FISH-DERIVED NUTRIENTS IN CALIFORNIA KELP FOREST ECOSYSTEMS

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INTRODUCTION TO THESIS

Kelp forests are one of the most productive ecosystems in the world. It is often assumed that kelp forests are sustained primarily by the delivery of inorganic nitrogen, a biolimiting nutrient essential for regulating macroalgal growth in the ocean, via external physical processes such as upwelling. Often overlooked as a nutrient source, fishes excrete metabolic waste products in the form of dissolved nutrients rich in nitrogen. For fishes that live in kelp forests, excretion of consumer-derived nutrients may serve to fertilize and fuel the growth of the habitat in which they live. The fish community may help maintain a consistent supply of limiting nitrogen to kelp forest ecosystems, which may be particularly important during low-nutrient periods (e.g. seasonal reductions in upwelling or climatic events such as El Niño-Southern Oscillation; Brzezinski et al. 2013, Smith et al. 2018)

Despite their potential importance in contributing to nutrient cycling in kelp forests, relatively little is known about the factors that drive nutrient excretion rates by kelp forest fishes. In this thesis, I provide the first comprehensive assessment of ammonium supplied by kelp forests fishes at the community level and explore the spatio-temporal patterns that drive excretion rates. In Chapter 1, I quantify the ammonium (NH_4^+) excretion rate of the 30 dominant species of fishes in kelp forests off the California coast as a function of body size and compare excretion among fish species, families, and trophic groups. In Chapter 2, I use the northern Channel Islands as a case study to examine how the overarching fish assemblage, which varies spatially and temporally, influences the overall magnitude of ammonium excreted by the fish community on an areal scale. I also examine how the magnitude of ammonium excreted by the total fish community differed in response to environmental drivers and protection from fishing inside a network of no-take marine reserves. While tested in California, this work provides a useful foundation for future studies on the enigmatic role of consumers in nutrient cycling in kelp forest ecosystems on a global scale.

CHAPTER 1: BODY SIZE, SPECIES, AND TROPHIC GUILD INFLUENCE RATES OF AMMONIUM EXCRETION IN KELP FOREST FISHES

ABSTRACT

In marine systems, fishes excrete dissolved nutrients rich in nitrogen, which is a biolimiting nutrient essential for regulating primary production and macroalgal growth in the ocean. Often overlooked in attempts to explain variability in kelp forest productivity, relatively little is known about the magnitude of nutrients excreted by fishes and what factors may influence nutrient excretion rates. I investigated the supply of nutrients excreted by the dominant fishes (30 species representing ~85% of total fish biomass) on nearshore rocky reefs in central and southern California. Using rapid field incubations, I measured the amount of dissolved ammonium (NH_4^+) released per individual ($n = 460$) as a function of body size and developed predictive models relating mass to excretion rates at the family-level. Mass-specific excretion rates ranged from 0.08 – 3.45 $\mu mol \cdot g^{-1} \cdot hr^{-1}$, and per capita ammonium excretion ranged from 5.9 – 2765 $\mu mol \cdot$ individual $\cdot\ hr^{-1}$. Ammonium excretion scaled with fish size; mass-specific excretion rates were higher in smaller fishes, but larger fishes contributed more ammonium per individual. When controlling for body size, ammonium excretion rates differed significantly among fish families with the highest excretion by surfperches (Embiotocidae) and the lowest excretion by scorpionfish (Scorpaenidae). By trophic guild, planktivores and micro-carnivores excreted more ammonium per gram of body mass than macro-carnivores, piscivores, and herbivores. However, when body size differences were considered, the highest mean excretion rates per individual were observed in larger-bodied fishes such as California sheephead (*Semicossyphus pulcher*), Kelp bass (*Paralabrax clathratus*), and Lingcod (*Ophiodon elongatus)*. The excretion rates reported here are consistent in magnitude with those for fishes inhabiting freshwater and tropical marine reefs, but are among the first measured in temperate kelp systems, enabling researchers to determine further quantify the role of consumers in nutrients cycling.

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INTRODUCTION

Complex multitrophic interactions are a central characteristic of ecosystem functioning in many ecosystems worldwide. Since the 1960's, ecologists have questioned the factors that control ecosystem structure and productivity by asking if an ecosystem is driven by "top-down" factors (e.g. food-web interactions), "bottom-up" effects (e.g. resource limitation), or a combination of the two (Hairston et al. 1960, Slobodkin et al. 1967, Hunter & Price 1992, Posey et al. 2002). While animal consumers have primarily been categorized as exerting a "top-down" effect on ecosystem structure via predation (Vanni and Layne 1997; Pauly et al. 1998), consumers may also play a pivotal "bottom-up" role through the excretion of excess nitrogen and phosphorous into the environment (Redfield 1934; later modified by Redfield 1958; Redfield et al. 1963; Caron et al. 2000, Haines and Wheeler 1978). The importance of nutrients supplied by consumers to maintain productivity is widely recognized in many ecosystems, including terrestrial (McNaughton et al. 1988), temperate tidepools (Bracken, Dolecal, & Long 2014, Bracken & Nielsen 2004), and open ocean environments (Pomeroy et al. 1963, Hernández-León et al. 2008, Roman & McCarthy 2010, Ratnarajah et al. 2014). In particular, the biotic processes of consumption, excretion, and egestion are tightly coupled and can significantly influence nutrient cycles at localized scales, such as when resident fishes feed and shelter within one biogenic habitat (e.g. Bray et al. 1986).

In many kelp forests, resident fishes may provide an important source of localized and easily-assimilated nutrients to primary producers year-round. Through the excretion of dissolved nutrients via their gills, urine, and feces (Smith 1929; Wood 1958; Sayer & Davenport 1987), fishes are recognized as important contributors to nutrient cycling in freshwater (Kitchell et al. 1979, Meyer et al. 1983, Sterner 1990; Devine & Vanni 2002) and tropical marine systems (Holbrook et al. 2008, McIntyre et al. 2008, Pfister et al. 2014). Despite the recognized importance of consumer-derived nutrients in other systems, few studies have systematically explored how animal consumers may affect nutrient cycling in kelp forest ecosystems. Two foundational papers in the 1980's revealed that ammonium production by Blacksmith (*Chromis punctipinnis*) is elevated at night in crevices near the base of giant kelp (*Macrocystis pyrifera*) on Santa Catalina Island and that kelp blades readily absorbed ammonium during incubation experiments conducted in the lab (Bray et al. 1986). Subsequent research by Bray et al. (1988) found that the rate of ammonium excreted by Blacksmith (250 μmol m^{-2} h^{-1}) was an order of magnitude greater than invertebrates and small crevice-dwelling fishes (30 μmol m^{-2} h^{-1}). Reef invertebrates in the Southern California Bight can also contribute to nutrient cycling, particularly California spiny lobster (*Panulirus interruptus*) and the Giant sea star (*Pisaster giganteus*) (Peters et al. 2019). Given the numerous potential benefits that animals may provide in enhancing and maintaining biogeochemical cycles, as evidenced in other systems, the paucity of studies on consumer-derived nutrients in kelp forests is somewhat surprising.

In aquatic systems, two conflicting theories have been developed to predict which variables best explain how individual demands for energy and nutrients influence growth and excretion rates in consumers: ecological stoichiometry theory (EST) and the metabolic theory of ecology (MTE). The EST was first proposed in 1986 (Reiners 1986) and predicted that elements within animals remain balanced with the environment. Animal excretion rates are affected by the nutrient content of prey (Sterner 1990, Elser & Urabe 1999, Sterner and Elser 2002, Welti et al. 2017), thus, species with a higher nitrogen-rich diet (e.g. predators), are predicted to excrete more ammonium than species (e.g. herbivores) that consume prey with a lower-nitrogen content (Schindler & Eby 1997, Elser & Urabe 1999). However, if two species feed on the same food source, then the species with a relatively low nutrient content in its body will allocate fewer nutrients to growth and will excrete more nutrients (Vanni et al. 2002). Under principles of EST, trophic level is also predicted to explain some of the variation in excretion rates among taxa as different prey types affect the quality of the food an individual consumes (Sterner & Elser 2002, Schindler & Eby 1997). Conversely, the metabolic theory of ecology (MTE), proposed in 2004 (Brown et al. 2004), identified body size and temperature as key variables influencing variability in excretion among taxa. The MTE recognizes that for most aquatic animals, excretion rates scale allometrically with body size, and larger taxa excrete ammonium at a lower rate per g of biomass than smaller taxa (Wen & Peters 1994, Brown et al. 2007). Thus, total biomass being equal, an assemblage with small animals will have greater animal-mediated nutrient fluxes than an assemblage composed of large-bodied animals, as allometric variation in structural tissue (e.g. P-rich bone) may alter ratios of excreted nutrients at larger body sizes. Secondly, MTE predicts that, due to relatively similar metabolic needs, organisms within a particular taxonomic or functional group will excrete nutrients at similar rates, while nutrient excretion will differ among disparate groups (Sterner & Elser 2002, Vanni et al. 2002, Allgeier et al. 2015).

Temperate marine kelp forests offer an excellent opportunity to study the role of consumers as mediators of nutrient cycles. Kelp forests are highly dynamic systems that contain a high diversity of animal species, complex food webs, and trophic levels that are well-established in the literature (Hobson & Chess 1986; Cailliet et al. 2000; Love et al. 2002). As limited research has been previously conducted on the role of fishes in nutrient cycling in kelp forests, my primary objective was to quantify the ammonium excretion rate of the full kelp forest fish assemblage and compare differences among the ammonium excretion rates of species as a function of taxonomic family, body size, and trophic group. I hypothesized that fish ammonium excretion rates will differ by family and that fishes that eat more digestible prey (e.g. Pomacentridae) will excrete ammonium faster than families that eat less digestible prey, such as algae (e.g. Kyphosidae). Similarly, I hypothesized that fishes in different trophic groups will excrete ammonium at different rates, depending on prey digestibility; planktivores will excrete ammonium the fastest compared to micro-carnivores, macro-carnivores, and piscivores.

METHODS

Given that limited studies exist on the role of fishes in kelp forest nutrient dynamics, I measured the excretion of dissolved ammonium for each of the dominant fish species inhabiting nearshore rocky reefs and kelp beds in central and southern California following commonly used methods for quantifying consumer-derived sources of nutrients in aquatic systems (Vanni et al. 2002; Whiles et al. 2009, McIntyre et al. 2008; Allgeier et al. 2014), and also tested the effect of experimental duration on excretion for kelp forest fishes. I selected a subset of 30 species, from 13 families, to represent the dominant fish species comprising the total fish biomass across California kelp forests. The selected species represented ~85% of total fish biomass, based on estimates of density and biomass from extensive underwater visual surveys conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) in central and southern California (Carr et al. 2020). I assigned each fish species to one of four trophic guilds based on discrete, fixed trophic delineations (herbivore, planktivore, micro-carnivore, macro-carnivore, and piscivore) as established in the literature (Hobson & Chess 1986; Cailliet et al. 2000; Love et al. 2011). Herbivores consist of species that eat mostly algae, planktivores eat zooplankton, micro-carnivores eat small crustaceans (e.g. amphipods, isopods, shrimps, crabs, and copepods), macro-carnivores eat larger invertebrates (e.g. seastars, gastropods, crabs, polychaetes, shrimps, sea urchins) and may occasionally eat small fishes, and piscivores eat primarily fishes. Since many fishes within California kelp forests are opportunistic predators, species with a mixed diet were classified into a single trophic group based on the dominant type of prey taxa (>50% of the diet) consumed at the adult stage.

FISH COLLECTIONS

Collections occurred from May 2016 – September 2017. Kelp forest fish communities are not uniform across coastal California; Point Conception is a recognized geographic break and distinct species typically associate with kelp forests north or south of this break (Allen et al. 2006, Horn & Allen 1978). In central and northern California, species evolutionarily linked to temperate environments and that are cold-water affiliated are dominant, whereas in southern California, species with tropical lineages and warm-water affiliated are dominant (Allen et al. 2006). To quantify excretion rates for species representative of kelp forests along the entire coast of California, I sampled both regions (Fig. S1). Species affiliated with cold water were collected from Stillwater Cove in Carmel Bay (36°33'42.8"N 121°56'48.5"W) and Point Lobos Marine Reserve in Monterey Bay (36°31'18.4"N 121°56'33.9"W), whereas species affiliated with warm water were collected on Santa Catalina Island (33°26'52.8"N 118°28'57.4"W) near the University of Southern California Wrigley Marine Science Center.

For each species, I collected *n* = 5 – 45 individuals across a range of body sizes via a variety of methods, including hook-and-line, baited fish traps, and barrier nets and hand nets while scuba diving. I collected fish during daylight hours between 0900 and 1500, and only individuals collected in good condition (i.e., not exhibiting signs of barotrauma) underwent experimental incubation to measure ammonium excretion rates. After capture, I placed the fish immediately in a prepared incubation chamber or in a communal holding tank for <10 minutes when my fishing yield exceeded the rate of experimental processing. To reduce handling time before the experiment, I weighed each individual for wet mass (in grams) and measured total and standard length (in centimeters) following the experiment, and released the fish following experimentation.

Previous studies indicated that ~20 – 30 individuals per species is sufficient to generate a strong relationship between body size and nutrient excretion rates (Vanni et al. 2002; Layman et al. 2011; Allgeier et al. 2014). For species that I could not collect a minimum of 20 individuals due to logistical limitations, I combined those excretion estimates with similarly related species in the same family during data analysis. All collections were permitted by the California Department of Fish and Wildlife (Permit: Hamilton #SC-6477). The San Jose State University Institutional Animal Care and Use Committee approved the protocols for the capture and handling of fish (protocol #1034).

EXPERIMENTAL INCUBATIONS TO MEASURE AMMONIUM EXCRETION

To calculate the ammonium excretion rate (NH_4^+ per individual per gram body weight per minute) for each individual fish, I conducted experimental incubations to test the change in ammonium over a set period. The experiments were conducted on a boat (e.g. Boston whaler) or on the shore of the sampling site with a research team of 3 – 4 people. Before adding a fish to an incubation tank, I prepared each tank identically and frequently ran 5 – 8 incubations concurrently. Each tank (e.g. a plastic bin or cooler) was lined with a 4 mm polyethylene bag, and the bag was changed between incubations. The tank was filled with a known volume of water (1 – 75 L) which varied according to the size of the fish. During data analysis, nutrient excretion rates were calculated by standardizing the measured nutrient concentration by the water volume used. Seawater was collected from the surface using a submersible pump and water temperatures were within 2°C of the temperatures from which the fishes were collected. Seawater was filtered to 1 μM using a sediment cartridge polypropylene filter (ANSI/NSF Standard 8" x 2.5"), which removed autotrophic bacteria and plankton that may otherwise have altered nutrient concentrations during the incubation period. Although some bacteria and plankton are smaller than 1 μm, it is unlikely that these organisms affected the nitrogen levels in the seawater during the experiment, as reflected by stable nutrient concentrations in the control incubations. To maintain water temperature within ±2°C throughout the duration of the experiment, incubations for fishes in southern California were conducted within insulated containers.

To start the experiment, I collected an initial sea water sample to represent the concentration of ambient ammonium without the fish in the tank. I then added the fish into the tank, and collected a water sample every 10 – 15 minutes. I collected 2.5 mL of seawater with a syringe affixed with a 0.45-μm Whatman nylon membrane filter, then placed the filtered sample into a 20 mL amber glass scintillation vial pre-filled with working reagent, and immediately placed the sample on ice for later nutrient analysis at the lab. After the addition of the fish, all containers were covered and aerated to limit stress on the test subjects. All excretion values calculated for each fish were compared to control samples each day using 2 – 4 identical treatment bags without fish.

The experimental duration intentionally varied between 30 – 60 minutes. Previous research suggested that 30 minutes was sufficient to accurately quantify the excretion of ammonium in tropical nearshore fishes (Allgeier et al. 2014), but since limited studies on kelp forest fishes existed, I tested the effects of incubation time on the ammonium excretion rate. I conducted experimental time trials on 135 of the 460 total individuals (5 – 15 individuals of each species) representative of a suite of size classes. For the time trials, I collected 7 samples per incubation in 10-minute intervals for one hour (e.g. an initial without fish, 10 minutes, 20 min., 30 min., 40 min., 50 min., 60 min.). After I determined that the excretion rate did not vary significantly as a function of experimental duration or between time bins for any of the species of interest, I shortened the experiment length to 30 minutes and collected three samples in 15-minute intervals (e.g. initial without fish), 15 min., and 30 min.). I kept time with stopwatches attached to each tank.

NUTRIENT ANALYSES

The fluorometric determination of ammonium is a well-established method that analyzes the fluorescent emission from a water sample and compares the light intensity from the unknown water sample to known concentrations of standards (Holmes et al. 1999; Protocol B). Samples for ammonium quantification underwent nutrient analysis on the day-of collection. In the field, I added seawater samples to amber vials containing working reagent to begin the reaction process. The working reagent contained a mix of ortho-phthalaldehyde (OPA), sodium sulfite, and sodium tetraborate (Holmes et al. 1999). OPA was the active ingredient in the working reagent, and although OPA is also used to measure amino acids, it loses sensitivity to amino acids when combined with sodium sulfite. Thus, it was essentially specific to ammonium and may be measured fluorometrically. The working reagent was kept in dark bottles and I mixed new working reagent every three months. For the samples, I used amber vials because the working reagent is light sensitive. Between experimentation days, I acid-washed the vials in alcohol and used each vial 3x before disposal. The same syringe and were used for each incubation (e.g. 3 – 7 water samples) and were then discarded to minimize the potential for contamination from different tanks.

Standards with known concentrations of ammonium were used daily to create a standard curve for calculating ammonium concentrations and underwent the same treatment in the field. In the morning of each field day, I created the standards ranging from 0 – 40 µM with an ammonium stock solution using low nutrient seawater. I made separate batches of the low nutrient seawater for each fish collection region in order to capture the background fluorescence in the water of that region (i.e., I made separate batches for experiments conducted in central California versus southern California). I collected 20L of water in a clear container and left it in the sun for three days with aeration to promote the utilization of the ambient nutrients by the bacteria and plankton in the water. To maintain temperature for the seawater, the container was 80% submerged in cool running water. After three days, I filtered the water to 1 µM and froze the low nutrient sea water in 20 mL batches. One vial of low nutrient sea water was thawed the night before a field day to make the standards. A sample of each low-nutrient seawater batch was run on a Lachet Quikchem 8000 Flow Injection Analyzer to confirm that it was low in nutrients.

Within 3 – 10 hours of collection (as recommended by Holmes et al. 1999), I analyzed the samples for ammonium analysis using a handheld Turner Designs AquaFluor Handheld Fluorometer. The fluorometer optical kit (No. 8000-402) consisted of an LED (CWL) lamp at 375 nm, a 350 nm excitation filter with an 80 nm bandpass, and a ≥420 nm combination emission filter. Samples are manually introduced into the fluorometer in plastic minicell cuvettes that achieved readings from 10–100 µM. Each minicell cuvette was used once.

DATA ANALYSES

Quantify the NH_4^+ excretion rate per individual

To calculate the mean excretion rate of each individual, I plotted NH_4^+ (µmol) over experimental time (minutes) in a series of linear regressions for 460 fishes and extracted the slope of the relationship. To quantify the role of body mass in predicting excretion rates for each individual, I used simple linear regressions to generate a mass-specific ammonium excretion rate where the change in ammonium excreted by each individual fish per min is divided by fish wet weight (in grams). To test if the excretion rate varied throughout the duration of an hour-long incubation, I calculated the change in ammonium excretion in ten-minute time bins (e.g. 0 – 10 minutes, 10 – 20 minutes, 20 – 30 minutes, etc.) and used an ANOVA to test if values differed among time bins. Data were $\log_{10}$ transformed to meet assumptions of normality. I also tested the effect of experimental duration on ammonium excretion rate at different intervals to test whether excretion estimates improve with longer duration incubations. To determine if the rate from the initial to differing endpoints stayed constant, I subtracted the mean mass-specific excretion rate at various secondary intervals (e.g. 10 minutes, 30 minutes, 60 minutes, etc.) from the initial value without a fish. I then used an ANOVA to test if excretion depended on the length of the interval.

Average the NH_4^+ excretion rate by species

Mass-specific excretion rates were calculated as total ammonium excreted per individual per hour, divided by the wet weight (g) of an individual. Per capita excretion rates were averaged over all sizes measured for that species, and reflect the total ammonium excreted, regardless of body size. In cases where the sample size of a specific species was not robust (usually $n < 5$), species with similar taxonomic identities and/or feeding habits were grouped together. To account for the effect of fish mass, I used bivariate linear regressions to examine the strength of the association between NH_4^+ excretion per individual per minute as a function of fish mass. Due to evidence of allometric scaling at the larger fish weights, I log-transformed excretion and body size to improve homoscedasticity and normality.

Test for family and trophic group differences in nutrient excretion rates

To test the hypothesis that the concentration of ammonium excreted by kelp forest fishes (NH_4^+ µmol · min^{-1}) differs based on phylogeny, I used an Analysis of Covariance (ANCOVA) with the factor of family identity, the covariate of body mass, and the interaction between family identity and body mass. Although I measured excretion on fishes from 13 total families, I excluded Cottidae, Gobiidae, and Malacanthidae from family analyses due to limited sample sizes and fish size ranges. I tested statistical assumptions of ANCOVAs: that errors are independent and identically distributed, the response-covariate relationship is linear, and that the slopes of response-covariate relationships are equal. To meet the assumptions of normality and homoscedasticity, I log_{10} transformed excretion and fish size values.

To test the hypothesis that the concentration of ammonium excreted by kelp forest fishes differs among trophic guilds, I used an Analysis of Covariance (ANCOVA) to test for statistically significant differences in mass-specific excretion rates with the factor of trophic guilds, the covariate of body size, and the interaction between the two. Similar to analyses on fish families, I $\log_{10}$ transformed excretion and fish size values to meet assumptions of the statistical test. All statistical analyses were conducted using JMP 14.

RESULTS

QUANTIFYING THE EFFECTS OF INCUBATION DURATION AND BODY SIZE ON NH_4^+ EXCRETION

Despite some apparent variability in excretion rates among individual 10-minute time bins for some families (Fig. 1), there was no statistically significant effect of time on excretion for any family (Table S1A). In addition, there was also not a significant effect of increasing incubation duration on ammonium excretion rates for any fish family (Fig. 2; Table S1B). Thus, conducting an experiment for 30 minutes yields the same excretion rate as an experiment for 60 minutes. These results also suggest that using a holding chamber for a short period (10 – 30 minutes) before starting the experiment did not significantly alter the excretion rate. Of the 460 incubations, per capita excretion rates scaled allometrically (Fig. 3A), thus, I log-transformed excretion and body size. Larger bodied fishes excreted more ammonium than smaller bodied fishes, however the rate of ammonium excretion per gram of body was not equivalent and scaled with mass using a multiplier of 0.75 (Fig. 3B).

EFFECTS OF TAXONOMY ON NH_4^+ EXCRETION RATES

By species, both the mass-specific and per capita rates of ammonium excretion rates varied. The mean mass-specific excretion rate was 0.70 $\mu mol \cdot g^{-1} \cdot hr^{-1}$ and ranged from 0.08 – 3.45 $\mu mol \cdot g^{-1} \cdot hr^{-1}$ for different species (Table 1). Kelp surfperch (*Brachyistius frenatus*) and Señorita (*Oxyjulis californica*) excreted ammonium at the highest rates per gram of body weight of the 30 species (3.45 and 3.18 $\mu mol \cdot g^{-1} \cdot hr^{-1}$, respectively). However, when the collinear variable of size was allowed to propagate through, the average magnitude of ammonium an individual fish excreted in an hour increased by 2 – 3 orders of magnitude. Fish excretion ranged from 5.9 – 2,765 µmol $NH_4^+ \cdot \text{individual}^{-1} \cdot \text{hr}^{-1}$, and the mean excretion rate was 412.1 ± 27.83. A large 4.6 kg Lingcod individual excreted the most ammonium (2,765 $\mu\text{mol} \cdot \text{hr}^{-1}$), which was nearly two times higher than a 3.5 kg California sheephead individual (965 $\mu\text{mol} \cdot \text{hr}^{-1}$). Smaller fishes, such as Island kelpfish and Blackeye goby (<5 g), excreted the least per individual at 5.9 and 9.3 µmol $NH_4^+ \cdot \text{individual}^{-1} \cdot \text{hr}^{-1}$, respectively.

Across all families, nutrient excretion increased with mass (Fig. 4A), however the excretion rate differed significantly among families when body mass was considered as a covariate (ANCOVA, family: $F_{7,394} = 17.32$, $P < 0.0001$; body mass: $F_{1,394} = 569.5$, $P < 0.0001$). The interaction between the terms was significant, indicating that the slopes were not constant and differed among families (ANCOVA, family*body mass: $F_{7,394} = 3.67$, $P = 0.0007$); although excretion was similar at small sizes, excretion differed as fish grew larger. As fish weight increased, fishes in the Labridae family excreted nearly double the concentration of ammonium per hour compared to individuals in the Sebastidae and Scorpaenidae families of the same body size. Overall, the fit of the linear regressions indicated high predictive potential (r^2 values ranged from 0.34 to 0.94). Higher r^2 values often reflected families that were better sampled in the dataset. For a full list of predictive ammonium excretion equations as a function of body mass for each family, see the Appendix (Table S2 and Fig. S2).

Of the thirteen families tested, the mean mass-specific excretion rate ranged from 0.4–2.4 $\mu\text{mol} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (Table 2). On average across all fish sizes, families differed in mean excretion rates per gram of fish weight (ANOVA: $F_{7,402} = 15.07$, $P < 0.0001$). Embiotocids, Pomacentrids, and Labrids on average excreted ammonium at higher rates per gram of body mass, excreting over two times more ammonium than individuals of the Serranidae, Kyphosidae, Scorpaenidae, and Sebastidae families (Fig. 4B; Table 2). However, when fish size was considered, families with bigger individual fish (Hexagrammidae, Kyphosidae, Labridae, Serranidae) excreted ammonium 2 – 3 times faster than the smaller-bodied fish families for individuals that I incubated (Table 2).

EFFECTS OF TROPHIC GROUP ON NH_4^+ EXCRETION RATES

As body size increased, fishes from each trophic group excreted ammonium at similar rates, as indicated by the non-significant interaction between trophic guild and body mass (ANCOVA, trophic guild: $F_{4,435} = 13.50$, $P < 0.0001$; body mass: $F_{1,435} = 246.0$, $P < 0.0001$; trophic guild x body mass: $F_{4,435} = 0.8603$, $P = 0.4877$). On average across all fish sizes per trophic group, mass-specific excretion rates were 2x greater among planktivores and micro-carnivores compared to macro-carnivores, piscivores, and herbivores (ANOVA: $F_{4,440} = 36.72$, $P < 0.0001$; Table 3; Fig. 5B). However, on the per individual basis of the fishes I tested, larger-bodied macro-carnivores excreted an order of magnitude more ammonium than small-bodied planktivores, and four times more ammonium than micro-carnivores.

