Title
Consumer-mediated nutrient dynamics of kelp forests in the wake of global change

Author
Peters, Joseph Richard

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Consumer-mediated nutrient dynamics of kelp forests in the wake of global change

A dissertation submitted in partial satisfaction of the requirements for the degree of
Doctor of Philosophy in Ecology, Evolution, and Marine Biology

by
Joseph R. Peters

Committee:
Professor Deron Burkepile, Co-Chair
Dr. Daniel Reed, Co-Chair
Professor Holly Moeller

September 2023

The dissertation of Joseph R. Peters is approved.

Holly Moeller

Daniel Reed, Committee Co-Chair

Deron Burkepile, Committee Co-Chair

August 2023

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VITA OF JOSEPH R. PETERS
August 2023

Education

2023	**Ph.D.** – Ecology, Evolution, & Marine Biology University of California, Santa Barbara
2016	**M.S.** – Environmental Science & Management Portland State University
2013	**B.S.** – Marine Biology, Honors in the Major; Minor in Chemistry Florida International University

Research Grants

2023	**NSF LTER Synthesis Working Group,** UCSB/NCEAS – *Consumer-mediated nutrient dynamics of marine ecosystems under the wake of global change* (**$54,590**)
2019	**UCSB Associated Students Coastal Fund** – *Lobster aggregations form biogeochemical hotspots that structure benthic communities in kelp forests* (**$7,400**)
2019	**Schmidt Family Foundation Research Accelerator Award,** UCSB – *Sea otters as keystone nutrient cyclers in southern California kelp forests* (**$8,000**)
2017	**UCSB Associated Students Coastal Fund** – *Consumer-mediated nutrient cycling in kelp forests: identifying how consumer hotspots drive primary production in the Santa Barbara Channel* **($9,363**)
2017	**UCSB EEMB Block Grant** - *Consumer-mediated nutrient cycling in kelp forests* (**$2,500**)

Fellowships and Awards

2020-2021	Bertelsen Doctoral Fellowship, UCSB **($41,860**)
2015-2016	Natural Resource Policy Fellowship, Oregon Sea Grant, (**$32,000**)
2015	Directorate Resource Fellowship, U.S. Fish & Wildlife Service, PSU **($5,500**)
2015	Dean's Award for Academic Achievement, PSU
2015	Outstanding Graduate Research Award, PSU
2014-2015	Robert E. Malouf Scholarship, Oregon Sea Grant, PSU (**$10,800**)
2013	Outstanding Academic Achievement in Marine Biology, FIU
2011-2013	Capt. Kevin Llorente Memorial Scholarship, Kiwanas Club, FIU (**$5,000**)
2011-2013	First Generation Scholarship, City of North Miami, FIU (**$2,000**)

Peer-Reviewed Publications

‡Undergraduate student author

2021 Munsterman KS, Allgeier JE, **Peters JR**, and Burkepile DE. A view from both ends: shifts in herbivore assemblages impact top-down and bottom-up processes on coral reefs. *Ecosystems* 24: 1702-1715.

2021 Lenihan, HS, Gallagher JP‡, **Peters JR**, Stier AC, Hofmeister J, and Reed DC. Evidence that spillover from Marine Protected Areas benefit the spiny lobster (*Panulirus interruptus*) fishery in southern California. *Scientific Reports* 11 (1) 1-9.

2019 **Peters, JR**, Reed, DC, and Burkepile DE. Climate and fishing drive regime shifts in consumer mediated nutrient cycling in kelp forests. *Global Change Biology* 25 (9) 3179-3192.

2017 **Peters, JR**, Granek, EF, de Rivera, CE, and Rollins, MA‡. Prozac in the water: Chronic fluoxetine exposure and predation risk interact to shape behaviors in an estuarine crab. *Ecology & Evolution* 7 (21) 9151-9161.

2016 **Peters, JR** and Granek EF. Long-term fluoxetine exposure reduces growth and reproductive potential in the dominant rocky intertidal mussel, *Mytilus californianus*. *Science of the Total Environment* 545-546, 621-628

2016 Catano, LB, Rojas MC, Malossi, RJ, **Peters, JR**, Heithaus, MR, Fourqurean, JW, and Burkepile DE. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behavior. *Journal of Animal Ecology* 85(1): 146-156.

2016 Yeager, LA, Stoner, EW, **Peters, JR**, and Layman, CA. Potential terrestrial-aquatic food web subsidy is mediated by multiple predator effects on an arboreal crab. *Journal of Experimental Marine Biology and Ecology* 475. 73-79.

2015 **Peters, JR**, Yeager, LA, and Layman CA. Comparison of fish assemblages between intact and restored mangroves along an urban shoreline. *Bulletin of Marine Science* 91 (2): 125-139. *Featured article

Manuscripts in Preparation & Review

Peters, JR, Reed, DC, Shrestha J, Hamilton S, and Burkepile DE. Frequent disturbance to a foundation species disrupts consumer-mediated nutrient cycling in giant kelp forests. *Ecology* (in prep)

Peters, JR, Diforte B, Reed DC, and Burkepile DE. Fishing spiny lobsters disrupts important hotspots of nitrogen for benthic macroalgae. *Ecosystems* (in prep)

Landfield, KM, **Peters, JR,** Munsterman, KS**,** Stier AC**,** Allgeier, JE and Burkepile DE. Coral characteristics and the presence of micro-predatory fishes influence ammonium contributions from associated small-bodied fish and invertebrates. Marine Ecology Progress Series (in prep)

Esaian, S, Bui, A, Husted K, Diforte B, **Peters, JR,** Wilbanks, L**,** and Moeller H**.** Giant kelp microbiome community compositions shift from stochastic to depth specialized as host blades mature. Environmental Microbiology (in prep)

Selected Presentations

2022 **Peters, J.R**. Ecological and socioeconomic effects on climate extremes and fishing on the foundational role of giant kelp. ***Poster***, LTER All Scientists Meeting, Monterrey, CA.

2020 **Peters, J.R**. Climate and fishing drive regime shifts in consumer mediated nutrient cycling in kelp forests. ***Talk***, AGU Ocean Sciences Meeting, San Diego, CA.

2018 **Peters, J.R.** Long-term data reveal climate- and human- induced alterations to consumer-mediated nutrient recycling in kelp forests. ***Poster***, Western Society of Naturalists, Tacoma, WA. *Awarded Best Poster

Academic Service & Outreach

Teaching Assistant/Instructor – Taught the following courses

-*Aquatic Communities* (EEMB 142A) – Fall 2016, Fall 2017
-*Aquatic Communities Lab* (EEMB 142AL) – Fall 2018
-*Introduction to Ecology* (EEMB 120) – Spring 2017, Spring 2019, Spring 2023
-*Biometry* (EEMB 146) – Winter 2017, Winter 2018
-*Introduction to Biology* (EEMB 2LL) – Spring 2022, Fall 2022
-*Coral Reefs* (EEMB 147) – Winter 2023
-*Introduction to Ecology* (EEMB 120)*as Instructor of Record

Mentor – Led six undergraduate students from diverse backgrounds in developing independent research projects, two of which led to published manuscripts. Each student has advanced either to graduate school or industry utilizing skill sets like statistical programming and technical writing.
Instructor – R workshops for ecologists (6 courses), UCSB – Fall 2016, Winter 2017, Spring 2017, Fall 2017, Winter 2018, Spring 2018**.**
Boat Captain & Scientific Diver – 2016-present - assist with data collection and field logistics
Reviewer – Ecology, Journal of Animal Ecology; Estuarine, Coastal and Shelf Science; Behavioural Ecology, Ecology & Evolution; Science of the Total Environment, Journal of Experimental Marine Biology and Ecology.

ABSTRACT

Consumer-mediated nutrient dynamics of kelp forests in the wake of global change

by

Joseph R. Peters

Globally, human impacts like habitat destruction, overfishing, and climate change are reducing or redistributing the abundances of marine consumers and altering ecosystems through modification of trophic or “top-down” interactions. Less considered are how the impacts of global change disrupt important “bottom-up” processes that these consumers influence, like nutrient recycling, which are critical for ecosystem functioning. Consumer-mediated nutrient dynamics (CND) are now considered integral biogeochemical components of most ecosystems, but lacking long-term studies it is difficult to predict how CND will respond to accelerating disturbances in the wake of global change. To aid in such predictions, we completed multiple studies on CND in kelp forests, which are highly dynamic, diverse, and among the most productive ecosystems on Earth. Nitrate is the major form of nitrogen believed to fuel this high productivity, yet its availability varies greatly among seasons and years. Forms of nitrogen, like ammonium, recycled by consumers are believed to sustain kelp growth during low nitrate availability, however the extent to which changes to CND in these temperate systems has received little attention. To address these gaps, we paired data of ammonium excretion rates of common fishes and macroinvertebrates with three different time series of their population dynamics in southern California kelp forests. First, we assessed how fishing, ocean warming, and disease altered the recycling of ammonium by reef macroinvertebrates in five kelp forests over an 18-year period. We discovered that California spiny lobster (*Panulirus interruptus*) became the dominant source of ammonium among reef invertebrates, following region-wide mass mortalities of sea stars. Following up on this finding, we evaluated how fishing disrupts the ability of lobster aggregations to form localized and reliable sources of ammonium, i.e. “hot spots”, that influence surrounding benthic communities. Finally, we examined how the loss of giant kelp as a foundation species may alter community-wide CND and the demand for nitrogen by kelp forest macroalgae by taking advantage of a 10-year kelp forest removal experiment that mimics frequent wave disturbance. Our findings from all three studies suggest that kelp forest consumers are resilient to disturbances and serve as reliable sources of ammonium, but are vulnerable to prolonged impacts from fishing, ocean warming, and loss of habitat.

I. Climate and fishing drive regime shifts in consumer-mediated nutrient cycling in kelp forests

Abstract

Globally, anthropogenic pressures are reducing the abundances of marine species and altering ecosystems through modification of trophic interactions. Yet, consumer declines also disrupt important bottom-up processes, like nutrient recycling, which are critical for ecosystem functioning. Consumer-mediated nutrient dynamics (CND) are now considered a major biogeochemical component of most ecosystems but lacking long-term studies it is difficult to predict how CND will respond to accelerating disturbances in the wake of global change. We coupled empirical excretion rates with an 18-year times series of the standing biomass of common benthic macroinvertebrates in southern California kelp forests. This time series of excretion rates encompassed an extreme warming period, disease outbreaks, and the abolishment of fishing at two of our study sites, allowing us to assess kelp forest CND across a wide range of environmental conditions. Reef invertebrates supplied on average 10.9 ± 1.0 μmol NH_4^+ m^{-2} h^{-1}, with rates as high as 18.3 ± 3.0 μmol NH_4^+ m^{-2} h^{-1} when sea stars, an important group of nutrient recyclers, reached their peak abundance. Yet, total ammonium excretion decreased by ~81 % during the 2014-2015 extreme warming period when disease drove mass mortalities in sea star populations. However, increased populations in the California spiny lobster, *Palinurus interupptus* (Randall, 1840), in response to reduced fishing pressure and warming temperatures, have compensated much of the recycled ammonium lost to sea star die offs. Both lobsters and sea stars are critical for regulating prey species, but our study demonstrates their importance in also driving nutrient cycling, further defining their roles in the ecosystem. Climate change has increased the frequency and magnitude of extreme temperature events and rising human populations are intensifying fishing pressure in coastal ecosystems worldwide. Our study demonstrates how these drivers can shift recycled nutrient regimes and highlights the importance of integrating long-term data with future CND research.

1. Introduction

Animals play a pivotal role in shaping the natural world and dramatic changes in their biomass and species composition represent some of the most pervasive and consequential impacts to the environment (Estes et al., 2011; McCauley et al., 2015). Natural fluctuations in climate, disturbance, resource availability, and pathogens can alter the sizes and geographic ranges of animal populations leading to dramatic shifts in community composition and state (Levin & Paine, 1974; Sousa, 1984; Harvell et al. 2002). Such changes are exacerbated by human actions that affect animal populations through overharvest (Jackson et al., 2001), species introductions (Mack et al., 2000), habitat degradation (Lotze et al., 2006), and anthropogenic climate change (Hoegh-Guldberg & Bruno, 2010). To date the vast majority of research on the importance of animals in structuring ecosystems has focused on their role as consumers in influencing food web structure, trophic interactions, and energy flow (Estes et al., 2011; Terborgh, 2015). Yet, as consumers, animals also serve as important mediators of biogeochemical cycles through their excretion and egestion of essential nutrients (Elser & Urabe, 1999; Vanni, 2002; Elser et al., 2007). Consequently, widespread changes in consumer populations have the potential to fundamentally disrupt community dynamics, primary production and other important functions as they mediate bottom-up as well as top-down regulation of ecosystems (Polis, 1999, Burkepile et al. 2013).

Consumer-mediated nutrient dynamics (herein CND) is a critical component of biogeochemical cycling in a wide range of terrestrial and aquatic systems, and the degree to which changes in consumer populations alter nutrient cycling is becoming increasingly recognized (see reviews by Vanni, 2002; Schmitz et al., 2010; Atkinson et al. 2017; Allgeier et al., 2017). CND may be especially important in hard bottom marine systems where the capacity to store nutrients is limited due to the absence of sediments. Such is the case for oligotrophic coral reefs where aggregations of fish serve as biogeochemical hotspots concentrating nutrients that otherwise limit primary production (Meyer et al., 1983; Layman et al., 2013; Shantz et al., 2015). Moreover, declines in reef fish populations due to fishing can significantly reduce the supply of nutrients to coral symbionts and reef macrophytes and lead to decreases in primary production (Layman et al. 2011; Layman et al. 2013).

Unlike coral reefs in the tropics, shallow reefs in temperate seas are typically dominated by forests of large brown macroalgae, i.e., kelps, whose net primary production rivals that of the most productive ecosystems on Earth (Mann, 1973; Reed & Brzezinksi, 2009). Nitrate is often considered to be the major form of nitrogen that fuels this high productivity, yet its availability in many temperate reef systems varies greatly among seasons and years (Jackson, 1977; Chapman and Craigie 1977; van Tussenbroek, 1989; Brzezinksi et al., 2013). Despite this high variability and the limited capacity for kelps to store nitrogen for less than a few weeks (Gerard 1982b), measurable growth occurs year-round in many kelp systems (Kirkman et al., 1989; van Tussenbroek, 1989: Vadas et al., 2004; Hepburn et al., 2007; Reed et al. 2008). Such observations have prompted suggestions that recycled forms of nitrogen (e.g. ammonium and urea) are important in sustaining kelp growth during extended periods of low nitrate availability (Wheeler and Druehl, 1986, Brzezinksi et al. 2013, Smith et al., 2018). While several investigators have drawn attention to the potential importance of CND in contributing to macrophyte productivity in temperate systems (Bray et al. 1986; Bray et al., 1988; Bracken & Nielsen, 2004; Hepburn & Hurd, 2005), the extent to which changes in consumer abundance alters nutrient dynamics in these systems has received little attention.

Like most coastal ecosystems, fishing has drastically reshaped the abundance and size structure of important consumers in kelp forests worldwide (Dayton et al., 1998; Tegner, 2000; Steneck et al., 2002). These impacts from fishing are being mitigated in part by the increased use of no-take marine protected areas (MPAs) as tools for fishery management, and for promoting and protecting ecosystem conservation (Gell & Roberts, 2003: Lester et al., 2009, Edgar et al. 2014). The use of MPAs in kelp forests have been particularly effective in restoring populations of top predators (Kelly et al., 2000; Lipcius et al., 2001; Goñi et al., 2006; Kay et al., 2012), which can have cascading effects on primary producers (Shears & Babcock, 2003; Caselle et al. 2018). Overharvesting is not the only threat to kelp forest consumers as ocean warming has been linked to large changes in their abundance and distribution, acerbating the adverse effects of increased temperature on forest macrophytes (Vergés et al. 2016, Wernberg et al. 2016). Moreover, overfishing of predators and high ocean temperature have been linked to outbreaks of infectious disease (Harvell et al., 1999, Lafferty et al. 2004a), which have led to dramatic population declines in important consumers such as sea urchins and sea stars (Lafferty 2004b, Lester et al., 2007; Eisenlord et al., 2016). How overfishing, disease and climate change interact to disrupt CND in kelp forests is entirely unknown, despite the potentially adverse consequences of their synergistic effects on the populations of many species (Lafferty 2004b, Ling et al. 2009).

In this study we examined CND of benthic macroinvertebrates inhabiting giant kelp (*Macrocystis pyrifera*, Linnaeus) forests of southern California, where year-round kelp growth coupled with extended periods of low concentrations of seawater nitrate and limited nitrogen storage are the norm (Brzezinski et al. 2013). Our 18-year time series of macroinvertebrate biomass spanned the most extreme warming event on record (Reed et al. 2016a), an epidemic disease outbreak that led to mass mortalities of an important consumer guild (Hewson, et al. 2014), and the establishment of no-take MPAs at two of our five long-term study sites (Gleason et al. 2013). We coupled species-specific estimates of excretion rates measured in the field to our biomass time series to: (1) assess the contributions of benthic invertebrates to the supply of recycled nitrogen, (2) characterize CND of kelp forest macroinvertebrates across a wide range of environmental conditions, and (3) determine how anomalous ocean warming, disease outbreak, and fishing altered CND through losses of top consumers and shifts in community structure.

2. Materials and Methods

2.1 Study System We focused our study on giant kelp forests located on shallow reefs (4-11 m depth) off the mainland coast of the Santa Barbara Channel, CA, USA. Kelp forests in this region support diverse assemblages of benthic invertebrates, fish, and other macroalgae that rely strongly on physical modification of habitat (e.g. light, space, temperature) by *M. pyrifera* (Bynres et al. 2011, Miller et al. 2018, Castorani et al. 2018). Data were collected at five kelp forests spanning ~75 km of coast: Arroyo Quemado (AQUE; 120.07 °W, 34.28 °N) , Naples (NAPL; 119.57 °W, 34.25 °N), Isla Vista (IVEE; 119.51 °W, 34.24 °N), Mohawk (MOHK; 119.43 °W, 34.23 °N), and Carpinteria (CARP; 119.32 °W, 34.23 °N). Between January 2014-December 2015, prolonged warming of bottom waters occurred throughout much of the Northeastern Pacific (Kintisch, 2015), including our study sites where daily and monthly bottom temperature anomalies as high as + 5.8°C and + 4.6°C, respectively were recorded (Reed et al. 2016a). Coinciding with this warming event, were epidemic disease outbreaks that caused populations of sea stars to decline by > 90% and sea urchins by ~50% (Reed et al. 2016a). In addition, a network of no-take MPAs was established in southern California in 2012 that included two of our study sites (NAPL & IVEE), which provided us with an opportunity to assess the impacts of fishing on CND.

2.2 Data collection and time series procedures

2.2.1 Time series of invertebrate biomass. Data on the size and abundances of common sessile and mobile reef macroinvertebrate species were collected annually in summer (July-August) from 2001-2018 within 80 m^2 fixed plots (n = 2-8 plots per site) by the Santa Barbara Coastal Long-Term Ecological Research (SBC LTER) program (Reed et al. 2018). Sizes and abundances of all species were converted into grams shell-free dry mass (herein SFDM) using species-specific power functions developed by Reed et al. (2016b). This 18-year time series of invertebrate biomass was used to model population and assemblage level ammonium excretion rates. Beginning in summer 2012, additional surveys were conducted for the California spiny lobster, *Panulirus interruptus*, and were expanded to 1200 m^2 per plot to provide more accurate population estimates for this highly mobile kelp forest predator (Reed 2019). Lobster excretion models based on this 7-year time series were used to assess population-level responses to no-take reserves and warming.

2.2.2 Ammonium excretion rates. We measured ammonium excretion rates from 331 individuals of 14 common benthic macroinvertebrate species (Table 1) in late summer and early fall of 2017 and 2018. Excretion was measured for a representative size range of each species following the methods of Layman et al. (2011) and Allgeier et al. (2013). Animals that could easily be collected by divers were brought to the surface and immediately transferred into 0.1- to 8.0-L acid-washed clear plastic bags (depending on animal size) with known volumes of pre-filtered (0.35 µm Whatman GF-filter), UV-sterilized seawater. Bags with animals were paired with control bags without animals (filtered seawater only) and allowed to incubate for 30-150 min (depending on animal size) in a closed cooler with ice packs to maintain ambient temperatures. Water collected from each bag at the end of the incubation period was filtered (0.45 µm Whatman GF) into 60 mL amber HDPE bottles and placed on ice for transport to the laboratory at UCSB for ammonium analysis. Animals used in incubations were also transported to the laboratory where they were weighed wet for subsequent conversion to SFDM using species-specific relationships developed by Reed et al. (2016b).

We performed *in situ* incubations for the anemone *Anthopleura sola* (Brandt, 1835) and the boring piddock clams *Chaceia ovoidea* (Gould, 1851) and *Parapholas californica* (Conrad, 1837) because they were difficult for divers to collect without causing them excessive physiological stress or physical harm. Incubations for these species consisted of placing a clear polypropylene chamber over the specimen for 60 min. Chambers (0.7 L volume) had an open bottom (6cm diameter) and were sealed to seafloor with a rubber gasket and a weighted flexible rubber skirt. Trials using rhodamine dye indicated the seal was effective and prevented water from flowing into or out of the chamber (J.R. Peters, personal observation). Incubation chambers were paired with control chambers (ambient seawater only). Following incubation, water samples for ammonium analysis were drawn from each chamber and the study specimen was collected. Water samples and animal specimens were transported to the laboratory and processed as described above.

The ammonium concentrations of all water samples were determined within 12 hours of collection following fluorometric methods outlined by Taylor et al. (2007). Concentrations were converted to per capita ammonium excretion rates (μmol NH_4^+ h^{-1} individual^{-1}) by factoring the bag/chamber volume (L) and incubation time (min) of each individual. Mass-specific ammonium excretion rates were calculated as the excretion rate divided by individual SFDM (μmol NH_4^+ h^{-1} dry g^{-1}). We adjusted excretion rates by subtracting ammonium concentrations measured in filtered and ambient seawater as well as changes within control bags/chambers paired with samples during the same incubation period.

2.2.3 Time series of excretion rates. Species-specific excretion data were used to develop generalized linear models to assess the relationship between the ammonium excretion rate and the SFDM of an individual. Because they had similar excretion rates, species of sea urchins (*Strongylocentrotus purpuratus* (Stimpson, 1857) *& M. franciscanus* (Agassiz, 1863)) and boring clams (*C. ovoidea & P. californica*) were pooled into their own respective models. Regressions were performed on log-transformed variables to estimate the slope, intercept, and root mean square error (RMSE) for each model (Appendix S1), and residuals were visually inspected to ensure assumptions of normality and homoscedasticity.

We generated an 18-year time series of ammonium excretion rates at our study sites by populating species-specific models with the standing biomass of species with excretion data. Specifically, per capita ammonium excretion rates (μmol NH_4^+ individual^{-1} h^{-1}) were calculated from the SFDM of an individual from a given family and multiplied by the mean density of a species to obtain areal N excretion (μmol NH_4^+ m^{-2} h^{-1}) for each species in a plot (Allgeier et al. 2013; Burkepile et al. 2013). Models developed for *Pisaster giganteus* (Stimpson, 1857) were used as proxies for *Pisaster brevispinus* (Stimpson, 1857) due to the few *P. brevispinus* remaining at our sites. We applied this procedure to the more spatially comprehensive data collected for spiny lobster during 2012-2018 to better characterize the impacts of fishing on the excretion rates of this important predator.

Model prediction uncertainty was propagated into our final excretion rate estimates using a Monte Carlo procedure. Simulated species-specific model coefficients and their 95% confidence intervals were used to calculate per capita ammonium excretion rates 1000 times at each site. Per capita rates were then converted to areal rates by multiplying by the density of each species. This Monte Carlo approach allowed us to propagate error in predicting individual rates into our estimates of mean areal N excretions for each species. We used the standard deviation of these values, which are normally distributed, to calculate the standard error of areal N excretion estimates. Monte Carlo iterations and modeling procedures were performed using the arm package (Gelman & Hill 2007) in R (R Core Team 2018).

2.3 Data analyses. To assess the contributions of benthic invertebrates to nitrogen recycling, we ranked species in order of their mass-specific excretion rates and compared their mean per capita and areal N excretions (Table 1). We then aggregated areal NH_4^+ excretions and standing biomass estimates into the following functional groups based on their contributions to total excretion and biomass: 'Sea stars' (*P. giganetus*, *P. brevispinus*, & *Patiria miniata* (Brandt, 1835)), 'Urchins' (*S. purpuratus* & *M. franciscanus*), 'Boring clams' (*C. ovoidea, P. californica*), 'Spiny lobsters' (*P. interruptus*), and 'Other taxa' (*M. californica* (Brandt, 1835)*, M. crenulata* (Sowerby, 1825)*, N. norrisii* (Sowerby, 1825)*, S. montereyensi* (Dall, 1872)*, K. kelletii* (Forbes, 1850)*, M. undosa* (Wood, 1828)*,* & *A. sola*). Both values were averaged across sites within each year of the time series. Species in "Other taxa" supplied < 10% of total NH_4^+ excretion and total biomass of invertebrates each year. Although we assessed the annual variability of areal N excretion and standing biomass of each species (Appendices S2 & S3), we performed subsequent analyses of CND on these five groups.

