilino et al., 2009), and among tidepools (fine-scale microhabitats; Bracken, 2004). Therefore, regenerated nitrogen may contribute substantially to meso-, small-, and fine-scale variation in nutrient availability, even in high-flow, upwelling-dominated nearshore coastal ecosystems.

Shallow subtidal rocky reefs and kelp forests are temperate nearshore habitats that attract dense aggregations of fishes and invertebrates, many of which are economically, ecologically, and culturally important (Steneck et al., 2002). Elevated NH₄⁺ excretion from the concentrated biodiversity and biomass of these communities may also contribute to nutrient hotspots on small to meso scales. Fast-growing canopy kelps, which form expansive underwater forests, may benefit from these excretions directly as a source of nitrogen (in the form of NH₄⁺), especially during low upwelling periods (Brzezinksi et al., 2013; Lees et al., 2024). These kelps, which comprise giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis leutkeana*) in the northeast Pacific, also influence the hydrodynamics and hydrochemistry of seawater, both slowing water flow within the forests and generating gradients of carbon content, pH, alkalinity, and oxygen (Gaylord et al., 2007; Jackson and Winant, 1983; Pfister et al., 2019). These modifications of the surrounding fluid environment by kelp forests could affect the productivity and community composition of other primary producers and contribute to small-scale spatial nutrient heterogeneity.

We aimed to quantify the contribution of animal-regenerated nitrogen to spatial variability of nutrients in a temperate, wave-swept upwelling region (Barkley Sound, British Columbia, Canada). This region is located on the traditional territories of the Huu-ay-aht Nation and comprises an archipelago of islands dotted with rocky reefs and kelp forests of heterogeneous structure. We hypothesized that animal-regenerated nutrients contribute to variability in resource availability across three distinct spatial scales. Specifically, we predicted that NH₄⁺ variation would be detectable at the meso-scale due to variation in animal abundance among sites. We also expected to observe variation in NH₄⁺ concentrations at small scales (within natural sites) and fine scales (between experimental cages), but only under conditions that allow for local enrichment (e.g., low tidal exchange). To test these predictions, we measured variation in NH₄⁺ concentrations among rocky reef sites (meso scale of ~10s of km), in and out of kelp forest sites (small scale of 5 m), and near experimentally caged consumers (fine scale of < 2 m, Fig. 1a, b, c). We quantified the abundance and diversity of fishes and invertebrates at each rocky reef and kelp forest site and measured kelp forest metrics and abiotic variables to explore potential drivers of variation in NH₄⁺ concentrations. By characterizing the scale at which animal-driven nutrients vary, we hope to uncover the extent to which consumers in temperate regions structure communities not only from the top down, but also the bottom up through CND.

**Methods**

*Site description*

Barkley Sound is located in an upwelling region on the west coast of Vancouver Island, Canada. Upwelling supplies nitrates in the spring and early summer, while storms flush riverine inputs into the nearshore in the winter and spring (Pawlowicz, 2017). Due to the proximity of the Bamfield Marine Sciences Centre (BMSC), this region has been a long-term focal area for studies seeking to document the response of kelps to marine heatwaves, establish ecological baselines, and unravel ecosystem dynamics (Attridge et al., 2024; Starko et al., 2024, 2022; Tanasichuk, 1998). Subtidal fish communities in this region include at least 18 families including gobies, surfperches, rockfishes, greenlings, and sculpins (E.G. Lim, unpubl.). Macroinvertebrate assemblages, which are made up of over 49 families, are dominated by sea urchins, turban snails, sea stars, sea cucumbers, and abalone (E.G. Lim, unpubl.).

*Surveys of meso-scale (among-site) variation*

To explore meso-scale variation in animal-regenerated nutrients among rocky reefs, we measured ammonium (NH₄⁺) concentrations and surveyed fish and invertebrate communities at 27 subtidal sites ranging from 0.06 – 24 km apart in Barkley Sound (Fig. 1d). We used a globally standardized method (i.e., Reef Life Survey, RLS) at each site to estimate fish and invertebrate abundance and collected subtidal NH4+ samples during each survey. We conducted our surveys in the spring (April-May) for three years (2021-2023), with all annual surveys occurring within two weeks of each other (Table S1.1). A full explanation of the Reef Life Survey method is available online (http://www.reeflifesurvey.com/methods) and provided by Edgar and Stuart-Smith (2009) and Edgar et al. (2020). Briefly, at each rocky reef site, a pair of RLS-trained SCUBA divers assessed fish and invertebrate abundance and diversity along each side of a 50 m transect line. First, fishes in the water column were counted and sized (total length, in various size class categories) within 5 m on either side of the transect line (500 m2), and then benthic cryptic fishes (also sized) and large mobile invertebrates (> 2.5 cm) were counted within 1 m on either side of the transect line (100 m2).

Immediately following each RLS survey, we collected three 60 mL subtidal seawater samples at 0, 25, and 50 m along the transect, 0 – 2 m above the substrate, and stored the syringes in sealed plastic bags upon collection to prevent contamination. Seawater samples were filtered into opaque amber bottles in the field and frozen for a maximum of two weeks before NH4+ analysis. We confirmed that freezing samples for this duration did not affect NH4+ concentration (E. G. Lim unpubl.). In 2021 and 2022, we followed the fluorometric method using 40 mL seawater samples (Holmes et al., 1999), and in 2023, we followed the fluorometric standard-additions protocol II (Taylor et al., 2007). These methods produce similar results, although the Holmes single spike method is associated with higher variability in measurements (Taylor et al., 2007). The three NH₄⁺ samples collected during each survey were averaged to determine the mean NH₄⁺ concentration for each site.

*Surveys of small-scale (within-site) variation*

To investigate small-scale variation of animal-regenerated nutrients, we measured NH4+ concentrations inside and outside kelp forests and surveyed the resident biological communities as potential moderators of this variation. Our 16 sites comprised forests of varying densities dominated by giant kelp or bull kelp, and two no-kelp control sites. We conducted surveys from July to September 2022 (Table S1.2). First, divers conducted RLS surveys (as above) along 50 m transect lines parallel to the edge of the kelp forest to quantify the abundance and biodiversity of fish and invertebrate communities associated with each kelp forest. Next, divers ran four 5 m-long transects perpendicular to the RLS transect (5 m apart) into the kelp forest to assess kelp density, canopy height, and kelp biomass (Fig. S1.1). Divers then counted the number of canopy kelp individuals (bull or giant kelp) within 0.5 m on either side of each kelp transect to measure kelp density. To estimate canopy height, we measured the length of five randomly selected kelp individuals per kelp transect; for bull kelp we measured the total length from holdfast to pneumatocyst in situ, but for giant kelp, we collected five random individuals to measure the length from holdfast to the tip of the apical meristem on dry land. To quantify bull kelp biomass, we measured the sub-bulb circumference (15 cm below the bottom of the bulb) of the same five bull kelps per transect in situ and calculated individual biomass using a quadratic diameter to biomass formula for Barkley Sound (C. M. Attridge unpubl.). For giant kelp biomass, we weighed (to the nearest 1 g or less) the same five individuals per transect that were collected for total length measurements. We multiplied the mean biomass estimate for each kelp species by the species density to calculate a biomass/m2 estimate for each kelp transect, which we then averaged over the four transects per forest to estimate overall mean forest biomass/m2. We estimated total forest area by swimming around the perimeter of the forest on the surface with a Garmin GPSMAP 78SC, which we used to calculate total forest biomass (kg).

Finally, to compare NH₄⁺ concentrations inside vs outside each kelp forest, we collected paired 60 mL syringes of seawater immediately outside the kelp forest within 0 – 2 m above the substrate, and 5 m into the kelp forest at the same depth. We collected three paired NH₄⁺ samples from each site, which were spaced 5 m apart, by matching them with the first three kelp transects. Outside each kelp forest, we also filled a plastic Ziplock bag with seawater to create standards. Samples and standards were filtered into amber bottles in the field and stored on ice for transportation back to the laboratory, at which point we measured NH4+ concentration in each sample bottle following the fluorometric standard-additions protocol II for 40 mL samples (Taylor et al., 2007). For each paired inside and outside kelp forest NH₄⁺ sample, we calculated ∆NH₄⁺ = inside NH₄⁺ - outside NH₄⁺.

*Surveys of fine-scale (microhabitat) variation*

To quantify the ability of animals to affect the NH₄⁺ concentration in their immediate vicinity we conducted two caging experiments in situ near Bamfield. We used California sea cucumbers (*Apostichopus californicus*) in the first caging experiment because they are a large, abundant invertebrate with a high excretion rate (Bray et al., 1988). The first experiment occurred May 27 – 28, 2021 at Scott’s Bay (48°50'05.2"N, 125°08'49.3"W), a wide, exposed bay that opens into Trevor Channel (Fig. 1d). We constructed 18 wire cages (26 x 26 x 26 cm), which we covered in 2 mm plastic mesh. These cages were spaced 3 m apart along two weighted lines (9 cages per line) and deployed at 3 to 5.8 m depth. We collected adult California sea cucumbers from the site via SCUBA, measured contracted sea cucumber length and girth, and immediately placed them into the cages in randomly assigned densities of 0, 1, or 2 sea cucumbers (n = 6 replicates per density). After 24 hours, we returned to collect water samples from each cage in situ. While underwater, we minimized water movement by reducing our fin and hand movements while opening the mesh lids, which were secured with wire and just wide enough to collect a 60 mL syringe of seawater. Once at the surface, we filtered 40 mL of each sample into amber bottles and transported them on ice to the lab, where we measured NH4+ using the fluorometric method (Holmes et al., 1999).

