



Spatial dynamics of animal-mediated nutrients in temperate waters

Journal:	<i>Limnology and Oceanography</i>
Manuscript ID	LO-24-0740.R1
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	25-Aug-2025
Complete List of Authors:	<p>Lim, Em; Simon Fraser University Faculty of Science, Department of Biological Sciences; Bamfield Marine Sciences Centre</p> <p>Attridge, Claire; Simon Fraser University Faculty of Science, Department of Biological Sciences</p> <p>Cox, Kieran; Simon Fraser University Faculty of Science, Department of Biological Sciences</p> <p>Schuster, Jasmin; Bamfield Marine Sciences Centre; University of Victoria Faculty of Science, Department of Biology; Hakai Institute</p> <p>Kattler, Kiara; Simon Fraser University Faculty of Science, Department of Biological Sciences</p> <p>Leedham, Emily; The University of Auckland Institute of Marine Science</p> <p>Maher, Bridget; University of Victoria Faculty of Science, Department of Biology</p> <p>Bickell, Andrew; Simon Fraser University Faculty of Science, Department of Biological Sciences</p> <p>Juanes, Francis; University of Victoria Faculty of Science, Department of Biology</p> <p>Côté, Isabelle; Simon Fraser University Faculty of Science, Department of Biological Sciences</p>
Keywords:	Excretion, Consumer-mediated nutrient cycling, Nitrogen, Kelp forest, Rocky reef, Bottom-up effects, Coastal marine ecosystems
Abstract:	<p>Consumer-mediated nutrient dynamics (CND), through which animals' metabolic waste products fertilize primary producers, drive variability in nutrient availability in tropical waters. This variability influences primary productivity and community functioning. Yet, examinations of CND as a driver of nutrient variability in temperate marine ecosystems are limited. Therefore, we assessed the existence and drivers of variation in CND in temperate waters at meso, small, and fine spatial scales. We quantified the occurrence of 48 fish and 92 macroinvertebrate taxa and measured in situ ammonium at 27 northeast Pacific rocky reefs for three years and 16 kelp forests of varying density for one year. Ammonium concentrations ranged from 0.01 to 2.5 μM across rocky reefs separated by tens of km. The relationship between animal abundance and ammonium among sites was mediated by water flow, where flood tides seemed to "wash away" the effect of nutrient regeneration by animals, although enrichment was possible on ebb tides. Ammonium concentration was significantly greater within than outside of kelp forests, a difference that increased with kelp</p>

	<p>biomass, tidal exchange, and to a lesser degree animal biomass. Caging experiments revealed that fine-scale (~2 m) ammonium variability and nutrient enrichment were only possible under low-flow conditions. Our results suggest that CND drives nutrient variability at scales ranging from two meters to over 20 km, acting on a finer scale than allochthonous nitrogen sources such as upwelling. Therefore, consumer-mediated nutrient dynamics are implicated as a previously overlooked driver of spatial variation in primary productivity in temperate marine systems.</p>

Scientific Significance Statement Topic

We investigated the drivers of variability in marine animal-mediated nutrients at three spatial scales. At scales of 10s of km, ammonium varied up to 16-fold across 27 rocky reefs, a larger difference than previously reported. The effect of reef-associated animal abundance on ammonium was positive but mediated by tidal exchange. At a smaller scale, ammonium concentrations were higher inside than outside 16 kelp forests, and ammonium retention increased with kelp biomass, tidal exchange, and animal biomass. Finally, by caging animals in situ, fine-scale enrichment on a scale of m was possible but only when flow was limited. Overall, animal-mediated nutrient cycling contributes to meso-, small-, and fine-scale variation in nutrients even in an upwelling region. This suggests animals may contribute more to bottom-up effects through excretion than previously considered. This work is the most extensive exploration of drivers of ammonium variability in temperate ecosystems to date.

Scientific Significance Statement Outlet

The readers of L&O will find value in our paper as it combines marine ecology with oceanography and includes both physical and biological considerations. Our research broadens our understanding of aquatic systems by documenting an overlooked driver of bottom-up effects in temperate upwelling-influenced ecosystems. This focus will appeal to all those interested in or tasked with ecosystem-based management of ocean resources.

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

Running title: Animals drive nutrient variability across scales

Authors: Em G Lim^{1,2*}, Claire M Attridge¹, Kieran D Cox¹, Jasmin M Schuster^{2,3,4}, Kiara R Kattler^{1§}, Emily J Leedham^{1¶}, Bridget Maher³, Andrew L Bickell^{1†}, Francis Juanes³, Isabelle M Côté¹

Affiliations:

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

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

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

⁴Hakai Institute, Campbell River, British Columbia, Canada

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

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

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

*Corresponding author: Em Lim, em_lim@sfu.ca

Keywords: Excretion, Consumer-mediated nutrient cycling, Nitrogen, Kelp forest, Rocky reef, Bottom-up effects, Coastal marine ecosystems

24 **Author ORCID and contact information:**

25 Em G Lim: 0000-0002-3586-2108; em_lim@sfu.ca

26 Claire M Attridge: 0009-0007-8777-2781; claire_attridge@sfu.ca

27 Kieran D Cox: 0000-0001-5626-1048; kieran_cox@sfu.ca

28 Jasmin M Schuster: 0000-0001-8681-0757; jasmin.schuster@kelprescue.org

29 Kiara R Kattler: 0009-0006-4181-5945; kkattler@ualberta.ca

30 Emily J Leedham: elee323@aucklanduni.ac.nz

31 Bridget Maher: 0000-0002-8061-9932; bridgetmaher@uvic.ca

32 Andrew L Bickell: 0000-0002-7808-7471; andrewbickell@uvic.ca

33 Francis Juanes: 0000-0001-7397-0014; juanes@uvic.ca

34 Isabelle M Côté: 0000-0001-5368-4061; imcote@sfu.ca

35

36 **Author Contribution Statement:**

37 EGL: Conceptualization (equal); formal analysis; investigation (lead); methodology (lead);

38 visualization; writing – original draft preparation. CMA: Conceptualization (supporting);

39 investigation (equal); methodology (equal). KDC: Conceptualization (supporting); funding

40 acquisition (supporting); investigation (equal); methodology (equal); project administration

41 (equal). JMS: Funding acquisition (supporting); investigation (supporting); project

42 administration (supporting). KKK: Investigation (supporting). EKL: Investigation (supporting).

43 BM: Investigation (supporting); methodology (supporting). ALB: Investigation (supporting). FJ:

44 Funding acquisition (equal); project administration (supporting). IMC: Conceptualization

45 (equal); funding acquisition (equal); methodology (equal); project administration (equal);

46 supervision. All authors contributed to writing – review & editing.

Abstract

Consumer-mediated nutrient dynamics (CND), through which animals' metabolic waste products fertilize primary producers, drive variability in nutrient availability in tropical waters. This variability influences primary productivity and community functioning. Yet, examinations of CND as a driver of nutrient variability in temperate marine ecosystems are limited. Therefore, we assessed the existence and drivers of variation in CND in temperate waters at meso, small, and fine spatial scales. We quantified the occurrence of 48 fish and 92 macroinvertebrate taxa and measured in situ ammonium at 27 northeast Pacific rocky reefs for three years and 16 kelp forests of varying density for one year. Ammonium concentrations ranged from 0.01 to 2.5 μM across rocky reefs separated by tens of km. The relationship between animal abundance and ammonium among sites was mediated by water flow, where flood tides seemed to "wash away" the effect of nutrient regeneration by animals, although enrichment was possible on ebb tides. Ammonium concentration was significantly greater within than outside of kelp forests, a difference that increased with kelp biomass, tidal exchange, and to a lesser degree animal biomass. Caging experiments revealed that fine-scale (~ 2 m) ammonium variability and nutrient enrichment were only possible under low-flow conditions. Our results suggest that CND drives nutrient variability at scales ranging from two meters to over 20 km, acting on a finer scale than allochthonous nitrogen sources such as upwelling. Therefore, consumer-mediated nutrient dynamics are implicated as a previously overlooked driver of spatial variation in primary productivity in temperate marine systems.

Introduction

Variation in resource availability across spatial and temporal scales can drive substantial heterogeneity in the growth, biomass and composition of primary producers (Tilman 1984; Leibold 1991; Dayton et al. 1999; McInturf et al. 2019). In many marine ecosystems, community structure is regulated through bottom-up control, i.e. structure depends on factors that generate variability in the resources available to lower trophic levels (Gruner et al. 2008). Although marine ecologists have historically focused on external, abiotic sources of nutrients (e.g., upwelling) as drivers of variability in nutrient availability, there is emerging evidence that consumers also contribute to bottom-up effects (Allgeier et al. 2017). Metabolic waste products (i.e., excretion and egestion) of animals fertilize primary producers via a process termed consumer-mediated nutrient dynamics (CND; Vanni, 2002). Consumers excrete metabolic waste in the form of ammonium (NH_4^+), which is preferentially taken up by primary producers over other forms of nitrogen like nitrate and nitrite (Lobban and Harrison 1994; Phillips and Hurd 2004). However, the ecological importance of consumer-regenerated nutrients at varied spatial scales remains unclear. Therefore, identifying the extent to which biologically relevant variation in nutrient availability contributes to heterogeneity in primary productivity remains an active area of research (Allgeier et al. 2017).

Heterogeneity in consumer habitat use greatly influences spatial and temporal variation in nutrients supplied by animal waste (Uthicke 2001; Roman and McCarthy 2010; Benkwitt et al. 2019). For example, tropical coral reefs provide habitat, shelter, and food sources that attract dense aggregations of vertebrate and invertebrate consumers which regenerate nutrients (Archer et al. 2015; Shantz et al. 2015). On a meso-scale (i.e., 10 to 100 km; Broitman et al., 2001), productivity increases with proximity to reefs with high densities of fishes (Layman et al. 2016),

while on a fine scale, sheltering schools of fish increase nitrogen concentrations around individual heads of corals relative to neighboring uninhabited corals (Holbrook et al. 2008). Ammonium supply can also vary with not only the body size, but also the diversity of the consumers (Allgeier et al. 2014). Diurnal migrations are another source of temporal and spatial variation in consumer-regenerated nutrients, as some fishes travel away from reefs to forage at night, then return to excrete waste around their hiding spots during the day (Meyer and Schultz 1985; Francis and Côté 2018). At an even larger-scale, variation can arise from the migration of megafauna; for instance, whales transport and deposit nutrients across thousands of kilometers as they travel from their feeding to breeding grounds (Doughty et al. 2016). However, the current understanding of animal-driven spatio-temporal variability of nitrogen is drawn substantially from tropical ecosystems (Meyer et al. 1983; Holbrook et al. 2008; Allgeier et al. 2013), often overlooking productive temperate marine ecosystems.

In temperate oceans, external sources of nutrients, such as upwelling and freshwater runoff, are generally considered the dominant drivers of nitrogen variability (Dayton et al. 1999; Lønborg et al. 2021). Due to the open nature of many nearshore environments, fast water flow from currents, tides, and wave action are believed to limit small-scale (1 to 100 m²) nutrient variation (Probyn and Chapman 1983). Therefore, research on intertidal and shallow subtidal ecosystems has traditionally focused on top-down trophic interactions as the drivers of community composition at small scales, while limiting considerations of resource limitation to large regional or continental scales (Paine 1986; Menge 1992). However, evidence suggests meso-scale variation in allochthonous nitrogen via upwelling and internal waves may contribute to bottom-up control of marine communities (Menge et al. 1997; Nielsen and Navarrete 2004; Leichter et al. 2023) and even weaken top-down control (Sellers et al. 2020). Consumer-

mediated nutrient dynamics may also contribute to smaller scales of nutrient variability than previously assumed. For instance, the abundance of intertidal mussel beds has been linked to variation in nitrogen concentrations along entire coastlines (Pfister et al. 2014), across 10s of meters (Aquilino et al. 2009), and among tidepools (fine-scale microhabitats; Bracken, 2004). Therefore, regenerated nitrogen may contribute substantially to meso-, small-, and fine-scale variation in nutrient availability, even in fast-flow, upwelling-dominated nearshore coastal ecosystems.

Shallow subtidal rocky reefs and kelp forests are temperate nearshore habitats that attract dense aggregations of fishes and invertebrates, many of which are economically, ecologically, and culturally important (Steneck et al. 2002). Elevated NH_4^+ excretion from the concentrated diversity and biomass of these communities may also contribute to nutrient hotspots on small to meso-scales and exceed NH_4^+ delivery from other sources (Shrestha et al. 2024). Fast-growing canopy kelps, which form expansive underwater forests, may benefit from these excretions directly as a source of nitrogen (in the form of NH_4^+), especially during low upwelling periods (Brzezinski et al. 2013; Lees et al. 2024). These kelps, which comprise giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis leutkeana*) in the northeast Pacific, also influence the hydrodynamics and hydrochemistry of seawater, both slowing water flow within the forests and generating gradients of carbon content, pH, alkalinity, and oxygen (Jackson and Winant 1983; Gaylord et al. 2007; Pfister et al. 2019). These modifications of the surrounding fluid environment by kelp forests could affect the productivity and community composition of other primary producers and contribute to small-scale spatial nutrient heterogeneity.

We aimed to quantify the contribution of animal-regenerated nitrogen to spatial variability of nutrients in a temperate, wave-swept upwelling region (Barkley Sound, British

Columbia, Canada). This region is located on the traditional territories of the Huu-ay-aht Nation and comprises an archipelago of islands dotted with rocky reefs and kelp forests of heterogeneous structure. We hypothesized that animal-regenerated nutrients contribute to variability in resource availability across three distinct spatial scales. Specifically, we predicted that NH_4^+ variation would be detectable at the meso-scale due to variation in animal abundance among sites. We also expected to observe variation in NH_4^+ concentrations at small scales (within natural sites) and fine scales (between experimental cages), but only under conditions that allow for local enrichment (e.g., low tidal exchange). To test these predictions, we measured variation in NH_4^+ concentrations among rocky reef sites (meso scale of ~10s of km), in and out of kelp forest sites (small scale of 5 m), and near experimentally caged consumers (fine scale of < 2 m, Fig. 1a–c). We quantified the abundance and diversity of fishes and invertebrates at each rocky reef and kelp forest site and measured kelp forest metrics and abiotic variables to explore potential drivers of variation in NH_4^+ concentrations. By characterizing the scale at which animal-driven nutrients vary, we hope to uncover the extent to which consumers in temperate regions structure communities not only from the top down, but also the bottom up through CND.

Methods

Site description

Barkley Sound is located in an upwelling region on the west coast of Vancouver Island, Canada. Upwelling supplies nitrates in the spring and early summer, while storms flush riverine inputs into the nearshore in the winter and spring (Pawlowicz 2017). Due to the proximity of the Bamfield Marine Sciences Centre (BMSC), this region has been a long-term focal area for studies seeking to document the response of kelps to marine heatwaves, establish ecological

baselines, and unravel ecosystem dynamics (Tanasichuk 1998; Starko et al. 2022, 2024; Attridge et al. 2024). Subtidal fish communities in this region comprise at least 18 families, including gobies, surfperches, rockfishes, greenlings, and sculpins (E.G. Lim, unpubl.). Macroinvertebrate assemblages, which are made up of over 49 families, are dominated by sea urchins, turban snails, sea stars, sea cucumbers, and abalone (E.G. Lim, unpubl.).

Surveys of meso-scale (among-site) variation

To explore meso-scale variation in animal-regenerated nutrients among rocky reefs, we measured ammonium (NH_4^+) concentrations and surveyed fish and invertebrate communities at 27 subtidal sites ranging from 0.07 – 24 km apart in Barkley Sound (Fig. 1d). We used a globally standardized method (i.e., Reef Life Survey, RLS) at each site to estimate fish and invertebrate abundance and collected subtidal NH_4^+ samples during each survey. We conducted our surveys in the spring (April-May) for three years (2021-2023), with all annual surveys occurring within two weeks of each other (Supporting Information; Table S1). A full explanation of the Reef Life Survey method is available online (<http://www.reeflifesurvey.com/methods>) and provided by Edgar and Stuart-Smith (2009) and Edgar et al. (2020). Briefly, at each rocky reef site, a pair of RLS-trained SCUBA divers assessed fish and invertebrate abundance and diversity along each side of a 50 m transect line. First, fishes in the water column were counted and sized (total length, in various size class categories) within 5 m on either side of the transect line (500 m²), and then benthic cryptic fishes (also sized) and large mobile invertebrates (> 2.5 cm) were counted within 1 m on either side of the transect line (100 m²).

Immediately following each RLS survey, we collected three 60 mL subtidal seawater samples at 0, 25, and 50 m along the transect, 0 – 2 m above the substrate, and stored the

syringes in sealed plastic bags upon collection to prevent contamination. Seawater samples were filtered into opaque amber bottles in the field and frozen for a maximum of two weeks before NH_4^+ analysis. We confirmed that freezing samples for this duration did not affect NH_4^+ concentration (E. G. Lim unpubl.). In 2021 and 2022, we followed the fluorometric method using 40 mL seawater samples (Holmes et al. 1999), and in 2023, we followed the fluorometric standard-additions protocol II (Taylor et al. 2007). These methods produce similar results, although the Holmes single spike method is associated with larger variability in measurements (Taylor et al. 2007). The three NH_4^+ samples collected during each survey were averaged to determine the mean NH_4^+ concentration for each site.

Surveys of small-scale (within-site) variation

To investigate small-scale variation of animal-regenerated nutrients, we measured NH_4^+ concentrations inside and outside kelp forests and surveyed the resident biological communities as potential moderators of this variation. Our 16 sites comprised forests of varying densities dominated by giant kelp or bull kelp, and two no-kelp control sites. We conducted surveys from July to September 2022 (Table S2). First, divers conducted RLS surveys (as above) along 50 m transect lines along the edge of the kelp forest to quantify the abundance and biodiversity of fish and invertebrate communities *associated* with each kelp forest (Fig. S1). We were unable to conduct RLS transects entirely within the kelp forests due to visual obstruction and concern with diver entanglement by the kelp. Next, divers ran four 5 m-long transects perpendicular to the RLS transect (5 m apart) into the kelp forest to assess kelp density, canopy height, and kelp biomass (Fig. S1). Divers then counted the number of canopy kelp individuals (bull or giant kelp) within 0.5 m on either side of each kelp transect to measure kelp density. To estimate

canopy height, we measured the length of five randomly selected kelp individuals per species per kelp transect; for bull kelp we measured the total length from holdfast to pneumatocyst in situ, but for giant kelp, we collected five random individuals to measure the length from holdfast to the tip of the apical meristem on dry land. To quantify bull kelp biomass, we measured the sub-bulb circumference (15 cm below the bottom of the bulb) of the same five bull kelps per transect in situ and calculated individual biomass using a quadratic diameter to biomass formula for Barkley Sound (C. M. Attridge unpubl.). For giant kelp biomass, we weighed (to the nearest 1 g or less) the same five individuals per transect that were collected for total length measurements. We multiplied the mean biomass estimate for each kelp species by the species density to calculate a biomass/m² estimate for each kelp transect, which we then averaged over the four transects per forest to estimate overall mean forest biomass/m². We estimated total forest area by swimming around the perimeter of the forest on the surface with a Garmin GPSMAP 78SC, which we used to calculate total forest biomass (kg).