We characterized kelp forest CND at the regional scale by assessing the temporal variability of areal NH_4^+ excretion and standing biomass of each functional group. Linear mixed models (LMM), were fitted with either areal NH_4^+ excretion/standing biomass as the response, survey year as the explanatory variable, and sites included as a random term to account for repeated sampling over time (lme4 package; Bates et al. 2014). We tested differences of both response variables over time with Type III One-way ANOVAs using Kenward-Roger's method (lmerTest package; Kuznetsova et al., 2017). Post-hoc Tukey pairwise contrasts were used to further investigate which years drove differences (emmeans package; Lenth 2018). Areal NH_4^+ excretions were square-root transformed and biomass were log-transformed prior to model-fitting. Assumptions of normality and homoscedasticity were assessed through visual inspection of model residuals. This procedure was also applied to total areal NH_4^+ excretion/total standing biomass to compare interannual differences among the entire assemblage.

We examined how warming, disease, and fishing affected CND by comparing areal NH_4^+ excretion of each group of species at different periods during the time series. For this purpose, we categorized the periods of the time series as pre-warming (2001-2013), warming (2014-2015), and post warming (2016-2018). Disease outbreaks resulting in high mortality of sea stars and sea urchins coincided with the warm period. Therefore, we examined the consequence of disease by comparing areal NH_4^+ excretions of these species during warming and post-warming periods to the pre-warming period using Welch's two-sample t-tests of unequal variances. Areal NH_4^+ excretions of *P interruptus*, a heavily-fished species, were compared during the same periods to assess the effects of warming as well as reduced fishing pressures at two of our sites between 2012-2018. Prior to t-tests, areal excretion rates were square-root transformed to meet normality assumptions.

Using an ordination procedure, we further examined whether warming, disease, and fishing were associated with major shifts at the community-level. We calculated a Bray-Curtis dissimilarity matrix of species-specific areal NH_4^+ excretions, which were normalized using Wisconsin square-root transformation (Legendre & Gallagher; 2001). We then used Permutational Multivariate Analysis of Variance (PERMANOVA) to detect changes in community structure across sites and years (Anderson, 2017). Yearly differences in the community supply of recycled ammonium were displayed graphically using a non-metric multidimensional scaling (NMDS) plot with convex hulls depicting dispersion among sites. A species biplot was also generated to determine correlations between species and ordination axes. Multivariate analyses and ordinations were conducted using the vegan package (Oksanen et al. 2018).

We assessed how warming and MPA establishment at two of our five sites altered lobster areal NH_4^+ excretions with a LMM using the 2012-2018 lobster time series. In this analysis reserve status (MPA vs. non-MPA) and survey year were considered fixed factors and site a random effect. We tested overall differences in the LMM with a Type III Two-way ANOVA using Satterthwaite's method (lmerTest package; Kuznetsova et al., 2017). Tukey pairwise contrasts were used to determine differences between reserve status and year and their interaction. Lobster excretion rates were square-root transformed prior to model-fitting. To examine changes in the population size structure of lobster over time, we fit kernel density estimates of carapace lengths (mm) for MPA and non-MPA sites and plotted changes in their size distributions for each year. All data analyses were performed using R (R Core Team 2018).

3. Results

3.1 Invertebrate contributions to kelp forest recycled nitrogen

Mass-specific and per capita (averaged over all sizes) ammonium excretion rates varied substantially among invertebrate species and were highest in the California spiny lobster, *P. interruptus* (Table 1). Mass-specific excretion rates of *P. interruptus* were ~3 times higher than that of the sea star *P. giganteus* and ~10 times that of *P. miniata*, whose excretion rates were the second and third highest. The sea urchins *S. purpuratus*, and *M. franciscanus* and the boring clams *C. ovoidea* and *P. californica* had relatively low mass-specific excretion rates (Table 1). When averaged over the entire study period, areal NH_4^+ excretions were highest for *P*. *giganteus* and *S. purpuratus*. Mean areal NH_4^+ excretion of *P. interruptus* was ~3 times lower than *P*. *giganteus*, due to extremely low biomass densities for the first 13 years of the study (Appendix S2). Collectively, benthic macroinvertebrates supplied kelp forests in the region with an average total areal N excretion of (mean

± SE) 10.9 ± 1.0 µmol NH_4^+ m^{-2} h^{-1}, with rates ranging between 3.5-18.3 µmol NH_4^+ m^{-2} h^{-1} over the study period.

Table 1. Mean excretion rates (mass-specific, per capita, and areal) of common kelp forest macroinvertebrates. Mass-specific excretion rates were calculated as total ammonium excretion divided by the wet mass (g) of an individual. Per capita excretion rates were averaged over all sizes measured for that species. Areal excretion rates were averaged across all sites and years. Species arranged in order of decreasing mass-specific excretion rates. Size ranges *n* = sample size of incubated individuals

			Wet mass (g)	Mass-specific excretion (μmol NH4^{+} dry g^{-1} h^{-1})	Per capita excretion (μmol NH$_4^{+}$ ind^{-1} h^{-1})	Areal excretion (μmol NH$_4^{+}$ m^{-2} h^{-1})
Species	Common name	*n*	Range	Mean ± SE	Mean ± SE	Mean ± SE
Panulirus interruptus	California spiny lobster	51	57.53 - 653.55	4.71 ± 0.3	173.54 ± 8.35	0.91 ± 0.71
Pisaster giganteus	Giant sea star	10	85.27 - 297.8	1.52 ± 0.12	22.41 ± 2.89	3.03 ± 1.27
Patiria miniata	Bat star	11	10.27 - 116.84	0.48 ± 0.04	3.28 ± 0.39	1.06 ± 1.20
Muricea californica	California golden gorgonian	18	6.26 - 69.96	0.27 ± 0.02	0.86 ± 0.09	0.15 ± 0.14
Megathura crenulata	Giant keyhole limpet	28	47.62 - 199.39	0.27 ± 0.01	4.52 ± 0.13	0.42 ± 0.21
Norrisia norrisi	Norris's top snail	13	34.00 - 80.78	0.15 ± 0.01	0.9 ± 0.1	0.002 ± 0.003
Styela montereyensi	Stalked tunicate	11	5.51 - 17.6	0.14 ± 0.01	0.23 ± 0.03	0.22 ± 0.19
Kelletia kelletii	Kellet's whelk	30	4.18 - 341.46	0.1 ± 0.01	0.2 ± 0.06	0.04 ± 0.03
Mesocentrotus franciscanus	Red urchin	30	60.31 - 357.69	0.08 ± 0.003	1.55 ± 0.11	0.76 ± 0.37
Stronglyocentrotus purpuratus	Purple urchin	32	52.04 - 155.52	0.07 ± 0.01	0.75 ± 0.07	2.23 ± 0.98
Megastraea undosa	Wavy turban snail	36	3.58 - 507.40	0.07 ± 0.01	0.48 ± 0.11	0.08 ± 0.08
Chaceia ovoidea	Wartneck piddock	31	153.6 - 331.09	0.03 ± 0.002	0.61 ± 0.08	1.05 ± 0.76
Parapholas californica	Scale-sided piddock	15	92.51 - 178.94	0.01 ± 0.001	0.12 ± 0.02	0.38 ± 0.25
Anthopleura sola	Starburst anemone	15	4.92 - 43.73	0.01 ± 0.001	0.04 ± 0.01	0.06 ± 0.02

3.2 Patterns of kelp forest CND

Over the study period, the 14 species that we examined (Table 1) comprised 85-97% of the total standing biomass of 84 species of benthic macroinvertebrates surveyed. Interannual fluctuations in their total mean biomass were substantial (Year: $F_{17, 68} = 6.7$, $P < 0.001$; Figure 1a), as a 4-fold decline occurred between 2001 and 2016 ($P < 0.001$), coinciding with the warming event. Fluctuations in the biomass of boring clams and sea urchins drove these differences, as they comprised ~65% and ~20% of the total biomass, respectively (Figure 1a). Despite their high biomass boring clams contributed on average only ~14% of mean total areal NH_4^+ excretions (Figure 1b), due to their low mass-specific excretion rates (Table 1). In contrast, urchins contributed ~28% of total areal NH_4^+ excretions as their mass-specific rates were ~3x higher than boring clams (Table 1, Figure 1b). Yet, urchin areal NH_4^+ excretion fluctuated over the study period (Year: $F_{17, 68} = 7.2$, $P < 0.001$) as there were two periods (2001-2002 & 2009-2014) with relatively high urchin biomass.

Sea stars and spiny lobsters both comprised < 5% of the total standing biomass of invertebrates (Figure 1a). Despite this, interannual patterns of total areal NH_4^+ excretion were driven primarily by their population dynamics, as each group dominated invertebrate regimes of recycled ammonium during two distinct periods of the study (sea stars: 2003-2013, spiny lobster: 2016-2018; Figure 1b). Total areal NH_4^+ excretion varied significantly between years ($F_{17, 68} = 6.9$, $P < 0.001$), with rates as high as 18.3 ± 3.0 $\mu mol\ NH_4^+\ m^{-2}\ h^{-1}$ between 2009-2012, a period when sea stars peaked in biomass and supplied ~60% of the total. Total areal NH_4^+ excretion decreased by ~81% between 2010 and 2015, as the biomass of sea stars, and subsequently their excretion rates, decreased by ~99%. Yet, total areal NH_4^+ excretion increased 3-fold between 2015 and 2018 as excretions from spiny lobster increased from 21 to 52 % of the total (Figure 1b). After no-take reserves were designated at NAPL and IVEE in 2012, we witnessed a 58-fold increase in lobster biomass ($F_{17, 68} = 3.2$, $P < 0.001$) and 40-fold increase their excretion rates ($F_{17, 68} = 3.3$; $P < 0.001$) across all of our sites (Figure 1a & b; Appendix S2 & S3).

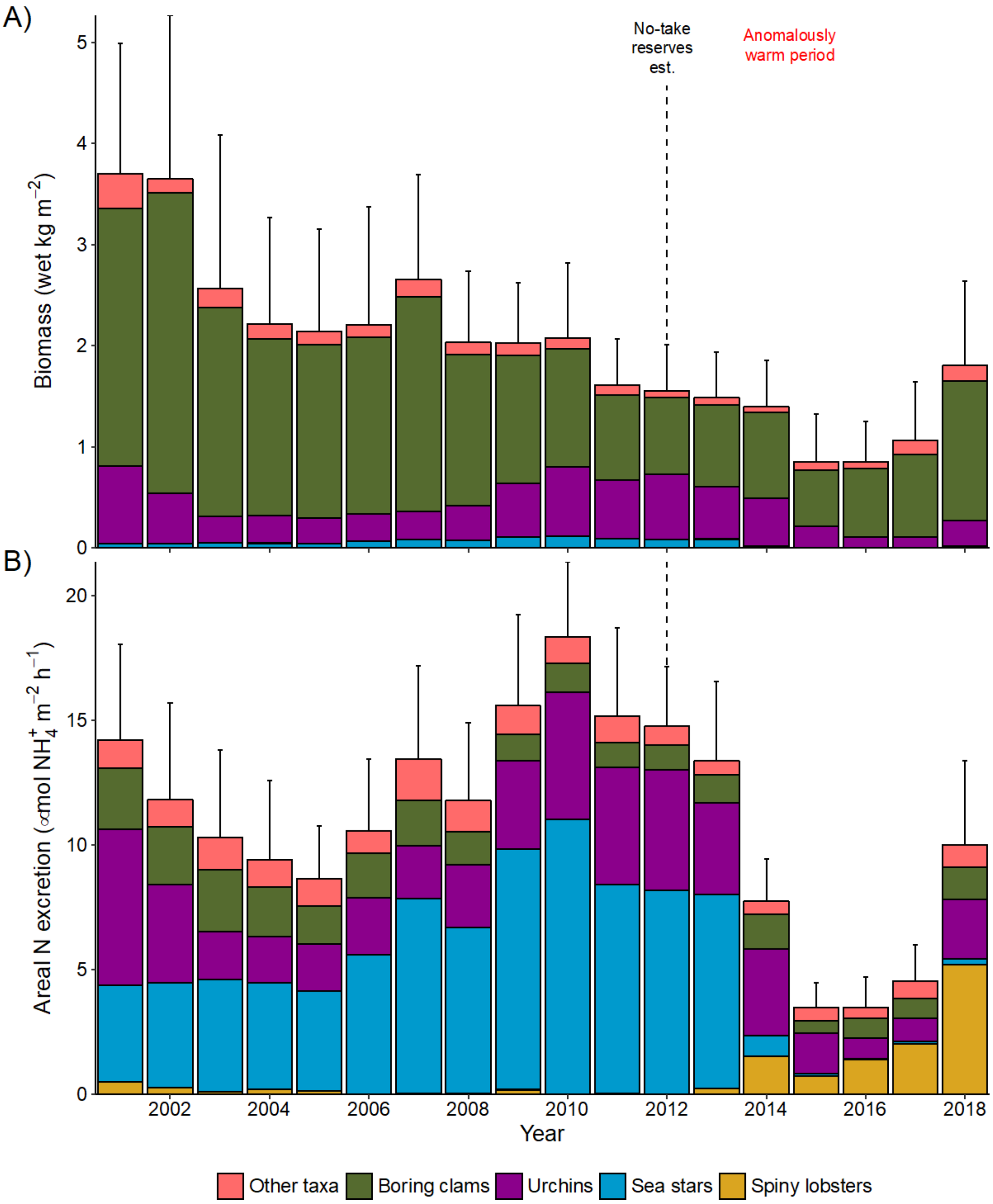
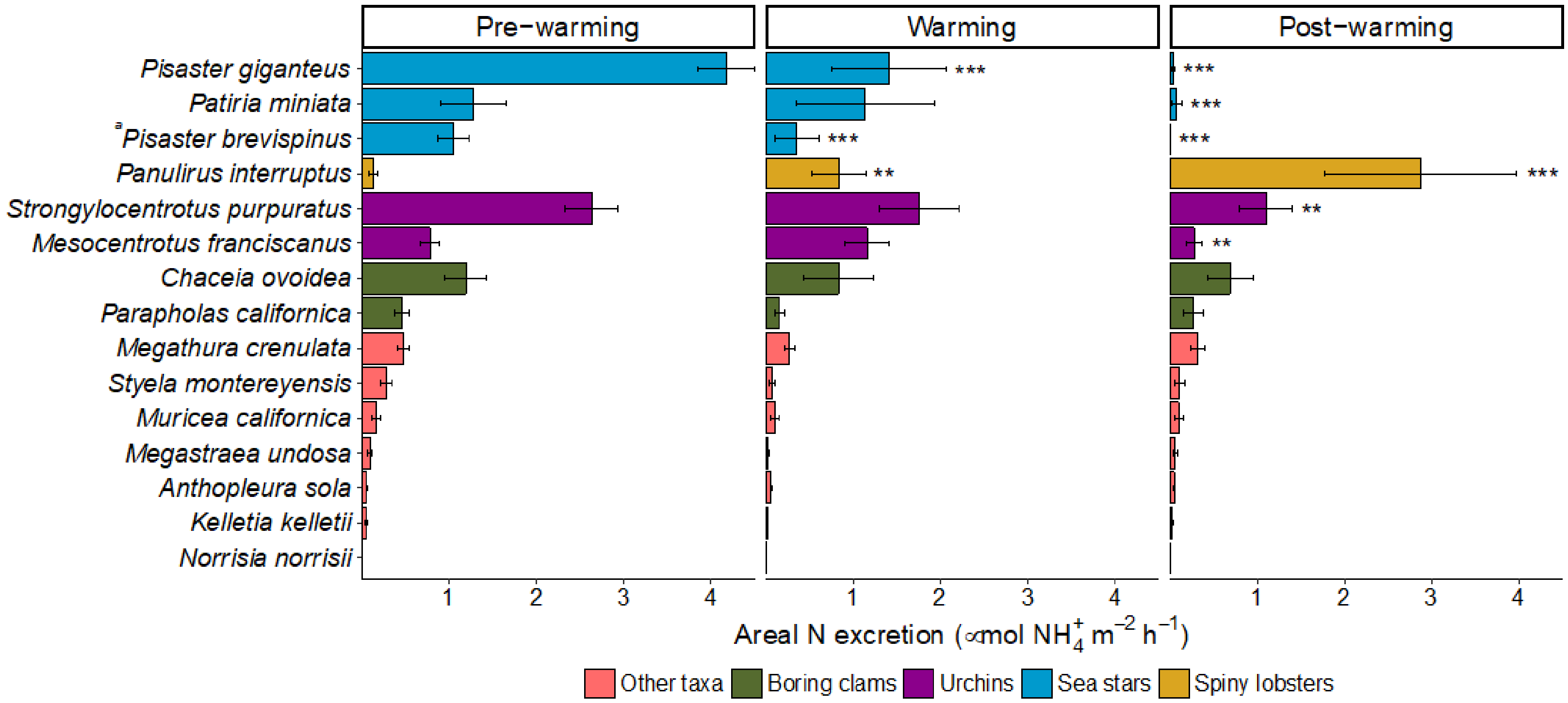


Figure 1. Annual means (mean ± SE) of the A) standing biomass and B) areal ammonium excretions of kelp forest macroinvertebrates averaged across sites (n=5). Taxa in stacked bars are grouped in order of their contribution to total areal excretions. MPAs established in 2012 (dashed line). Red band depicts the 2014-2015 warming period.

3.3 Effects of warming, disease, and fishing on CND

Impacts of warming and disease were most apparent in the sea stars *P. giganteus* and *P. brevispinus*, who each excreted substantial amounts of ammonium in pre-warming years but went functionally extinct by 2014 (Pre vs. Warming: t=4.7, *P* < 0.001, t=3.2, *P*=0.004 respectively, Figure 2). Outbreaks of disease drove declines in the areal excretions of the sea star *P. miniata*, and the sea urchins *S. purpuratus*, and *M. franciscanus* but significant alterations were not detected until 2016 (Pre vs. Post-warming: t=4.5, *P* < 0.001, t=2.8, *P* < 0.001, t=2.9, *P*=0.00, respectively; Figure 2). *P. interruptus* was the only species to show a significant increase in areal NH_4^+ excretion rates during and after the warming event (t= -2.8*, P*=0.01, t= -3.5, *P*=0.003, respectively; Figure 2). Population-level areal NH_4^+ excretion rates of boring clams and the ten species that comprised the “other taxa” group did not change appreciably between periods (Figure 2).

Figure 2. Areal ammonium excretion rates of common kelp forest invertebrates in pre-warming (2001-2013), during (2014-2015), and post-warming (2016-2018) years. Data are mean ± SE averaged across sites and years within each period. Means during the warming and post-warming periods were contrasted with those in the pre-warming period using pairwise t-tests, and significant differences denoted by asterisks (****P* < 0.001, ***P* < 0.01, **P* < 0.05). [a]*Pisaster brevispinus* areal excretion rates were estimated from the *P. giganteus* excretion model.



Following sea star declines, spiny lobsters contributed the most to recycled ammonium. Community-level patterns in areal NH_4^+ excretions corroborate this as a significant shift occurred between 2013-2014, coinciding with the onset of the warming event (PERMANOVA: Years: $F_{17, 68} = 6.0$, $R^2=0.24$; $P < 0.001$), though the magnitude of community restructuring varied substantially by site (Site: $F_{4, 68} = 63.7$, $R^2=0.60$; $P < 0.001$; Figure 3a). Relative dispersion between the pre-warming period (2001-2013) with the warming and post-warming periods (2014-2018) was high for the two MPA sites (IVEE and NAPL) due to larger increases in lobster abundances following no-take protections designated in 2012 (Figure 3a). This effect was most pronounced at IVEE as no lobsters were observed prior to 2012. Regime shifts from sea stars to lobsters as the dominant NH_4^+ recycler was apparent across all sites, despite strong site-to-site variability (Figure 3a). Indeed, all three sea star species were strongly correlated with the 13 years preceding this event, while *P. interruptus* was correlated with the years following (2014-2018; Figure 3b). Further, several invertebrates unaffected by the warming event (e.g. *N. norrisii*, *M. undosa*, Figure 2) were also strongly correlated with post-warming years, but effects were site dependent (Figure 3b).

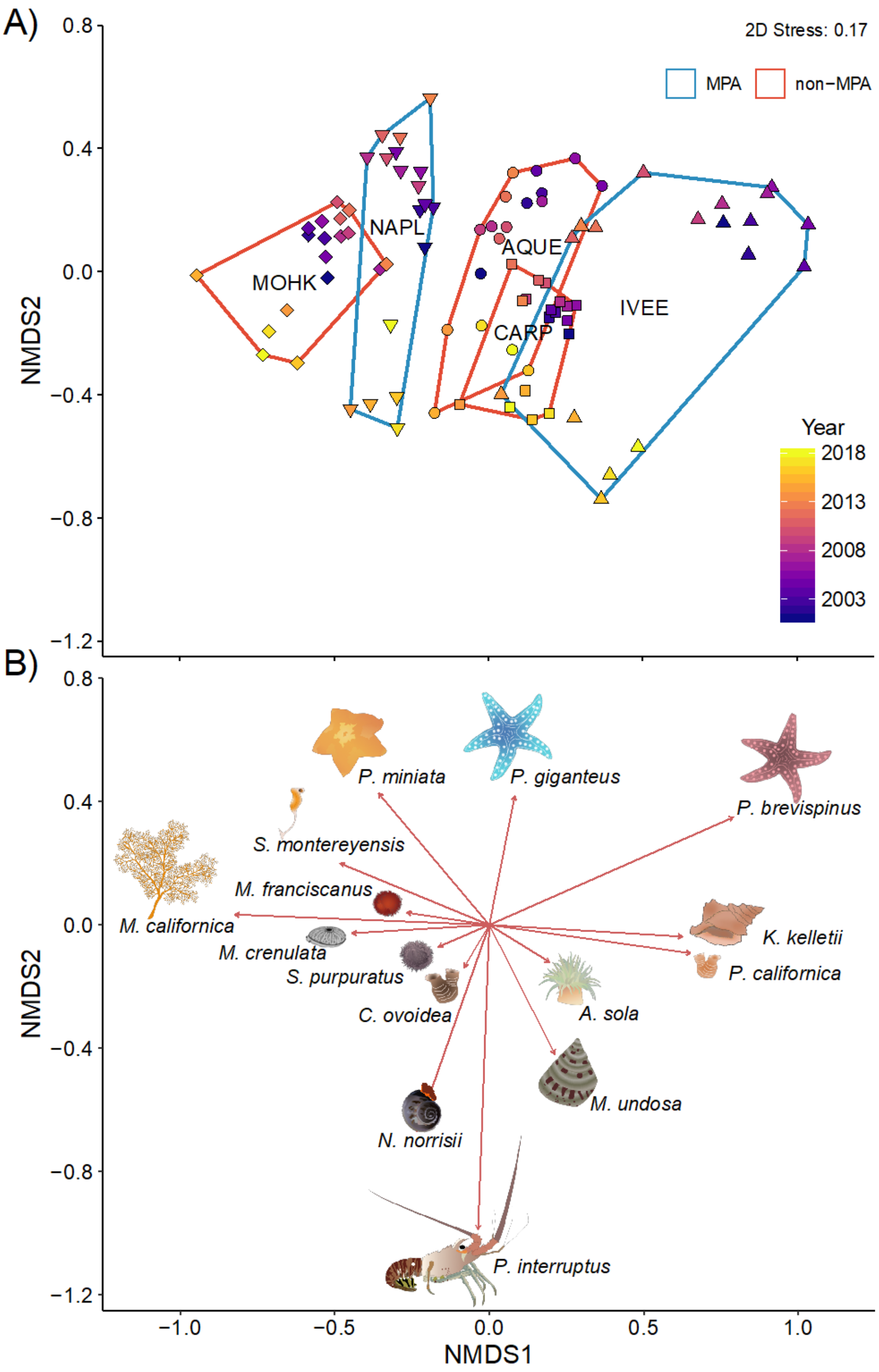


Figure 3. Non-metric multidimensional scaling plots depicting A) yearly assemblage-wide shifts in areal ammonium excretion among sites and B) family-level associations in excretion rates. Magnitude and direction of vectors indicate strength of correlation with ordination axes.

While there were substantial yearly increases in areal N excretion by lobsters since 2012, there were no prominent differences between MPAs and non-MPAs (Two-way ANOVA: Reserve status: $F_{1,\,3} = 0.19$, $P = 0.7$; Year: $F_{6,\,18} = 7.9$, $P < 0.001$; Reserve status*Year: $F_{6,\,18} = 2.2$, $P = 0.1$; Figure 4a). However, yearly changes in lobster population size structure were different between MPA and non-MPAs, as more large-sized individuals were observed at MPAs in most years following designation (Figure 4b; Note that 2012 data were collected before the fishing season in the year MPAs were established). Interestingly, in 2015 more small lobsters were observed at non-MPA sites than MPA sites.