We used red rock crabs (*Cancer productus*) in the second caging experiment to see if a species with an even higher individual-level excretion rate could produce fine-scale nutrient variation. The second experiment occurred over nine days from June 10 – 19, 2023 in Bamfield Inlet (48°49'53"N 125°08'11"W), a narrow, sheltered inlet (Fig. 1d). We replicated this experiment from June 19 – 28, 2023 following the same methodology. We collected red rock crabs from the site using crab traps and kept them at BMSC in flow-through sea tables for 2 – 10 days. Crabs were fed salmon every 2 – 4 days, and all crabs were fed the night before each experiment started. We constructed 12 cages from clear plastic (40 x 28 x 17 cm), with two 15 x 9 cm windows covered in a dual layer of 10 mm plastic mesh and 1 mm mesh to allow for water flow. The cages were randomly distributed every 2 m along a lead line anchored with cement blocks 0.8 m below chart datum. Each cage contained either one large crab (carapace 15.0 – 15.9 cm), one medium crab (11.6 – 14.4 cm), or a control (i.e., a small rock, scraped clean, so weight was similar across all cages) (n = 4 replicates per experiment). During both experiments, we replaced the crabs after 4 days with freshly fed, similar-sized crabs, at this point, we re-randomized the order of the cages along the line to minimize any effect of cage location. We measured seawater NH₄⁺ concentration via snorkel at low tide at the beginning, middle, and end of each nine-day experiment by drawing water samples using a 60 mL syringe and a fixed narrow rubber tube that began in the centre of the cage and extended several inches outside the mesh window. We filtered 40 mL of each sample into amber bottles, which were stored on ice before NH₄⁺ analysis via fluorometric standard-additions protocol II (Taylor et al., 2007).

*Statistical analyses*

All statistical analysis were conducted in R (v4.1.2, R Core Team, 2019) using RStudio (v1.3.1093, RStudio Team, 2016). We used tidyverse packages for data manipulation and visualization (Wickham et al., 2019), ‘glmmTMB’ for all modelling (Brooks et al., 2017), and DHARMa to check model fit (Hartig, 2022). We ensured all models met assumptions by inspecting residuals using the DHARMa simulateResiduals function and checked for collinearity between variables using the vif function from the car package with a cutoff value of 2.

For each Reef Life Survey conducted, we calculated fish biomass from fish length following the formula:

W is fish weight, L is the fish length, a and b are species-specific constants from FishBase (Froese et al., 2014). All mobile invertebrates were counted, but only sunflower sea stars (*Pycnopodia helianthoides*) and economically important species (abalone [*Haliotis kamtschatkana*] and scallops [*Crassadoma gigantea*]) were sized. We used published length–weight relationships to calculate wet weight from length for these three species. For all other invertebrates, we used published wet weights to estimate biomass for each taxon. We used shell-free wet weight for species with large shells, such as hermit crabs and snails. When biomass information was unavailable for a species, we used estimates from the closest relative or most similarly sized species available (Table S1.3). Animal abundance per m2 was calculated as the total number of fishes and invertebrates counted on each survey (divided by 500 m2 for pelagic fishes and by 100 m2 for cryptic fishes and macroinvertebrates), and we used the ‘vegan’ package to calculate Shannon and Simpson diversity indices (Oksanen et al., 2022). We calculated the tide exchange by computing the percent change of the tide height every minute, averaged over the hour-long survey.

Meso-scale (among-site) variation

To explore meso-scale variation in NH₄⁺, we constructed generalized linear mixed-effect models (GLMMs) with NH₄⁺ concentration as the response variable, and animal abundance, tide exchange, an interaction between abundance and tide, Shannon diversity, and survey depth as predictors, and random effects of site and year. All predictors were scaled and centered around the mean using the scale function. We used a gamma distribution (link = ‘log’). To test the robustness of our modelling approach, we considered animal biomass as a predictor instead of abundance, and Simpson’s diversity instead of Shannon diversity; alternative models including these predictors were not better supported by AIC (Table S1.4). We ran additional models considering the effect of only the most abundant families of fishes and invertebrates, which are fully described in Electronic Supplement 2.

Small-scale (within-site) variation

To determine whether NH₄⁺ concentration differed inside and outside of kelp forests, we used a linear mixed-effects model (LMM) with ∆NH₄⁺ as the response variable (n = 3 estimates per site), and kelp species, mean forest kelp biomass (per m2), tide exchange, animal biomass, survey depth, Shannon diversity, and interactions between kelp biomass and tide exchange, kelp biomass and animal biomass, and animal biomass and tide exchange as fixed effects. All continuous predictors were scaled and centered around the mean as above. We included site as a random effect (1|site) as each site contributed three estimates to the analysis and used a Gaussian distribution. As above, we chose our final set of predictors upon comparing AIC values of models with alternate predictors (Table S1.5). We then ran additional models considering the effect of only the most abundant families of fishes and invertebrates (Electronic Supplement 2).

Fine-scale (microhabitat) variation

We constructed separate linear models for each caging experiment to quantify the impact of caged animals on adjacent NH₄⁺ concentration. For the sea cucumber experiment, we regressed cage NH₄⁺ concentration against the treatment (i.e., sea cucumber density: 0, 1, or 2 sea cucumbers) and cage depth (centered) using a Gaussian distribution. We calculated the NH₄⁺ excretion rate for each sea cucumber using a previously generated size-to-excretion relationship (Table S1.6). For the red rock crab experiment, we constructed a generalized linear mixed-effects model (GLMM) with cage NH₄⁺ concentration as the response variable and treatment (no crab, medium crab, or large crab) as the predictor variable with a gamma distribution (link = ‘log’). We included a random effect of sampling day because we measured NH₄⁺ three times per experiment, and a random effect of experimental week, because we replicated the whole experiment twice. We used a previously developed carapace-to-excretion relationship to calculate NH₄⁺ excretion rates for each crab (Table S1.7).

**Results**

We found evidence of meso-scale variation in ammonium (NH₄⁺) concentrations, which ranged from 0.07 μM – 2.06 μM among rocky reefs in Barkley Sound (Fig. 1d). Overall, we found no evidence that NH₄⁺ concentration was correlated with animal abundance (GLMM, p = 0.57), tide exchange (p = 0.99), Shannon diversity (p = 0.41), or survey depth (p = 0.61; Fig. 2a). However, we did find a significantly negative interaction between animal abundance and tide exchange (p = 0.01; Fig. 2b), revealing a weakly positive effect of total animal abundance per m2 on NH₄⁺ concentration, but only at ebb tide. In the models considering only the abundance of one animal family at a time, we found evidence for a positive relationship between the abundance of greenlings (Hexagrammidae) and whitecap limpets (Acmaeidae) and NH₄⁺ (p = 0.03; Fig. S2.1). The single-family models did not reveal a significant effect of any other predictors (Fig. S2.1 and Table S2.1).

We also documented evidence of significant small-scale, within-site variation of NH₄⁺ (Fig. 3).; concentrations were 1.3x higher inside giant kelp forests and 1.6x higher inside bull kelp forests than outside (LMM, p < 0.001; Fig. 3b). The ‘excess’ NH₄⁺ concentration inside kelp forests increased with kelp biomass (p < 0.001; Fig. 3c), and tide exchange (p = 0.007; Fig. 3a). We found limited evidence for an effect of animal biomass (p = 0.07; Fig. 3a), survey depth (p = 0.07; Fig. 3a), and Shannon diversity on ∆NH₄⁺ (p = 0.09; Fig. 3a). There was a positive interaction between kelp forest biomass and tide exchange, whereby the positive effect of kelp biomass on ∆NH₄⁺ increased with tide exchange (p < 0.001; Fig. 3a & c). We also identified a negative interaction between kelp biomass and animal biomass (p = 0.006; Fig. 3a & d), and a negative interaction between tide exchange and animal biomass (p = 0.004; Fig. 3a & e). The change in NH₄⁺ was negative between samples taken 5 m apart at the no-kelp control sites (p = 0.003; Fig. 3b). For the single-family models, five families displayed significant relationships between biomass and ∆NH₄⁺, while the biomass of Gobiidae was negatively correlated with ∆NH₄⁺ (Fig. S2.2 and Table S2.2).

We found mixed evidence for animal-related fine-scale variability in NH₄⁺ concentration. For sea cucumbers, we found no effect of sea cucumber density on cage NH₄⁺ concentration despite a supply rate of 14 μM/h and 28 μM/h for the low and high treatments, respectively. Overall, the mean NH₄⁺ concentration was 0.92 ± 0.04 μM across all cages (LM, p > 0.75 for both treatments; Fig. 4a). However, we see a positive effect of cage depth, whereby NH₄⁺ increased by 0.38 ± 0.05 μM per m increase in depth (p < 0.001). For red rock crabs, both medium and large crabs significantly increased the cage NH₄⁺ concentration relative to control cages, by 8.7x and 12.1x respectively (GLMM, p < 0.001 for all; Fig. 4b). Medium crabs excreted on average 88 μM/h while large crabs excreted 150 μM/h.

**Discussion**

We found evidence of variability of animal-regenerated nutrients from the largest to the smallest scale examined, although the strength of the signal varied. Ammonium (NH₄⁺) varied by up to 16x between rocky reef sites within a year, 1.9x inside vs outside kelp forests, and 40x between cages with and without crabs. Water flow (i.e., tidal exchange and wave exposure) mediated the capacity for animals to saturate the water column with nutrients. Among sites a flooding tide seemed to “wash away” the impact of animals on NH₄⁺ concentrations; in contrast, within sites, moving water made kelps’ ability to slow flow and trap animal-regenerated nutrients more pronounced. In the fine-scale caging experiments we only detected an effect when the nutrient providers were crabs – an effect that we attribute mainly to the low water flow in the protected inlet rather than to the taxa. Nevertheless, across all three scales, there was animal-mediated spatial heterogeneity in nutrient availability, which may contribute to bottom-up effects.

*Meso-scale (among-site) variation*

In rocky reef habitats, we detected a 16-fold difference in NH₄⁺ among sites with the lowest and highest concentrations. This difference is substantially greater than previous measurements of among-site variation in nitrate (3.7x and 6.5x) and ammonium (0.4x and 0.8x) from the same region (Druehl et al., 1989; Hurd et al., 2000). It is also larger than among-site NH₄⁺ differences measured in nearby Washington State (1.1x, Pfister et al., 2014). We had predicted that variation in NH₄⁺ concentration among sites would be driven primarily by animal abundance. We were partly correct since the only significant predictor of among-site differences in NH₄⁺ was a negative interaction between tide exchange and animal abundance, whereby animal excretions may enrich the seawater when the tide is ebbing or slack, but the effect of animal abundance is washed away when the tide comes in. Although marine species diversity sometimes covaries with animal abundance or biomass (Müller et al., 2018; Yee and Juliano, 2007), we found no relationship between Shannon diversity and NH₄⁺. We did not quantify intertidal animals or microbial regeneration, which are additional sources of NH₄⁺ (Aquilino et al., 2009; Lowman et al., 2023), but these may be more important in shallower waters and soft-sediment areas than on the subtidal rocky reefs we studied. We conclude that CND likely contributes to meso-scale variation in NH₄⁺ in an unexpected, dynamic, tide-associated manner, which could drive among-site variation in primary productivity and thus bottom-up control.