DISCUSSION

Excretion rates of kelp forest fish were comparable with that of fishes in freshwater and tropical systems, and were similar to the first values published for a subset of kelp forest fishes and invertebrates over thirty years ago (Table 4). Initial estimates of ammonium excretion rates were published using the dry weight of the fish, thus, if I assume that dry mass was 25% of wet mass as suggested in the literature (Schaus et al. 1997, Gido 2002), then the excretion estimates fall within similar ranges. Bray et al. (1986) found that Blacksmith excreted ammonium at a mean rate of 0.53 μmol g wet wt^{-1} h^{-1}, and the mean excretion rate of ammonium for Blacksmith in my study was 1.63 ± 0.22 μmol g wet wt^{-1} h^{-1}. Bray et al. (1988) reported that the mass-specific excretion for a series of five fish species (California sheephead, Kelp bass, Blackeye goby, Bluebanded goby, Island kelpfish) ranged from 0.75 – 1.75 μmol wet weight g^{-1} h^{-1}, which is comparable to the range I observed in my study (0.01 – 3.5 μmol wet weight g^{-1} h^{-1}). Peters et al. (2019) calculated ammonium excretion rates for 14 common benthic macroinvertebrates in southern California following similar methods used in this study. Similarly, assuming that dry mass is 25% of wet mass, then the range of mass-specific excretion rates for invertebrates (0.0025 – 0.8525 μmol · g^{-1} wet weight · hr^{-1}) is ~25%

less than the mass-specific excretion rate range for fishes (0.01 – 3.5 µmol wet weight g^{-1} h^{-1}). Interestingly, although the mass-specific excretion ranges were similar to fishes, the per capita excretion ranges are drastically different due to the increased body mass of fishes. Fishes excrete ammonium at faster rates than invertebrates by nearly 2 – 3 orders of magnitude (fish: 5.9 – 2765 µmol · hr^{-1} versus invertebrates: 0.04 – 189 µmol · hr^{-1}). Pairing the invertebrate excretion calculations with fishes will enable further studies to investigate changes in consumer community assemblages and anthropogenic effects on the magnitude of nutrients excreted.

FISH CONTRIBUTIONS TO KELP FOREST NITROGEN CYCLING

My results suggest that principles of the metabolic theory of ecology (MTE) likely drive excretion rates in kelp forest fishes more so than principles of the ecological stoichiometry theory (EST). My results support the hypothesis that body size and taxonomy, principles of MST, predict excretion rates among kelp forest fishes. Individual excretion rates scaled to the 0.75 power of body mass, implying that larger fishes excreted at a lower rate for their size than smaller fishes. This result is in accordance with prior studies on animals in aquatic systems (Wen & Peters 1994, Schaus et al. 1997), and it has been suggested that the mechanisms for the less than proportional increase in excretion rate is likely linked to metabolism, which also scales as the ¾ power of body size (Brown et al. 2004). Under principles of MST, it is also predicted that organisms within a particular taxonomic group will excrete nutrients at similar rates due to relatively similar metabolic needs (Sterner & Elser 2002, Vanni et al. 2002, Allgeier et al. 2015). Kelp forest fish excretion rates were similar among a species but varied a by family, providing further support for the principles of MST.

I expected that my trophic group analyses would support the hypothesis that fish diet and other principles of EST would drive ammonium excretion by fish consumers in kelp forests (Elser & Urabe 1999). I expected that the piscivorous predators, with higher nitrogen-rich diets, would excrete more ammonium than invertivores, planktivores, and herbivores with a lower-nitrogen diet. I did not see this trend among mass-specific estimates of excretion; instead, I observed a faster mass-specific excretion rate by planktivores and micro-carnivores compared to macro-carnivores, piscivores, and herbivores. This result may have been due to the 100 – 300% faster digestibility of plankton and invertebrates compared to fish prey, as has been observed in studies on digestion by Kelp rockfish (Van Dykhuizen 1983). The relatively slow digestion rate by herbivores in my study may also be explained by the slower digestion rate typical of herbivores in numerous ecosystems; generally, herbivores have longer intestines to help digest difficult prey, such as algae and detritus, and the absorption efficiency of different foods may contribute to variability in excretion rates. For example, foods richer in lipids and proteins have a higher absorption efficiency compared to foods richer in carbohydrates. Thus, carnivorous fishes, feeding on soft-bodied and highly digestible prey rich in proteins have a higher absorption efficiency (~90%) compared to herbivores (~40 – 65%) which have a lower absorption efficiency (see Kapoor et al. 1975 for an extensive review).

Researchers testing the prevalence of the EST in aquatic systems report conflicting results. In pelagic systems, trophic level is a key determinant of consumer-derived excretion (Sterner 1990), however trophic level is not as important in freshwater (Vanni et al. 2002) or nearshore tropical systems (Allgeier et al. 2015). In freshwater systems, invertivores and generalized carnivores were reported to excrete nitrogen at rates substantially lower than herbivores, omnivores, and piscivores (Vanni and McIntyre 2016). In the Caribbean, mesopredators (e.g. Haemulidae, Lutjanidae, Serranidae) excreted a lower ratio of nitrogen to phosphorous compared to herbivores, which was reflective of the more phosphorous-rich diet of predators (Allgeier et al. 2013). However, subsequent studies revealed that trophic level is confounded by fish body mass and ultimately explained little of the overall variation (Allgeier et al. 2015). In kelp forests, my differing results may have been due to my method of classifying trophic guilds. I classified fishes into broad categories intended to reflect an increasing rank order of dietary nitrogen content, however, many of the fishes in California kelp forests are opportunistic and generalist predators. Under the principles of EST, it is predicted that if two animals feed on the same food, then the animal with a relatively low nutrient content in its body will allocate fewer nutrients to growth and will therefore excrete more nutrients (Vanni et al. 2002). Therefore, if the fishes are feeding opportunistically then it would be expected that the trophic groups with relatively low nitrogen in its body (e.g. invertivores or herbivores) would excrete more nitrogen. Further testing of the nitrogen storage among fishes with the collection of δ^{15} N values (as a proxy for trophic position) in kelp forests would be a worthy direction of future research to continue disentangling the effects of trophic guild and predictors of EST in kelp forests.

For this study, I chose to focus on the effects of body mass and taxonomic identity because these variables were the primary predictors of fish excretion in tropical systems (Allgeier et al. 2015). However, numerous additional variables (e.g. temperature, diet, prey energy content, growth rates, and ontogenetic shifts) may alter or interact with the effects of body size on fish-derived excretion rates in kelp forests. Some of the variability I observed may be explained by changing diets between seasons; many kelp forest fish species feed opportunistically and the cascading effects of a diet shift may alter the excretion rate at different times of year. In California kelp forests, changes in prey availability may alter consumptive patterns (Van Dykhuizen 1983); during the summer-fall season, when kelp canopies are largest, food is readily available, but it declines during the winter season when waves remove much of the kelp canopy, during which fishes have been observed to have largely empty stomachs (Roberts 1979). Furthermore, fish trophic guild classifications were based upon adult feeding habits, however, shifts in physiology and diet as an animal ages may alter ammonium excretion rates and may explain some of the variability over the size range of a species. For example, excretion by freshwater American gizzard shad (*Dorosoma cepedianum*) shifts with diet and the subsequent variation in N:P ratios in the food, however, excretion by Zebrafish (*Danio rerio*) is driven by ontogenetic changes in physiology (e.g. bone formation) as the fish ages (Pilati & Vanni 2007). I also focused on quantifying the excretion of ammonium but not the other nutrients excreted by fishes, including urea, creatine, and phosphorous (Smith 1929), and recent work suggests that urea may be an additional important source of nitrogen in kelp forests (Smith et al. 2018). Further testing of additional variables that influence nutrient excretion rates will help explain variability among kelp forest fish species, and will contribute valuable empirical evidence supporting the integration (or separation) of metabolic and ecological stoichiometry theory frameworks.

RECOMMENDATIONS FOR INCUBATION EXPERIMENTS

The calculation of accurate excretion rates is essential for linking consumers to biogeochemical processes. As the methods to quantify ammonium supplied by kelp forest fishes is not well-established in the literature, I have identified a set of recommendations for future experiments. First, I recommend that experiments follow procedures established for consumers in freshwater (Whiles et al. 2009) and tropical marine systems (Allgeier et al. 2015, Peters et al. 2019). Thirty-minute incubations were deemed appropriate for freshwater fishes, because longer experiments (>2 hours) confounded increasing concentrations of excretory products (see Whiles et al. 2009 for a review), and in tropical marine systems, fish excretion rates reached an asymptote within 30 minutes and remained relatively constant (Allgeier et al. 2014). For kelp forest fishes, I recommend that empirical excretion studies follow previously recommended guidelines of 30-minute trials. My results suggested that excretion did not vary significantly between the 10-minute time bins or the time elapsed since the start of the experiment, however, I did occasionally observe patterns of variability within the first 10 – 20 minutes. Thus, I recommend incubations are conducted for a minimum of 20 minutes, but I expect that incubations with a duration of 30 minutes will yield similar results as those lasting 60 minutes. It is also likely not necessary to collect a water sample every 10 minutes, and for logistical ease and cost, taking one sample before the start of the incubation and final samples at the end of the incubation is likely sufficient. However, if there is a specific species of interest not tested in this study, I recommend the use of preliminary experimental time trials with more frequent collections of seawater samples for nutrient analysis following methods presented in this paper.

FUTURE DIRECTIONS

Since the first publications that tested the effects of fish-derived nutrients in kelp forests in the 1980s (Bray et al. 1986, 1988), further elucidation on the rates and ratios to which kelp forest fishes store and excrete nutrients remained untested until this study. To further advance our understanding of the role fishes play in kelp forest nutrient dynamics, four priorities for future research are to: (1) investigate the nature and occurrence of fish-derived ammonium on an areal scale for regions of interest (see next chapter in my thesis using the northern Channel Islands as a case study), (2) examine the capacity for kelp forest fishes to store nutrients, (3) test predictor variables of ecological theory (e.g. EST vs. MTE, or a combination of the two) and, (4) examine the role of additional fish-derived nutrients, including urea and phosphorus. As part of my research, I collected extra seawater samples and determined the phosphate in each sample, but I have not yet analyzed the results for trends by species, family, or trophic group. My next steps will be to conduct those analyses and investigate the ratio of N:P excreted by kelp forest fishes, which will help further our understanding of the ecological theories at play in kelp forests.

CONCLUSION

This study provides evidence that fishes contribute nutrients to kelp forest ecosystems via excretion processes. Ammonium excretion rates were affected by fish body mass, family identity, and trophic group, suggesting that maintaining large-bodied fishes, as well as taxonomic diversity, could have important effects on mediating nearshore nitrogen cycles in kelp forests. The quantification of family-specific predictive excretion rates provides a baseline for modeling fish-derived nutrients in kelp forests on an areal scale, which I explore in Chapter 2.

TABLES

Table 1. Mean ammonium excretion rates of common kelp forest fishes by species. [a]Mass-specific excretion rates were calculated as total ammonium excretion divided by the wet weight (g) of an individual. [b]Per capita excretion rates were averaged over all sizes measured for that species. Species are arranged in order of decreasing per capita excretion rates. Sample size n = the number of incubated individuals. In the cases where the sample size of a specific species was not robust, individuals of closely-related species by taxonomic identity and trophic group were grouped together.

			Wet Mass (g per indiv.)		**Mass-specific excretion**[a] (μmol $NH_4^+\cdot g^{-1}\cdot hr^{-1}$)	**Per capita excretion**[b] (μmol $NH_4^+\cdot hr^{-1}$)
Species	**Common name**	**N**	**MIN**	**MAX**	**MEAN ± SE**	**MEAN ± SE**
Ophiodon elongatus	Lingcod	10	910	4670	0.63 ± 0.33	2765 ± 420
Other *Sebastes spp.*	Treefish, Bocaccio, Vermilion RF	8	250	2600	0.79 ± 0.45	1133 ± 436
Semicossyphus pulcher	California sheephead	56	34	3470	0.56 ± 0.07	965 ± 86
Myliobatis californica	Bat Ray	11	1100	17600	0.42 ± 0.03	838 ± 105
Scorpaenichthys marmoratus	Cabezon	12	890	2250	0.50 ± 0.32	581 ± 111
Girella nigricans	Opaleye	21	295	705	0.71 ± 0.39	464 ± 40
Medialuna californiensis	Halfmoon	22	130	625	1.44 ± 0.34	417 ± 53
Sebastes auriculatus/caurinus	Brown RF, Copper RF	9	200	2000	0.26 ± 0.09	410 ± 81
Paralabrax clathratus	Kelp bass	44	19	2240	0.76 ±0.07	374 ± 62
Hexagrammos decagrammus	Kelp greenling	4	460	630	1.39 ± 1.41	342 ± 96

Caulolatilus princeps	Ocean whitefish	12	75	590	0.48 ± 0.30	297 ± 40
Embiotocidae spp.	Black, Striped, Rainbow, Pile surfperches	14	15	605	0.73 ± 0.27	287 ± 54
Hypsypops rubicundus	Garibaldi	28	23	470	0.42 ± 0.14	273 ± 28.2
Sebastes atrovirens	Kelp rockfish	14	0.3	670	0.47 ± 0.12	235 ± 28
Sebastes serranoides/flavidus/melanops	Olive, Yellowtail, Black rockfish	16	1.4	1320	0.37 ± 0.10	256 ± 56
Sebastes chrysomelas	Black and yellow rockfish	11	330	500	0.70 ± 0.47	254 ± 27.1
Halichoeres semicinctus	Rock wrasse	43	5.8	204	1.90 ± 0.26	161 ± 15.2
Scorpaena guttata	California scorpionfish	16	14	840	0.48 ± 0.13	132 ± 40
Sebastes carnatus	Gopher rockfish	11	1.0	580	0.46 ± 0.13	130 ± 37.2
Brachyistius frenatus	Kelp surfperch	10	4.0	75	3.45 ±0.70	110 ± 28.5
Sebastes mystinus	Blue rockfish	12	2.7	510	0.65 ± 0.11	112 ± 42.7
Oxyjulis californica	Señorita	13	11	55	3.18 ± 0.64	80 ± 18.1
Chromis punctipinnis	Blacksmith	36	0.4	85	1.63 ± 0.22	59 ± 7.6
Oxylebius pictus	Painted greenling	12	2.3	50	1.57 ± 0.46	43 ± 7.8
Rhinogobiops nicholsii	Blackeye goby	10	1.7	14	0.24 ± 0.51	9.3 ± 2.0
Alloclinus holderi	Island kelpfish	5	4.9	21	0.08 ± 0.33	5.9 ± 1.8
	TOTAL	**460**				

Table 2. Mean excretion rates of kelp forest fishes by family. [a]Mass-specific excretion rates were calculated as total ammonium excretion divided by the wet weight (g) of an individual. [b]Per capita excretion rates were averaged over all sizes measured for that species. Species are arranged in order of decreasing per capita excretion rates. Sample size n = the number of incubated individuals. In the cases where the sample size of a specific species was not robust, individuals of similar taxonomic identity were grouped together.

			Wet Mass (g per individual)			**Mass-specific excretion[a] (μmol · $indiv^{-1} \cdot g^{-1} \cdot hr^{-1}$)**	**Per capita excretion[b] (μmol $NH_4^+ \cdot indiv^{-1} \cdot hr^{-1}$)**
Family	**Species**	**N**	**MIN**	**MEAN**	**MAX**	**MEAN ± SE**	**MEAN ± SE**
Hexagrammidae	Lingcod, Greenlings	26	2.33	1112	4670	1.29 ± 0.13	1136.0 ± 302.0
Myliobatidae	Bat rays	11	1100	1888	2630	0.43 ± 0.02	837.7 ± 105.0
Cottidae	Cabezon	12	890	1383	2250	0.42 ± 0.07	581.2 ± 111.0
Labridae	Wrasses	112	5.81	518.1	3470	1.85 ± 0.11	553.8 ± 58.2
Kyphosidae	Opaleye, Halfmoon	43	130	440.5	705	1.03 ± 0.07	439.9 ± 33.3
Serranidae	Kelp bass	44	19.2	384.7	2240	1.29 ± 0.12	374.4 ± 62.4
Sebastidae	Rockfishes	81	0.3	549.4	2600	1.17 ± 0.19	317.5 ± 54.1
Malacanthidae	Ocean whitefish	12	75	199.1	590	1.86 ± 0.42	297.5 ± 39.7
Embiotocidae	Surfperches	24	4.11	131.9	605	2.41 ± 0.37	213.2 ± 37.7
Pomacentridae	Damselfishes	64	0.4	133.6	820	1.86 ± 0.15	152.8 ± 18.6
Scorpaenidae	Scorpionfish	16	14	181.5	840	0.94 ± 0.18	131.6 ± 39.7
Gobiidae	Gobies	10	1.72	5.546	14.25	2.66 ± 0.88	9.3 ± 2.0
Labrisomidae	Island kelpfish	5	4.9	9.685	21.18	0.77 ± 0.25	0.8 ± 0.2
	TOTAL	**460**					

Table 3. Mean excretion rates by trophic group. [a]Mass-specific excretion rates were calculated as total ammonium excretion divided by the wet weight (g) of an individual. [b]Per capita excretion rates were averaged over all sizes measured for that species. Trophic groups are arranged in order of decreasing per capita excretion rates. Sample size n = the number of incubated individuals.

			Wet Mass (g per individual)			**Mass-specific excretion**[a] ($\mu mol \cdot g^{-1} \cdot hr^{-1}$)	**Per capita excretion**[b] ($\mu mol \cdot hr^{-1}$)
Trophic group	**Species**	**N**	**MIN**	**MAX**	**MEAN**	**MEAN ± SE**	**MEAN ± SE**
Macro-carnivore	CA sheephead Kelp greenling Pile perch	62	33.8	3470	1066	1.26 ± 0.09	900.1 ± 81.55
Piscivore	Lingcod Kelp bass CA scorpionfish Cabezon Rockfishes	151	1100	2630	700.0	1.08 ± 0.11	513.7 ± 66.15
Herbivore	Opaleye Halfmoon	43	130	705	440.5	1.03 ± 0.07	440.0 ± 33.26
Micro-carnivore	Kelp surfperch Black surfperch Striped surfperch Rainbow surfperch Garibaldi Rock wrasse Painted greenling	117	2.33	820	136.4	2.00 ± 0.13	200.0 ± 13.96
Planktivore	Blacksmith Blue rockfish Señorita	61	0.4	510	53.0	2.24 ± 0.17	74.1 ± 10.32
	TOTAL	**436**					

Table 4. A comparison of consumer-derived ammonium excretion rates in aquatic ecosystems. Range and mean values represent the mass-specific ammonium excretion rates (µmol $NH_4^+ \cdot g^{-1} \cdot hr^{-1}$). N/A = Value not reported. Asterisk (*) indicates studies that calculated excretion rates with the dry weight of the individual fish instead of wet weight.

Source	**Year**	**System**	**Range**	**Mean**	**Notes**
Shrestha et al.	This paper	Marine	0.08 – 3.5	0.7	30 kelp forest species
Peters et al.*	2019	Marine	0.01 – 3.41	0.47	14 kelp forest invertebrates
Bray et al.*	1986	Marine	2.1 – 3.3	N/A	*Chromis punctipinnis*
Bray et al.*	1988	Marine	0.5 – 7	0.9	Kelp forest; 5 fishes and 20 invertebrate species
Weisberg & Lotrich*	1982	Marine	N/A	12.5	*Fundulus heteroclitus*
Whitledge & Packard*	1971	Marine	N/A	4.58	*Engraulis ringens*
McCarthy & Whitledge*	1972	Marine	N/A	9.58	*Engraulis ringens*
McCarthy & Whitledge*	1972	Marine	N/A	7.5	*Engraulis mordax*
McCarthy & Whitledge*	1972	Marine	N/A	3.75	*Trachurus symmetricus*
Durbin and Durbin	1981	Marine	N/A	0.54	*Brevoortia tyrannus*
Allgeier et al.	2015	Marine	.0001 – 19.5	N/A	100 species of fishes and inverts in tropical systems
Meyer & Schultz	1985	Marine	0.0016 – 2.5	N/A	*Haemulid* spp.
Schaus et al.	1997	Freshwater	1.85 – 2.9	N/A	Gizzard shad
Mather et al.	1995	Freshwater	0.4 – 7.2	N/A	Gizzard shad
Mather et al.	1995	Freshwater	2.5 – 3.4	N/A	Bluegill (lab study)
Vanni et al.	2002	Freshwater	0.5 – 1.67	N/A	Gizzard shad and zebrafish

FIGURES

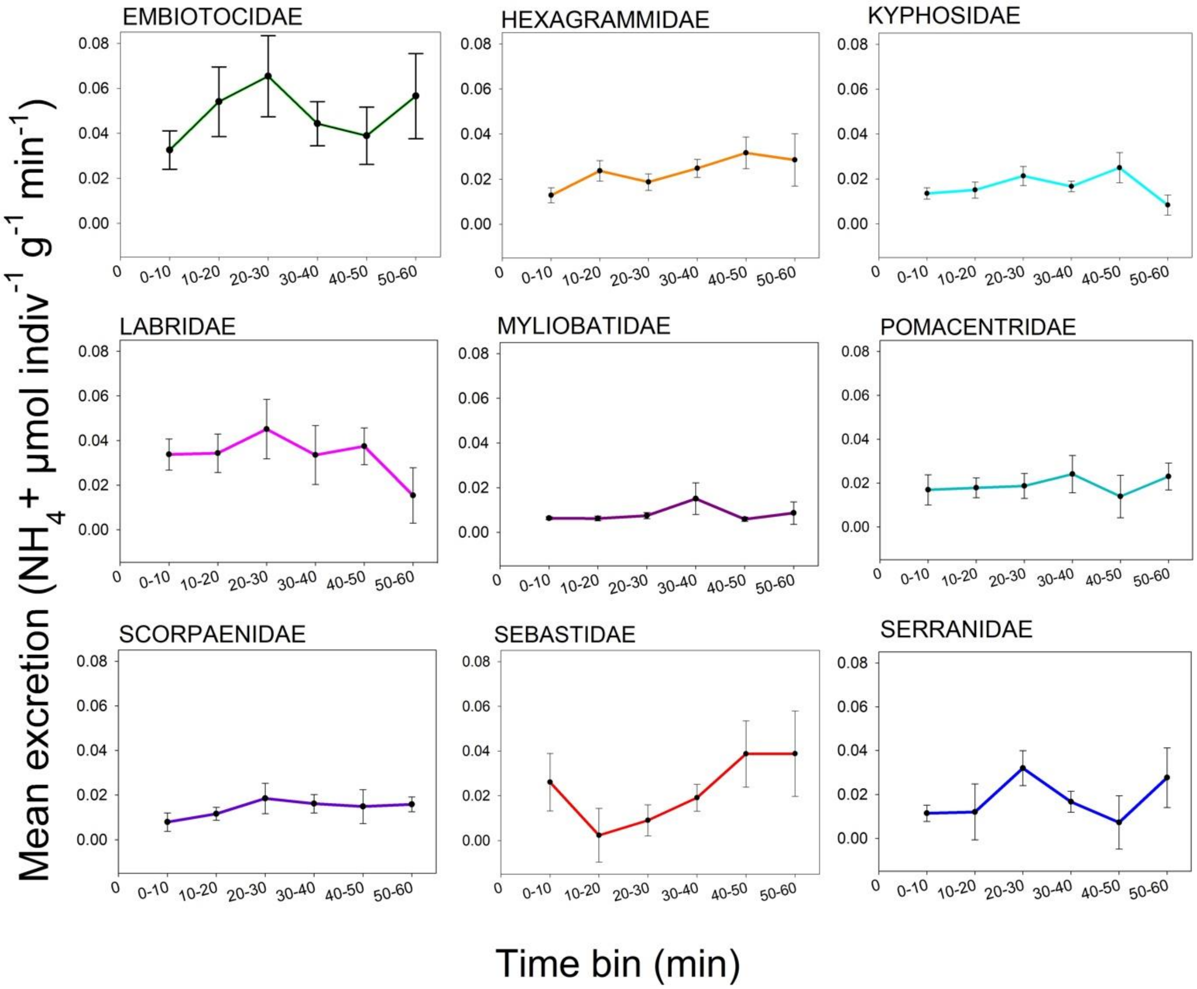

Figure 1. Fish excretion rates over the duration of the experiment. Each point represents the mean (± 1 standard error) change in ammonium excretion per individual compared to the previous 10-minute time bin for each family.