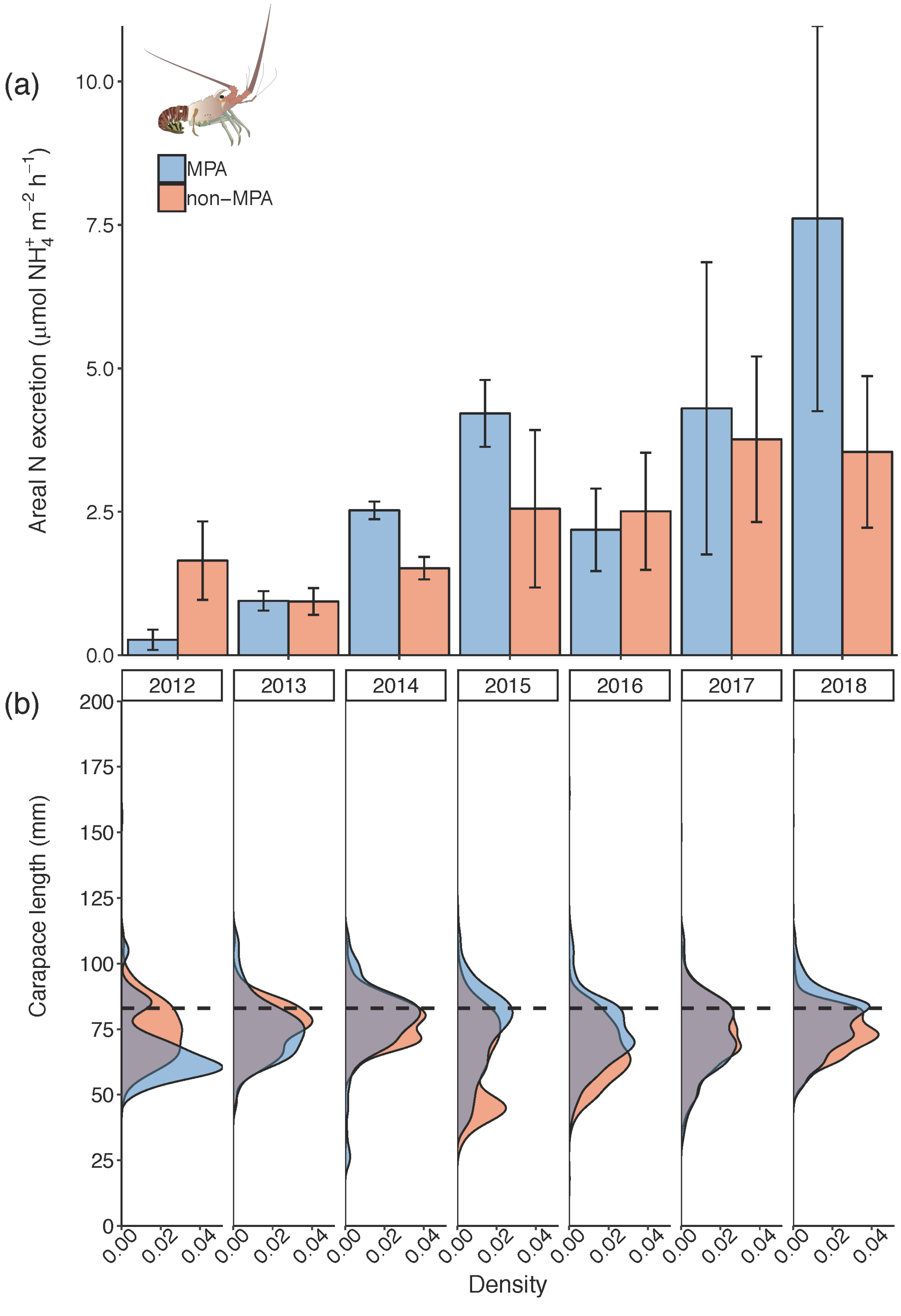


Figure 4. Annual trends in *P. interruptus* (A) ammonium excretion rates and (B) population size structures (carapace lengths in mm) at MPA and non-MPA sites following MPA designation. Values are means averaged over sites with the same MPA designation. Error bars in (A) represent ± 1 SE. Dashed line in panel B depicts the legal carapace length for take (83mm).

4. Discussion

Our study revealed the impacts of climate anomalies, disease, and fishing pressure on kelp forest consumers and links changes in community composition with a region-wide shift in CND. Reef invertebrates contribute substantial amounts of ammonium to kelp forests through their excretions, however changes in the consumer community following these events fundamentally altered this ecosystem function. Following a two-year warming period coupled with a disease outbreak affecting sea stars and sea urchins, reduced inputs of excreted ammonium from reef macroinvertebrates by ~80%. Prior to their demise, sea stars accounted for up to 62% of the ammonium excreted by invertebrates, yet the loss of this source of recycled nitrogen was compensated in part by a concomitant increase in the abundance of spiny lobster associated with the warming and increased protections from fishing, resulting in a shift in recycled nutrient regimes (Figure 5). Climate extremes, disease outbreaks, and fishing pressure increasingly affect coastal ecosystems. Our study provides a novel decadal scale perspective of how changes in consumer abundances in response to these processes can affect ecosystem functioning.

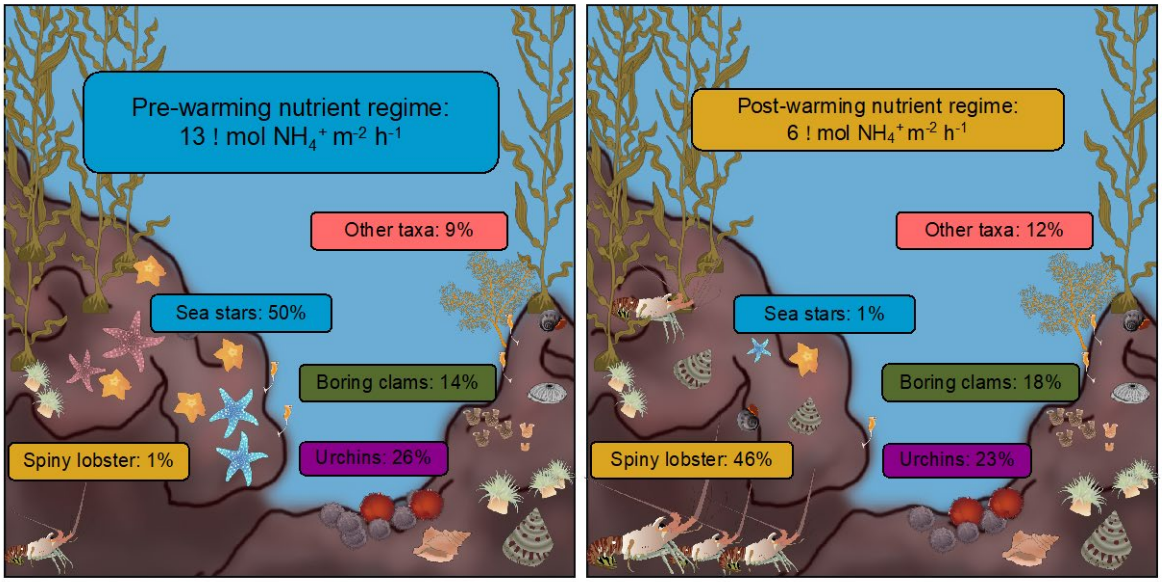


Figure 5. Conceptual diagram depicting shifts in recycled nutrient regimes following the 2014-2015 warming period and designation of MPAs in 2012. Group percentages comprise the mean total areal ammonium excretion for pre- and post-warming periods.

Linked to a densovirus that has been present off the Pacific coast since 1979, the 2013-2015 epidemic sea star wasting disease was unprecedented in magnitude and scale given the number of species affected and its broad geographical extent (Hewson et al., 2014). Anomalously warm ocean temperatures have been implicated as the cause for accelerating its spread and mortality rate in sea stars (Eisenlord et al., 2016) and are consistent with temporal patterns observed at our sites (Reed et al., 2016a). Before the onset of the 2014 warming period, sea star populations were increasing in kelp forests along the Santa Barbara coast. Yet, by 2015 their densities had declined to near zero. Mass mortalities of sea stars could have wide-reaching implications for trophic dynamics and mediation of regime shifts through top-down control (Burt et al., 2018). However, our study also highlights how sea stars may serve as “keystone recyclers” (Small et al., 2011), further defining their role in regulating ecosystem processes. Following mass mortalities of sea stars from our sites, total recycled nitrogen supplied to the reef by invertebrates declined by ~80%, as stars generated the majority of the total in years when they were abundant. Therefore, climate-induced mortality events not only disrupt trophic interactions (Menge et al., 2016; Bonaviri et al., 2017; Burt et al., 2018) but also fundamentally alter consumer-mediated biogeochemical cycling in ecosystems.

Overfishing has drastic implications for coastal ecosystems as widescale removal of consumers disrupts trophic interactions (Dayton et al. 1998), reduces food web complexity (Jackson et al., 2001), and restructures top-down regulation of primary producers (Tegner, 2000). Yet removing consumers also alters the supply and storage of nutrients, which are integral to energy flow in ecosystems (Allgeier et al., 2017). Much of our knowledge of how fishing pressure impacts ecosystems is inferred from the recovery of degraded states following designation of no-take marine reserves (Lester et al. 2009). Worldwide, species of spiny lobster have experienced significant population recoveries following protections from no-take reserves (Kelly et al., 2000; Lipcius et al., 2001; Goñi et al., 2006). In California, populations of *P. interruptus* had been severely reduced by commercial and recreational fishing pressures (Kay et al., 2012). Since designation of two no-take reserves in 2012, we witnessed a 58-fold increase in lobster biomass across our sites, even in unprotected areas. Region-wide increases in spiny lobster may be due to synergies between increased protections from fishing and ocean warming, as they are warm-water associated species (Ling et al. 2009). Indeed, we observed many juvenile lobsters during summer 2014 (Figure 4b), which may indicate a recruitment event resulting from increasing populations of breeding adults and ideal ambient temperatures. Lobsters serve an important trophic role by regulating populations of urchins (Breen & Mann, 1976) presumably influencing the abundance of kelp by keeping populations of important herbivores in check (Shears & Babcock, 2002). Yet, we found that lobsters excrete more nitrogen per gram of biomass than any other invertebrate in our study, with rates similar to kelp forest fish (Bray et al. 1986; Bray et al. 1988), suggesting they also serve critical bottom-up roles in kelp forest nutrient cycling. In our system, lobsters have replaced sea stars as the dominant invertebrate nitrogen recycler and have nearly compensated for the loss of ammonium recycling from sea stars as their populations continue to grow each year. This demonstrates how release of consumers from fishing may mitigate the impacts on nutrient recycling resulting from climate-induced mortality events.

Ammonium is one of the most available N substrate for marine primary producers (Mulholland & Lomas, 2008), and is readily taken up by *M. pyrifera* (Bray et al. 1986; Hepburn & Hurd, 2005) and understory macroalgae (Haines & Wheeler, 1978; Thomas & Harrison, 1987; Young et al., 2009; Pritchard et al., 2015). Giant kelp has a limited capacity to store N (Gerard 1982a) and their growth is sustained only when ambient N concentrations are > 1μM (Gerard 1982b). In southern California, rates of advective nitrate supply easily meet these demands during winter and spring (McPhee-Shaw et al., 2007). Yet, *M. pyrifera* growth rates are often just as high during summer and fall when available nitrate consistently falls below this threshold (Fram et al., 2008; Brzezinski et al., 2013, Rassweiler et al. 2018). Our data demonstrate that benthic consumers supply substanital amounts of ammonium to kelp forests, and their excretion may be particularly important for primary production during the summer when available nitrate is low. Previous work in the same study system detected strong signals of a near-continuous supply of ammonium originating from the reef benthos (Brzezinski et al., 2013), suggesting that benthic invertebrates may be an important and persistent source of ammonium near the benthos. Therefore, it is plausible that consumer-derived nutrients may sustain primary production during periods when advective sources of N are minimal (McPhee-Shaw et al., 2007; Fram et al., 2008).

Research in other kelp forests (Bray et al., 1986; Bray et al., 1988; Hepburn & Hurd, 2005) and temperate intertidal systems (Bracken & Nielsen, 2004; Bracken et al., 2014) have found that consumers enhance nutrient cycling and primary production. Bray et al. (1988) found that benthic communities excreted 25-30 μmol NH_4^+ m^{-2} h^{-1} in kelp forests off Catalina Island, CA. Other published excretion rates from temperate and tropical reef macrofauna generally range between 10-500 μmol NH_4^+ m^{-2} h^{-1} (Bronk & Steinberg, 2008). Our estimates may appear low in comparison, but they are based on an 18-year average that more appropriately depict temporal and spatial heterogeneity in animal biomass and therefore rates of excretion. Indeed, total reef excretion rates had tremendous spatial variability with rates between 0.06-58.6 μmol NH_4^+ m^{-2} h^{-1}. And excretion rates in a given plot can vary by 20-fold over an 18-year period. We focused our study on benthic macroinvertebrates because they comprised the majority of animal biomass on reefs at our sites (Miller et al., 2015; Reed et al. 2016b). Other studies have highlighted the importance of consumers such as fish (Burkepile et al., 2013), zooplankton (Dugdale and Goering 1967), birds (McCauley et al., 2012), and mammals (Roman & McCarthy, 2010), in contributing sources of recycled N to marine ecosystems and are all potentially important in kelp forests (Bray et al. 1986). Future studies aiming to quantify these different sources would benefit from temporally and spatially replicated time series data to account for the high year-round productivity of kelp forests and other coastal marine ecosystems subjected to intermittent supplies of advected nitrate.

Climate- and human-driven regime shifts are frequently detected in long-term studies of aquatic (Daskalov et al. 2007; deYoung et al., 2008) and terrestrial (Ripple et al. 2006; Romme et al., 2011) consumer populations, and have altered important ecosystem functions via modification of top-down and bottom-up mechanisms (Andersen et al., 2009). Our study is unique in that it highlights how anthropogenic defaunation can shift regimes of recycled nutrients and disrupt CND over annual or decadal scales. Many conclusions about the importance of CND are based on studies taking place over one or two field seasons (Burkepile et al. 2013, Allgeier et al. 2013), which do not effectively characterize natural variation in consumer populations or capture important disturbance events that impact consumer communities. Indeed, we saw several major alterations to CND in kelp forests over the course of this study and these transitions between different consumer regimes over time likely occur in ecosystems worldwide (Folke et al., 2004). As aspects of global change continue to alter consumer populations, restructure communities, and lead to altered states, research that fuses empirical excretion models and long-term data will more effectively describe how human drivers impact nutrient cycling and ecosystem function. Consumer regime shifts alter top-down control, but our data suggest that they also impact inputs of limited nutrients necessary for macroalgal production. More evidence that describe recycled nutrient regime shifts in other systems are needed to predict how these impacts alter primary production in a rapidly changing world.

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Appendices

Table S1. Model coefficients (a = intercept, b = slope), R^2 and P values for log-log linear regressions of per capita excretion rates (μmol NH_4^+ h^{-1}) vs. shell-free dry mass (g) for n individuals from 14 benthic kelp forest invertebrate species. The root mean square error (RMSE) depict the model prediction uncertainty in our estimates of per capita excretion rates.

Species	Common name	*n*	Range (wet g)	a	b	R^2	RMSE	*P*
Panulirus interruptus	California spiny lobster	51	57.53 - 653.55	3.71	0.38	0.23	0.34	< 0.001
Pisaster giganteus	Giant sea star	10	85.27 - 297.80	0.96	0.78	0.57	0.34	0.01
Patiria miniata	Bat star	11	10.27 - 116.84	0.02	0.58	0.73	0.24	< 0.001
Muricea californica	California golden gorgonian	18	6.26 - 69.96	-0.99	0.66	0.68	0.31	< 0.001
Megathura crenulata	Giant keyhole limpet	34	47.62 - 220.49	0.55	0.33	0.6	0.11	< 0.001
Norrisia norrisii	Norris's top snail	13	34.00 - 80.78	-2.34	1.25	0.68	0.24	< 0.001
Styela montereyensi	Stalked tunicate	11	5.51 - 17.60	-1.92	0.79	0.55	0.36	< 0.001
Kelletia kelletii	Kellet's whelk	30	4.18 - 341.46	-2.29	0.74	0.89	0.26	< 0.001
Stronglyocentrotus purpuratus	Purple urchin	62	52.04 - 357.69	-2.77	1.03	0.63	0.38	< 0.001
Mesocentrotus franciscanus	Red urchin							
Megastraea undosa	Wavy turban snail	36	3.58 - 507.40	-2.54	0.83	0.79	0.56	< 0.001
Chaceia ovoidea	Wartneck piddock	46	92.51 - 331.09	-10.14	3.04	0.81	0.48	< 0.001
Parapholas californica	Scale-sided piddock							
Anthopleura sola	Starburst anemone	15	4.92 - 43.73	-4.22	0.91	0.82	0.35	< 0.001

Figure S2. Annual means (mean ± SE) of wet biomass averaged across sites (n=5) of common kelp forest invertebrates. MPAs established in 2012 (dashed line). Red band represents 2014-2015 warming event.

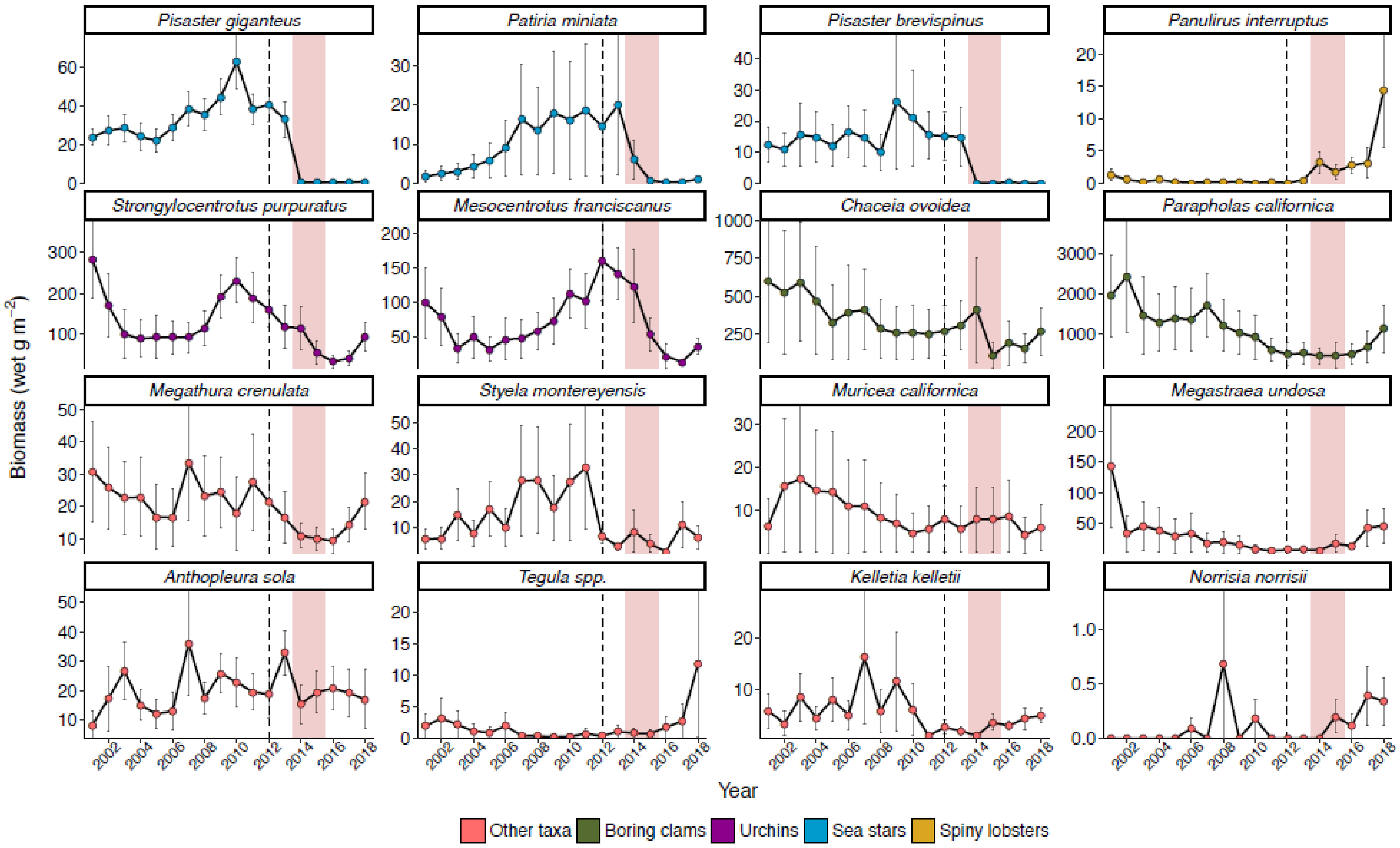
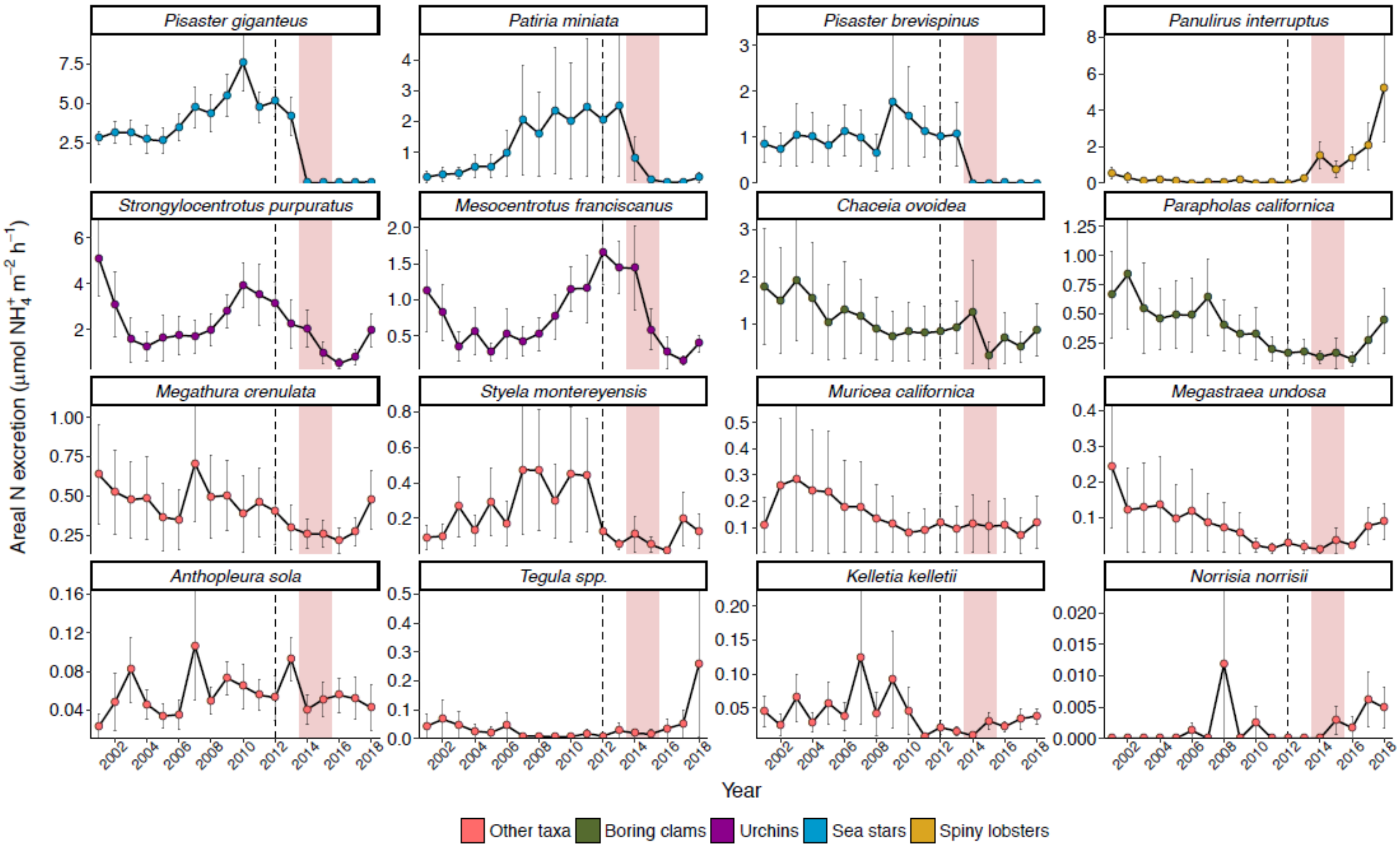


Figure S3. Annual means (mean ± SE) of areal N excretions averaged across sites (n=5) of common kelp forest invertebrates. MPAs established in 2012 (dashed line). Red band represents 2014-2015 warming event.



II. Fishing of spiny lobsters disrupts nutrient hot spots that influence benthic communities

Abstract

Aggregations of consumers can form nutrient “hot spots” that are capable of influencing the abundance, species composition, and growth of primary producers. Ammonium, the major form of nitrogen excreted by aquatic consumers can be particularly important for primary production when other sources of nitrogen are low. However, fishing and other human impacts can alter consumer densities and therefore nutrient supplies and few studies have quantified the direct impacts of fishing on consumer-mediated nutrient dynamics (CND). To help fill this knowledge gap, we conducted a study on the intensively fished California spiny lobster (*Panulirus interruptus*, Randall 1840), which excrete significant quantities of ammonium. Further, lobsters regularly aggregate for several hours each day, giving them the potential to form nutrient hot spots that influence local communities of primary producers. Using a gradient of lobster densities inside and outside of no-take reserves, we investigated the extent to which lobsters form ammonium hot spots and influence the abundance and species composition of benthic macroalgae. We also examined the impacts of fishing on CND by comparing fished and unfished lobster populations over a three-month period that encompassed the transition from closed to open fishing season. Plots with high lobster densities supplied on average ~20 times more ammonium excretion than habitats with low densities, which were twice as variable. Although lobster hot spots did not appear to influence the overall cover of macroalgae, the percent cover by filamentous turfs was 3-fold greater in high excretion plots compared to low excretion plots while the cover of brown macroalgae was significantly lower, suggesting that the nutrients excreted by lobster influence primary producer communities. Fishing reduced the amount of ammonium excreted by lobster nearly 3-fold within the first month of the fishing season and it doubled the temporal variability in the rate of ammonium excreted in in fished but not unfished study plots. Thus, fishing can fundamentally disrupt the size, distribution, and persistence of nutrient hot spots formed by animal aggregations which in turn influences nutrient cycling and community composition.