*Small-scale (within-site) variation*

We found evidence of kelp-mediated nutrient variation on a smaller scale (5 m) than previously established. Although higher NH₄⁺ inside high-density kelp forests has been documented (e.g., Pfister et al., 2019), these studies compared nutrient samples taken from the middle of very large kelp forests to sites more than 50 m away from the forest edges (Pfister et al., 2019; Stewart et al., 2009; Traiger et al., 2022). By sampling inside and outside forests across a gradient of kelp densities we further demonstrate a positive relationship between kelp biomass and NH₄⁺ retention. The retention of NH₄⁺ observed is likely due to the dampening of flow within the kelp forest bed and subsequent flow acceleration around the edges (Gaylord et al., 2007; Rosman et al., 2007). Indeed, as predicted, we found the effect of kelp biomass on NH₄⁺ retention was more pronounced when the tide was rising (flood tide). Unfortunately, we never sampled on ebbing tides, and did not quantify water motion due to waves or currents, so we could only contrast slack and flooding tides. Nevertheless, it seems that water flow due to tidal exchange enhances NH₄⁺ variability within kelp forests instead of masking it.

We uncovered additional drivers of differences in NH₄⁺ concentration inside and outside kelp forests, namely kelp species and animal biomass. We found higher ∆NH₄⁺ (NH₄⁺ inside - NH₄⁺ outside) in bull kelp forests compared to giant kelp forests, which may be due to their different allocations of biomass in the water column and thus different alterations of water flow. Indeed, Traiger et al., (2022) found the effect of giant kelp forests on water chemistry was smaller than that of bull kelp forests, previously described by Murie and Bourdeau (2020). Somewhat surprisingly, at the no kelp sites, NH₄⁺ was lower in the “inside” samples, which were closer to shore, compared to the “outside” samples, which were taken 5 m farther from shore and often slightly deeper despite our efforts to maintain a consistent sampling depth. NH₄⁺ tends to *increase* with depth (Brzezinksi et al., 2013), which might explain this result. As we found the opposite trend at our kelp sites, where the “inside” kelp forest samples had more NH₄⁺ than the possibly deeper “outside” samples, we are confident this result is due to retention of NH₄⁺ by kelp, instead of an artifact of our sampling procedure.

Even though kelp forests attract dense aggregations of fishes and invertebrates, the positive effect of animal biomass on ∆NH₄⁺ was weak and mediated by water flow and kelp biomass. Shannon diversity was positively associated with both animal and kelp biomass (Fig. S1.2), but weakly negatively affected ∆NH₄⁺. The negative interactions between animal biomass and both tide and kelp biomass suggest a potentially saturating relationship among these variables. When animal biomass was low, increased kelp biomass or tidal exchange increased ∆NH₄⁺, whereas at high animal biomass, increasing kelp or flow had no effect. There may therefore be a threshold for how much animals can saturate and therefore increase ∆NH₄⁺ in kelp forest ecosystems. Beyond this point, increased water motion or kelp biomass no longer enhances NH₄⁺ inside kelp forests relative to the forest edge.

*Fine-scale (microhabitat) variation*

At the smallest scale of variability tested, we found evidence of variation in NH₄⁺ only in our cage experiments in the sheltered inlet, which may suggest that water motion mediates variation at this scale as well. Under laboratory conditions we confirmed that NH₄⁺ enrichment by animals declines with increasing flow rates (Fig. S1.3). Alternative or complementary explanations include a taxonomic effect and/or an experimental effect. The crabs in the sheltered cages excreted NH₄⁺ at a rate roughly 6x higher than the sea cucumbers caged in the more exposed location. This difference in NH₄⁺ production could have given us more scope to detect differences among treatments in the protected inlet. In addition, the crab cages were constructed with only two mesh windows, in contrast to the fully meshed cages of sea cucumbers, which could have promoted nutrient retention in the former. The experimental duration was also shorter for the sea cucumber experiment, but NH₄⁺ concentrations in the crab cages were consistent across the three sampling days (day one, four, and nine) so cumulative enrichment is unlikely.

Fine-scale NH₄⁺ enrichment by animals is nevertheless possible in wave-exposed conditions; for example, seawater above mussel beds had ~16x higher NH₄⁺ compared to neighbouring rock without mussels on the northern California coast (Aquilino et al., 2009). Our cage experiments were not designed to test why variation was found in one experiment and not the other, but rather to see whether fine-scale variation might arise at all. Therefore, we simply conclude that at least in sheltered conditions, variation on the scale of meters driven by animal biomass is possible.

*Implications for primary productivity*

Heterogeneity in primary productivity arises from variation in resource supply. Increased primary productivity has been seen with orders of variation (i.e., 1.3 – 9x) in NH₄⁺ (Arzul, 2001; Uthicke and Klumpp, 1998; Vinther and Holmer, 2008; West et al., 2009), which is within the range of variation we saw at all three spatial scales considered here. Regardless of nitrate availability, ammonium (NH₄⁺) is less costly for primary producers to use, and can even inhibit nitrate uptake (MacIsaac and Dugdale, 1972, 1969). In nitrate-replete upwelling ecosystems of the west coast of North America, a 15.8x increase in NH₄⁺ (from 0.08 uM to 1.26 uM) was linked to increased tissue nitrogen and percent cover of an intertidal seaweed (Aquilino et al., 2009), while a 1.8x increase in NH₄⁺ increased growth in subtidal seaweeds (Druehl et al., 1989). Furthermore, the mismatch of timing between upwelling and the growing season at temperate latitudes leads to an increased reliance on NH₄⁺ over time as nitrate becomes depleted (Brzezinksi et al., 2013; Druehl et al., 1989).

Heterogeneity in NH₄⁺ availability likely impacts primary productivity in Barkley Sound at each spatial scale studied. At the meso-scale, nitrate varies among sites (Druehl et al., 1989; Hurd et al., 2000). However, Pawlowicz (2017) determined that external nutrient supply (upwelling) does not control primary productivity in Barkley Sound, and instead suggested that local factors may be more important. The meso-scale NH₄⁺ variability we documented may be one such local factor driving primary productivity. At a small scale, nitrate from external sources (e.g., upwelling and run-off) becomes depleted or unchanged as it flows through a kelp forest (Pfister et al., 2019; Stewart et al., 2009), in contrast to NH4+ which is continuously regenerated by animals within and around the forest and seemingly retained. Kelp forests effectively concentrate their preferred form of nitrogen. This likely facilitates not only the growth of these canopy kelps but also understory seaweeds and phytoplankton in the water column. As urchin overgrazing and climate change decimate kelp forests, we may lose this important ecosystem function. At fine scales, invertebrates and fishes living in close contact with primary producers can enrich seaweeds directly. Many seaweeds are capable of surge uptake of NH₄⁺ (Cedeno et al., 2021), allowing them to maximize the benefit from animal excretion directly on their thalli. Indeed, given turnover rates of water and NH₄⁺ uptake rates, seaweeds in New Zealand were estimated to derive up to 79% of their needed nitrogen from direct epifauna excretion (Taylor and Rees, 1998).

*Conclusion*

Despite the mixing forces of currents, tides and waves, and underlying spatial heterogeneity in NH₄⁺, concentration of? was detectable at meso, small, and fine spatial scales. Given the annual depletion of nitrates each summer (Druehl et al., 1989), primary producers’ preference for NH₄⁺ over nitrate (Phillips and Hurd, 2004), and the capacity for surge uptake of NH₄⁺ (Cedeno et al., 2021), it seems likely that the animal-driven variation in NH₄⁺ we observed could be contributing to heterogeneity in primary productivity. Our results disrupt the dominant paradigm that bottom-up effects in temperate waters are primarily driven by external sources of nutrients acting on large scales, while animals contribute to smaller-scale variation mainly through top-down, consumptive effects. Instead, animals in temperate waters likely drive bottom-up effects across multiple spatial scales while also contributing to top-down effects. Animal-driven spatio-temporal variability of nitrogen is known to drive bottom-up effects in the tropics, and our results suggest animal-regenerated nutrients also play a previously unappreciated role in shaping nutrient availability in temperate regions.

**Acknowledgements**

We are grateful to the volunteers who conduct annual Reef Life Surveys and to Dr. Amanda Bates and the Canada Research Chairs Program for funding this critical long-term monitoring work. Thank you to Siobhan Gray, Dave Porter, Phil Lavoie, Kelly Clement, and all the Bamfield Marine Sciences Center staff for their ongoing support. Thank you to Brittnie Spriel and Kayla Holloway for their assistance with the crab cages. Hailey Davies illustrated the red rock crabs and California sea cucumbers, and Jane Thomas provided the kelp symbols through the Integration and Application Network (ian.umces.edu/media-library). This work was funded by National Sciences and Engineering Research Council of Canada (NSERC) scholarships to EGL (CGS-M and CGS-D), CMA (CGS-M), KDC (PDF), KRK (USRA), EJL (USRA), and ALB (USRA).). NSERC Discovery Grants supportsupportgrants to IMC and FJ. The, Liber Ero Foundation supportssupportsfunding to FJ (Liber Ero Chair)), MITACS and KDC (Liber Ero Chair).