Finally, to compare NH₄⁺ concentrations inside vs outside each kelp forest, we collected paired 60 mL syringes of seawater immediately outside the kelp forest within 0 – 2 m above the substrate, and 5 m into the kelp forest at the same depth. We collected three paired NH₄⁺ samples from each site, which were spaced 5 m apart, by matching them with the first three kelp transects (Fig. S1). At our two control, no-kelp sites, we followed the same procedure in terms of number and spacing of samples, with the ‘inside’ samples taken ~ 5 m closer to shore than the ‘outside’ samples. Outside each kelp forest and at each control site, we also collected seawater to create a standard curve, following the standard-additions protocol II for the fluorometric detection of NH₄⁺ in 40 mL samples (Taylor et al. 2007). 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 NH_4^+ concentration in each sample bottle following the protocol above (Taylor et al. 2007). For each paired inside and outside kelp forest NH_4^+ sample, we calculated $\Delta\text{NH}_4^+ =$ inside NH_4^+ - outside NH_4^+ .

Surveys of fine-scale (microhabitat) variation

To quantify the ability of animals to affect the NH_4^+ concentration in their immediate vicinity we conducted two caging experiments in situ near Bamfield, BC. We used California sea cucumbers (*Apostichopus californicus*) in the first caging experiment because this species is a large, abundant invertebrate with a high excretion rate (Bray et al. 1988). The first experiment occurred May 27 – 28, 2021 at Scott's Bay ($48^\circ50'05.2''\text{N}$, $125^\circ08'49.3''\text{W}$), a wide, exposed bay that opens into Trevor Channel (Fig. 1d). We constructed 18 wire cages (26 x 26 x 26 cm), which we covered in 2 mm plastic mesh. These cages were spaced 3 m apart along two weighted lines (9 cages per line) and deployed at 3 to 5.8 m depth. We collected adult California sea cucumbers from the site via SCUBA, measured contracted sea cucumber length and girth, and immediately placed them into the cages in randomly assigned densities of 0, 1, or 2 sea cucumbers ($n = 6$ replicates per density). After 24 hours, we returned to collect water samples from each cage in situ. While underwater, we minimized water movement by reducing our fin and hand movements while opening the mesh lids, which were secured with wire and just wide enough to collect a 60 mL syringe of seawater. Once at the surface, we filtered 40 mL of each sample into amber bottles and transported them on ice to the lab, where we measured NH_4^+ using the fluorometric method (Holmes et al. 1999).

We used red rock crabs (*Cancer productus*) in the second caging experiment to see if a species with an even larger individual-level excretion rate could produce fine-scale nutrient

variation. The second experiment occurred over nine days from June 10 – 19, 2023 in Bamfield Inlet (48°49'53"N 125°08'11"W), a narrow, sheltered inlet (Fig. 1d). We replicated this experiment from June 19 – 28, 2023 following the same methodology. We collected red rock crabs from the site using crab traps and kept them at BMSC in flow-through sea tables for 2 – 10 days. Crabs were fed salmon every 2 – 4 days, and all crabs were fed the night before each experiment started. We constructed 12 cages from clear plastic (40 x 28 x 17 cm), with two 15 x 9 cm windows covered in a dual layer of 10 mm plastic mesh and 1 mm mesh to allow for water flow. The cages were randomly distributed every 2 m along a lead line anchored with cement blocks 0.8 m below chart datum. Each cage contained either one large crab (carapace 15.0 – 15.9 cm), one medium crab (11.6 – 14.4 cm), or a control (i.e., a small rock, scraped clean, so weight was similar across all cages) ($n = 4$ replicates per experiment). During both experiments, we replaced the crabs after 4 days with freshly fed, similar-sized crabs, at this point, we re-randomized the order of the cages along the line to minimize any effect of cage location. We measured seawater NH_4^+ concentration via snorkel at low tide at the beginning, middle, and end of each nine-day experiment. A fixed narrow rubber tube that began in the centre of the cage and extended several inches outside the mesh window allowed us to draw water samples using a 60 mL syringe without disturbing the cages. We filtered 40 mL of each sample into amber bottles, which were stored on ice before NH_4^+ analysis via fluorometric standard-additions protocol II (Taylor et al. 2007).

Statistical analyses

All statistical analysis were conducted in R (v4.1.2, R Core Team, 2019) using RStudio (v1.3.1093, RStudio Team, 2016). We used ‘tidyverse’ packages for data manipulation and

visualization (Wickham et al. 2019), ‘glmmTMB’ for all modelling (Brooks et al. 2017), and ‘DHARMA’ to check model fit (Hartig 2022). We ensured models met assumptions by inspecting residuals using the ‘DHARMA’ simulateResiduals function and checked for collinearity between variables using the vif function from the ‘car’ package with a cutoff value of 2.

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

$$W = aL^b$$

W is fish weight, L is the fish length, a and b are species-specific constants from FishBase (Froese et al. 2014). All mobile invertebrates were counted, but only sunflower sea stars (*Pycnopodia helianthoides*) and economically important species (abalone [*Haliotis kamtschatkana*] and scallops [*Crassadoma gigantea*]) were sized. We used published length–weight relationships to calculate wet weight for these three species. For all other invertebrates, we used published wet weights to estimate biomass for each taxon. We used shell-free wet weight for species with large shells, such as hermit crabs and snails. When biomass information was unavailable for a species, we used estimates from the closest relative or most similarly sized species available (Table S3). Animal abundance per m² was calculated as the total number of fishes and invertebrates counted on each survey, and animal biomass per m² was calculated as the total wet weight of all animals on each survey (divided by 500 m² for pelagic fishes and by 100 m² for cryptic fishes and macroinvertebrates). We used the ‘vegan’ package to calculate Shannon and Simpson diversity indices (Oksanen et al. 2022). We calculated tidal exchange by computing the percent change of the tide height every minute, averaged over the hour-long survey.

299 Meso-scale (among-site) variation

300 To explore meso-scale variation in NH_4^+ , we constructed generalized linear mixed-effect models
301 (GLMMs) with NH_4^+ concentration as the response variable, and animal abundance (per m^2),
302 tidal exchange, an interaction between abundance and tide, Shannon diversity, and survey depth
303 as predictors, and random effects of site and year. All predictors were scaled and centered around
304 the mean using the scale function. We used a gamma distribution (link = 'log'). To test the
305 robustness of our modelling approach, we considered animal biomass/ m^2 as a predictor instead
306 of abundance/ m^2 , and Simpson's diversity instead of Shannon diversity; alternative models
307 including these predictors were not better supported by AIC (Table S4).

308

309 Small-scale (within-site) variation

310 To determine whether NH_4^+ concentration differed inside and outside of kelp forests, we used a
311 linear mixed-effects model (LMM) with ΔNH_4^+ as the response variable ($n = 3$ estimates per
312 site), and kelp species, mean forest kelp biomass (per m^2), tidal exchange, animal biomass (per
313 m^2), survey depth, Shannon diversity, and interactions between kelp biomass and tidal exchange,
314 kelp biomass and animal biomass, and animal biomass and tide exchange as fixed effects. All
315 continuous predictors were scaled and centered around the mean as above. We included site as a
316 random effect (1|site) as each site contributed three estimates to the analysis and used a Gaussian
317 distribution. As above, we chose our final set of predictors upon comparing AIC values of
318 models with alternative predictors (Table S5).

319

320 Fine-scale (microhabitat) variation

We constructed separate linear models for each caging experiment to quantify the impact of caged animals on adjacent NH_4^+ concentration. For the sea cucumber experiment, we regressed cage NH_4^+ concentration against the treatment (i.e., sea cucumber density: 0, 1, or 2 sea cucumbers) and cage depth (centered) using a Gaussian distribution. For the red rock crab experiment, we constructed a GLMM with cage NH_4^+ concentration as the response variable and treatment (no crab, medium crab, or large crab) as the predictor variable with a gamma distribution (link = 'log'). We included a random effect of sampling day because we measured NH_4^+ three times per experiment, and a random effect of experimental week, because we replicated the whole experiment twice. We also calculated the respective NH_4^+ supply rates by sea cucumbers and red rock crabs using a previously generated size-excretion relationship for each sea cucumber (Table S6), and a carapace-excretion relationship for each crab (Table S7).

Results

We found evidence of meso-scale variation in ammonium (NH_4^+) concentrations, which ranged from 0.07 μM – 2.06 μM among rocky reefs in Barkley Sound (Fig. 1d). Overall, we found no evidence that NH_4^+ concentration was correlated with animal abundance (GLMM, $p = 0.57$), tidal exchange ($p = 0.99$), Shannon diversity ($p = 0.41$), or survey depth ($p = 0.61$; Fig. 2a; Table S8). However, we did find a significantly negative interaction between animal abundance and tidal exchange ($p = 0.01$; Fig. 2b), revealing a weakly positive effect of total animal abundance per m^2 on NH_4^+ concentration, but only at ebb tide.

We also documented evidence of significant small-scale, within-site variation of NH_4^+ (Fig. 3; Table S9).; concentrations were 1.3x greater inside giant kelp forests and 1.6x greater inside bull kelp forests than outside (LMM, $p < 0.001$; Fig. 3b). The 'excess' NH_4^+ concentration

inside kelp forests increased with kelp biomass ($p < 0.001$; Fig. 3c), and tidal exchange ($p = 0.02$; Fig. 3a). We found limited evidence for an effect of animal biomass ($p = 0.10$; Fig. 3a), and no evidence of an effect of survey depth ($p = 0.19$; Fig. 3a), or Shannon diversity on ΔNH_4^+ ($p = 0.23$; Fig. 3a). There was a positive interaction between kelp forest biomass and tidal exchange, whereby the positive effect of kelp biomass on ΔNH_4^+ increased with tidal exchange ($p < 0.001$; Fig. 3a,c). We also identified a negative interaction between kelp biomass and animal biomass ($p = 0.04$; Fig. 3a,d), and a negative interaction between tidal exchange and animal biomass ($p = 0.001$; Fig. 3a,e). The change in NH_4^+ was negative between samples taken 5 m apart at the no-kelp control sites ($p = 0.004$; Fig. 3b).

We found mixed evidence for animal-related fine-scale variability in NH_4^+ concentration. For sea cucumbers, we found no effect of one or two sea cucumbers on cage NH_4^+ concentration despite a supply rate of 14 $\mu\text{M}/\text{h}$ and 28 $\mu\text{M}/\text{h}$, respectively. Overall, the mean NH_4^+ concentration was $0.92 \pm 0.04 \mu\text{M}$ across all cages (LM, $p > 0.75$ for both treatments; Fig. 4a; Table S10). However, we saw a positive effect of cage depth, whereby NH_4^+ increased by $0.38 \pm 0.05 \mu\text{M}$ per m increase in depth ($p < 0.001$). For red rock crabs, both medium and large crabs significantly increased the cage NH_4^+ concentration relative to control cages, by 8.7x and 12.1x respectively (GLMM, $p < 0.001$ for all; Fig. 4b; Table S11). Medium crabs excreted on average 88 $\mu\text{M}/\text{h}$ while large crabs excreted 150 $\mu\text{M}/\text{h}$.

Discussion

We found evidence of variability of animal-regenerated nutrients from the largest to the smallest scale examined, although the strength of the signal varied. Ammonium (NH_4^+) varied by up to 16x between rocky reef sites within a year, 1.9x inside vs outside kelp forests, and 40x between

cages with and without crabs. Water flow (i.e., tidal exchange and wave exposure) mediated the capacity for animals to saturate the water column with nutrients. Among sites a flooding tide seemed to “wash away” the impact of animals on NH_4^+ concentrations; in contrast, within sites, moving water made kelps’ ability to slow flow and trap animal-regenerated nutrients more pronounced. In the fine-scale caging experiments we only detected an effect when the nutrient providers were crabs – an effect that we attribute mainly to the low water flow in the protected inlet rather than to the taxa. Nevertheless, across all three scales, there was animal-mediated spatial heterogeneity in nutrient availability, which may contribute to bottom-up effects.

Meso-scale (among-site) variation

In rocky reef habitats, we detected a 16-fold difference in NH_4^+ among sites with the lowest and highest concentrations. This difference is substantially greater than previous measurements of among-site variation in nitrate (3.7x and 6.5x) and ammonium (0.4x and 0.8x) from the same region (Druehl et al. 1989; Hurd et al. 2000). It is also larger than among-site NH_4^+ differences measured in nearby Washington State (1.1x, Pfister et al., 2014). We had predicted that variation in NH_4^+ concentration among sites would be driven primarily by animal abundance. However, the only significant predictor of among-site differences in NH_4^+ was a negative interaction between tidal exchange and animal abundance, whereby animal excretions may enrich the seawater when the tide is ebbing, but the effect of animal abundance is washed away when the tide comes in. Although marine species diversity sometimes covaries with animal abundance or biomass (Yee and Juliano 2007; Müller et al. 2018), we found no relationship between Shannon diversity and NH_4^+ . We did not quantify intertidal animals or microbial regeneration, which are additional sources of NH_4^+ (Aquilino et al. 2009; Lowman et al. 2023), but these sources may be

more important in shallower waters and soft-sediment areas than on the subtidal rocky reefs we studied. We conclude that CND likely contributes to meso-scale variation in NH_4^+ in an unexpected, dynamic, tide-associated manner, which could drive among-site variation in primary productivity and thus bottom-up control.

Small-scale (within-site) variation

We found evidence of kelp-mediated nutrient variation on a smaller scale (5 m) than previously established. Although greater NH_4^+ concentrations inside high-density kelp forests have been documented (e.g., Pfister et al., 2019), these studies compared nutrient samples taken from the middle of very large kelp forests to sites more than 50 m away from the forest edges (Stewart et al. 2009; Pfister et al. 2019; Traiger et al. 2022). By sampling inside and outside forests across a gradient of kelp densities we further demonstrate a positive relationship between kelp biomass and NH_4^+ retention. The retention of NH_4^+ observed is likely due to the dampening of flow within the kelp forest bed and subsequent flow acceleration around the edges (Gaylord et al. 2007; Rosman et al. 2007). Indeed, as predicted, we found the effect of kelp biomass on NH_4^+ retention was more pronounced when the tide was rising (flood tide). Unfortunately, we never sampled on ebbing tides, and did not quantify water motion due to waves or currents, so we could only contrast slack and flooding tides. Nevertheless, it seems that water flow due to tidal exchange enhances, rather than masks, NH_4^+ variability within kelp forests.

We uncovered additional drivers of differences in NH_4^+ concentration inside and outside kelp forests, namely kelp species and animal biomass. We found greater ΔNH_4^+ (NH_4^+ inside - NH_4^+ outside) in bull kelp forests compared to giant kelp forests, which may be due to their different allocations of biomass in the water column and thus different alterations of water flow.

Indeed, Traiger et al., (2022) found the effect of giant kelp forests on water chemistry was smaller than that of bull kelp forests, previously described by Murie and Bourdeau (2020). Species-specific NH_4^+ uptake rates may also impact NH_4^+ retention, as giant kelp may have higher NH_4^+ uptake rates than bull kelp (Ahn et al. 1998; Lees et al. 2024). Somewhat surprisingly, NH_4^+ was lower in the “inside” samples than in the “outside” samples at the no-kelp sites. Despite our efforts to maintain a consistent sampling depth, the “inside” samples were taken at slightly shallower depths since they were closer to shore. This result is therefore in line with the observation that NH_4^+ tends to *increase* with depth (Brzezinski et al. 2013). The fact that we found the opposite trend at our kelp sites increases our confidence that kelp help to retain NH_4^+ within forests.

Even though kelp forests attract dense aggregations of fishes and invertebrates, the positive effect of animal biomass on ΔNH_4^+ was weak and mediated by water flow and kelp biomass. Shannon diversity was positively associated with both animal and kelp biomass (Fig. S2) but had no effect on ΔNH_4^+ . The negative interactions between animal biomass and both tide and kelp biomass suggest a potentially saturating relationship among these variables. When animal biomass was low, increased kelp biomass or tidal exchange increased ΔNH_4^+ , whereas at high animal biomass, increasing kelp or flow had no effect. There may therefore be a threshold for how much animals can saturate and therefore increase ΔNH_4^+ in kelp forest ecosystems. Beyond this point, increased water motion or kelp biomass no longer enhances NH_4^+ inside kelp forests relative to the forest edge. Our RLS surveys captured kelp forest associated communities, but we did not pair RLS surveys inside and outside forests. Therefore, we were unable to account for animal biomass outside forests, which might have reduced noise in the model.

Fine-scale (microhabitat) variation

At the smallest scale of variability tested, we found evidence of variation in NH_4^+ only in our cage experiments in the sheltered inlet, which may suggest that water motion mediates variation at this scale as well. Under laboratory conditions we confirmed that NH_4^+ enrichment by animals declines with increasing flow rates (Fig. S3). Alternative or complementary explanations include a taxonomic effect and/or an experimental effect. The crabs in the sheltered cages excreted NH_4^+ at a rate roughly 6x greater than the sea cucumbers caged in the more exposed location. This difference in NH_4^+ production could have given us more scope to detect differences among treatments in the protected inlet. In addition, the crab cages were constructed with only two mesh windows, in contrast to the fully meshed cages of sea cucumbers, which could have promoted nutrient retention in the former. The experimental duration was also shorter for the sea cucumber experiment, but NH_4^+ concentrations in the crab cages were consistent across the three sampling days (day one, four, and nine) so cumulative enrichment is unlikely.

Fine-scale NH_4^+ enrichment by animals is nevertheless possible in wave-exposed conditions; for example, seawater above mussel beds had ~16x greater NH_4^+ compared to neighbouring rock without mussels on the northern California coast (Aquilino et al. 2009). Our cage experiments were not designed to test why variation was found in one experiment and not the other, but rather to see whether fine-scale variation might arise at all. Therefore, we simply conclude that at least in sheltered conditions, variation on the scale of meters driven by animal biomass is possible.

Implications for primary productivity

Heterogeneity in primary productivity arises from variation in resource supply. Increased primary productivity has been seen with orders of variation (i.e., 1.3 – 9x) in NH_4^+ (Uthicke and Klumpp 1998; Arzul 2001; Vinther and Holmer 2008; West et al. 2009), which is within the range of variation we observed at all three spatial scales considered here. Regardless of nitrate availability, NH_4^+ is less costly for primary producers to use, and can even inhibit nitrate uptake (MacIsaac and Dugdale 1969, 1972). In nitrate-replete upwelling ecosystems of the west coast of North America, a 15.8x increase in NH_4^+ (from 0.08 μM to 1.26 μM) was linked to increased tissue nitrogen and percent cover of an intertidal seaweed (Aquilino et al. 2009), while a 1.8x increase in NH_4^+ increased growth in subtidal seaweeds (Druehl et al. 1989). Furthermore, the mismatch of timing between upwelling and the growing season at temperate latitudes leads to an increased reliance on NH_4^+ over time as nitrate becomes depleted (Druehl et al. 1989; Brzezinski et al. 2013). For example, oceanographic processes may only provide half of the nitrogen needed to sustain giant kelp growth between late summer and early fall in southern California (Fram et al. 2008).