1. Introduction

Consumers can play important roles in nutrient cycling (Kitchell et al. 1979; McNaughton et al. 1988) and influence the local abundance, growth, and species composition of primary producers (Anderson and Polis 1999, Atkinson et al. 2018). By releasing nutrients like nitrogen and phosphorous through excretion, egestion, and decomposition of their carcasses, consumers serve as important recyclers of locally-derived nutrients within an ecosystem (Kitchell et al. 1979; Vanni 2002), as well as effective importers of nutrients derived from neighboring ecosystems (e.g., from sea to land, from rivers to forests; Anderson and Polis 1999; Wainwright et al. 1998; Holtgrieve et al. 2009). Such consumer-mediated nutrient dynamics (herein: “CND”) are important in structuring communities and contributing to the functioning of many ecosystems (reviewed by Vanni 2002; Allgeier et al. 2017; Schmitz et al.

2010). But human impacts such as overharvesting and habitat loss coupled with global climate change threaten to upend CND because they alter the abundance, size structure, species composition and distributions of consumers. Given that human impacts are increasing with global change, it is imperative to examine their consequences for CND and the ecosystems processes they support (Subalusky and Post 2019).

The importance of CND to the structure and function of ecosystems is likely greatest when and where consumers amass, with these aggregations forming 'hot spots' where nutrient concentrations exceed that of surrounding habitats (McClain et al. 2003; McIntyre et al. 2009). For example, migrating salmon (Holtgrieve et al. 2009; Tiegs et al. 2011), wildebeest (Subalusky et al. 2017), and bison (Knapp et al. 1999; Steinauer and Collins 2001) form large seasonal nutrient hot spots that fertilize streams, forests, and grasslands. Aggregations that form breeding colonies like seabirds (Wainright et al. 1998; Anderson et al. 1999; Otero et al. 2018), pinnipeds (Fariña et al. 2003; Bokhorst et al. 2019), and bats (Duchamp et al. 2010) can serve as near continuous sources of nutrients to nearby habitats for several months. At finer spatial scales, smaller aggregations of fishes and invertebrates can form nutrient hot spots that influence production and community structure in tide pools (Bracken et al. 2004), around coral colonies (Meyer et al. 1983; Holbrook et al. 2008; Shantz et al. 2015), and within seagrass meadows (Allgeier et al. 2013; Layman et al. 2013). Although hot spots can influence the growth and species composition of producers, their importance depends on the magnitude and consistency of nutrients supplied by consumers, as well as the relative ecosystem demand for their nutrients (Subalusky and Post 2019). Myriad factors may influence consumer densities such as habitat quality, access to mates, and predator avoidance (Subalusky and Post 2019; Schmitz et al. 2010), which in turn determine the size and consistency of hot spots.

CND in many ecosystems worldwide is being altered by factors that influence the abundance and distribution of consumers such as climate change, habitat loss/fragmentation, and harvest (Estes et al. 2011; McCauley et al. 2015; Su et al. 2021; Tucker et al. 2018; Barbarossa et al. 2020; Doughty et al. 2015). For example, over the past 140 years, fisheries, land development, dams, and other human impacts to watersheds in the Pacific Northwest USA (Washington, Oregon, Idaho, and California) have led to a ~93% reduction in the amount of marine-derived nutrients delivered to streams and riparian forests by migrating anadromous fish (Gresh et al. 2011). Overfishing Caribbean reef fishes has reduced the supply and storage of nutrients on coral reefs by ~50% (Allgeier et al. 2016), while ocean warming and disease contributed to ~83% reduction in nitrogen recycled by sea stars in giant kelp forests of southern California (Peters et al. 2019). Yet, ocean warming coupled with the establishment of no-take reserves also increased nitrogen inputs from the California spiny lobster, *Panulirus interruptus* (Randall 1940), which compensated for nutrients previously supplied by sea stars (Peters et al. 2019). These examples demonstrate how multiple human impacts act in concert to influence CND, yet studies examining their effects on ecosystems are lacking.

In marine ecosystems, ammonium is the primary form of nitrogen excreted by fish and invertebrates and is readily taken up by benthic macroalgae and phytoplankton (Dugdale and Goering 1967; Haines and Wheeler 1978; Eppley et al. 1979; Thomas and Harrison 1987, Young et al. 2009). Ammonium excreted by consumers can be important in sustaining productivity on tropical coral reefs and seagrass meadows, which thrive in warm, oligotrophic waters (Allgeier et al. 2013; Burkepile et al. 2013; Munsterman et al. 2021). Yet, animal-derived ammonium may also be important in contributing to the high productivity of cooler, more nutrient-rich temperate reefs dominated by forests of large brown macroalgae (i.e. kelps). The high productivity of kelp forests is typically attributed to high concentrations of nitrate advected by upwelling, internal waves and other oceanographic processes (Zimmerman and Kramer 1984; Washburn and McPhee-Shaw 2013), varies substantially among seasons and years (Vadas et al. 2004; Jackson 1977; van Tussenbroek 1989; Haines and Wheeler 1978). Yet, kelp forest macroalgae often maintain year-round growth even when nitrate concentrations are low, leading to suggestions that ammonium recycled locally by consumers may sustain kelp forest production during these periods (Gerard 1982, Brzezinski et al. 2013; Smith et al. 2018). However, we know little about how harvesting can impact animal populations, their impact on CND (but see Allgeier et al 2016), and the potential cascading impacts on benthic communities in this system.

Aggregations of marine fishes and invertebrates are often targeted for harvesting and when this occurs nutrients are effectively removed from the ecosystem rather than recycled (Allgeier et al. 2017). This in turn may cause cascading detrimental effects on primary producers that rely on locally excreted nitrogen to sustain their growth in the absence of other sources of nitrogen. Such may be the case for the extensively fished California spiny lobster which forage at night and consistently aggregate in shelters during the day (Zimmer-Faust and Spanier 1987; Mai and Hovell 2007; Withy-Allen et al. 2013). Our previously finding that spiny lobster excrete significant quantities of ammonium led us to hypothesize that their excretion may be particularly important for primary production by reef macroalgae during periods when nitrate concentrations are low (Peters et al. 2019)

Here we examined the potential for the California spiny lobster, *P. interruptus,* (herein: “lobsters”) to generate hot spots of ammonium that in turn influence the abundance and species composition of reef-associated macroalgae. In Southern California, ammonium from lobsters is likely to be most important during summer through autumn when nitrate concentrations average < 1 µmol L^{-1} (Brzezinski et al. 2013). Lobsters in this region are most intensively fished in autumn (CDFW 2019), and their harvest may reduce the size and/or abundance of ammonium hot spots by reducing their aggregations. We investigated the extent to which lobsters form ammonium hot spots during a three-month period in autumn that encompassed the transition from closed to open fishing season using a gradient of lobster densities in plots established inside and outside of a no-take reserve. Within each plot we estimated rates of ammonium excretion and the coverage of benthic macroalgae to determine whether hot spots formed by sheltering lobsters influenced the abundance and species composition of benthic macroalgae. Specifically, we asked: (1) How do lobster aggregations affect spatiotemporal heterogeneity in ammonium excretion? (2) Does the abundance and species composition of benthic macroalgae differ among plots with different densities of lobsters? and 3) What are the impacts of fishing on ammonium excreted by lobsters?

2. Methods

2.1 Study design and field observations

We conducted our study along the eastern shore of Santa Catalina Island, CA, USA, where lobsters are heavily fished commercially and recreationally (comprising 15.6% of California's reported catch for lobsters in 2019-2020; CDFW 2019). Commercial traps account for 57% of reported lobster catch at Catalina Island while the remaining 43% are caught by hand or hoop nets by recreational fishers (CDFW 2019). Fishing season for lobsters in California begins the first week of October and ends the first week of the following April, and the minimum size for legal take is 82.5 mm carapace length. Fishing of lobsters was central to our questions about their capacity to form nutrient hot spots, therefore we established four 20 m x 20 m fixed plots within the Blue Cavern Onshore State Marine Conservation Area (established 2012; herein "unfished") and outside the reserve boundaries (herein “fished”; Figure 1; Appendix S1 for coordinates). Plots were located in rocky-reef habitat at 3 - 8 m depth with features such as ledges, cracks, and boulders where lobsters took shelter.

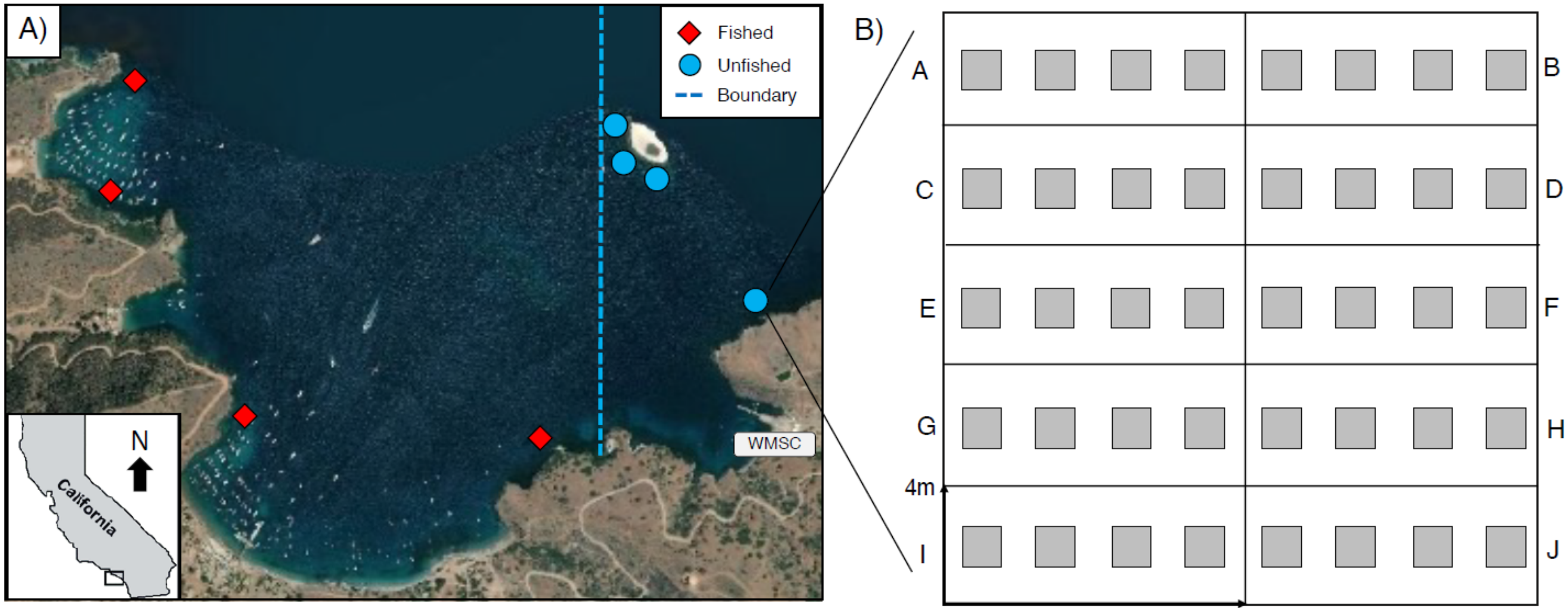


Figure 1. A) Fixed plots located within fished and unfished zones (n=4 each) along the eastern coast of Catalina Island, CA, and a B) schematic of our sampling design where all lobsters were censused within 4m x 10m subplots (A-J; n=10 per plot), and benthic macroalgae were sampled using 1m^2 quadrats (n=4 per subplot).

To determine the extent to which lobsters influence spatiotemporal heterogeneity in ammonium excretion (*Question 1*), we subdivided each plot into ten 4 m x 10 m subplots (A-J in Figure 1b). We recorded the size (estimated carapace length to the nearest mm) and location (distance to the nearest cm along a transect) of every lobster observed within each subplot (Figure 1b). Individual carapace lengths were converted to the carapace-free dry mass of an individual (herein "dry mass") using the power function $M = 1.0 \times 10^{-3}L^{2.914}$ to convert carapace length (L) to wet mass (M) and a wet mass / carapace free dry mass ratio of 15.7 (Reed et al. 2016b). Estimates of per capita dry mass were converted to per capita ammonium excretion rates using power functions developed for a representative size range of lobsters (see below) collected from outside our plots, but within the study region. In order to evaluate whether lobster ammonium excretion alters the abundance or composition of producers (*Question 2*), we visually estimated the percentage cover of benthic macroalgae and different substrate types in each subplot using four $1m^2$ quadrats (grey squares in Figure 1b). Macroalgae were classified as foliose browns, foliose reds and filamentous turfs, and substrate was classified as either rock or unconsolidated (i.e., sand, gravel, and shell rubble). To determine how fishing lobsters affects ammonium excretion (*Question 3*), we conducted our surveys of lobster size and abundance in each subplot three times during the final two weeks of the closed fishing season (September 15, 24, and 27) and twice within the first month of the fishing season (October 12 and November 1).

2.2 Measuring ammonium excretion by lobsters

We measured per capita ammonium excretion rates (µmol NH_4^+ h^{-1} individual^{-1}) from lobsters (n = 119) collected from representative size range of those sampled at our study sites following the methods of Layman et al. (2011) and Allgeier et al. (2013). Lobsters were hand collected by divers, brought to the surface and immediately transferred into 3.8 to 75.0 L polyethylene bags (depending on lobster size) with known volumes of pre-filtered (0.35 µm Whatman GF-filters), UV-sterilized seawater. Bags with lobsters were paired with control bags without lobsters (filtered seawater only) and incubated for ~30 min in insulated containers with ice packs to maintain ambient seawater temperatures (18-20 °C). Following incubations, lobsters were weighed to obtain wet mass for subsequent conversion to dry mass using the relationships described above. Samples collected from incubations were filtered (0.45 µm Whatman GF) into 60 mL amber HDPE bottles and placed on ice for transport to the laboratory for quantification at University of Southern California Wrigley Marine Science Center (WMSC). Following fluorometric methods outlined by Holmes et al. (1999) and Taylor et al. (2007) Ammonium concentrations were determined within 12 hours of collection. Per capita ammonium excretion rates (µmol NH_4^+ h^{-1} individual^{-1}) were determined from concentrations by factoring the bag volume (L) and incubation time (min) of each individual lobster. We accounted for any background ammonium flux in the filtered seawater by subtracting values measured in control bags paired with samples during the same incubation period. Mass-specific ammonium excretion rates were calculated by dividing each per capita excretion rate by individual dry mass (μmol NH_4^+ h^{-1} dry g^1).

To determine how lobster abundance influenced ammonium concentrations near lobster aggregations (*Question 1*), we collected water samples around shelters across a gradient of lobster biomass represented in our study plots (n=13 shelters). Using acid-washed 50mL syringes, we took water samples (within 0.5 m from the bottom) within shelters, and at distances of 0.25, 0.5, 1, 2, and 4 m away from shelters. Samples taken at 4m away served as controls to reflect background concentrations in similar habitats and depth without lobsters. We also counted the number of lobsters in each shelter and estimated their size (carapace lengths). We determined the total biomass of lobsters residing in shelters by converting individual carapace lengths to dry mass using the power function from Reed et al. (2016b) and summing the dry mass of all lobsters within a shelter. Ammonium concentrations of water samples were determined following the same procedure as described for ammonium excretions.

2.3 Data Analyses

2.3.1. Spatiotemporal heterogeneity in lobster ammonium excretion

Lobster excretion data from incubations were used to developed generalized linear models to predict per capita ammonium excretion per unit dry mass for each lobster observed in our study plots (Allgeier et al. 2013; Burkepile et al. 2013;

Peters et al. 2019). Regressions were performed on log-transformed variables to estimate the model slope, intercept, and root mean square error (RMSE), and residuals were visually inspected to ensure assumptions of normality and homoscedasticity were met. Model prediction uncertainty was propagated into final excretion rate estimates using a Monte Carlo procedure. Simulated model coefficients and their 95% confidence intervals were used to calculate per capita excretions 1000 times for each subplot and sample date. We used the standard deviation of these values, which are normally distributed, to calculate the standard error. Monte Carlo iterations and modeling procedures were performed using the *arm* package (Gelman and Hill, 2007) in R (R Core Team 2023).

We used lobster counts, dry mass, and per capita ammonium excretion for each shelter and sample date to developed a simple linear model to predict total ammonium excretion as a function of the lobster dry mass within a shelter. Aggregations were divided into three ranges (each 33rd percentile: low, moderate, and high) according to their shelter lobster dry mass. To determine how total dry mass of lobsters in a shelter influenced ambient ammonium concentrations near shelters, we fit exponential decay functions across each level of total dry mass. Using the *drc* package, we performed t-tests to compare model parameters: y-intercepts (i.e., concentrations within shelters), slopes (i.e., decay rates), and horizontal asymptotes (i.e., distances where concentrations saturate with measured background levels at 4m away). Model residuals were inspected for assumptions of normality and homoscedasticity and no violations were found. Only concentrations within shelters differed with increasing levels of lobster dry mass as there was no effect on rates of decay or the distance at which concentrations approached background levels (see Results). Therefore, we used a single exponential decay function to predict concentration gradients of excreted ammonium around each lobster shelter. We corrected for background concentrations in all modelled outputs for each distance by subtracting the mean ammonium concentration determined from controls collected at 4m from each shelter.

We used a twofold approach to characterize the spatiotemporal heterogeneity of ammonium excretion by lobsters (*Question 1*). First, we used the package *tidyverse* (Wickham 2019) to populate our decay model with the total mass of lobsters within each shelter to generate visual depictions of the size and distribution of ammonium hot spots within each plot on the different sampling dates. Second, we scaled our estimates of ammonium excretion to the area of each subplot (40 m^2) to calculate mean lobster density, biomass (dry g) and ammonium excretion (μmol NH_4^+ h^{-1}) per m^2. Eight out of the 80 subplots consistently had no lobsters and considering we were interested in the spatiotemporal heterogeneity of lobster ammonium excretion we excluded them from our analyses. We calculated the mean and coefficient of variation (CV: mean/standard deviation (μ/σ)) of ammonium excretion for each subplot over the study period (n=5) and categorized them into one of three levels of ammonium excretion (each 33rd percentile: low, moderate, and high, n=24 each). We compared the magnitude and temporal variability (as CV) of across the three levels of lobster ammonium excretion using

One-Way ANOVAs. Post hoc Tukey tests were used to determine differences among levels of ammonium excretion where ANOVAs were significant. We hypothesized that temporal variability of ammonium excretion would decrease with increasing lobster densities. To test this hypothesis, we fit an exponential decay model using the *drc* package and assessed the relationship between mean lobster density and the CV of ammonium excretion for subplots over the study period. Model residuals were inspected for assumptions of normality and homoscedasticity and no violations were found.

2.3.2. Influence of lobster ammonium excretion on benthic macroalgae

Benthic data collected for *Question 2* was evaluated by comparing the mean percent cover of macroalgae in subplots among different levels of lobster ammonium excretion. Percent cover estimates for each of the three dominant groups of macroalgae (foliose browns, foliose reds and filamentous turfs) and for all macroalgae combined were averaged over the four quadrats sampled within each subplot (n= 24 subplots for each level of ammonium excretion). Using the *lme4* package, we fit LMMs to test whether the percent cover of each macroalgal cover varied as a function of ammonium excretion. Plot was included as a random effect to account for correlations between subplots within a plot. Percent cover data were arc-sine transformation prior to model-fitting to meet assumptions of normality and homoscedasticity. We used *emmeans* (Lenth 2020) for post hoc Tukey HSD comparisons among levels of ammonium excretion while controlling for any effect of unconsolidated substrate, which represents unsuitable habitat for macroalgal colonization.

2.3.3. Effects of fishing on ammonium excretion from lobsters

We assessed how fishing influenced ammonium excretion from lobsters (*Question 3*), by comparing differences in lobster size, density and the mean and CV of ammonium excretion among fished and unfished plots immediately before and shortly after the start of the fishing season. This time the CV of ammonium excretion was calculated for subplots across fished and unfished plots within closed and open fishing seasons. For each response variable we fit a linear mixed model (LMM) using the package *lme4* (Bates et al. 2015) with protection status (herein: status) and fishing season (herein: season) as fixed variables and plot as random term to account for repeated sampling over the period of study. Data for density, carapace length, and the mean and CV of ammonium excretion were log10 (+1) transformed prior to model-fitting to meet assumptions of normality and homoscedasticity. Using the *lmerTest* package (Kuznetsova et al., 2017) we analyzed each model with a two-way analysis of variance (ANOVAs) to examine the main and interactive effects of status (fished vs. unfished) and season (closed vs. open) on each variable. No lobsters were observed in two fished plots (CC2 & CC4) on one of the sampling dates during the fished season. These two plots were excluded in the analysis of carapace length given there were no lobsters. Heat maps generated for *Question 1* were used to help visualize the range in the size and distribution and temporal variability of ammonium hot spots along a gradient of lobster densities before and after the start of the lobster fishing season in fished and non-fished plots.

3. Results

3.1. Spatiotemporal heterogeneity in lobster ammonium excretion

Individual dry mass explained 65% of the variation in ammonium excretion (Figure 2a, slope = 0.57; t=14.8l; $p < 0.001$; $R^2 = 0.65$) and an average-sized lobster (~70 mm CL) excreted (mean ± SE) 191.9 ± 9.9 μmol NH_4^+ h^{-1}. Lobsters observed in our plots ranged in size from 48-140 mm CL or 16.8 - 380.9 g dry mass. Total ammonium excretion was highly variable among shelters (96.7- 8457.6 μmol NH_4^+ h^{-1}), but increased linearly with increasing lobster dry mass within shelters (Figure 2b; t=156.8; $p < 0.001$; $R^2 = 0.97$). Ambient ammonium concentrations were twofold greater in shelters with high lobster biomass compared to low biomass (Figure 2c; t-test of y-intercepts: $p < 0.02$ in both cases). Ammonium concentrations outside of shelters decreased by ~50% at a distance of 1 m irrespective of the mass of lobster within a shelter (Figure 2c; t-tests of slopes: $p > 0.3$ in each case), and ammonium concentrations near all shelters converged to background levels at a distance of ~3 m (Figure 2c; t-tests of horizontal asymptotes; p > 0.9 in each case).

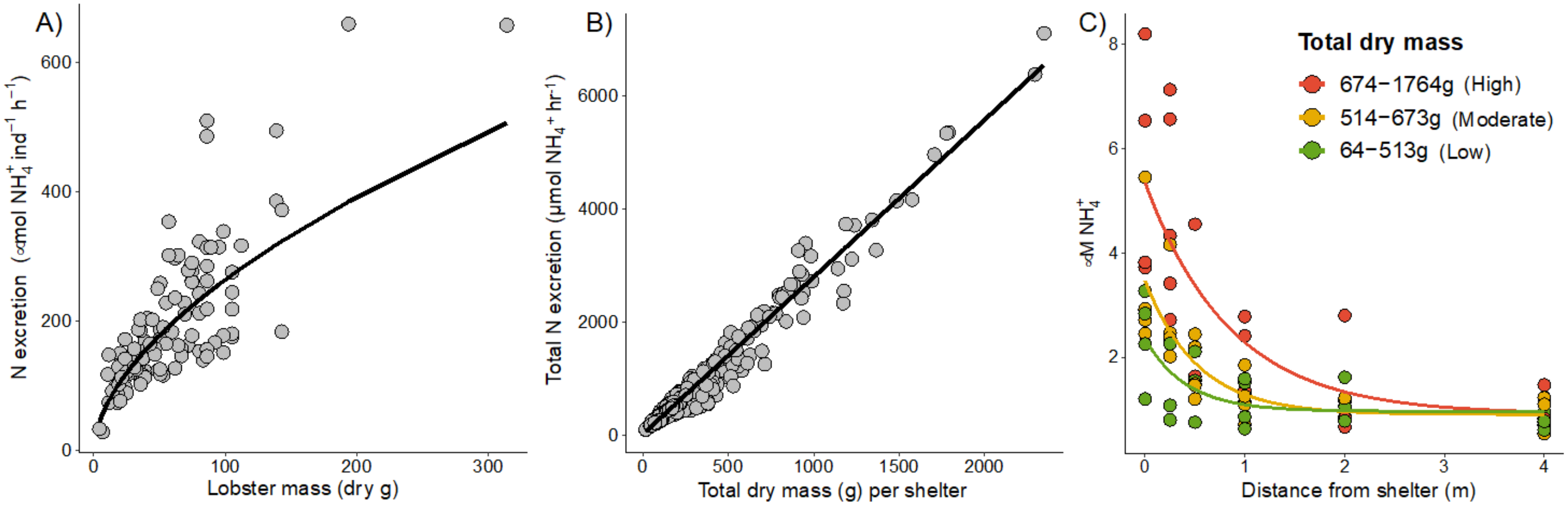


Figure 2. Lobster ammonium excretions were calculated by first A) predicting per capita excretion rates from carapace free dry mass (g) and were summed to estimate B) total ammonium excretion as a function of total lobster dry mass (g) in each shelter (gray dot). Ambient water samples were used to C) compare decreases in ammonium concentrations across shelters with three ranges (each 33rd percentile: low, moderate, and high) of lobster dry mass (g) in shelters.