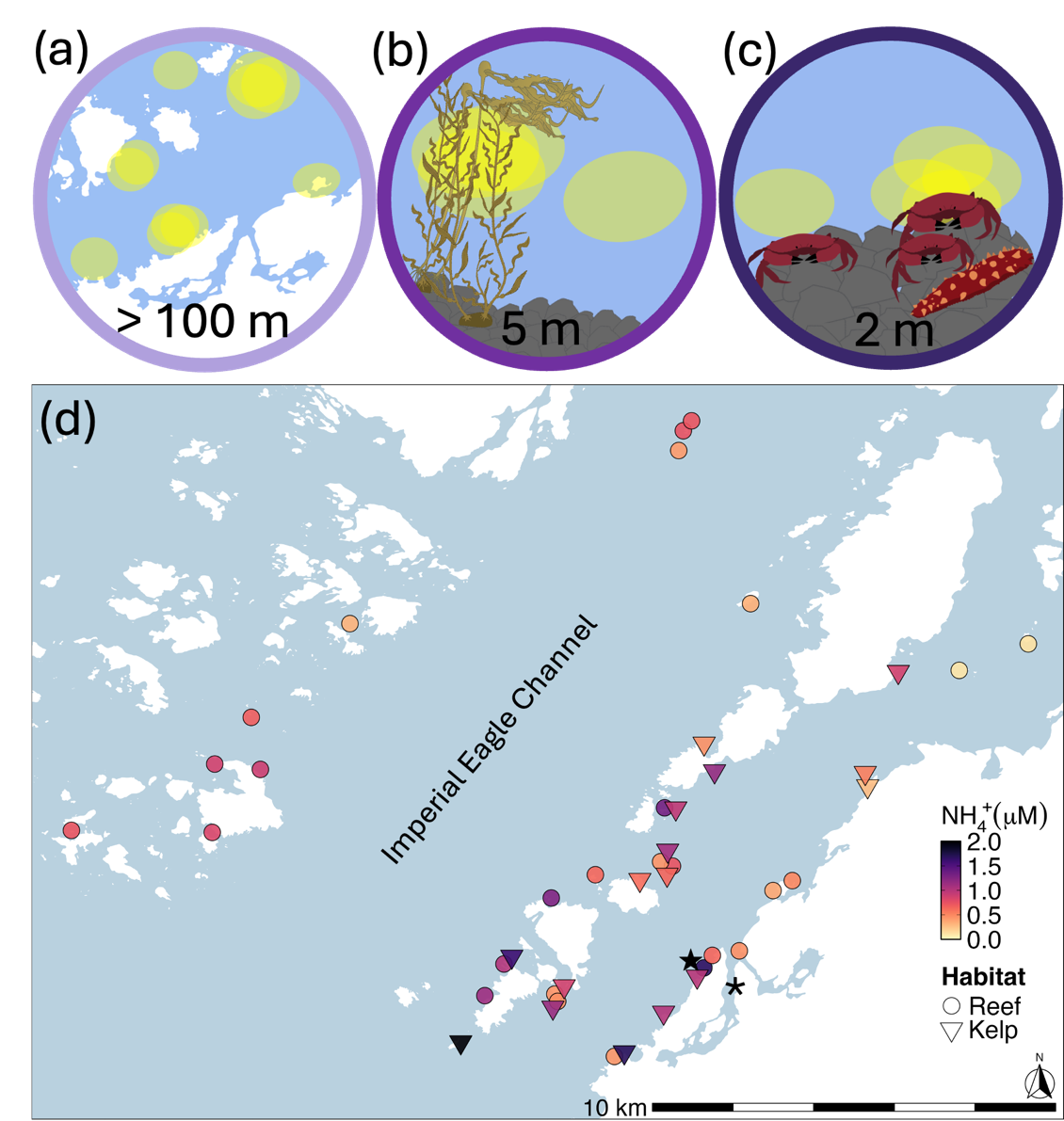
HakaiJMS,

Data Availability Statement

Conflict of Interest Statement

The authors declare no conflict of interest.

**Figures**

****

**Figure 1.** Scales of study and site locations in Barkley Sound, British Columbia, Canada.(a) Meso-scale (among-site), (b) small-scale (within-site), and (c) fine-scale (microhabitat) schematics of the three spatial scales of variability investigated. (d) Rocky reefs (circles) surveyed for meso-scale ammonium variation, and kelp forests surveyed (triangles) for small-scale ammonium variation. Site colour indicates mean ammonium concentration found at each site across all three years, with darker points having higher concentrations of ammonium. (★) Indicates the location of the fine scale sea cucumber caging experiment and (\*) denotes location of the crab caging experiment.

**A comparison of different colored lines

Description automatically generated with medium confidence**

**Figure 2.** Ecological drivers of seawater ammonium concentration observed across 27 rocky reef sites (meso-scale) in Barkley Sound, British Columbia, Canada. (a)Model coefficients with 95% confidence intervals, and (b) model-generated predictions with shaded 95% confidence intervals of the effect of the interaction between animal abundance and tide exchange on among-site variation in ammonium concentration. The coefficients were generated from a generalized linear mixed-effects model with a gamma distribution (link = ‘log’), so coefficients are presented in log space. Continuous predictors were centred and scaled to compare effect sizes between predictors with varying units.

A screenshot of a graph

Description automatically generated

**Figure 3.** Drivers of variation in ammonium concentration inside vs outside kelp forests across 16 sites (small-scale) in Barkley Sound, British Columbia, Canada. (a) Model coefficients with 95% confidence intervals and (b-e) model-generated predictions with shaded 95% confidence intervals of the effects of significant drivers of within-site variation in ammonium concentration. Continuous variables were scaled and centered to facilitate comparisons between variables measured in different units. Nereo = *Nereocystis luetkeana*, Macro = *Macrocystis pyrifera*, None = no kelp control.

****

**Figure 4.** Fine scale effect of California sea cucumbers (*Apostichopus californicus*) and red rock crabs (*Cancer productus*) on ammonium concentration. Mean ammonium concentration in experimental cages containing (a) zero (control), one, or two California sea cucumbers (n = 6), and (b) zero (control), one medium, or one large red rock crab (n = 8 for control and medium, n = 7 for large). Error bars indicate 95% confidence intervals.

**Electronic Supplement 1.** Supplementary tables and figures.

**A green hill with yellow dots and a black text

Description automatically generated**

**Figure S1.1.** Schematic of methods used to survey biological communities adjacent to a kelp forest, kelp forest density, and NH₄⁺ inside vs outside the forest. We first ran a 50 m Reef Life Survey transect parallel to the kelp forest (green shaded area) and counted fishes in the water column within 5 m on either side of the transect (light blue shaded areas), and cryptic fishes and macroinvertebrates within 1 m on either side of the transect (darker blue shaded area). Next, we ran four 5 m long transects into the kelp forest, 5 m apart from each other, to assess kelp density and biomass within 0.5 m on either side of the transect (four perpendicular black lines). Finally, we took NH₄⁺ samples at the beginning and end of the first three kelp transects (yellow circles) to compare NH₄⁺ inside vs outside kelp forests.

A comparison of different types of mass

Description automatically generated

**Figure S1.2**. Relationship between Shannon diversity and (a) kelp forest biomass and (b) animal biomass in kelp forests across 16 sites (small-scale) in Barkley Sound, British Columbia, Canada. Nereo = *Nereocystis luetkeana*, Macro = *Macrocystis pyrifera*, None = no kelp control.

**A diagram of a flow rate

Description automatically generated**

**Figure S1.3.** Change in ammonium in containers containing zero or four California sea cucumbers (*Apostichopus californicus*) relative to initial ammonium concentration after 24 hours in mesocosms with varying flow rates. Shaded areas indicate 95% confidence intervals, and raw data are plotted as points. While NH₄⁺ concentration remained the same across flow rates in the control mesocosms, sea cucumbers enriched NH₄⁺ concentration when flow was low. This enrichment declined as flow rate increased.

**Table S1.1.** Rocky reef sites sampled using Reef Life Survey methods, with the associated coordinates and years each site was surveyed.

|  |  |  |  |
| --- | --- | --- | --- |
| **Site code** | **Site name** | **Coordinates** | **Years sampled** |
| BMSC1 | Dodger Channel | 48.82894897, -125.1975708 | 2021, 2022, 2023 |
| BMSC2 | Kirby | 48.85039902, -125.1987686 | 2021, 2023 |
| BMSC3 | Ohiat | 48.85558319, -125.1837997 | 2021, 2022, 2023 |
| BMSC4 | Kii xin | 48.81511688, -125.1753311 | 2021, 2023 |
| BMSC5 | Taylor Rock | 48.82733154, -125.1966019 | 2021, 2022, 2023 |
| BMSC6 | Baeria Rocks South Island | 48.95023346, -125.1555481 | 2021, 2022, 2023 |
| BMSC7 | Baeria Rocks N Island Southside | 48.95464325, -125.1539917 | 2021 |
| BMSC8 | Baeria Rocks N Island Northside | 48.95508194, -125.1533737 | 2021, 2022, 2023 |
| BMSC9 | Eagle Bay | 48.83478928, -125.1470261 | 2021, 2022, 2023 |
| BMSC10 | Ross Islets Slug Island | 48.87051773, -125.160347 | 2021, 2022, 2023 |
| BMSC11 | Wizard Island South | 48.85746765, -125.1582336 | 2021, 2022, 2023 |
| BMSC12 | Wizard Island North | 48.858284, -125.1609192 | 2021, 2022, 2023 |
| BMSC13 | Effingham West | 48.8650322, -125.3137207 | 2021, 2022 |
| BMSC14 | Effingham Archipelago | 48.87908173, -125.2974014 | 2021, 2022 |
| BMSC15 | Raymond Kelp Rock | 48.88028336, -125.3128815 | 2021, 2022 |
| BMSC16 | Faber Islets | 48.89070129, -125.300499 | 2021, 2022 |
| BMSC17 | Wouwer Channel | 48.86548233, -125.3614807 | 2021, 2022 |
| BMSC18 | Eussen Rock | 48.91161728, -125.2670364 | 2021, 2022 |
| BMSC19 | Ed King SW Pyramid | 48.82860184, -125.2212982 | 2021, 2022, 2023 |
| BMSC20 | Ed King East | 48.83566666, -125.214798 | 2021, 2022, 2023 |
| BMSC21 | Dixon SW | 48.85205078, -125.1235657 | 2021, 2022, 2023 |
| BMSC22 | Dixon Inside | 48.85426712, -125.1170349 | 2021, 2022, 2023 |
| BMSC23 | Aguilar Point | 48.837589, -125.144145 | 2022, 2023 |
| BMSC24 | Swiss Boy | 48.916073, -125.131174 | 2023 |
| BMSC25 | Goby Town | 48.838595, -125.135015 | 2023 |
| BMSC26 | Hosie South | 48.9071, -125.037017 | 2023 |
| BMSC27 | San Jose North Island | 48.901183, -125.060433 | 2023 |

