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

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**Abstract**

Consumer-mediated nutrient dynamics (CND), through which animals’ metabolic waste products fertilize primary producers, drives variability in nutrient availability and thus primary productivity and community functioning in tropical waters. Yet, examinations of CND as a driver of variation in nutrient availability in temperate marine ecosystems are limited. To assess the scale and drivers of spatial variation in CND within temperate marine ecosystems, we quantified the occurrence of 48 fish and 92 macroinvertebrate taxa and measured their ammonium excretions at 27 northeast Pacific rocky reefs for three years and 17 kelp forests of varying density for a single year. Ammonium concentrations ranged from 0.01 to 2.5 uM across rocky reefs, and the relationship between animal biomass and ammonium was weakly positive at slack and ebb tides, but weakly negative at flood tide. Ammonium was significantly higher within than adjacent to kelp forests, a difference that increased with tide exchange, kelp biomass, and animal biomass. Using caging experiments, we found that fine-scale ammonium variability and nutrient enrichment on a scale of meters was only possible under low-flow conditions. Our results suggest CND-driven variability acts on scales ranging from a few meters to over 20 km, contributing to finer-scale variation in nutrient availability than allochthonous nutrient sources such as upwelling. Therefore, CND may play a previously unrecognized role in structuring temperate marine ecosystems from the bottom up.

**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 under 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, such as upwelling, as drivers of variability in nutrient availability, there is now substantial evidence that consumers also contribute to bottom-up effects (Allgeier et al., 2017). Animals’ metabolic waste products (i.e., excretion and egestion) fertilize primary producers via a process termed consumer-mediated nutrient dynamics (Vanni, 2002). However, the ecological importance of consumer-regenerated nutrients across scales remains unclear. Therefore, identifying the scales at which biologically relevant variation in nutrient availability contributes to community structure remains an active area of research (Allgeier et al., 2017).

Heterogeneity in consumer habitat use contributes substantially to spatial and temporal variation in nutrients supplied by animal waste (Benkwitt et al., 2019; Roman and McCarthy, 2010; Uthicke, 2001a). 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; Meyer et al., 1983; Shantz et al., 2015). On a broad scale, productivity increases with proximity to reefs with high densities of fishes (Layman et al., 2016), while on a finer 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 a source of temporal variation as some fishes travel from their nighttime feeding grounds to daytime hiding spots, transporting substantial quantities of nitrogen in their tissues with them (Francis and Côté, 2018; Meyer and Schultz, 1985). Even larger-scale temporal and spatial variation can arise from the migration of megafauna; 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 waters, external sources of nutrients, such as upwelling and freshwater runoff, are generally thought to be dominant drivers of nitrogen variability (Dayton et al., 1999; Mann, 1973). Due to the open nature of nearshore environments, high water flow due to currents, tides, and wave action are theorized to limit small-scale nutrient variation (Probyn and Chapman, 1983). Therefore, research on intertidal and shallow subtidal ecosystems has traditionally focused on top-down, trophic interactions as drivers of community composition at small scales (1 to 100 m2), and considered resource limitation mainly at 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 benthic and pelagic marine communities (Menge et al., 1997; Nielsen and Navarrete, 2004) and even weaken top-down control (Sellers et al., 2020). For example, the amount of nitrogen regenerated by intertidal mussel beds varies with mussel cover along an entire coastline (Pfister et al., 2014). In a nearby wave-exposed shoreline, mussels also contribute to nutrient regeneration on small, local scales by increasing the concentration of nitrogen in the water column directly over the beds (Aquilino et al., 2009). Vertical gradients in ammonium concentration in the water column can also arise from microbial remineralization in marine sediments (Lowman et al., 2023). Therefore, regenerated nitrogen may contribute substantially to large-, meso-, and small-scale variation in nutrient availability, even in high-flow, upwelling nearshore coastal ecosystems.

Shallow subtidal rocky reefs and kelp forests are two charismatic temperate nearshore communities that attract dense aggregations of fishes and invertebrates, many of which are economically, ecologically, and culturally important (Steneck et al., 2002). These animals 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). The elevated levels of biomass and biodiversity that occur within these habitats 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, especially during low upwelling periods (Brzezinksi et al., 2013). These kelps, which comprise giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis leutkeana*) in the northeast Pacific region, also affect seawater hydrodynamics and physical composition, both slowing water flow within forests and creating gradients of carbon content, pH, alkalinity, and oxygen (Gaylord et al., 2007; Jackson and Winant, 1983; Pfister et al., 2019). These modifications to the physical environment could affect the productivity and community composition of other primary producers, also contributing to small-scale spatial heterogeneity.