Heterogeneity in NH_4^+ availability likely influences primary productivity in Barkley Sound at each spatial scale studied. Although nitrate varies among sites at the meso-scale (Druehl et al. 1989; Hurd et al. 2000), external nutrient supply (upwelling) may not control primary productivity as strongly as local factors (Pawlowicz 2017). The meso-scale NH_4^+ variability we documented may be one such local factor. At a small scale, nitrate from external sources (e.g., upwelling and run-off) becomes depleted or unchanged as it flows through a kelp forest (Pfister et al., 2019; Stewart et al., 2009), in contrast to NH_4^+ which is continuously regenerated by animals within and around the forest and seemingly retained. As such, kelp forests effectively concentrate their preferred form of nitrogen. This process likely facilitates not

only the growth of these canopy kelps but also understory seaweeds and phytoplankton in the water column. As urchin overgrazing and climate change continue to degrade kelp forests, this important ecosystem function may be lost. At fine scales, invertebrates and fishes living in close contact with primary producers can enrich kelps directly. Many seaweeds are capable of surge uptake of NH_4^+ (Cedeno et al. 2021), allowing them to maximize the benefit from animal excretion directly on their thalli. Indeed, given turnover rates of water and NH_4^+ uptake rates, seaweeds in New Zealand were estimated to derive up to 79% of their needed nitrogen from direct epifauna excretion (Taylor and Rees 1998).

Conclusion

Despite the mixing forces of currents, tides and waves, spatial heterogeneity in NH_4^+ concentration was detectable at meso, small, and fine spatial scales. Given the annual depletion of nitrates each summer (Druehl et al. 1989), primary producers' preference for NH_4^+ over nitrate (Phillips and Hurd 2004), and capacity for surge uptake of NH_4^+ (Cedeno et al. 2021), it seems likely that the animal-driven variation in NH_4^+ we observed could be contributing to heterogeneity in primary productivity. Our results disrupt the dominant paradigm that bottom-up effects in temperate waters are primarily driven by external sources of nutrients acting on large scales, while animals contribute to smaller-scale variation mainly through top-down, consumptive effects. Instead, animals in temperate waters likely drive bottom-up effects across multiple spatial scales while also contributing to top-down effects. Animal-driven spatio-temporal variability of nitrogen is known to drive bottom-up effects in the tropics, and our results suggest animal-regenerated nutrients also play a previously unappreciated role in shaping nutrient availability in temperate regions as well.

504

505 **Acknowledgements**

506 We are grateful to the volunteers who conduct annual Reef Life Surveys and to Dr. Amanda
507 Bates and the Canada Research Chairs Program for funding this critical long-term monitoring
508 work. Thank you to Siobhan Gray, Dave Porter, Phil Lavoie, Kelly Clement, and all the
509 Bamfield Marine Sciences Center staff for their ongoing support. Thank you to Brittanie Spriel
510 and Kayla Holloway for their assistance with the crab cages. Hailey Davies illustrated the red
511 rock crabs and California sea cucumbers, and Jane Thomas provided the kelp symbols through
512 the Integration and Application Network (ian.umces.edu/media-library). This work was funded
513 by National Sciences and Engineering Research Council of Canada (NSERC) scholarships to
514 EGL (CGS-M and CGS-D), CMA (CGS-M), KDC (PDF), KRK (USRA), EJJ (USRA), and
515 ALB (USRA). NSERC Discovery Grants support IMC and FJ. The Liber Ero Foundation
516 supports FJ (Liber Ero Chair) and KDC (Liber Ero Fellow). MITACS and the Hakai Institute
517 funding supports JMS. Thank you to the anonymous reviewers for their comments, which
518 improved the manuscript.

519

520 **Data Availability Statement**

521 All datasets generated during the current study and code are available in the GitHub repository:
522 https://github.com/em-lim13/Ch2_Spatial_pee and the OSF repository: <https://osf.io/hk4tf/>

523

524 **Conflict of Interest Statement**

525 The authors declare no conflict of interest.

526

References

- Ahn, O., R. J. Petrell, and P. J. Harrison. 1998. Ammonium and nitrate uptake by *Laminaria saccharina* and *Nereocystis luetkeana* originating from a salmon sea cage farm. *J. Appl. Phycol.* **10**: 333–340. doi:10.1023/A:1008092521651
- Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. *Glob Change Biol* **23**: 2166–2178. doi:10.1111/gcb.13625
- Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2014. Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Glob. Change Biol.* **20**: 2459–2472. doi:10.1111/gcb.12566
- Allgeier, J. E., L. A. Yeager, and C. A. Layman. 2013. Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology* **94**: 521–529. doi:https://doi.org/10.1890/12-1122.1
- Aquilino, K. M., M. E. S. Bracken, M. N. Faubel, and J. J. Stachowicz. 2009. Local-scale nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an upwelling system. *Limnol Oceanogr* **54**: 309–317. doi:https://doi.org/10.4319/lo.2009.54.1.0309
- Archer, S. K. and others. 2015. Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling. *Coral Reefs* **34**: 19–23. doi:10.1007/s00338-014-1208-4
- Arzul, G. 2001. Effect of marine animal excretions on differential growth of phytoplankton species. *ICES J. Mar. Sci.* **58**: 386–390. doi:10.1006/jmsc.2000.1038

- 549 Attridge, C. M., K. D. Cox, B. Maher, S. Gross, E. G. Lim, K. R. Kattler, and I. M. Côté. 2024.
550 Studying kelp forests of today to forecast ecosystems of the future. *Fisheries* **49**: 181–
551 187. doi:10.1002/fsh.11065
- 552 Benkwitt, C. E., S. K. Wilson, and N. A. J. Graham. 2019. Seabird nutrient subsidies alter
553 patterns of algal abundance and fish biomass on coral reefs following a bleaching event.
554 *Glob Change Biol* **25**: 2619–2632. doi:https://doi.org/10.1111/gcb.14643
- 555 Bracken, M. E. S. 2004. Invertebrate-mediated nutrient loading increases growth of an intertidal
556 macroalga. *J. Phycol.* **40**: 1032–1041. doi:https://doi.org/10.1111/j.1529-
557 8817.2004.03106.x
- 558 Bray, R. N., A. C. Miller, S. Johnson, P. R. Krause, D. L. Robertson, and A. M. Westcott. 1988.
559 Ammonium excretion by macroinvertebrates and fishes on a subtidal rocky reef in
560 southern California. *Mar. Biol.* **100**: 21–30. doi:10.1007/BF00392951
- 561 Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of
562 southeastern Pacific intertidal communities. *Mar. Ecol. Prog. Ser.* **224**: 21–34.
563 doi:10.3354/meps224021
- 564 Brooks, M. E. and others. 2017. glmmTMB balances speed and flexibility among packages for
565 zero-inflated generalized linear mixed modeling. *The R Journal* **9**: 378. doi:10.32614/RJ-
566 2017-066
- 567 Brzezinski, M., D. Reed, S. Harrer, A. Rassweiler, J. Melack, B. Goodridge, and J. Dugan. 2013.
568 Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner
569 continental shelf of the Santa Barbara Channel. *Oceanog* **26**: 114–123.
570 doi:10.5670/oceanog.2013.53

- 571 Cedeno, T. H., M. A. Brzezinski, R. J. Miller, and D. C. Reed. 2021. An evaluation of surge
572 uptake capability in the giant kelp (*Macrocystis pyrifera*) in response to pulses of three
573 different forms of nitrogen. *Mar Biol* **168**: 166. doi:10.1007/s00227-021-03975-z
- 574 Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales
575 of kelp demography: The role of oceanographic climate. *Ecol. Monogr.* **69**: 219–250.
576 doi:10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2
- 577 Doughty, C. E. and others. 2016. Global nutrient transport in a world of giants. *Proc Natl Acad*
578 *Sci USA* **113**: 868–873. doi:10.1073/pnas.1502549112
- 579 Druehl, L. D., P. J. Harrison, K. E. Lloyd, and P. A. Thompson. 1989. Phenotypic variation in N
580 uptake by *Laminaria groenlandica* Rosenvinge (Laminariales, Phaeophyta). *J. Exp. Mar.*
581 *Bio. Ecol* **127**: 155–164. doi:10.1016/0022-0981(89)90181-0
- 582 Edgar, G. J. and others. 2020. Establishing the ecological basis for conservation of shallow
583 marine life using Reef Life Survey. *Biol. Conserv.* **252**: 108855.
584 doi:10.1016/j.biocon.2020.108855
- 585 Edgar, G., and R. Stuart-Smith. 2009. Ecological effects of marine protected areas on rocky reef
586 communities—a continental-scale analysis. *Mar. Ecol. Prog. Ser.* **388**: 51–62.
587 doi:10.3354/meps08149
- 588 Fram, J. P., H. L. Stewart, M. A. Brzezinski, B. Gaylord, D. C. Reed, S. L. Williams, and S.
589 MacIntyre. 2008. Physical pathways and utilization of nitrate supply to the giant kelp,
590 *Macrocystis pyrifera*. *Limnol Oceanogr* **53**: 1589–1603. doi:10.4319/lo.2008.53.4.1589
- 591 Francis, F. T., and I. M. Côté. 2018. Fish movement drives spatial and temporal patterns of
592 nutrient provisioning on coral reef patches. *Ecosphere* **9**: e02225. doi:10.1002/ecs2.2225

- 593 Froese, R., J. T. Thorson, and R. B. Reyes Jr. 2014. A Bayesian approach for estimating length-
594 weight relationships in fishes. *J. Appl. Ichthyol.* **30**: 78–85. doi:10.1111/jai.12299
- 595 Gaylord, B. and others. 2007. Spatial patterns of flow and their modification within and around a
596 giant kelp forest. *Limnol Oceanogr* **52**: 1838–1852. doi:10.4319/lo.2007.52.5.1838
- 597 Gruner, D. S. and others. 2008. A cross-system synthesis of consumer and nutrient resource
598 control on producer biomass. *Ecol Lett* **11**: 740–755. doi:10.1111/j.1461-
599 0248.2008.01192.x
- 600 Hartig, F. 2022. DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression
601 models. R package version 0.4.6.
- 602 Holbrook, S. J., A. J. Brooks, R. J. Schmitt, and H. L. Stewart. 2008. Effects of sheltering fish on
603 growth of their host corals. *Mar Biol* **155**: 521–530. doi:10.1007/s00227-008-1051-7
- 604 Holmes, R. M., A. Aminot, R. Kerouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and
605 precise method for measuring ammonium in marine and freshwater ecosystems. *Can. J.*
606 *Fish. Aquat. Sci.* **56**: 1801–1808. doi:https://doi.org/10.1139/f99-128
- 607 Hurd, C. L., K. M. Durante, and P. J. Harrison. 2000. Influence of bryozoan colonization on the
608 physiology of the kelp *Macrocystis integrifolia* (Laminariales, Phaeophyta) from
609 nitrogen-rich and -poor sites in Barkley Sound, British Columbia, Canada. *Phycologia*
610 **39**: 435–440. doi:10.2216/i0031-8884-39-5-435.1
- 611 Jackson, G. A., and C. D. Winant. 1983. Effect of a kelp forest on coastal currents. *Continental*
612 *Shelf Research* **2**: 75–80. doi:10.1016/0278-4343(83)90023-7
- 613 Layman, C. A., J. E. Allgeier, and C. G. Montaña. 2016. Mechanistic evidence of enhanced
614 production on artificial reefs: A case study in a Bahamian seagrass ecosystem. *Ecol Eng*
615 **95**: 574–579. doi:10.1016/j.ecoleng.2016.06.109

- 616 Lees, L. E., S. N. Z. Jordan, and M. E. S. Bracken. 2024. Kelps may compensate for low nitrate
617 availability by using regenerated forms of nitrogen, including urea and ammonium. *J*
618 *Phycol* **60**: 768–777. doi:10.1111/jpy.13459
- 619 Leibold, M. A. 1991. Biodiversity and nutrient enrichment in pond plankton communities. *Evol.*
620 *Ecol. Res* **1**: 73–95.
- 621 Leichter, J. J., L. B. Ladah, P. E. Parnell, M. D. Stokes, M. T. Costa, J. Fumo, and P. K. Dayton.
622 2023. Persistence of southern California giant kelp beds and alongshore variation in
623 nutrient exposure driven by seasonal upwelling and internal waves. *Front. Mar. Sci.* **10**.
624 doi:10.3389/fmars.2023.1007789
- 625 Lobban, C. S., and P. J. Harrison. 1994. Seaweed ecology and physiology, Cambridge University
626 Press.
- 627 Lønborg, C. and others. 2021. Nutrient cycling in tropical and temperate coastal waters: Is
628 latitude making a difference? *Estuar. Coast. Shelf Sci.* **262**: 107571.
629 doi:10.1016/j.ecss.2021.107571
- 630 Lowman, H. E., M. E. Hirsch, M. A. Brzezinski, and J. M. Melack. 2023. Examining the
631 potential of sandy marine sediments surrounding giant kelp forests to provide recycled
632 nutrients for growth. *J. Coast. Res.* **39**: 442–454. doi:10.2112/JCOASTRES-D-22-
633 00035.1
- 634 MacIsaac, J. J., and R. C. Dugdale. 1969. The kinetics of nitrate and ammonia uptake by natural
635 populations of marine phytoplankton. *Deep-Sea Res. Oceanogr. Abstr.* **16**: 45–57.
636 doi:10.1016/0011-7471(69)90049-7

- 637 MacIsaac, J. J., and R. C. Dugdale. 1972. Interactions of light and inorganic nitrogen in
638 controlling nitrogen uptake in the sea. *Deep-Sea Res. Oceanogr. Abstr.* **19**: 209–232.
639 doi:10.1016/0011-7471(72)90032-0
- 640 McInturf, A. G., L. Pollack, L. H. Yang, and O. Spiegel. 2019. Vectors with autonomy: what
641 distinguishes animal-mediated nutrient transport from abiotic vectors? *Biological*
642 *Reviews* **94**: 1761–1773. doi:10.1111/brv.12525
- 643 Menge, B. A. 1992. Community regulation: Under what conditions are bottom-up factors
644 important on rocky shores? *Ecology* **73**: 755–765. doi:10.2307/1940155
- 645 Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997.
646 Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-
647 down control? *Proc Natl Acad Sci USA* **94**: 14530–14535. doi:10.1073/pnas.94.26.14530
- 648 Meyer, J. L., and E. T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and
649 organic matter on coral reefs. *Limnol Oceanogr* **30**: 146–156.
- 650 Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools: An asset to corals. *Science*
651 **220**: 1047–1049. doi:10.1126/science.220.4601.1047
- 652 Müller, J. and others. 2018. LiDAR-derived canopy structure supports the more-individuals
653 hypothesis for arthropod diversity in temperate forests. *Oikos* **127**: 814–824.
654 doi:10.1111/oik.04972
- 655 Murie, K. A., and P. E. Bourdeau. 2020. Fragmented kelp forest canopies retain their ability to
656 alter local seawater chemistry. *Sci Rep* **10**: 11939. doi:10.1038/s41598-020-68841-2
- 657 Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up:
658 intertidal interactions between consumers and upwelling. *Ecol. Lett.* **7**: 31–41.
659 doi:10.1046/j.1461-0248.2003.00542.x

- Oksanen, J. and others. 2022. vegan: Community ecology package. R package version 2.6-4.
- Paine, R. T. 1986. Benthic community—water column coupling during the 1982-1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence?1. *Limnol Oceanogr* **31**: 351–360. doi:10.4319/lo.1986.31.2.0351
- Pawlowicz, R. 2017. Seasonal cycles, hypoxia, and renewal in a coastal fjord (Barkley Sound, British Columbia). *Atmos.-Ocean* **55**: 264–283. doi:10.1080/07055900.2017.1374240
- Pfister, C. A., M. A. Altabet, and D. Post. 2014. Animal regeneration and microbial retention of nitrogen along coastal rocky shores. *Ecology* **95**: 2803–2814. doi:10.1890/13-1825.1
- Pfister, C. A., M. A. Altabet, and B. L. Weigel. 2019. Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. *Ecology* **100**: e02798. doi:https://doi.org/10.1002/ecy.2798
- Phillips, J. C., and C. L. Hurd. 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. *J Phycol* **40**: 534–545. doi:10.1111/j.1529-8817.2004.03157.x
- Posit team. 2024. RStudio: Integrated Development Environment for R.
- Probyn, T. A., and A. R. O. Chapman. 1983. Summer growth of *Chordaria flagelliformis* (O.F. Muell.) C. Ag.: Physiological strategies in a nutrient stressed environment. *J. Exp. Mar. Bio. Ecol* **73**: 243–271. doi:10.1016/0022-0981(83)90050-3
- R Core Team. 2024. R: A language and environment for statistical computing.
- Roman, J., and J. J. McCarthy. 2010. The whale pump: Marine mammals enhance primary productivity in a coastal basin P. Roopnarine [ed.]. *PLoS ONE* **5**: e13255. doi:10.1371/journal.pone.0013255

- 682 Rosman, J. H., J. R. Koseff, S. G. Monismith, and J. Grover. 2007. A field investigation into the
683 effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. J.
684 Geophys. Res. Oceans **112**. doi:10.1029/2005JC003430
- 685 Sellers, A. J., B. Leung, and M. E. Torchin. 2020. Global meta-analysis of how marine upwelling
686 affects herbivory. Glob. Ecol. Biogeogr. **29**: 370–383.
687 doi:https://doi.org/10.1111/geb.13023
- 688 Shantz, A. A., M. C. Ladd, E. Schrack, and D. E. Burkepile. 2015. Fish-derived nutrient hotspots
689 shape coral reef benthic communities. Ecol Appl **25**: 2142–2152. doi:10.1890/14-2209.1
- 690 Shrestha, J., J. R. Peters, J. E. Caselle, and S. L. Hamilton. 2024. Marine protection and
691 environmental forcing influence fish-derived nutrient cycling in kelp forests. Funct. Ecol.
692 1–15. doi:10.1111/1365-2435.14708
- 693 Starko, S. and others. 2024. Local and regional variation in kelp loss and stability across coastal
694 British Columbia. Mar. Ecol. Prog. Ser. **733**: 1–26. doi:10.3354/meps14548
- 695 Starko, S., C. J. Neufeld, L. Gendall, B. Timmer, L. Campbell, J. Yakimishyn, L. Druehl, and J.
696 K. Baum. 2022. Microclimate predicts kelp forest extinction in the face of direct and
697 indirect marine heatwave effects. Ecol Appl **32**: e2673. doi:10.1002/eap.2673
- 698 Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J.
699 Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future.
700 Environ. Conserv. **29**: 436–459. doi:10.1017/S0376892902000322
- 701 Stewart, H., J. Fram, D. Reed, S. Williams, M. Brzezinski, S. MacIntyre, and B. Gaylord. 2009.
702 Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis*
703 *pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Mar. Ecol.
704 Prog. Ser. **375**: 101–112. doi:10.3354/meps07752