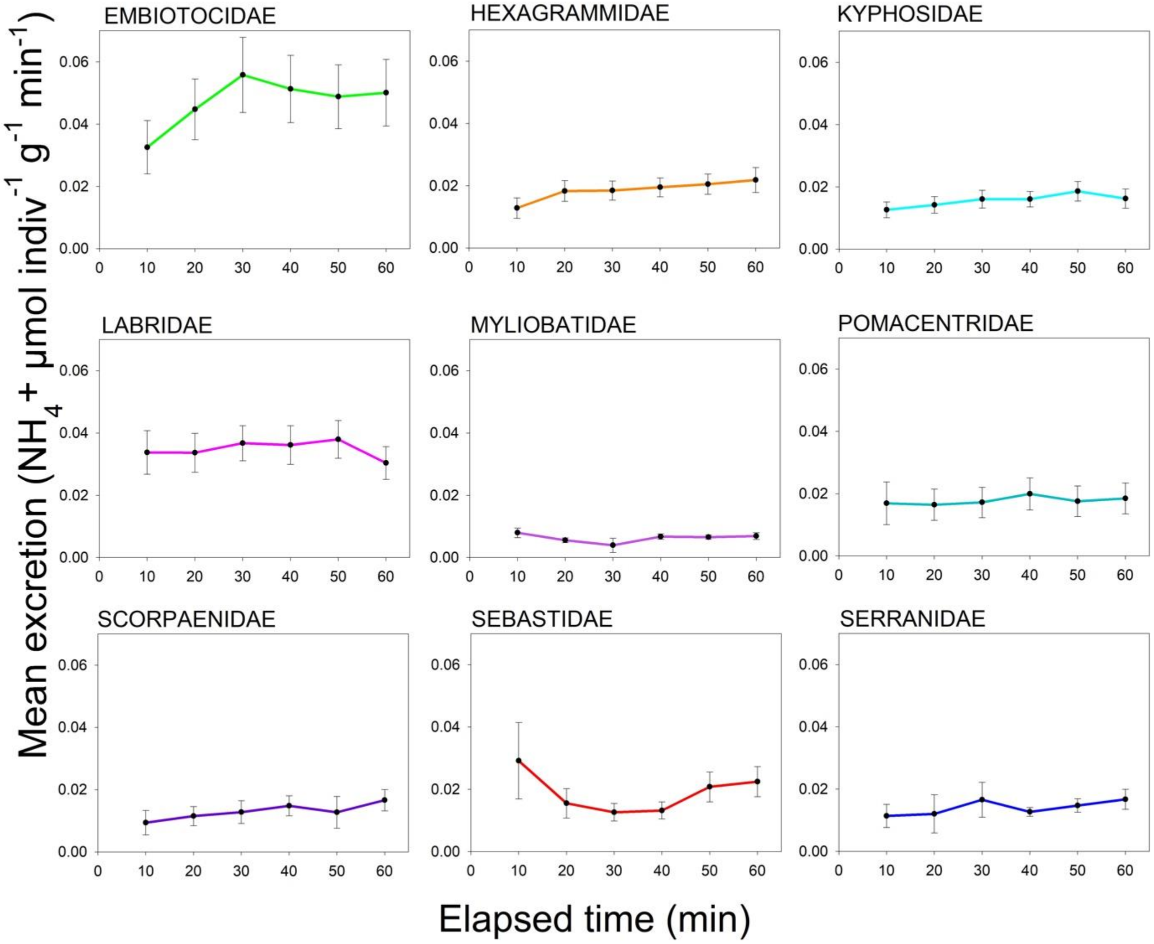

Figure 2. Fish excretion rates at different incubation intervals. Each point represents the mean (± 1 standard error) change in ammonium excretion from the initial excretion value per individual fish by family.

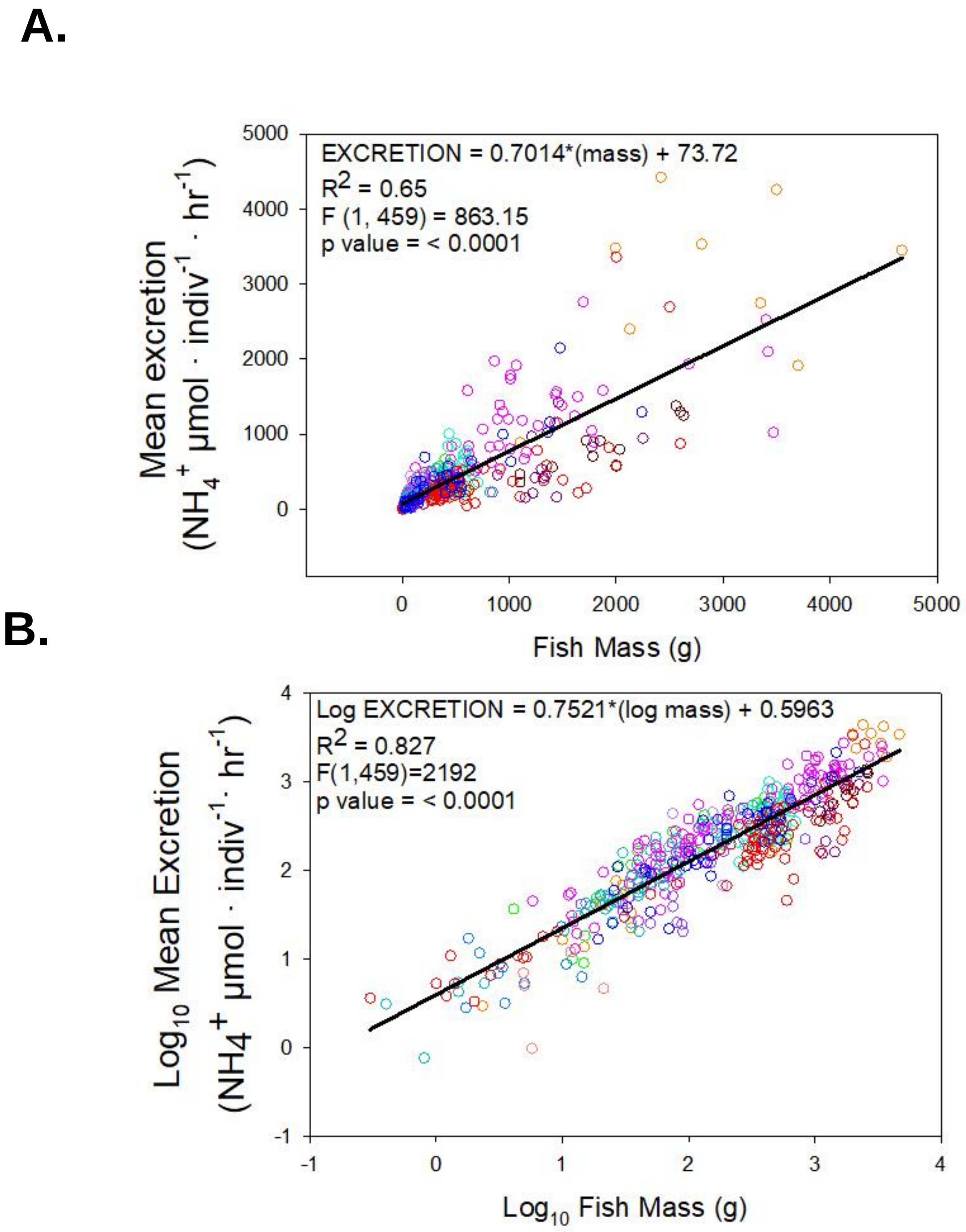

Figure 3. Linear regression of ammonium excretion rates of individual organisms. Bivariate fit of NH4+ excretion rate by fish weight using log10 transformed data. Each point represents an individual fish, and each color denotes unique families. A) Excretion rates with raw data and (B) excretion rates $\log_{10}$ transformed.

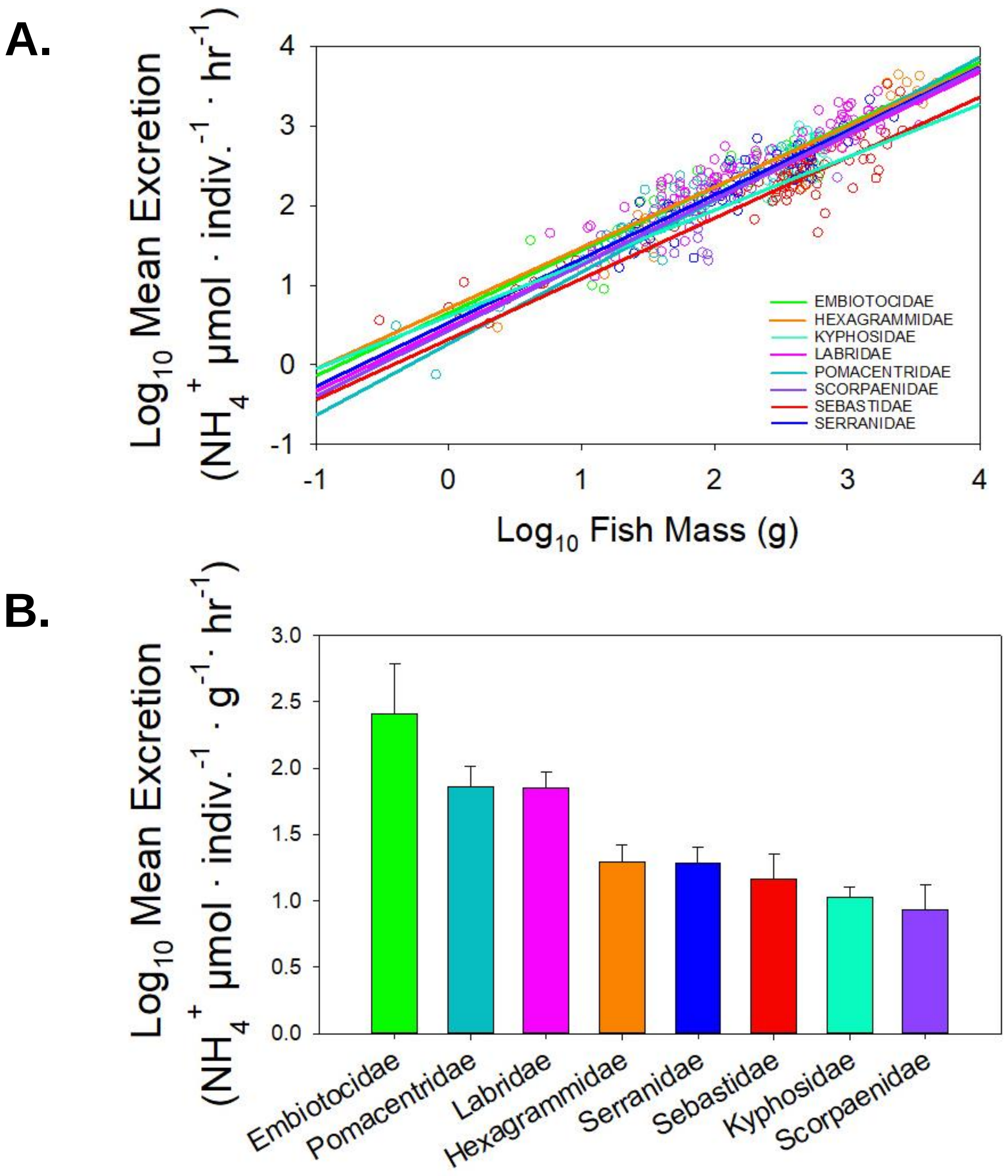

Figure 4. Mean ammonium excretion rates by family. (A) Multiple linear regressions depict taxonomic variability in ammonium excretion by fish family. The covariate (body weight) is shown on the x-axis, and the response variable (excretion rate) is shown on the y-axis. Each point represents an individual fish, and each line represents a family. Values were log$_{10}$ transformed. (B) Mass-specific mean excretion by family; values were calculated from the per capita excretion rates and divided by fish weight to remove the collinear variable.

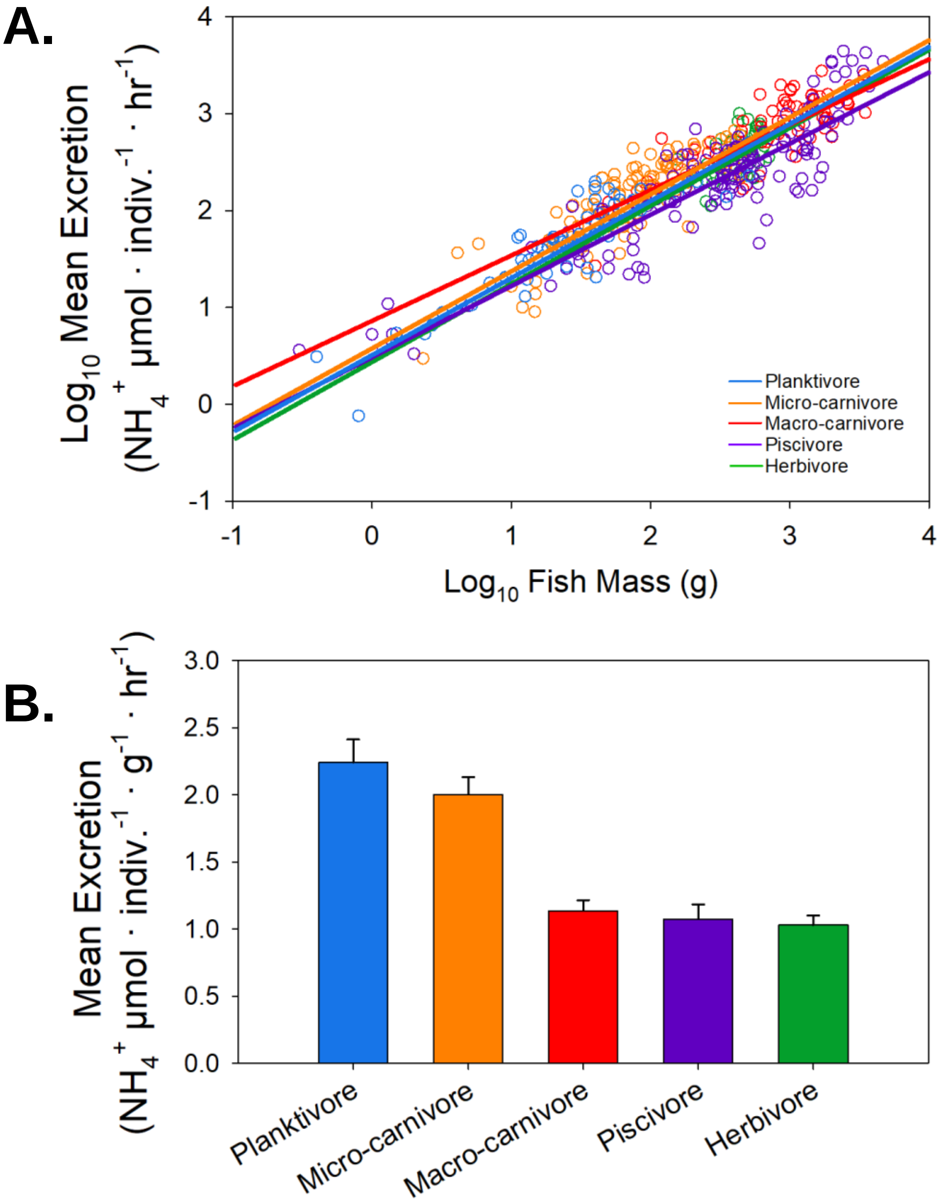

Figure 5. Mean ammonium excretion rates by trophic group. (A) Multiple linear regressions by trophic group. The covariate (body weight) is shown on the x-axis, and the response variable (excretion rate) is shown on the y-axis. Each point represents an individual fish and each line represents a trophic group. All values were log$_{10}$ transformed. (B) Mean mass-specific excretion rate by trophic group; values were calculated from the per capita excretion rates and divided by fish weight to remove the collinear variable.

APPENDIX

Table S1. Comparison of excretion rates over duration of experiment ANOVA results by (A) time bin and (B) compared to initial. Data were $\log_{10}$ transformed prior to analysis.

A. Excretion rates compared by time bin

Family	**DF**	**Error**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Embiotocidae	5	73	0.7711	0.1542	0.6104	0.6922
Hexagrammidae	5	76	1.1457	0.2291	0.5202	0.7602
Kyphosidae	5	67	0.8478	0.1696	1.6513	0.1586
Labridae	5	108	1.3581	0.2716	1.646	0.1540
Myliobatidae	5	17	0.2794	0.0559	0.9076	0.4990
Pomacentridae	5	61	1.5267	0.3053	0.6461	0.6654
Scorpaenidae	5	67	1.2336	0.2467	0.6399	0.6700
Sebastidae	5	125	2.2733	0.4547	1.2532	0.2885
Serranidae	5	17	0.5414	0.1083	0.9413	0.4796

B. Excretion rates compared to initial

Family	**DF**	**Error**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Embiotocidae	5	75	0.4577	0.0915	0.7206	0.6100
Hexagrammidae	5	76	0.0919	0.0184	0.0554	0.9980
Kyphosidae	5	68	0.1945	0.0389	0.6761	0.6430
Labridae	5	115	0.2586	0.0517	0.4261	0.8297
Myliobatidae	5	17	0.0485	0.0097	0.6069	0.6958
Pomacentridae	5	62	1.4983	0.2997	0.396	0.8497
Scorpaenidae	5	69	0.3471	0.0694	0.3112	0.9046
Sebastidae	5	137	0.4774	0.0955	0.3123	0.9049
Serranidae	5	20	0.1567	0.0313	0.4157	0.8322

Table S2. Excretion rate models by family. Coefficients (m = slope; b= intercept), R^2 and P values for log-log linear regressions of per capita excretion rates ($NH_4^+ \cdot indiv^{-1} \cdot hr^{-1}$) vs. weight mass (g) for n individuals from 8 benthic kelp forest fish families. The root mean square error (RMSE) depict the model prediction uncertainty in my estimates of per capita excretion rate.

Family	**Common name**	**n**	**Range (wet g)**	**m**	**b**	**R2**	**RMSE**	**P**
Embiotocidae	Surfperch	24	4.11 – 605	0.7855	0.6775	0.7014	0.2855	<.0001
Hexagrammidae	Lingcod, Greenling	26	2.33 – 4670	0.8958	0.2933	0.9447	0.2245	<.0001
Kyphosidae	Opaleye, Halfmoon	43	130 – 705	0.7981	0.5000	0.3419	0.1908	<.0001
Labridae	Wrasses	112	5.81 – 3470	0.7573	0.7401	0.8763	0.1951	<.0001
Pomacentridae	Damselfish	64	0.4 – 820	0.7981	0.5585	0.8873	0.1962	<.0001
Scorpaenidae	Scorpionfish	16	14 – 840	0.7573	0.3489	0.5835	0.3110	0.0006
Sebastidae	Rockfish	81	0.3 – 2600	0.6620	0.6394	0.8765	0.2316	<.0001
Serranidae	Bass	44	19.2 – 2240	0.8195	0.4593	0.8044	0.2185	<.0001

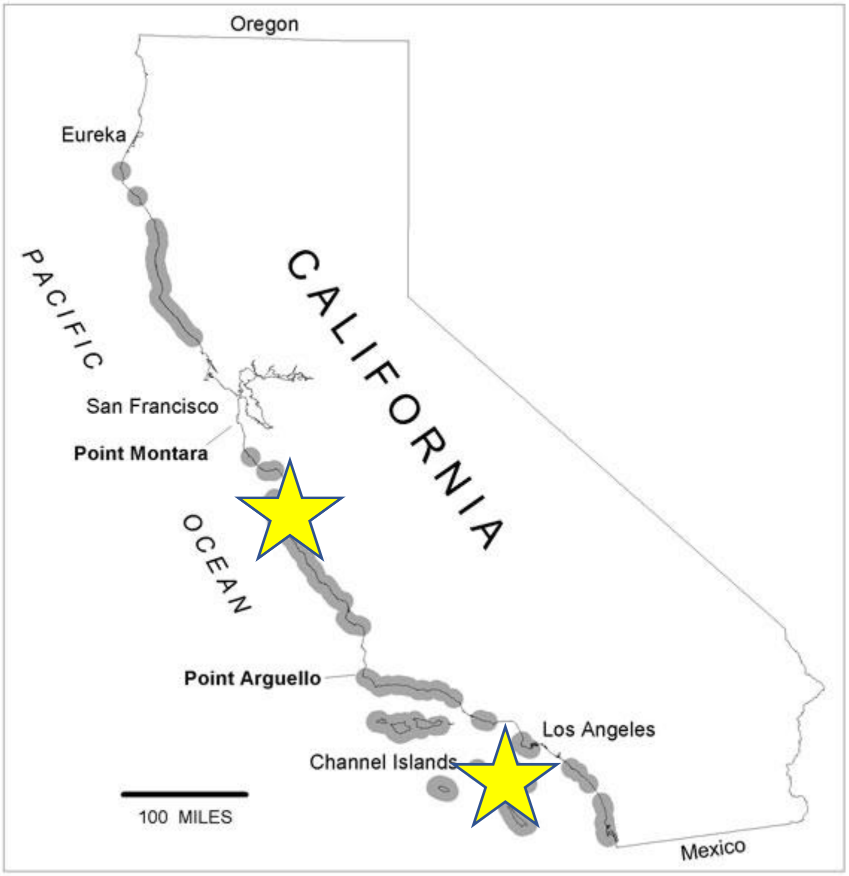

Figure S1. Location of sampling sites. Species affiliated with cold water were collected from Stillwater Cove in Carmel Bay (36°33'42.8"N 121°56'48.5"W) and Point Lobos Marine Reserve in Monterey Bay (36°31'18.4"N 121°56'33.9"W), whereas species affiliated with warm water were collected on Santa Catalina Island (33°26'52.8"N 118°28'57.4"W) near the University of Southern California Wrigley Marine Science Center.

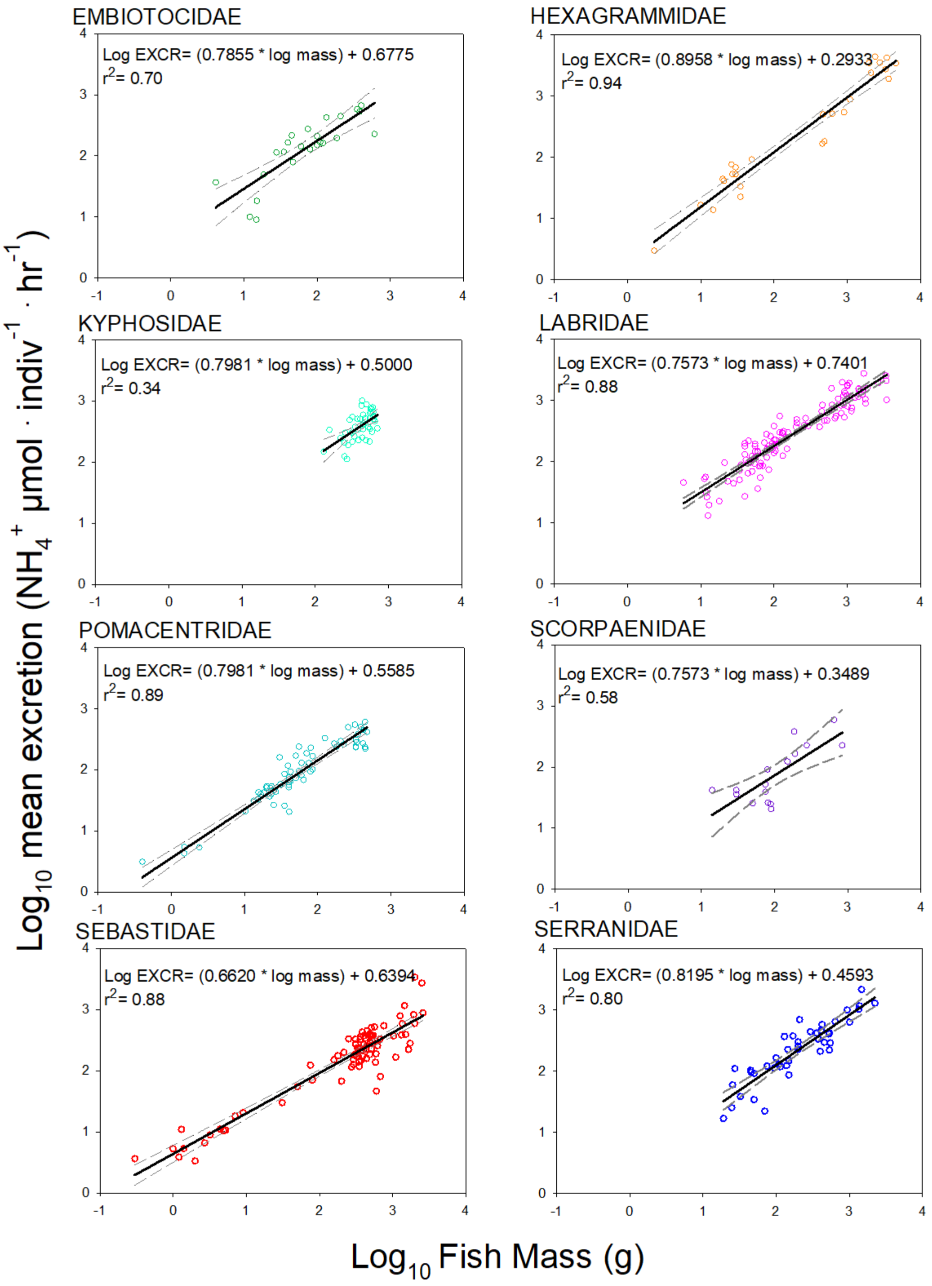

Figure S2. Ammonium excretion rates as a function of body size for each fish family. All values were $\log_{10}$ transformed and each point represents an individual fish. The independent variable (fish body weight) is shown on the x-axis, and the response variable (excretion rate) is shown on the y-axis. Solid line depicts the best fit linear equation, while the dashed curves indicated 95% confidence intervals on the best-fit line. Each panel represents a different family.

CHAPTER 2: SPATIAL PROTECTION AND ENVIRONMENTAL CHANGE INFLUENCE FISH-DERIVED NUTRIENT CYCLING IN SOUTHERN CALIFORNIA KELP FORESTS

ABSTRACT

Consumers excrete dissolved nutrients rich in nitrogen, a biolimiting nutrient essential for regulating primary production and macroalgal growth in the ocean. Often overlooked in attempts to explain kelp forest productivity, relatively little is known about the role of consumers in nutrient cycling in temperate systems, such as the magnitude of nutrients excreted and the factors that influence spatial and temporal variability in consumer-derived nutrients. To investigate the supply of ammonium (NH_4^+) excreted by the dominant members of the nearshore rocky reef fish community in the northern Channel Islands (nine families representing 95% of resident bony fish biomass), I combined empirically-measured relationships between excretion rate and body mass for each species with data on fish density and size structure from visual SCUBA surveys conducted from 2005-2018 at 46 sites across 4 islands. The fish community excreted a substantial amount of nitrogen to the kelp forest (mean: 131.3 $\mu mol \cdot m^{-2} \cdot hr^{-1}$) but excretion rates differed among sites and over time (range: 59.84 – 247.9 $\mu mol \cdot m^{-2} \cdot hr^{-1}$). Variability in areal excretion rates were associated with the establishment of marine protected areas (MPAs) and environmental characteristics resulting in geographic and temporal shifts in the overarching fish community structure. Areal excretion rates were 30% greater inside of marine reserves than outside of marine reserves, and environmental and habitat characteristics (e.g., habitat vertical relief, kelp biomass, wave exposure, chlorophyll a, etc.) explained 85% of the spatial variation in community excretion rates. In contrast, large-scale oceanographic phenomena (e.g. North Pacific Gyre Oscillation index) and past patterns of fish recruitment explained 57% of the temporal variation in nutrient excretion over the 14-year time series. Results suggest that fish-derived nutrients may provide an important and underrepresented nutrient source to kelp beds, particularly during low-nutrient periods (e.g. seasonal reductions in upwelling or El Niño-Southern Oscillation events), and that fishing may interfere with these nutrient cycling pathways. Areal rates of ammonium excretion – consistent with those reported for tropical reefs, but among the first measured in temperate systems – reveal that fishes may play a critical role in supporting the resiliency of kelp forest ecosystems in southern California by supplying a relatively constant source of reduced nitrogen that can be utilized by giant kelp and other macroalgae to fuel primary production of biogenic habitat.