We aimed to quantify the contribution of regenerated nutrients to spatial variability of nutrients in a temperate, wave-swept upwelling region: Barkley Sound in British Columbia (BC), Canada. This region is located on the traditional territories of the Huu-ay-aht First Nations and comprises an archipelago of islands dotted with rocky reefs and kelp forests. Specifically, we measured variation in ammonium (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 (smaller 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, measured kelp forest metrics, and other abiotic variables to explore drivers of potential variation in NH₄⁺ concentrations. Despite this region’s external nutrient sources and high flow, we hypothesize consumer-mediated nutrient dynamics will contribute to meso-, small-, and smaller-scale nutrient variability. By characterizing the scale at which animal-driven nutrients vary in this temperate region, we hope to elucidate the potential for consumers to structure communities not only from the top down, but also the bottom up.

**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 unravel ecosystem dynamics, document large-scale patterns of kelp response to heatwaves and establish ecological baselines (Attridge et al., 2024; Howard et al., 2019; Starko et al., 2024, 2022; Tanasichuk, 1998). Subtidal fish communities comprise at least 18 families including gobies, surfperches, rockfishes, greenlings, and sculpins (cite RLS?). Invertebrate assemblages, which are made up of over 49 families, are dominated by urchins, turban snails, sea stars, abalone, and sea cucumbers (cite RLS).

*Surveys of among-site (meso-scale) 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 collected subtidal NH4+ samples paired with fish and invertebrate surveys using a globally standardized method (i.e., Reef Life Survey, RLS) at each site. We conducted our surveys between the end of April and middle of May for three years (2021-2023), with all annual surveys occurring within 2 weeks of each other (Supplemental Table 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 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 at consistent depths and stored the syringes in sealed plastic bags upon collection to prevent contamination. Seawater samples were filtered into 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 (Lim, unpublished data). 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 increased 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 within-site (small-scale) variation*

To investigate within-site variation in animal-regenerated nutrients, we measured NH4+ concentrations in and around kelp forests and surveyed the neighbouring biological communities as potential moderators of this variation. Our 16 sites comprised forests of varying densities dominated by giant kelp or bull kelp, as well as two no-kelp control sites. We conducted our surveys from July to September 2022 (Supplemental Table 2). First, to quantify the abundance and biodiversity of animal communities associated with each kelp forest, divers surveyed fish and invertebrate communities along 50 m transect lines placed immediately adjacent to the edge of the kelp forest following the RLS protocol as above. Next, we ran four 1 m-wide, 5 m-long transects, 5 m apart, into the kelp forest to assess kelp density, canopy height, and biomass (Supplemental Fig. 1). Divers then counted the number of canopy kelp individuals (bull or giant kelp) within 0.5 m on either side of the kelp transect to measure kelp density. To estimate canopy height, we measured the length of five randomly chosen 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 from holdfast to 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 (Attridge, unpublished data). For giant kelp biomass, we weighed using X brand scale 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 GPS, 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 from 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 Whirl-PakTM sample bag with seawater for creating 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 within-meters (smaller-scale) 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. The first caging experiment took place at Scott’s Bay (48°50'05.2"N, 125°08'49.3"W), a wide, exposed bay that opens on Trevor Channel (Fig. 1d), on May 27 – 28, 2021. 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 and deployed at 3 to 5.8 m depth (9 cages per line). We collected California sea cucumbers (*Apostichopus californicus*) 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 h, 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, 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).

The second caging experiment took place in Bamfield Inlet (48°49'53"N 125°08'11"W), a narrow, sheltered inlet (Fig. 1d), from June 10 – 19, 2023, and we replicated it from June 19 – 28, 2023 following the same methodology. For these experiments, we used red rock crabs (*Cancer productus*). We collected 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 buckets 0.8 m below chart datum. Each cage contained either one large crab (carapace 15.0 – 15.9 cm), one medium size crab (11.6 – 14.4 cm), or a control (i.e., a small rock, scraped clean, to weight the cages similarly to the crabs) (n = 4 replicates per experiment). During both experiments, we replaced the crabs after 4 days with freshly fed, similar-sized crabs, at which point we re-randomized the order of the cages along the line. 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). All data and code are available at https://github.com/em-lim13/Ch2\_Spatial\_pee.

For each Reef Life Survey conducted, we calculated fish biomass from fish length following the formula (W = a\*Lb) where W is fish weight, L is the fish length, a and b are species-specific constants from FishBase (Froese et al., 2014). For invertebrates, sunflower sea stars and economically important species (abalone and scallops) were measured, so we used published length-weight relationships to calculate wet weight from size. For all other invertebrates, we used published wet weight estimates from this region to estimate rough average biomass estimates 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 (Supplemental Table 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, starting from the time each survey started and ending one hour later, and taking the average of those values. We downloaded tide height data from the website: <http://tbone.biol.sc.edu/tide/tideshow.cgi?site=Bamfield%2C+British+Columbia>.

Among-site (meso-scale) variation

To determine whether there was significant variation in NH₄⁺ among sites, 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 (1|site) and year (1|year). All predictors were scaled and centered around the mean using the scale function. We used a gamma distribution (link = ‘log’). We constructed additional models with animal biomass as a predictor instead of abundance, and Simpson’s diversity instead of Shannon diversity, but we determined that abundance and Shannon diversity were the best metrics by comparing alternative models using AIC (Supplemental Table 4). We checked for collinearity of variables using car::vif, and all values were below 1.9. We visually inspected model residuals by plotting the output from DHARMa::simulateResiduals, and the model met all assumptions. 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.