- 705 Tanasichuk, R. 1998. Interannual variations in the population biology and productivity of
706 *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and
707 1993 warm ocean years. Mar. Ecol. Prog. Ser. **173**: 163–180. doi:10.3354/meps173163
- 708 Taylor, B. W., C. F. Keep, R. O. Hall, B. J. Koch, L. M. Tronstad, A. S. Flecker, and A. J.
709 Ulseth. 2007. Improving the fluorometric ammonium method: matrix effects, background
710 fluorescence, and standard additions. J.N. Am. Benthol. Soc. **26**: 167–177.
711 doi:10.1899/0887-3593(2007)26[167:ITFAMM]2.0.CO;2
- 712 Taylor, R., and T. A. V. Rees. 1998. Excretory products of mobile epifauna as a nitrogen source
713 for seaweeds. Limnol Oceanogr **43**: 600–606. doi:10.4319/lo.1998.43.4.0600
- 714 Tilman, G. D. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65**:
715 1445–1453. doi:10.2307/1939125
- 716 Traiger, S. B. and others. 2022. Limited biogeochemical modification of surface waters by kelp
717 forest canopies: Influence of kelp metabolism and site-specific hydrodynamics. Limnol
718 Oceanogr **67**: 392–403. doi:10.1002/lno.11999
- 719 Uthicke, S. 2001. Nutrient regeneration by abundant coral reef holothurians. J. Exp. Mar. Biol.
720 Ecol. **265**: 153–170. doi:10.1016/S0022-0981(01)00329-X
- 721 Uthicke, S., and D. W. Klumpp. 1998. Microphytobenthos community production at a near-shore
722 coral reef: seasonal variation and response to ammonium recycled by holothurians. Mar
723 Ecol Prog Ser **169**: 1–11.
- 724 Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst
725 **33**: 341–370. doi:10.1146/annurev.ecolsys.33.010802.150519

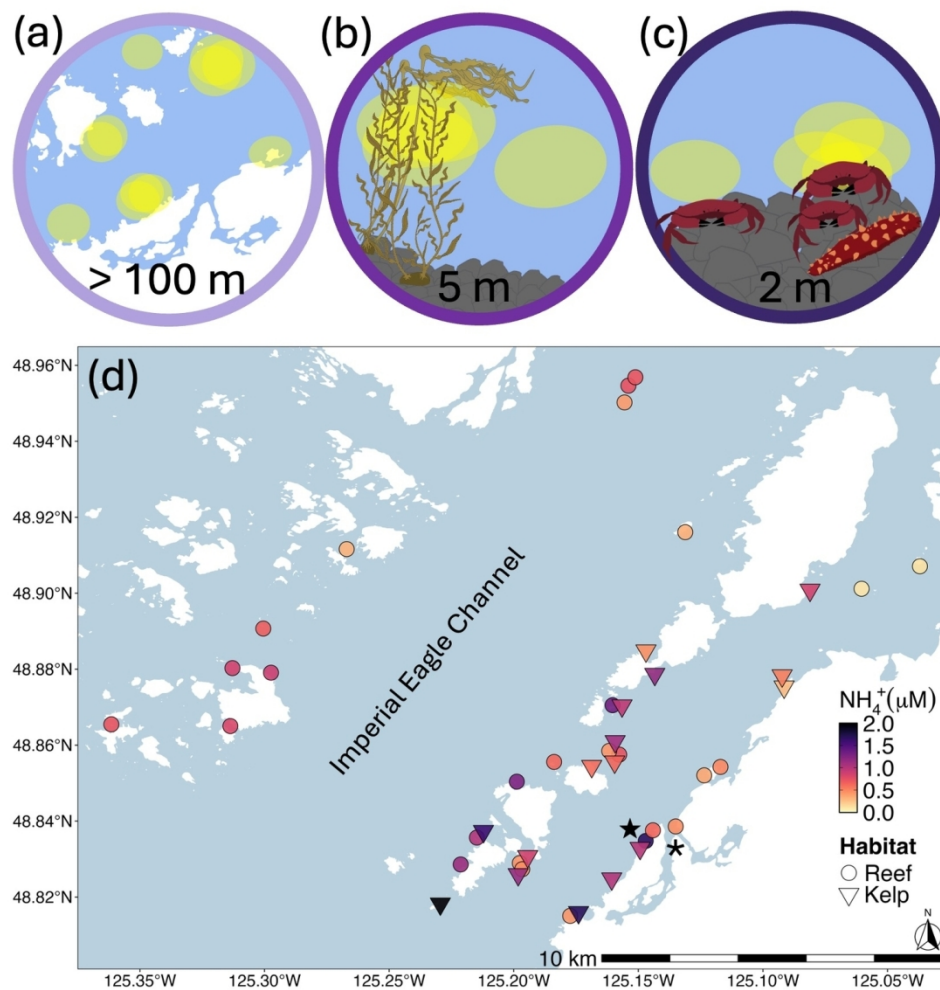
726 Vinther, H. F., and M. Holmer. 2008. Experimental test of biodeposition and ammonium
727 excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance.
728 J. Exp. Mar. Bio. Ecol **364**: 72–79. doi:10.1016/j.jembe.2008.07.003

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

732 Wickham, H. and others. 2019. Welcome to the tidyverse. JOSS **4**: 1686.
733 doi:10.21105/joss.01686

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

737



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

135x137mm (300 x 300 DPI)

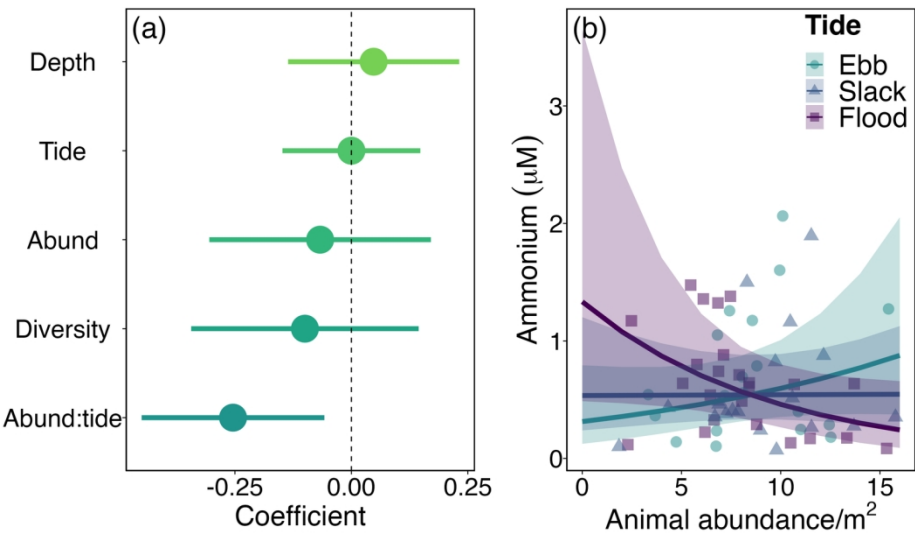


Figure 2. Ecological drivers of seawater ammonium concentration observed across 27 rocky reef sites (meso-scale) in Barkley Sound, British Columbia, Canada. (a) Model coefficients with 95% confidence intervals, and (b) model-generated predictions with shaded 95% confidence intervals of the effect of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

152x88mm (300 x 300 DPI)

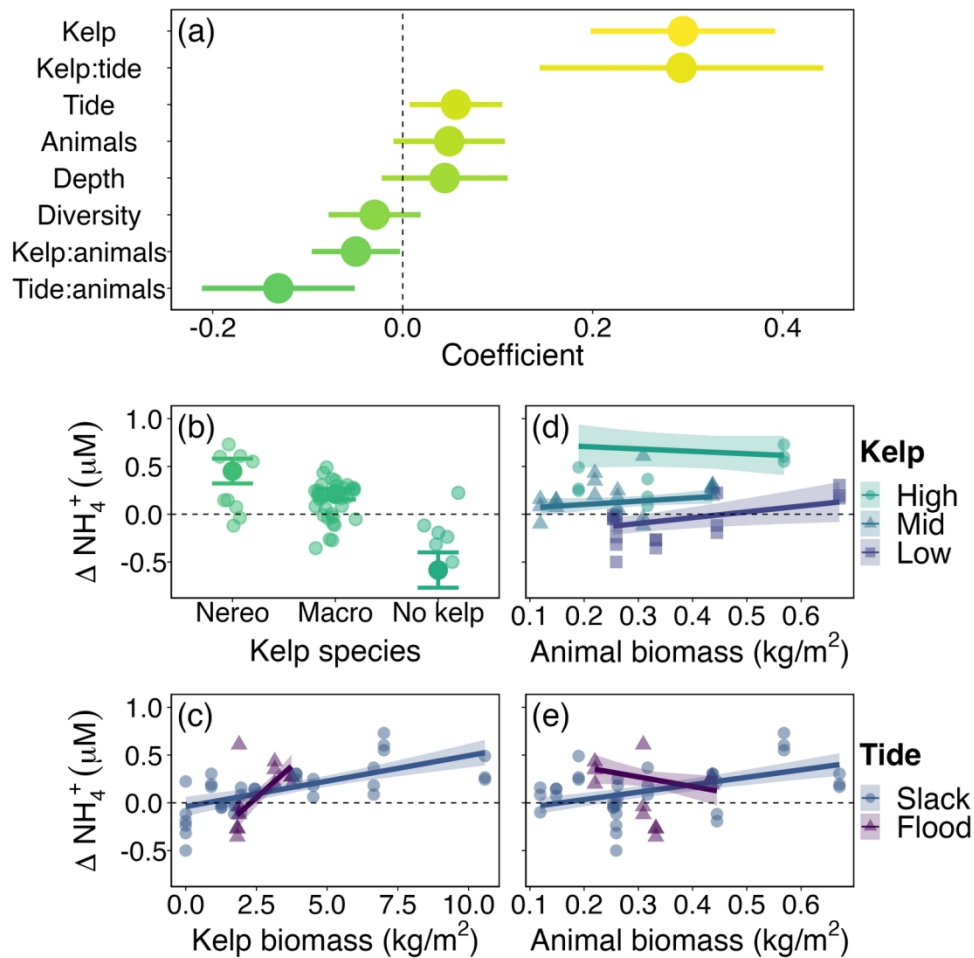


Figure 3. Drivers of variation in ammonium concentration inside vs outside kelp forests across 16 sites (small-scale) in Barkley Sound, British Columbia, Canada. (a) Model coefficients with 95% confidence intervals and (b-e) model-generated predictions with shaded 95% confidence intervals of the effects of significant drivers of within-site variation in ammonium concentration. ΔNH_4^+ is the concentration of ammonium inside - outside kelp forests. Continuous variables were scaled and centered to facilitate comparisons between variables measured in different units. Nereo = *Nereocystis luetkeana*, Macro = *Macrocystis pyrifera*, No kelp = no kelp control.

139x139mm (300 x 300 DPI)

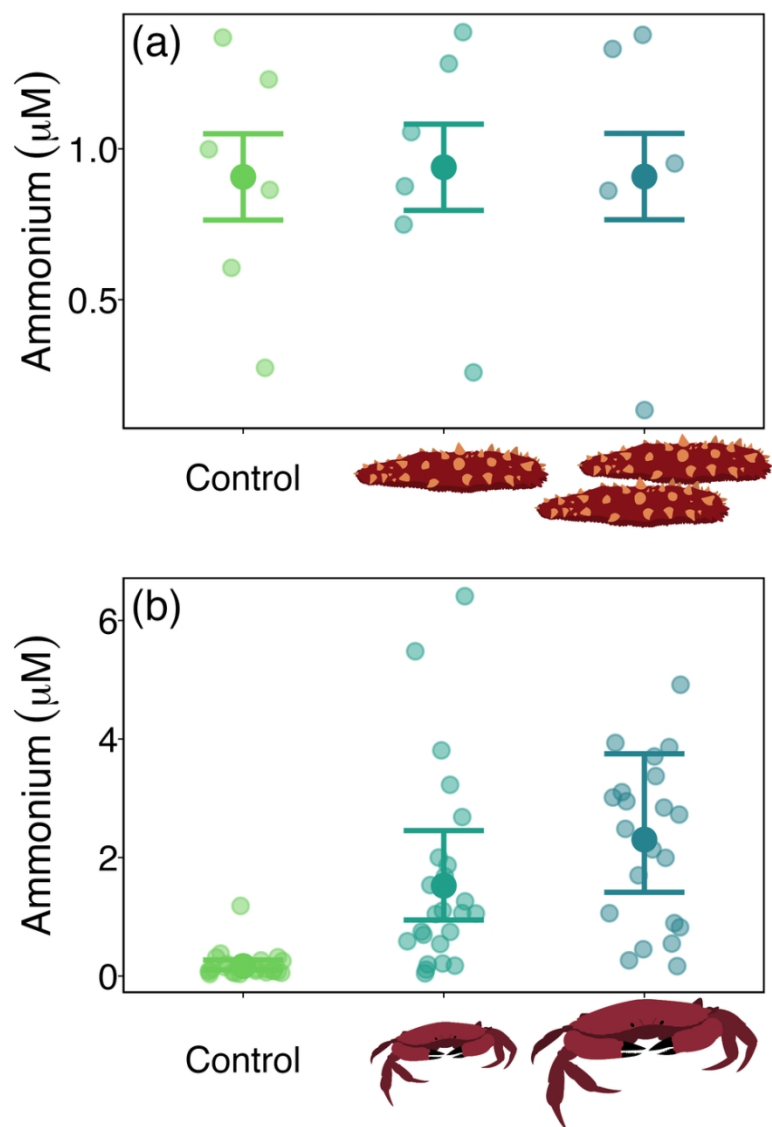


Figure 4. Fine scale effect of caged California sea cucumbers (*Apostichopus californicus*) and red rock crabs (*Cancer productus*) on ammonium concentration. Mean ammonium concentration in experimental cages containing (a) zero (control), one, or two California sea cucumbers ($n = 6$), and (b) zero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

88x127mm (300 x 300 DPI)

Supporting Information for:

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

Authors: Em G Lim^{1,2*}, Claire M Attridge¹, Kieran D Cox¹, Jasmin M Schuster^{2,3,4}, Kiara R Kattler^{1§}, Emily J Leedham^{1¶}, Bridget Maher³, Andrew L Bickell^{1†}, Francis Juanes³, Isabelle M Côté¹

Affiliations:

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

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

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

⁴Hakai Institute, Campbell River, British Columbia, Canada

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

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

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

*Corresponding author: Em Lim, em_lim@sfu.ca

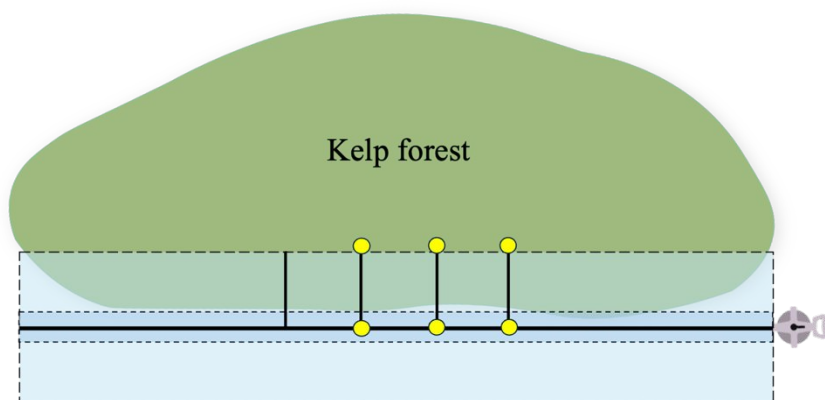


Figure S1. Schematic of methods used to survey biological communities associated with a kelp forest, kelp forest density, and NH_4^+ inside vs outside the forest. We first ran a 50 m Reef Life Survey transect parallel to the kelp forest (green shaded area) and counted fishes in the water column within 5 m on either side of the transect (light blue shaded areas), and cryptic fishes and macroinvertebrates within 1 m on either side of the transect (darker blue shaded area). Next, we ran four 5 m long transects into the kelp forest, 5 m apart from each other, to assess kelp density and biomass within 0.5 m on either side of the transect (four perpendicular black lines). Finally, we took NH_4^+ samples at the beginning and end of the first three kelp transects (yellow circles) to compare NH_4^+ inside vs outside kelp forests.

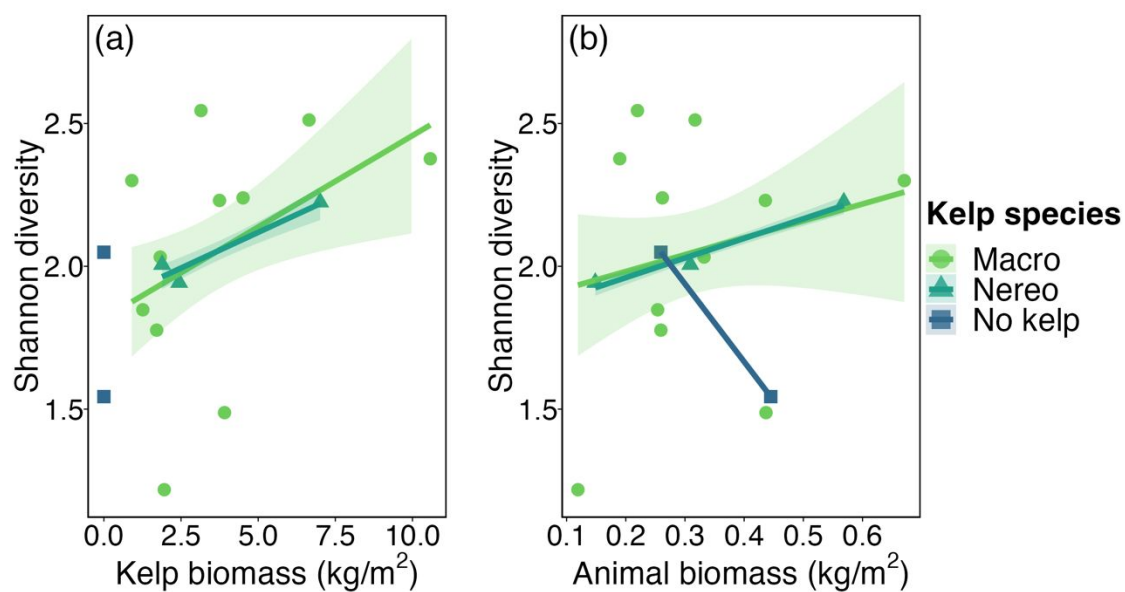


Figure S2. Relationship between Shannon diversity and (a) kelp forest biomass and (b) animal biomass in kelp forests across 16 sites (small-scale) in Barkley Sound, British Columbia, Canada. Macro = *Macrocystis pyrifera*, Nereo = *Nereocystis luetkeana*, No kelp = no kelp control.