**Table S1.2.** Kelp forest site names, coordinates, survey dates and dominant kelp forest species. Macro = giant kelp (*Macrocystis pyrifera*), Nereo = bull kelp (*Nereocystis luetkeana*).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Site code** | **Site name** | **Coordinates** | **Date** | **Kelp** |
| KCCA1 | Ross Islet Slug Island | 48.87039, -125.1599 | 2022-07-04 | Macro |
| KCCA2 | Between Scott & Brady | 48.83287, -125.1493 | 2022-07-05 | Macro |
| KCCA3 | Dodger Channel 1 | 48.83072, -125.19439 | 2022-07-06 | Macro |
| KCCA4 | Flemming 112 | 48.87868, -125.1434 | 2022-07-07 | Macro |
| KCCA6 | Less Dangerous Bay | 48.87535, -125.0915 | 2022-07-24 | None |
| KCCA7 | Ed King East Inside | 48.83608, -125.2131 | 2022-07-25 | Macro |
| KCCA9 | Wizard Islet South | 48.85728, -125.1595 | 2022-07-27 | Macro |
| KCCA12 | North Helby Rock | 48.85831, -125.1649 | 2022-08-03 | Macro |
| KCCA14 | Danvers Danger Rock | 48.877, -125.0923 | 2022-08-06 | Macro |
| KCCA15 | Cable Beach | 48.82484, -125.16067 | 2022-08-07 | Nereo |
| KCCA16 | Tzartus 116 | 48.90084, -125.0811 | 2022-08-18 | Macro |
| KCCA17 | Turf Island 2 | 48.884864, -125.146937 | 2022-08-20 | Macro |
| KCCA18 | Second Beach | 48.815969, -125.174 | 2022-08-21 | Nereo |
| KCCA19 | Wizard Islet North | 48.85916, -125.15908 | 2022-08-22 | None |
| KCCA21 | Bordelais Island | 48.81822, -125.2294516 | 2022-09-01 | Nereo |
| KCCA22 | Taylor Rock | 48.82721, -125.19717 | 2022-09-05 | Macro |

**Table S1.3**. Wet weight estimates for each invertebrate species used to calculate total biomass for Reef Life Survey data. We used shell-free wet weight for species with large shells (e.g., hermit crabs, snails). When weight information was unavailable for a species, we used estimates from the closest relative or most similarly sized species available. For the three species we sized in situ (*Pycnopodia helianthoides*, *Crassadoma gigantea*, and *Haliotis kamtschatkana*), we used published length-weight relationships to calculate wet weight from size.

|  |  |  |
| --- | --- | --- |
| **Species** | **Weight (g)** | **Source, proxy species if applicable** |
| *Cancer productus* | 200 | E.G. Lim, unpubl. |
| *Glebocarcinus oregonensis* | 3 | Hines 1982, small crabs |
| *Romaleon antennarium* | 3 | Hines 1982, small crabs |
| *Chorilia longipes* | 1.235 | Hines 1982, *Pugettia richii* |
| *Pugettia foliata* | 1.235 | Hines 1982, *Pugettia richii* |
| *Pugettia gracilis* | 1.235 | Hines 1982, *Pugettia richii* |
| *Pugettia producta* | 46 | Hines 1982 |
| *Pugettia richii* | 1.235 | Hines 1982 |
| *Scyra acutifrons* | 2 | Hines 1982 |
| *Scyra spp.* | 1.235 | Hines 1982 |
| *Cryptolithodes sitchensis* | 3 | Hines 1982, small crabs |
| *Cryptolithodes typicus* | 3 | Hines 1982, small crabs |
| *Hapalogaster mertensii* | 65 | Stewart et al 2015, *Phyllolithodes papillosus* |
| *Lopholithodes mandtii* | 65 | Stewart et al 2015, *Phyllolithodes papillosus* |
| *Phyllolithodes papillosus* | 65 | Stewart et al 2015 |
| *Oregonia gracilis* | 3 | Hines 1982, small crabs |
| *Paguroidea spp.* | 0.43 | McKinney et al 2004, Paguroidea |
| *Pagurus beringanus* | 0.43 | McKinney et al 2004, Paguroidea |
| *Pagurus hemphilli* | 0.43 | McKinney et al 2004, Paguroidea |
| *Pandalus danae* | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| *Pandalus gurneyi* | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| *Pandalus spp.* | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| *Pandulus spp.* | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| *Lophopanopeus bellus* | 3 | Hines 1982, small crabs |
| *Pachycheles pubescens* | 4.25 | Stillman and Somero 1996, *Petrolisthes spp.* |
| *Petrolisthes eriomerus* | 4.25 | Stillman and Somero 1996, *Petrolisthes spp.* |
| *Heptacarpus stylus* | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| Brachyura spp. | 3 | Hines 1982, small crabs |
| Unidentified shrimp | 0.11 | McKinney et al 2004, *Palaemonetes pugio* |
| *Polyorchis penicillatus* | 0.01 | Båmstedt 2015, *Bolinopsis infundibulum* |
| *Mitrocoma cellularia* | 0.01 | Båmstedt 2015, *Bolinopsis infundibulum* |
| *Pleurobrachia bachei* | 0.01 | Båmstedt 2015, *Bolinopsis infundibulum* |
| *Bolinopsis infundibulum* | 0.01 | Båmstedt 2015 |
| *Evasterias troschelii* | 66.5 | O'Clair 1985 |
| *Leptasterias hexactis* | 5.5 | Menge 1975, *Leptasterias spp.* |
| *Leptasterias spp.* | 5.5 | Menge 1975, *Leptasterias spp.* |
| *Orthasterias koehleri* | 66.5 | O'Clair 1985, *Evasterias troschelii* |
| *Pisaster brevispinus* | 146.18 | Peters et al 2019, Pisaster giganteus |
| *Pisaster ochraceus* | 128 | Sanford 2002 |
| *Pycnopodia helianthoides* | 0.018\*size^3.13 | Lee 2016 |
| *Stylasterias forreri* | 66.5 | O'Clair 1985, *Evasterias troschelii* |
| *Patiria miniata* | 26.97 | Peters et al 2019 |
| *Henricia pumila* | 10 | Menge 1975, *Henricia spp*. |
| *Henricia spp.* | 10 | Menge 1975 |
| *Dermasterias imbricata* | 92 | Montgomery 2014 |
| *Mediaster aequalis* | 10 | Menge 1975, *Henricia spp*. |
| *Solaster dawsoni* | 486 | Montgomery 2014, *Solaster stimpsoni* |
| *Solaster stimpsoni* | 486 | Montgomery 2014 |
| *Pteraster tesselatus* | 10 | Menge 1975, *Henricia spp.* |
| *Mesocentrotus franciscanus* | 29.51 | Schuster and Bates 2023 |
| *Strongylocentrotus droebachiensis* | 20 | Stewart et al 2015, *Strongylocentrotus polyacanthus* |
| *Strongylocentrotus purpuratus* | 20 | Stewart et al 2015, *Strongylocentrotus polyacanthus* |
| *Apostichopus californicus* | 319.31 | Peters et al 2019, *Apostichopus parvimensis* |
| *Chlamys hastata* | 2.5 | MacDonald 1991, *Chlamys spp.* |
| *Crassadoma gigantea* | 0.038\*size^2.39 | MacDonald 1991 |
| *Enteroctopus dofleini* | 137.5 | Osborn 1995, *Octopus rubescens* |
| *Octopus rubescens* | 80 | Osborn 1995 |
| *Opalia wroblewskyi* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Diodora aspera* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Megathura crenulata* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Haliotis kamtschatkana* | 0.00058\*size^3.2 | Zhang 2007 |
| *Neverita lewisii* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Ceratostoma foliatum* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Nucella lamellosa* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Armina californica* | 0.54 | McKinney et al 2004, gastropods |
| *Cadlina luteomarginata* | 0.54 | McKinney et al 2004, gastropods |
| *Cadlina modesta* | 0.54 | McKinney et al 2004, gastropods |
| *Cadlina sylviaearleae* | 0.54 | McKinney et al 2004, gastropods |
| *Coryphella verrucosa* | 0.54 | McKinney et al 2004, gastropods |
| *Dendronotus iris* | 0.54 | McKinney et al 2004, gastropods |
| *Dirona albolineata* | 0.54 | McKinney et al 2004, gastropods |
| *Dirona pellucida* | 0.54 | McKinney et al 2004, gastropods |
| *Diaulula odonoghuei* | 0.54 | McKinney et al 2004, gastropods |
| *Diaulula sandiegensis* | 0.54 | McKinney et al 2004, gastropods |
| *Peltodoris nobilis* | 0.54 | McKinney et al 2004, gastropods |
| *Doris montereyensis* | 0.54 | McKinney et al 2004, gastropods |
| *Doris odhneri* | 0.54 | McKinney et al 2004, gastropods |
| *Antiopella fusca* | 0.54 | McKinney et al 2004, gastropods |
| *Hermissenda crassicornis* | 0.54 | McKinney et al 2004, gastropods |
| *Acanthodoris hudsoni* | 0.54 | McKinney et al 2004, gastropods |
| *Acanthodoris nanaimoensis* | 0.54 | McKinney et al 2004, gastropods |
| *Onchidoris bilamellata* | 0.54 | McKinney et al 2004, gastropods |
| *Limacia cockerelli* | 0.54 | McKinney et al 2004, gastropods |
| *Polycera tricolor* | 0.54 | McKinney et al 2004, gastropods |
| *Triopha catalinae* | 0.54 | McKinney et al 2004, gastropods |
| *Triopha modesta* | 0.54 | McKinney et al 2004, gastropods |
| *Triopha spp.* | 0.54 | McKinney et al 2004, gastropods |
| *Melibe leonina* | 0.54 | McKinney et al 2004, gastropods |
| *Tritonia festiva* | 0.54 | McKinney et al 2004, gastropods |
| *Acmaea mitra* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Lottia scutum* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Berthella chacei* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Calliostoma ligatum* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Tegula funebralis* | 0.91 | Palmer 1982, *Nucella spp.* |
| *Pomaulax gibberosus* | 31 | Schuster and Bates 2023 |
| *Eurylepta leoparda* | 0.54 | McKinney et al 2004, gastropods |

**Table S1.4**. Akaike’s Information Criterion (AIC) values calculated for each model of ammonium concentration in relation to animal abundance (AA) or animal biomass (AB), Shannon diversity (SHD) or Simpson diversity (SID), tide exchange rate (T), depth (D), and an interaction term. RE = random effect of both site and year. k is the number of parameters in the model. The model with the lowest AIC score is the “best” model; ΔAIC is the difference in AIC score between a given model and the “best” model; AIC weight represents the probability that a model is the best model, given the data and the set of candidate models.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictors** | **k** | **AIC** | **ΔAIC** | **AIC weight** |
| AA + SHD + T + D + AA:T + RE | 9 | 45.60 | 0.00 | 0.50 |
| AA + SID + T + D + AA:T + RE | 9 | 46.09 | 0.50 | 0.39 |
| AB + SHD + T + D + AB:T + RE | 9 | 49.70 | 4.10 | 0.06 |
| AB + SID + T + D + AB:T + RE | 9 | 49.98 | 4.38 | 0.06 |