Within-site (small-scale) 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/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) to account for the fact that each site contributed 3 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 animal abundance instead of biomass, and Simpson’s diversity instead of Shannon diversity (Supplemental Table 5). We inspected residuals using DHARMa::simulateResiduals, checked for collinearity between variables, and the model met all assumptions. We also ran our final model with centred continuous variables instead of scaled variables to facilitate interpretation of coefficients in the results. Finally, 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.

Within-meters (smaller-scale) variation

To quantify the impact of caged animals on NH₄⁺ concentration, we constructed separate linear models for each caging experiment. 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. The model met all assumptions upon inspection of the residuals. We calculated the NH₄⁺ excretion rate for each sea cucumber using a previously generated size index (sqrt(length\*girth)) to excretion relationship (Supplement???). For the red rock crab experiment, we constructed a generalized linear mixed-effects model with cage NH₄⁺ concentration as the response variable and treatment (no crab, medium crab, or large crab) as the predictor variable. 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 gamma distribution (link = ‘log’) to ensure model residuals met all assumptions. We used a previously developed carapace to excretion relationship to calculate NH₄⁺ excretion rates for each crab. `

**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. 3a). However, we did find a significantly negative interaction between animal abundance and tide exchange (p = 0.01, Fig. 3b), revealing a weakly positive effect of total animal abundance per m2 on NH₄⁺ concentration, but only at ebb tide.

We also found evidence of small-scale, within-site variation; NH₄⁺ concentrations were significantly higher inside than outside giant kelp forests (LMM, mean difference ± SE; 0.16 ± 0.03 μM, p < 0.001) and bull kelp forests (0.41 ± 0.06 μM, p < 0.001). The ‘excess’ NH₄⁺ concentration inside kelp forests increased by 0.54 ± 0.09 μM per unit of kelp biomass (kg/m2) (p < 0.001), and with tide exchange (p = 0.007). We found limited evidence for an effect of animal biomass (p = 0.07, Fig. 4a, b), survey depth (p = 0.07) (Fig. 4a), and Shannon diversity on ∆ NH₄⁺ (p = 0.09). We found evidence of a positive interaction between kelp forest biomass and tide exchange, whereby the positive effect of kelp biomass on ∆ NH₄⁺ increased with tide exchange (2.65 ± 0.71, p < 0.001, Fig. 4b). We also found a negative interaction between kelp biomass and animal biomass (- 0.83 ± 0.30, p = 0.006), and a negative interaction between tide exchange and animal biomass (- 4.23 ± 1.45, p = 0.004, Fig. 4a). ∆ NH₄⁺ was negative between samples taken 5 m apart at the no-kelp control sites (-0.24 ± 0.08 μM, p = 0.003, Fig. 4a).

We found mixed evidence for animal-related variability in ammonium concentration at the smallest scale studied. For sea cucumbers, we found no effect of sea cucumber density on cage NH₄⁺ concentration despite a supply rate of 14 μM/hour and 28 μM/hour 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. 5a). However, we did find 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. 5b). Medium crabs excreted on average 88 μM/hour while large crabs excreted 150 μM/hour.

**Discussion**

We found evidence of meso- and small-scale variability, and mixed evidence for smaller-scale variability of animal-regenerated nutrients. Ammonium varied up to 16x between rocky reef sites, 1.9x inside vs outside kelp forests, and 40x between cages with crabs vs control cages which supports our hypothesis that animal-driven variability in nutrients is possible across all three spatial scales. Water flow 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, but within sites moving water made kelps’ ability to slow flow and trap animal-regenerated nutrients more pronounced. In the very-small scale caging experiments we only detected an effect of animals in the protected, low flow inlet. –need a hook here ----

*Meso-scale*

Among rocky reef sites, we detected a 16-fold difference in NH₄⁺ between the lowest and highest sites, which doesn’t even represent the highest difference (533x) the authors have measured in this region. This is substantially larger than measurements of among-site variation in nitrate (3.7x and 6.5x differences) and ammonium (0.4x and 0.8x) from the same region, (Druehl et al., 1989; Hurd et al., 2000), and larger than among-site NH₄⁺ differences measured in a nearby region (1.1x, Pfister et al., 2014). We found a negative interaction between tide exchange and animal abundance, whereby animal excretions may enrich the seawater when the tide is going out and standing still, but when the tide comes in it washes away the effect of animal abundance. We did not quantify intertidal animals or microbial regeneration, which are additional sources of NH₄⁺ (Aquilino et al., 2009; Lowman et al., 2023). However, given the positive relationship between animal abundance and NH₄⁺, we propose animal-regenerated nutrients likely contribute to meso-scale variation in NH₄⁺ which could drive among-site variation in primary productivity and thus bottom-up control.

