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

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**Abstract**

Consumer-mediated nutrient cycling (CNC), which is the fertilization of primary producers by animals’ metabolic waste products, is known to drive variability in nutrient availability and thus primary productivity and community functioning in tropical waters. Yet, CNC may be an unappreciated contributor of variability in temperate systems. Therefore, we aimed to quantify and explain spatial variation in CNC by surveying fish and macroinvertebrates via Reef Life Survey methods and measuring their ammonium excretions at 27 rocky reefs (3 years) and 17 kelp forests of varying density (1 year) in Barkley Sound, British Columbia. Ammonium concentrations varied from 0.009 to 2.5 uM across rocky reefs, and the relationship between animal biomass and ammonium varied with tidal exchange–weakly positive at slack and ebb tides, but weakly negative at flood tide. Ammonium was significantly higher within than near kelp forests, a difference that increased with kelp forest biomass. Ammonium variation between kelp forests was described by complex interactions between animal biomass, kelp density, and tide exchange. We also explored fine-scale ammonium variability and found nutrient enrichment on a scale of meters was possible, but only under low flow conditions. Our results suggest CNC-driven variability acts on scales ranging from a few meters to entire reefs, contributing to finer-scale variability in nutrient availability than allochthonous nutrient sources such as upwelling. CNC may therefore play a larger role than assumed in structuring temperate marine ecosystems from the bottom up.

**Introduction**

Variability in resource availability can drive substantial variation in the growth, biomass and composition of primary producers (Dayton et al., 1999; Leibold, 1991; Tilman, 1984). As producers are generally limited by resources (CITE theory papers), and productivity determines the flow of energy up the food chain and thus trophic interactions (CITE), variation in nutrient availability contributes to a mosaic of diverse assemblages across small and large scales (CITE). In some cases, these resource-limited effects can propagate up the food chain and substantially structure ecosystem composition and dynamics, exceeding even the impacts of top-down control (Gruner et al., 2008). However, in some cases bottom-up effects are difficult to detect, and top-down ecosystem control seems more likely (CITE). Identifying the contexts under which these bottom-up effects contribute meaningfully to ecosystem structure remains an active area of research (CITE). Therefore, elucidating the scale of biologically relevant variation in nutrient availability is the first step towards identifying whether such variation structures primary productivity, and thus propagates up food chains to structure ecosystems.

Nutrient regeneration by animals through a process termed consumer-mediated nutrient dynamics (CND) can contribute substantially to variation in nutrient availability (Allgeier et al., 2017). On small – meso-scales, variability in nutrients supplied by animal excretion and egestion stems from heterogeneity in consumers’ habitat use. For example, tropical coral reefs provide habitat, shelter, and food sources which attract dense aggregations of consumers, and thus regenerated nutrients (Archer et al., 2015; Shantz et al., 2015). At the fine scale, individual heads of coral inhabited by schools of fish have higher concentrations of nutrients than neighboring uninhabited corals (Holbrook et al., 2008). Diurnal variation arises as fishes travel from their feeding grounds to nighttime hiding spots, transporting substantial quantities of nutrients with them (Meyer and Schultz, 1985). Large-scale temporal and spatial variation can arise from the migration of megafauna; whales transport nutrients across thousands of kilometers as they travel from their feeding to breeding grounds (Doughty et al., 2016). However, the understanding of animal-driven variability of nutrients is drawn substantially from tropical ecosystems, often disregarding productive temperate marine ecosystems.

In temperate waters, external sources of nutrients, such as upwelling and freshwater runoff, are generally thought to dominate drivers of nutrient variability (CITE). High water flow due to currents, tides, and wave action in these regions are thought to limit small-scale nutrient variation in intertidal and shallow subtidal waters (CITE). Therefore, research on intertidal and shallow subtidal ecosystems has traditionally focused on top-down, trophic interactions as drivers of community composition at the small-scale, and considered resource limitation mainly at large, continental or regional scales (Menge, 1992). However, evidence suggests mesoscale variation in allochthonous nutrients via upwelling may contribute to bottom-up control of benthic marine communities (Nielsen and Navarrete, 2004). Intertidal mussel beds, which form dense aggregations of bivalves, contributed to meso-scale variation in nutrients via regenerative processes along a coastline with varying mussel cover (Pfister et al., 2014). In a nearby wave exposed shoreline, mussels also contributed to small-scale variation by increasing the concentration of nitrogen in the water column directly over the mussel beds (Aquilino et al., 2009). Therefore, regenerated nutrients may contribute substantially to large-, meso-, and small-scale variation in nutrient availability in high flow, upwelling nearshore coastal ecosystems.