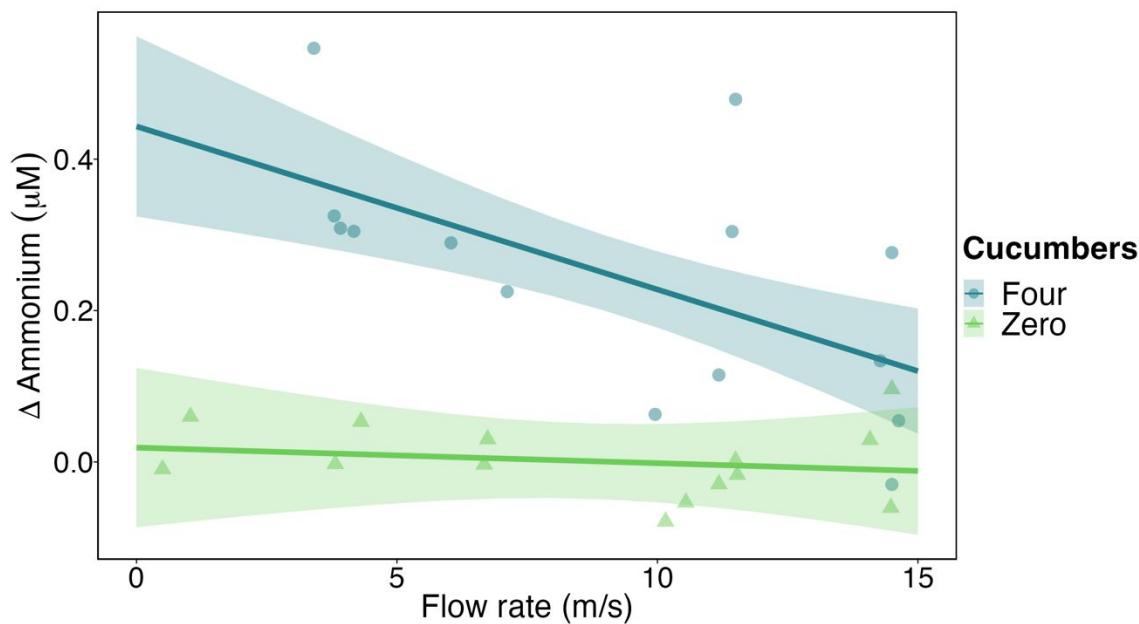


Figure S3. Change in ammonium in containers containing zero or four California sea cucumbers (*Apostichopus californicus*) relative to initial ammonium concentration after 24 hours in mesocosms with varying flow rates. Shaded areas indicate 95% confidence intervals, and raw data are plotted as points. While NH_4^+ concentration remained the same across flow rates in the control mesocosms, sea cucumbers enriched NH_4^+ concentration when flow was low. This enrichment declined as flow rate increased.

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

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

Table S2. Kelp forest site names, coordinates, survey dates and dominant kelp forest species.

Macro = giant kelp (*Macrocystis pyrifera*), Nereo = bull kelp (*Nereocystis luetkeana*), None = no kelp control.

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

Table S3. Wet weight estimates for each invertebrate species used to calculate total biomass for Reef Life Survey data. We used shell-free wet weight for species with large shells (e.g., hermit crabs, snails). When weight information was unavailable for a species, we used estimates from the closest relative or most similarly sized species available. For the three species we sized in situ (*Pycnopodia helianthoides*, *Crassadoma gigantea*, and *Haliotis kamtschatkana*), we used published length-weight relationships to calculate wet weight from size.

Species	Weight (g)	Source, proxy species if applicable
<i>Cancer productus</i>	200	E.G. Lim, unpubl.
<i>Glebocarcinus oregonensis</i>	3	Hines 1982, small crabs
<i>Romaleon antennarium</i>	3	Hines 1982, small crabs
<i>Chorilia longipes</i>	1.235	Hines 1982, <i>Pugettia richii</i>
<i>Pugettia foliata</i>	1.235	Hines 1982, <i>Pugettia richii</i>
<i>Pugettia gracilis</i>	1.235	Hines 1982, <i>Pugettia richii</i>
<i>Pugettia producta</i>	46	Hines 1982
<i>Pugettia richii</i>	1.235	Hines 1982
<i>Scyra acutifrons</i>	2	Hines 1982
<i>Scyra</i> spp.	1.235	Hines 1982
<i>Cryptolithodes sitchensis</i>	3	Hines 1982, small crabs
<i>Cryptolithodes typicus</i>	3	Hines 1982, small crabs
<i>Hapalogaster mertensii</i>	65	Stewart et al. 2015, <i>Phyllolithodes papillosus</i>
<i>Lopholithodes mandtii</i>	65	Stewart et al. 2015, <i>Phyllolithodes papillosus</i>
<i>Phyllolithodes papillosus</i>	65	Stewart et al. 2015
<i>Oregonia gracilis</i>	3	Hines 1982, small crabs
<i>Paguroidea</i> spp.	0.43	McKinney et al. 2004, Paguroidea
<i>Pagurus beringanus</i>	0.43	McKinney et al. 2004, Paguroidea
<i>Pagurus hemphilli</i>	0.43	McKinney et al. 2004, Paguroidea
<i>Pandalus danae</i>	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>
<i>Pandalus gurneyi</i>	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>
<i>Pandalus</i> spp.	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>

<i>Pandulus</i> spp.	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>
<i>Lophopanopeus bellus</i>	3	Hines 1982, small crabs
<i>Pachycheles pubescens</i>	4.25	Stillman and Somero 1996, <i>Petrolisthes</i> spp.
<i>Petrolisthes eriomerus</i>	4.25	Stillman and Somero 1996, <i>Petrolisthes</i> spp.
<i>Heptacarpus stylus</i>	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>
<i>Brachyura</i> spp.	3	Hines 1982, small crabs
Unidentified shrimp	0.11	McKinney et al. 2004, <i>Palaemonetes pugio</i>
<i>Polyorchis penicillatus</i>	0.01	Båmstedt and Martinussen 2015, <i>Bolinopsis infundibulum</i>
<i>Mitrocoma cellularia</i>	0.01	Båmstedt and Martinussen 2015, <i>Bolinopsis infundibulum</i>
<i>Pleurobrachia bachei</i>	0.01	Båmstedt and Martinussen 2015, <i>Bolinopsis infundibulum</i>
<i>Bolinopsis infundibulum</i>	0.01	Båmstedt and Martinussen 2015
<i>Evasterias troschelii</i>	66.5	O'Clair and Rice 1985
<i>Leptasterias hexactis</i>	5.5	Menge 1975, <i>Leptasterias</i> spp.
<i>Leptasterias</i> spp.	5.5	Menge 1975, <i>Leptasterias</i> spp.
<i>Orthasterias koehleri</i>	66.5	O'Clair and Rice 1985, <i>Evasterias troschelii</i>
<i>Pisaster brevispinus</i>	146.18	Peters et al. 2019, <i>Pisaster giganteus</i>
<i>Pisaster ochraceus</i>	128	Sanford 2002
<i>Pycnopodia helianthoides</i>	0.018*size ^{3.13}	Lee et al. 2016
<i>Stylasterias forreri</i>	66.5	O'Clair and Rice 1985, <i>Evasterias troschelii</i>
<i>Patiria miniata</i>	26.97	Peters et al. 2019
<i>Henricia pumila</i>	10	Menge 1975, <i>Henricia</i> spp.
<i>Henricia</i> spp.	10	Menge 1975
<i>Dermasterias imbricata</i>	92	Montgomery 2014
<i>Mediaster aequalis</i>	10	Menge 1975, <i>Henricia</i> spp.
<i>Solaster dawsoni</i>	486	Montgomery 2014, <i>Solaster stimpsoni</i>
<i>Solaster stimpsoni</i>	486	Montgomery 2014
<i>Pteraster tessellatus</i>	10	Menge 1975, <i>Henricia</i> spp.
<i>Mesocentrotus franciscanus</i>	29.51	Schuster and Bates 2023
<i>Strongylocentrotus droebachiensis</i>	20	Stewart et al. 2015, <i>Strongylocentrotus polyacanthus</i>
<i>Strongylocentrotus purpuratus</i>	20	Stewart et al. 2015, <i>Strongylocentrotus polyacanthus</i>
<i>Apostichopus californicus</i>	319.31	Peters et al. 2019, <i>Apostichopus parvimensis</i>
<i>Chlamys hastata</i>	2.5	MacDonald et al. 1991, <i>Chlamys</i> spp.
<i>Crassadoma gigantea</i>	0.038*size ^{2.39}	MacDonald et al. 1991

<i>Enteroctopus dofleini</i>	137.5	Osborn 1995, <i>Octopus rubescens</i>
<i>Octopus rubescens</i>	80	Osborn 1995
<i>Opalia wroblewskyi</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Diodora aspera</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Megathura crenulata</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Haliotis kamtschatkana</i>	$0.00058 \cdot \text{size}^3$	Zhang et al. 2007
<i>Neverita lewisii</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Ceratostoma foliatum</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Nucella lamellosa</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Armina californica</i>	0.54	McKinney et al. 2004, gastropods
<i>Cadlina luteomarginata</i>	0.54	McKinney et al. 2004, gastropods
<i>Cadlina modesta</i>	0.54	McKinney et al. 2004, gastropods
<i>Cadlina sylviaeaeleae</i>	0.54	McKinney et al. 2004, gastropods
<i>Coryphella verrucosa</i>	0.54	McKinney et al. 2004, gastropods
<i>Dendronotus iris</i>	0.54	McKinney et al. 2004, gastropods
<i>Dirona albolineata</i>	0.54	McKinney et al. 2004, gastropods
<i>Dirona pellucida</i>	0.54	McKinney et al. 2004, gastropods
<i>Diaulula odonoghuei</i>	0.54	McKinney et al. 2004, gastropods
<i>Diaulula sandiegensis</i>	0.54	McKinney et al. 2004, gastropods
<i>Peltodoris nobilis</i>	0.54	McKinney et al. 2004, gastropods
<i>Doris montereyensis</i>	0.54	McKinney et al. 2004, gastropods
<i>Doris odhneri</i>	0.54	McKinney et al. 2004, gastropods
<i>Antiopella fusca</i>	0.54	McKinney et al. 2004, gastropods
<i>Hermisenda crassicornis</i>	0.54	McKinney et al. 2004, gastropods
<i>Acanthodoris hudsoni</i>	0.54	McKinney et al. 2004, gastropods
<i>Acanthodoris nanaimoensis</i>	0.54	McKinney et al. 2004, gastropods
<i>Onchidoris bilamellata</i>	0.54	McKinney et al. 2004, gastropods
<i>Limacia cockerelli</i>	0.54	McKinney et al. 2004, gastropods
<i>Polycera tricolor</i>	0.54	McKinney et al. 2004, gastropods
<i>Triopha catalinae</i>	0.54	McKinney et al. 2004, gastropods
<i>Triopha modesta</i>	0.54	McKinney et al. 2004, gastropods
<i>Triopha</i> spp.	0.54	McKinney et al. 2004, gastropods
<i>Melibe leonina</i>	0.54	McKinney et al. 2004, gastropods

<i>Tritonia festiva</i>	0.54	McKinney et al. 2004, gastropods
<i>Acmaea mitra</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Lottia scutum</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Berthella chacei</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Calliostoma ligatum</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Tegula funebris</i>	0.91	Palmer 1982, <i>Nucella</i> spp.
<i>Pomaulax gibberosus</i>	31	Schuster and Bates 2023
<i>Eurylepta leoparda</i>	0.54	McKinney et al. 2004, gastropods

Table S4. Akaike’s Information Criterion (AIC) values calculated for each model of ammonium concentration in relation to animal abundance/m² (AA) or animal biomass/m² (AB), Shannon diversity (SHD) or Simpson diversity (SID), tidal exchange rate (T), depth (D), and an interaction term. RE = random effect of both site and year. k is the number of parameters in the model. The model with the lowest AIC score is the “best” model; ΔAIC is the difference in AIC score between a given model and the “best” model; AIC weight represents the probability that a model is the best model, given the data and the set of candidate models.

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

Table S5. Akaike's Information Criterion (AIC) values calculated for each model of delta ammonium concentration in vs outside kelp forests in relation to animal abundance/m² (AA) or animal biomass/m² (AB), Shannon diversity (SHD) or Simpson diversity (SID), kelp species (KS), kelp biomass (KB), tidal exchange rate (T), depth (D), and three interaction terms. RE = random effect of site. k is the number of parameters in the model. The model with the lowest AIC score is the "best" model; Δ AIC is the difference in AIC score between a given model and the "best" model; AIC weight represents the probability that a model is the best model, given the data and the set of candidate models.

Predictors	k	AIC	Δ AIC	AIC weight
AB + SHD + KS + KB + T + D + AB:T + AB:KB + KB:T + RE	13	-33.16	0.00	0.30
AA + SHD + KS + KB + T + D + AA:T + AA:KB + KB:T + RE	13	-32.89	0.27	0.26
AA + SID + KS + KB + T + D + AA:T + AA:KB + KB:T + RE	13	-32.80	0.36	0.25
AB + SID + KS + KB + T + D + AB:T + AB:KB + KB:T + RE	13	-32.38	0.78	0.20

Table S6. Excretion rate model to determine log transformed NH₄⁺ excretion rate (uM/hour/L) for California sea cucumbers (*Apostichopus californicus*) based on size index: sqrt(length*girth). Adjusted R-squared for this model is 0.39.

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

Table S7. Excretion rate model to determine log transformed NH_4^+ excretion rate (uM/hour/L) for red rock crabs (*Cancer productus*) based on carapace width (mm). Adjusted R-squared for this model is 0.82.

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

Table S8. Meso-scale linear mixed-effect model describing drivers of among-site variability in ammonium concentration. The model was constructed with a gamma distribution (link = ‘log’), so coefficients are presented in log space. Continuous predictors were centred and scaled to compare effect sizes between predictors with varying units.

	Estimate	Std. error	z value	p value
Intercept	-0.61	0.25	-2.48	0.01
Abundance	-0.07	0.12	-0.55	0.58
Tidal exchange	0.00	0.08	0.00	1.00
Diversity	-0.10	0.12	-0.80	0.42
Depth	0.05	0.09	0.51	0.61
Abundance:tide	-0.25	0.10	-2.54	0.01

Table S9. Small-scale linear mixed effect model describing drivers of ammonium concentration inside – outside kelp forests. Continuous predictors were centred and scaled. Kelp species is a categorical predictor with three levels: macro = *Macrocystis pyrifera* (intercept level), nereeo = *Nereocystis luetkeana*, none = no kelp control.

	Estimate	Std. error	z value	p value
Intercept	0.16	0.03	5.91	< 0.001
Kelp nereeo	0.24	0.07	3.64	< 0.001
Kelp none	-0.40	0.10	-4.13	< 0.001
Kelp biomass	0.29	0.05	5.95	< 0.001
Tidal exchange	0.06	0.02	2.25	0.02
Animal biomass	0.05	0.03	1.64	0.10
Diversity	-0.03	0.02	-1.20	0.23
Depth	0.04	0.03	1.31	0.19
Kelp:tide	0.29	0.08	3.85	< 0.001
Kelp:animals	-0.05	0.02	-2.08	0.04
Tide:animals	-0.13	0.04	-3.19	0.001

Table S10. Fine-scale linear model describing ammonium variation between cages with zero (intercept level), one, or two California sea cucumbers (*Apostichopus californicus*).

	Estimate	Std. error	z value	p value
Intercept	0.91	0.07	12.43	< 0.001
Cukes - one	0.03	0.10	0.31	0.76
Cukes - two	0.00	0.10	0.01	0.99
Depth	0.38	0.05	8.07	< 0.001

Table S11. Fine-scale model describing ammonium variation between cages with zero (intercept level), medium, or large red rock crabs (*Cancer productus*). The model was constructed with a gamma distribution (link = ‘log’), so coefficients are presented in log space.

	Estimate	Std. error	z value	p value
Intercept	-1.78	0.25	-7.25	< 0.001
Crabs - medium	2.20	0.26	8.48	< 0.001
Crabs - large	2.61	0.27	9.83	< 0.001

References

- Båmstedt, U., and M. B. Martinussen. 2015. Ecology and behavior of *Bolinopsis infundibulum* (Ctenophora; Lobata) in the Northeast Atlantic. *Hydrobiologia* **759**: 3–14. doi:10.1007/s10750-015-2180-x
- Hines, A. H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.* **69**: 309–320. doi:10.1007/BF00397496
- Lee, L. C., J. C. Watson, R. Trebilco, and A. K. Salomon. 2016. Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. *Ecosphere* **7**: e01604. doi:10.1002/ecs2.1604
- MacDonald, B. A., R. J. Thompson, and N. F. Bourne. 1991. Growth and reproductive energetics of three scallop species from British Columbia (*Chlamys hastata*, *Chlamys rubida*, and *Crassadoma gigantea*). *Can. J. Fish. Aquat. Sci.* **48**: 215–221. doi:10.1139/f91-029
- McKinney, R. A., S. M. Glatt, and S. R. Williams. 2004. Allometric length-weight relationships for benthic prey of aquatic wildlife in coastal marine habitats. *Wildlife Biology* **10**: 241–249. doi:10.2981/wlb.2004.029
- Menge, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.* **31**: 87–100. doi:10.1007/BF00390651
- Montgomery, E. M. 2014. Predicting crawling speed relative to mass in sea stars. *J. Exp. Mar. Bio. Ecol* **458**: 27–33. doi:10.1016/j.jembe.2014.05.009
- O'Clair, C. E., and S. D. Rice. 1985. Depression of feeding and growth rates of the seastar *Evasterias troschelii* during long-term exposure to the water-soluble fraction of crude oil. *Mar. Biol.* **84**: 331–340. doi:10.1007/BF00392503
- Osborn, S. A. 1995. Fecundity and embryonic development of *Octopus rubescens* Berry from Monterey Bay, California. Master of Science. San Jose State University.
- Palmer, A. R. 1982. Growth in marine gastropods: a non-destructive technique for independently measuring shell and body weight. *Malacologia* **23**: 63–74.
- Peters, J. R., D. C. Reed, and D. E. Burkepile. 2019. Climate and fishing drive regime shifts in consumer-mediated nutrient cycling in kelp forests. *Glob Change Biol* **25**: 3179–3192. doi:10.1111/gcb.14706

- Sanford, E. 2002. The feeding, growth, and energetics of two rocky intertidal predators (*Pisaster ochraceus* and *Nucella canaliculata*) under water temperatures simulating episodic upwelling. *J. Exp. Mar. Biol. Ecol.* **273**: 199–218. doi:10.1016/S0022-0981(02)00164-8
- Schuster, J. M., and A. E. Bates. 2023. The role of kelp availability and quality on the energetic state and thermal tolerance of sea urchin and gastropod grazers. *J. Exp. Mar. Bio. Ecol.* **569**: 151947. doi:10.1016/j.jembe.2023.151947
- Stewart, N. L., B. Konar, and M. T. Tinker. 2015. Testing the nutritional-limitation, predator-avoidance, and storm-avoidance hypotheses for restricted sea otter habitat use in the Aleutian Islands, Alaska. *Oecologia* **177**: 645–655. doi:10.1007/s00442-014-3149-6
- Stillman, J. H., and G. N. Somero. 1996. Adaptation to temperature stress and aerial exposure in congeneric species of intertidal porcelain crabs (genus *Petrolisthes*): correlation of physiology, biochemistry and morphology with vertical distribution. *J. Exp. Biol.* **199**: 1845–1855. doi:10.1242/jeb.199.8.1845
- Zhang, Z., A. Campbell, and J. Lessard. 2007. Modeling northern abalone, *Haliotis kamtschatkana*, population stock and recruitment in British Columbia. *J. Shellfish Res.* **26**: 1099–1107. doi:10.2983/0730-8000(2007)26[1099:MNAHKP]2.0.CO;2

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

Running title: Animals drive nutrient variability across scales

Authors: Em G Lim^{1,2*}, Claire M Attridge¹, Kieran D Cox¹, Jasmin M Schuster^{2,3,4}, Kiara R Kattler^{1§}, Emily J Leedham^{1¶}, Bridget Maher³, Andrew L Bickell^{1†}, Francis Juanes³, Isabelle M Côté¹

Affiliations:

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

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

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

⁴Hakai Institute, Campbell River, British Columbia, Canada

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

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

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

*Corresponding author: Em Lim, em_lim@sfu.ca

Keywords: Excretion, Consumer-mediated nutrient cycling, Nitrogen, Kelp forest, Rocky reef, Bottom-up effects, Coastal marine ecosystems

24 **Author ORCID and contact information:**

25 Em G Lim: 0000-0002-3586-2108; em_lim@sfu.ca

26 Claire M Attridge: 0009-0007-8777-2781; claire_attridge@sfu.ca

27 Kieran D Cox: 0000-0001-5626-1048; kieran_cox@sfu.ca

28 Jasmin M Schuster: 0000-0001-8681-0757; jasmin.schuster@kelprescue.org

29 Kiara R Kattler: 0009-0006-4181-5945; kkattler@ualberta.ca; kiara_kattler@sfu.ca

30 Emily J Leedham: elee323@aucklanduni.ac.nz

31 Bridget Maher: 0000-0002-8061-9932; bridgetmaher@uvic.ca

32 Andrew L Bickell: 0000-0002-7808-7471; andrewbickell@uvic.ca

33 Francis Juanes: 0000-0001-7397-0014; juanes@uvic.ca

34 Isabelle M Côté: 0000-0001-5368-4061; imcote@sfu.ca

35

36 **Author Contribution Statement:**

37 EGL: Conceptualization (equal); formal analysis; investigation (lead); methodology (lead);

38 visualization; writing – original draft preparation. CMA: Conceptualization (supporting);

39 investigation (equal); methodology (equal). KDC: Conceptualization (supporting); funding

40 acquisition (supporting); investigation (equal); methodology (equal); project administration

41 (equal). JMS: Funding acquisition (supporting); investigation (supporting); project

42 administration (supporting). KRK: Investigation (supporting). EJJ: Investigation (supporting).