**Table S1.5**. Akaike’s Information Criterion (AIC) values calculated for each model of delta ammonium concentration in vs outside kelp forests in relation to animal abundance (AA) or animal biomass (AB), Shannon diversity (SHD) or Simpson diversity (SID), kelp species (KS), kelp biomass (KB), tide exchange rate (T), depth (D), and three interaction terms. RE = random effect of site. k is the number of parameters in the model. The model with the lowest AIC score is the “best” model; ΔAIC is the difference in AIC score between a given model and the “best” model; AIC weight represents the probability that a model is the best model, given the data and the set of candidate models.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Predictors** | **k** | **AIC** | **ΔAIC** | **AIC weight** |
| AB + SHD + KS + KB + T + D + AB :T + AB :KB + KB:T + RE | 13 | -34.76 | 0.00 | 0.33 |
| AA + SHD + KS + KB + T + D + AA:T + AA:KB + KB:T + RE | 13 | -34.56 | 0.2 | 0.30 |
| AA + SID + KS + KB + T + D + AA:T + AA:KB + KB:T + RE | 13 | -34.12 | 0.64 | 0.24 |
| AB + SID + KS + KB + T + D + AB:T + AB:KB + KB:T + RE | 13 | -33.01 | 1.75 | 0.14 |

**Table S1.6.** Excretion rate model to determine log transformed NH₄⁺ excretion rate (uM/hour/L) for California sea cucumbers (*Apostichopus californicus*) based on size index: sqrt(length\*girth). Adjusted R-squared for this model is 0.39.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **t value** | **p value** |
| Intercept | 1.40 | 0.22 | 6.23 | < 0.001 |
| Size index | 0.05 | 0.009 | 5.52 | < 0.001 |

**Table S1.7.** Excretion rate model to determine log transformed NH₄⁺ excretion rate (uM/hour/L) for red rock crabs (*Cancer productus*) based on carapace width (mm). Adjusted R-squared for this model is 0.82.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Estimate** | **Std. error** | **t value** | **p value** |
| Intercept | 1.22 | 0.32 | 3.76 | 0.002 |
| Carapace | 0.02 | 0.003 | 8.73 | < 0.001 |

**Electronic Supplement 2.** Effect of individual families of fishes and invertebrates on meso-scale (among-site) and small-scale (within-site) variation in ammonium.

**Regional (meso-scale) variation**

We further explored the effect of animals on variation in NH₄⁺ concentration among rocky reef sites by considering only the abundance of one animal family at a time. For each of the top 15 most abundant families observed on our surveys, we constructed an GLMM identical to the top model shown in Table S4, using only the abundance of that family (NH₄⁺ regressed against family abundance, tide exchange, an interaction between family abundance and tide, Shannon diversity, survey depth, with a random effect of site and year and a gamma distribution). Here, we present the three fish families (Hexagrammidae, Gobiidae, and Sebastidae) and three invertebrate families (Muricidae, Asteriidae, and Acmaeidae) with the highest R2 values. These six families constitute 17% of the total abundance.

We found evidence of a positive relationship between NH₄⁺ concentration and the abundance of greenlings (Hexagrammidae, GLMM, p = 0.03, Fig. S2.1), weak evidence of an interaction between greenling abundance and tide (p = 0.09), but no evidence for an effect of any other predictors (p > 0.10). We also found evidence of a positive relationship between NH₄⁺ concentration and the abundance of whitecap limpets (Acmaeidae, GLMM, p = 0.03), but no evidence of an effect of any other predictors (p > 0.40). We found no evidence of an effect of any predictors on NH₄⁺ concentration in the models for the families Sebastidae, Gobiidae, Asteriidae, or Muricidae (p > 0.10). Full model outputs are available in Table S2.1.

**A graph of different types of numbers

Description automatically generated with medium confidence**

**Figure S2.1.** Model-generated predictions of ammonium concentrations in relation to abundance across rocky reef sites for the 6 animal families with the highest R2.

**Table S2.1.** Model summaries from the meso-scale (among-site) models including only the biomass of one family (indicated in the top left cell) for each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sebastidae** (R2 = 0.67) | **Estimate** | **Std. error** | **z-value** | **p-value** |
| Intercept | 0.13 | 1.23 | 0.11 | 0.91 |
| Abundance | 1.98 | 3.22 | 0.61 | 0.54 |
| Tide exchange | -0.53 | 1.00 | -0.53 | 0.60 |
| Biodiversity | -0.10 | 0.13 | -0.75 | 0.45 |
| Depth | -0.02 | 0.13 | -0.18 | 0.86 |
| Abundance:Tide | -1.79 | 2.82 | -0.63 | 0.53 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Muricidae** (R2 = 0.54) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | -0.43 | 0.33 | -1.30 | 0.19 |
| Abundance | 0.79 | 0.51 | 1.55 | 0.12 |
| Tide exchange | 0.05 | 0.12 | 0.44 | 0.66 |
| Biodiversity | 0.00 | 0.10 | -0.04 | 0.97 |
| Depth | 0.04 | 0.09 | 0.43 | 0.67 |
| Abundance:Tide | 0.12 | 0.55 | 0.22 | 0.83 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Asterinidae** (R2 = 0.651) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | -0.58 | 0.26 | -2.28 | 0.02 |
| Abundance | 0.21 | 0.26 | 0.80 | 0.42 |
| Tide exchange | 0.12 | 0.07 | 1.80 | 0.07 |
| Biodiversity | -0.12 | 0.09 | -1.29 | 0.20 |
| Depth | 0.06 | 0.09 | 0.62 | 0.54 |
| Abundance:Tide | 0.07 | 0.27 | 0.26 | 0.80 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Hexagrammidae** (R2 = 0.47) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 4.96 | 2.54 | 1.95 | 0.05 |
| Abundance | 14.67 | 6.69 | 2.19 | 0.03 |
| Tide exchange | -3.35 | 2.01 | -1.67 | 0.10 |
| Biodiversity | 0.01 | 0.09 | 0.11 | 0.91 |
| Depth | 0.02 | 0.09 | 0.25 | 0.81 |
| Abundance:Tide | -9.01 | 5.35 | -1.68 | 0.09 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Acmaeidae** (R2 = 0.46) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | -0.19 | 0.33 | -0.59 | 0.56 |
| Abundance | 1.42 | 0.67 | 2.13 | 0.03 |
| Tide exchange | 0.03 | 0.16 | 0.21 | 0.84 |
| Biodiversity | -0.01 | 0.09 | -0.09 | 0.93 |
| Depth | 0.00 | 0.09 | 0.05 | 0.96 |
| Abundance:Tide | -0.16 | 0.58 | -0.28 | 0.78 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Gobiidae** (R2 = 0.44) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | -0.64 | 0.29 | -2.19 | 0.03 |
| Abundance | 0.17 | 0.23 | 0.75 | 0.45 |
| Tide exchange | 0.04 | 0.07 | 0.52 | 0.61 |
| Biodiversity | -0.01 | 0.10 | -0.11 | 0.91 |
| Depth | -0.06 | 0.11 | -0.55 | 0.58 |
| Abundance:Tide | 0.13 | 0.17 | 0.80 | 0.43 |

**Within-site (small-scale) variation**

As above, we further explored the effect of animals on ∆NH₄⁺ – the difference in NH₄⁺ concentration between inside and outside kelp forests – by rerunning the top LMM in Table S5 with the biomass of only one animal family at a time. We ran models for the 15 most abundant families, but only present the three fish families (Gobiidae, Cottidae, and Embiotocidae) and three invertebrate families (Echinasteridae, Strongylocentrotidae, and Asteriidae) with the highest R2 values. These six families contribute almost half (48%) of the total biomass observed on the surveys.

We found a negative relationship between ∆NH₄⁺ and the biomass of gobies (Gobiidae) and evidence of positive kelp:goby biomass and tide:goby biomass interactions (GLM, p < 0.003, Fig. S2.2). ∆NH₄⁺ was positively correlated with the biomass of sculpins (Cottidae; p = 0.046) and surfperches (Embiotocidae; p < 0.001), but no interactions with biomass were significant (p > 0.06). Sea stars in the family Echinasteridae displayed a positive relationship with ∆NH₄⁺, a negative kelp:sea star biomass interaction, and a positive tide:sea star biomass interaction (p < 0.001). We found evidence for a smaller but still positive relationship between the biomass of urchins in the family Strongylocentrotidae and sea stars in the family Asteropseidae and ∆NH₄⁺ (p < 0.005), but no interactions with biomass were significant (p > 0.17). Full model outputs are available in Table S2.2.



**Figure S2.2.** Model-generated predictions of difference in ammonium concentrations between inside and outside kelp forests in relation to animal biomass for the 6 animal families with the highest R2.