Contrary to other experiments which focused on intertidal animals as sources of nitrogen, here we consider shallow subtidal rocky reef and kelp forest communities. Both of these habitats attract dense aggregations of fishes and invertebrates, many of which are economically, ecologically, and culturally important (CITE). 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). These biomass and biodiversity hot spots may also contribute to nutrient hotspots and meso- and small-scale nutrient variability. – better segue here – Fast growing, canopy kelps, which form expansive kelp forests, may benefit from these excretions directly as a source of nitrogen during low upwelling periods (Brzezinksi et al., 2013). These kelps, which comprise giant kelp (*Macrocystis* pyrifera) and bull kelp (*Nereocystis leutkeana*), also affect seawater hydrodynamics and physical composition, both slowing flow within forests and creating a gradient of carbon content, pH, alkalinity, and oxygen (Traiger 2022???). These modifications to their physical environment could affect the productivity and community composition of other primary producers, such as understory kelps and phytoplankton.

To assess the potential for regenerated nutrients to contribute to spatial variability, we aimed to characterize the extent and drivers of meso-, small-, and fine-scale variability in a wave-exposed, high flow upwelling temperate system: Barkley Sound, Canada. This region is located on the traditional territories of the Huu-ay-aht First Nations and comprises an archipelago of islands. Due to the proximity of the Bamfield Marine Science Centre, this region has been used throughout time to identify ecosystem dynamics, etc etc…. External sources of nutrients are delivered via upwelling in the spring and early summer and riverine input in the winter and spring (Pawlowicz, 2017), contributing to both spatial and temporal variation in nutrient availability. Specifically, these external sources provide nitrogen, a limiting nutrient in nearshore marine waters (Elser et al., 2007), in the form of nitrate and nitrite. ….. We specifically set out to test the extent of variability in ammonium concentrations both amoung and within sites. Additionally, we surveyed biotic communities and measured abiotic variables to determine drivers and modifiers of this variability. – explain experiments more -- Due to this region’s external nutrient sources and high flow, CND would not be expected to contribute substantially to small- and fine-scale nutrient variability, but we hypothesize that meso-scale variation may be possible under normal mixing conditions. By characterizing the meaningful scale of animal-driven nutrient variability, we hope to contribute to better understanding the contexts under which bottom-up ecosystem control is detectable.

1. Nutrients + variability in nutrient availability are super important for pp. (stay broad here, terrestrial, aquatic, and marine)
   1. Variation in nutrient availability 🡪 variation in pp 🡪 variation in ecosystems
   2. But not always! Sometimes bottom-up, sometimes top-down, relative importance of the two = big field
   3. Why does nutrients 🡪 pp not 🡪 ecosystem always?
   4. If we want to know when nutrients var 🡪 pp 🡪 ecosystems, need to know when/what scale nutrients vary! important!
2. Sources of temporal and spatial nutrient variability in the ocean
   1. Abiotic/external nutrient source examples:
      1. upwelling, run-off, atmospheric deposition.
         1. All vary in space + time
   2. Biotic/internal/regenerative examples?
      1. Nitrogen fixation + regeneration by microbes
         1. Seasonal differences in rates?
      2. Animal excretion + egestion
         1. Timing (migrations), spatial (animals concentrate on some reefs and not others)
   3. Talk about abiotic/biotic and temporal/spatial and large/small?
3. Temperate paragraph
   1. Why don’t we think CND matters in temperate?
      1. We think nutrients only vary on large scales due to external nutrients
         1. We think any smaller scale variation would be washed away by water motion
      2. We think small scale community stuff is driven by trophic interactions
   2. Why does it matter?
      1. External nutrients can matter on smaller scales!
      2. Regenerated nutrients can matter on meso and small scales!
      3. Small scale var is possible even with water motion!
      4. Cite Pfister mussel paper and the Aquilino paper
   3. So maybe it does matter!
4. Set up what we’re doing?
   1. Intro Barkley Sound region?
   2. Intro into kelp forests and rocky reefs?
   3. explain why this is the coolest/most important system???
5. Set up what we’re doing
   1. intro experiment and set up hypothesis/questions
   2. end on a really killer hook!

Graveyard:

Biologically important nutrient variation can arise from both external and internal sources across scales of magnitude. Wind-driven upwelling of deep, nutrient rich water drives large-scale regional and continental spatial patterns which can moderate plant-herbivore interactions (Sellers et al., 2020). Nutrient delivery can also vary seasonally; both upwelling and freshwater run-off vary with weather conditions (Pawlowicz, 2017). Variation doesn’t just arise from abiotic sources, though.