43 BM: Investigation (supporting); methodology (supporting). ALB: Investigation (supporting). FJ:

44 Funding acquisition (equal); project administration (supporting). IMC: Conceptualization

45 (equal); funding acquisition (equal); methodology (equal); project administration (equal);

46 supervision. All authors contributed to writing – review & editing.

Abstract

Consumer-mediated nutrient dynamics (CND), through which animals' metabolic waste products fertilize primary producers, drive variability in nutrient availability in tropical waters. This variability influences primary productivity and community functioning. Yet, examinations of CND as a driver of nutrient variability in temperate marine ecosystems are limited. Therefore, we assessed the existence and drivers of variation in CND in temperate waters at meso, small, and fine spatial scales. ~~W~~~~To do so, we~~ quantified the occurrence of 48 fish and 92 macroinvertebrate taxa and measured in situ ammonium at 27 northeast Pacific rocky reefs for three years and 16 kelp forests of varying density for one year. Ammonium concentrations ranged from 0.01 to 2.5 μM across rocky reefs separated by tens of km. The relationship between animal abundance and ammonium among sites was mediated by water flow, where flood tides seemed to “wash away” the effect of nutrient regeneration by animals, although enrichment was possible on ebb tides. Ammonium concentration was significantly ~~higher-greater~~ within than outside of kelp forests, a difference that increased with kelp biomass, ~~tidale~~ exchange, and to a lesser degree animal biomass. Caging experiments revealed that fine-scale (~ 2 m) ammonium variability and nutrient enrichment were only possible under low-flow conditions. Our results suggest that CND drives nutrient variability at scales ranging from two meters to over 20 km, acting on a finer scale than allochthonous nitrogen sources such as upwelling. Therefore, consumer-mediated nutrient dynamics are implicated as a previously overlooked driver of spatial variation in primary productivity in temperate marine systems.

69 Introduction

70 Variation in resource availability across spatial and temporal scales can drive substantial
71 heterogeneity in the growth, biomass and composition of primary producers (Tilman 1984;
72 Leibold 1991; Dayton et al. 1999; McInturf et al. 2019). In many marine ecosystems, community
73 structure is regulated through bottom-up control, i.e., ~~the~~ its structure depends on factors that
74 generate variability in the resources available to lower trophic levels (Gruner et al. 2008).
75 Although marine ecologists have historically focused on external, abiotic sources of nutrients
76 (e.g., upwelling) as drivers of variability in nutrient availability, there is emerging evidence that
77 consumers also contribute to bottom-up effects (Allgeier et al. 2017). Metabolic waste products
78 (i.e., excretion and egestion) of animals fertilize primary producers via a process termed
79 consumer-mediated nutrient dynamics (CND; Vanni, 2002). Consumers excrete metabolic waste
80 in the form of ammonium (NH_4^+), which is preferentially taken up by primary producers over
81 other forms of nitrogen like nitrate and nitrite (Lobban and Harrison 1994; Phillips and Hurd
82 2004). However, the ecological importance of consumer-regenerated nutrients at varied spatial
83 scales remains unclear. Therefore, identifying the extent to which biologically relevant variation
84 in nutrient availability contributes to heterogeneity in primary productivity remains an active
85 area of research (Allgeier et al. 2017).

86 Heterogeneity in consumer habitat use greatly influences spatial and temporal variation in
87 nutrients supplied by animal waste (Uthicke 2001; Roman and McCarthy 2010; Benkwitt et al.
88 2019). For example, tropical coral reefs provide habitat, shelter, and food sources that attract
89 dense aggregations of vertebrate and invertebrate consumers which regenerate nutrients (Archer
90 et al. 2015; Shantz et al. 2015). On a meso-scale (i.e., 10 to 100 km; Broitman et al., 2001),
91 productivity increases with proximity to reefs with high densities of fishes (Layman et al. 2016),

while on a fine scale, sheltering schools of fish increase nitrogen concentrations around individual heads of corals relative to neighboring uninhabited corals (Holbrook et al. 2008). Ammonium NH_4^+ supply can also vary with not only the body size, but also the diversity of the consumers (Allgeier et al. 2014). Diurnal migrations are another source of temporal and spatial variation in consumer-regenerated nutrients, as some fishes travel away from reefs to forage at night, then return to excrete waste around their hiding spots during the day (Meyer and Schultz 1985; Francis and Côté 2018). At an even larger-scale, variation can arise from the migration of megafauna; for instance, whales transport and deposit nutrients across thousands of kilometers as they travel from their feeding to breeding grounds (Doughty et al. 2016). However, the current understanding of animal-driven spatio-temporal variability of nitrogen is drawn substantially from tropical ecosystems (Meyer et al. 1983; Holbrook et al. 2008; Allgeier et al. 2013), often overlooking productive temperate marine ecosystems.

In temperate oceans, external sources of nutrients, such as upwelling and freshwater runoff, are generally considered the dominant drivers of nitrogen variability (Dayton et al. 1999; Lønborg et al. 2021). Due to the open nature of many nearshore environments, high-fast water flow from currents, tides, and wave action are believed to limit small-scale (1 to 100 m²) nutrient variation (Probyn and Chapman 1983). Therefore, research on intertidal and shallow subtidal ecosystems has traditionally focused on top-down trophic interactions as the drivers of community composition at small scales, while limiting considerations of resource limitation to large regional or continental scales (Paine 1986; Menge 1992). However, evidence suggests meso-scale ~~(10 to 100 km; Broitman et al., 2001)~~ variation in allochthonous nitrogen via upwelling and internal waves may contribute to bottom-up control of marine communities (Menge et al. 1997; Nielsen and Navarrete 2004; Leichter et al. 2023) and even weaken top-

down control (Sellers et al. 2020). Consumer-mediated nutrient dynamics may also contribute to smaller scales of nutrient variability than previously assumed. For instance, the abundance of intertidal mussel beds has been linked to variation in nitrogen concentrations along entire coastlines (Pfister et al. 2014), across 10s of meters (Aquilino et al. 2009), and among tidepools (fine-scale microhabitats; Bracken, 2004). Therefore, regenerated nitrogen may contribute substantially to meso-, small-, and fine-scale variation in nutrient availability, even in ~~high~~fast-flow, upwelling-dominated nearshore coastal ecosystems.

Shallow subtidal rocky reefs and kelp forests are temperate nearshore habitats that attract dense aggregations of fishes and invertebrates, many of which are economically, ecologically, and culturally important (Steneck et al. 2002). Elevated NH_4^+ excretion from the concentrated ~~bio~~diversity and biomass of these communities may also contribute to nutrient hotspots on small to meso-scales and exceed NH_4^+ delivery from other sources (Shrestha et al. 2024). Fast-growing canopy kelps, which form expansive underwater forests, may benefit from these excretions directly as a source of nitrogen (in the form of NH_4^+), especially during low upwelling periods (Brzezinski et al. 2013; Lees et al. 2024). These kelps, which comprise giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis leutkeana*) in the northeast Pacific, also influence the hydrodynamics and hydrochemistry of seawater, both slowing water flow within the forests and generating gradients of carbon content, pH, alkalinity, and oxygen (Jackson and Winant 1983; Gaylord et al. 2007; Pfister et al. 2019). These modifications of the surrounding fluid environment by kelp forests could affect the productivity and community composition of other primary producers and contribute to small-scale spatial nutrient heterogeneity.

We aimed to quantify the contribution of animal-regenerated nitrogen to spatial variability of nutrients in a temperate, wave-swept upwelling region (Barkley Sound, British

Columbia, Canada). This region is located on the traditional territories of the Huu-ay-aht Nation and comprises an archipelago of islands dotted with rocky reefs and kelp forests of heterogeneous structure. We hypothesized that animal-regenerated nutrients contribute to variability in resource availability across three distinct spatial scales. Specifically, we predicted that NH_4^+ variation would be detectable at the meso-scale due to variation in animal abundance among sites. We also expected to observe variation in NH_4^+ concentrations at small scales (within natural sites) and fine scales (between experimental cages), but only under conditions that allow for local enrichment (e.g., low tidal exchange). To test these predictions, we measured variation in NH_4^+ concentrations among rocky reef sites (meso scale of ~10s of km), in and out of kelp forest sites (small scale of 5 m), and near experimentally caged consumers (fine scale of < 2 m, Fig. 1a–c). We quantified the abundance and diversity of fishes and invertebrates at each rocky reef and kelp forest site and measured kelp forest metrics and abiotic variables to explore potential drivers of variation in NH_4^+ concentrations. By characterizing the scale at which animal-driven nutrients vary, we hope to uncover the extent to which consumers in temperate regions structure communities not only from the top down, but also the bottom up through CND.

Methods

Site description

Barkley Sound is located in an upwelling region on the west coast of Vancouver Island, Canada. Upwelling supplies nitrates in the spring and early summer, while storms flush riverine inputs into the nearshore in the winter and spring (Pawlowicz 2017). Due to the proximity of the Bamfield Marine Sciences Centre (BMSC), this region has been a long-term focal area for studies seeking to document the response of kelps to marine heatwaves, establish ecological

baselines, and unravel ecosystem dynamics (Tanasichuk 1998; Starko et al. 2022, 2024; Attridge et al. 2024). Subtidal fish communities in this region ~~include~~ comprise at least 18 families, including gobies, surfperches, rockfishes, greenlings, and sculpins (E.G. Lim, unpubl.).

Macroinvertebrate assemblages, which are made up of over 49 families, are dominated by sea urchins, turban snails, sea stars, sea cucumbers, and abalone (E.G. Lim, unpubl.).

Surveys of meso-scale (among-site) variation

To explore meso-scale variation in animal-regenerated nutrients among rocky reefs, we measured ammonium (NH_4^+) concentrations and surveyed fish and invertebrate communities at 27 subtidal sites ranging from 0.07 – 24 km apart in Barkley Sound (Fig. 1d). We used a globally standardized method (i.e., Reef Life Survey, RLS) at each site to estimate fish and invertebrate abundance and collected subtidal NH_4^+ samples during each survey. We conducted our surveys in the spring (April-May) for three years (2021-2023), with all annual surveys occurring within two weeks of each other (~~Supporting Information~~ Supplemental Material; Table ~~S1-0S~~ S1). A full explanation of the Reef Life Survey method is available online (<http://www.reeflifesurvey.com/methods>) and provided by Edgar and Stuart-Smith (2009) and Edgar et al. (2020). Briefly, at each rocky reef site, a pair of RLS-trained SCUBA divers assessed fish and invertebrate abundance and diversity along each side of a 50 m transect line. First, fishes in the water column were counted and sized (total length, in various size class categories) within 5 m on either side of the transect line (500 m²), and then benthic cryptic fishes (also sized) and large mobile invertebrates (> 2.5 cm) were counted within 1 m on either side of the transect line (100 m²).

Immediately following each RLS survey, we collected three 60 mL subtidal seawater samples at 0, 25, and 50 m along the transect, 0 – 2 m above the substrate, and stored the syringes in sealed plastic bags upon collection to prevent contamination. Seawater samples were filtered into opaque amber bottles in the field and frozen for a maximum of two weeks before NH_4^+ analysis. We confirmed that freezing samples for this duration did not affect NH_4^+ concentration (E. G. Lim unpubl.). In 2021 and 2022, we followed the fluorometric method using 40 mL seawater samples (Holmes et al. 1999), and in 2023, we followed the fluorometric standard-additions protocol II (Taylor et al. 2007). These methods produce similar results, although the Holmes single spike method is associated with ~~higher-larger~~ variability in measurements (Taylor et al. 2007). The three NH_4^+ samples collected during each survey were averaged to determine the mean NH_4^+ concentration for each site.

Surveys of small-scale (within-site) variation

To investigate small-scale variation of animal-regenerated nutrients, we measured NH_4^+ concentrations inside and outside kelp forests and surveyed the resident biological communities as potential moderators of this variation. Our 16 sites comprised forests of varying densities dominated by giant kelp or bull kelp, and two no-kelp control sites. We conducted surveys from July to September 2022 (Table ~~S1-0~~S2). First, divers conducted RLS surveys (as above) along 50 m transect lines ~~parallel to~~along the edge of the kelp forest to quantify the abundance and biodiversity of fish and invertebrate communities *associated* with each kelp forest (Fig. S1). We were unable to conduct RLS transects entirely within the kelp forests due to visual obstruction and concern with diver entanglement by the kelp. Next, divers ran four 5 m-long transects perpendicular to the RLS transect (5 m apart) into the kelp forest to assess kelp density, canopy

height, and kelp biomass (Fig. S1.0S1). Divers then counted the number of canopy kelp individuals (bull or giant kelp) within 0.5 m on either side of each kelp transect to measure kelp density. To estimate canopy height, we measured the length of five randomly selected kelp individuals per species per kelp transect; for bull kelp we measured the total length from holdfast to pneumatocyst in situ, but for giant kelp, we collected five random individuals to measure the length from holdfast to the tip of the apical meristem on dry land. To quantify bull kelp biomass, we measured the sub-bulb circumference (15 cm below the bottom of the bulb) of the same five bull kelps per transect in situ and calculated individual biomass using a quadratic diameter to biomass formula for Barkley Sound (C. M. Attridge unpubl.). For giant kelp biomass, we weighed (to the nearest 1 g or less) the same five individuals per transect that were collected for total length measurements. We multiplied the mean biomass estimate for each kelp species by the species density to calculate a biomass/m² estimate for each kelp transect, which we then averaged over the four transects per forest to estimate overall mean forest biomass/m². We estimated total forest area by swimming around the perimeter of the forest on the surface with a Garmin GPSMAP 78SC, which we used to calculate total forest biomass (kg).

Finally, to compare NH₄⁺ concentrations inside vs outside each kelp forest, we collected paired 60 mL syringes of seawater immediately outside the kelp forest within 0 – 2 m above the substrate, and 5 m into the kelp forest at the same depth. We collected three paired NH₄⁺ samples from each site, which were spaced 5 m apart, by matching them with the first three kelp transects (Fig. S1.0S1). At our two control, no-kelp sites, we followed the same procedure in terms of number and spacing of samples, with the ‘inside’ samples taken ~ 5 m closer to shore than the ‘outside’ samples. Outside each kelp forest and at each control site, we also collected seawater to create a standard curve, following the standard-additions protocol II for the fluorometric

detection of NH_4^+ in 40 mL samples (Taylor et al. 2007). ~~filled a plastic Ziplock bag with~~
~~seawater to create standards.~~ Samples and standards were filtered into amber bottles in the field
and stored on ice for transportation back to the laboratory, at which point we measured NH_4^+
concentration in each sample bottle following the ~~fluorometric standard additions protocol II for~~
~~40 mL samples protocol above~~ (Taylor et al. 2007). For each paired inside and outside kelp forest
 NH_4^+ sample, we calculated $\Delta\text{NH}_4^+ = \text{inside } \text{NH}_4^+ - \text{outside } \text{NH}_4^+$.

Surveys of fine-scale (microhabitat) variation

To quantify the ability of animals to affect the NH_4^+ concentration in their immediate vicinity we
conducted two caging experiments in situ near Bamfield, BC. We used California sea cucumbers
(*Apostichopus californicus*) in the first caging experiment because ~~this species is~~ ~~ey are~~ a large,
abundant invertebrate with a high excretion rate (Bray et al. 1988). The first experiment occurred
May 27 – 28, 2021 at Scott's Bay (48°50'05.2"N, 125°08'49.3"W), a wide, exposed bay that
opens into Trevor Channel (Fig. 1d). We constructed 18 wire cages (26 x 26 x 26 cm), which we
covered in 2 mm plastic mesh. These cages were spaced 3 m apart along two weighted lines (9
cages per line) and deployed at 3 to 5.8 m depth. We collected adult California sea cucumbers
from the site via SCUBA, measured contracted sea cucumber length and girth, and immediately
placed them into the cages in randomly assigned densities of 0, 1, or 2 sea cucumbers ($n = 6$
replicates per density). After 24 hours, we returned to collect water samples from each cage in
situ. While underwater, we minimized water movement by reducing our fin and hand movements
while opening the mesh lids, which were secured with wire and just wide enough to collect a 60
mL syringe of seawater. Once at the surface, we filtered 40 mL of each sample into amber

bottles and transported them on ice to the lab, where we measured NH_4^+ using the fluorometric method (Holmes et al. 1999).

We used red rock crabs (*Cancer productus*) in the second caging experiment to see if a species with an even ~~higher~~ larger individual-level excretion rate could produce fine-scale nutrient variation. The second experiment occurred over nine days from June 10 – 19, 2023 in Bamfield Inlet (48°49'53"N 125°08'11"W), a narrow, sheltered inlet (Fig. 1d). We replicated this experiment from June 19 – 28, 2023 following the same methodology. We collected red rock crabs from the site using crab traps and kept them at BMSC in flow-through sea tables for 2 – 10 days. Crabs were fed salmon every 2 – 4 days, and all crabs were fed the night before each experiment started. We constructed 12 cages from clear plastic (40 x 28 x 17 cm), with two 15 x 9 cm windows covered in a dual layer of 10 mm plastic mesh and 1 mm mesh to allow for water flow. The cages were randomly distributed every 2 m along a lead line anchored with cement blocks 0.8 m below chart datum. Each cage contained either one large crab (carapace 15.0 – 15.9 cm), one medium crab (11.6 – 14.4 cm), or a control (i.e., a small rock, scraped clean, so weight was similar across all cages) ($n = 4$ replicates per experiment). During both experiments, we replaced the crabs after 4 days with freshly fed, similar-sized crabs, at this point, we re-randomized the order of the cages along the line to minimize any effect of cage location. We measured seawater NH_4^+ concentration via snorkel at low tide at the beginning, middle, and end of each nine-day experiment. A fixed narrow rubber tube that began in the centre of the cage and extended several inches outside the mesh window allowed us to draw water samples using a 60 mL syringe without disturbing the cages. We filtered 40 mL of each sample into amber bottles, which were stored on ice before NH_4^+ analysis via fluorometric standard-additions protocol II (Taylor et al. 2007).