*Small-scale*

We found evidence of kelp-mediated variation in nutrients on a smaller scale (5 m) than previously established by other studies that compared samples taken over 100 m apart (Pfister et al., 2019; Stewart et al., 2009; Traiger et al., 2022). Increased NH₄⁺ inside high density kelp forests has been documented (Pfister et al., 2019), but by sampling 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 acceleration of flow around the edges (Gaylord et al., 2007; Rosman et al., 2007). Indeed, 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, so we can only contrast slack and flooding tides. Nevertheless, it seems as though water flow due to tidal exchange enhances NH₄⁺ variability within kelp forests instead of masking it.

Nitrate, which is supplied externally via upwelling or run-off, becomes depleted or unchanged as it flows through kelp forests (Pfister et al., 2019; Stewart et al., 2009), opposed to NH₄⁺ which is regenerated by animals within and around the forest, and seemingly retained there. Although the positive relationship between animal biomass and ∆ NH₄⁺ was weak, the negative interactions between animal biomass and both tide and kelp suggest a potentially saturating relationship between these variables. When animal biomass was low, increased kelp or tidal exchange increased the ∆ NH₄⁺ but at high animal biomass, increasing the kelp or flow had no effect. There may be a threshold for how much animals can saturate and therefore increase NH₄⁺ inside vs outside kelp forests beyond which increased water motion or kelp no longer continues to increase ∆ NH₄⁺ indefinitely.

We found higher ∆ NH₄⁺ in bull kelpforests compared to giant kelp forests, which may be due to different allocations of biomass in the water column and thus different alterations of water flow. Indeed, (Murie and Bourdeau, 2020) found larger differences in dissolved oxygen and pH between inside vs outside bull kelp forests compared to the differences found inside vs outside giant kelp forests by Traiger et al (2021). We found a negative ∆ NH₄⁺ at our no kelp control sites, which may be a result of the slope of the substrate. NH₄⁺ increases with depth, (CITE), a trend that our data show weekly, so samples collected “outside” the control sites may have been deeper than the “inside” samples. We cannot say for certain what caused this result, but we take comfort in the fact that the trend we observed at control sites is opposite to the trend we found in kelp forests.

We did not find a significant effect of biodiversity among- or within-sites. Elucidating the tangled relationships between the abundances of each species in communities is challenging, as some families may be sources of NH₄⁺, while others may benefit from increases in primary productivity due to NH₄⁺ production by other families. As surveys were conducted at the edges of kelp forests due to difficulties conducting a 5 m wide fish belt survey in thick kelp, our communities are more representative of kelp forest associated species, and not necessarily the species living immediately within the kelp. Nevertheless, we did find more species at our kelp sites compared to the rocky reef sites, supporting extensive research on the positive effect of kelp on biodiversity (CITE).

*Smaller scale*

When we zoom into the smallest scale of variability tested, we only found evidence of smaller-scale variation in NH₄⁺ in our cage experiments in the sheltered inlet, which may suggest water motion mediates variation at this scale as well. However, NH₄⁺ enrichment by animals is possible in wave-exposed conditions; seawater above mussel beds had 15.9x higher NH₄⁺ compared to neighbouring rock (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 it might be possible at all. The crabs in the sheltered cages excreted NH₄⁺ at a rate roughly 6x higher than the sea cucumbers caged in the more exposed location, and the crab cages were constructed with only two mesh windows instead of the fully mesh sea cucumber cages. Therefore, we simply conclude that at least in sheltered conditions, smaller-scale variation driven by animal biomass is possible

Finally, we must consider whether the NH₄⁺ variation described by our studies could translate into meaningful variation in primary productivity. Increased primary productivity has been seen at orders of variation from 1.3 – 9x in NH₄⁺ (Allgeier et al., 2020; Arzul, 2001; Meyer et al., 1983; Sandoval-Gil et al., 2016; Savage, 2019; Shantz et al., 2015; Uthicke, 2001b; 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. Even in nutrient-replete upwelling ecosystems, an increase in NH₄⁺ from 0.08 uM to 1.26 uM (15.8x difference) was linked to increased tissue nitrogen and coverage of an intertidal seaweed (Aquilino et al., 2009), and a 1.8x increase in NH₄⁺ increased growth in subtidal seaweeds in Barkley Sound (Druehl et al., 1989). Given the annual depletion of nitrates each summer (Druehl et al., 1989), and primary producers preference for NH₄⁺ over nitrate (Phillips and Hurd, 2004), it’s likely that the NH₄⁺ variation we documented at meso-, small-, and smaller-scales contribute to variation in primary productivity and potentially bottom-up control.

Conclusion paragraph??????

Discussion outline:

Paragraph 1: restate results from each spatial scale and address hypotheses. We found evidence of meso-scale, small-scale, and smaller-scale variation in NH₄⁺. Flow and animals were important at all three scales.

Paragraph 2: Among-site. How does that measure up to other drivers of variability (nitrates from upwelling!)