Shelters consisting of boulders, reef ledges, and crevices housed up to 36 lobsters. Shelters with up to two lobsters (i.e. low biomass) were commonly observed in our plots but were more randomly distributed in our plots than shelters with moderate or high biomass of lobsters (Figure 3). In many cases shelters with differing densities of lobsters were in close proximity of one another (< 1 m) and modelled ammonium excretion estimates show accumulation of ammonium across multiple shelters, while those further apart generated separate supplies of ammonium (Figure 3). Shelters with high lobster biomass generated on average 1613.4 ± 96.9 µmol NH_4^+ h^{-1}, which was ~4 and ~8 times greater than ammonium excreted by moderate and low biomass shelters, respectively (Figure 3).

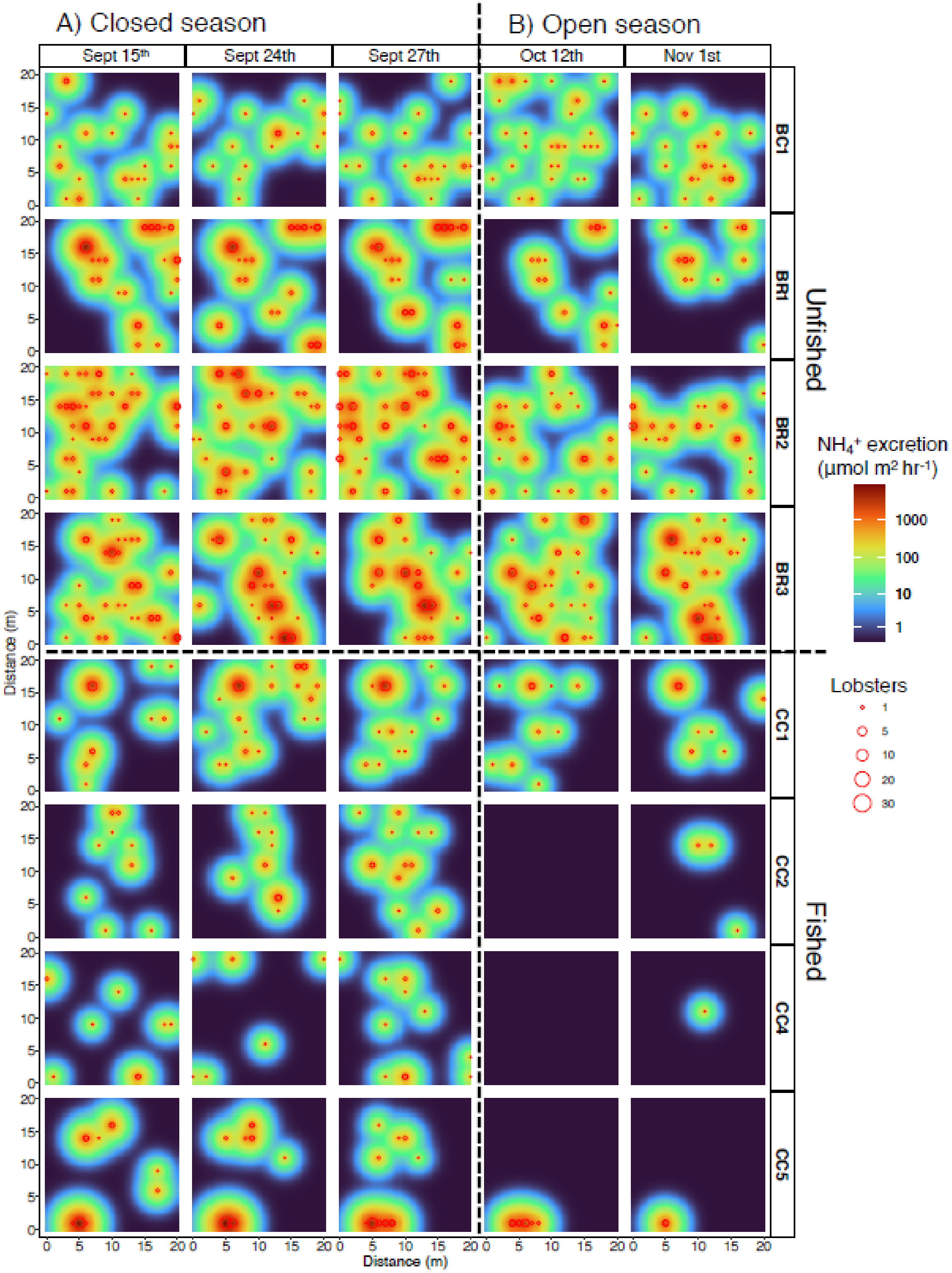


Figure 3. Size and distribution of ammonium hot spots from sheltering lobsters (counts indicated by circle size) during A) 1-13 days before and B) 14 and 33 days after the beginning of fishing season. No lobsters were observed in CC2 and CC4 on 10/12/19.

Subplots often contained multiple shelters with densities ranging between 1-56 lobsters per $40m^{-2}$, thus areal ammonium excretion varied greatly and ranged between 3.4-317.5 μmol NH_4^+ m^{-2} h^{-1} (Figure S1). On average, ammonium excretion in low, moderate, and high excretion subplots ranged between: 0.9-7.9, 8.0-21.5, and 21.6-199.1 μmol NH_4^+ m^{-2} h^{-1}, respectively. Mean ammonium excretion in subplots with high excretion were 72.3 ± 9.1 μmol NH_4^+ m^{-2} h^{-1}, which were ~5x and ~19x greater than moderate and low excretion subplots, respectively. High excretion subplots had, on average, 12.8 ± 1.7 lobsters per $40m^{-2}$ while moderate and low biomass subplots had 2.5 ± 0.13 and 0.8 ± 0.1 lobsters per $40m^{-2}$, respectively. Temporal variation in ammonium excretion of subplots decreased exponentially with increasing lobster density up to a density of 8 lobsters per subplot (Figure 4; slope: $t_{1,69} = 3.5$; $p < 0.001$). Subplots with high lobster densities were more reliable sources of ammonium excretion (level of ammonium excretion: $F_{2,69} = 28.8$; $p < 0.001$), as the CV was more than 2-fold greater in subplots with low excretion (Tukey HSD, $p < 0.001$).

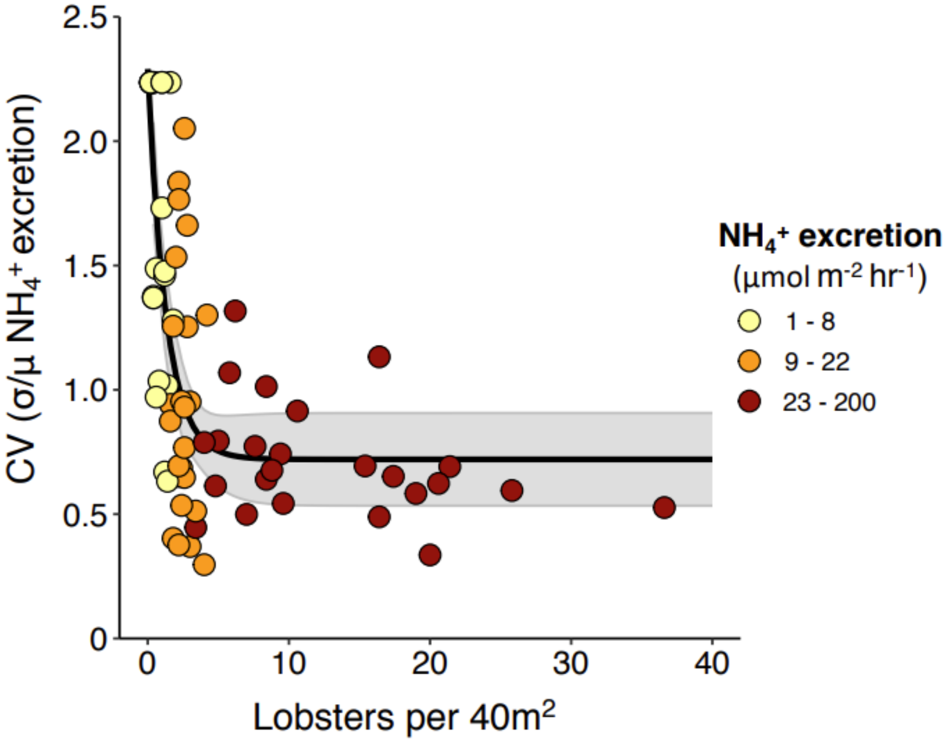


Figure 4. Temporal variation (CV) in ammonium excretion as a function of mean lobster densities over the study period (n=72). Points are subplot means and are colored according to their percentile ranges in ammonium excretion (n=24 subplots for each percentile).

3.2. Influence of lobster ammonium excretion on benthic macroalgae

Macroalgae covered on average ~75% of the benthos in both fished and unfished areas (protection status: $F_{1,69} = 0.2$; $p = 0.68$), with the remainder of the benthos comprised of ~18% unconsolidated substrate, and ~7% bare rock (sessile invertebrate cover was very low in our plots). Cover by all macroalgae did not vary across levels of ammonium excretion (Figure 5; $F_{2,69} = 0.1$; $p = 0.9$), but there were differences in community composition. Foliose brown macroalgae comprised ~57% of benthic cover in subplots with low ammonium excretion, which was 2-fold greater than cover of brown macroalgae under high excretion (Figure 5; $F_{2,69} = 5.8$; $p <$

0.01). Filamentous turfs covered ~13% of the benthos in low ammonium excretion subplots, but were 3-fold greater in high ammonium excretion subplots (Figure 5; $F_{2,69} = 4.1$; $p = 0.02$). Cover of foliose red macroalgae did not differ significantly among subplots characterized by different levels of ammonium (Figure 5; $F_{2,69} = 1.4$; $p = 0.3$).

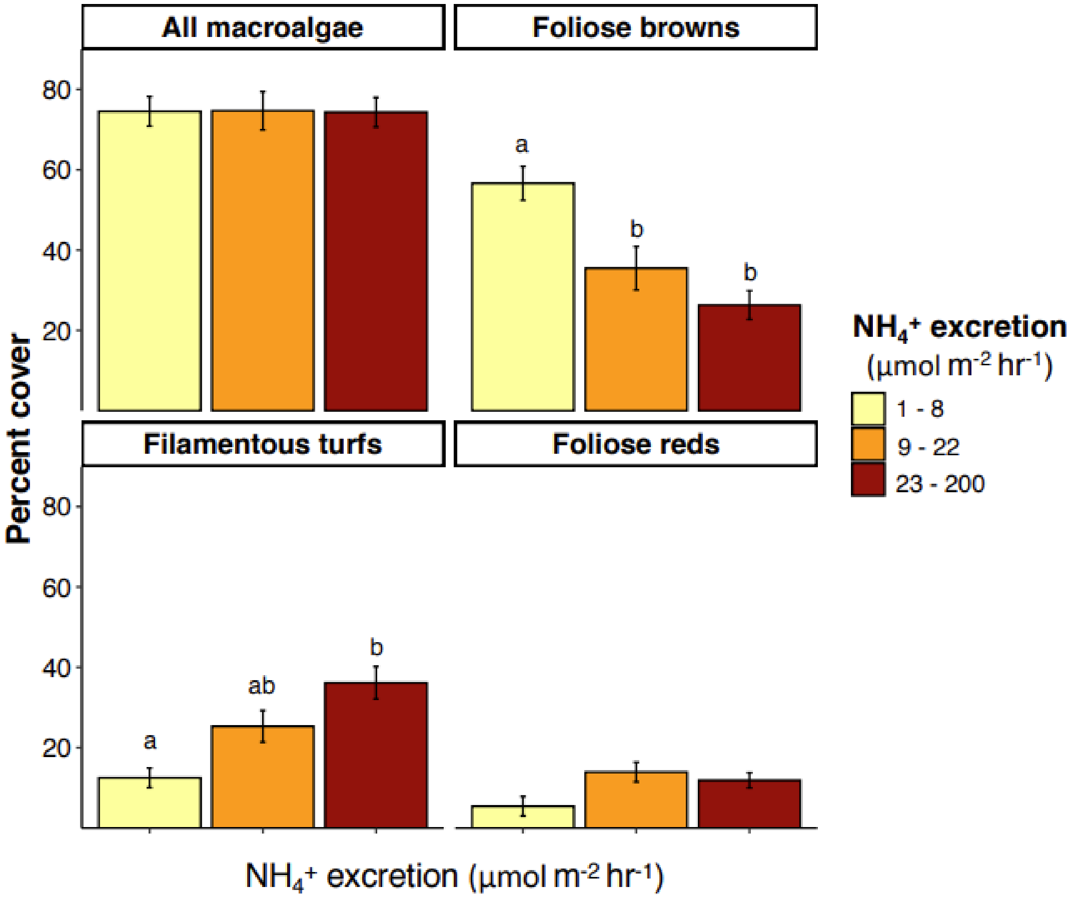


Figure 5. Benthic macroalgal cover (mean ± SE) in subplots divided into three percentiles of ammonium excretion (range reported in figure key). Significant contrasts between estimated marginal means denoted by letters.

3.3. Effects of fishing on lobster nutrient hot spots

Fishing had a strong influence on lobster densities (Figure 6a; season: $F_{1,3} = 18.5$; $p < 0.001$), which were consistently greater in unfished areas (protection status: $F_{1,6} = 15.9$; $p < 0.01$). During closed season, lobster densities were ~3-fold greater in unfished areas and ~5-fold greater after season opened (Figure 6a; Tukey HSD: unfished vs. fished: $p < 0.05$ in both cases). Densities decreased by ~70% in fished areas from closed to open season ($p < 0.001$), but only by half as much (~36%) in unfished areas ($p = 0.04$). Carapace lengths were consistently larger in unfished areas (Figure 2b; status: $F_{1,6} = 9.5$; $p = 0.02$) and did not change between seasons (Figure 6b; season: $F_{1,3} = 3.0$; $p = 0.08$). The effects of fishing on mean lobster densities or carapace lengths did not change with season (Figure 6a-b; protection status*season: $p > 0.2$ in each case). The rate of ammonium excretion from subplots in unfished areas was generally higher than in fished areas, but the magnitude of this difference was ~6 times greater during the open season compared to the closed season (Figure 6c; protection status*season: $F_{1,3} = 5.3$ $p = 0.02$). After season opened ammonium excretion decreased in fished plots by ~71%. Temporal variation in ammonium excretion was generally lower in unfished areas, however during the closed season this difference was ~3 times greater (Figure 6d; protection status*season: $F_{1,3} = 4.3$ $p = 0.04$). Moreover, temporal variation nearly doubled in fished areas once fishing season opened, while it remained unchanged in unfished areas.

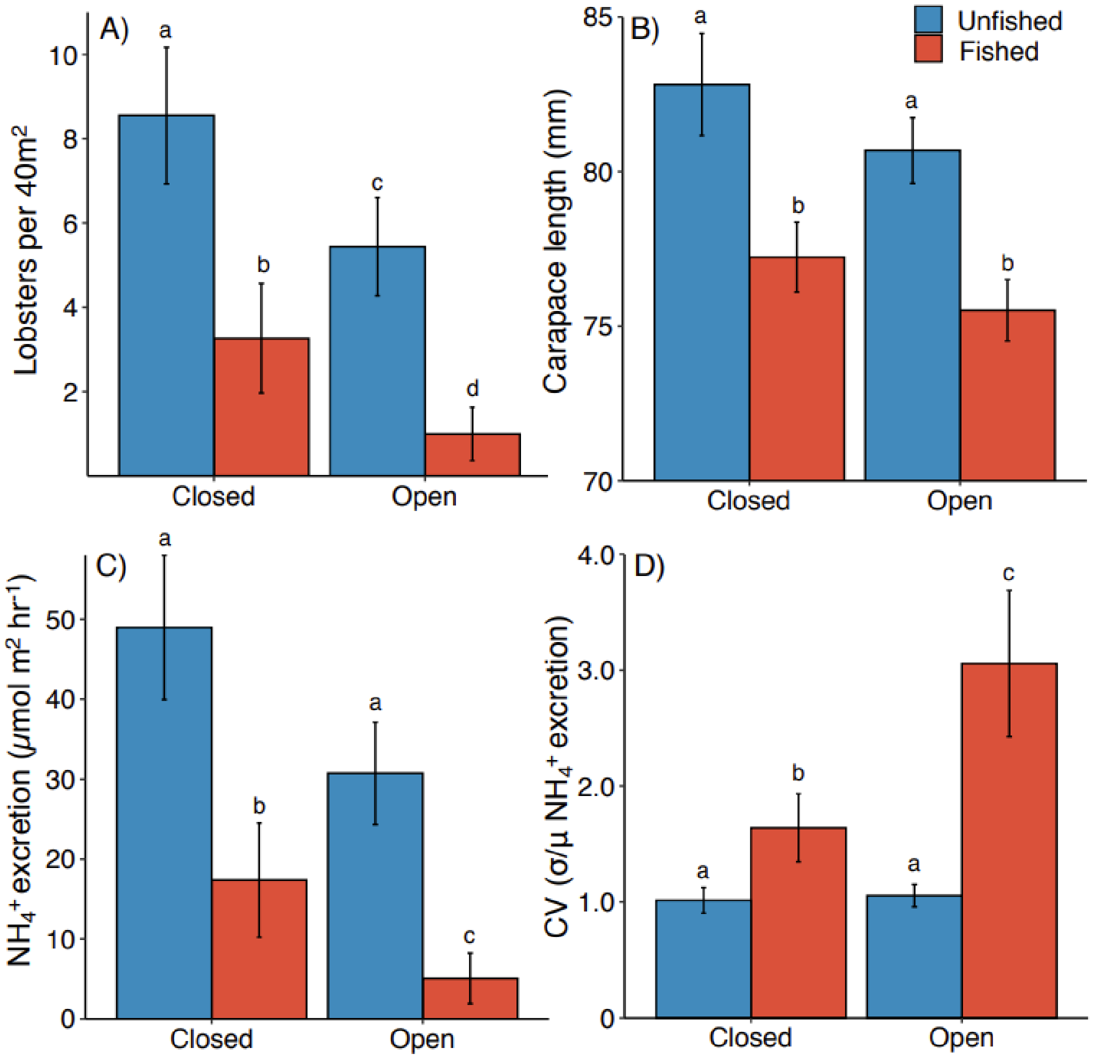


Figure 6. Effect of fishing on lobster a) density, b) carapace lengths, c) ammonium excretion, and d) temporal variation of ammonium excretion (expressed as the CV) during closed and open fishing season in unfished and fished areas. Data are means ± SE averaged over subplots and means with different letters denote significant Tukey contrasts at α =0.05).

4. Discussion

Consumer aggregations can generate large and persistent nutrient hot spots that influence the nutrient landscape and shape community structure (McClain et al. 2003; McIntyre et al. 2008; Duchamp et al. 2010; Shantz et al. 2015). Yet, aggregations of consumers are also often targeted for harvest or are vulnerable to other impacts like habitat degradation and climate change. By focusing our study on the spatiotemporal dynamics of lobster-derived nutrients, we showed that lobster fishing disrupted nutrient hot spots which have the potential to alter the species composition of benthic macroalgae. Ammonium excretion was nearly 20-fold greater and twice as consistent in habitats with high rather than low lobster biomass. Consistently high rates of ammonium excretion may explain compositional differences we found in benthic macroalgae, as filamentous turfs were three times more abundant where lobster excretion was highest while foliose brown macroalgae were twice as abundant where lobster excretion was lowest. Connections between nutrient hot spots and local producer assemblages may be threatened by human impacts like fishing, as we found ammonium excretion decreased by ~70% and became twice as variable in fished habitats within one month of season opening. By contrast, in unfished habitats we found no appreciable difference in the mean or variability of ammonium excretion between fishing seasons. Our work demonstrates how fishing can strongly impact CND by disrupting the formation and persistence of nutrient hot spots, which can influence rates of nutrient cycling and community composition.

Our data reveal the importance of consumer density in mediating the size and distribution of nutrient hot spots. Plots with dense lobster aggregations supplied nearly 20 times more ammonium on average than similar habitats with few lobsters. Similarly, coral heads sheltering high biomass of reef fishes generated ~10 times more nitrogen than those with low biomass of these fishes (Shantz et al. 2015). In both cases, aggregating animals concentrate excretion near their reef habitats while sheltering during the day, driving spatial heterogeneity in nitrogen availability which is a condition required for consumers to establish a nutrient hot spot (McClain et al. 2003). For example, heterogenous distributions of fishes and freshwater mussels drove 47-fold (McIntyre et al. 2008) and 68-fold (Atkinson and Vaughn 2015) variation in nitrogen excretion among various runs in freshwater streams. Likewise, ammonium excretion varied 93-fold across the full range of lobsters in subplots at our sites. Further we show that consumer densities mediate the consistency of nutrient hot spots. Temporal variation of ammonium excretion decreased precipitously with increasing lobster density until reaching higher densities observed at our sites and afterward was on average half as variable as habitats with few lobsters. Perhaps similar thresholds in consumer densities determine the consistency of nutrient hot spots in other systems, yet to our knowledge no other studies have examined this relationship. If the persistence of nutrient hot spots are density dependent then better management practices that preserve minimum sizes of dense aggregations may be set in place to conserve CND.

High rates of nutrient delivery can influence the composition and dominance of producer assemblages, rates of primary production, nutrient storage, and ecosystem function (McClain et al. 2003; Allgeier et al. 2017, Subalusky and Post 2019). For example, seasonal salmon runs transfer marine-derived nutrients to rivers and streams forming hot spots that can extend into riparian and boreal forests influencing nutrient cycling (Holtgrieve et al. 2009), production (Holtgrieve and

Schindler 2011), and community structure (Naiman et al. 2002). Local rates of nutrient delivery from reef fishes can exceed inputs from physical forces (e.g. atmospheric deposition, upwelling; Burkepile et al. 2013), and influence the growth (Meyer et al. 1983; Holbrook et al. 2008) and distribution of corals and benthic macroalgae (Shantz et al. 2015). Like reef fishes, localized hot spots of ammonium excretion from lobsters may explain compositional differences we found in benthic macroalgae. Relative high cover of filamentous turf near high inputs of ammonium excretion from lobsters is consistent with previous reports of turfs flourishing on reefs exposed to nitrogen loading (Gorgula and Connell 2004; Zaneveld et al. 2016). Abundant turf algae can inhibit larger macroalgae such as kelps and fucoid algae (reviewed by Filbee-Dexter et al. 2018), possibly explaining why brown macroalgae were less abundant in areas of high lobster excretion. Differences in benthic cover may also be influenced by other factors like physical disturbance from lobster movement or potentially increased herbivory of macrophytes enriched by nitrogen from excretion as demonstrated in coral reefs (Shantz et al. 2015) and grasslands (Augustine et al. 2003). But, we were unable to test the roles of these mechanisms in influencing the benthic community. Although we found differences in benthic macroalgal composition among different levels of lobster ammonium excretion, additional research is needed to investigate potential mechanisms driving these differences and the potential feedbacks they have on community dynamics and ecosystem functioning.

Spiny lobsters (genus Panulirus) are important consumers that can influence community structure in coastal systems like kelp forests (Shears and Babcock 2002; Ling et al. 2009) coral reefs (Shaver et al. 2020), and seagrass meadows (Cox et al. 1998). Most research has focused on their roles as predators in maintaining prey populations (reviewed in Phillips et al. 2013), with less consideration of their potential to mediate ecosystem nutrient cycles, as is the case with many predators (reviewed in Schmitz et al. 2010). Our work with *P. interruptus* is the first to demonstrate how spiny lobsters can form large and consistent hot spots of ammonium that can influence benthic community structure. Ammonium supplied by *P. interruptus* and other consumers may be important for maintaining production demands on temperate reefs in Southern California when nitrate is low between summer and fall (Brzenzski et al. 2013). Coincidentally, *P. interruptus* migrate to shallow inshore reefs to reproduce during these warm summer months, as their breeding is strongly temperature dependent (Vega Velázquez 2003). Thus, *P. interruptus* may be even more important due to this seasonal overlap in the supply and demand for nitrogen (Subalusky and Post 2019). Moreover, when lobsters forage outside of ecosystem boundaries (e.g. from kelp forest to shallow surfgrass habitats: Robles et al. 1990; Barksy 2001), the nutrients they release around their shelters may serve as subsidies, similar to many reef fishes (Meyer and Schultz 1985), pinnipeds (Fariña et al. 2003), and seabirds (Anderson and Polis 1998 and 1999).