**Methods**

*RLS meso-scale*

We considered meso-scale variation as the differences in ammonium (NH₄⁺) concentrations between rocky reef sites, which ranged from X – X km apart. We collected subtidal NH4+ samples paired with fish and invertebrate surveys using a globally standardized method (Reef Life Survey) at 27 subtidal sites in Barkley Sound, BC from the end of April – early May each year from 2021 – 2023 (Table 1). A full explanation of the Reef Life Survey method are available online (http://www.reeflifesurvey.com/methods) and provided by Edgar and Stuart-Smith, (2009 and Edgar et al., (2020). 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. First, fishes were counted and sized within 5 meters of the transect on either side, and then cryptic fishes (also sized) and large mobile invertebrates (> 2.5 cm) were counted within 2.5 meters on either side of the transect.

Immediately following the RLS survey, we collected three 60 mL subtidal seawater samples along the transect (at 0, 25, and 50 m) 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. The first two years, we followed the fluorometric method using 40 mL seawater samples (Holmes et al., 1999), and in the third year we followed the fluorometric standard-additions protocol II (Taylor et al., 2007). For each survey, we took the average of the three NH4+ samples as the mean NH4+ concentration. Detailed ammonium analysis methodology is available in the supplement (???).

*Kelp pee small-scale*

To explore within site variability, we explored NH4+ variability in and around kelp forests of varying density and composition at 16 sites in Barkley Sound, BC from July – September 2022 (Table 2). Our sites comprised forest of varying densities dominated by giant kelp or bull kelp, as well as a bare site as a no kelp control. First, to quantify the abundance and biodiversity of the kelp forest communities, trained SCUBA divers counted and identified fish and invertebrate along 50 m transects placed immediately outside kelp forests following standardized Reef Life Survey protocols as above. Next, we ran four 5 m long transects 5 m apart into the kelp forest to assess kelp density, canopy height, and biomass (Figure 1). We counted the number of canopy kelp individuals (bull or giant kelp) within 0.5 m of either side of the 5 m kelp transect to measure kelp density. To estimate canopy height, we measured the length of five random kelps 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 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* in order to calculate individual biomass using a quadratic diameter to biomass formula (info here?). For giant kelp, we weighed the same five individuals per transect which were collected for total length measurements using X scale. We multiplied the mean biomass estimate for each kelp species by the species density in order to calculate a biomass/m2 estimate for each kelp transect, which we averaged over the four transects per forest to estimate overall mean forest biomass. We estimated total forest area by swimming around the perimeter of the forest on the surface with a Garmin GPS.

Finally, to compare NH₄⁺ concentration inside vs outside the kelp forest, we collected paired 60 mL syringes of seawater immediately outside the kelp forest within 0 – 2 meters from the substrate, and 5 m into the kelp forest (n = 3). These paired seawater samples were matched to the first three kelp density, biomass, and canopy height transects. We attempted to maintain a consistent depth for all three paired collections, and to fill a whirlpak of seawater from outside the kelp forest. Upon surfacing, we filtered 40 mL of each sample into amber bottles and also filled 8 amber bottles for use as standards with 40 mL of filtered seawater from the whirlpak. We stored all samples 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 (Taylor et al., 2007). For each paired inside vs outside NH₄⁺ sample, we calculated ∆ NH₄⁺ = inside NH₄⁺ - outside NH₄⁺.

Biological and abiotic variable calculations for both meso- and small-scale experiments

For each Reef Life Survey, we calculated fish biomass from fish length following the formula (W = exp(log(a) + b\*log(L))) 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, only economically important species (abalone and scallops) and sunflower stars were sized, so we were only able to calculate weights for those species. For all others, we used published weight estimates from this region to estimate rough average weights for each taxon (Table 3). Animal abundance was calculated as simply the total number of fishes and invertebrates counted on the surveys. We calculated Shannon diversity, simpson diversity and species richness for each survey. We calculated the tide exchange by computing the rate of 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>. In order to define ebb, slack, and flood tide, we considered the rate of exchange over all six survey weeks (two weeks per year, three years) and <<< I did something with means and SD and centering and ended up with: ebb < - 0.1897325 < slack < 0.1897325 < flood. Come back to this >>>>.