* How does that measure up to other drivers of variability (nitrates from upwelling!)
  + (Pfister et al., 2014)
    - 110% (2.607-1.238) variation between onshore sites in NH₄⁺
    - 725% (2.607-0.316) onshore vs offshore
    - Nitrates varied 24% between sites (24.665-19.868)
  + (Hurd et al., 2000)
    - 370% (1.17-5.5) uM surface nitrate Dixon vs Kii xin
    - 40% (2.25-3.15) uM surface ammonium Dixon vs Kii xin
  + Druehl et al 1989
    - 7.5x (0.6-4.5 uM) surface nitrate site vs site in summer
    - 1.83 (0.6 - 1.1 uM) surface ammonium site vs site in summer

Paragraph 3. Within-site. Kelp forests impacted small-scale variation in nutrients by retaining NH₄⁺

* More kelp and more flow = increased delta, and positive interaction so that relationship really cranks up!
* Magnitude of variability vs differences found in other in vs out kelp forests. Cite those kelp slows flow of water papers.
  + (Pfister et al., 2019) found lower nitrate and phosphate in kelp but higher ammonium
  + (Stewart et al., 2009) similar nitrate in vs out
* Sounds like nitrates don’t concentrate in kelp but animal regenerated nutrients = preferred nutrient = concentrated around kelp! Cool! Limitation: only sampled on flood and slack, didn’t catch ebb.

Paragraph 4. Address the other in vs out predictors here! Why was delta nh4+ larger in Nereo vs Macro? Why the no kelp sites had negative delta ammonium. Negative interactions: almost an asymptote relationship? If you have a high level of one variable, increasing the other doesn’t infinitely increase the delta. Talk about animal biomass here. Address depth and biodiversity, both had near significant effects. Limitations: RLS surveys were on edge of kelp, not inside the forest, only one year of data.

Paragraph 5. Small scale! Magnitude of diff, has anyone else done super small scale stuff? Compare to that. Maybe the crabs had a diff bc that area had lower flow? But also address diff in flow between cages! Limitations: didn’t standardize cage design but these experiments weren’t to test the conditions under which fine-scale variation was possible, only to see if it WAS possible.

Paragraph 6: Do we think the amount of variability we found at each scale will amount to any effect on pp? Cite some CNC = growth papers that have similar levels of enrichment. Cite the papers that show nitrates in the summer are low?

Paragraph 7. Conclusions. Animals are contributing to variability! Mention magnitude of variability vs other sources (upwelling, run-off) BUT… do we know if this impacts pp? Set up Ch 3 kelp outplant experiment!