Fishing can profoundly alter ecological communities through major reductions in consumer densities and changes to population size structure (Jackson et al. 2001, McCauley et al. 2015). CND can be disrupted not only by the removal of nutrients from the ecosystem (Laymen et al. 2011; Allgeier et al. 2016), but also through changes in size structure (Munsterman et al. 2020) as excretion rates are predominately determined by body size (Vanni and McIntyre 2016). Nutrient hot spots may be particularly vulnerable as aggregations are often the targets of fishing (Layman et al. 2011). Our work is novel in that we demonstrate how fishing can reduce the size, distribution, and persistence of nutrient hot spots. Within one month of fishing season opening excretions decreased in fished areas by ~70%, yet they remained unchanged in unfished areas. Our data suggest this was driven by reductions in both densities and individual sizes of lobsters persisting in fished areas. Protections from no-take reserves can result in large increases in both the biomass and size of lobsters, even after only five years of designation (Shears and Babcock 2001; Kay et al. 2012). Indeed, lobster densities were three-fold greater in unfished areas during closed season and six-fold greater after season opened. When released from fishing pressure in no-take reserves, many species of spiny lobsters are recovering from overfishing (Davidson et al. 2002; Alzugaray et al. 2018; Cox and Hunt 2005), including *P. interruptus* (Kay et al. 2012; Lenihan et al. 2021), which we have shown previously can increase nutrients to local reefs over time (Peters et al. 2019). Importantly, our study found that fishing doubled the variation in ammonium excretion in fished areas following season opening. For nutrient hot spots to be effective in influencing rates of nutrient cycling or primary production, they must maintain some consistency increasing nutrient availability above the surrounding habitat matrix (McClain et al. 2003). While CND may be reduced by impacts like fishing that remove or redistribute aggregations, more research is needed to understand how impacts affect their persistence.

The relative importance of CND depends on the quality, quantity, timing, and the duration of nutrients supplied by consumers as well as the need by producers in recipient ecosystems (Subalusky and Post 2019). Nutrient hot spots from consumer aggregations are important phenomenon that are integral for the functioning of many ecosystems yet are particularly vulnerable to harvest, as we have demonstrated in our study. Even after a few weeks of fishing in a highly regulated fishery, ammonium excretions by lobster decreased by 3-fold and were twice as variable. Overharvest, habitat destruction, and climate change are responsible for global defaunation that lead to widescale changes in many terrestrial and marine ecosystems (McCauley et al 2015; Estes et al. 2011; Dirzo et al. 2014). Understanding the roles of CND in the Anthropocene are essential for preserving or restoring important ecosystem functions like nutrient cycling or primary production. Our study provides context for these phenomena, demonstrating how harvest can diminish the ability for consumers to concentrate nutrients that may be important for determining community dynamics and maintaining ecosystem processes. Teasing apart the mechanisms that drive or disrupt CND requires investigation at multiple spatiotemporal scales such as the formation and disruption of hot spots like we have demonstrated in our study.

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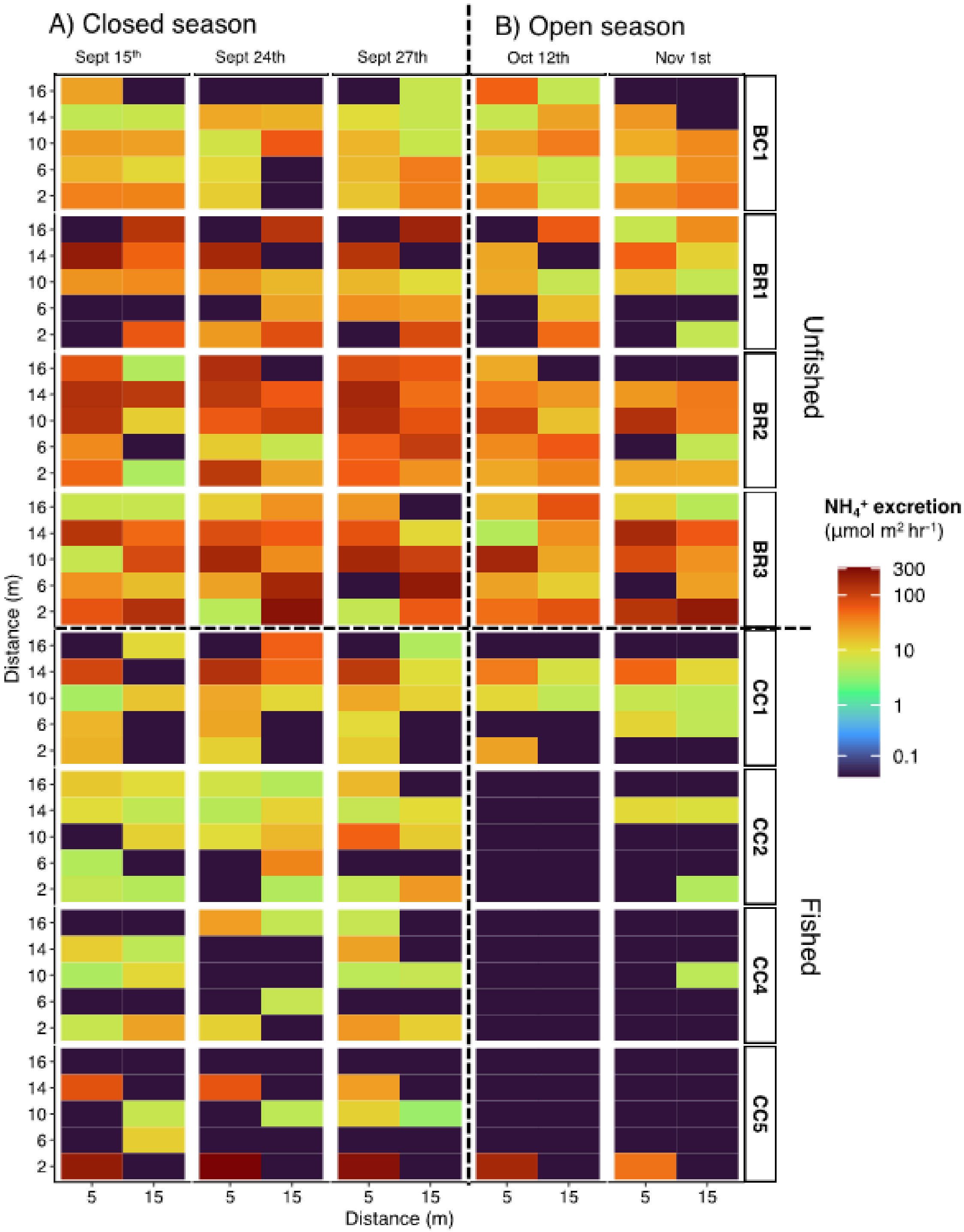
APPENDICES

Table S1. Coordinates of our study plots near the University of Southern California Wrigley Marine Science Center (WMSC) on Catalina Island, California

Status	Plot	Lat	Long
Unfishable	BR1	N33.45205°	W118.48806°
Unfishable	BR2	N33.45100°	W118.48803°
Unfishable	BR3	N33.45061°	W118.48759°
Unfishable	BC1	N33.44752°	W118.48313°
Fishable	CC1	N33.44448°	W118.48980°
Fishable	CC2	N33.44526°	W118.49794°
Fishable	CC4	N33.45260°	W118.50081°
Fishable	CC5	N33.44983°	W118.50165°

Figure S1. Average ammonium excretion from sheltering lobsters in the 10 m x 2 m subplots (n = 10) of each 20 m x 20 m plot (n = 4) in unfished and fished areas on (A) three days immediately before and (B) two days soon after the start of the fishing season (i.e. September 28). The three-character alpha-numeric code for each plot is shown on the right. No lobsters were observed in CC2 and CC4 on October 12.



III. Frequent disturbance to a foundation species disrupts consumer-mediated nutrient cycling in giant kelp forests

Abstract

Structure-forming foundation species facilitate consumers by providing habitat and refugia. In return, consumers can benefit foundation species by reducing top-down pressures and increasing the supply of nutrients. Consumer-mediated nutrient dynamics (CND) fuel the growth of autotrophic foundation species and generate more habitat for consumers, forming reciprocal mutualisms or feedbacks. Such feedbacks are threatened when foundation species are lost to disturbances, yet testing these interactions require long-term studies which are rare. Here, we ask how disturbance affects CND in a marine forest community supported by giant kelp and to what extent this diminishes nutrient feedbacks that help sustain forest primary production during extended periods of low nitrate? We addressed these questions using a 10-yr field experiment where we removed giant kelp annually during the winter to mimic frequent wave disturbance. We paired temporal changes in the forest community in kelp removal and control plots with estimates of taxon-specific ammonium excretion rates (fishes and invertebrates) and nitrogen demand (giant kelp and understory macroalgae) to determine the effects of disturbance on ammonium excretion, nitrogen demand by kelp forest macroalgae, and the percentage of nitrogen demand met by reef fishes and invertebrates. We found that reductions in giant kelp biomass decreased ammonium excretion by 56% over the study period, with most losses due to declines in fishes which excreted the most ammonium and utilize giant kelp as habitat. Apart from a few fish species that dominated CND, most reef-associated consumers were unaffected by disturbance. Disturbance to giant kelp reduced its nitrogen demand 15-fold and increased that of the understory by 30-fold when compared to controls. Consumers supported 11-12% of the nitrogen required by all kelp forest macroalgae in both disturbance regimes. Yet, the same excretion supported an average of 48% of N demand by the understory macroalgae near the benthos, where most reef-associated consumers reside. Our findings suggest that kelp forest CND can be resilient to disturbances and serve as a reliable source of nitrogen that may facilitate the recovery of reef macrophytes.

1. Introduction

As consumers, animals exert trophic pressure on primary producers to alter producer biomass and species composition (Estes et al., 2011; Terborgh, 2015), which in turn modifies the demand of nutrients to fuel primary production (Schmitz et al. 2010). Consumers also increase local nutrient availability by releasing nutrients via excretion and egestion (Vanni 2002; Allgeier et a. 2017; Subalusky & Post 2019). Such consumer-mediated nutrient dynamics (herein CND) are a critical component of nutrient cycling in a wide range of terrestrial and aquatic systems (see reviews by Allgeier et al. 2017, Atkinson et al. 2017, Sitters et al. 2017). CND can significantly influence primary production (Sharitt et al. 2021), yet the importance of consumers as nutrient sources depends on nutrient limitation of primary producers as well as factors that influence population dynamics of producers and consumers (Subalusky & Post 2019).

Foundation species (e.g., trees, kelps, hermatypic corals, grasses) form some of the most productive and diverse ecosystems because they provide habitat, resources, and refugia for myriad consumers (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011). In exchange, consumers can benefit foundation species by reducing competitive and consumptive pressures (Estes & Palmisano 1974) and by increasing the availability of limiting nutrients, as most foundation species are autotrophs or contain autotrophic symbionts (Meyer et al. 1983; Bray et al. 1986; Holbrook et al. 2008; Allgeier et al. 2013). Yet, foundation species can be disproportionately susceptible to disturbances (Ellison et al. 2005; Smale et al 2019), which jeopardize positive relationships with consumers if disturbance events are too frequent or severe and critical habitat is destroyed. Moreover, the loss of foundation species to disturbances may facilitate inferior competitors, which in turn benefit from nutrients supplied by consumers and may keep communities in degraded states (Burkepile et al. 2013). Understanding the impacts form disturbance on foundation species and their effects on consumers and the ecosystem processes they govern is becoming increasingly important given the predicted changes in disturbance frequency and intensity due to climate change (Ummenhofer & Meehl 2017).

Unfortunately, few studies have examined how disturbances (e.g., storms, heatwaves, wildfires) alter CND and their potential impacts on foundation species (but see Peters et al. 2019). Such events are typically only captured by long-term studies that can reveal how these dynamic ecosystem processes vary over seasonal to decadal scales. Kelp forests are ideal systems for examining the impacts of disturbance on CND, as they are among the most productive habitats on Earth (Mann 1973; Brady-Campbell et al. 1984; Reed & Brzezinksi 2009) and support diverse consumer assemblages that play pivotal roles in maintaining community structure and ecosystem function (Steneck et al. 2002; Schiel & Foster 2015, Teagle et al. 2017). Moreover, disturbance is key for influencing kelp forest ecosystems via the removal of kelp and alterations of consumer communities that rely on kelp-generated habitat (Johnson & Mann 1988; Dayton et al. 1992; Tegner et al. 1997; Norderhaug et al. 2020).

Many kelp ecosystems undergo extended periods of nutrient limitation (Chapman and Craigie 1977, van Tussenbroek 1989, Brown et al. 1997, Brzezinski et al. 2013, due to seasonal and internal variability in coastal transport processes (e.g. upwelling, internal waves, coastal eddies) that deliver nitrate-rich water (reviewed in Washburn et al. 2013). Yet, kelps in many regions maintain year-round growth even when these processes are relatively inactive (Vadas et al. 2004; van Tussenbroek 1989; Brzezinksi et al. 2013). Recycled forms of nitrogen (i.e., ammonium and urea) are consistently available (Bray et al. 1988; Peters et al. 2019; Smith et al. 2018) and utilized by kelps and other macroalgae (Haines & Wheeler 1978; Thomas & Harrison 1987; Smith et al. 2020). Ammonium can enhance productivity in temperate systems when ambient nitrate is low (Bracken &

Nielsen 2004; Bray et al. 1986; Pfister et al. 2014), thus CND may sustain kelp growth during these periods. The extent to which CND meets the nitrogen demands of kelp forest macroalgae may be dependent on the extent to which high densities of consumers that regenerate significant quantities of nitrogen rely on kelp for habitat. Yet, frequent loss of kelp from disturbance can reduce ecosystem productivity, biodiversity and food web complexity (Steneck et al. 2002; Byrnes et al. 2011; Castorani et al. 2018), which could fundamentally alter CND, as many kelp forest consumers rely on kelp for habitat (Graham 2004; Miller et al. 2018; Lamy et al. 2020). Resolving whether frequent disturbance disrupts the role of animals as nutrient recyclers through changes in habitat structure is essential for understanding the potential feedbacks between consumers and foundation species across many different ecosystems.

Here, we used a 10-y field experiment to test how frequent disturbance to a foundation species, giant kelp (*Macrocystis pyrifera*), impacts the supply of, and demand for, consumer-derived nitrogen in kelp forests of southern California. Our experiment involved mimicking frequent wave disturbance by removing giant kelp annually in winter from 2,000 m^2 plots, spatially replicated at four sites along ~75km of shoreline. We tracked changes in the biomass of 34 species of fishes and macroinvertebrates in kelp removal ('disturbance') and control plots at each of the four sites and paired these data with taxon-specific ammonium excretion rates measured in the field to estimate the supply of nitrogen excreted by fishes and invertebrates. We also followed changes in the biomass and primary production of giant kelp and 52 species of understory macroalgae for which we estimated their nitrogen demand. We used these data to ask: (1) how does frequent disturbance affect habitat structure, CND, and the demand for nitrogen by macroalgae in giant kelp forests? and (2) To what extent do consumers support the nitrogen demand of kelp forest macroalgae under different disturbance regimes?

2. Methods

2.1. Study System

We focused our study on giant kelp forests occurring on shallow reefs (5-10 m depth) off the mainland coast of the Santa Barbara Channel, CA, USA. Kelp forests in this region support diverse assemblages of benthic invertebrates, fish, and other macroalgae that are strongly affected by *M. pyrifera's* physical modification of habitat (e.g., light, space, water motion) (Byrnes et al., 2011; Miller et al., 2018; Castorani et al., 2018). As per Castorani et al. (2018) we experimentally tested the effects of increased disturbance to giant kelp at four kelp forests (sites) separated by at least 10 km: Arroyo Quemado (120.12 °W, 34.47 °N), Naples (119.95 °W, 34.42 °N), Isla Vista (119.73 °W, 34.39 °N), and Mohawk (119.73 °W, 34.39 °N). The experiment began in winter (January) 2008 at Arroyo Quemado, Mohawk, and Naples and later extended to Isla Vista in autumn (October) 2011. Naples was overgrazed by sea urchins from 2008 until the end of 2010, precluding our ability to remove giant kelp; therefore, we commenced our experiment at this site in winter

(January) 2011. We ceased experimental clearing of giant kelp in winter 2016 at Naples and Isla Vista, and in winter 2017 at Arroyo Quemado and Mohawk.

2.2. Experimental design and kelp forest community sampling.

We manipulated disturbance frequency of giant kelp using a paired design in which two adjacent 40 m x 50 m plots were established at each of the 4 sites (8 total plots), with one plot subjected to annual experimental kelp removal ("disturbed") and the other serving as an unmanipulated control ("control"). In disturbed plots, all giant kelp was removed by divers each winter (mid-February) to simulate large storm-driven waves that disproportionately remove giant kelp during this time of the year (Reed et al. 2011, Bell et al. 2015). Control plots were only subjected to natural disturbances, which on average remove significant amounts of kelp once every 3 to 4 years in our study region (Byrnes et al. 2011).

We hypothesized that CND would be most important for giant kelp forest communities during the summer and fall months when nitrate availability tends to be low at our study sites. Therefore, each summer (July-August) and autumn (September - November), we used non-destructive sampling methods to estimate the standing biomass of kelp forest producers and consumers in fixed 40 m x 2 m transects centered within each disturbed and control plot. Depending on their size and abundance, we counted and measured giant kelp, solitary macroalgae, benthic mobile invertebrates and reef associated fish (i.e., those occurring within 2 m of the bottom) within either the entire transect area, or within six 1 m^2 quadrats uniformly spaced within the transect area. The abundance of sessile invertebrates and understory macroalgae that are impractical to count as individuals were measured as percent cover of the transect area using a uniform point contact (UPC) method at 80 paired points spaced every 1 m on either side of a 1 m wide band centered on each transect. Percentages for each species were determined from the proportion observed out of 80 points in each transect. We converted measurements of abundance and size of all species to dry mass using taxon-specific relationships developed for the study region (see Reed and Miller 2021a for detailed methods).

2.3. Ammonium excretion rates of fishes and invertebrates

We measured ammonium excretion rates of benthic macroinvertebrates (13 species, n=338) and reef fishes (21 species, n=373) common to giant kelp forests in southern California. These species comprised 85-97% of the total standing biomass of macroinvertebrates and fishes surveyed at our sites over the study period (Tables S1 & S2). Excretion data were collected for a representative size range of each species between late summer to early autumn following the methods of Layman et al. (2011) and Allgeier et al. (2013). We collected fishes by hook-and-line, fish traps, barrier nets, or hand nets and mobile invertebrates by hand using SCUBA. Upon collection, specimens were brought to the surface and immediately transferred into 0.1- to 75.0-L polyethylene bags (depending on animal size) with known volumes of pre-filtered (0.35 or 1.0 μm Whatman GF-filters for invertebrates and fishes, respectively), UV-sterilized seawater. Organisms were allowed to incubate at ambient temperature in insulated containers for 30-150 min (depending on animal size). Control bags without animals (filtered seawater only) were also incubated to account for background changes in ammonium concentrations. Water collected from each bag at the end of the incubation period was filtered (0.45 µm Whatman GF) into 20 mL glass scintillation vials or 60 mL amber HDPE bottles and placed on ice for transport to the laboratory for ammonium analysis. Animals used in incubations were weighed wet for subsequent conversion to dry mass (shell-free dry mass for invertebrates) using taxon-specific relationships for invertebrates (Reed et al. 2016) and a conversion factor of 0.26 wet weight to dry weight for fishes (Taylor 1997).

We performed *in situ* incubations for the anemone *Anthopleura sola* (Brandt, 1835) and the boring piddock clams *Chaceia ovoidea* (Gould, 1851) and *Parapholas californica* (Conrad, 1837) because they were difficult for divers to collect without causing them excessive physiological stress or physical harm. Incubations for these species consisted of placing a clear polypropylene chamber over the specimen for 60 min. Chambers (0.7 L volume) had an open bottom (6cm diameter) and were sealed to seafloor with a rubber gasket and a weighted flexible rubber skirt. Trials using rhodamine dye indicated the seal was effective and prevented water from flowing into or out of the chamber (J.R. Peters, personal observation). Incubation chambers were paired with control chambers (ambient seawater only) to account for background changes in ammonium concentration. Following incubation, water samples for ammonium analysis were drawn from each chamber and the study specimen was collected. Water samples and animal specimens were transported to the laboratory and processed as described above.

Ammonium concentrations of all water samples were determined within 12 hours of collection following fluorometric methods described by Taylor et al. (2007). Concentrations were converted to per capita ammonium excretion rates (μmol NH_4^+ h^{-1} individual^{-1}) by factoring the bag/chamber volume (L) and incubation time (min) of each individual. Mass-specific ammonium excretion rates (μmol NH_4^+ h^{-1} dry g^{-1}) were calculated as the excretion rate divided by individual dry mass. We adjusted excretion rates by subtracting ammonium concentrations measured in filtered and ambient seawater as well as changes within control bags/chambers paired with samples during the same incubation period to account for any ammonium detected in controls.

2.4. Time series of kelp forest CND

Species-specific ammonium excretion rates were used to develop generalized linear models at the family level to predict ammonium excretion rate from the dry mass of an individual. Regressions were performed on log-transformed variables to calculate the slope, intercept, and root mean square error (RMSE) for each model (Appendix S1), and residuals were visually inspected to ensure assumptions of normality and homoscedasticity. We used these models to generate a time series of ammonium excretion for the dominant 21 fish and 13 invertebrate species surveyed during our experiment. Specifically, per capita ammonium excretion rates (μmol

NH_4^+ individual^{-1} h^{-1}) were calculated from the dry mass of an individual and multiplied by the mean density of a species to obtain areal excretion rates (μmol NH_4^+ m^{-2} h^{-1}; herein ‘N excretions’) for each species in a plot (Allgeier et al. 2013; Burkepile et al. 2013). Model prediction uncertainty was propagated into our final excretion rate estimates using a Monte Carlo procedure. Simulated model coefficients and their 95% confidence intervals were used to calculate per capita ammonium excretion rates 1000 times for a given species at each site and then converted to N excretions by multiplying by the density of each species. This Monte Carlo approach allowed us to propagate error in predicting individual excretion rates into our estimates of N excretions for each species at the population level. We used the standard deviation of these values, which are normally distributed, to calculate the standard error of N excretion estimates. Monte Carlo iterations and modeling procedures were performed using the *arm* package (Gelman & Hill, 2007) in R (R Core Team 2020).

2.5. Time series of nitrogen demand by kelp forest macroalgae

For each plot, we estimated the summer and autumn nitrogen (N) demand of 63 species of understory macroalgae (including juvenile *M. pyrifera* < 1m tall), based on modeled estimates of their net primary production (Harrer et al. 2021). We used the same procedure to estimate N demand by adult *M. pyrifera* (≥ 1m tall), even though most of its biomass was outside of the area that we surveyed for consumers (i.e., >2 m above the sea floor). Taxon-specific estimates of NPP were generated by combining time series data of standing biomass and hourly bottom irradiance with relationships between irradiance, photosynthesis, and respiration (see Harrer et al. 2021 for details). Specifically, taxon-specific NPP was calculated as the sum of gross production over all daylight hours and respiration over all hours of darkness for each plot for each day of the year over the time series. For adult *M. pyrifera*, NPP was estimated by multiplying the interpolated value of its biomass by the slope of the relationship between biomass and mean daily NPP developed for a given month (Rassweiler et al 2018).

Daily taxon-specific estimates of NPP for species of understory macroalgae (in units of g C m^{-2} d^{-1}) were converted to g N m^{-2} d^{-1} (i.e., N demand) based on the average C:N ratio of each species (Harrer et al. 2021). For adult *M. pyrifera*, we used the 19-year mean C:N ratio measured monthly in adult blades between July and November at Arroyo Quemado and Mohawk (Reed et al. 2021). Taxon-specific estimates of N demand (g N m^{-2} d^{-1}) were converted to μmol N m^{-2} hr^{-1}, and summed for all species of understory macroalgae, and all macroalgae (including adult giant kelp).

2.6. Statistical analyses

2.6.1. Effects of disturbance on kelp forest habitat structure, CND, and nitrogen demand

Because we were interested in the effects of winter disturbance on kelp forest communities during the summer-autumn months when nitrate availability is low (McPhee-Shaw et al. 2007; Brzezinski et al. 2013), we calculated the average from summer and autumn samples (herein: “summer”) to generate annual estimates of biomass, N excretion, and N demand to be used in subsequent analyses below.

Kelp forest habitat structure was defined as the total dry biomass of both giant kelp and understory macroalgae. N excretion was summed for different functional groups of similar species based on their contributions to the total N excretion (ranked in order in Table S2): “Major fishes” (*E. jacksoni, S. pulcher, P. clathratus, O. californica, G. nigricans,* and *R. vacca*), “Minor fishes” (*M. californiensis, S. atrovirons, H. caryi, O. pictus, B. frenatus, C. punctipinnis, O. elongatus, H. semicinctus, E. lateralis, S. mystinus, H. rubicundus, S. chrysomelas, S. carnatus, S. serranoides,* and *S. auriculatus*), “Spiny lobsters” (*P. interruptus*), “Sea stars and urchins” (*P. giganteus, P. miniata, S. purpuratus,* and *M. franciscanus*), and “Minor invertebrates” (*S. montereyensi, M. crenulata, M. californica, C. oviodea, P. californica, A. sola, M. undosa,* and *K. kelletii*). N excretion was also aggregated into following coarser groupings: fishes, invertebrates, and total N excretion (fishes + invertebrates). Similarly, N demand was aggregated into the following groups: giant kelp, understory, and all macroalgae (giant kelp + understory). For each group listed above we calculated their percentage contribution to total biomass, N excretion, or N demand for each year of the experiment. To determine the effects of the disturbance on kelp forest habitat structure, CND, and N demand, we used two general approaches: 1) comparing effect sizes for each response variable over time, calculated as the absolute difference between disturbed and control plots and by 2) assessing how annual changes in each response varied as a function of disturbance treatment.