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INTRODUCTION

Kelp forests are among the most productive ecosystems in the world (Steneck et al. 2002; Graham et al. 2016). Giant kelp (*Macrocystis pyrifera*) serves as a foundation species that provisions habitat and energy, supporting a highly diverse community (Graham et al. 2016). To support growth, giant kelp requires a consistent supply of nutrients year-round; at a minimum, it requires 1 – 2 μM nitrogen in seawater and has a limited ability to store nitrogen for future needs (Jackson 1977, Gerard 1982). At the base of this productivity, it is well-known that kelp forests rely upon physical processes, particularly upwelling and internal waves, to hydrodynamically transport essential nutrients to the kelp forest (Zimmerman & Kremer 1984, Fram et al. 2008). However, the delivery of nutrients, primarily nitrate, via offshore oceanographic processes can be spatially variable and sporadic. From late summer to fall, wind-driven coastal upwelling in Southern California relaxes, thermocline and nutricline depth increases (McPhee-Shaw et al. 2007), and it is estimated that oceanographic processes provide only half of the nitrogen required by giant kelp (Fram et al. 2008). Yet, giant kelp continues to grow during low-nutrient seasons when the minimum threshold is not met (Rassweiler et al. 2008), and it can only store nitrogen internally for ~2 – 4 weeks in the absence of significant external nutrients (Gerard 1982, Zimmerman & Kremer 1986)

To account for the lack of nitrogen, it has been hypothesized that animal consumers may help sustain giant kelp biomass during periods of low advective delivery from oceanographic sources (Brzezinski et al. 2013, Smith et al. 2018). Consumers are widely recognized as an important localized source of nutrients via the excretion of key limiting nutrients, such as ammonium (NH_4^+) to help maintain ecosystem productivity in aquatic systems worldwide. For example, coral reef growth has been shown to increase by 50 – 70% on colonies with resident fishes (Meyer et al. 1983, Meyer & Schultz 1985, Holbrook et al. 2008, Shantz et al. 2015), and hot spots of ammonium around groups of sheltering fish are up to 10x greater than surrounding areas without fish (Meyer et al. 1983, Shantz et al. 2015). In kelp forests along the coast of California, ambient levels of ammonium have been observed to exceed nitrate levels during poor upwelling conditions that typify the summer months

(Brzezinski et al. 2013) and consumer-derived ammonium may represent a previously underappreciated source of nitrogen. Importantly, ammonium is the preferred form of nitrogen for the majority of primary producers because it is energetically more efficient and can be used immediately for amino acid synthesis, unlike nitrate which requires energy for reduction to a useable form (Raven 1992). Furthermore, in the presence of various forms of nitrogen, ammonium can suppress the uptake and assimilation of nitrate and nitrite (Haines & Wheeler 1978). Thus, consumer-derived ammonium may dominate nitrogen uptake in kelp forests even when nitrate is in greater supply.

Consumers have immense potential to help fuel kelp forest productivity, yet empirical studies that test the role of consumers in kelp forests nutrient dynamics are lacking. Two foundational studies, conducted in the 1980's on Santa Catalina Island, California, revealed that Blacksmith (*Chromis punctipinnis)*, an abundant planktivorous fish, excreted ammonium that is utilized by giant kelp (Bray et al. 1986), and that the five focal fish species tested excreted ammonium on an areal scale one order of magnitude greater than invertebrates (Bray et al. 1988). In New Zealand, epifaunal invertebrates supply up to 122% of the nitrogen needed for giant kelp to maintain positive growth (Hepburn & Hurd 2005) and the ammonium excreted by invertebrates is utilized by giant kelp (Hepburn et al. 2012). In the Santa Barbara Channel, the invertebrate community was found to contribute substantial amounts of ammonium to the kelp forest ecosystem, but the supply was reduced following periods of warming and disease (Peters et al. 2019). Furthermore, excretion by the California spiny lobster (*Palinurus interruptus*), a species widely targeted by recreational fishermen in kelp forests, increased from 21% to 52% of the total invertebrate ammonium supply following the establishment of marine reserves in 2012 (Peters et al. 2019). Similar management measures have been shown to increase the community-level excretion rates among fishes in other ecosystems; for example, excretion is 50% greater among fishes protected from fishing on tropical reefs (Allgeier et al. 2016) and protection of key species (e.g. Gray snapper) can increase ammonium supply by an impressive 450% (Layman et al. 2011). Given the extensive lack of knowledge regarding the magnitude of fish-derived nutrient excretion in kelp forests, and how it varies across space and throughout time, a further investigation is warranted.

To address these knowledge gaps, I quantified the ammonium excretion rate supplied by the total fish community in kelp forests using the northern Channel Islands as a case study. I estimated community-level contributions of ammonium from fishes on an areal scale by combining empirical excretion estimates (generated in Chapter 1) with estimates of fish abundance and size structure from visual SCUBA surveys. I investigated spatial differences in excretion across the northern Channel Islands, as well as the temporal trajectories of change across the islands in a network of Marine Protected Areas (MPAs) over a 14-year time period, to test how excretion changes over time in response to underlying geographical differences in community structure, environmental conditions, and anthropogenic effects. I hypothesized that differences in fish assemblages (e.g. trophic groups, species composition) among islands would influence patterns of nutrient excretion. My analyses focused on differences in excretion by the whole community, as well as between groupings of targeted species (i.e. fished or exploited), non-targeted species (i.e. unfished and unexploited), and trophic groups (e.g. piscivore, carnivore, planktivore, herbivore). I expected that spatial variation in excretion rates may be driven by similar habitat and environmental conditions that drive biomass due to the correlation between biomass and excretion rates as observed in Chapter 1. I expected that changing oceanographic conditions over a 14-year period (e.g. ocean temperature anomalies, El Niño-Southern Oscillation [ENSO] events) would affect the magnitude of the excretion rate by the total fish community. To test the effects of marine reserves on the fish-derived nutrient supply, I hypothesized that the total excretion of ammonium supplied by fishes would be greater inside of marine reserves (i.e. protected areas) than outside of them (i.e. fished areas) due to increased biomass inside reserves caused by the elimination of fishing pressure, and that the differences in ammonium excretion between reserves and fished areas would increase over time as fish biomass increased since the establishment of the MPA network. To better understand the importance of fish-derived sources of ammonium relative to other sources of nutrients, I also compared the flux convergence of nutrients derived from the fish community to oceanographic sources (e.g. upwelling, internal waves) and invertebrate consumers.

METHODS

The northern Channel Islands, located off the coast of southern California, provided an excellent opportunity to investigate the factors influencing spatial and temporal variation in fish-derived nutrients. Located in the middle of a dynamic oceanographic boundary formed by the cold California Current to the west and the warmer Southern California Countercurrent to the east, the convergence and mixing of the currents results in substantial variation in productivity and the formation of strong thermal gradients from west to east that influence the structure of fish assemblages at the island scale (Hamilton et al. 2010). In addition, spatial variation in fish biomass throughout the wider Southern California Bight, including the northern Channel Islands, is strongly associated with physical environmental and habitat characteristics (Pondella et al. 2019). Fish abundance and biomass has also been observed to vary across the Channel Islands in response to the establishment of a network of MPAs that are a part of the Channel Islands National Park and National Marine Sanctuary, with biomass nearly doubling for species targeted by fishing activities since 2003 (Hamilton et al. 2010, Caselle et al. 2015). Lastly, estimates of nitrate delivery via oceanographic processes (McPhee-Shaw et al. 2002) and ammonium excretion by invertebrates (Peters et al. 2019) are also well-studied in the Santa Barbara Channel just north of the islands, thus I was able to compare the flux convergence of nutrients derived from the fish community to other sources of nitrogen in kelp forests.

COMMUNITY SURVEY METHODOLOGY

Visual surveys of fish assemblages collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) were used to quantify abundance, biomass, and to estimate nutrient excretion by the fish community. Since 1999, PISCO has conducted annual subtidal SCUBA surveys at rocky reef sites in the Channel Islands, including sites inside and outside of the state network of MPAs along the California coast (Carr et al. 2020). There is no evidence that MPAs were originally placed in either degraded or richer areas compared to non-MPA sites, and there are no significant differences in habitat among the protected and unprotected sites within each island (Hamilton et al. 2010), although strong habitat differences do exist among islands (Caselle et al. 2015). Sampling effort has changed over time, but included 46 sites in the northern Channel Islands at the peak of effort. At each site, PISCO divers conducted eight to 12 fish transects (30 m long × 2 m wide × 2 m high) at multiple levels in the water column: benthic, midwater, and canopy in depths from 0-20 m. Transects were laid out in a stratified-random design, with multiple non-permanent transects located in fixed strata (i.e., outer, middle, and inner edges of the reef). At each level in the water column, one diver counted and sized the total length (in centimeters) of all the fishes per transect.

Observations of fish abundance and size structure were compiled in a database covering the years 2005-2018. Although PISCO surveys started in 1999, I included only the year 2005 onwards in order to encompass when the survey effort expanded to include sufficient sites for analysis over time. To focus only on resident kelp forest species, I excluded elasmobranchs, highly migratory species. Small cryptic species were not enumerated using these survey techniques, but they likely contribute little to community excretion given their small size. Although over 125 species associate with rocky reefs in the Southern California Bight (Allen et al. 2006), I focused only on the 50 resident species comprising 95% of the bony fish biomass in the northern Channel Islands. I assigned each species in the PISCO dataset to a trophic group (e.g. herbivore, planktivore, carnivore, and piscivore) based on published diet studies (Hobson & Chess 1986; Cailliet et al. 2000; Love et al. 2011) and past assessment for MPA evaluations (Hamilton et al. 2010). I assigned each species to a targeted status based on recreational records from Recreational Fisheries Information Network (RecFIN), a coordinated fishery data collection and analysis monitoring program, from 2005-2018. All classifications per species by trophic group and target status may be found in Table S1.

ESTIMATING FISH COMMUNITY EXCRETION

To estimate nitrogen excretion by the fish community on an areal scale, I first calculated the concentration of nutrients excreted by each individual observed on a transect (NH_4^+ µmol · m^{-2} · hr^{-1}) using the family-level mass-specific equations determined in Chapter 1 and presented in Supplementary Table S1. The formulas estimate ammonium excretion by fish weight; thus, I converted the estimated lengths of each fish observed on a transect to weight (in grams) using published weight-length formulas (e.g. Cailliet et al. 2000; Love 2011, Jones et al. 1999). The relationship between fish weight and fish length is expressed by the following power function, [$W = aL^b$], where W is the observed fish weight, L is the observed fish length, and a and b are constants unique to each species. In the cases where length-weight equation information did not exist for a given species, the parameters from closely related taxa and those of similar body morphology were used. I then summed the excretion of each individual observed on a transect over the three levels of the water column to estimate total ammonium excreted by all fish per transect per area of benthos. The total rate of excretion per unit area at each site was then averaged across transects each year, with the mean excretion in a site-year as the lowest level of replication (Hamilton et al. 2010, Caselle et al. 2015).

TESTING SPATIAL AND TEMPORAL VARIABILITY IN FISH COMMUNITY EXCRETION

Using the excretion database, I evaluated spatial and temporal variability in community-level fish nutrient excretion and the potential environmental, habitat, and anthropogenic drivers of variability in consumer nutrient excretion in the Channel Islands. I used ArcGIS to generate maps of average nutrient excretion for each of the sites around the northern Channel Islands to identify hotspots of total fish-derived nutrients. Additional maps were generated to identify unique spatial patterns of nutrient excretion for 8 key species that contribute disproportionately to total nutrient excretion. To compare spatial patterns in excretion for the total fish community, I used a two-way ANOVA to test whether community excretion differed as a function of reserve status, island, or the interaction between reserve status and island. Similarly, I conducted additional two-way ANOVAs, with the factors of reserve and island, to examine spatial differences in excretion rate as a function of trophic group and for targeted vs. non-targeted groups of fishes separately.

I also explored concurrent spatial and temporal patterns in excretion. To evaluate whether changes in total fish excretion differed by reserve status following the establishment of MPAs in 2003, I performed a general linear model with year as a continuous variable and tested for the effects of marine protection, time, and island. Similarly, I tested for spatial and temporal variability in excretion by island for targeted and non-targeted species and by trophic groups using the same general linear model framework. To explore which species contributed most to excretion in different locations throughout the time series (2005-2018), I tested whether the contribution by 18 of the dominant species changed geographically or over time in consistent ways. I transformed the data using a $\log_{10}$ transformation to achieve assumptions of normality and homogeneity, then created a Bray Curtis Similarity index using the excretion rates of each fish species at each site in a given year. I used the similarity index to perform a permutational multivariate analysis of variance (PERMANOVA) using the factors of island and year, and their interaction. Differences in nutrient excretion by the fish community among islands over time were visualized using a nonmetric multidimensional scaling plot (nMDS). A permutation test for homogeneity of multivariate dispersions was then used to detect mean differences of each point from their centroids and 95% confidence intervals were generated to examine differences among islands in the species contributing to community-level nutrient excretion. Lastly, I developed a species biplot to explore correlations between species and ordination axes, in order to identify which species contributed most to community-level nutrient excretion across the four islands and over time.

ENVIRONMENTAL AND HABITAT DRIVERS OF FISH COMMUNITY EXCRETION

I used a suite of statistical tests to disentangle the relative importance of 14 oceanographic and habitat variables (e.g., sea surface temperature, cholorphyll-*a*, maximum wave height, kelp canopy biomass, mean vertical relief, etc.) to total fish community nutrient supply at various spatial and temporal scales (see Table S2 and Pondella et al. (2019) for detailed explanations of predictor variables and data sources). Also, I tested the relative importance of the environmental variables individually for eight key species that accounted for 80.6% of total fish community excretion when averaged across all sites over the 14-year time period. To determine the variables that best explained spatial variability in total community fish excretion across the northern Channel Islands, I used stepwise model selection techniques to fit models containing the full set of explanatory variables and then selected the best fit model using Akaike's Information Criteria corrected for small sample sizes (AIC_c). The best fit model had the lowest AIC_c, and models with $\Delta AIC > 2$ were deemed significantly different. Highly collinear variables (Pearson's correlation > 0.8) were not allowed in the same model (Table S3), and all variance inflation factor (VIF) values in the top-ranked models were less than the *a priori* threshold of 10 (Zuur et al. 2017). Explanatory variables were standardized prior to analysis. I examined the relative importance of each variable included in the confidence model set, which gives the sum total weight of all models containing a particular variable (Burnham and Anderson 2002), indicating variables that occur in a large proportion of highly ranked models. I also examined models within the confidence set for uninformative parameters, where the model was within AICc < 2, but the maximized log-likelihood was essentially the same as the best model (Burnham & Anderson 2002). For the total fish community excretion estimates, mean ammonium excretion conformed to assumptions of a normal distribution and displayed homogeneity in variance, however, excretion calculations for single species were $\log_{10}$ transformed due to positively skewed distributions.

To test whether temporal variation in total fish ammonium excretion was associated with large-scale oceanographic phenomena and past patterns of fish recruitment, I used the 14-year time series along with a number of oceanographic indices and patterns of recruitment from visual SCUBA surveys. I obtained data and calculated annual indices per year on five different oceanographic indices: sea surface temperature (SST), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), Oceanic Nino Index (ONI), and Multivariate Ocean Climate Index (MOCI) (see Table S4 for detailed explanation of descriptor variables and sources). To calculate fish recruitment from 2005-2018, I examined the PISCO dataset and considered observations of fish individuals <8 cm total length as young-of-year recruits.

Metrics of total fish recruit density and the recruit density of the top 18 species were used to investigate which species best explained the temporal fluctuations in excretion. I then calculated lagged values (1, 2, or 3 years) for each variable to test whether conditions in the past better explained current total excretion patterns across the islands. I used the average combined community excretion rates for all sites in a year as the response variable, because many of the indices reflected oceanographic patterns covering a large spatial domain. I selected the best fit model with the lowest AIC_c to explain temporal variability in fish excretion. Highly correlated variables were not included in the same model (Pearson's correlation > 0.8; Supplementary Table 5).

QUANTIFYING THE RELATIVE IMPORTANCE OF FISH-DERIVED NUTRIENTS

To compare fish community ammonium excretion to the flux of nitrogen delivered by oceanographic sources and invertebrate kelp forest consumers, I converted my values to a volumetric rate (NH_4^+ μmol $L^{-1} \cdot day^{-1}$). I integrated excretion over the depth (z) of the water column using the following equation:

$$Excretion = \frac{\mu mol}{m^2 * hr} * \frac{1}{z} * \frac{1\, m^3}{1{,}000\, L}$$

Depth (in meters) was calculated from the average maximum depth of each transect survey conducted by PISCO. I used a similar conversion to calculate the nutrient flux of ammonium by invertebrates in the Santa Barbara Channel from published data (Peters et al. 2019). I compared the consumers to oceanographic sources of nitrogen using data published by McPhee-Shaw et al. (2002). The published nitrate and nitrite delivery rates did not need to be converted. To compare the delivery of ammonium by upwelling and internal waves, I multiplied the nitrate values by 0.066, the estimated ratio of NH_4^+ to NO_3^- below the nutricline (Bronk & Ward 2005). Lastly, to compare the availability of fish-derived nutrients to nitrate available during an ENSO event, I calculated 80% of the average upwelling value to reflect the 80% reduced availability of nitrate in California surface waters during the 1997 – 1998 ENSO event (Chavez et al. 2002).

RESULTS

SPATIAL VARIABILITY

Aggregate excretion estimates

The mean ammonium excretion rate by the resident bony fish assemblage was 95.5 μmol · m^{-2} · hr^{-1}, ranging from 23.1 – 183.0 μmol · m^{-2} · hr^{-1} depending on site. Spatial hotspots of fish excretion emerged for the total fish community (Fig. 1A), notably, fish excretion was greatest on Santa Cruz Island compared to the other islands. Excretion was generally elevated inside of marine reserves, where fishing is prohibited, compared to sites open to fishing on all four islands (Fig. 1). Total fish community excretion differed significantly as a function of island and reserve status (Table 1A, Fig. 1B), with excretion being highest at Santa Cruz Island and at sites inside marine reserves. The interaction between island and reserve was not significant, indicating that the reserve effect on nutrient excretion was consistent across islands.

Spatial differences in excretion occurred at the species level (Fig. 2). For example, California sheephead exhibited high levels of nutrient excretion inside reserves on Anacapa, Santa Cruz, and Santa Rosa Islands, but negligible excretion on San Miguel Island. Total excretion rates by Kelp bass was greater on the eastern islands and inside of reserves compared to the western islands. In contrast, excretion by Blue rockfish was elevated in the western islands and excretion by Black surfperch was relatively consistent across all sites and islands. Of all the sites, Gull Island State Marine Reserve (SMR) on Santa Cruz Island recorded the greatest mean ammonium excretion rate (200 μmol m^{-2} hr^{-1}), driven primarily by California sheephead, Kelp bass, and Señorita. Sites on the north coast of Santa Cruz Island (e.g. Painted Cave SMCA, sites in/around the Scorpion SMR, and one non-MPA site on the central north shore) were also hot spots of ammonium excretion, driven mostly by Kelp bass, Blacksmith, and California sheephead. On the western-most San Miguel Island, the non-MPA site Tyler Bight is a surprising hot spot of excretion, driven by Striped surfperch, Blue rockfish, and Kelp rockfish. On Anacapa, excretion was consistently greater on the north shore within the MPAs than on the sites on the south coast where fishing is permitted.

Multivariate approaches indicated that the contribution of individual species to total community nutrient excretion differed geographically across the Channel Islands. The species that dominated excretion in the community varied from island to island (Fig. 3). Sites within an island were more similar to each other than they were to sites on other islands in community excretion patterns (nMDS axis 1 in Fig. 3A explains geographic differences; PERMANOVA for the factor of Island: $r^2 = 0.48$, $F_{3,236}= 93.92$, $P = 0.001$). Cold-water species (e.g. Lingcod, Rockfishes) contributed most to community excretion on the western-most islands of San Miguel and Santa Rosa, whereas warm-water species (e.g. California sheephead, Blacksmith, Kelp rockfish) dominated excretion on the eastern islands of Santa Cruz and Anacapa (Fig. 3B).

Characterized by trophic group, fishes excreted ammonium in different patterns spatially across the northern Channel Islands (Figure 1B). Overall, carnivores contributed the greatest percentage of ammonium excretion (39%), followed by planktivores (30%), piscivores (22%), and herbivores (8.5%). Interestingly, the excretion response by each trophic group depended in different ways on the factors of island, reserve status, and the interaction of island and reserve status (Table 1C). Among piscivores, carnivores and herbivores, excretion was greater on the eastern islands (Santa Cruz and Anacapa) compared to the western islands (San Miguel and Santa Rosa), whereas planktivores did not differ significantly by island (Tukey's HSD, $P<0.05$). In response to protection from fishing, excretion was consistently greater inside marine reserves for piscivores, carnivores, and planktivores, but not significantly different for herbivores. Among herbivores, excretion was significantly greater outside of MPAs on Anacapa, greater inside MPAs on Santa Cruz, and exhibited no difference on Santa Rosa (Tukey's HSD, $P<0.05$). The island*reserve interaction was also significant among piscivores and planktivores; piscivores excreted significantly more ammonium inside of MPAs only on the eastern islands but not the other islands, and planktivores excreted more ammonium outside of marine reserves on Anacapa (Tukey's HSD, $P<0.05$).

By target status, mean excretion was consistently greater inside marine reserves among both targeted and non-targeted species (Table 1B; Fig. S1). Among species targeted by fishing, three of the four islands showed a large MPA effect, with higher rates of excretion by targeted species inside MPAs. There was no significant interaction between island and reserve status, suggesting that excretion by targeted species was consistently elevated within MPAs on each of the islands. By contrast, the island*reserve interaction among non-targeted species was significant; excretion differed by reserve status but this effect differed by island. In particular, excretion by non-targeted species outside of marine reserves was greater than inside reserves on the eastern-most Anacapa Island (Fig. S2).

Environmental and habitat drivers of spatial patterns

Spatial variability in total community nutrient excretion was strongly associated with environmental and habitat-specific variables. From the stepwise model selection, the best model contained 6 of the 14 oceanographic and habitat variables and explained 85% of the spatial variation in total fish community excretion (AICc >2, P = 0.0019, Table 2). Excretion by the fish community was positively correlated with vertical relief of the habitat, kelp canopy biomass, and chlorophyll *a* levels, while excretion was negatively correlated with the distance of each site to the 200 m isobath, maximum wave height, and understory kelp stipe density (Fig. 4). Thus, excretion was highest in locations with complex topography, lots of giant kelp, high primary productivity in the water column, and areas close to the 200 m isobath, that were protected from waves, and where understory algae were sparse.

The best fit models for the most abundant eight species across the islands were correlated with some of the same variables, in addition to other variables not included in the total community response (Fig. 4). For the predictors that occurred most frequently, the directionality of the relationship was generally conserved across taxa. The mean relief of the habitat was significant and positively correlated in 50% of the focal species (4 of 8: Kelp bass, Blacksmith, Opaleye, Black surfperch). The distance to the continental shelf break (i.e., the 200 m isobath) was significant and negatively correlated with fish excretion in half of the focal species (4 out of 8: Kelp bass, California sheephead, Opaleye, Black surfperch), such that excretion is predicted to be greater at reefs situated closer to the shelf break. Wave action was significant and negatively correlated as a predictor of excretion by the total fish community and was negatively correlated with excretion in 3 species (Kelp bass, Opaleye, and Black surfperch). Interestingly, kelp canopy biomass was not a significant predictor variable for any of the key focal species, although it was a significant and positive predictor for the total fish community excretion response. Chlorophyll-*a* was significant and positively correlated with fish excretion rates in 4 species (Kelp bass, California sheephead, Opaleye and Black surfperch). Somewhat surprisingly, sea surface temperature was not included in the best-fit models for the total fish community. Instead, it was a significant variable for the individual species models, however the directionality of response varied widely depending on species; SST was positively correlated with excretion rates for 3 species (Kelp bass, Garibaldi, and Opaleye) and negatively-correlated with the excretion rate for one species (Blue rockfish). Lastly, for some species, none of the variables in the total community model were significantly correlated (e.g. Señorita). Four additional variables were significant in top-ranked models of individual species: sea surface temperature (positively correlated with Kelp bass, Garibaldi, Opaleye; negatively correlated with Blue rockfish), giant kelp stipes (negatively correlated with Garibaldi), and reef slope (positively correlated with Garibaldi and Black surfperch).

TEMPORAL VARIABILITY

Underlying the spatial variation, I found substantial differences in fish excretion from 2005-2018. Since the establishment of marine reserves in 2003, total fish excretion rates increased dramatically over time, particularly for communities within marine reserves (Fig. 5A). From the General Linear Model, year was a significant factor (Table 3), indicating that excretion tended to increase over time across the 14-year time series. The year*island, year*reserve, and year*island*reserve interactions were not significant, indicating that trends in total excretion rates over time were consistent across islands and by reserve status. Excretion increased most over time for the eastern-most islands of Santa Cruz and Anacapa; exhibiting a nearly 2-3x increase over the 14-year time period both inside and outside of MPAs for the total fish community. On the western islands of Santa Rosa and San Miguel, excretion was greater inside of reserves than outside, and excretion outside of reserves declined slightly over time (Fig. S3). Over time, targeted species increasingly excreted significantly more ammonium inside MPAs than outside of MPAs (Fig. 5B, Table 4), yet among non-targeted species, excretion patterns did not deviate dramatically by reserve status. Only after 2010 did non-targeted species excrete more ammonium inside protected areas than outside of them (Fig. 5C), and excretion patterns over time by target status mirrored the total fish community trends.

By species, areal fish excretion varied temporally over the 15-year time period and this pattern was consistent across islands. Excretion by key species, such as Kelp bass, Blacksmith, and California sheephead, increased nearly 3x over the duration of the time series (Fig. 6). Interestingly, the species that contributed significant proportions of the total community supply shifted as time progressed (Fig. 3). In early years of the timeseries (2005-2009), surfperches contributed the majority of ammonium excretion on the eastern islands, however in later years (2010-2018), warm-water species (e.g. California sheephead, Blacksmith, Kelp rockfish) dominated. Island explained most of the variation in community excretion patterns, as mentioned previously (PERMANOVA, Island: r^2 = 0.48, $F_{3,236}$= 93.92, P = 0.001), however, annual changes to fish community structure were also important in explaining which species contributed most to community excretion patterns (PERMANOVA: Year, r^2 = 0.11, $F_{13,236}$ = 5.074, P = 0.001). The interaction between island and year was not significant (PERMANOVA, Island*Year, $F_{36,200}$=1.0371, P = 0.383) and thus was dropped from the model.