**Figures**

**A screenshot of a map

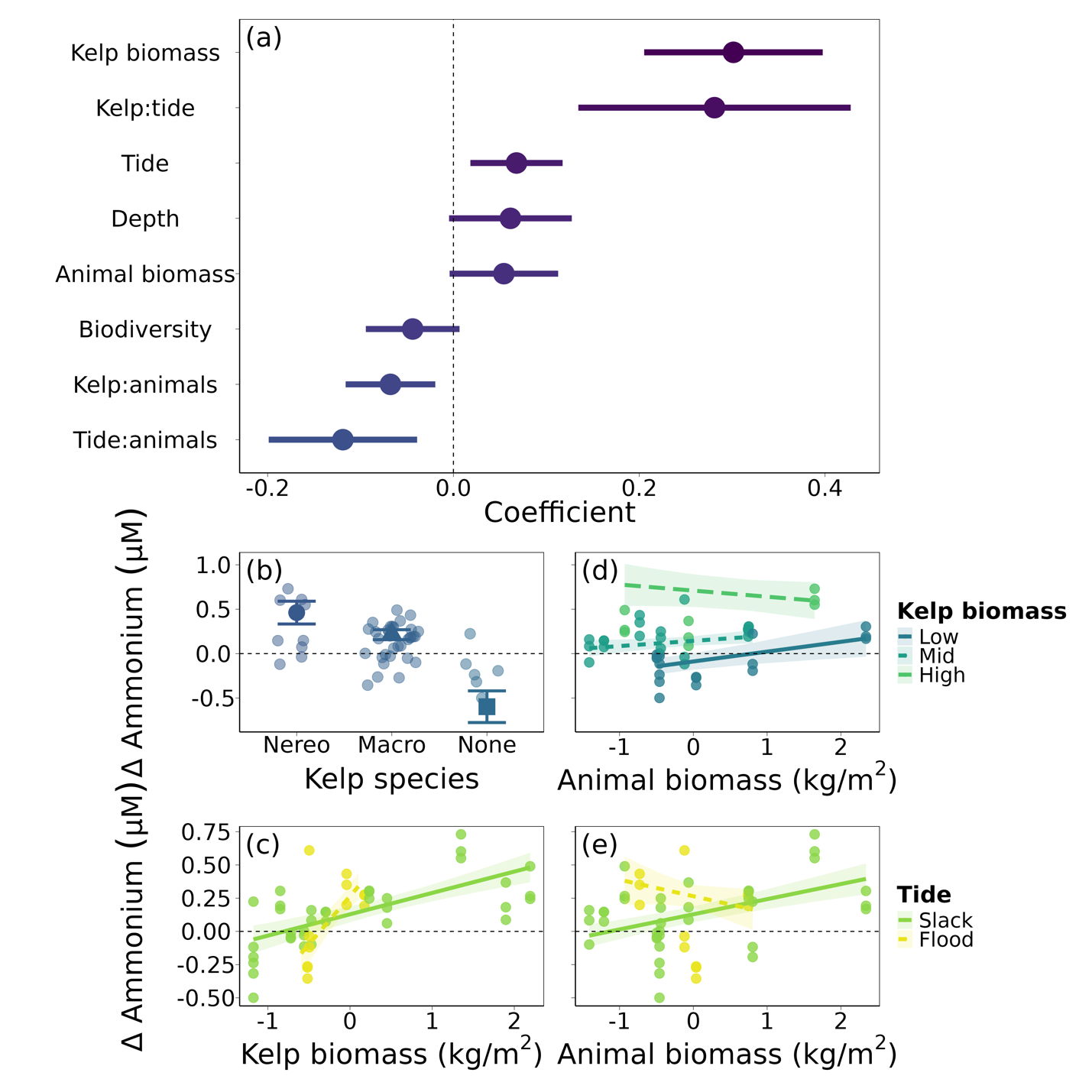
Description automatically generated**

**Figure 1.** (b Among-site, (c) within-site, and (d) within-meters schematics of our three spatial scales of variability investigated. (d) Rocky reefs (circles) surveyed for among-site, meso-scale ammonium variation, and kelp forests surveyed (triangles) for within-site, small-scale ammonium variation in Barkley Sound, BC. Site colour indicates mean ammonium concentration found at each site across all three years, with darker points having higher concentrations of ammonium. Image credit to …….

**A graph of an abundance

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**Figure 3.** Ecological drivers of seawater ammonium concentration observed across 27 rocky reef sites in Barkley Sound, British Columbia, Canada. (a)Model coefficients surrounded by 95% confidence intervals, and (b) model-generated predictions for the investigation of among-site variation in ammonium concentration. The coefficients were generated from a generalized linear mixed-effects model, which used a gamma distribution (link = ‘log’) so coefficients are presented in log space. Continuous predictors were centred and scaled for comparison of effect sizes between predictors with varying units.



**Figure 4.** Drivers of variation in ammonium concentration inside vs outside kelp forests across 16 sites in Barkley Sound, British Columbia, Canada. (a) Model coefficients surrounded by 95% confidence intervals and (b) model-generated predictions for the investigation of within-site variation in ammonium concentration. Continuous variables were scaled and centered to facilitate comparisons between variables measured in different units.

**A diagram of ammonium and ammonium

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**Figure 5.** Smaller-scale effect of animals on ammonium concentration. Mean ammonium concentration in experimental cages containing (a) zero, one, or two California sea cucumbers, and (b) control, medium size, or large size red rock crab. Error bars indicate 95% confidence intervals. Image credit to Hailey Davis

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

**A drawing of a seaweed and syringes

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**Supplemental Figure 1.** Placeholder schematic for the kelp pee samples. Still need to tidy this up! Image credit to ------

**Supplemental Table 1.** List of rocky reef sites sampled using Reef Life Survey methods, and the 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 |

**Supplemental Table 2.** List of kelp forest sites and the date of each survey.

|  |  |  |  |
| --- | --- | --- | --- |
| **Site code** | **Site name** | **Coordinates** | **Date** |
| KCCA1 | Ross Islet Slug Island | 48.87039, -125.1599 | 2022-07-04 |
| KCCA2 | Between Scott’s and Brady’s | 48.83287, -125.1493 | 2022-07-05 |
| KCCA3 | Dodger Channel 1 | 48.83072, -125.19439 | 2022-07-06 |
| KCCA4 | Flemming 112 | 48.87868, -125.1434 | 2022-07-07 |
| KCCA6 | Less Dangerous Bay | 48.87535, -125.0915 | 2022-07-24 |
| KCCA7 | Ed King East Inside | 48.83608, -125.2131 | 2022-07-25 |
| KCCA9 | Wizard Islet South | 48.85728, -125.1595 | 2022-07-27 |
| KCCA12 | North Helby Rock | 48.85831, -125.1649 | 2022-08-03 |
| KCCA14 | Danvers Danger Rock | 48.877, -125.0923 | 2022-08-06 |
| KCCA15 | Cable Beach (Blow Hole) | 48.82484, -125.16067 | 2022-08-07 |
| KCCA16 | Tzartus 116 | 48.90084, -125.0811 | 2022-08-18 |
| KCCA17 | Turf Island 2 | 48.884864, -125.146937 | 2022-08-20 |
| KCCA18 | Second Beach | 48.815969, -125.174 | 2022-08-21 |
| KCCA19 | Wizard Islet North | 48.85916, -125.15908 | 2022-08-22 |
| KCCA21 | Bordelais Island | 48.81822, -125.2294516 | 2022-09-01 |
| KCCA22 | Taylor Rock | 48.82721, -125.19717 | 2022-09-05 |

**Supplemental Table 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 (eg. 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 measured *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 | Lim, unpublished data |
| *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 |

**Supplemental Table 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. df is the degrees of freedom 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** | **df** | **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 |

**Supplemental Table 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. df is the degrees of freedom 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** | **df** | **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 |

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

**Among-site (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, Supplemental Figure 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 Supplemental Table 1.