*Cage experiments fine-scale*

To assess the potential for animals to contribute to small-scale nutrient variability, we conducted two caging experiments *in situ* to measure animals’ effect on the NH4+ concentration in their immediate surroundings. Both experiments were conducted near Bamfield, BC; the first caging experiment took place at Scott’s Bay (48°50'05.2"N 125°08'49.3"W) using California sea cucumbers (*Apostichopus californicus*). We caged sea cucumbers in densities of 0, 1, or 2 individuals per X x X x X m mesh cage, which were spaced 3 m apart along two weighted lines (9 cages per line, n = 6, N = 18). We collected sea cucumbers from the site via SCUBA, measured contracted sea cucumber length and girth, and immediately placed them into the cages. Cage depth ranged from 3 – 5.8 meters, and sea cucumbers were left in the cages for 24 hours before we returned to collect water samples from each cage via SCUBA on May 28, 2021. We opened 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 fluorometry (Holmes et al., 1999).

The second caging experiment took place in Bamfield inlet (48°49'53"N 125°08'11"W) using red rock crabs (*Cancer productus*). Our 12 cages contained either one large crab (carapace 15.9 – 15.0 cm), one medium size crab (14.4 – 11.6 cm), or a small control rock, scraped clean, to weight the cages similarly to the crabs (n = 4). We collected the crabs from the site using crab traps, and they were kept in flow through conditions in the lab for 2 – 10 days. Crabs were fed salmon every 2 - 4 days, and all crabs were fed the night before the experiment started. We constructed the cages from clear plastic X x X x X cm enclosures, with two X x X cm windows covered in a dual layer of X mm plastic mesh and X m 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, which allowed samples to be collected by snorkel. We measured seawater ammonium concentration at the beginning, middle, and end of the nine-day experiment at slack tide by drawing water samples using a 60 mL syringe and a narrow tube attached to the center of the cage. We swapped We filtered 40 mL of each sample into amber bottles which were stored on ice, before ammonium analysis via fluorometric standard-additions protocol II (Taylor et al., 2007). We ran the experiment from June 10 – 19, 2023 and replicated it a second time from June 19 – 28, 2023 following the same methodology. 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. Mention that we weighed each crab? Mention that each cage had ulva??

*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), ‘vegan’ to calculate biodiversity indices (Oksanen et al., 2022), ‘glmmTMB’ for all modelling (Brooks et al., 2017), and DHARMa to check model fit (residuals?) (Hartig, 2022). All data and code are available at https://github.com/em-lim13/Ch2\_Spatial\_pee.

RLS meso-scale

To determine whether there is significant variation in NH₄⁺ amoung sites, we constructed generalized linear mixed effect models with NH₄⁺ as the response variable, and animal abundance, tide exchange, an interaction between abundance:tide, Shannon diversity, and survey depth included as predictors, and a random effect of both site (1|site) and year (1|year). All predictors were centered around the mean using the scale function, with scale = FALSE. We used a gamma distribution (link = ‘log’). We constructed additional models with animal biomass instead of abundance, simpson’s diversity or species richness instead of Shannon diversity, but we determined abundance and Shannon diversity were the best metrics by comparing alternate models using AIC (report AIC values). We checked for collinearity of variables using car::vif, and all values were below 1.75. We visually inspected model residuals by plotting the output from DHARMa::simulateResiduals, and the model met all assumptions.

Kelp pee small-scale

To determine whether NH₄⁺ concentration varies inside vs outside of kelp forests, we used a linear mixed effects model with ∆ NH₄⁺ (inside NH₄⁺ - outside NH₄⁺) as the response variable (n = 3 per site), and kelp species, mean forest kelp biomass, tide exchange, animal biomass, survey depth, Shannon diversity, and interactions between kelp biomass:tide exchange, kelp biomass:animal biomass, and animal biomass:tide exchange as fixed effects. All continuous predictors were centered around the mean using the scale function, with scale = FALSE. We included site as a random effect (1|site) to account for the fact that each site contributed three paired samples to the analysis and used a gaussian distribution. We inspected residuals and checked for collinearity as above, and the model met all assumptions. Should I mention models with alt variables?

Cage experiments fine-scale

To quantify the effect of each caged animal on its surrounding NH₄⁺ concentration, we constructed separate linear models for each caging experiment. For the sea cucumber cage experiment, we regressed cage NH₄⁺ concentration against the treatment (0, 1, or 2 sea cucumbers) and cage depth (centered). Inspection of the residuals revealed no significant problems. For the red rock crab cage experiment, we constructed a generalized linear mixed-effects model with cage NH₄⁺ concentration as the response variable, treatment (no crab, medium crab, or large crab) as the predictor variable, and a random effect of sampling day. We used a gamma distribution (link = ‘log’) to ensure model residuals met all assumptions.