274

275 *Statistical analyses*

276 All statistical analysis were conducted in R (v4.1.2, R Core Team, 2019) using RStudio

277 (v1.3.1093, RStudio Team, 2016). We used ‘tidyverse’ packages for data manipulation and

278 visualization (Wickham et al. 2019), ‘glmmTMB’ for all modelling (Brooks et al. 2017), and

279 ‘DHARMa’ to check model fit (Hartig 2022). We ensured ~~all~~ models met assumptions by

280 inspecting residuals using the ‘DHARMa’ simulateResiduals function and checked for

281 collinearity between variables using the vif function from the ‘car’ package with a cutoff value

282 of 2.

283 For each Reef Life Survey conducted, we calculated fish biomass from fish length

284 following the formula:

285
$$W = aL^b$$

286 W is fish weight, L is the fish length, a and b are species-specific constants from FishBase

287 (Froese et al. 2014). All mobile invertebrates were counted, but only sunflower sea stars

288 (*Pycnopodia helianthoides*) and economically important species (abalone [*Haliotis*289 *kamtschatkana*] and scallops [*Crassadoma gigantea*]) were sized. We used published length–

290 weight relationships to calculate wet weight for these three species. For all other invertebrates,

291 we used published wet weights to estimate biomass for each taxon. We used shell-free wet

292 weight for species with large shells, such as hermit crabs and snails. When biomass information

293 was unavailable for a species, we used estimates from the closest relative or most similarly sized

294 species available (Table ~~S1.0~~S3). Animal abundance per m² was calculated as the total number295 of fishes and invertebrates counted on each survey, and animal biomass per m² was calculated as296 the total wet weight of all animals on each survey (divided by 500 m² for pelagic fishes and by

100 m² for cryptic fishes and macroinvertebrates). ~~and We~~ we used the ‘vegan’ package to calculate Shannon and Simpson diversity indices (Oksanen et al. 2022). We calculated ~~the tide~~ tide exchange by computing the percent change of the tide height every minute, averaged over the hour-long survey.

Meso-scale (among-site) variation

To explore meso-scale variation in NH₄⁺, we constructed generalized linear mixed-effect models (GLMMs) with NH₄⁺ concentration as the response variable, and animal abundance (per m²), tide exchange, an interaction between abundance and tide, Shannon diversity, and survey depth as predictors, and random effects of site and year. All predictors were scaled and centered around the mean using the scale function. We used a gamma distribution (link = ‘log’). To test the robustness of our modelling approach, we considered animal biomass/m² as a predictor instead of abundance/m², and Simpson’s diversity instead of Shannon diversity; alternative models including these predictors were not better supported by AIC (Table ~~S1.0~~S4). ~~We ran additional models considering the effect of only the most abundant families of fishes and invertebrates, which are fully described in Supplemental Material Section 2.~~

Small-scale (within-site) variation

To determine whether NH₄⁺ concentration differed inside and outside of kelp forests, we used a linear mixed-effects model (LMM) with ΔNH₄⁺ as the response variable ($n = 3$ estimates per site), and kelp species, mean forest kelp biomass (per m²), tide exchange, animal biomass (per m²), survey depth, Shannon diversity, and interactions between kelp biomass and tide exchange, kelp biomass and animal biomass, and animal biomass and tide exchange as fixed

effects. All continuous predictors were scaled and centered around the mean as above. We included site as a random effect (1|site) as each site contributed three estimates to the analysis and used a Gaussian distribution. As above, we chose our final set of predictors upon comparing AIC values of models with alternative predictors (Table S1.0S5). ~~We then ran additional models considering the effect of only the most abundant families of fishes and invertebrates (Supplemental Material Section 2).~~

Fine-scale (microhabitat) variation

We constructed separate linear models for each caging experiment to quantify the impact of caged animals on adjacent NH_4^+ concentration. For the sea cucumber experiment, we regressed cage NH_4^+ concentration against the treatment (i.e., sea cucumber density: 0, 1, or 2 sea cucumbers) and cage depth (centered) using a Gaussian distribution. ~~We calculated the NH_4^+ excretion rate for each sea cucumber using a previously generated size-to-excretion relationship (Table S1.06).~~ For the red rock crab experiment, we constructed a ~~generalized linear mixed-effects model (GLMM)~~ with cage NH_4^+ concentration as the response variable and treatment (no crab, medium crab, or large crab) as the predictor variable with a gamma distribution (link = 'log'). We included a random effect of sampling day because we measured NH_4^+ three times per experiment, and a random effect of experimental week, because we replicated the whole experiment twice. ~~We also computed~~ calculated the respective NH_4^+ supply rates by sea cucumbers and red rock crabs using a previously generated size-to-excretion relationship for each sea cucumber (Table S6), and a ~~We used a previously developed~~ carapace-to-excretion relationship to calculate NH_4^+ excretion rates for each crab (Table S1.0S7).

Results

We found evidence of meso-scale variation in ammonium (NH_4^+) concentrations, which ranged from 0.07 μM – 2.06 μM among rocky reefs in Barkley Sound (Fig. 1d). Overall, we found no evidence that NH_4^+ concentration was correlated with animal abundance (GLMM, $p = 0.57$), tidal exchange ($p = 0.99$), Shannon diversity ($p = 0.41$), or survey depth ($p = 0.61$; Fig. 2a; Table S1.0S8). However, we did find a significantly negative interaction between animal abundance and tidal exchange ($p = 0.01$; Fig. 2b), revealing a weakly positive effect of total animal abundance per m^2 on NH_4^+ concentration, but only at ebb tide. ~~In the models considering only the abundance of one animal family at a time, we found evidence for a positive relationship between the abundance of greenlings (Hexagrammidae) and whitecap limpets (Acmidae) and NH_4^+ ($p = 0.03$; Fig. S2.01). The single family models did not reveal a significant effect of any other predictors (Fig. S2.01 and Table S2.01).~~

We also documented evidence of significant small-scale, within-site variation of NH_4^+ (Fig. 3; Table S1.0S9).; concentrations were 1.3x ~~higher-greater~~ inside giant kelp forests and 1.6x ~~higher-greater~~ inside bull kelp forests than outside (LMM, $p < 0.001$; Fig. 3b). The ‘excess’ NH_4^+ concentration inside kelp forests increased with kelp biomass ($p < 0.001$; Fig. 3c), and tidal exchange ($p = 0.02$; Fig. 3a). We found limited evidence for an effect of animal biomass ($p = 0.10$; Fig. 3a), and no evidence of an effect of survey depth ($p = 0.19$; Fig. 3a), or Shannon diversity on ΔNH_4^+ ($p = 0.23$; Fig. 3a). There was a positive interaction between kelp forest biomass and tidal exchange, whereby the positive effect of kelp biomass on ΔNH_4^+ increased with tidal e-exchange ($p < 0.001$; Fig. 3a,c). We also identified a negative interaction between kelp biomass and animal biomass ($p = 0.04$; Fig. 3a,d), and a negative interaction between tidal exchange and animal biomass ($p = 0.001$; Fig. 3a,e). The change in NH_4^+ was negative between

samples taken 5 m apart at the no-kelp control sites ($p = 0.004$; Fig. 3b). ~~For the single-family models, five families displayed significant relationships between biomass and ΔNH_4^+ , while the biomass of Gobiidae was negatively correlated with ΔNH_4^+ (Fig. S2.02 and Table S2.02).~~

We found mixed evidence for animal-related fine-scale variability in NH_4^+ concentration. For sea cucumbers, we found no effect of ~~one or two~~ sea cucumbers ~~density~~ on cage NH_4^+ concentration despite a supply rate of $14\ \mu\text{M/h}$ and $28\ \mu\text{M/h}$ ~~for the low and high treatments~~, respectively. Overall, the mean NH_4^+ concentration was $0.92 \pm 0.04\ \mu\text{M}$ across all cages (LM, $p > 0.75$ for both treatments; Fig. 4a; Table S1.10). However, we ~~see~~ saw a positive effect of cage depth, whereby NH_4^+ increased by $0.38 \pm 0.05\ \mu\text{M}$ per m increase in depth ($p < 0.001$). For red rock crabs, both medium and large crabs significantly increased the cage NH_4^+ concentration relative to control cages, by 8.7x and 12.1x respectively (GLMM, $p < 0.001$ for all; Fig. 4b; Table S1.11). Medium crabs excreted on average $88\ \mu\text{M/h}$ while large crabs excreted $150\ \mu\text{M/h}$.

Discussion

We found evidence of variability of animal-regenerated nutrients from the largest to the smallest scale examined, although the strength of the signal varied. Ammonium (NH_4^+) varied by up to 16x between rocky reef sites within a year, 1.9x inside vs outside kelp forests, and 40x between cages with and without crabs. Water flow (i.e., tidal exchange and wave exposure) mediated the capacity for animals to saturate the water column with nutrients. Among sites a flooding tide seemed to “wash away” the impact of animals on NH_4^+ concentrations; in contrast, within sites, moving water made kelps’ ability to slow flow and trap animal-regenerated nutrients more pronounced. In the fine-scale caging experiments we only detected an effect when the nutrient providers were crabs – an effect that we attribute mainly to the low water flow in the protected

inlet rather than to the taxa. Nevertheless, across all three scales, there was animal-mediated spatial heterogeneity in nutrient availability, which may contribute to bottom-up effects.

Meso-scale (among-site) variation

In rocky reef habitats, we detected a 16-fold difference in NH_4^+ among sites with the lowest and highest concentrations. This difference is substantially greater than previous measurements of among-site variation in nitrate (3.7x and 6.5x) and ammonium (0.4x and 0.8x) from the same region (Druehl et al. 1989; Hurd et al. 2000). It is also larger than among-site NH_4^+ differences measured in nearby Washington State (1.1x, Pfister et al., 2014). We had predicted that variation in NH_4^+ concentration among sites would be driven primarily by animal abundance. However, the only significant predictor of among-site differences in NH_4^+ was a negative interaction between tidal exchange and animal abundance, whereby animal excretions may enrich the seawater when the tide is ebbing, but the effect of animal abundance is washed away when the tide comes in. Although marine species diversity sometimes covaries with animal abundance or biomass (Yee and Juliano 2007; Müller et al. 2018), we found no relationship between Shannon diversity and NH_4^+ . We did not quantify intertidal animals or microbial regeneration, which are additional sources of NH_4^+ (Aquilino et al. 2009; Lowman et al. 2023), but these sources may be more important in shallower waters and soft-sediment areas than on the subtidal rocky reefs we studied. We conclude that CND likely contributes to meso-scale variation in NH_4^+ in an unexpected, dynamic, tide-associated manner, which could drive among-site variation in primary productivity and thus bottom-up control.

Small-scale (within-site) variation

We found evidence of kelp-mediated nutrient variation on a smaller scale (5 m) than previously established. Although ~~higher-greater~~ NH_4^+ ~~concentrations~~ inside high-density kelp forests ~~has~~ been documented (e.g., Pfister et al., 2019), these studies compared nutrient samples taken from the middle of very large kelp forests to sites more than 50 m away from the forest edges (Stewart et al. 2009; Pfister et al. 2019; Traiger et al. 2022). By sampling inside and outside forests across a gradient of kelp densities we further demonstrate a positive relationship between kelp biomass and NH_4^+ retention. The retention of NH_4^+ observed is likely due to the dampening of flow within the kelp forest bed and subsequent flow acceleration around the edges (Gaylord et al. 2007; Rosman et al. 2007). Indeed, as predicted, we found the effect of kelp biomass on NH_4^+ retention was more pronounced when the tide was rising (flood tide). Unfortunately, we never sampled on ebbing tides, and did not quantify water motion due to waves or currents, so we could only contrast slack and flooding tides. Nevertheless, it seems that water flow due to tidal exchange enhances ~~rather than masks~~ NH_4^+ variability within kelp forests ~~instead of masking it~~.

We uncovered additional drivers of differences in NH_4^+ concentration inside and outside kelp forests, namely kelp species and animal biomass. We found ~~higher-greater~~ ΔNH_4^+ (NH_4^+ inside - NH_4^+ outside) in bull kelp forests compared to giant kelp forests, which may be due to their different allocations of biomass in the water column and thus different alterations of water flow. Indeed, Traiger et al., (2022) found the effect of giant kelp forests on water chemistry was smaller than that of bull kelp forests, previously described by Murie and Bourdeau (2020).

Species-specific NH_4^+ uptake rates may also impact NH_4^+ retention, as giant kelp may have higher NH_4^+ uptake rates than bull kelp (Ahn et al. 1998; Lees et al. 2024). Somewhat surprisingly, ~~at the no kelp sites~~, NH_4^+ was lower in the “inside” samples ~~than in, which were closer to shore, compared to the “outside” samples, which were taken 5 m farther from shore at~~

the no-kelp sites. ~~And often slightly deeper~~ despite our efforts to maintain a consistent sampling depth, the “inside” samples were taken at slightly shallower depths since they were closer to shore. This result is therefore in line with the observation that NH_4^+ tends to increase with depth (Brzezinski et al. 2013), ~~which might explain this result. The fact that we~~ As we found the opposite trend at our kelp sites ~~increases our~~, where the “inside” kelp forest samples had more NH_4^+ than the possibly deeper “outside” samples, we are confident ~~this result is due to that kelp help to retain retention of NH_4^+ by kelp, instead of an artifact of our sampling procedure within forests.~~

Even though kelp forests attract dense aggregations of fishes and invertebrates, the positive effect of animal biomass on ΔNH_4^+ was weak and mediated by water flow and kelp biomass. Shannon diversity was positively associated with both animal and kelp biomass (Fig. S1.0S2) but had no effect on ΔNH_4^+ . The negative interactions between animal biomass and both tide and kelp biomass suggest a potentially saturating relationship among these variables. When animal biomass was low, increased kelp biomass or tidal exchange increased ΔNH_4^+ , whereas at high animal biomass, increasing kelp or flow had no effect. There may therefore be a threshold for how much animals can saturate and therefore increase ΔNH_4^+ in kelp forest ecosystems. Beyond this point, increased water motion or kelp biomass no longer enhances NH_4^+ inside kelp forests relative to the forest edge. Our RLS surveys captured kelp forest associated communities, but we did not pair RLS surveys inside and outside forests. Therefore, we were unable to account for animal biomass outside forests, which might have reduced noise in the model.

Fine-scale (microhabitat) variation

At the smallest scale of variability tested, we found evidence of variation in NH_4^+ only in our cage experiments in the sheltered inlet, which may suggest that water motion mediates variation at this scale as well. Under laboratory conditions we confirmed that NH_4^+ enrichment by animals declines with increasing flow rates (Fig. S1.0S3). Alternative or complementary explanations include a taxonomic effect and/or an experimental effect. The crabs in the sheltered cages excreted NH_4^+ at a rate roughly 6x ~~higher-greater~~ than the sea cucumbers caged in the more exposed location. This difference in NH_4^+ production could have given us more scope to detect differences among treatments in the protected inlet. In addition, the crab cages were constructed with only two mesh windows, in contrast to the fully meshed cages of sea cucumbers, which could have promoted nutrient retention in the former. The experimental duration was also shorter for the sea cucumber experiment, but NH_4^+ concentrations in the crab cages were consistent across the three sampling days (day one, four, and nine) so cumulative enrichment is unlikely.

Fine-scale NH_4^+ enrichment by animals is nevertheless possible in wave-exposed conditions; for example, seawater above mussel beds had ~16x ~~higher-greater~~ NH_4^+ compared to neighbouring rock without mussels on the northern California coast (Aquilino et al. 2009). Our cage experiments were not designed to test why variation was found in one experiment and not the other, but rather to see whether fine-scale variation might arise at all. Therefore, we simply conclude that at least in sheltered conditions, variation on the scale of meters driven by animal biomass is possible.

Implications for primary productivity

Heterogeneity in primary productivity arises from variation in resource supply. Increased primary productivity has been seen with orders of variation (i.e., 1.3 – 9x) in NH_4^+ (Uthicke and

Klumpp 1998; Arzul 2001; Vinther and Holmer 2008; West et al. 2009), which is within the range of variation we observed at all three spatial scales considered here. Regardless of nitrate availability, NH_4^+ is less costly for primary producers to use, and can even inhibit nitrate uptake (MacIsaac and Dugdale 1969, 1972). In nitrate-replete upwelling ecosystems of the west coast of North America, a 15.8x increase in NH_4^+ (from 0.08 μM to 1.26 μM) was linked to increased tissue nitrogen and percent cover of an intertidal seaweed (Aquilino et al. 2009), while a 1.8x increase in NH_4^+ increased growth in subtidal seaweeds (Druehl et al. 1989). Furthermore, the mismatch of timing between upwelling and the growing season at temperate latitudes leads to an increased reliance on NH_4^+ over time as nitrate becomes depleted (Druehl et al. 1989; Brzezinski et al. 2013). For example, oceanographic processes may only provide half of the nitrogen needed to sustain giant kelp growth between late summer and early fall in southern California (Fram et al. 2008).

Heterogeneity in NH_4^+ availability likely influences primary productivity in Barkley Sound at each spatial scale studied. Although nitrate varies among sites at the meso-scale (Druehl et al. 1989; Hurd et al. 2000), external nutrient supply (upwelling) may not control primary productivity as strongly as local factors (Pawlowicz 2017). The meso-scale NH_4^+ variability we documented may be one such local factor. At a small scale, nitrate from external sources (e.g., upwelling and run-off) becomes depleted or unchanged as it flows through a kelp forest (Pfister et al., 2019; Stewart et al., 2009), in contrast to NH_4^+ which is continuously regenerated by animals within and around the forest and seemingly retained. As such, kelp forests effectively concentrate their preferred form of nitrogen. This process likely facilitates not only the growth of these canopy kelps but also understory seaweeds and phytoplankton in the water column. As urchin overgrazing and climate change continue to degrade kelp forests, this

important ecosystem function may be lost. At fine scales, invertebrates and fishes living in close contact with primary producers can enrich kelps directly. Many seaweeds are capable of surge uptake of NH_4^+ (Cedeno et al. 2021), allowing them to maximize the benefit from animal excretion directly on their thalli. Indeed, given turnover rates of water and NH_4^+ uptake rates, seaweeds in New Zealand were estimated to derive up to 79% of their needed nitrogen from direct epifauna excretion (Taylor and Rees 1998).