**A graph of different types of numbers

Description automatically generated with medium confidence**

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

**Supplemental Table 1.** Model summaries from the among-site, meso-scale models including only the biomass of one family for each model.

Sebastidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.13333 1.23129 0.108 0.914

fam\_den\_scale 1.97572 3.21833 0.614 0.539

tide\_scale -0.52577 1.00087 -0.525 0.599

shannon\_scale -0.09965 0.13231 -0.753 0.451

depth\_avg\_scale -0.02276 0.12990 -0.175 0.861

fam\_den\_scale:tide\_scale -1.78560 2.81804 -0.634 0.526

Muricidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.434858 0.333427 -1.304 0.192

fam\_den\_scale 0.793932 0.513936 1.545 0.122

tide\_scale 0.053399 0.121424 0.440 0.660

shannon\_scale -0.003838 0.097453 -0.039 0.969

depth\_avg\_scale 0.039007 0.091700 0.425 0.671

fam\_den\_scale:tide\_scale 0.122610 0.553062 0.222 0.825

Asterinidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.58081 0.25501 -2.278 0.0228 \*

fam\_den\_scale 0.20689 0.25841 0.801 0.4233

tide\_scale 0.12450 0.06909 1.802 0.0715 .

shannon\_scale -0.11586 0.09008 -1.286 0.1984

depth\_avg\_scale 0.05520 0.08902 0.620 0.5352

fam\_den\_scale:tide\_scale 0.06921 0.27150 0.255 0.7988

Hexagrammidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 4.960945 2.539162 1.954 0.0507 .

fam\_den\_scale 14.671724 6.691550 2.193 0.0283 \*

tide\_scale -3.349292 2.012201 -1.665 0.0960 .

shannon\_scale 0.009674 0.088138 0.110 0.9126

depth\_avg\_scale 0.021288 0.086719 0.246 0.8061

fam\_den\_scale:tide\_scale -9.007885 5.353635 -1.683 0.0925 .

Acmaeidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.194057 0.329224 -0.589 0.5556

fam\_den\_scale 1.424749 0.669551 2.128 0.0333 \*

tide\_scale 0.032068 0.155457 0.206 0.8366

shannon\_scale -0.007977 0.093207 -0.086 0.9318

depth\_avg\_scale 0.004841 0.092253 0.052 0.9582

fam\_den\_scale:tide\_scale -0.162030 0.577448 -0.281 0.7790

Gobiidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.64053 0.29309 -2.185 0.0289 \*

fam\_den\_scale 0.17168 0.22942 0.748 0.4543

tide\_scale 0.03806 0.07359 0.517 0.6050

shannon\_scale -0.01094 0.09648 -0.113 0.9098

depth\_avg\_scale -0.06208 0.11275 -0.551 0.5819

fam\_den\_scale:tide\_scale 0.13329 0.16709 0.798 0.4250

**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 our 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, Supplemental Figure 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 Supplemental Table 2.

A graph of different types of growth

Description automatically generated with medium confidence

**Supplemental Figure 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

**Supplemental Table 2.** Model summaries from the within-site, small scale models including only the biomass of one family for each model.

Echinasteridae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 3.22472 0.70794 4.555 5.24e-06 \*\*\*

kelp\_spnereo 0.23457 0.03453 6.793 1.10e-11 \*\*\*

kelp\_spnone -0.08853 0.06650 -1.331 0.183088

kelp\_bio\_scale -2.81761 0.88787 -3.173 0.001506 \*\*

tide\_scale 3.01942 0.75719 3.988 6.67e-05 \*\*\*

weight\_den\_fam\_scale 7.35886 1.67832 4.385 1.16e-05 \*\*\*

shannon\_scale -0.12606 0.02115 -5.959 2.53e-09 \*\*\*

depth\_scale 0.04027 0.01837 2.192 0.028381 \*

kelp\_bio\_scale:tide\_scale 0.20281 0.03761 5.392 6.97e-08 \*\*\*

kelp\_bio\_scale:weight\_den\_fam\_scale -7.65598 2.14144 -3.575 0.000350 \*\*\*

tide\_scale:weight\_den\_fam\_scale 6.87200 1.78273 3.855 0.000116 \*\*\*

Gobiidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) -0.55547 0.23654 -2.348 0.018857 \*