**Results**

We found evidence of meso-scale ammonium variation amoung both rocky reefs and kelp forests sites in Barkley Sound (Fig. 2). Amoung rocky reefs, NH₄⁺ concentrations ranged from 0.01 μM – 2.54 μM. Overall, we found no evidence that [NH₄⁺] is correlated with animal abundance (estimate ± SE; - 0.61 ± 0.26, p = 0.90), tide exchange (0.02 ± 0.08, p = 0.82), Shannon diversity (- 0.04 ± 0.11, p = 0.071), or survey depth (0.04 ± 0.09, p = 0.65, Fig. 3a). However, we did find a significantly negative interaction between animal abundance and tide exchange (- 0.24 ± 0.10, p = 0.02, Fig. 3b).

We found evidence of medium-scale variability; NH₄⁺ concentrations were significantly higher inside vs outside giant kelp forests (mean increase ± SE; 0.15 ± 0.04 μM, p < 0.001) and bull kelp forests (0.33 ± 0.06, p < 0.001), a difference that increased with kelp forest biomass (coefficient ± SE; 0.42 ± 0.06, p < 0.001), tide exchange (0.12 ± 0.03, p < 0.001), and animal biomass (0.15 ± 0.06, p = 0.02, Fig. 4a, b). NH₄⁺ did not vary between samples taken 5 m apart at the no kelp control site (0.08 ± 0.11, p = 0.48). ∆ NH₄⁺ (inside NH₄⁺ - outside NH₄⁺ decreased with Shannon diversity (- 0.18 ± 0.04, p < 0.001) and there was no effect of survey depth (0.01 ± 0.03, p = 0.82) on ∆ NH₄⁺. We found evidence of a positive interaction between kelp forest biomass and tide exchange (0.29 ± 0.09, p < 0.001, Fig. 4b), but the other two interactions (kelp:animal biomass and tide:animal biomass) were not significant (p > 0.60).

We found mixed evidence for small-scale variability. For sea cucumbers, we found no effect of sea cucumber density on cage NH₄⁺ concentration (p > 0.75 for both treatments, Fig. 5a). However, we did find a positive effect of cage depth (0.38 ± 0.05, p < 0.001). For red rock crabs, both medium and large crabs significantly increased the NH₄⁺ concentration relative to control cages (convert coeffs back out of log space?, Fig. 5b).