Characterized by trophic group, fishes excreted ammonium in different patterns over time (Fig. S4) (General Linear Model; Table 3). Piscivores and carnivores excreted ammonium differently across time on different islands, as evidenced by the significant year*island interaction term. On the eastern islands of Santa Cruz and Anacapa, excretion increased steadily from 2005-2018 (increasing nearly 3x for piscivores and carnivores) whereas excretion on the other islands fluctuated over time. Among herbivores, excretion differed between years with an overall increase in excretion over time, and uniquely, the three-way year*island*reserve interaction was significant. On Santa Cruz, excretion by herbivores increased dramatically by nearly 400% from 2013 to 2018 inside of marine reserves, whereas excretion steadily declined outside of the reserves. On Anacapa, excretion from 2008 – 2015 was significantly greater outside of the marine reserves than inside of them, and on Santa Rosa, excretion fluctuated by reserve status across the timeseries.

Environmental variation over time

Temporal variation in excretion across the 14-year time series could best be explained by a model that included both biological and climatic variables. The best fit model, which included a two-year lagged response in fish recruitment density and a two-year lagged response of the NPGO index, explained 57% of the variability in fish excretion over time (Stepwise modeling; Table 4). The next-best fit models, which included SST and the Oceanic Nino Index (ONI), explained 60 – 70% of the variability, however the models were not significant. PDO, which characterizes anomalous SST on a longer time scale was not included in any model. Similarly, MOCI, which is a relatively new index featuring a more comprehensive model of California conditions, was not included in any of the best fit models.

Each variable in the best fit model was positively correlated with areal excretion rates, indicating that excretion was greater two years following a recruitment event and time periods with greater NPGO values. A decline in fish excretion rates from 2005 – 2008 is correlated with lower-than-average NPGO values from 2005 – 2006. The increase in excretion in 2009 – 2010 is correlated with a strong recruitment events observed in 2008, as well as the increase in NPGO to above-average values from 2007-2012. From 2013-2018, NPGO values returned to below-average levels, which likely explains the initial excretion rate decline in 2014. Although fish excretion increased dramatically in 2016, this response is likely due to the strong recruitment event in 2014 – 2015, when I observed a 300% increase in multi-species fish recruitment in 2014 – 2015. This effect was particularly strong within marine reserves and among fish species with warm-water affinities. For example, Blacksmith recruited strongly in 2015 (10x greater), as did Kelp bass (5x greater) and Señorita (6x greater) before mean densities returned to pre-recruitment levels in 2016. Community excretion rates declined again in 2017 – 2018, likely as a staggered response to the below-average NPGO index values observed from 2013 – 2018.

FISH-DERIVED NUTRIENTS RELATIVE TO OTHER SOURCES OF NITROGEN

On a volumetric scale, the fish community excreted 0.30 µmol $NH_4^+ \cdot L^{-1} \cdot day^{-1}$ (Fig. 7). Compared to oceanographic sources, ammonium excretion by the fish community integrated over the whole water column provided 70 – 85% less nitrogen than the nitrate supplied during spring upwelling (1.0 - 1.9 µmol $NO_3^- \cdot L^{-1} \cdot day^{-1}$). However, ammonium excretion by fishes was nearly equivalent to the nitrate flux due to internal waves (mean: 0.30 µmol $NO_3^- \cdot L^{-1} \cdot day^{-1}$; McPhee-Shaw et al. 2002). Compared to nitrate availability during an ENSO event, the fish-derived source of ammonium is comparable to nitrate available in the surface waters. Considering only ammonium, fish excretion was the greatest source of ammonium compared to oceanographic and invertebrate excretion. Fish excretion provided an additional 50 – 75% more ammonium that than supplied by upwelling (0.07 – 0.13 µmol $NH_4^+ \cdot L^{-1} \cdot day^{-1}$) and 92% more ammonium than that supplies by internal waves (0.02 µmol $NH_4^+ \cdot L^{-1} \cdot day^{-1}$). The fish community excreted 85% more ammonium compared to the invertebrate community at sites along the mainland coast near Santa Barbara (0.05 µmol $NH_4^+ \cdot L^{-1} \cdot day^{-1}$; calculated from Peters et al. (2019) using conversions established in Bronk & Ward 2005).

DISCUSSION

My comprehensive assessment of areal nutrient excretion by the total community of fishes in the kelp forests (representing 95% of total resident fish biomass) in the northern Channel Islands is comparable to initial studies on key fish species in California (Bray et al. 1986, 1988), and were consistent with those reported for fishes in tropical marine and freshwater systems (Table 5). Compared to coral reefs with similar fish biomass, kelp forest fishes excrete ammonium at a similar rate (e.g. Allgeier et al. 2013, Burkepile et al. 2013). At sites in the northern Channel Islands characterized by high fish biomass (e.g. the hotspots in Fig. 1A), my excretion values are comparable to those reported for the full fish communities in tropical ecosystems. Overall, my results are consistent with reef habitats throughout the world, especially considering my focus on resident species and exclusion of highly migratory species or spawning aggregations that might skew excretion estimates. For instance, in studies that tested ammonium excretion in large dense fish aggregations of a single population (e.g. haemulid groupers/grunts), excretion was greater than the average excretion rate I report for the full kelp forest community (Archer et al. 2015, Layman et al. 2011, Meyer et al. 1983), however the aggregations are characterized by dramatic increases in biomass density during the spawning event. Furthermore, my estimates of fish excretion by the total fish community presented in this study are likely an underestimate. Surveys integrated fish excretion from 3 levels of the water column (2 x 2 x 2 m volumes surveyed), but likely underestimated the total biomass over the full area of the water column when depths exceeded 6 m, especially at sites where 3-dimensional structure was provided by giant kelp. The pulse of nutrients from migratory species and elasmobranchs, which I excluded, will likely increase the total community nutrient supply. I also excluded the Giant sea bass (*Stereolepis gigas*); although a kelp forest species, its high biomass at aggregation sites (mean: 20,000 kg m^{-2}; House et al. 2016) and tendency to occur at low densities with daily movements over large scales skewed spatial and temporal trends. Since biomass and excretion are closely correlated, I expect that this species in particular could excrete a substantial additional concentration of ammonium to kelp forests in certain locations and times. I also expect that areal fish excretion rates will increase as targeted species continue to recover from recreational fishing.

Compared to invertebrate consumers in the kelp forests in the Santa Barbara Channel, fish excretion rates were 6x greater than invertebrate excretion on the areal scale (Peters et al. (2019). Similarly to my results, invertebrate excretion varied spatiotemporally following the establishment of marine reserves along the mainland reefs in 2012 and changing environmental conditions in the Santa Barbara Channel. For invertebrates, the heat wave reduced excretion by nearly 80% in 2014 – 2015 (Peters et al. 2019), however it did not noticeably affect excretion by fishes in my study. Instead, my results suggest that fish excretion increased during the warming period, particularly in the marine reserves. The differing response between invertebrates and fishes may be due to the species that comprise the majority of excretion respond differently to warming temperatures. Whereas the primary nutrient contributor, sea stars, declined during that period, partially due to sea star wasting disease, there were no significant losses of fish species during the timeseries and fish recruitment generally increased during warmer periods (Caselle et al. 2010).

EFFECTS OF MARINE PROTECTION ON FISH COMMUNITY EXCRETION

My study demonstrates how human impacts from fishing can reduce the fish-derived nutrient supply by nearly 30% across the northern Channel Islands. The establishment of marine reserves in 2003 reduced fishing pressure inside MPAs and likely contributed to the observed positive net change in excretion over the 14-year time period, as evidenced by the noticeable increase in total excretion within marine reserves closest to the mainland and among key species targeted by fishermen. Excretion by the highly-targeted Kelp bass and California sheephead comprised nearly a third of the excretion contributed by the entire fish community (18.1 and 13.1%, respectively), and their extraction contributed to the substantial loss in fish-derived nutrient capacity outside of marine reserves. However, Kelp bass and California sheephead did not dominate excretion throughout the whole time period; instead, the species that contributed to total fish excretion shifted over time. In the early years of the time series (2005 – 2009), surfperches contributed proportionally more to ammonium excretion across all of the islands, relative to other taxa. In later years, however, as the effects from the establishment of marine reserves became more pronounced and populations recovered from fishing effects, populations of top excreting species (e.g. larger fishes such as Kelp bass, California sheephead) and trophic groups (e.g. piscivores, carnivores) became relatively more important to total community nutrient excretion. Notably, non-targeted Blacksmith populations excreted an impressive concentration of ammonium on areal scales that frequently rivaled that of Kelp bass and California sheephead (Fig. S6). Although physically smaller, Blacksmith school in dense aggregations in the midwater and it is likely that their sheer number led to greater excretion rates.

Patterns of increased excretion over time following the establishment of marine reserves varied by site and island as well. On Anacapa and Santa Cruz, excretion by the total fish community increased nearly 2 – 3 fold over time inside MPAs, likely due to reduced fishing pressure that occurred following the establishment of the marine reserve network.

Responses to MPA protection were likely greater at these islands due to their proximity to fishing ports on the mainland and historically high fishing pressure compared to the western islands. Yet on Anacapa, non-targeted species also excreted more ammonium outside of marine reserves. This surprising result may be explained by the increased predation pressure upon non-targeted species by predatory fishes released from fishing pressure within marine reserves. Interestingly, on San Miguel Island, the establishment of marine reserves did not significantly change the total community excretion. This may be due to a low level of fishing pressure on San Miguel, even prior to the establishment of marine reserves, due to its distance from the mainland. Alternatively, the western-islands are also comprised of cold-water associated species (e.g. rockfishes) that are older and slower-growing than many of the warm-water species. Thus, recovery after protection from fishing is likely to take longer, as has been observed as the biomass/density response to marine reserve protection in aquatic systems (Starr et al. 2015). Furthermore, recruitment of juveniles to the cooler western islands is reduced and highly intermittent in this region compared to the warmer eastern islands, which may have led to a slower response to protection from fishing (Caselle et al. 2010).

As expected by marine reserve theory, the establishment of marine reserves also affected other fish responses. Fish biomass differed significantly by reserve status (Fig. S1), especially among targeted species, and there were more larger fish inside of MPAs compared to fished areas. Conversely, fish densities did not differ greatly between MPAs and fished sites (Fig. S1), and although non-targeted species in the northern Channel Islands were four times more dense than targeted species, targeted species drove many of the excretion patterns. Since excretion is better predicted by biomass rather than density, my results suggest that conserving biomass instead of density is more critical for maintaining localized nutrient cycling pathways in kelp forests. Especially during the establishment of marine protected areas or expanding the network, choosing sites with more biomass and not necessarily more density of fishes will help conserve nutrient recycling. Furthermore, my results have management implications as well. While it is well established that protecting bigger fish from fish harvest improves reproductive output of the population (Hixon et al.

2014), the results from this study provide evidence that bigger fish should also be protected for their ability to contribute substantial amounts of ammonium to the ecosystem.

SPATIAL AND ENVIRONMENTAL DRIVERS OF FISH-DERIVED NUTRIENT EXCRETION

Spatial variation

Individual reefs that maintain high excretion can do so for multiple reasons. Several hot spots resulted from high nutrient excretion in response to marine protection, such as excretion by the California sheephead within the Gull Island SMR on Santa Cruz. Similarly, high excretion by Kelp bass contributed disproportionately to excretion in the Scorpion SMR site on Santa Cruz Island. Excretion rates at other sites, however, may be driven by oceanographic and habitat characteristics as predicted by the modeling results. Most notably, indicators of high primary productivity and availability of nutrient-rich waters linked primary productivity to fish community structure and areal ammonium excretion rates. For example, chlorophyll-*a* (used as a proxy for bottom-up productivity) was positively associated with excretion, likely due to the influence of primary production on the base of the food chain, which supports high fish biomass and thus nutrient excretion rates. Sites closer to the shelf break also exhibited higher nutrient excretion, potentially because these locations closer to the shelf break are more strongly influenced by bottom-up processes related to upwelling, currents, and internal waves (Vanney and Stanley 1983). The negative association between wave exposure and excretion likely results from both direct and indirect effects on the fish community. High wave action removes giant kelp and limits kelp productivity in California (Reed et al. 2011, Bell et al. 2015), thereby reducing the abundance of giant kelp, a key foundation species, that supports fish communities (Graham 2004). Wave exposure can also directly impact fish communities by producing a high energy environment that makes it difficult for fish to maintain position and forage efficiently (Fulton and Bellwood 2003), and numerous studies have reported lower fish biomass in locations of high wave exposure (Romer 1990, Friedlander et al. 2003).

It is well known that reef fishes associate with structure (Allen et al. 2006), and increased structural complexity both biotic (e.g. presence of macrophytes) and physical (e.g. rocky reefs) in nature increases shelter available to fish while providing habitat for the prey species (Jessee et al. 1985, Levin & Hay 1996). In my study, the inclusion of the mean vertical relief in the best fit excretion model suggests that greater vertical relief enhances community excretion, likely by supporting high fish biomass (Ambrose and Swarbrick 1989). The model, however, did not include other reef characteristics such as variation of mean vertical relief or mean substrate, indicative of substrate type (e.g. sand, rock). This was somewhat surprising, as previous research by Pondella et al. (2019) reported that variables associated with habitat heterogeneity (e.g. reef standard deviation and reef slope) were positively correlated with total fish biomass in the Southern California Bight, suggesting that habitat heterogeneity is important in explaining high fish biomass. These variables were not selected in the best fit model for total community excretion, and it may be due to the greater number of sites on a larger spatial scale included in the Pondella et al. (2019) study, whereas my study focuses only on the northern Channel Islands.

The inclusion of two kelp variables as significant predictors of total community excretion reinforces the paradigm that fishes are attracted to biotic sources of structure as well. However, the structure provided by kelp does not influence excretion equally, and the differing directions of kelp canopy biomass and kelp understory density in the top-ranked model reflects this distinction. Kelp canopy biomass is predicted to be positively correlated with fish excretion; as fishes utilize the structure-forming canopy of the foundational species giant kelp, the community excretes more nutrients than in areas without kelp canopy. While it may not at first be expected that understory kelp density should be negatively correlated with excretion, the understory kelp consists of other species (e.g. *Desmarestia ligulata*, *Laminaria* spp.) that do not provide as much vertical structure compared to giant kelp that can grow 30 – 50ft, and understory algae are often negatively correlated with kelp biomass since kelp is the dominant competitor that reduces light and space for other species. Since many fish prefer to associate with giant kelp (Holbrook et al. 1990) this effect is likely due to competition between giant kelp and other kelp species.

To conduct this modeling, I used 14 of the same variables described in an extensive study that tested the drivers of rocky reef biomass density variability in the Southern California Bight (Pondella et al. 2019). Surprisingly, my findings differed noticeably from leading variables that were selected to best predict biomass density in the region. Only two of the variables in my top-ranked model for excretion are consistent with the model that best predicts biomass (chlorophyll-*a*: positively correlated; distance to shelf break: negatively correlated), and some notable differences by species emerged. For example, six explanatory variables predicted Kelp bass excretion, however only one variable (mean substrate index) was included in the biomass density model, and it had confidence intervals that crossed 0. In a second example, wave height was significant and negatively correlated in 4 of my excretion models (total fish community, Kelp bass, Opaleye, and Black surfperch), but it was only included in one biomass density model (Blue rockfish), and conversely, it was positively correlated.

Temporal drivers of nutrient excretion

I observed dramatic spikes in excretion rates in 2009 – 2010 and 2016 – 2017, which may be partially explained by warming and favorable multi-species recruitment events during the 1 – 2 years prior (Caselle et al. 2015). The delayed effect on excretion is likely caused by the fact that it takes a few years for pulses of newly recruited fishes to grow to a size at which their increased numbers are sufficient to influence excretion by the total fish community. My observation that recruitment increased during the heatwave with subsequent effects on fish responses (e.g. biomass) is consistent with other studies on numerous species across the Channel Islands, Kelp bass and Kelp rockfish (Watson et al. 2010), and larval rockfishes (Caselle et al. 2010). Most notably, excretion by Blacksmith responded dramatically following each warming event and likely reflected the favorable recruitment conditions, as they are known to recruit extremely well following warming periods (Stephens et al. 1986). Blacksmith also drove excretion patterns for the planktivore trophic group; although I classified six other conspicuous species as planktivores (e.g. Señorita, Blue rockfish), temporal patterns of planktivore excretion mirrored Blacksmith excretion, including a noticeable spike in excretion in 2009 and 2016 indicative of the recruitment events.

Over the 14-year time series, the northern Channel Islands also faced changing oceanographic and climatic conditions. An unprecedented marine heat wave from 2014 –

2016 featured record-high sea surface temperatures, followed by an ENSO event in 2015 – 2016 that rivaled those of the record 1997–98 ENSO event, indicated by high ONI index values (>0.5˚C), PDO index values (>2), and MOCI values (>3) (Jacox et al. 2016, García-Reyes & Sydeman 2017, Wells et al. 2017). Extremely low NPGO values from 2013 – 2017 indicated a substantial loss of sea surface salinity, nutrients, and chlorophyll values (Di Lorenzo & Mantua 2016), leading to decreased production during this period. Interestingly, only the positively-correlated NPGO index lagged by two years was included as the best climatic index to explain temporal variability, suggesting that primary production and prey availability may influence fish community structure and subsequent fish excretion more so than sea surface temperature. As a low frequency signal of sea surface height indicative of variations in the circulation of the North Pacific Subtropical Gyre and Alaskan Gyre positive values of the NPGO are linked with increased equatorward flow in the California Current resulting in increased surface salinities, nutrients, and chlorophyll values Conversely, negative NPGO values are associated with decreases in these variables, inferring less subarctic source waters, fewer nutrients, reduced upwelling and lower production (Di Lorenzo et al. 2008). The delayed effect on excretion was likely caused by the delayed influence of increased productivity to propagate through trophic interactions.

The inclusion of NPGO and not SST, PDO, or ONI indexes in the best fit model suggests that basin-scale gyre circulation patterns that capture fluctuations in nutrient availability and productivity more than solely SST may help explain temporal variation in excretion patterns among kelp forest fishes. The inclusion of NPGO and not a different index may also be due to a number of additional reasons: 1) PDO events are a long-lived pattern of Pacific climate variability (20-30 years) and my study only spanned 14 years, 2) although ONI is useful in explaining SST anomalies, it is not a localized metric for California and my study area is narrow, and 3) MOCI, a relatively new index that synthesized over 10 climatic and oceanographic variables, may have included too many variables and prevented us from disentangling the variables of importance.

RELEVANCE OF FISH-DERIVED NUTRIENTS FOR KELP FORESTS IN CALIFORNIA

While much of the productivity in kelp forests off the coast of California is attributed to the supply of allochthonous nitrogen via oceanographic processes, my results suggest that the fish community plays a critically important role in maintaining nutrient cycles during low-nutrient periods. Seasonally, fish-derived nitrogen may be particularly important during the late summer-fall months when wind-driven coastal upwelling relaxes dramatically in the Southern California Bight resulting in a 50% reduction of nutrients to the euphotic zone (McPhee-Shaw et al. 2007). As a result of climate change, the annual frequency and severity of basin-scale climatic variability (e.g. ENSO, PDO, and NPGO events) is predicted to increase in the next century (Easterling et al. 2000, Xiu et al. 2018). Observations from the 1997-1998 ENSO event reported an 80% decrease in surface water nitrate availability and a 70% reduction in new production (Chavez et al. 2002). If future ENSO events result in similar reductions in nitrate, then fish-derived ammonium could surpass nitrate availability. Given that giant kelp has a limited ability to store nitrogen (Gerard 1982), and that the minimum concentration of nitrogen required for kelp growth is not met solely by the nitrate supply during low-nutrient periods (Reed et al. 2011, Brzezinski et al. 2013), the localized delivery of ammonium may be a key source of nitrogen to support kelp growth during low-nutrient seasonal periods. Furthermore, while nitrogen delivery from oceanographic sources is greater than that from consumers when integrated over the full water column, consumer-derived sources are concentrated near the benthos where the animals predominately live. Thus, there are certain parts of the water column where consumer-derived inputs of nutrients may be relatively more important to primary producers than that depicted in Figure 7 for the whole water column.

The role of fish-derived ammonium in kelp forest nutrient cycling may also be amplified by metabolic and thermodynamic processes. Ammonium is the preferred source of nitrogen for most algal species (Raven 1992) due to its reduced energy cost for use in metabolic processes. The redox state of nitrogen in organic tissues is predominantly -III, the same as ammonium. In contrast, the redox state of nitrate is +V. The uptake and incorporation of nitrate-N into organic matter, thus involves a multi-step redox process (assimilative nitrate reduction). This process consumes large amounts of photosynthetic energy in the form of ATP and reduced NADPH in the presence of metabolically expensive enzymes such as nitrate reductase. However, no change in redox state is required for the incorporation of ammonium-N. Thus, these nutrients are not simply taken up in proportion to their relative metabolic preference. It appears that ammonium may down-regulate the uptake of nitrate in giant kelp in order to preserve metabolic resources. Thus, when ammonium is present, even in small quantities, nitrate uptake may be inhibited. Haines and Wheeler (1978) demonstrated in lab experiments that the presence of ammonium inhibited nitrate uptake in giant kelp by a factor of 2. Using these assumptions of a 2:1 preference for ammonium-N, fish-derived excretion may dominate nitrogen uptake in kelp forests even when nitrate-N is in greater supply (see modified ammonium fluxes for fish and invertebrates to account for this process in Fig. 7).

FUTURE DIRECTIONS

Since the first publications that tested the effects of consumer-derived nutrients in kelp forests in the 1980s (Bray et al. 1986, 1988), further elucidation on the role of consumers in kelp beds largely remained untested until recent years (Hepburn & Hurd 2005; Peters et al. 2019). As such, there are numerous directions for future research that would benefit the field; for example, 1) the testing of the relationship between consumers and productivity in kelp forests via experimental manipulations, 2) the comparison of consumer nutrient supply rates to nutrient demand in both kelps and additional primary producers (e.g. phytoplankton), particularly at different levels of the water column, and 3) the species-specific translocation of nutrients within kelp beds and/or neighboring ecosystems as a result of diel or seasonal migrations. As climate change and anthropogenic impacts continue to affect nearshore ecosystems, an improved understanding of the feedbacks linking consumers to nutrient dynamics will be critical to preserving the resiliency of kelp forest ecosystems along the coast of California.

CONCLUSION

Nutrient subsidies supplied by the fish community play an important role in mediating nutrient cycling in kelp forests. Both oceanographic forcing and geologic parameters explained spatial and temporal variation in fish excretion across a 14-year time period in the northern Channel Islands, providing evidence for the pivotal role fishes may play in contributing to bottom-up forcing in kelp forest ecosystems and challenging the way we view trophic interactions in kelp systems. Fish-derived ammonium may support resiliency in kelp forests, as during these low-nutrient periods, the fish community fertilizes their own habitat with a consistent supply of limiting nitrogen to kelp forests ecosystems. Anthropogenic impacts, such as fishing, can negatively affect nutrient cycling in kelp forest ecosystems by removing fish biomass and consequently reducing nutrient excretion. However, management measures that protect fish biomass can reverse the lost nutrient cycling functions caused by fishing. Our improved understanding of the ecological, environmental, and anthropogenic factors that control spatial and temporal variation in the fish-derived nutrient supply allows for more accurate forecasting of how nutrient recycling regimes may change in the future in response to climate change, and provide evidence for the continued support of adaptive and ecosystem-based management of MPAs in coastal California.

TABLES

Table 1. Two-way ANOVA results of fish excretion rates in the northern Channel Islands by the (A) total fish community, (B) target status, and (C) trophic group.

Y	Factor	N	DF	Error df	Sum of Squares	F Ratio	Prob > F
A. Total fish community							
Total	ISLAND	3	3	97	34615	9.692	<**0.0001**
Total	RESERVE	1	1	97	25384	21.32	<**0.0001**
Total	ISLAND*RESERVE	3	3	97	8406	2.354	0.0768
B. Target status							
Targeted	ISLAND	3	3	97	4093	5.066	**0.0027**
Targeted	RESERVE	1	1	97	11370	42.22	<**0.0001**
Targeted	ISLAND*RESERVE	3	3	97	1269	1.571	0.2014
Non-targeted	ISLAND	3	3	97	19400	12.82	<**0.0001**
Non-targeted	RESERVE	1	1	97	2777	5.503	**0.0210**
Non-targeted	ISLAND*RESERVE	3	3	97	6841	4.519	**0.0052**
C. Trophic group							
Piscivore	ISLAND	3	3	97	5626	22.49	<**0.0001**
Piscivore	RESERVE	1	1	97	2190	26.26	<**0.0001**
Piscivore	ISLAND*RESERVE	3	3	97	763.4	3.051	**0.0322**
Carnivore	ISLAND	3	3	97	6081	10.62	<**0.0001**
Carnivore	RESERVE	1	1	97	2201	11.53	**0.0010**
Carnivore	ISLAND*RESERVE	3	3	97	1190	2.080	0.1079
Planktivore	ISLAND	3	3	97	1008	0.9427	0.4232
Planktivore	RESERVE	1	1	97	4170	11.69	**0.0009**
Planktivore	ISLAND*RESERVE	3	3	97	3307	3.091	**0.0306**
Herbivore	ISLAND	3	3	97	4200	58.11	<**0.0001**
Herbivore	RESERVE	1	1	97	2.681	0.111	0.7394
Herbivore	ISLAND*RESERVE	3	3	97	863	11.94	<**0.0001**

Table 2. Model selection results showing the best statistical models testing the effects of environmental drivers on spatial variation in total fish community nutrient excretion rates in the northern Channel Islands. Explanatory variables were standardized prior to analysis, and highly correlated variables (Pearson's correlation coefficient > 0.8) were not allowed in the same model.

Parameters	**No. of parameters**	**R^2**	**AICc**	**BIC**	**P-value**
Relief_mean, Wave height, Kelp biomass, Kelp density, Dist200, SS Chlorophyll-*a*	7	0.8465	236.1	236.8	**0.0019**
Relief_mean, Wave height, Kelp biomass, Kelp density, Dist200, SS Chlorophyll-*a*, Stipes	8	0.8566	239.4	238.4	0.2895
Relief_mean, Wave height, Kelp biomass, Kelp density, Dist200, SS Chlorophyll-*a*, Stipes, Substrate index mean	9	0.8609	244.3	240.8	0.4937
Relief_mean, Wave height, Kelp biomass, Kelp density, Dist200	6	0.7345	245.4	247.3	0.0749
Relief_mean, Wave height, Kelp biomass, Kelp density	5	0.6849	245.7	248.4	0.0819
Relief_mean, Wave height, Kelp biomass	4	0.6320	246.1	249.0	0.0796
Relief_mean, Wave height	3	0.5726	246.7	249.6	0.0847

Table 3. Full-factorial results of the General Linear Model with the factors of year, island, and reserve for excretion rates by the (A) total fish community, (B) target status, and (C) trophic group.