kelp\_spnone 0.88797 0.34010 2.611 0.009031 \*\*

kelp\_bio\_scale 1.06405 0.37849 2.811 0.004934 \*\*

tide\_scale 4.79062 0.98052 4.886 1.03e-06 \*\*\*

weight\_den\_fam\_scale -1.71304 0.56978 -3.006 0.002643 \*\*

shannon\_scale 0.13727 0.03868 3.549 0.000387 \*\*\*

depth\_scale -0.00280 0.02937 -0.095 0.924042

kelp\_bio\_scale:tide\_scale 0.11384 0.08461 1.345 0.178486

kelp\_bio\_scale:weight\_den\_fam\_scale 2.64764 0.98325 2.693 0.007087 \*\*

tide\_scale:weight\_den\_fam\_scale 12.21684 2.47943 4.927 8.34e-07 \*\*\*

Cottidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 1.23122 0.56070 2.196 0.028102 \*

kelp\_spnereo 0.11919 0.07321 1.628 0.103523

kelp\_spnone -0.43416 0.09321 -4.658 3.19e-06 \*\*\*

kelp\_bio\_scale -0.35380 0.36761 -0.962 0.335844

tide\_scale -0.67897 1.14142 -0.595 0.551943

weight\_den\_fam\_scale 2.55957 1.28229 1.996 0.045924 \*

shannon\_scale -0.15608 0.03545 -4.402 1.07e-05 \*\*\*

depth\_scale 0.10973 0.02875 3.817 0.000135 \*\*\*

kelp\_bio\_scale:tide\_scale 0.17294 0.08104 2.134 0.032851 \*

kelp\_bio\_scale:weight\_den\_fam\_scale -1.58585 0.85911 -1.846 0.064904 .

tide\_scale:weight\_den\_fam\_scale -1.88287 2.68459 -0.701 0.483077

Strongylocentrotidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.0004341 0.0570275 0.008 0.99393

kelp\_spnereo 0.0661813 0.0798662 0.829 0.40730

kelp\_spnone -0.6711153 0.1241935 -5.404 6.52e-08 \*\*\*

kelp\_bio\_scale 0.1965326 0.0574934 3.418 0.00063 \*\*\*

tide\_scale 0.0663294 0.0669569 0.991 0.32187

weight\_den\_fam\_scale 0.0808835 0.0251885 3.211 0.00132 \*\*

shannon\_scale 0.0400143 0.0349902 1.144 0.25280

depth\_scale 0.0994891 0.0310032 3.209 0.00133 \*\*

kelp\_bio\_scale:tide\_scale 0.1472693 0.0605091 2.434 0.01494 \*

kelp\_bio\_scale:weight\_den\_fam\_scale -0.0168616 0.0150645 -1.119 0.26301

tide\_scale:weight\_den\_fam\_scale -0.0239569 0.0225873 -1.061 0.28886

Embiotocidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.27008 0.04271 6.324 2.55e-10 \*\*\*

kelp\_spnereo -0.03453 0.07745 -0.446 0.655717

kelp\_spnone -0.28231 0.13383 -2.109 0.034908 \*

kelp\_bio\_scale 0.24745 0.04663 5.307 1.11e-07 \*\*\*

tide\_scale 0.15179 0.04062 3.736 0.000187 \*\*\*

weight\_den\_fam\_scale 0.55061 0.11968 4.601 4.21e-06 \*\*\*

shannon\_scale -0.08701 0.03058 -2.846 0.004434 \*\*

depth\_scale 0.07119 0.02975 2.393 0.016713 \*

kelp\_bio\_scale:tide\_scale 0.18242 0.06991 2.609 0.009068 \*\*

kelp\_bio\_scale:weight\_den\_fam\_scale -0.05275 0.10959 -0.481 0.630243

tide\_scale:weight\_den\_fam\_scale 0.31241 0.19648 1.590 0.111832

Asteriidae

Estimate Std. Error z value Pr(>|z|)

(Intercept) 0.056277 0.041953 1.341 0.17978

kelp\_spnereo 0.047528 0.092364 0.515 0.60685

kelp\_spnone -0.242165 0.111039 -2.181 0.02919 \*

kelp\_bio\_scale 0.234677 0.074798 3.138 0.00170 \*\*

tide\_scale -0.018518 0.081987 -0.226 0.82131

weight\_den\_fam\_scale 0.126168 0.045779 2.756 0.00585 \*\*

shannon\_scale -0.098288 0.031823 -3.089 0.00201 \*\*

depth\_scale 0.047207 0.030279 1.559 0.11898

kelp\_bio\_scale:tide\_scale 0.115009 0.075756 1.518 0.12898

kelp\_bio\_scale:weight\_den\_fam\_scale 0.004679 0.028540 0.164 0.86978

tide\_scale:weight\_den\_fam\_scale 0.125188 0.095002 1.318 0.18759

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Discussion notes

* Talk about Cedeno et al., 2021 paper!!! They suggest nitrates = temporal variation in nutrients, but ammonium/regeneration = spatial variation in where animals are! Show surge uptake in Macro, so they just need to be exposed to a burst of strong fish pee = take up and store tons of nitrogen.
* Pfister, Altabet and Weigel 2019 also did pee inside vs out, but only 3 forests and inside vs offshore
* Stewart et al 2009 also did inside vs out
* Make sure to compare magnitudes of variation! 0 – 20 umol nitrite, what increases did Pfister or Aquilio find?