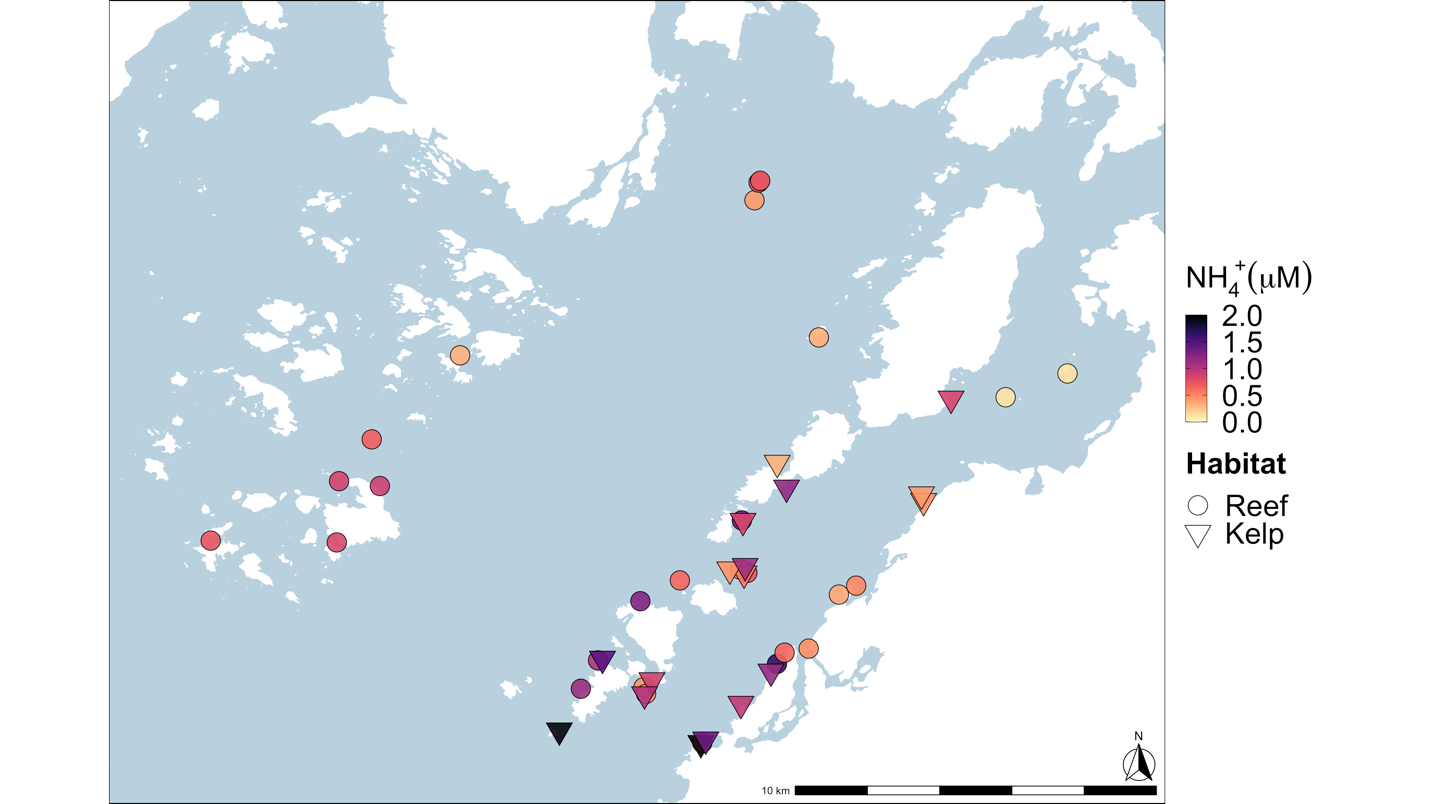
Discussion

* 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?