Y	Factor	N	DF	Error	Sum of Squares	F Ratio	Prob > F
A. Total fish community							
Total	year	1	1	89	16458	17.68	**<0.0001**
Total	ISLAND	3	3	89	32697	11.71	**<0.0001**
Total	year*ISLAND	3	3	89	6311	2.261	0.0869
Total	RESERVE	1	1	89	24620	26.45	**<0.0001**
Total	year*RESERVE	1	1	89	2880	3.095	0.0820
Total	ISLAND*RESERVE	3	3	89	8107	2.904	**0.0392**
Total	year*ISLAND*RESERVE	3	3	89	4596	1.646	0.1845
B. Target status							
Targeted	year	1	1	89	5769	33.25	**<0.0001**
Targeted	ISLAND	3	3	89	3734	7.172	**0.0002**
Targeted	year*ISLAND	3	3	89	2582	4.959	**0.0031**
Targeted	RESERVE	1	1	89	11168	64.36	**<0.0001**
Targeted	year*RESERVE	1	1	89	529	3.047	0.0843
Targeted	ISLAND*RESERVE	3	3	89	1058	2.033	0.1150
Targeted	year*ISLAND*RESERVE	3	3	89	1120	2.152	0.0993
Non-targeted	year	1	1	89	2739	5.757	**0.0185**
Non-targeted	ISLAND	3	3	89	18982	13.30	**<0.0001**
Non-targeted	year*ISLAND	3	3	89	1164	0.816	0.4885
Non-targeted	RESERVE	1	1	89	2624	5.517	**0.0210**
Non-targeted	year*RESERVE	1	1	89	941	1.978	0.1631
Non-targeted	ISLAND*RESERVE	3	3	89	6813	4.774	**0.0039**
Non-targeted	year*ISLAND*RESERVE	3	3	89	1230	0.8618	0.4641
C. Trophic group							
Piscivore	year	1	1	89	1752	33.54	**<0.0001**
Piscivore	ISLAND	3	3	89	5361	34.22	**<0.0001**
Piscivore	year*ISLAND	3	3	89	1057	6.749	**0.0004**
Piscivore	RESERVE	1	1	89	2116	40.52	**<0.0001**
Piscivore	year*RESERVE	1	1	89	140.8	2.697	0.1041
Piscivore	ISLAND*RESERVE	3	3	89	688.1	4.392	**0.0063**
Piscivore	year*ISLAND*RESERVE	3	3	89	242.8	1.550	0.2072
Carnivore	year	1	1	89	191.3	1.230	0.2704
Carnivore	ISLAND	3	3	89	6292	13.48	**<0.0001**
Carnivore	year*ISLAND	3	3	89	3243	6.950	**0.0003**

Carnivore	RESERVE	1	1	89	2206	14.18	**0.0003**
Carnivore	year*RESERVE	1	1	89	164.1	1.055	0.3071
Carnivore	ISLAND*RESERVE	3	3	89	1119	2.399	**0.0732**
Carnivore	year*ISLAND*RESERVE	3	3	89	905.0	1.940	0.1289
Planktivore	year	1	1	89	4257	13.02	**0.0005**
Planktivore	ISLAND	3	3	89	1235	1.259	0.2934
Planktivore	year*ISLAND	3	3	89	599.0	0.610	0.6100
Planktivore	RESERVE	1	1	89	4034	12.33	**0.0007**
Planktivore	year*RESERVE	1	1	89	358.1	1.095	0.2982
Planktivore	ISLAND*RESERVE	3	3	89	3297	3.360	**0.0223**
Planktivore	year*ISLAND*RESERVE	3	3	89	240.7	0.245	0.8645
Herbivore	year	1	1	89	81.0	4.116	**0.0455**
Herbivore	ISLAND	3	3	89	4107	69.55	**<0.0001**
Herbivore	year*ISLAND	3	3	89	59.1	1.000	0.3966
Herbivore	RESERVE	1	1	89	1.2	0.062	0.8041
Herbivore	year*RESERVE	1	1	89	70.9	3.601	0.0610
Herbivore	ISLAND*RESERVE	3	3	89	818.2	13.86	**<0.0001**
Herbivore	year*ISLAND*RESERVE	3	3	89	351.5	5.953	**0.0010**

Table 4. Model selection results showing the best statistical models testing the effects of environmental drivers on temporal variation in total fish community nutrient excretion rates in the northern Channel Islands.

Parameters	**Number of parameters**	**R^2**	**AICc**	**BIC**	**P-value**
REC DENSITY-2, NPGO-2	3	0.5710	128.8	126.9	**0.0155**
REC DENSITY-2	2	0.2523	132.5	132.0	0.0672
REC DENSITY-2, NPGO-2, ONI-2	4	0.6041	132.7	128.4	0.3827
REC DENSITY-2, NPGO-2, ONI-2, SST-3	5	0.6875	135.9	127.8	0.1555

Table 5. A comparison of consumer-derived excretion rates of ammonium in aquatic ecosystems. FW = Freshwater system; NA = not available.

			Areal nutrient supply (µmol NH_4^+ m^{-2} hr^{-1})		
Source	**System**	**Assembly**	**Range**	**Mean**	**Notes**
Shrestha et al. (this study)	Marine	community	23 – 183	96	Fish community in the Channel Islands
Peters et al. (2019)	Marine	community	0.06 – 59	18	Invertebrates in kelp forests of the Santa Barbara Channel
Bray et al. (1988)	Marine	community	25 – 30	NA	Benthic macroinvertebrates and 6 species of fish in California
Bray et al. (1986)	Marine	population	NA	43	Blacksmith in kelp forests
Allgeier et al. (2014)	Marine	community	0.69 – 46	23	Fish on tropical reefs in the Bahamas
Burkepile et al. (2013)	Marine	community	NA	83	Fish in tropical reefs - Florida keys
Shantz et al. (2015)	Marine	population	12 – 116	NA	Tropical haemulid grunts
Archer et al. (2015)	Marine	population	NA	806	Tropical fish spawning aggregations of groupers (> 1,500 fish)
Haertel-Borer et al. (2004)	Marine	community	NA	155	Fish in temperate tidal creek
Layman et al. (2011)	Marine	population	NA	138	Gray snapper in tropical tidal creek
Meyer et al. (1983)	Marine	population	NA	237	Fish in tropical coral reef
Allgeier et al. (2013)	Marine	community	NA	96	Fish in artificial tropical reefs
Schaus et al. (1997)	FW	population	77 – 121	NA	Gizzard shad in eutrophic lake
McIntyre et al. (2008)	FW	community	NA	76	Fish in tropical river
Small et al. (2011)	FW	community	NA	48	Fish in tropical river
Verant et al. (2007)	FW	community	0.05 – 11	NA	Fish in temperate lake
Vanni et al. (2006)	FW	population	0.97 – 12	NA	Fish in temperate lakes
Hernández-Léon, Fraga & Ikeda (2008)	Marine	population	29 – 45	NA	Mesozooplankton in temperate regions

FIGURES

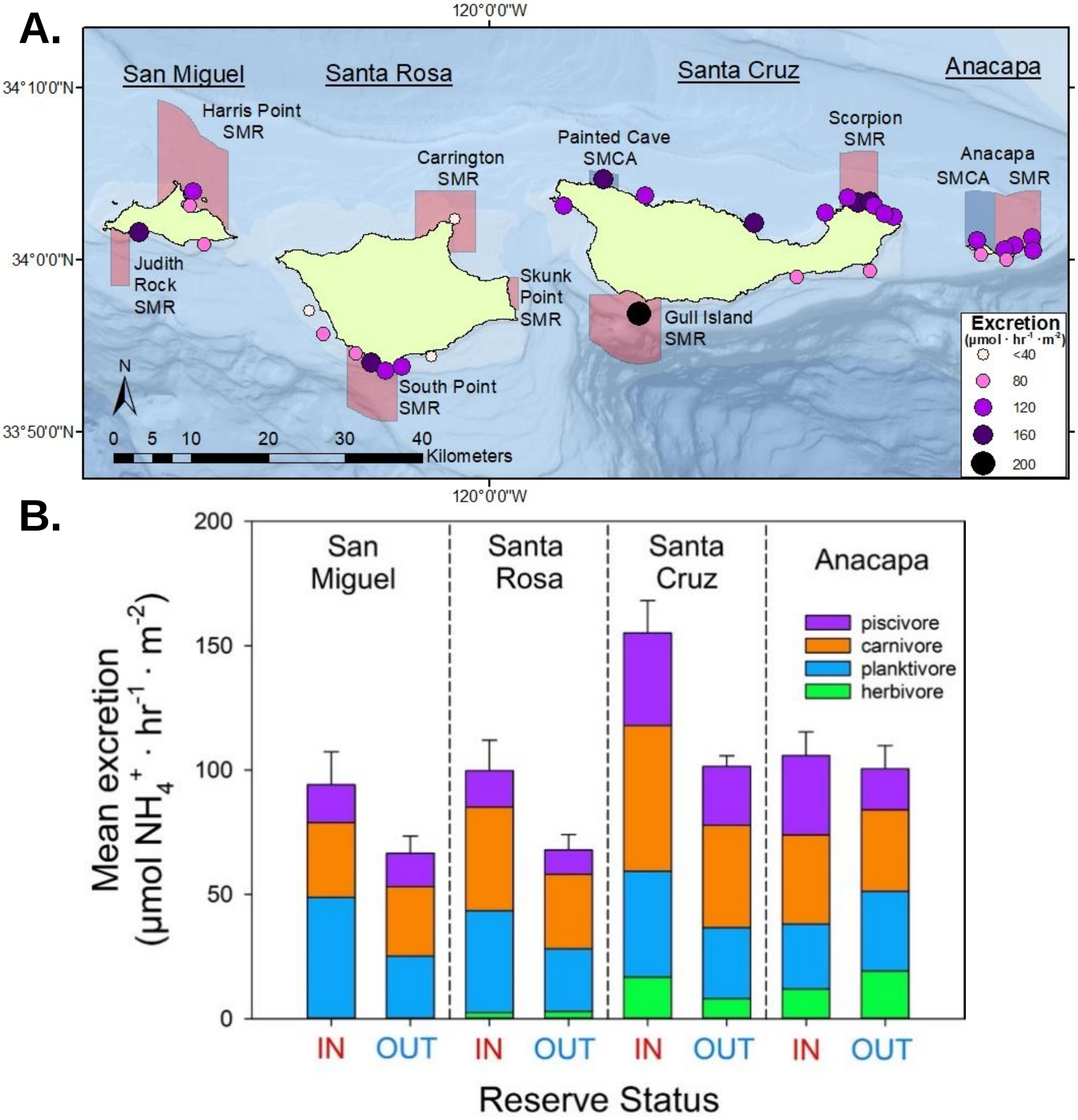


Figure 1. Average ammonium excretion rates by the total fish community in the Northern Channel Islands.(A) Map of ammonium excreted at the study sites; darker shades and larger bubbles reflect greater community-level nutrient excretion. State Marine Reserves, where fishing is prohibited, are indicated by red boxes. State Marine Conservation Areas are indicated with blue boxes; however, fishing on the species included in this study is not permitted and they functionally serve as marine reserves. (B) Bar plot depicting excretion by trophic group by reserve status on each island. Error bars are ± 1 standard error on the overall mean excretion inside and outside of reserves per island.

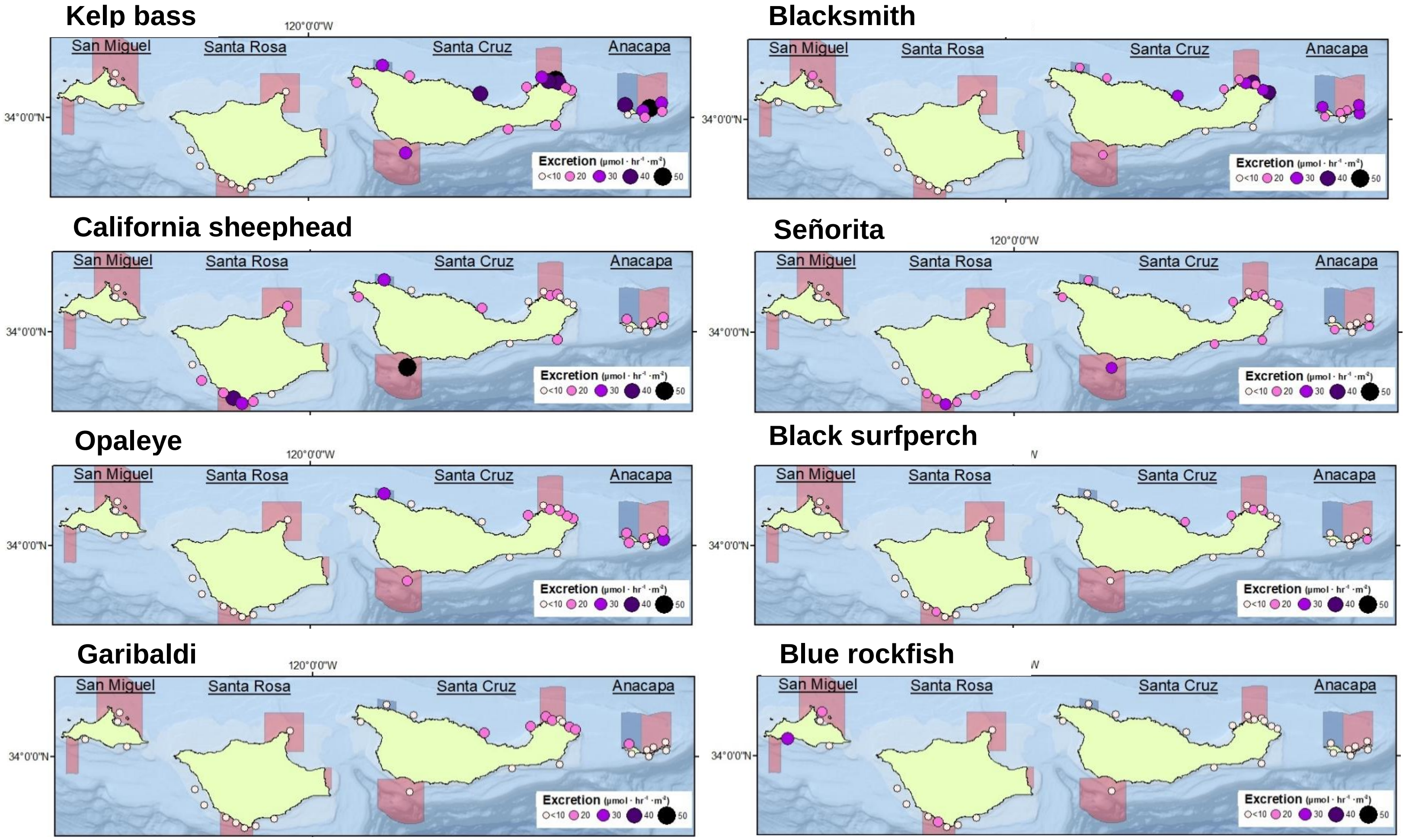


Figure 2. Maps of the ammonium excretion rates by the focal fish species at the study reef sites in the northern Channel Islands. Averaged across all sites over the 15-year time period, these eight species accounted for 80.6% of total fish community excretion. Darker shades and larger bubbles reflect higher nutrient excretion by individual species. State Marine Reserves, where fishing is prohibited, are indicated by red boxes. State Marine Conservation Areas are indicated with blue boxes.

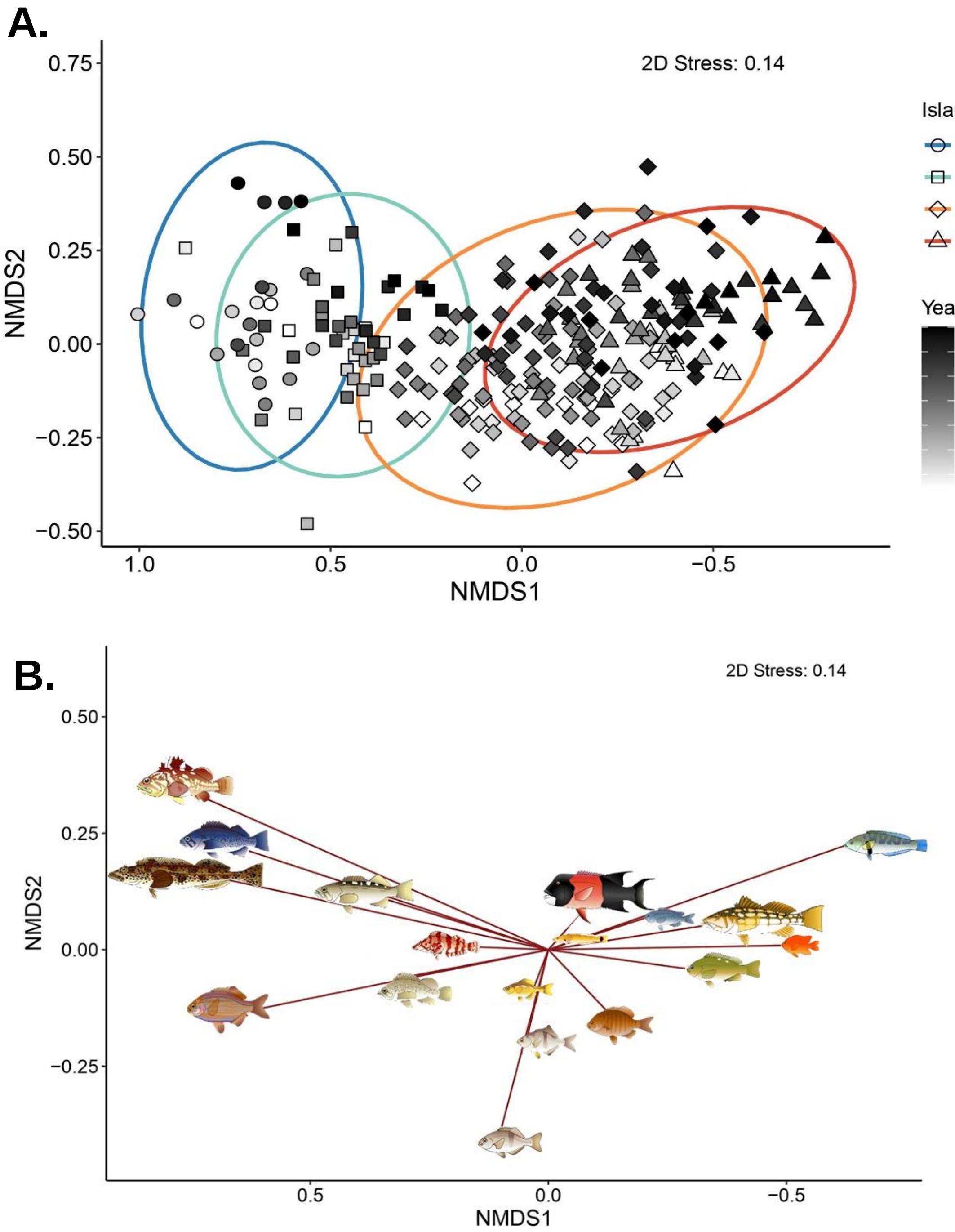


Figure 3. Nonmetric multidimensional scaling plots depicting (A) spatial and temporal shifts in areal ammonium excretion rates by the fish assemblage in the northern Channel Islands and (B) vectors indicating which species contribute most to ammonium excretion among islands and years. The magnitude and direction of vectors indicate strength of correlation of individual species excretion rates with the ordination axes.

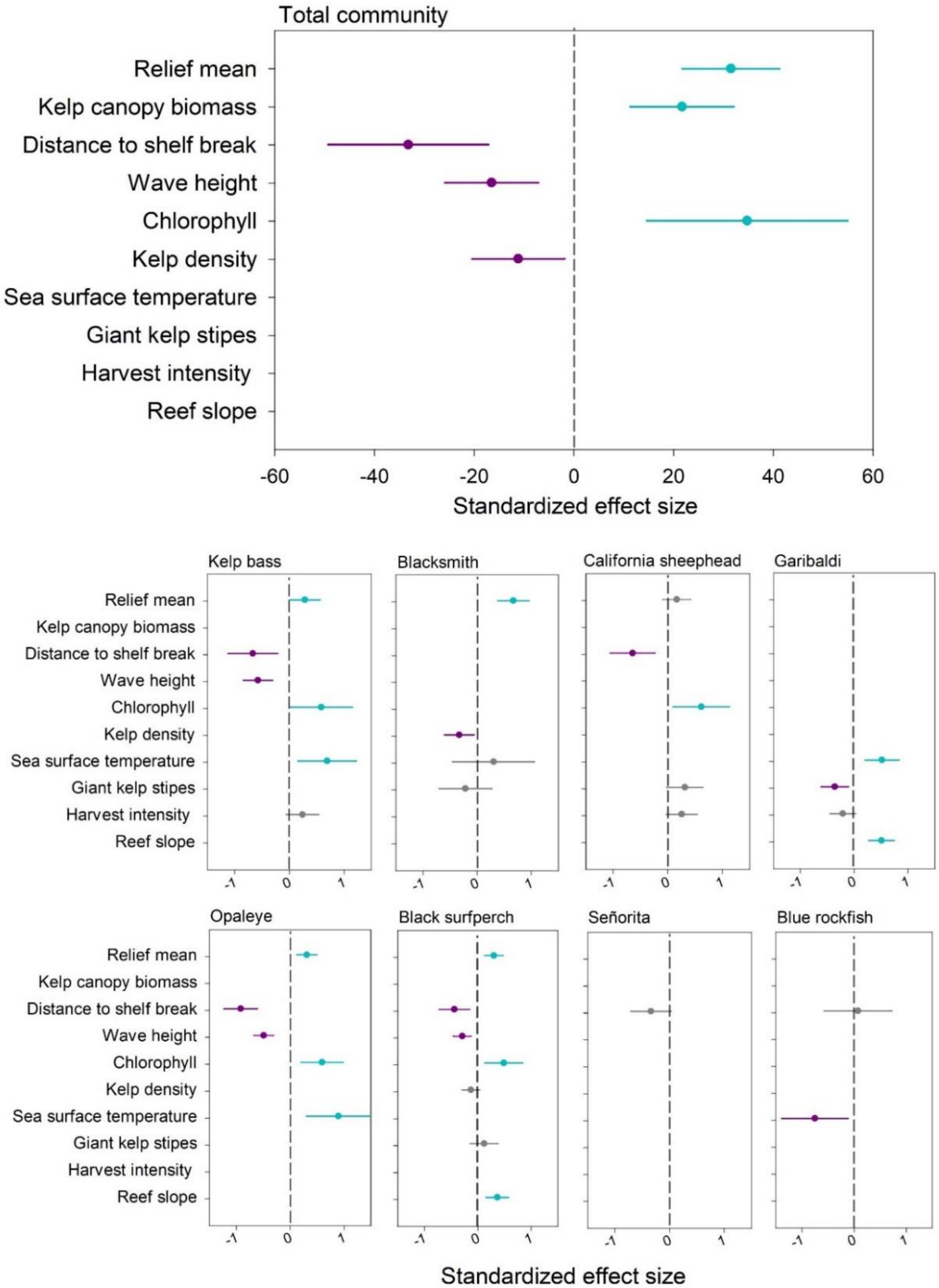


Figure 4. Predictor variables explaining spatial variability in fish nutrient excretion rates included in the top-ranked models for the total fish community (top panel) and 8 key species (bottom panels). Parameter estimates are the mean standardized effect size and 95% confidence interval. Positive (teal symbols) and negative (purple symbols) effect sizes denote a significant association, whereas gray symbols are not significantly different than zero.

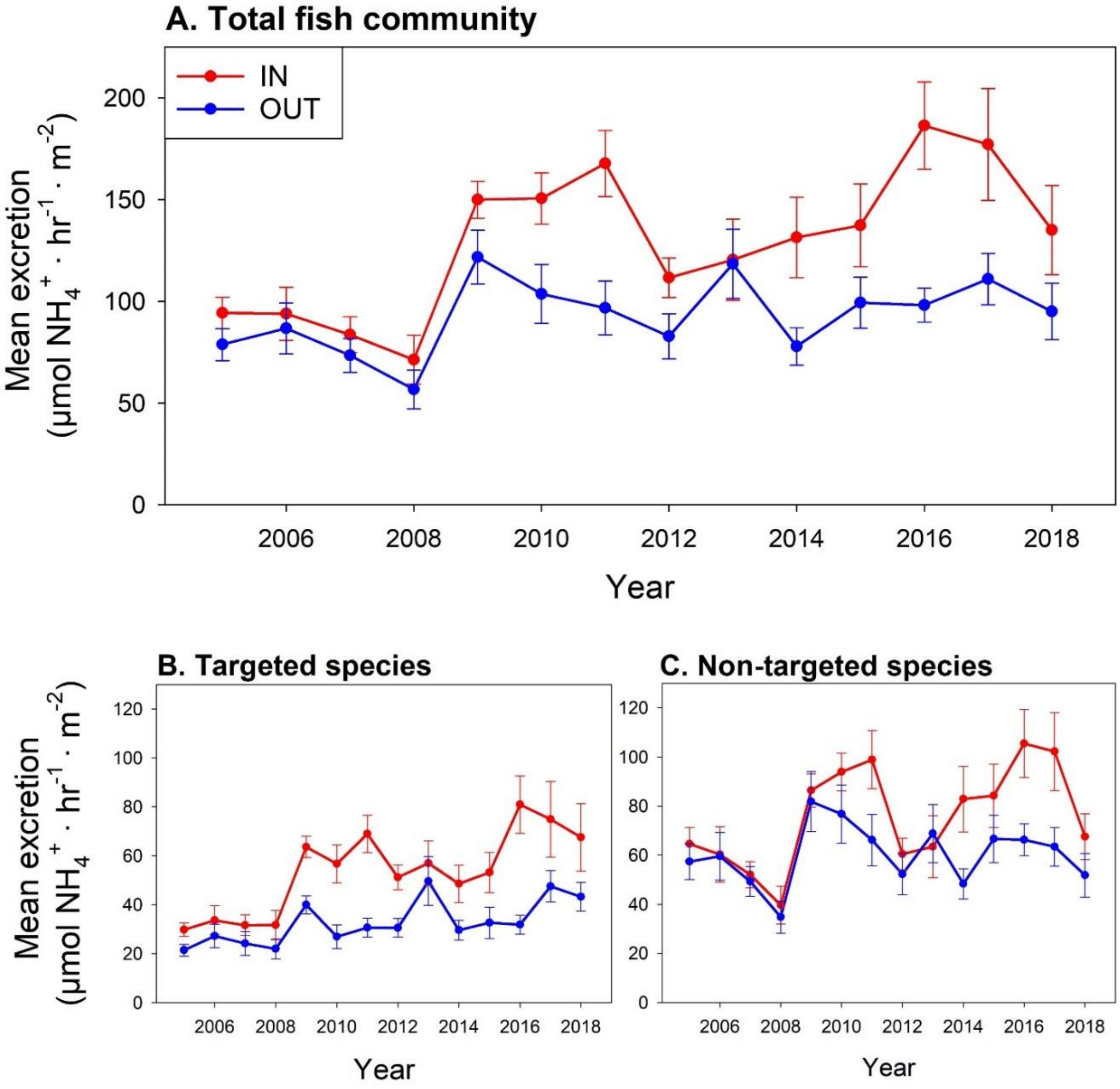


Figure 5. Mean fish excretion rates per year over the 15-year time period inside and outside MPAs for the (A) total fish community, (B) targeted species, and (C) non-targeted species. Red lines indicate excretion within reserves, while blue lines indicate mean excretion outside of reserves. Error bars are ± 1 standard error.