**Table S2.2.** Model summaries from the small scale (within-site) models including only the biomass of one family (indicated in the top left cell) for each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Echinasteridae** (R2 = 0.97) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 3.22 | 0.71 | 4.56 | < 0.01 |
| Kelp nereo | 0.23 | 0.03 | 6.79 | < 0.01 |
| Kelp none | -0.09 | 0.07 | -1.33 | 0.18 |
| Kelp biomass | -2.82 | 0.89 | -3.17 | < 0.01 |
| Tide exchange | 3.02 | 0.76 | 3.99 | < 0.01 |
| Animal biomass | 7.36 | 1.68 | 4.39 | < 0.01 |
| Biodiversity | -0.13 | 0.02 | -5.96 | < 0.01 |
| Depth | 0.04 | 0.02 | 2.19 | 0.03 |
| Kelp:tide | 0.20 | 0.04 | 5.39 | < 0.01 |
| Kelp:animals | -7.66 | 2.14 | -3.58 | < 0.01 |
| Tide:animals | 6.87 | 1.78 | 3.86 | < 0.01 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Gobiidae** (R2 = 0.92) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | -0.56 | 0.24 | -2.35 | 0.02 |
| Kelp none | 0.89 | 0.34 | 2.61 | 0.01 |
| Kelp biomass | 1.06 | 0.38 | 2.81 | < 0.01 |
| Tide exchange | 4.79 | 0.98 | 4.89 | < 0.01 |
| Animal biomass | -1.71 | 0.57 | -3.01 | < 0.01 |
| Biodiversity | 0.14 | 0.04 | 3.55 | < 0.01 |
| Depth | 0.00 | 0.03 | -0.10 | 0.92 |
| Kelp:tide | 0.11 | 0.08 | 1.35 | 0.18 |
| Kelp:animals | 2.65 | 0.98 | 2.69 | 0.01 |
| Tide:animals | 12.22 | 2.48 | 4.93 | < 0.01 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Cottidae** (R2 = 0.92) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 1.23 | 0.56 | 2.20 | 0.03 |
| Kelp nereo | 0.12 | 0.07 | 1.63 | 0.10 |
| Kelp none | -0.43 | 0.09 | -4.66 | < 0.01 |
| Kelp biomass | -0.35 | 0.37 | -0.96 | 0.34 |
| Tide exchange | -0.68 | 1.14 | -0.60 | 0.55 |
| Animal biomass | 2.56 | 1.28 | 2.00 | 0.05 |
| Biodiversity | -0.16 | 0.04 | -4.40 | < 0.01 |
| Depth | 0.11 | 0.03 | 3.82 | < 0.01 |
| Kelp:tide | 0.17 | 0.08 | 2.13 | 0.03 |
| Kelp:animals | -1.59 | 0.86 | -1.85 | 0.06 |
| Tide:animals | -1.88 | 2.68 | -0.70 | 0.48 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Strongylocentrotidae** (R2 = 0.87) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 0.00 | 0.06 | 0.01 | 0.99 |
| Kelp nereo | 0.07 | 0.08 | 0.83 | 0.41 |
| Kelp none | -0.67 | 0.12 | -5.40 | < 0.01 |
| Kelp biomass | 0.20 | 0.06 | 3.42 | < 0.01 |
| Tide exchange | 0.07 | 0.07 | 0.99 | 0.32 |
| Animal biomass | 0.08 | 0.03 | 3.21 | < 0.01 |
| Biodiversity | 0.04 | 0.03 | 1.14 | 0.25 |
| Depth | 0.10 | 0.03 | 3.21 | < 0.01 |
| Kelp:tide | 0.15 | 0.06 | 2.43 | 0.01 |
| Kelp:animals | -0.02 | 0.02 | -1.12 | 0.26 |
| Tide:animals | -0.02 | 0.02 | -1.06 | 0.29 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Embiotocidae** (R2 = 0.88) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 0.27 | 0.04 | 6.32 | < 0.01 |
| Kelp nereo | -0.03 | 0.08 | -0.45 | 0.66 |
| Kelp none | -0.28 | 0.13 | -2.11 | 0.03 |
| Kelp biomass | 0.25 | 0.05 | 5.31 | < 0.01 |
| Tide exchange | 0.15 | 0.04 | 3.74 | < 0.01 |
| Animal biomass | 0.55 | 0.12 | 4.60 | < 0.01 |
| Biodiversity | -0.09 | 0.03 | -2.85 | < 0.01 |
| Depth | 0.07 | 0.03 | 2.39 | 0.02 |
| Kelp:tide | 0.18 | 0.07 | 2.61 | 0.01 |
| Kelp:animals | -0.05 | 0.11 | -0.48 | 0.63 |
| Tide:animals | 0.31 | 0.20 | 1.59 | 0.11 |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Asteriidae** (R2 = 0.88) | **Estimate** | **Std. error** | **z value** | **p value** |
| Intercept | 0.06 | 0.04 | 1.34 | 0.18 |
| Kelp nereo | 0.05 | 0.09 | 0.52 | 0.61 |
| Kelp none | -0.24 | 0.11 | -2.18 | 0.03 |
| Kelp biomass | 0.23 | 0.07 | 3.14 | < 0.01 |
| Tide exchange | -0.02 | 0.08 | -0.23 | 0.82 |
| Animal biomass | 0.13 | 0.05 | 2.76 | 0.01 |
| Biodiversity | -0.10 | 0.03 | -3.09 | < 0.01 |
| Depth | 0.05 | 0.03 | 1.56 | 0.12 |
| Kelp:tide | 0.12 | 0.08 | 1.52 | 0.13 |
| Kelp:animals | 0.00 | 0.03 | 0.16 | 0.87 |
| Tide:animals | 0.13 | 0.10 | 1.32 | 0.19 |

**References**

Allgeier, J.E., Burkepile, D.E., Layman, C.A., 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world’s changing oceans. Glob Change Biol 23, 2166–2178. https://doi.org/10.1111/gcb.13625

Allgeier, J.E., Yeager, L.A., Layman, C.A., 2013. Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. Ecology 94, 521–529. https://doi.org/10.1890/12-1122.1

Aquilino, K.M., Bracken, M.E.S., Faubel, M.N., Stachowicz, J.J., 2009. Local-scale nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an upwelling system. Limnol Oceanogr 54, 309–317. https://doi.org/10.4319/lo.2009.54.1.0309

Archer, S.K., Allgeier, J.E., Semmens, B.X., Heppell, S.A., Pattengill-Semmens, C.V., Rosemond, A.D., Bush, P.G., McCoy, C.M., Johnson, B.C., Layman, C.A., 2015. Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling. Coral Reefs 34, 19–23. https://doi.org/10.1007/s00338-014-1208-4

Arzul, G., 2001. Effect of marine animal excretions on differential growth of phytoplankton species. ICES J. Mar. Sci. 58, 386–390. https://doi.org/10.1006/jmsc.2000.1038

Attridge, C.M., Cox, K.D., Maher, B., Gross, S., Lim, E.G., Kattler, K.R., Côté, I.M., 2024. Studying Kelp Forests of Today to Forecast Ecosystems of the Future. Fisheries 49, 181–187. https://doi.org/10.1002/fsh.11065

Benkwitt, C.E., Wilson, S.K., Graham, N.A.J., 2019. Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Glob Change Biol 25, 2619–2632. https://doi.org/10.1111/gcb.14643

Bracken, M.E.S., 2004. Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. J Phycol 40, 1032–1041. https://doi.org/10.1111/j.1529-8817.2004.03106.x

Bray, R.N., Miller, A.C., Johnson, S., Krause, P.R., Robertson, D.L., Westcott, A.M., 1988. Ammonium excretion by macroinvertebrates and fishes on a subtidal rocky reef in southern California. Marine Biology 100, 21–30. https://doi.org/10.1007/BF00392951

Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., 2001. Geographic variation of southeastern Pacific intertidal communities. Mar. Ecol. Prog. Ser. 224, 21–34. https://doi.org/10.3354/meps224021

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9, 378. https://doi.org/10.32614/RJ-2017-066

Brzezinksi, M., Reed, D., Harrer, S., Rassweiler, A., Melack, J., Goodridge, B., Dugan, J., 2013. Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner continental shelf of the Santa Barbara Channel. Oceanog 26, 114–123. https://doi.org/10.5670/oceanog.2013.53

Cedeno, T.H., Brzezinski, M.A., Miller, R.J., Reed, D.C., 2021. An evaluation of surge uptake capability in the giant kelp (Macrocystis pyrifera) in response to pulses of three different forms of nitrogen. Mar Biol 168, 166. https://doi.org/10.1007/s00227-021-03975-z

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1999. Temporal and Spatial Scales of Kelp Demography: The Role of Oceanographic Climate. Ecological Monographs 69, 219–250. https://doi.org/10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2

Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., Svenning, J.-C., 2016. Global nutrient transport in a world of giants. Proc Natl Acad Sci USA 113, 868–873. https://doi.org/10.1073/pnas.1502549112

Druehl, L.D., Harrison, P.J., Lloyd, K.E., Thompson, P.A., 1989. Phenotypic variation in N uptake by Laminaria groenlandica Rosenvinge (Laminariales, Phaeophyta). J. Exp. Mar. Bio. Ecol 127, 155–164. https://doi.org/10.1016/0022-0981(89)90181-0

Edgar, G., Stuart-Smith, R., 2009. Ecological effects of marine protected areas on rocky reef communities—a continental-scale analysis. Mar. Ecol. Prog. Ser. 388, 51–62. https://doi.org/10.3354/meps08149

Edgar, G.J., Cooper, A., Baker, S.C., Barker, W., Barrett, N.S., Becerro, M.A., Bates, A.E., Brock, D., Ceccarelli, D.M., Clausius, E., Davey, M., Davis, T.R., Day, P.B., Green, A., Griffiths, S.R., Hicks, J., Hinojosa, I.A., Jones, B.K., Kininmonth, S., Larkin, M.F., Lazzari, N., Lefcheck, J.S., Ling, S.D., Mooney, P., Oh, E., Pérez-Matus, A., Pocklington, J.B., Riera, R., Sanabria-Fernandez, J.A., Seroussi, Y., Shaw, I., Shields, D., Shields, J., Smith, M., Soler, G.A., Stuart-Smith, J., Turnbull, J., Stuart-Smith, R.D., 2020. Establishing the ecological basis for conservation of shallow marine life using Reef Life Survey. Biological Conservation 252, 108855. https://doi.org/10.1016/j.biocon.2020.108855

Francis, F.T., Côté, I.M., 2018. Fish movement drives spatial and temporal patterns of nutrient provisioning on coral reef patches. Ecosphere 9, e02225. https://doi.org/10.1002/ecs2.2225

Froese, R., Thorson, J.T., Reyes Jr, R.B., 2014. A Bayesian approach for estimating length-weight relationships in fishes. J. Appl. Ichthyol. 30, 78–85. https://doi.org/10.1111/jai.12299

Gaylord, B., Rosman, J.H., Reed, D.C., Koseff, J.R., Fram, J., MacIntyre, S., Arkema, K., McDonald, C., Brzezinski, M.A., Largier, J.L., Monismith, S.G., Raimondi, P.T., Mardian, B., 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. Limnol Oceanogr 52, 1838–1852. https://doi.org/10.4319/lo.2007.52.5.1838

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H., Harpole, W.S., Elser, J.J., Cleland, E.E., Bracken, M.E.S., Borer, E.T., Bolker, B.M., 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol Lett 11, 740–755. https://doi.org/10.1111/j.1461-0248.2008.01192.x

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6.