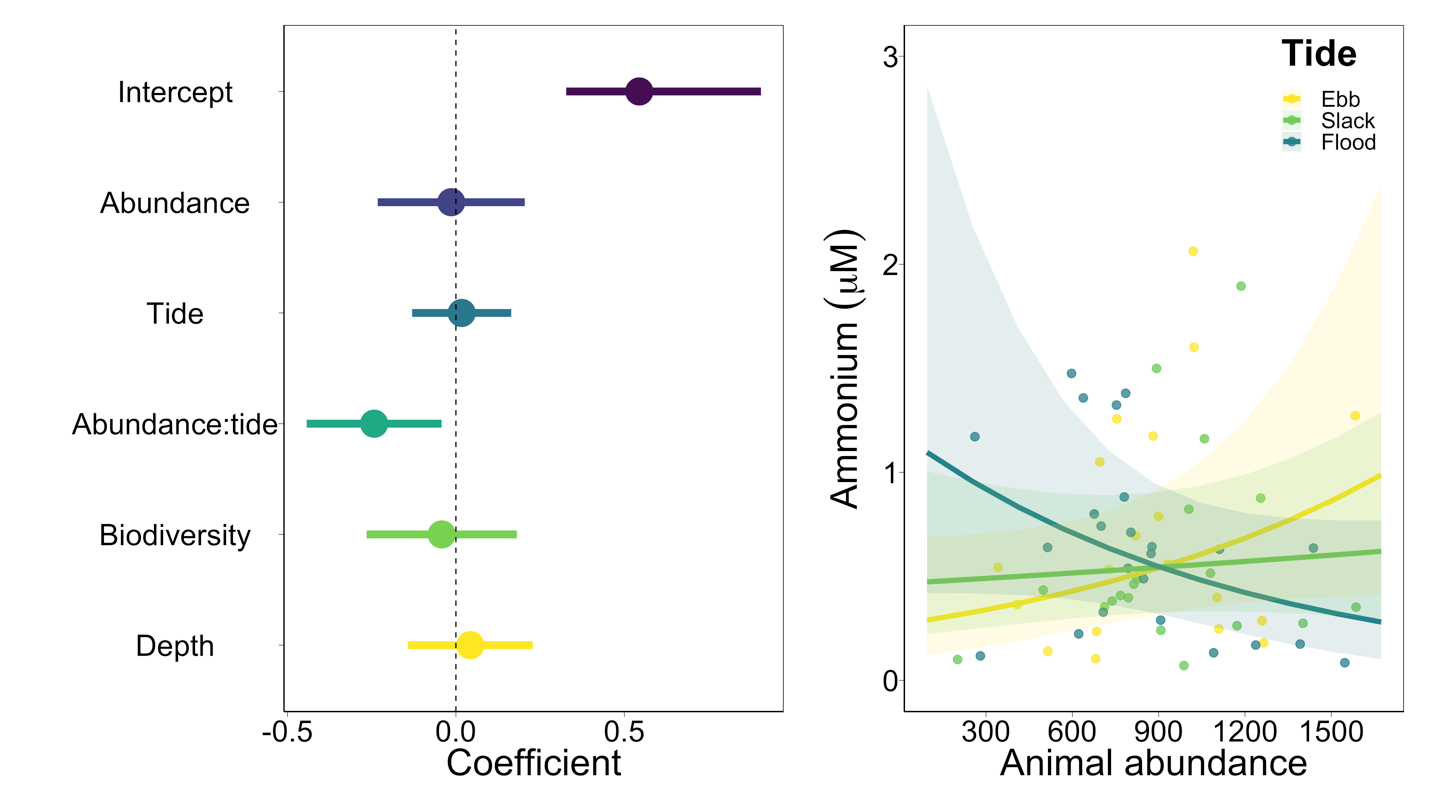
**Figures**

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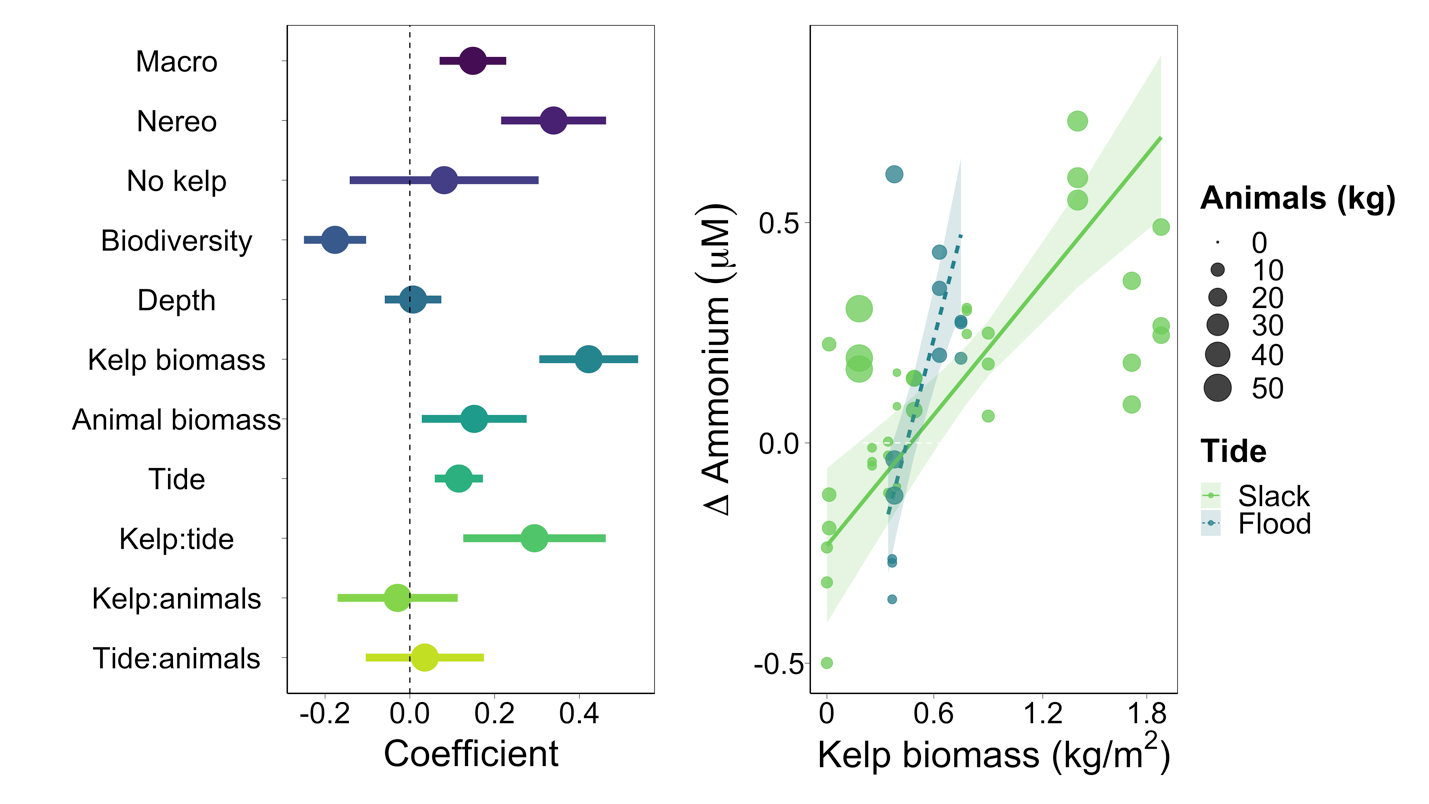
**Figure 1.** Schematic for the kelp pee samples!