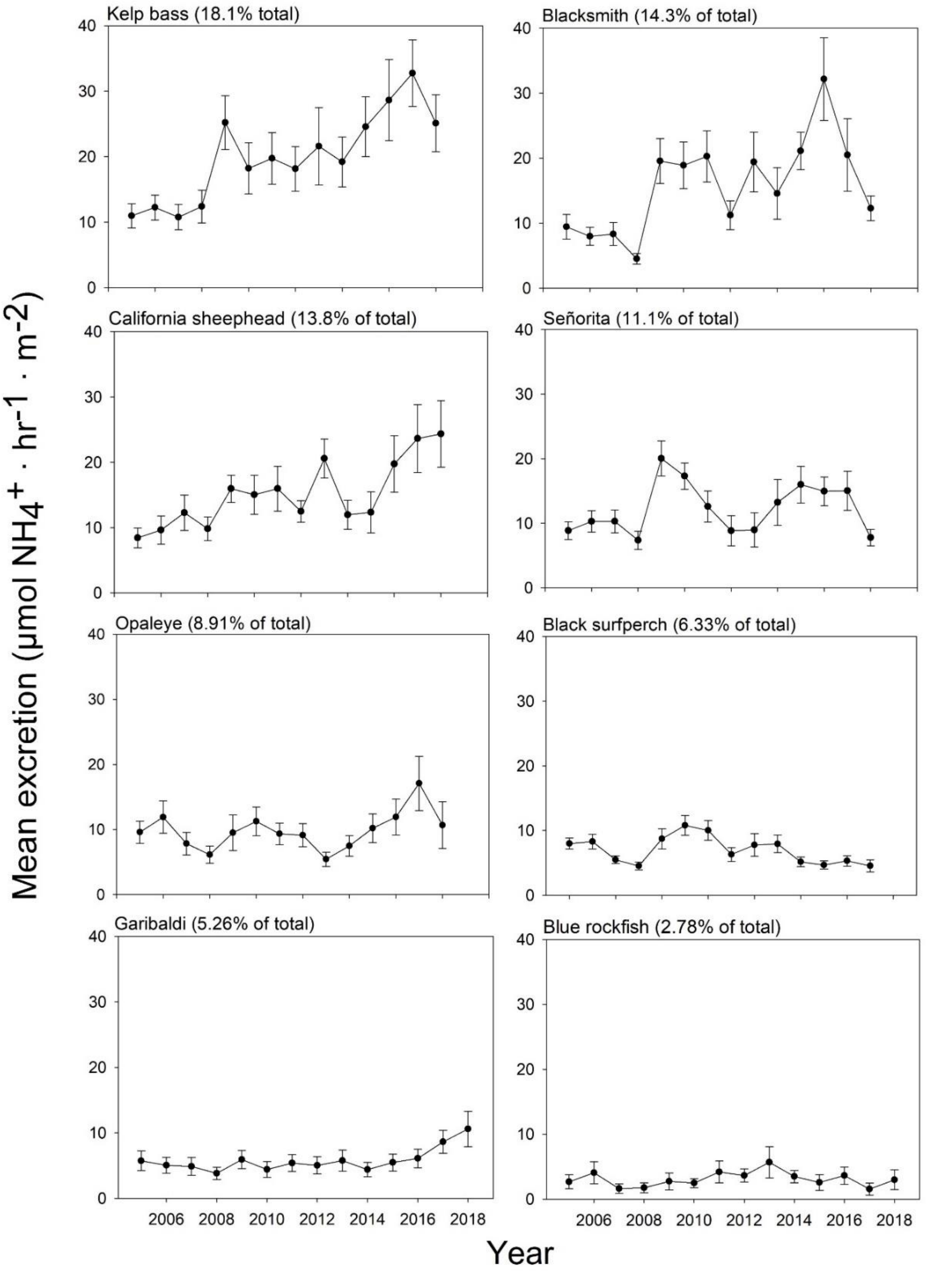


Figure 6. Mean excretion rates by focal species over time. Selected species excrete 80.6% of the total community ammonium supply. Shown are mean values ± 1 standard error.

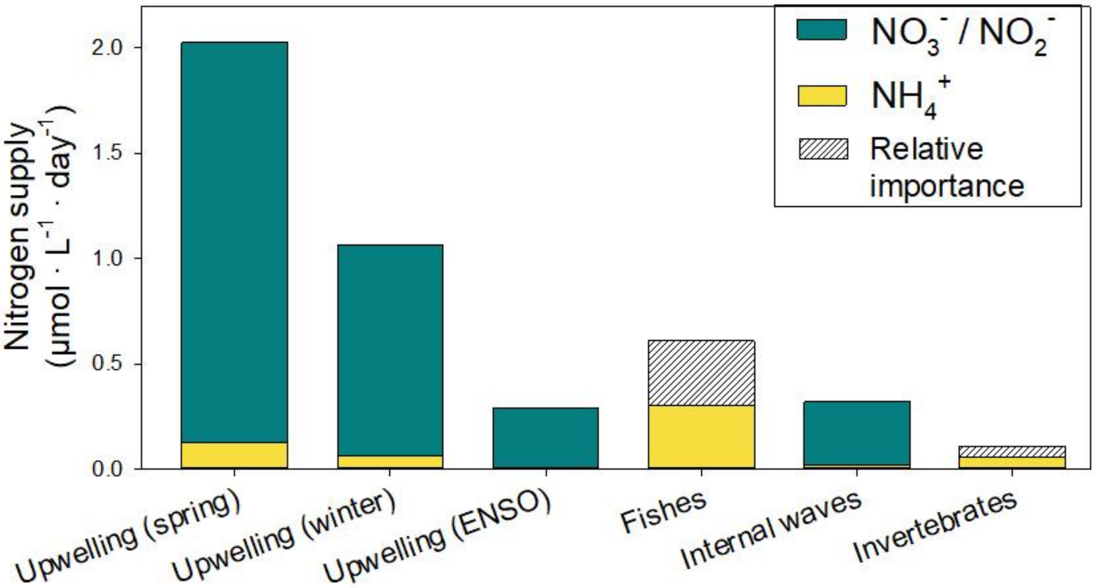


Figure 7. Comparison of fish-derived nitrogen fluxes relative to other nitrogen sources in southern California kelp forests. Oceanographic nitrate and nitrite values from McPhee-Shaw et al. (2007) and the oceanographic delivery of ammonium was calculated by the multiplication of nitrate rate by 0.066, the estimated ratio of NH_4^+ to NO_3^- below the nutricline (Bronk & Ward 2005). The nitrate delivery rate during an El Niño -Southern Oscillation (ENSO) event was estimated from the reduced ambient nitrate availability during the 1997 – 1998 ENSO event (Chavez et al. 2002). Volumetric invertebrate-derived ammonium excretion rate was calculated from Peters et al. (2019). The striped portion of the bar above the fish and invertebrate excretion rates denotes the potential significance of consumer-derived nutrients; ammonium inhibits nitrate uptake in giant kelp by a factor of 2 (Haines & Wheeler 1978).

APPENDIX

Table S1. Study species by classification status and predictive excretion rate.Targeted status based on Recreational Fisheries Information Network (RecFIN) recreational catch records from 2005-2018. Each species in the PISCO dataset was assigned to a trophic group (herbivore, planktivore, carnivore, and piscivore) based on published diet studies. N refers to the number of times the species was observed on a transect throughout the 14-year time series.

Family Excretion Equation (µmol indiv^{-1} g^{-1} hr^{-1})				
Scientific name	Common name	Target status	Trophic group	N
1. Embiotocidae $y = 0.7855\,(x) + 0.6775$				
Brachyistius frenatus	Kelp surfperch	Non-targeted	Carnivore	9071
Cymatogaster aggregata	Shiner surfperch	Non-targeted	Carnivore	252
Embiotoca jacksoni	Black surfperch	Targeted	Carnivore	9682
Embiotoca lateralis	Striped surfperch	Targeted	Carnivore	4553
Hyperprosopon analis	Spotfin surfperch	Non-targeted	Carnivore	33
Hyperprosopon argenteum	Walleye surfperch	Non-targeted	Carnivore	2
Hyperprosopon ellipticum	Silver surfperch	Non-targeted	Carnivore	1034
Hypsurus caryi	Rainbow surfperch	Non-targeted	Carnivore	3
Micropetrus minimus	Dwarf surfperch	Non-targeted	Carnivore	2
Phanerodon atripes	Sharpnose surfperch	Non-targeted	Carnivore	9
Phanerodon furcatus	White surfperch	Non-targeted	Carnivore	117
Rhacochilus toxotes	Rubberlip surfperch	Targeted	Carnivore	750
Rhacochilus vacca	Pile surfperch	Targeted	Carnivore	3483
2. Hexagrammidae $y = 0.8958\,(x) + 0.2933$				
Hexagrammos decagrammus	Kelp greenling	Targeted	Carnivore	42
Hexagrammos lagocephalus	Rock greenling	Targeted	Carnivore	1
Ophiodon elongatus	Lingcod	Targeted	Piscivore	236
Oxylebius pictus	Painted greenling	Non-targeted	Carnivore	7468
3. Kyphosidae $y = 0.7981\,(x) + 0.5000$				
Girella nigricans	Opaleye	Non-targeted	Herbivore	4957
Medialuna californiensis	Halfmoon	Non-targeted	Herbivore	3013
4. Labridae $y = 0.7573\,(x) + 0.7401$				
Halicoeres semicinctus	Rock wrasse	Non-targeted	Carnivore	5891
Oxyjulis californica	Señorita	Non-targeted	Planktivore	17346
Semicossyphus pulcher	California sheephead	Targeted	Carnivore	11484
5. Pomacentridae $y = 0.7981\,(x) + 0.5585$				
Chromis punctipinnis	Blacksmith	Non-targeted	Planktivore	15375
Hypsypops rubicundus	Garibaldi	Non-targeted	Carnivore	5963
6. Scorpaenidae $y = 0.7573\,(x) + 0.3489$				

Scorpaena guttata	California scorpionfish	Targeted	Piscivore	44

7. Sebastidae $\mathbf{y = 0.6620\ (x) + 0.6394}$

Sebastes atrovirens	Kelp rockfish	Targeted	Piscivore	6569
Sebastes auriculatus	Brown rockfish	Targeted	Piscivore	147
Sebastes carnatus	Gopher rockfish	Targeted	Piscivore	566
Sebastes caurinus	Copper rockfish	Targeted	Piscivore	823
Sebastes chrysomelas	Black-and-yellow rockfish	Targeted	Piscivore	722
Sebastes dallii	Calico rockfish	Targeted	Piscivore	3
Sebastes diploproa	Splitnose rockfish	Targeted	Planktivore	1
Sebastes entomelas	Widow rockfish	Targeted	Planktivore	1
Sebastes flavidus	Yellowtail rockfish	Non-targeted	Planktivore	3915
Sebastes hopkinsi	Squarespot rockfish	Targeted	Planktivore	4
Sebastes melanops	Black rockfish	Targeted	Piscivore	142
Sebastes miniatus	Vermilion rockfish	Targeted	Piscivore	259
Sebastes mystinus	Blue rockfish	Targeted	Planktivore	6028
Sebastes nebulosus	China rockfish	Targeted	Piscivore	1
Sebastes paucispinis	Bocaccio	Targeted	Piscivore	162
Sebastes pinniger	Canary rockfish	Targeted	Piscivore	13
Sebastes rastrelliger	Grass rockfish	Targeted	Piscivore	85
Sebastes rosaceus	Rosy rockfish	Targeted	Carnivore	3
Sebastes rubrivinctus	Flag rockfish	Targeted	Carnivore	4
Sebastes saxicola	Stripetail rockfish	Targeted	Planktivore	7
Sebastes semicinctus	Halfbanded rockfish	Targeted	Carnivore	6
Sebastes serranoides	Olive rockfish	Non-targeted	Planktivore	3915
Sebastes serriceps	Treefish	Targeted	Piscivore	764
Sebastes spp.	Rockfish YOY	Non-targeted	Planktivore	1239

8. Serranidae $\mathbf{y = 0.8195\ (x) + 0.4593}$

Paralabrax clathratus	Kelp bass	Targeted	Piscivore	17028
Paralabrax nebulifer	Barred sandbass	Targeted	Piscivore	2

Table S2. Summary of reef-scale explanatory variables in the northern Channel Islands. Data were sourced from Pondella et al. (2019); see paper for detailed explanations on predictor variables, collection methods, and data sources. [a]The temporal resolution of each variable was calculated as the grand mean 2-10 years preceding the survey and inclusive of the sampling year. Surveys were conducted in 2004, 2008, 2011, and 2012.

Variable	Abbrev.	Unit	Spatial resolution	[a]Temporal resolution
Distance to the shelf break	DIST	m	200 m^2	Not applicable
Reef slope	SLOP	°	200 m^2; steepest downhill descent in cell	Not applicable
Maximum wave height	WHM	m	Buoys located closest to site	Preceding 2 years
Kelp Canopy Biomass	KBIO	Wet kg m-2	900 m^2 radius around site	Preceding 2 years
Sea Surface Chlorophyll *a*	CHL	Mg m-2	1 km^2; mean of four grid cells adjacent to site	Preceding 5 years
Sea Surface Temperature	SST	°C	1 km^2 – mean of four grid cells adjacent to site	Preceding 5 years
Harvest Intensity Index	HII	MT yr^{-1} km^{-1}	100 km^2	Preceding 10 years
Urchin density	UD	No. m^{-2}	SCUBA collection	Day of survey
Giant Kelp Stipes	STIP	No. m^{-2}	SCUBA count of stipes per individual	Day of survey
Kelp Understory Spp. Density	KUSP	No. m^{-2}	SCUBA collection	Day of survey
Mean Relief Index	MRI	No. m^{-2}	SCUBA quantification of relief types	Day of survey
Relief Index Standard Deviation	RISD	No. m^{-2}	SCUBA collection	Day of survey
Mean Substrate Index	MSI	No. m^{-2}	SCUBA quantification of substrate types	Day of survey
Substrate Index Standard Deviation	SISD	No. m^{-2}	SCUBA collection	Day of survey

Table S3. Pearson's correlation table of environmental variables used in the spatial analysis of geographic variation in total community nutrient excretion rates. Variables that were highly correlated (>0.8) were not included in the same model, and all variables were standardized.

	Relief mean	**Wave height**	**Dist 200**	**SS Chl**	**Kelp biomass**	**Kelp density**	**substrate index SD**	**SST**	**Urchin density**	**stipes**	**Relief sd**	**Substrate index mean**	**MT reef**	**Reef slope**
relief_ mean	1.0	-0.24	-0.24	-0.04	-0.50	0.04	0.27	0.27	0.37	-0.45	0.95	0.12	-0.13	0.72
Wave height	-0.24	1.0	0.32	0.38	0.32	0.02	-0.40	-0.62	-0.38	0.18	-0.18	0.48	-0.28	-0.56
Dist 200	-0.24	0.32	1.0	0.79	0.12	-0.25	-0.06	-0.66	-0.27	0.15	-0.24	0.21	-0.01	-0.26
SS Chl	-0.04	0.38	0.79	1.0	-0.15	-0.31	-0.25	-0.52	-0.09	-0.06	-0.10	0.32	0.25	-0.04
kelp biomass	-0.50	0.32	0.12	-0.15	1.0	0.21	-0.24	-0.57	-0.58	0.75	-0.34	0.25	-0.41	-0.57
kelp density	0.04	0.02	-0.25	-0.31	0.21	1.0	0.17	0.07	-0.33	0.36	0.12	-0.01	-0.18	-0.05
substrate index SD	0.27	-0.40	-0.06	-0.25	-0.24	0.17	1.0	0.20	-0.06	0.04	0.29	-0.47	0.10	0.23
SST	0.27	-0.62	-0.66	-0.52	-0.57	0.07	0.20	1.0	0.53	-0.46	0.16	-0.66	0.36	0.51
urchin density	0.37	-0.38	-0.27	-0.09	-0.58	-0.33	-0.06	0.53	1.0	-0.74	0.23	-0.17	0.31	0.46
stipes	-0.45	0.18	0.15	-0.06	0.75	0.36	0.04	-0.46	-0.74	1.0	-0.35	0.02	-0.36	-0.31
relief sd	0.95	-0.18	-0.24	-0.10	-0.34	0.12	0.29	0.16	0.23	-0.35	1.0	0.16	-0.22	0.53
substrate index mean	0.12	0.48	0.21	0.32	0.25	-0.01	-0.47	-0.66	-0.17	0.02	0.16	1.0	-0.39	-0.19
MT_reef	-0.13	-0.28	-0.01	0.25	-0.41	-0.18	0.10	0.36	0.31	-0.36	-0.22	-0.39	1.0	0.12
Reef slope	0.72	-0.56	-0.26	-0.04	-0.57	-0.05	0.23	0.51	0.46	-0.31	0.53	-0.19	0.12	1.0

Table S4. Summary of oceanographic indices used to test temporal variation in total ammonium excretion rates. The temporal resolution for each index was from 2002 – 2018. See sources for further details on how the indices are calculated.

Index name	**Abbv.**	**Description**	**Spatial resolution**	**Source**
Sea surface temperature	SST	Mean sea surface temperature	-120°W, 34°N	NOAA[1]
Pacific Decadal Oscillation	PDO	Long-lived (20-60 years) pattern of climate variability in the north Pacific. Index variables include: - SST - sea level pressure - surface wind stress	North of 20°N	NOAA[2] (based on Mantua et al. 1997)
North Pacific Gyre Oscillation	NPGO	Correlation between sea level height and fluctuations in salinity, nutrients, and chlorophyll-*a*.	180°W - 110°W 25°N –62°N	Lorenzo et al. (2008)[3]
Oceanic Niño Index	ONI	Short-term indicator of El Niño-Southern Oscillation events calculated as the 3-month mean of SST.	5°N-5°S, 120°-170º°W	NOAA[4]
Multivariate Ocean Climate Index	MOCI	Indicator that synthesizes ocean and atmospheric conditions in California, including: - ENSO index - PDO - NPGO - Northern Oscillation - Bakun Upwelling Index - Sea level - Wind stress - Sea surface temperature - Sea level pressure - Sea air temperature	32°N - 34.5°N	García-Reyes & Sydeman (2017)[5]

Sources:

[1] https://giovanni.gsfc.nasa.gov/

[2] https://www.ncdc.noaa.gov/teleconnections/pdo/

[3] http://www.o3d.org/npgo/npgo.php

[4] https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php

[5] http://www.faralloninstitute.org/moci

Table S5. Pearson's correlation table of environmental variables used in the temporal analysis of drivers associated with nutrient excretion rates over the 15-year timeseries. Variables listed here represent only the parameters included in the top models, and variables that were highly correlated (>0.8) were not included in the same model. Lagged values of each variable are indicated by the number of years at which the lag was applied (e.g. "REC-2" refers to the mean recruit density offset by two years).

	REC -2	**NPGO-2**	**ONI-2**	**SST-3**
REC-2	1.0	-0.67	0.66	0.39
NPGO-2	-0.67	1.0	-0.64	-0.53
ONI-2	0.66	-0.64	1.0	0.68
SST-3	0.39	-0.53	0.68	1.0

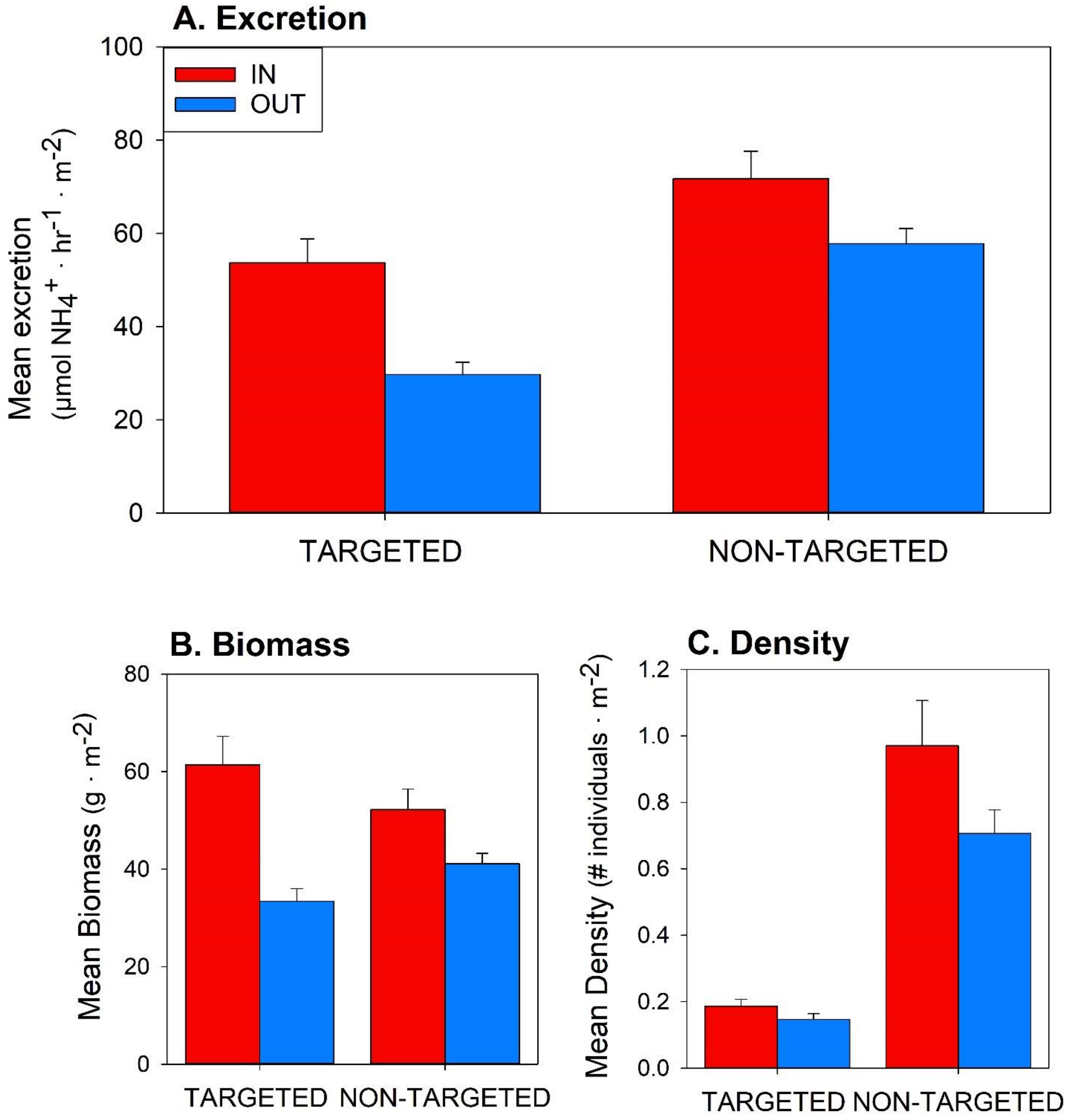
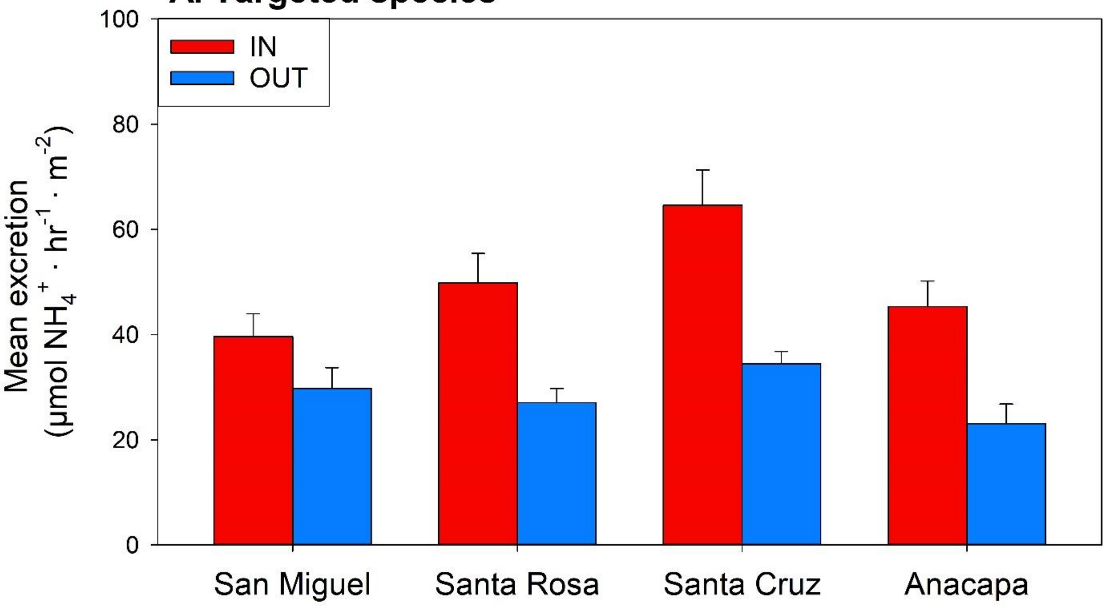


Figure S1. Effect of target status on average fish (A) excretion rates, (B) biomass, and (C) density by marine reserve status. Shown are mean values ± 1 standard error.