Holbrook, S.J., Brooks, A.J., Schmitt, R.J., Stewart, H.L., 2008. Effects of sheltering fish on growth of their host corals. Mar Biol 155, 521–530. https://doi.org/10.1007/s00227-008-1051-7

Holmes, R.M., Aminot, A., Kerouel, R., Hooker, B.A., Peterson, B.J., 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Can. J. Fish. Aquat. Sci. 56, 1801–1808. https://doi.org/10.1139/f99-128

Hurd, C.L., Durante, K.M., Harrison, P.J., 2000. Influence of bryozoan colonization on the physiology of the kelp Macrocystis integrifolia (Laminariales, Phaeophyta) from nitrogen-rich and -poor sites in Barkley Sound, British Columbia, Canada. Phycologia 39, 435–440. https://doi.org/10.2216/i0031-8884-39-5-435.1

Jackson, G.A., Winant, C.D., 1983. Effect of a kelp forest on coastal currents. Continental Shelf Research 2, 75–80. https://doi.org/10.1016/0278-4343(83)90023-7

Layman, C.A., Allgeier, J.E., Montaña, C.G., 2016. Mechanistic evidence of enhanced production on artificial reefs: A case study in a Bahamian seagrass ecosystem. Ecol Eng 95, 574–579. https://doi.org/10.1016/j.ecoleng.2016.06.109

Lees, L.E., Jordan, S.N.Z., Bracken, M.E.S., 2024. Kelps may compensate for low nitrate availability by using regenerated forms of nitrogen, including urea and ammonium. J Phycol 60, 768–777. https://doi.org/10.1111/jpy.13459

Leibold, M.A., 1991. Biodiversity and nutrient enrichment in pond plankton communities. Evol. Ecol. Res 1, 73–95.

Lobban, C.S., Harrison, P.J., 1994. Seaweed Ecology and Physiology. Cambridge University Press.

Lønborg, C., Müller, M., Butler, E.C.V., Jiang, S., Ooi, S.K., Trinh, D.H., Wong, P.Y., Ali, S.M., Cui, C., Siong, W.B., Yando, E.S., Friess, D.A., Rosentreter, J.A., Eyre, B.D., Martin, P., 2021. Nutrient cycling in tropical and temperate coastal waters: Is latitude making a difference? Estuar. Coast. Shelf Sci. 262, 107571. https://doi.org/10.1016/j.ecss.2021.107571

Lowman, H.E., Hirsch, M.E., Brzezinski, M.A., Melack, J.M., 2023. Examining the Potential of Sandy Marine Sediments Surrounding Giant Kelp Forests to Provide Recycled Nutrients for Growth. J. Coast. Res. 39, 442–454. https://doi.org/10.2112/JCOASTRES-D-22-00035.1

MacIsaac, J.J., Dugdale, R.C., 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. Deep-Sea Res. Oceanogr. Abstr. 19, 209–232. https://doi.org/10.1016/0011-7471(72)90032-0

MacIsaac, J.J., Dugdale, R.C., 1969. The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. Deep-Sea Res. Oceanogr. Abstr. 16, 45–57. https://doi.org/10.1016/0011-7471(69)90049-7

McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? Biological Reviews 94, 1761–1773. https://doi.org/10.1111/brv.12525

Menge, B.A., 1992. Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? Ecology 73, 755–765. https://doi.org/10.2307/1940155

Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proc Natl Acad Sci USA 94, 14530–14535. https://doi.org/10.1073/pnas.94.26.14530

Meyer, J.L., Schultz, E.T., 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol Oceanogr 30, 146–156.

Meyer, J.L., Schultz, E.T., Helfman, G.S., 1983. Fish schools: An asset to corals. Science 220, 1047–1049. https://doi.org/10.1126/science.220.4601.1047

Müller, J., Brandl, R., Brändle, M., Förster, B., de Araujo, B.C., Gossner, M.M., Ladas, A., Wagner, M., Maraun, M., Schall, P., Schmidt, S., Heurich, M., Thorn, S., Seibold, S., 2018. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127, 814–824. https://doi.org/10.1111/oik.04972

Murie, K.A., Bourdeau, P.E., 2020. Fragmented kelp forest canopies retain their ability to alter local seawater chemistry. Sci Rep 10, 11939. https://doi.org/10.1038/s41598-020-68841-2

Nielsen, K.J., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecology Letters 7, 31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. vegan: Community Ecology Package. R package version 2.6-4.

Paine, R.T., 1986. Benthic community—water column coupling during the 1982-1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence?1. Limnology and Oceanography 31, 351–360. https://doi.org/10.4319/lo.1986.31.2.0351

Pawlowicz, R., 2017. Seasonal cycles, hypoxia, and renewal in a coastal fjord (Barkley Sound, British Columbia). Atmosphere-Ocean 55, 264–283. https://doi.org/10.1080/07055900.2017.1374240

Pfister, C.A., Altabet, M.A., Post, D., 2014. Animal regeneration and microbial retention of nitrogen along coastal rocky shores. Ecology 95, 2803–2814. https://doi.org/10.1890/13-1825.1

Pfister, C.A., Altabet, M.A., Weigel, B.L., 2019. Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. Ecology 100, e02798. https://doi.org/10.1002/ecy.2798

Phillips, J.C., Hurd, C.L., 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. J Phycol 40, 534–545. https://doi.org/10.1111/j.1529-8817.2004.03157.x

Probyn, T.A., Chapman, A.R.O., 1983. Summer growth of Chordaria flagelliformis (O.F. Muell.) C. Ag.: Physiological strategies in a nutrient stressed environment. J. Exp. Mar. Bio. Ecol 73, 243–271. https://doi.org/10.1016/0022-0981(83)90050-3

R Core Team, 2019. R: A language and environment for statistical computing.

Roman, J., McCarthy, J.J., 2010. The Whale Pump: Marine Mammals Enhance Primary Productivity in a Coastal Basin. PLoS ONE 5, e13255. https://doi.org/10.1371/journal.pone.0013255

Rosman, J.H., Koseff, J.R., Monismith, S.G., Grover, J., 2007. A field investigation into the effects of a kelp forest (Macrocystis pyrifera) on coastal hydrodynamics and transport. J. Geophys. Res. Oceans 112. https://doi.org/10.1029/2005JC003430

RStudio Team, 2016. RStudio: Integrated development for R.

Sellers, A.J., Leung, B., Torchin, M.E., 2020. Global meta-analysis of how marine upwelling affects herbivory. Glob. Ecol. Biogeogr. 29, 370–383. https://doi.org/10.1111/geb.13023

Shantz, A.A., Ladd, M.C., Schrack, E., Burkepile, D.E., 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. Ecol Appl 25, 2142–2152. https://doi.org/10.1890/14-2209.1

Starko, S., Neufeld, C.J., Gendall, L., Timmer, B., Campbell, L., Yakimishyn, J., Druehl, L., Baum, J.K., 2022. Microclimate predicts kelp forest extinction in the face of direct and indirect marine heatwave effects. Ecol Appl 32, e2673. https://doi.org/10.1002/eap.2673

Starko, S., Timmer, B., Reshitnyk, L., Csordas, M., McHenry, J., Schroeder, S., Hessing-Lewis, M., Costa, M., Zielinksi, A., Zielinksi, R., Cook, S., Underhill, R., Boyer, L., Fretwell, C., Yakimishyn, J., Heath, W., Gruman, C., Hingmire, D., Baum, J., Neufeld, C., 2024. Local and regional variation in kelp loss and stability across coastal British Columbia. Mar. Ecol. Prog. Ser. 733, 1–26. https://doi.org/10.3354/meps14548

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J., 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29, 436–459. https://doi.org/10.1017/S0376892902000322

Stewart, H., Fram, J., Reed, D., Williams, S., Brzezinski, M., MacIntyre, S., Gaylord, B., 2009. Differences in growth, morphology and tissue carbon and nitrogen of Macrocystis pyrifera within and at the outer edge of a giant kelp forest in California, USA. Mar. Ecol. Prog. Ser. 375, 101–112. https://doi.org/10.3354/meps07752

Tanasichuk, R., 1998. Interannual variations in the population biology and productivity of Euphausia pacifica in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. 173, 163–180. https://doi.org/10.3354/meps173163

Taylor, B.W., Keep, C.F., Hall, R.O., Koch, B.J., Tronstad, L.M., Flecker, A.S., Ulseth, A.J., 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. J.N. Am. Benthol. Soc. 26, 167–177. https://doi.org/10.1899/0887-3593(2007)26[167:ITFAMM]2.0.CO;2

Taylor, R., Rees, T.A.V., 1998. Excretory products of mobile epifauna as a nitrogen source for seaweeds. Limnol Oceanogr 43, 600–606. https://doi.org/10.4319/lo.1998.43.4.0600

Tilman, G.D., 1984. Plant Dominance Along an Experimental Nutrient Gradient. Ecology 65, 1445–1453. https://doi.org/10.2307/1939125

Traiger, S.B., Cohn, B., Panos, D., Daly, M., Hirsh, H.K., Martone, M., Gutierrez, I., Mucciarone, D.A., Takeshita, Y., Monismith, S.G., Dunbar, R.B., Nickols, K.J., 2022. Limited biogeochemical modification of surface waters by kelp forest canopies: Influence of kelp metabolism and site-specific hydrodynamics. Limnol Oceanogr 67, 392–403. https://doi.org/10.1002/lno.11999

Uthicke, S., 2001. Nutrient regeneration by abundant coral reef holothurians. J. Exp. Mar. Biol. Ecol. 265, 153–170. https://doi.org/10.1016/S0022-0981(01)00329-X

Uthicke, S., Klumpp, D.W., 1998. Microphytobenthos community production at a near-shore coral reef: seasonal variation and response to ammonium recycled by holothurians. Mar Ecol Prog Ser 169, 1–11.

Vanni, M.J., 2002. Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33, 341–370. https://doi.org/10.1146/annurev.ecolsys.33.010802.150519

Vinther, H.F., Holmer, M., 2008. Experimental test of biodeposition and ammonium excretion from blue mussels (Mytilus edulis) on eelgrass (Zostera marina) performance. Journal of Experimental Marine Biology and Ecology 364, 72–79. https://doi.org/10.1016/j.jembe.2008.07.003

West, E.J., Pitt, K.A., Welsh, D.T., Koop, K., Rissik, D., 2009. Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages. Limnol Oceanogr 54, 2058–2071. https://doi.org/10.4319/lo.2009.54.6.2058

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. Journal of Open Source Software 4, 1686. https://doi.org/10.21105/joss.01686

Yee, D.A., Juliano, S.A., 2007. Abundance matters: a field experiment testing the more individuals hypothesis for richness–productivity relationships. Oecologia 153, 153–162. https://doi.org/10.1007/s00442-007-0707-1

**Data Availability Statement**

All datasets generated during the current study and code are available in the GitHub repository: <https://github.com/em-lim13/Ch2_Spatial_pee>.