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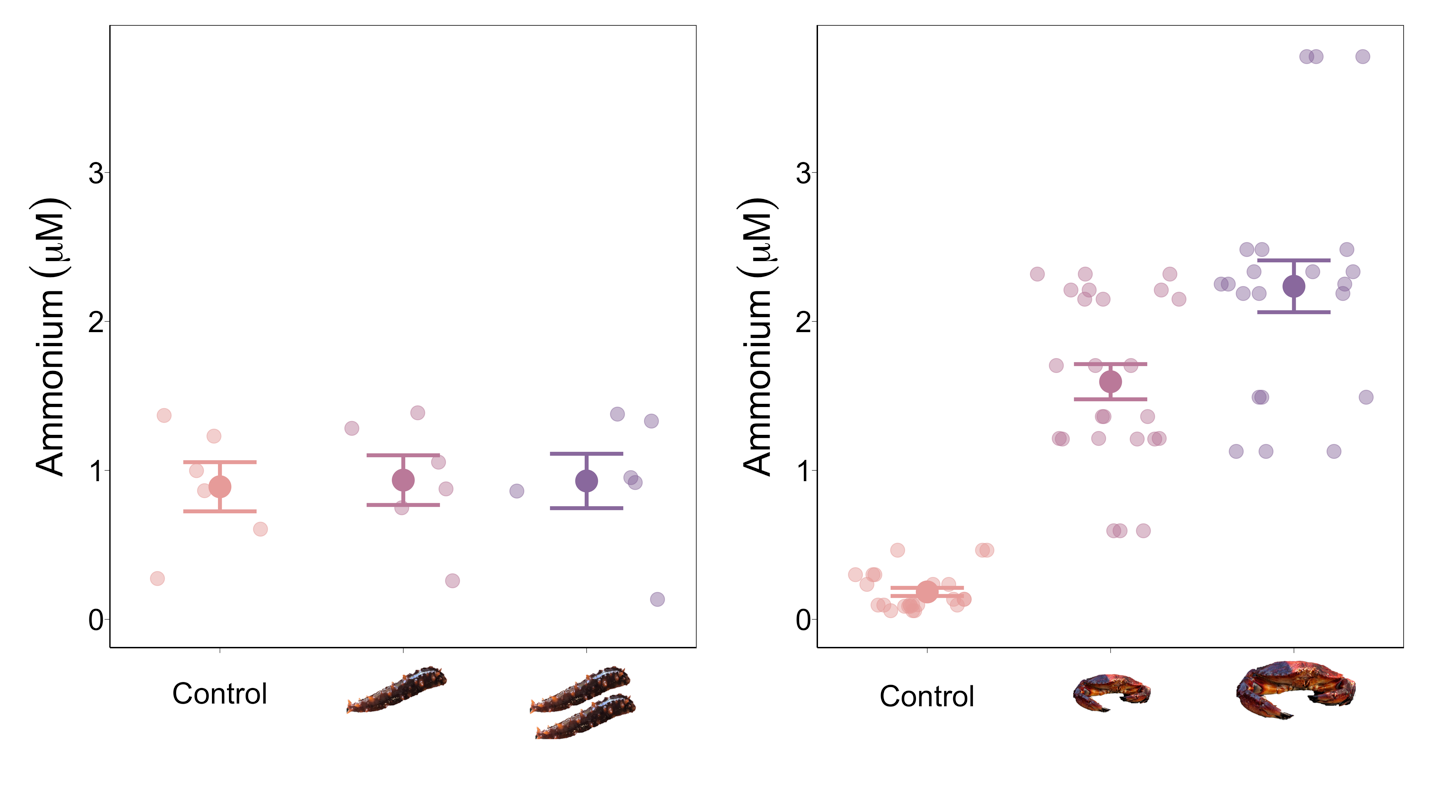
**Figure 2.** Study site map

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**Figure 3.** RLS large-scale model



**Figure 4.** Kelp pee medium-scale model output

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**Figure 5.** Crab and cuke cage experiments

**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 North Island Southside | 48.95464325, -125.1539917 | 2021 |
| BMSC8 | Baeria Rocks North 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 2. Sites used in kelp forest medium-scale experiment -add dates?-

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

**References**