A. Targeted species

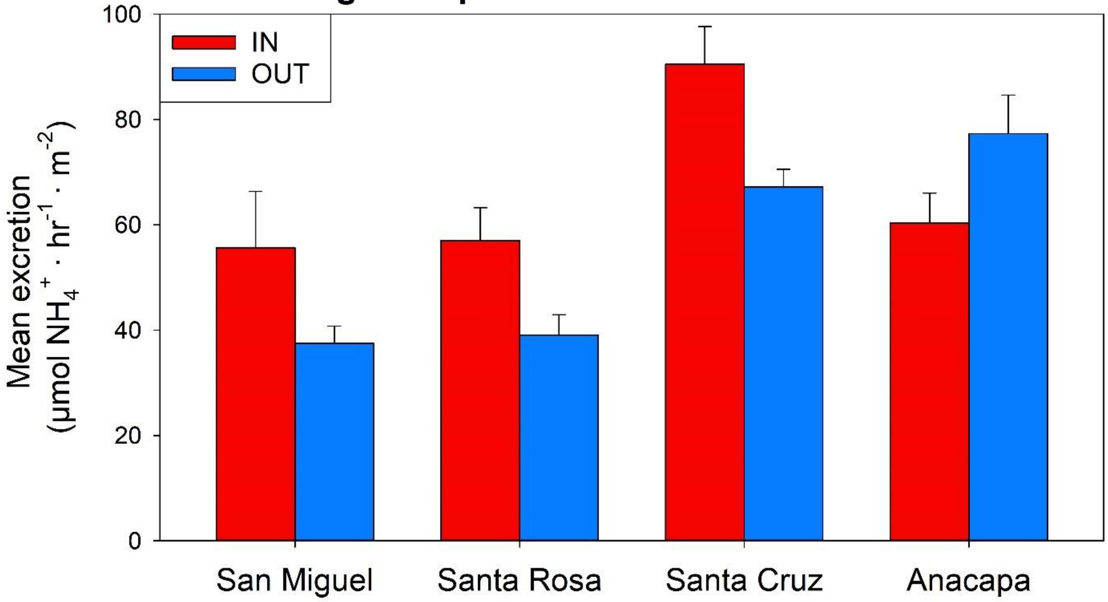

B. Non-targeted species

Figure S2. Fish excretion rates by island and marine reserve status for (A) targeted species and (B) non-targeted species. Shown are mean values ± 1 standard error.

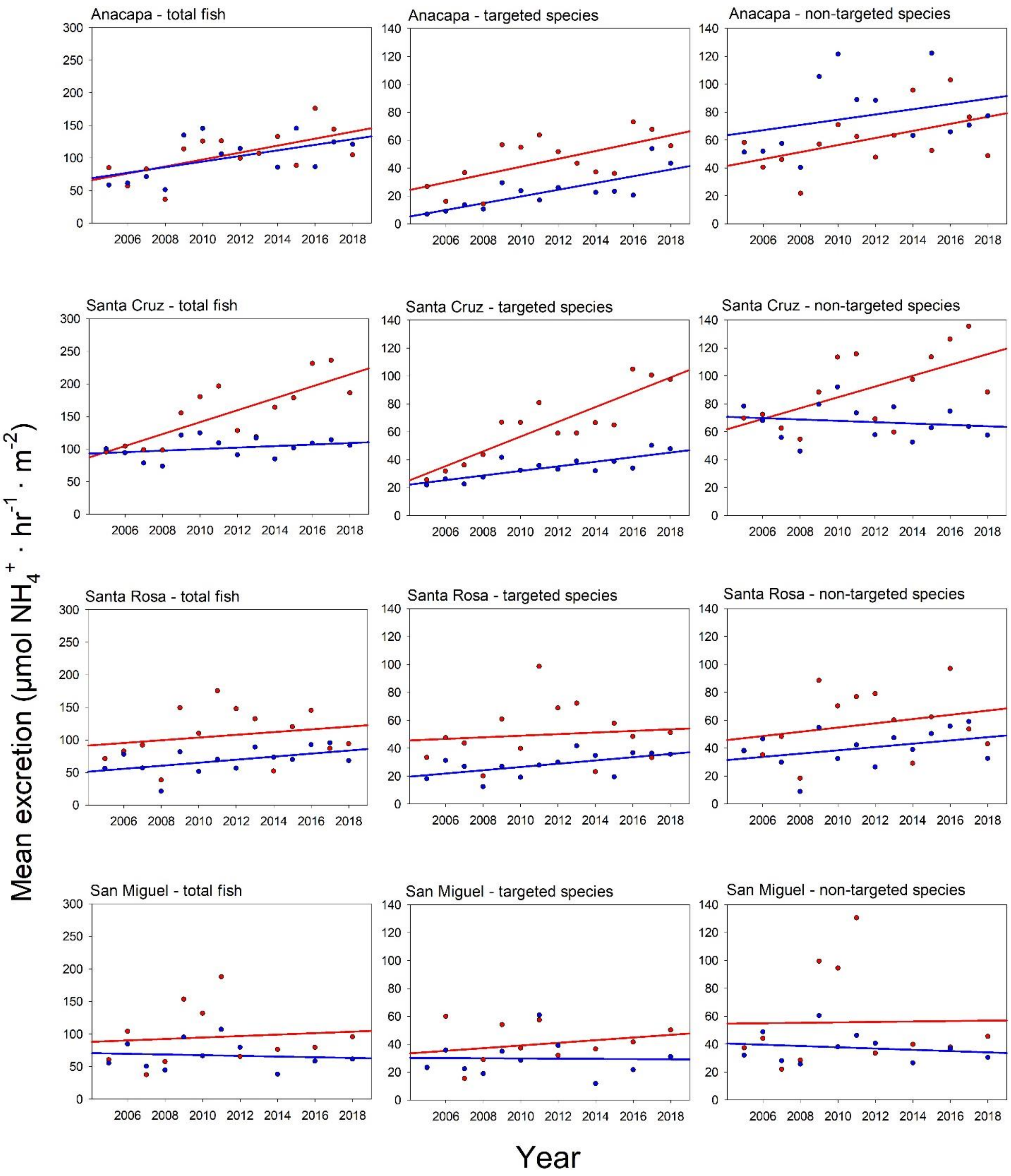


Figure S3. Trajectories of change in fish excretion rates inside (red) and outside (blue)MPAs across the islands in the Northern Channel Islands. Shown are total excretion rates (left panels), targeted species (middle panels), and non-targeted species (right panels) on each island.

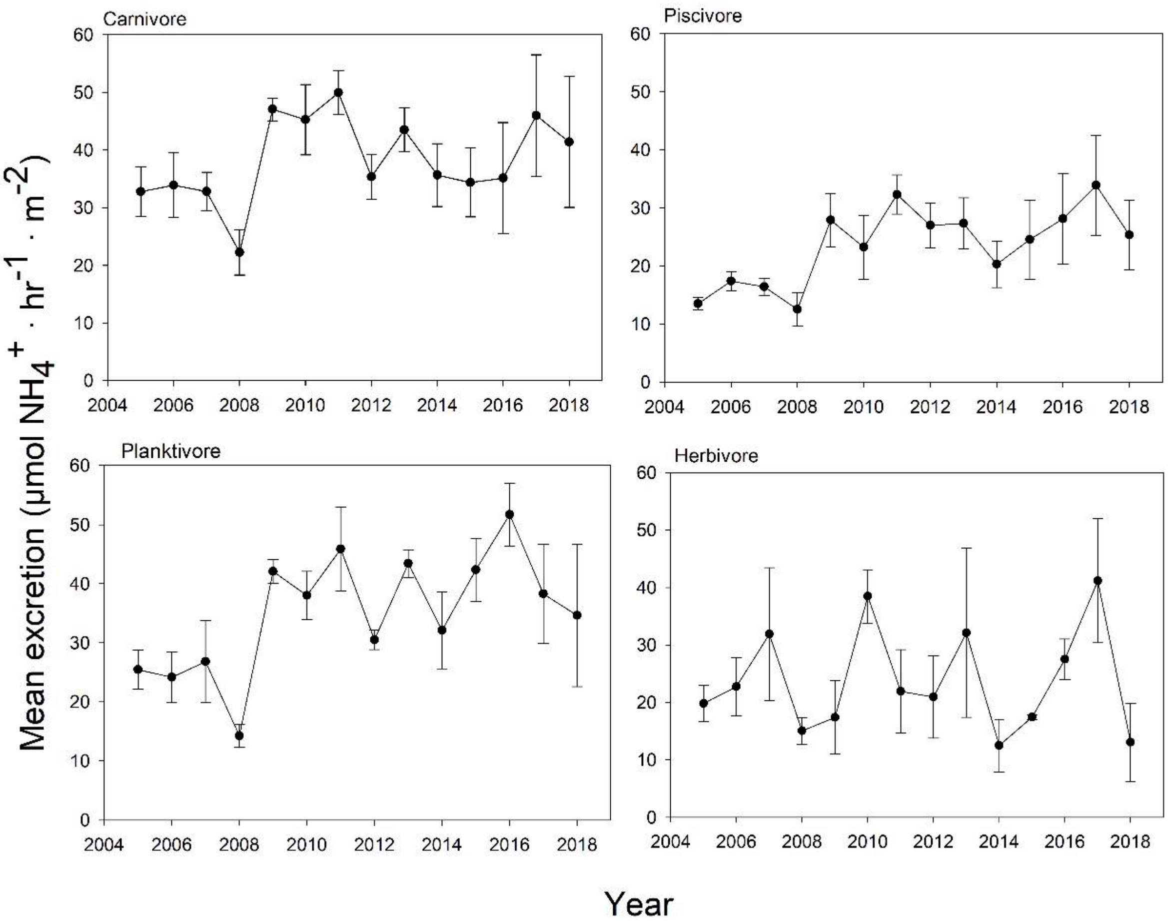


Figure S4. Trajectories of change in fish excretion rates by trophic group. Shown are mean values ± 1 standard error.

REFERENCES

Allen LG, Pondella DJ, Horn MH (2006) Biogeography. In: The Ecology of Marine Fishes: California and Adjacent Waters, University of California Press, pp 3-25

Allgeier JE, Yeager LA, Layman CA (2013) Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. Ecology 94: 521–529

Allgeier JE, Layman CA, Mumby PJ, Rosemond AD (2014) Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. Global Change Biology 20:2459–2472

Allgeier JE, Wenger SJ, Rosemond AD, Schindler DE, Layman CA (2015a) Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food web

Allgeier JE, Valdivia A, Cox C, Layman CA (2016) Fishing down nutrients on coral reefs. Nature Communications 7:1–5

Archer SK et al. (2015) Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling. Coral Reefs 34(1): 19-23.

Bracken MS, Dolecal RE, Long JD (2014) Community context mediates the top-down vs. bottom-up effects of grazers on rocky shores. Ecology 95(6)1458-1463

Bracken MS, Nielsen KJ (2004) Diversity of intertidal macroalgae increases with nitrogen loading by invertebrates. Ecology 85(10):2828-2836

Bray RN, Purcell LJ, Miller AC (1986) Ammonium excretion in a temperate-reef community by a planktivorous fish, *Chromis punctipinnis* (Pomacentridae), and potential uptake by young giant kelp, *Macrocystis pyrifera* (Laminariales). Marine Biology 90:327–334

Bray RN, Miller AC, Johnson S, Krause PR, Robertson DL, Westcott AM (1988) Ammonium excretion by macroinvertebrates and fishes on a subtidal rocky reef in southern California. Marine Biology 100:21-30

Bronk DA, Ward BB (2005) Inorganic and organic nitrogen cycling in the Southern California Bight. Deep Sea Research Part I: Oceanographic Research Papers 52(12): 2285-2300

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85(7):1771-1789

Brown JH, Allen AP, Gilloly JF (2007) The metabolic theory of ecology and the role of body size in marine and freshwater ecosystems. Hildrew A, Raffaelli D, Edmonds Brown R (eds) In: Body Size: The Structure and Function of Aquatic Ecosystems. Cambridge University Press, Cambridge pp. 1–15

Brzezinski MA, Reed DC, Harrer S, Rassweiler A, Melack JM, Goodridge BM, Dugan JE (2013) Multiple sources and forms of nitrogen sustain year-round kelp growth on the inner continental shelf of the Santa Barbara channel. Oceanography 26:114– 123.

Burkepile DE, Allgeier JE, Shantz AA, Pritchard CE, Lemoine NP, Bhatti LH, Layman CA (2013) Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Scientific Reports 3:1493–1501

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: a Practical Information-theoretical Approach, 2nd edn. New York: Springer

Caselle JE, Malone DP, Wilson JR, Wendt DE (2010) Predicting nearshore populations of rockfishes. CalCOFI Report 51:1–16

Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Scientific Reports 5(14102)

Cailliet GM, Burton EJ, Cope JM, Kerr LA, Larson RJ, Lea RN, VenTresca D, Knaggs E (2000) Biological characteristics of nearshore fishes of California: a review of existing knowledge and proposed additional studies. California Dept. of Fish and Game, Sacramento

Caron DA, Lim EL, Sanders RW, Dennett MR, Berninger UG (2000) Responses of bacterioplankton and phytoplankton to organic carbon and inorganic nutrient addition in two oceanic ecosystems Aquatic Microbial Ecology 22:175-184. doi: 10.3354/ame022175

Carr MH, Caselle JE, Koehn KD, Malone DP (2020) PISCO Kelp Forest Community Surveys. PISCO MN. doi:10.6085/AA/PISCO_kelpforest.1.6.

Chavez FP, Pennington JT, Castro CG, Ryan JP, Michisaki RP, Schlining B, Waltz P, Buck KR, McFaydyen A, Collins CA (2002) Biological and chemical consequences of the 1997-1998 El Niño in central California waters. Progress in Oceanography 54:205-232

Devine MJ, Vanni JA (2002) Spatial and seasonal variation in nutrient excretion by benthic invertebrates in a eutrophic reservoir. Freshwater Biology 47:1107–1121

Di Lorenzo E, Schneider N, Cobb KM, Franks PJS, Chhak K, Miller AJ, McWilliams JC, Bograd SJ, Arango H, Curchitser E, Powell TM, Riviere P (2008) North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophysical Research Letters, 35(8)

Di Lorenzo E, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change 6(11): 1042-1048 doi:10.1038/nclimate3082

Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P (2000) Observed variability and trends in extreme climate events: a brief review. Bulletin of the American Meteorological Society 81(3):417-426

Elser JJ, Urabe J (1999) The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology. 80(3) 735-751

Fram JP, Steward HL, Brzezinski MA, Gaylord B, Reed DC, Williams SL, MacIntyre S (2008) Physical pathways and utilization of nitrate supply to the giant kelp, *Macrocystis pyrifera*. Limnology and Oceanography 53(4): 1589-1603

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305 doi: 10.1007/s00338-003-0317-2

Fulton CJ, Bellwood DR (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. Marine Biology 144:429–437 doi: 10.1007/s00227-003-1216-3

García-Reyes M, Sydeman WJ (2017) California Multivariate Ocean Climate Indicator (MOCI) and marine ecosystem dynamics. Ecological Indicators 72:521-529

Gerard VA (1982) Growth and utilization of internal nitrogen reserves by the giant kelp Macrocystis pyrifera in a low-nitrogen environment. Marine Biology 66:27-35

Gido KB, Hargrave CW, Matthews WJ, Schnell GD, Pogue DW, Sewell GW (2002) Structure of littoral-zone fish communities in relation to habitat, physical, and chemical gradients in a southern reservoir. Environmental Biology of Fishes 63:253-263

Graham MH, Vasquez JA, and Buschmann AH (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. Oceanography and Marine Biology: An Annual Review 45:39-88

Graham MH, Fox MD, Hamilton SL (2016) Macrophyte productivity and the provisioning of energy and habitat to nearshore systems. In: Olafsson E (ed) Marine Macrophytes as Foundation Species, CRC Press, Boca Raton, FL, pp 131-160

Haines KC, Wheeler PA (1978) Ammoniun and nitrate uptake by the marine macrophytes *Hypnea musvuformis* (Rhodophyta) and *Macrocystis pyrifera* (Phaeophyta). Journal of Phycology 14:319-324

Hairston NG, Smith FE, and Slobodkin LB (1960) Community structure, population control, and competition. The American Naturalists 94:421-425

Hamilton SL, Caselle JE, Malone DP, Carr MH (2010) Incorporating biogeography into evaluations of the Channel Islands marine reserve network. PNAS 107(43):18272-18277

Hepburn CD, Hurd CL (2005) Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. Marine Ecology Progress Series 302: 37-48

Hernández-León S, Fraga C, Ikeda T (2008) A global estimation of mesozooplankton ammonium excretion in the open ocean, Journal of Plankton Research 30:577–585. doi: 10.1093/plankt/fbn021

Hixon MA, Johnson DW, Sogard SM (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71:2171–2185.

Hobson ES, Chess JR (1986) Relationships among fishes and their prey in a nearshore sand community off southern California. Environmental Biology of Fishes 17:201-226

Holbrook SJ, Schmitt RJ, Ambrose RF (1990) Biogenic habitat structure and characteristics of temperate reef fish assemblages. Australian Journal of Ecology 15:489-503

Holbrook SJ, Brooks AJ, Schmitt RJ, Stewart HL (2008) Effects of sheltering fish on growth of their host corals. Marine Biology 155:521-530

Holmes RM, Aminot A, Kerouel R, Hooker BA, Peterson BJ (1999) A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56:1801-1808

Horn MH, Allen LG (1978) A distributional analysis of California coastal marine fishes. Journal of Biogeography 5:23-42

House PH, Clark, BL, Allen LG (2016) The return of the king of the kelp forest: Distribution, abundance, and biomass of Giant sea bass (Stereolepis gigas) off Santa Catalina Island, California, 2014-2015. Bulletin, Southern California Academy of Sciences 115(1): 1-14

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732

Jackson GA (1977) Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. Limnology and Oceanography 22(6)979-995

Jacox MG, Bograd SJ, Hazen EL, Fiechter J (2015) Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. Geophysical Research Letters 42:5950– 5957 doi:10.1002/2015GL065147

Jacox MG, Hazen EL, Zaba KD, Rudnick DL, Edwards CA, Moore AM, Bograd SJ (2016) Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. Geophysical Research Letters, 43(13):7072-7080.

Jessee WN, Carpenter AL, Carter JW (1985) Distribution patterns and density estimates of fishes on a southern California artificial reef with comparisons to natural kelp-reef habitats. Bulletin of Marine Science 37(1):214-226

Jones RE, Petrell RJ, Pauly D (1999) Using modified length-weight relationships to assess the condition of fishes. Aquacultural Engineering 20:261-276

Kapoor BB, Smit H, Verighina IA (1975) The alimentary canal and digestion in teleosts. Advancements in Marine Biology 13:109-239

Kitchell JF, Oneill RV, Webb D, Gallepp GW, Bartell SM, Koonce JF, Ausmus BS (1979) Consumer regulation of nutrient cycling. BioScience 29:28–34

Layman CA, Allgeier JE, Rosemond AD, Dahlgren CP, Yeager LA (2011) Marine fisheries declines viewed upside down: human impacts on consumer-driven nutrient recycling. Ecological Applications 21:343-349

Levin PS, Hay ME (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. Marine Ecology Progress Series 134:37-47

Love MS, Yoklavich M, Thorsteinson L (2002) The rockfishes of the northeast Pacific. University of California Press, Berkeley, CA

Love Milton S. (2011) Certainly more than you want to know about the fishes of the Pacific Coast: a postmodern experience. Really Big Press

McIntyre PB, Flecker AS, Vanni MJ, Hood JM, Taylor BW, Thomas SA (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? Ecology 89:2335–2346

McNaughton SJ, Ruess RW, Seagle SW (1988) Large Mammals and process dynamics in African ecosystems. Bioscience 38(11)794-800

McPhee-Shaw EE, Siegel DA, Washburn L, Brzezinski MA, Jones JL, Leydecker A, Melack J (2007) Mechanisms for nutrient delivery to the inner shelf: Observations from the Santa Barbara Channel. Limnology and Oceanography 52:1748–1766

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: an asset to corals. Science 220:1047-1049

Meyer JL, Schultz ET (1985) Tissue condition and growth rate of corals associated with schooling fish. Limnology and Oceanography 30:157-166

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing Down Marine Food Webs. Science Report 279:860-863

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

Pilati A, Vanni MJ (2007). Ontogeny, diet shifts, and nutrient stoichiometry in fish. Oikos 116:1663-1674

Pfister CA, Altabet MA, Post D (2014) Animal regeneration and microbial retention of nitrogen along coastal rocky shores. Ecology. 95:2803–2814

Pomeroy LR, Mathews HM, Min HS (1963) Excretion of phosphate and soluble organic phosphorus compounds by zooplankton. Limnology and Oceanography 8:50–55

Pondella DJ, Piacenza SE, Claisse JT, Williams CM, Williams JP, Zellmer AJ, Caselle JE (2019) Assessing drivers of rocky reef fish biomass density from the Southern California Bight. Marine Ecology Progress Series 628:125-140

Posey MH, Alphin TD, Cahoon LB, Lindquist DG (2002) Top-down versus bottom-up limitation in benthic infaunal communities: direct and indirect effects. Estuaries 25(5):999-1014

Rassweiler A, Arkema KK, Reed DC, Brzezinski MA, Zimmerman RC (2008) Net primary production, growth and standing crop of *Macrocystis pyrifera* in southern California. Ecology 89:2068

Ratnarajah L, Bowie AR, Lannuzel D, Meiners KM, Nicol S (2014) The biogeochemical role of baleen whales and krill in Southern Ocean nutrient cycling. PLOS ONE 10(4) e0125134 doi: 10.1371/journal.pone.0125134

Raven JA, Wollenweber B, Handley LL (1992) A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. New Phytologist 121:19-32

Redfield AC (1934) On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: Daniel RJ (ed) James Johnstone Memorial Volume. University Press of Liverpool, pp 177–92

Redfield AC (1958) The biological control of chemical factors in the environment. American Science 46:205–21

Redfield A, Ketchum B, Richards, F (1963) The influence of organisms on the composition of seawater. In: Hill M (ed) The Sea. Interscience, New York, pp 26–77

Reed DC, Rassweiler A, Carr MH, Cavanaugh KC, Malone DP, Siegel DA (2011). Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92(11): 2108-2116

Reiners WA (1986) Complementary Models for Ecosystems. The American Naturalist 127(1) 59-73

Roberts DA (1979) Food habits as an ecological partitioning mechanism in the nearshore rockfishes (Sebastes) of Carmel Bay, California. Thesis, San Francisco State University. 82 pp

Roman J, McCarthy JJ (2010) The whale pump: marine mammals enhance primary productivity in a coastal basin. PLOS ONE 5(10):e13255 doi: 10.1371/journal.pone.0013255

Romer, G.S. (1990) Surf zone fish community and species response to a wave energy gradient. Journal of Fish Biology 36:279-287 doi: 10.1111/j.1095-8649.1990.tb05609.x

Sayer MD, Davenport J (1987) The relative importance of the gills to ammonia and urea excretion in five seawater and one freshwater teleost species. Journal of Fish Biology 31:561-570

Schaus MH, Vanni MJ, Wissing TE (2002) Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem

Schindler DE, Eby LA (1997) Stoichiometry of fishes and their prey: implications for nutrient recycling.

Shantz AA, Ladd MC, Schrack E, Burkepile DE (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. Ecological Applications 25(5) 2142-2152.

Smith HW (1929) The excretion of ammonia and urea by the gills of fish. Journal of Biological Chemistry 81:727-742

Smith JM, Brzezinski MA, Melack JM, Miller RJ, Reed DC (2018) Urea as a source of nitrogen to giant kelp (Macrocystis pyrifera). Letter: Limnology and Oceanography 3(4)365-373

Slobodkin LB, Smith FE, Hairston NG (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. American Society of Naturalist 101(918)109-124

Starr RM, Wendt DE, Barnes CL, Marks CI, Malone D, Waltz G, et al. (2015) Variation in Responses of Fishes across Multiple Reserves within a Network of Marine Protected Areas in Temperate Waters. PLoS ONE 10(3): e0118502. doi: 10.1371/journal.pone.0118502

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, and Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience, and future. Environmental Conservation 29(4):436-459

Stephens JS, Jordan GA, Morris PA, Singer MM (1986) Larval fish recruitment. CalCOFI Report 27

Sterner RW (1990) The ratio of nitrogen to phosphorus resupplied by herbivores - zooplankton and the algal arena. The American Naturalist 136:209–229

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, NJ

Van Dykhuizen G (1983). Activity patterns and feeding chronology of the kelp rockfish, *Sebastes atrovirens,* in a central California kelp forest. Thesis, California State University, San Jose. 61 pp

Vanney JR, Stanley DJ (1983) Shelfbreak Physiography: An Overview. In Stanley DJ & Moore GT (eds.), The Shelfbreak: Critical Interface on Continental Margins, SEPM Special Publication 33 pp 1-24

Vanni MJ, Layne CD (1997) Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. Ecology 78:21-40. doi: 10.2307/2265976

Vanni MJ, Flecker AS, Hood JM, Headworth JL (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. Ecology Letters 5:285–293

Vanni MJ, McIntyre PB (2016) Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. Ecology 97(12):3460-3471

Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the Southern California Bight. Marine Ecology Progress Series 401:31-48 doi: 10.3354/meps08376

Wells BK et al. (2017) State of the California Current 2016-2017: Still anything but “normal” in the north. CalCOFI Report 58

Welti N, Striebel M, Ulseth AJ, Cross WF, DeVilbiss S, Glibert PM, Guo L, Hirst AG, Hood J, Kominoski JS, MacNeill KL, Mehring AS, Welter JR and Hillebrand H (2017) Bridging food webs, ecosystem metabolism, and biogeochemistry using ecological stoichiometry theory. Frontiers in Microbiology 8:1298 doi: 10.3389/fmicb.2017.01298

Wen YH, Peters RH (1994) Empirical models of phosphorus and nitrogen excretion rates by zooplankton. Limnological Oceanography 39(7) 1669-1679

Whiles MR, Huryn AD, Taylor BW, Reeve JD (2009) Influence of handling stress and fasting on estimates of ammonium excretion by tadpoles and fish: recommendations for designing excretion experiments? Limnology and Oceanography: Methods 7:1-7

Wood JD (1958) Nitrogen excretion in some marine teleosts. Canadian Journal of Biochemistry and Physiology. 36(12):1237-1242, doi: 10.1139/o58-134

Xiu P, Chai F, Curchitser EN, Castruccio FS (2018) Future changes in coastal upwelling ecosystems with global warming: The case of the California Current System Scientific reports 8(1):2866 doi:10.1038/s41598-018-21247-7

Zimmerman RC, Kremer JN (1984) Episodic nutrient supply to a kelp forest ecosystem in Southern California. Journal of Marine Research 42:591-604

Zuur AF, Ieno EN, Saveliev AA (2017) Beginner's guide to spatial, temporal and spatial-temporal ecological data analysis with R-INLA. Newburgh, UK: Highland Statistics