Conclusion

Despite the mixing forces of currents, tides and waves, spatial heterogeneity in NH_4^+ concentration was detectable at meso, small, and fine spatial scales. Given the annual depletion of nitrates each summer (Druehl et al. 1989), primary producers' preference for NH_4^+ over nitrate (Phillips and Hurd 2004), and capacity for surge uptake of NH_4^+ (Cedeno et al. 2021), it seems likely that the animal-driven variation in NH_4^+ we observed could be contributing to heterogeneity in primary productivity. Our results disrupt the dominant paradigm that bottom-up effects in temperate waters are primarily driven by external sources of nutrients acting on large scales, while animals contribute to smaller-scale variation mainly through top-down, consumptive effects. Instead, animals in temperate waters likely drive bottom-up effects across multiple spatial scales while also contributing to top-down effects. Animal-driven spatio-temporal variability of nitrogen is known to drive bottom-up effects in the tropics, and our results suggest animal-regenerated nutrients also play a previously unappreciated role in shaping nutrient availability in temperate regions as well.

Acknowledgements

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

Data Availability Statement

All datasets generated during the current study and code are available in the GitHub repository: https://github.com/em-lim13/Ch2_Spatial_peek and the OSF repository: <https://osf.io/hkttf4/>.

Conflict of Interest Statement

The authors declare no conflict of interest.

References

- 548 Ahn, O., R. J. Petrell, and P. J. Harrison. 1998. Ammonium and nitrate uptake by *Laminaria*
549 *saccharina* and *Nereocystis luetkeana* originating from a salmon sea cage farm. J. Appl.
550 Phycol. **10**: 333–340. doi:10.1023/A:1008092521651
- 551 Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-
552 mediated nutrient dynamics in the world's changing oceans. Glob Change Biol **23**: 2166–
553 2178. doi:10.1111/gcb.13625
- 554 Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2014. Consistent nutrient
555 storage and supply mediated by diverse fish communities in coral reef ecosystems. Glob.
556 Change Biol. **20**: 2459–2472. doi:10.1111/gcb.12566
- 557 Allgeier, J. E., L. A. Yeager, and C. A. Layman. 2013. Consumers regulate nutrient limitation
558 regimes and primary production in seagrass ecosystems. Ecology **94**: 521–529.
559 doi:https://doi.org/10.1890/12-1122.1
- 560 Aquilino, K. M., M. E. S. Bracken, M. N. Faubel, and J. J. Stachowicz. 2009. Local-scale
561 nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an
562 upwelling system. Limnol Oceanogr **54**: 309–317.
563 doi:https://doi.org/10.4319/lo.2009.54.1.0309
- 564 Archer, S. K. and others. 2015. Hot moments in spawning aggregations: implications for
565 ecosystem-scale nutrient cycling. Coral Reefs **34**: 19–23. doi:10.1007/s00338-014-1208-
566 4
- 567 Arzul, G. 2001. Effect of marine animal excretions on differential growth of phytoplankton
568 species. ICES J. Mar. Sci. **58**: 386–390. doi:10.1006/jmsc.2000.1038

- 569 Attridge, C. M., K. D. Cox, B. Maher, S. Gross, E. G. Lim, K. R. Kattler, and I. M. Côté. 2024.
570 Studying kelp forests of today to forecast ecosystems of the future. *Fisheries* **49**: 181–
571 187. doi:10.1002/fsh.11065
- 572 Benkwitt, C. E., S. K. Wilson, and N. A. J. Graham. 2019. Seabird nutrient subsidies alter
573 patterns of algal abundance and fish biomass on coral reefs following a bleaching event.
574 *Glob Change Biol* **25**: 2619–2632. doi:https://doi.org/10.1111/gcb.14643
- 575 Bracken, M. E. S. 2004. Invertebrate-mediated nutrient loading increases growth of an intertidal
576 macroalga. *J. Phycol.* **40**: 1032–1041. doi:https://doi.org/10.1111/j.1529-
577 8817.2004.03106.x
- 578 Bray, R. N., A. C. Miller, S. Johnson, P. R. Krause, D. L. Robertson, and A. M. Westcott. 1988.
579 Ammonium excretion by macroinvertebrates and fishes on a subtidal rocky reef in
580 southern California. *Mar. Biol.* **100**: 21–30. doi:10.1007/BF00392951
- 581 Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of
582 southeastern Pacific intertidal communities. *Mar. Ecol. Prog. Ser.* **224**: 21–34.
583 doi:10.3354/meps224021
- 584 Brooks, M. E. and others. 2017. glmmTMB balances speed and flexibility among packages for
585 zero-inflated generalized linear mixed modeling. *The R Journal* **9**: 378. doi:10.32614/RJ-
586 2017-066
- 587 Brzezinski, M., D. Reed, S. Harrer, A. Rassweiler, J. Melack, B. Goodridge, and J. Dugan. 2013.
588 Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner
589 continental shelf of the Santa Barbara Channel. *Oceanog* **26**: 114–123.
590 doi:10.5670/oceanog.2013.53

- 591 Cedeno, T. H., M. A. Brzezinski, R. J. Miller, and D. C. Reed. 2021. An evaluation of surge
592 uptake capability in the giant kelp (*Macrocystis pyrifera*) in response to pulses of three
593 different forms of nitrogen. *Mar Biol* **168**: 166. doi:10.1007/s00227-021-03975-z
- 594 Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales
595 of kelp demography: The role of oceanographic climate. *Ecol. Monogr.* **69**: 219–250.
596 doi:10.1890/0012-9615(1999)069[0219:TASSOK]2.0.CO;2
- 597 Doughty, C. E. and others. 2016. Global nutrient transport in a world of giants. *Proc Natl Acad*
598 *Sci USA* **113**: 868–873. doi:10.1073/pnas.1502549112
- 599 Druehl, L. D., P. J. Harrison, K. E. Lloyd, and P. A. Thompson. 1989. Phenotypic variation in N
600 uptake by *Laminaria groenlandica* Rosenvinge (Laminariales, Phaeophyta). *J. Exp. Mar.*
601 *Bio. Ecol* **127**: 155–164. doi:10.1016/0022-0981(89)90181-0
- 602 Edgar, G. J. and others. 2020. Establishing the ecological basis for conservation of shallow
603 marine life using Reef Life Survey. *Biol. Conserv.* **252**: 108855.
604 doi:10.1016/j.biocon.2020.108855
- 605 Edgar, G., and R. Stuart-Smith. 2009. Ecological effects of marine protected areas on rocky reef
606 communities—a continental-scale analysis. *Mar. Ecol. Prog. Ser.* **388**: 51–62.
607 doi:10.3354/meps08149
- 608 Fram, J. P., H. L. Stewart, M. A. Brzezinski, B. Gaylord, D. C. Reed, S. L. Williams, and S.
609 MacIntyre. 2008. Physical pathways and utilization of nitrate supply to the giant kelp,
610 *Macrocystis pyrifera*. *Limnol Oceanogr* **53**: 1589–1603. doi:10.4319/lo.2008.53.4.1589
- 611 Francis, F. T., and I. M. Côté. 2018. Fish movement drives spatial and temporal patterns of
612 nutrient provisioning on coral reef patches. *Ecosphere* **9**: e02225. doi:10.1002/ecs2.2225

- 613 Froese, R., J. T. Thorson, and R. B. Reyes Jr. 2014. A Bayesian approach for estimating length-
614 weight relationships in fishes. *J. Appl. Ichthyol.* **30**: 78–85. doi:10.1111/jai.12299
- 615 Gaylord, B. and others. 2007. Spatial patterns of flow and their modification within and around a
616 giant kelp forest. *Limnol Oceanogr* **52**: 1838–1852. doi:10.4319/lo.2007.52.5.1838
- 617 Gruner, D. S. and others. 2008. A cross-system synthesis of consumer and nutrient resource
618 control on producer biomass. *Ecol Lett* **11**: 740–755. doi:10.1111/j.1461-
619 0248.2008.01192.x
- 620 Hartig, F. 2022. DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression
621 models. R package version 0.4.6.
- 622 Holbrook, S. J., A. J. Brooks, R. J. Schmitt, and H. L. Stewart. 2008. Effects of sheltering fish on
623 growth of their host corals. *Mar Biol* **155**: 521–530. doi:10.1007/s00227-008-1051-7
- 624 Holmes, R. M., A. Aminot, R. Kerouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and
625 precise method for measuring ammonium in marine and freshwater ecosystems. *Can. J.*
626 *Fish. Aquat. Sci.* **56**: 1801–1808. doi:https://doi.org/10.1139/f99-128
- 627 Hurd, C. L., K. M. Durante, and P. J. Harrison. 2000. Influence of bryozoan colonization on the
628 physiology of the kelp *Macrocystis integrifolia* (Laminariales, Phaeophyta) from
629 nitrogen-rich and -poor sites in Barkley Sound, British Columbia, Canada. *Phycologia*
630 **39**: 435–440. doi:10.2216/i0031-8884-39-5-435.1
- 631 Jackson, G. A., and C. D. Winant. 1983. Effect of a kelp forest on coastal currents. *Continental*
632 *Shelf Research* **2**: 75–80. doi:10.1016/0278-4343(83)90023-7
- 633 Layman, C. A., J. E. Allgeier, and C. G. Montaña. 2016. Mechanistic evidence of enhanced
634 production on artificial reefs: A case study in a Bahamian seagrass ecosystem. *Ecol Eng*
635 **95**: 574–579. doi:10.1016/j.ecoleng.2016.06.109

- 636 Lees, L. E., S. N. Z. Jordan, and M. E. S. Bracken. 2024. Kelps may compensate for low nitrate
637 availability by using regenerated forms of nitrogen, including urea and ammonium. *J*
638 *Phycol* **60**: 768–777. doi:10.1111/jpy.13459
- 639 Leibold, M. A. 1991. Biodiversity and nutrient enrichment in pond plankton communities. *Evol.*
640 *Ecol. Res* **1**: 73–95.
- 641 Leichter, J. J., L. B. Ladah, P. E. Parnell, M. D. Stokes, M. T. Costa, J. Fumo, and P. K. Dayton.
642 2023. Persistence of southern California giant kelp beds and alongshore variation in
643 nutrient exposure driven by seasonal upwelling and internal waves. *Front. Mar. Sci.* **10**.
644 doi:10.3389/fmars.2023.1007789
- 645 Lobban, C. S., and P. J. Harrison. 1994. Seaweed ecology and physiology, Cambridge University
646 Press.
- 647 Lønborg, C. and others. 2021. Nutrient cycling in tropical and temperate coastal waters: Is
648 latitude making a difference? *Estuar. Coast. Shelf Sci.* **262**: 107571.
649 doi:10.1016/j.ecss.2021.107571
- 650 Lowman, H. E., M. E. Hirsch, M. A. Brzezinski, and J. M. Melack. 2023. Examining the
651 potential of sandy marine sediments surrounding giant kelp forests to provide recycled
652 nutrients for growth. *J. Coast. Res.* **39**: 442–454. doi:10.2112/JCOASTRES-D-22-
653 00035.1
- 654 MacIsaac, J. J., and R. C. Dugdale. 1969. The kinetics of nitrate and ammonia uptake by natural
655 populations of marine phytoplankton. *Deep-Sea Res. Oceanogr. Abstr.* **16**: 45–57.
656 doi:10.1016/0011-7471(69)90049-7

- 657 MacIsaac, J. J., and R. C. Dugdale. 1972. Interactions of light and inorganic nitrogen in
658 controlling nitrogen uptake in the sea. *Deep-Sea Res. Oceanogr. Abstr.* **19**: 209–232.
659 doi:10.1016/0011-7471(72)90032-0
- 660 McInturf, A. G., L. Pollack, L. H. Yang, and O. Spiegel. 2019. Vectors with autonomy: what
661 distinguishes animal-mediated nutrient transport from abiotic vectors? *Biological*
662 *Reviews* **94**: 1761–1773. doi:10.1111/brv.12525
- 663 Menge, B. A. 1992. Community regulation: Under what conditions are bottom-up factors
664 important on rocky shores? *Ecology* **73**: 755–765. doi:10.2307/1940155
- 665 Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997.
666 Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-
667 down control? *Proc Natl Acad Sci USA* **94**: 14530–14535. doi:10.1073/pnas.94.26.14530
- 668 Meyer, J. L., and E. T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and
669 organic matter on coral reefs. *Limnol Oceanogr* **30**: 146–156.
- 670 Meyer, J. L., E. T. Schultz, and G. S. Helfman. 1983. Fish schools: An asset to corals. *Science*
671 **220**: 1047–1049. doi:10.1126/science.220.4601.1047
- 672 Müller, J. and others. 2018. LiDAR-derived canopy structure supports the more-individuals
673 hypothesis for arthropod diversity in temperate forests. *Oikos* **127**: 814–824.
674 doi:10.1111/oik.04972
- 675 Murie, K. A., and P. E. Bourdeau. 2020. Fragmented kelp forest canopies retain their ability to
676 alter local seawater chemistry. *Sci Rep* **10**: 11939. doi:10.1038/s41598-020-68841-2
- 677 Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up:
678 intertidal interactions between consumers and upwelling. *Ecol. Lett.* **7**: 31–41.
679 doi:10.1046/j.1461-0248.2003.00542.x

- Oksanen, J. and others. 2022. vegan: Community ecology package. R package version 2.6-4.
- Paine, R. T. 1986. Benthic community—water column coupling during the 1982-1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence?1. *Limnol Oceanogr* **31**: 351–360. doi:10.4319/lo.1986.31.2.0351
- Pawlowicz, R. 2017. Seasonal cycles, hypoxia, and renewal in a coastal fjord (Barkley Sound, British Columbia). *Atmos.-Ocean* **55**: 264–283. doi:10.1080/07055900.2017.1374240
- Pfister, C. A., M. A. Altabet, and D. Post. 2014. Animal regeneration and microbial retention of nitrogen along coastal rocky shores. *Ecology* **95**: 2803–2814. doi:10.1890/13-1825.1
- Pfister, C. A., M. A. Altabet, and B. L. Weigel. 2019. Kelp beds and their local effects on seawater chemistry, productivity, and microbial communities. *Ecology* **100**: e02798. doi:https://doi.org/10.1002/ecy.2798
- Phillips, J. C., and C. L. Hurd. 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. *J Phycol* **40**: 534–545. doi:10.1111/j.1529-8817.2004.03157.x
- Posit team. 2024. RStudio: Integrated Development Environment for R.
- Probyn, T. A., and A. R. O. Chapman. 1983. Summer growth of *Chordaria flagelliformis* (O.F. Muell.) C. Ag.: Physiological strategies in a nutrient stressed environment. *J. Exp. Mar. Bio. Ecol* **73**: 243–271. doi:10.1016/0022-0981(83)90050-3
- R Core Team. 2024. R: A language and environment for statistical computing.
- Roman, J., and J. J. McCarthy. 2010. The whale pump: Marine mammals enhance primary productivity in a coastal basin P. Roopnarine [ed.]. *PLoS ONE* **5**: e13255. doi:10.1371/journal.pone.0013255

- 702 Rosman, J. H., J. R. Koseff, S. G. Monismith, and J. Grover. 2007. A field investigation into the
703 effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. J.
704 Geophys. Res. Oceans **112**. doi:10.1029/2005JC003430
- 705 Sellers, A. J., B. Leung, and M. E. Torchin. 2020. Global meta-analysis of how marine upwelling
706 affects herbivory. Glob. Ecol. Biogeogr. **29**: 370–383.
707 doi:https://doi.org/10.1111/geb.13023
- 708 Shantz, A. A., M. C. Ladd, E. Schrack, and D. E. Burkepile. 2015. Fish-derived nutrient hotspots
709 shape coral reef benthic communities. Ecol Appl **25**: 2142–2152. doi:10.1890/14-2209.1
- 710 Shrestha, J., J. R. Peters, J. E. Caselle, and S. L. Hamilton. 2024. Marine protection and
711 environmental forcing influence fish-derived nutrient cycling in kelp forests. Funct. Ecol.
712 1–15. doi:10.1111/1365-2435.14708
- 713 Starko, S. and others. 2024. Local and regional variation in kelp loss and stability across coastal
714 British Columbia. Mar. Ecol. Prog. Ser. **733**: 1–26. doi:10.3354/meps14548
- 715 Starko, S., C. J. Neufeld, L. Gendall, B. Timmer, L. Campbell, J. Yakimishyn, L. Druehl, and J.
716 K. Baum. 2022. Microclimate predicts kelp forest extinction in the face of direct and
717 indirect marine heatwave effects. Ecol Appl **32**: e2673. doi:10.1002/eap.2673
- 718 Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J.
719 Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future.
720 Environ. Conserv. **29**: 436–459. doi:10.1017/S0376892902000322
- 721 Stewart, H., J. Fram, D. Reed, S. Williams, M. Brzezinski, S. MacIntyre, and B. Gaylord. 2009.
722 Differences in growth, morphology and tissue carbon and nitrogen of *Macrocystis*
723 *pyrifera* within and at the outer edge of a giant kelp forest in California, USA. Mar. Ecol.
724 Prog. Ser. **375**: 101–112. doi:10.3354/meps07752

- 725 Tanasichuk, R. 1998. Interannual variations in the population biology and productivity of
726 *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and
727 1993 warm ocean years. Mar. Ecol. Prog. Ser. **173**: 163–180. doi:10.3354/meps173163
- 728 Taylor, B. W., C. F. Keep, R. O. Hall, B. J. Koch, L. M. Tronstad, A. S. Flecker, and A. J.
729 Ulseth. 2007. Improving the fluorometric ammonium method: matrix effects, background
730 fluorescence, and standard additions. J.N. Am. Benthol. Soc. **26**: 167–177.
731 doi:10.1899/0887-3593(2007)26[167:ITFAMM]2.0.CO;2
- 732 Taylor, R., and T. A. V. Rees. 1998. Excretory products of mobile epifauna as a nitrogen source
733 for seaweeds. Limnol Oceanogr **43**: 600–606. doi:10.4319/lo.1998.43.4.0600
- 734 Tilman, G. D. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65**:
735 1445–1453. doi:10.2307/1939125
- 736 Traiger, S. B. and others. 2022. Limited biogeochemical modification of surface waters by kelp
737 forest canopies: Influence of kelp metabolism and site-specific hydrodynamics. Limnol
738 Oceanogr **67**: 392–403. doi:10.1002/lno.11999
- 739 Uthicke, S. 2001. Nutrient regeneration by abundant coral reef holothurians. J. Exp. Mar. Biol.
740 Ecol. **265**: 153–170. doi:10.1016/S0022-0981(01)00329-X
- 741 Uthicke, S., and D. W. Klumpp. 1998. Microphytobenthos community production at a near-shore
742 coral reef: seasonal variation and response to ammonium recycled by holothurians. Mar
743 Ecol Prog Ser **169**: 1–11.
- 744 Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst
745 **33**: 341–370. doi:10.1146/annurev.ecolsys.33.010802.150519

746 Vinther, H. F., and M. Holmer. 2008. Experimental test of biodeposition and ammonium
747 excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance.
748 J. Exp. Mar. Bio. Ecol **364**: 72–79. doi:10.1016/j.jembe.2008.07.003

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

752 Wickham, H. and others. 2019. Welcome to the tidyverse. JOSS **4**: 1686.
753 doi:10.21105/joss.01686

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

757
758