To determine whether there were changes in the effect sizes for each response variable (biomass, N excretion, and N demand) over time, we fit each with a linear mixed model (LMMs) using *lme4* (Bates et al. 2015) and evaluated changes in effect sizes since the start of the experiment (Time_{eff}), with sites included as random terms to account for correlations between observations over time. Some temporal trends were nonlinear, therefore quadratic functions were specified for giant kelp biomass and Weibull Type I functions were specified for fish and total N excretions. We performed t-tests to assess the significance of time on the effect size of each response variable. Assumptions of normality and homoscedasticity were assessed through visual inspection of model residuals, and in each case were met without need for transformation. We reported both absolute and percent differences as effect sizes of the experiment.

We further characterized the effects of disturbance by evaluating whether annual changes in each response variable varied as a function of disturbance treatment. Separate LMMs were fitted to determine if the response varied by disturbance treatment (“Disturbance”) over the years since the start of the experiment (“Time”). We performed *F* tests with the *lmerTest* package (Kuznetsova et al., 2017) to evaluate the significance of main terms and their interaction. Sites were included as a random term to account for repeated sampling over time (*lme4* package; Bates et al. 2014). Where the interaction with time was not significant, we refit LMMs with the same random term, but with disturbance treatment as the only factor. We used the package *emmeans* (Lenth 2021) to estimate marginal means and/or trends that describe the unbiased effects of disturbance and to calculate treatment contrasts. Response variables were either square-root or log-transformed to meet assumptions of normality and homoscedasticity, which were assessed through visual inspection of model residuals

2.6.2. Contributions of CND to kelp forest N demand

Finally, we determined the extent to which excretion by kelp forest consumers met the N demands of kelp forest macroalgae by dividing total N excretion by the N demand of each algal group: giant kelp, understory, and all macroalgae. Because fish and invertebrates were surveyed close to the benthos (i.e., within 2 m from the seafloor), we hypothesized that their N excretions would have a greater influence on the N demand of the understory than the N demand of giant kelp, whose biomass is mostly above 2m from the seafloor. Nevertheless, we were interested in contributions of N excretion that support each macroalgal grouping among disturbance treatments over the study period. Thus, we evaluated whether the percentage contribution of N excretion to N demand varied due to disturbance treatment over time using the same mixed modeling procedure for testing the interaction between disturbance and time detailed in the previous paragraph. Each response variable was transformed using a log-transformation to meet the assumptions of normality and homoscedasticity.

3. Results

3.1. Effects of disturbance on kelp forest habitat structure

Disturbance had an increasingly negative effect on giant kelp biomass (Fig 1a; $\text{Time}_{\text{eff:}}$ $t_{1,27\,=}$ -2.7, P = 0.03) and was consistently negative five years into the experiment after which giant kelp biomass was on average -427.5 ± 56.9 dry grams or ~62% less in disturbed plots. By the end of the experiment, mean giant kelp biomass had decreased by ~67% in disturbed plots while it increased by ~173% in control plots (Fig S2a; Disturbance*Time: $F_{1,56\,=}$ 6.0, P = 0.02). By contrast, disturbance had only a marginally significant positive effect on understory biomass over time (Fig 1b; Time_{eff}: $t_{1,27\,=}$ 1.9, P = 0.06). Understory biomass was highly variable in both treatments over the experiment, with no temporal trend (Fig S2b; Disturbance*Time: $F_{1,56\,=}$ 2.2, P = 0.14), rather it was on average ~80% higher in disturbed plots for the majority of the experiment (Fig S2b inset; Disturbance: $F_{1,\,56}$ = 15.9, P < 0.001). Disturbance also altered macroalgal composition over the experiment, as the proportion of dry biomass comprised of giant kelp increased from 0.6 to 0.9 in control plots but decreased from 0.6 to 0.4 in disturbed plots (Fig S2c; Disturbance*Time: $F_{1,56\,=}$ 6.9, P = 0.01).

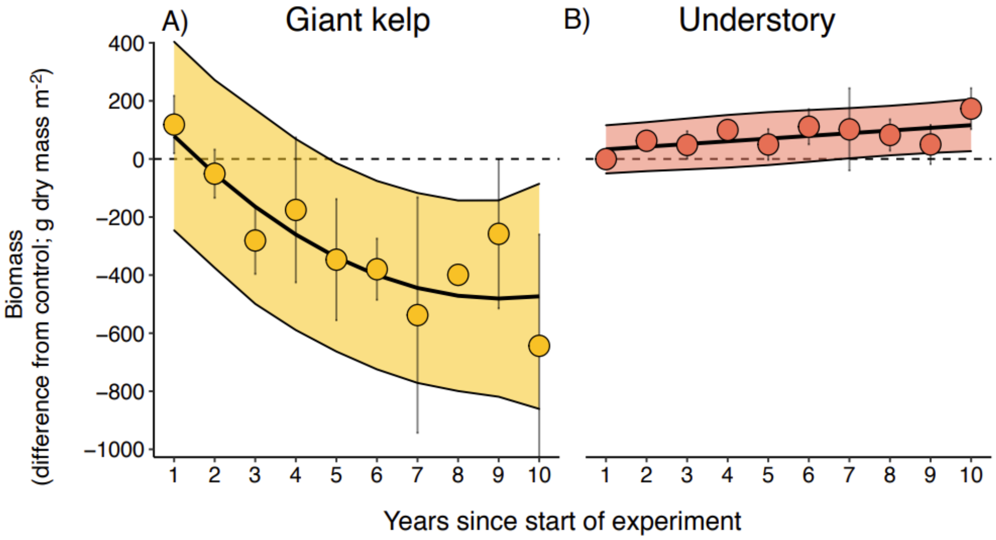


Figure 1. Effect of disturbance on the summer biomass of a) giant kelp and b) understory macroalgae. Points are annual mean treatment differences ± SE. Solid lines are estimated marginal trends with 95% CI. Dashed line at 0 indicates no effect while negative and positive values indicate negative and positive effects of disturbance, respectively.

3.2. Effects of disturbance on kelp forest CND

Total N excretion was similar among both treatments at the start of the experiment, but by the end it decreased 2.0-fold in disturbed plots while it remained unchanged in controls (Fig 2; Disturbance*Time: $F_{1,56} = 4.7$, $P = 0.03$). Fishes drove much of this variation over time, as they comprised on average ~68% of total N excretion at our sites and their excretions decreased in disturbed plots by 2.4-fold while remaining unchanged in control plots (major + minor fishes in Fig 2; Disturbance*Time: $F_{1,56} = 4.7$, $P = 0.03$). N excretion by major fishes decreased by nearly twofold in disturbed plots but increased by twofold in control plots (Fig 2; Disturbance*Time: $F_{1,56} = 9.1$, $P < 0.01$). Disturbance had no effect on minor fish N excretion (Fig 2; Disturbance*Time: $F_{1,56} = 0.2$, $P = 0.7$), yet it decreased by 2-3-fold in both treatments over time (Time: $F_{1,56} = 4.3$, $P = 0.04$).

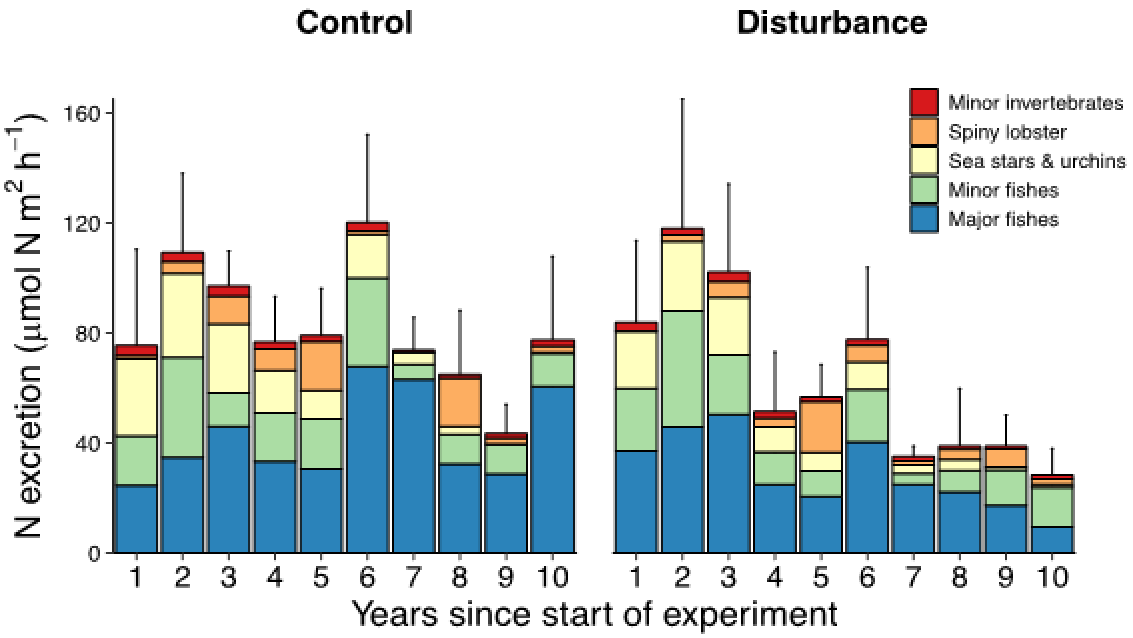


Figure 2. Annual variability in kelp forest in control and disturbance plots over the course of the kelp removal experiment. Values are summer means (mean ± SE) of ammonium (N) excretions of kelp forest consumers averaged across sites (n=4). Taxa in stacked bars are grouped in order of their contribution to total ammonium excretions.

Invertebrates comprised on average ~32% of total N excretion at our study sites, and their excretion did not vary by disturbance treatment (Fig 2; Disturbance*Time: $F_{1, 56} = 0.3$, $P = 0.6$), however they decreased by 3-4-fold in both treatments by the end of the study (Time: $F_{1, 56} = 20.3$, $P < 0.001$). Trends in total invertebrate N excretion were driven mostly by patterns in excretions by sea stars and sea urchins, whose excretion decreased by ~95% over the study period (Fig 2; Time: $F_{1, 56} = 64.6$, $P < 0.001$). Spiny lobster N excretion were also unaffected by disturbance (Fig 2; Disturbance*Time: $F_{1, 56} = 0.3$, $P = 0.6$), however there were 10-17-fold increases across both treatments over the experiment (Time: $F_{1, 56} = 13.3$, P

< 0.001). Minor invertebrates only contributed ~3% to the total N excretion, but decreased by nearly 3-fold in both treatments (Time: $F_{1, 56} = 14.0$, $P < 0.001$).

Effects of disturbance on fish N excretion were not apparent until 4-5 years into the experiment after which fish N excretion were 3-fold less than controls (Fig 3a; $\mathrm{Time}_{\mathrm{eff}}$: $t_{1,27} = -2.4$, $P = 0.02$). Fish N excretion steadily declined in disturbed plots during the experiment, but showed no significant temporal trajectory in control plots (Figure S2c; Disturbance*Time: $F_{1, 56} = 5.4$, $P = 0.02$). Effects of disturbance on invertebrate N excretion were increasingly positive over time, but only marginally significant (Fig 3b; $\mathrm{Time}_{\mathrm{eff}}$: $t_{1,27} = 1.9$, $P = 0.06$). Over the course of the experiment disturbance drove nearly 8-fold decreases in total N excretion relative to controls (Fig 3c; $\mathrm{Time}_{\mathrm{eff}}$: $F_{1,27} = -2.3$, $P = 0.03$), or by -5.6 µmol N m^{-2} h^{-1} (slope in Figure 3c) each year.

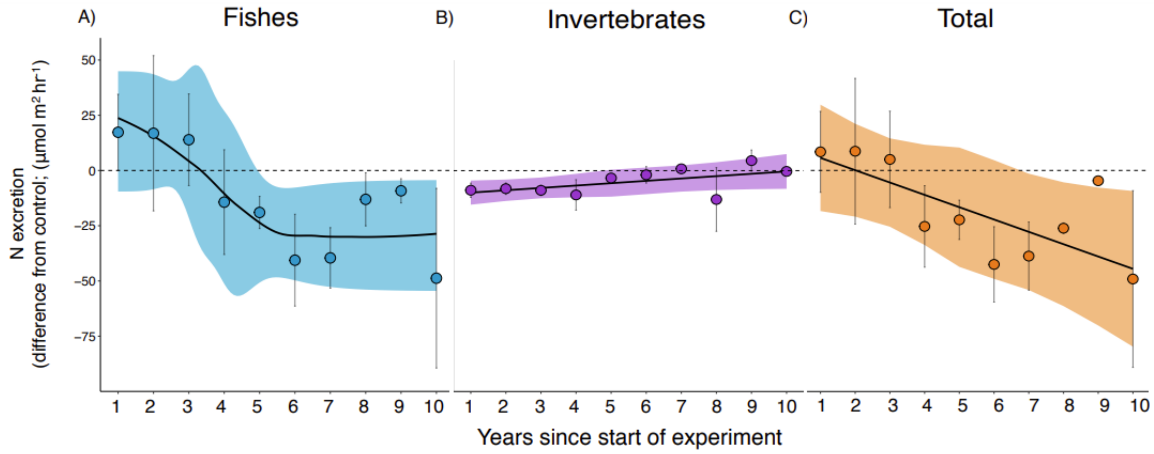


Figure 3. Effect of disturbance on N excretion by a) fishes, b) invertebrates, and c) their total. Points are annual mean treatment differences ± SE. Solid lines are estimated marginal trends with 95% CI. Dashed line at 0 indicates no effect while negative and positive values indicate negative and positive effects of disturbance, respectively.

3.3. Effects of disturbance on kelp forest N demand

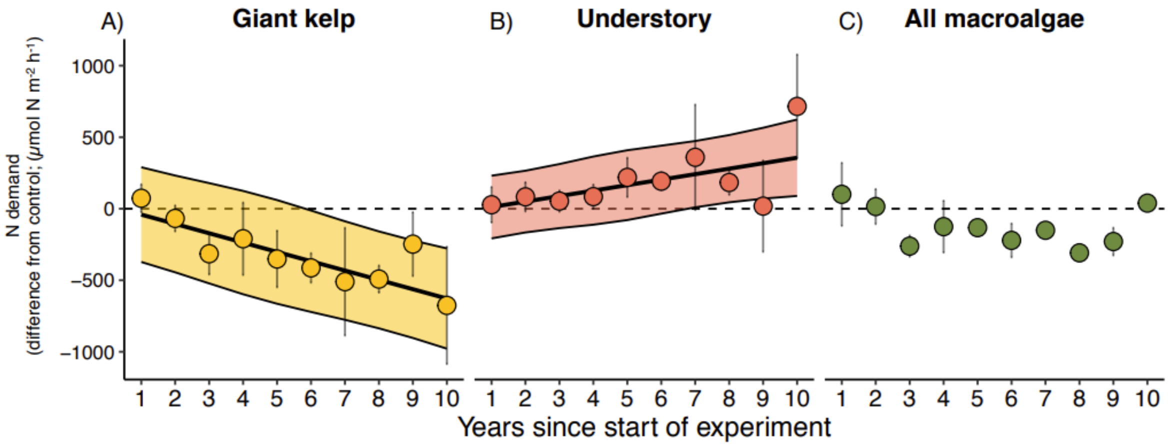


Figure 4. Effect of disturbance on the nitrogen demand of a) giant kelp, b) understory, and c) all macroalgae over the study period. Points are annual mean treatment differences ± SE. Lines are estimated marginal mean trends over time. Dashed line at 0 indicates no disturbance effect while negative and positive values indicate negative and positive effects, respectfully.

Disturbance decreased giant kelp N demand by ~15-fold by the end of the experiment (Fig 4a; $\text{Time}_{\text{eff:}}$ $t_{1,27} =$ -3.6, $P < 0.01$), or by -65.2 µmol N m^{-2} h^{-1} (slope in Figure 4a) each year. Such a strong effect was due to 2.3-fold decreases and 2.4-fold increases in disturbed and control plots, respectfully (Fig S3a; Disturbance*Time: $F_{1,56} =$ 6.2, $P = 0.01$). Conversely, disturbance to giant kelp drove ~30-fold increases in N demand by understory macroalgae relative to controls over time (Fig 4b; Time_{eff}: $t_{1,27} =$ 2.3, $P = 0.03$), increasing annually by 38.3 µmol N m^{-2} h^{-1} (slope in Fig 4b). Increases in N demand of the macroalgal understory were driven by 10 species whose N demand increased between 29-123.1% in disturbed plots relative to control plots over the 10-year experiment (Table S3). Disturbance had no effect on the N demand of all macroalgae over time (Fig 4c; Time_{eff}: $t_{1,27} =$ -1.5, $P =$ 0.15), as there were no treatment differences over the entirety of the study (Fig S3c; Disturbance*Time: $F_{1,56} =$ 6.2, $P = 0.01$).

3.4. Contributions of consumer excretion to kelp forest N demand

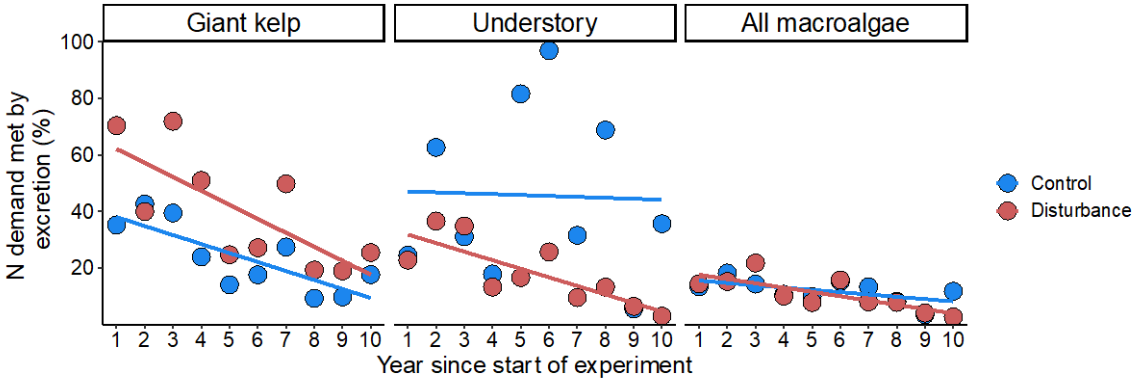


Figure 5. Percent of understory nitrogen demand supported by excretion in disturbance (red) and control (blue) plots over the study period.

As a consequence of the rapid decline in the biomass and N demand of giant kelp in disturbed plots relative to control plots (Figures 1a, 4a), the contribution of consumer excretion to the N demand of giant kelp in disturbed plots was consistently higher than that in control plots, averaging 42.8% and 25.6%, respectively during the experiment (Fig 5a, Disturbance: $F_{1,54} = 7.6$, $P < 0.01$; Disturbance*Time: $F_{1,56} = 0.66$, $P = 0.42$). Consumers initially supported ~31% of understory N demand in disturbed plots, which deceased to ~8% by the end of the experiment (Fig 5b; Disturbance*Time: $F_{1,56} = 4.4$, $P = 0.01$) as understory biomass increased gradually over time relative to control plots (Fig 1b; Time_{eff}: $F_{1,27} = 3.6$, $P = 0.06$). By contrast, the N demand of the understory met by consumer N excretion in the control plots varied substantially over time averaging 46% with no directional trend (Fig 5b). The strong and opposite effects of giant kelp on understory and consumer biomass likely accounted for there being little difference between disturbed and control plots in the percent of the N demand of all macroalgae supplied by excretion (12.4% and 11.9 % for disturbed and control plots, respectively (Fig 5c; Disturbance: $F_{1,56} = 0.6$, $P = 0.45$)).

4. Discussion

Our study reveals how frequent disturbance to a foundation species can diminish CND though declines in the abundances of closely associated consumers, thereby reducing nutrient sources that could otherwise help to sustain primary production. Ammonium recycled by fishes and invertebrates is an important nitrogen source utilized by kelp forest macroalgae (Haines & Wheeler 1978; Thomas & Harrison 1987; Smith et al. 2020), yet major reductions in giant kelp biomass following disturbance lowered consumer excretions by ~56% over the 10-year period. Nearly all of the losses were due to declines in fishes, which supplied ~68% of the recycled ammonium and typically rely on giant kelp as habitat (Holbrook et al. 1990; Schmitt & Holbrook 1990; Allen 2006). Despite reductions in excretion from major fishes, most consumers at our sites were unaffected by disturbance and their nutrients could support on average ~43% of the nitrogen demand by giant kelp in disturbed plots. Conversely, consumer N excretion represented ~46% of nitrogen demand by the understory in plots where giant kelp was left undisturbed. Under both disturbance regimes, consumers supported 11-12% of the nitrogen required by kelp forest macroalgae, regardless of changes to habitat structure and CND. Thus, reef-associated fishes and invertebrates appear to be resilient and reliable source of ammonium that may help facilitate recovery of macrophytes following disturbance events.

Species identity and diversity are likely important determinants for the resilience of CND in kelp forests and other ecosystems that undergo periodic disturbances. Standing biomass alone does not account for species-specific traits like trophic position, foraging behavior, and movement that ultimately determine rates of nutrient excretion (Elser & Urabe 1999; Vanni & McIntyre 2016). Reef fishes recycled ~68% of ammonium in kelp forests yet accounted for only ~10% of total consumer biomass. Of those fishes, only six species were negatively impacted by disturbance events, yet they contributed 51% of the ammonium excretion at our sites. Therefore, a few key species with high excretion rates which closely associate with foundation species may dominate CND, yet may also be more vulnerable to disturbances. Indeed, frequent disturbance to giant kelp in the same study system has been shown to lower food web complexity due to decreases in the abundances of fishes and invertebrates at higher trophic levels (Byrnes et al. 2011; Castorani et al. 2018). Diverse consumer assemblages may buffer the effects of disturbance on CND as some species may not rely on foundation species for essential habitat. Such was the case in our study, as 84% of consumers were unaffected by losses of giant kelp, suggesting that kelp forest CND may be resilient to these disturbances. However, the magnitude of nutrient inputs by consumers may depend on the impacts from multiple stressors like ocean warming, fishing, and disease (Peters et al. 2019; Munsterman et al. 2021; Allgeier et al. 2017). For example, four species of sea stars and urchins supplied up to 40% of total N excretion in both disturbance regimes before ocean warming and outbreaks of disease drove ~95% regional declines in their abundances (Peters et al. 2019). And following the abolishment of fishing at two of our study sites in 2012, ammonium excretion by spiny lobsters increased by up to 17-fold in both disturbed and control plots. Spiny lobsters and fishes had the highest mass-specific excretion rates and thus supplied more ammonium per gram of biomass than most invertebrates. Therefore, evaluating species contributions to CND would better inform management to preserve important ecosystem functions like nutrient cycling.

As a structure-forming foundation species, giant kelp provides habitat to consumers throughout the water column (Schiel & Foster 2015) and our estimates of CND do not include inputs from consumers within giant kelp holdfasts, in the midwater column, or in the canopy near most of the kelp fronds. Reed et al (2006) found reef fishes within 2 m of the bottom accounted for ~44% of all fish (by density) in kelp forests off southern California, while midwater and canopy fishes accounted for 36% and 20%, respectively (Reed et al. 2006). Thus, we are likely underestimating the supply of nutrients from fishes by up to ~50%. Given that reductions in giant kelp biomass led to over 2-fold reductions in fish N excretion at our sites, impacts to midwater and canopy fishes that are more closely associated with kelp would likely be even more severe. We also did not account for inputs from zooplankton that excrete daily pulses of nitrogen throughout the water column (Hernández-León et al. 2008) or for epifaunal consumers, such as fouling bryozoans and hydroids, that can supply individual kelp blades with up to 122% of the demand needed for growth (Hepburn and Hurd 2005). Moreover, we did not factor in sources of urea, which can be an additional source of nitrogen from fishes and invertebrates (Weihrauch et al. 2009), as well as from the breakdown of uric acid excreted by birds and marine mammals (Bokhorst et al. 2019; Otero et al., 2018), and is readily taken up by giant kelp at our study sites (Smith et al. 2018, 2020). Thus, when one considers the full suite of animals that rely on kelp as foundation species, the amount of nitrogen excreted by consumers in kelp forests as well as its contribution to sustaining macroalgal productivity is likely to be considerably higher than our estimates suggest.

Giant kelp's limited capacity to store nitrogen (Gerard, 1982b) requires it to have a near continuous supply of nitrogen to support its year-round growth (Brzezinski et al. 2013). Modeling studies indicate that nitrate concentrations in southern California in the summer and autumn are inadequate to support its growth and nitrogen demand measured during this time of year (Gerard, 1982a; Fram et al. 2008), suggesting other forms of nitrogen sustain it during periods of low nitrate availability (Gerard 1982b, Brzezinski et al 2013; Smith et al 2018). Ammonium, the dominant form of nitrogen recycled by kelp forest consumers, is one of the most available and metabolically efficient forms of nitrogen for marine primary producers (Mulholland & Lomas, 2008), including *M. pyrifera* (Haines and Wheeler 1978; Bray et al 1986; Smith et al. 2018) and understory macroalgae (Thomas & Harrison, 1987; Young et al., 2009; Pritchard et al., 2015). Our data show that during the nitratedepleted summer and autumn ammonium excreted by consumers living near the sea floor was sufficient to support 11-12% of the N demand by all kelp forest macroalgae throughout the entire water column.

Competitors capitalize on resources (e.g., space, light, nutrients) when dominant foundation species are removed by disturbances (Amarasekare 2003). This occurs in many kelp ecosystems when waves remove canopy-forming kelps, and understory macroalgae proliferate with increased light and space on the reef (Toohey et al. 2007; Harrer et al. 2013; Pessarrodona et al. 2019; Norderhaug et al. 2020). Indeed, giant kelp removal yielded an ~81% increase in understory biomass at our sites and comprised more than ~60% of total macroalgal biomass by the end of the experiment. Although consumer N excretions were reduced by the loss of giant kelp habitat, they met a significant portion of N demand by the understory which could potentially facilitate understory and suppress giant kelp. It is possible that a negative feedback could form whereby frequent disturbance facilitates understory macroalgae by increasing light, space, and consumer nutrients on the benthos. Similar interactions may occur on coral reefs when the foundation species of corals are lost to disturbances and the nutrients recycled by fishes facilitates algal abundance and may prevent the recovery of corals (Burkepile et al. 2013).

Our research shows the importance of time series and long-term experiments for unraveling the importance of CND in marine ecosystems and the key roles of foundation species. Many of the important patterns in our data showed up after multiple years into the experiment. In contrast, many previous conclusions about the importance of CND in many ecosystems are based on studies taking place over one or two field seasons (Burkepile et al., 2013; Allgeier et al., 2013). These once off studies do not effectively characterize natural variation in consumer populations or capture disturbances or anthropogenic impacts to consumer communities as they are in long-term studies (see Peters et al. 2019; Munsterman et al. 2021; Sharitt et al. 2021). Disturbance drove major reductions in kelp forest CND over the course of this study. Similar alterations to CND likely occur in habitats formed by other foundation species as accelerating rates of disturbances and other global-scale impacts (climate change, disease outbreaks, overharvest) have resulted in widescale defaunation, diminishing the important roles consumers play in ecosystems (McCauley et al. 2012; Estes et al. 2011; Terbough 2015). Management practices that protect foundation species and enhance consumer populations (e.g., no-take reserves) may help to minimize these impacts by preserving diverse assemblages that promote self-reinforcing feedbacks that can stabilize communities against disturbances. It is widely acknowledged that consumers mediate trophic interactions that enhance the persistence of foundation species (Estes et al. 2011, Burkeholder et al. 2013; Terborgh 2015). In the Anthropocene, management of ecosystem function will rely on conservation practices that target both foundation species and consumers in order to maintain the critical positive feedbacks that are needed for ecosystems to function properly.

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Appendices

Table S1. Model coefficients (a = intercept, b = slope), R^2 and *P* values for log-log linear regressions of per capita excretion rates (μmol NH_4^+ h^{-1}) vs. grams dry mass (shell-free dry mass for invertebrates) for n individuals from common benthic kelp forest consumers (34 species from 18 families) The root mean square error (RMSE) depict the model prediction uncertainty in our estimates of per capita excretion rates.

Family	**Species**	***n***	**Range (wet g)**	**a**	**b**	***R*²**	**RMSE**	***P***
1. Fishes								
Embiotocidae	*Brachyistius frenatus, Embiotoca jacksoni, Embiotoca lateralis, Hypsurus caryi, Rhacochilus vacca*	23	4.11- 605.00	1.14	0.77	0.69	0.24	< 0.001
Hexagrammidae	*Ophiodon elongatus, Oxylebius pictus*	26	2.00 - 4670.00	0.75	0.89	0.78	0.53	< 0.001
Kyphosidae	*Girella nigricans, Medialuna californiensis*	43	130.00 - 705.00	0.97	0.8	0.34	0.19	< 0.001
Labridae	*Semicossyphus pulcher, Halichoeres semicinctus, Oxyjulis californica*	113	5.81 - 3470.00	1.16	0.76	0.83	0.24	< 0.001
Pomacentridae	*Chromis punctipinnis, Hypsypops rubicundus*	65	0.40 - 820.00	1.05	0.78	0.87	0.21	< 0.001
Sebastidae	*Sebastes atrovirens, S. auriculatus, S. carnatus, S. chrysomelas, S. mystinus, S. serranoides*	59	0.30 - 1320.00	1.04	0.66	0.95	0.16	< 0.001
Serranidae	*Paralabrax clathratus*	44	19.20 - 2240.00	0.95	0.82	0.8	0.22	< 0.001
2. Invertebrates								
Actiniidae	*Anthopleura sola*	15	4.92 - 43.73	-4.22	0.91	0.82	0.35	< 0.001
Asteriidae	*Pisaster giganteus*	10	85.27 - 297.80	0.96	0.78	0.57	0.34	0.01
Asterinidae	*Patiria miniata*	11	10.27 - 116.84	0.02	0.58	0.73	0.24	< 0.001
Buccinidae	*Kelletia kelletii*	30	4.18 - 341.46	-2.29	0.74	0.89	0.26	< 0.001
Fissurellidae	*Megathura crenulata*	34	47.62 - 220.49	0.55	0.33	0.60	0.11	< 0.001
Palinuridae	*Panulirus interruptus*	71	57.53 - 653.55	3.22	0.48	0.40	0.32	< 0.001
Pholadidae	*Chaceia ovoidea, Parapholas californica*	46	92.51 - 331.09	-10.14	3.04	0.81	0.48	< 0.001
Plexauridae	*Muricea californica*	18	6.26 - 69.96	-0.99	0.66	0.68	0.31	< 0.001
Strongylocentrotidae	*Stronglyocentrotus purpuratus, Mesocentrotus franciscanus*	62	52.04 - 357.69	-2.77	1.03	0.63	0.38	< 0.001
Styelidae	*Styela montereyensi*	11	5.51 - 17.60	-1.92	0.79	0.55	0.36	< 0.001
Turbinidae	*Megastraea undosa*	36	3.58 - 507.40	-2.54	0.83	0.79	0.56	< 0.001

Table S2. Mean mass-specific and per capita ammonium excretion rates of common kelp forest 1) fishes and 2) invertebrates. Mass-specific excretion rates were calculated as the ammonium excretion rate divided by grams dry mass (shell-free dry mass for invertebrates) of an individual. Per capita excretion rates were averaged over all sizes measured for that species. Species arranged in order of decreasing areal-N excretion rates for fish and invertebrate species. Size ranges n = sample size of incubated individuals.

			Wet mass (g)	Mass-specific excretion (µmol NH4$^+$ dry g^{-1} h^{-1})	Per capita excretion (µmol NH_4^+ ind^{-1} h^{-1})	Areal excretion (µmol NH_4^+ m^{-2} h^{-1})	Dry mass (g dry m^{-2})
Species	Common name	*n*	Range	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
1. Fishes							
Embiotoca jacksoni	Black Surfperch	5	80.00 - 400.00	6.13 ± 0.20	410.92 ± 113.27	10.21 ± 1.27	1.69 ± 0.20
Semicossyphus pulcher	California Sheephead	57	33.79 - 3470.00	5.18 ± 0.39	998.46 ± 102.53	8.12 ± 1.30	2.00 ± 0.34
Paralabrax clathratus	Kelp Bass	44	19.20 - 2240.00	5.04 ± 0.46	373.86 ± 62.46	7.96 ± 1.24	2.09 ± 0.33
Oxyjulis californica	Senorita	13	11.15 - 55.00	11.34 ± 1.54	79.93 ± 18.12	7.16 ± 0.73	0.82 ± 0.09
Girella nigricans	Opaleye	21	295.00 - 705.00	3.41 ± 0.29	464.30 ± 40.04	4.91 ± 1.57	1.53 ± 0.50
Rhacochilus vacca	Pile surfperch	2	110.00 - 605.00	3.71 ± 2.23	197.13 ± 30.39	2.65 ± 0.47	0.44 ± 0.09
Medialuna californiensis	Halfmoon	22	130.00 - 625.00	4.63 ± 0.43	416.72 ± 53.05	2.07 ± 0.93	0.48 ± 0.22
Sebastes atrovirens	Kelp rockfish	14	0.30 - 670.00	5.32 ± 3.24	235.28 ± 27.72	1.76 ± 0.26	0.62 ± 0.10
Hypsurus caryi	Rainbow surfperch	5	15.00 - 185.00	7.64 ± 2.15	139.44 ± 34.58	1.73 ± 0.36	0.23 ± 0.05
Oxylebius pictus	Painted greenling	14	2.00 - 50.00	10.24 ± 4.59	48.58 ± 12.38	1.60 ± 0.18	0.34 ± 0.04
Brachyistius frenatus	Kelp surfperch	10	4.11 - 74.52	12.96 ± 2.98	109.83 ± 28.46	1.33 ± 0.54	0.54 ± 0.12
Chromis punctipinnis	Blacksmith	37	0.40 - 85.00	8.99 ± 0.87	64.32 ± 8.13	1.23 ± 0.30	0.15 ± 0.04
Ophiodon elongatus	Lingcod	12	910.00 - 4670.00	3.64 ± 0.59	2370.58 ± 437.09	0.93 ± 0.44	0.31 ± 0.14
Halichoeres semicinctus	Rock Wrasse	43	5.81 - 204.00	8.17 ± 0.80	149.91 ± 15.79	0.90 ± 0.27	0.11 ± 0.03
Embiotoca lateralis	Striped surfperch	1	133.8	12.42	423.96	0.50 ± 0.15	0.09 ± 0.03
Sebastes mystinus	Blue rockfish	12	2.70 - 510.00	6.45 ± 0.98	117.87 ± 43.41	0.46 ± 0.12	0.07 ± 0.02
Hypsypops rubicundus	Garibaldi	28	23.10 - 820.00	5.59 ± 0.64	274.58 ± 27.72	0.38 ± 0.15	0.10 ± 0.04
Sebastes chrysomelas	Black & Yellow rockfish	11	540.00 - 565.00	2.48 ± 0.24	254.19 ± 27.11	0.29 ± 0.07	0.09 ± 0.02
Sebastes carnatus	Gopher rockfish	11	1.00 - 580.00	8.40 ± 3.01	129.52 ± 37.16	0.15 ± 0.05	0.04 ± 0.01
Sebastes serranoides	Olive rockfish	9	1.40 - 1320.00	4.92 ± 1.47	257.75 ± 85.33	0.15 ± 0.06	0.01 ± 0.006
Sebastes auriculatus	Brown rockfish	2	250.00 - 368.00	3.16 ± 0.42	446.91 ± 69.51	0.14 ± 0.03	0.03 ± 0.01
2. Invertebrates							
Panulirus interruptus	California Spiny Lobster	71	77.82 - 1511.15	3.41 ± 0.18	188.84 ± 9.31	5.99 ± 1.39	1.60 ± 0.35
Pisaster giganteus	Giant Spined Sea Star	10	85.27 - 297.8	1.52 ± 0.12	22.41 ± 2.89	4.64 ± 0.51	4.73 ± 0.53
Patiria miniata	Bat star	11	10.27 - 116.84	0.48 ± 0.04	3.28 ± 0.39	3.81 ± 0.91	7.72 ± 1.81
Stronglyocentrotus purpuratus	Purple urchin	32	52.04 - 155.52	0.07 ± 0.01	0.75 ± 0.07	3.63 ± 0.42	70.91 ± 8.10
Mesocentrotus franciscanus	Red urchin	30	60.31 - 357.69	0.08 ± 0.003	1.55 ± 0.11	2.14 ± 0.36	65.63 ± 11.07
Styela montereyensi	Stalked tunicate	11	5.51 - 17.6	0.14 ± 0.01	0.23 ± 0.03	0.65 ± 0.11	2.71 ± 0.48
Megathura crenulata	Giant keyhole limpet	28	47.62 - 199.39	0.27 ± 0.01	4.52 ± 0.13	0.64 ± 0.09	3.21 ± 0.48
Muricea californica	California golden gorgonian	18	6.26 - 69.96	0.27 ± 0.02	0.86 ± 0.09	0.57 ± 0.10	6.96 ± 1.08
Chaceia ovoidea	Wartneck piddock	31	153.6 - 331.09	0.03 ± 0.002	0.61 ± 0.08	0.53 ± 0.06	82.73 ± 9.29
Parapholas californica	Scale-sided piddock	15	92.51 - 178.94	0.01 ± 0.001	0.12 ± 0.02	0.07 ± 0.02	61.46 ± 22.19
Anthopleura sola	Starburst anemone	15	4.92 - 43.73	0.01 ± 0.001	0.04 ± 0.01	0.05 ± 0.005	1.88 ± 0.20
Megastraea undosa	Wavy turban snail	36	3.58 - 507.40	0.07 ± 0.01	0.48 ± 0.11	0.02 ± 0.005	5.03 ± 1.42
Kelletia kelletii	Kellet's whelk	30	4.18 - 341.46	0.1 ± 0.01	0.2 ± 0.06	0.01 ± 0.001	0.91 ± 0.18

Note: Sample size (n) indicates count of each species used to collect empirical ammonium excretion data. Wet mass, mass-specific, and per capita ammonium excretions are based on emprical data. Areal excretion rates and grams dry mass (shell-free dry mass for invertebrates) are based on modeled estimates from our 10-yr time series of biomass and excretion rates and were averaged across all treatments plots and sampling periods. Species arranged in order of decreasing areal excretion rates for both 1) fishes and 2) invertebrates.

Figure S1. Annual treatment means ± SE of A) giant kelp and B) understory biomass, as well as the C) proportion of giant kelp biomass out of the total macroalgal biomass in control (grey) and disturbance (red) plots over the course of the experiment. Trend lines indicate estimated marginal trends, where significant. Inset *** indicates significant contrast between treatments; $P < 0.001$.

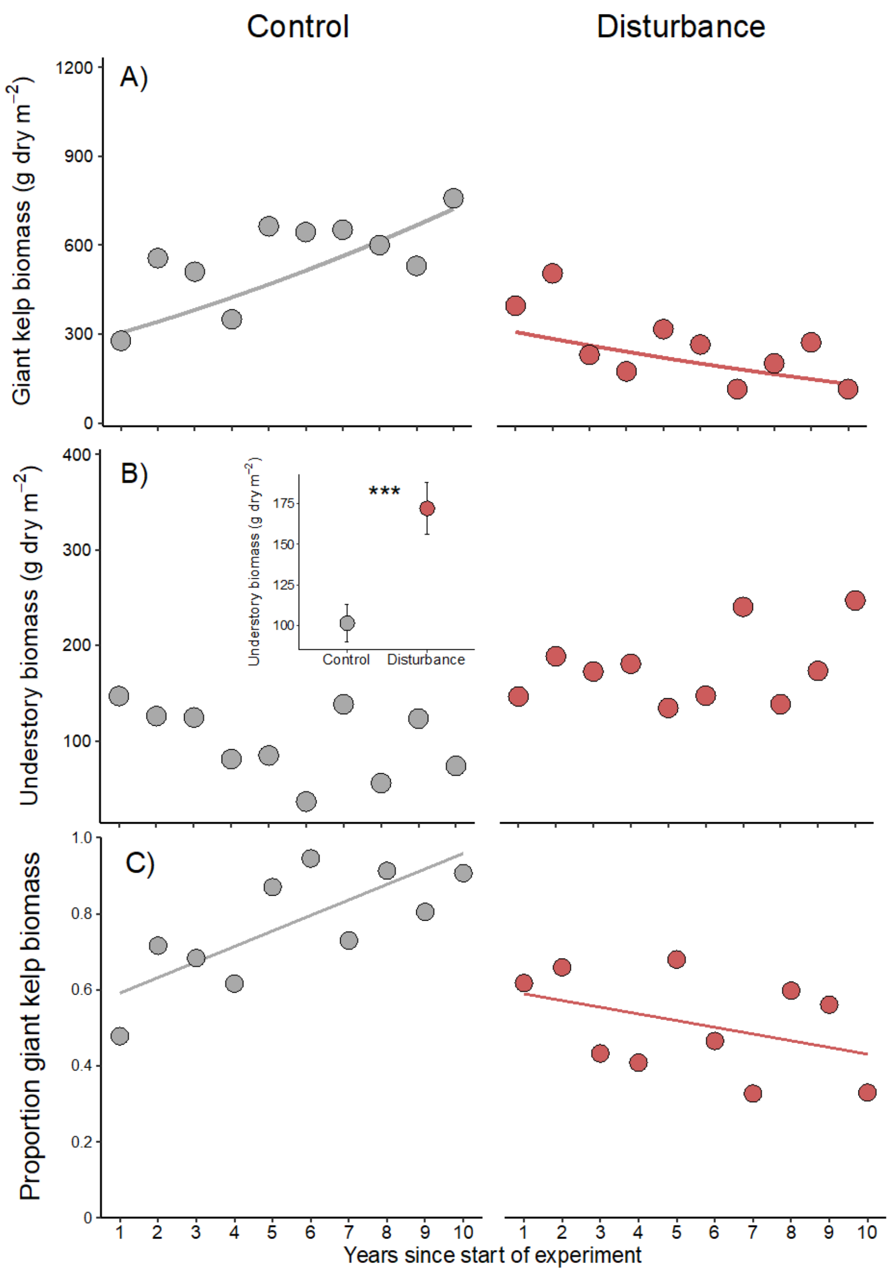

Figure S2. Annual treatment means ± SE of A) fish and B) invertebrate N excretion in control (grey) and disturbance (red) plots over the course of the experiment. Trend lines indicate estimated marginal trends, where significant.

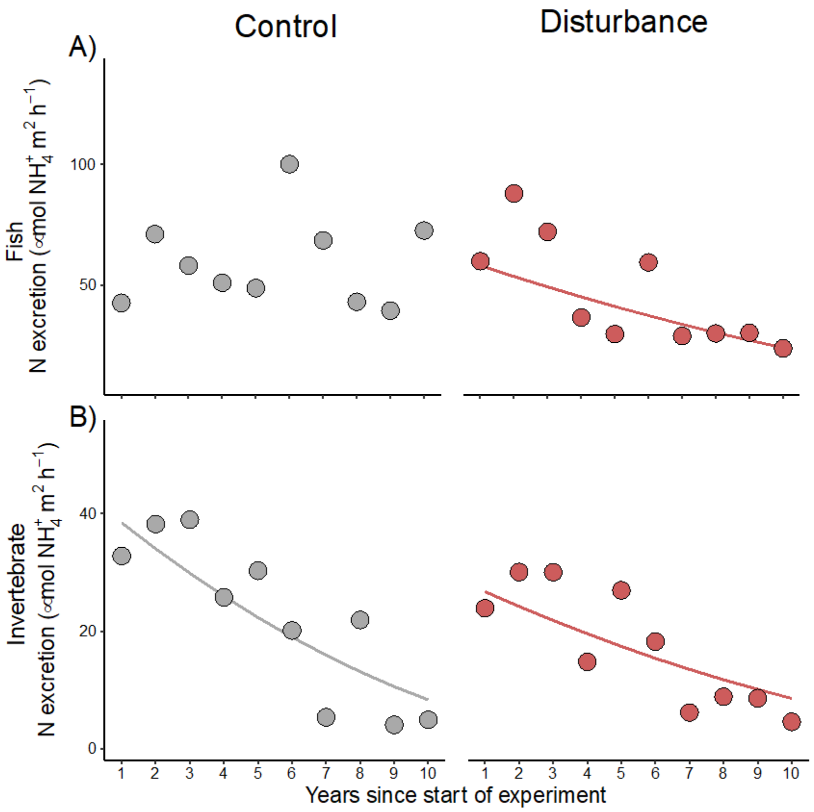

Figure S3. Annual nitrogen demand for A) giant kelp, B) understory, and C) all macroalgae in control (grey) and disturbance (red) plots for the duration of the experiment. Data are means ± SE and trend lines indicate estimated marginal trends with time, where significant.

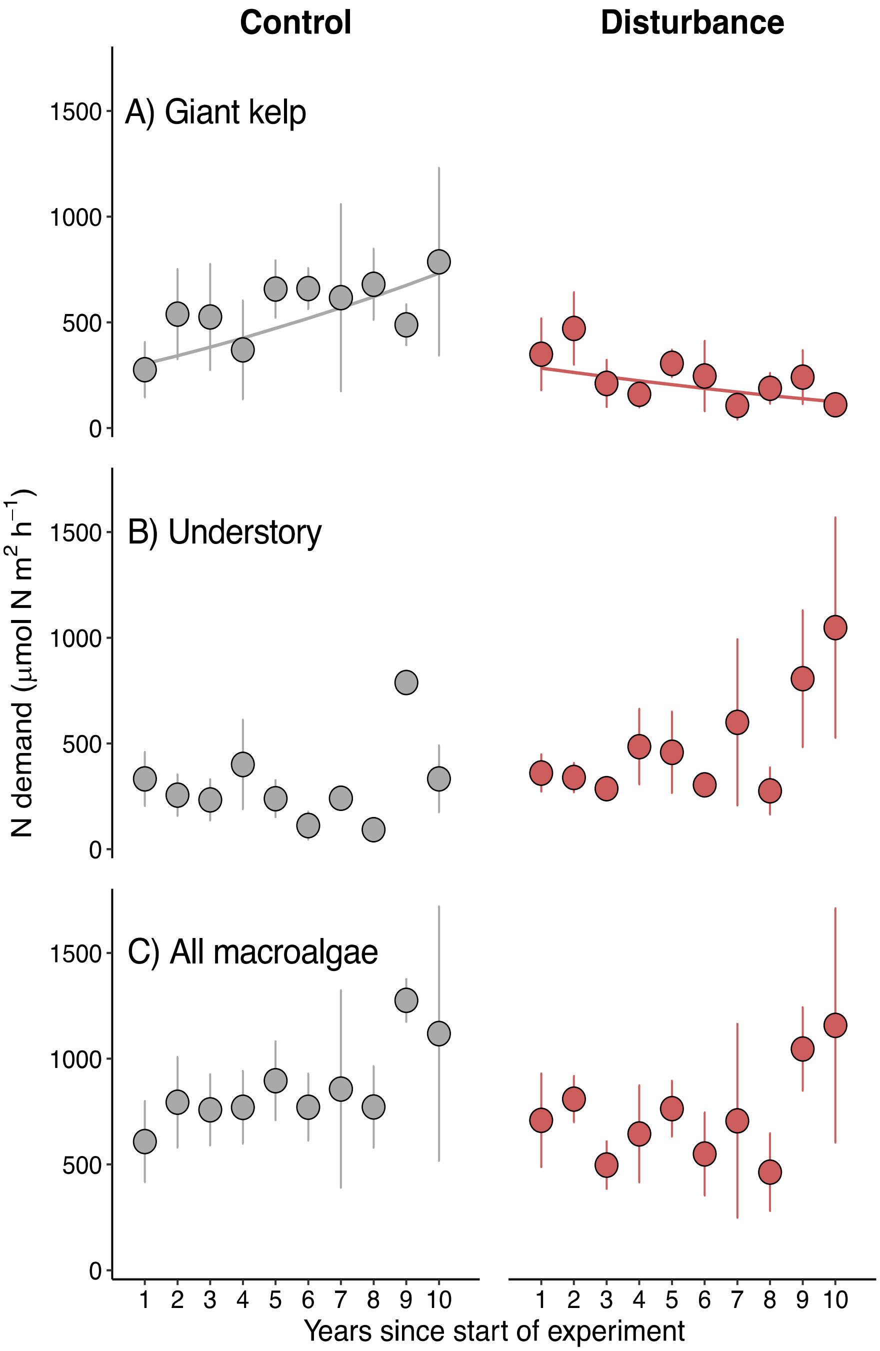

Table S3. N demand by major understory species comprising 92-95% of understory N demand in each disturbance treatment. Data are averages of each disturbance treatment over the study period ± SE; % = percent of total N demand, % difference = percent differences between treatments. Species below dashed line were negatively affected by disturbance, while species above were positively affected.

	N Demand (mean ± SE)								
Understory macroalgae	**Contol**			**%**	**Disturbance**			**%**	**% difference**
Sargassum muticum	5.2	±	4.3	2.3	21.7	±	21.1	1.1	123.1
Nienburgia andersoniana	6.0	±	2.3	2.8	20.8	±	8.0	1.5	110.3
Taonia lennebackerae	2.0	±	0.6	3.1	6.8	±	3.2	0.9	107.6
Stephanocystis osmundacea	22.4	±	4.3	12.9	66.8	±	20.1	9.0	99.4
Pterygophora californica	28.8	±	9.3	17.5	61.8	±	10.8	9.5	72.8
Chondracanthus spp.	18.8	±	4.3	8.1	36.4	±	6.7	7.5	63.8
Desmarestia ligulata	25.8	±	7.7	9.6	44.7	±	18.4	8.2	53.6
Rhodymenia californica	30.9	±	4.9	12.6	53.2	±	8.5	15.3	53.2
Ectocarpaceae spp.	3.9	±	1.1	2.8	5.6	±	2.3	1.9	35.5
Corallina officinalis	20.7	±	9.3	2.9	27.8	±	13.7	4.4	29.3
Bossiella orbigniana	5.3	±	2.2	1.7	5.0	±	3.0	0.7	-6.2
Macrocystis pyrifera (juvenile)	5.1	±	1.6	1.4	4.7	±	1.5	1.5	-8.7
Ceramiaceae spp.	35.3	±	7.4	9.0	32.1	±	6.0	15.8	-9.4
Crustose coralline algae spp.	6.9	±	1.8	2.0	6.3	±	1.2	4.3	-9.7
Acrosorium ciliolatum	14.0	±	8.5	1.0	7.7	±	4.7	2.1	-58.1
Polyneura latissima	39.9	±	25.4	5.1	21.4	±	13.7	8.6	-60.3
Total				94.7				92.5	