Consumer resilience suppresses the recovery of overgrazed ecosystems.

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Abstract

Food availability is among the strongest determinants of fitness. For many systems, ecosystem-wide collapse in food availability can result from overgrazing with cascading ecological impacts. Yet, the mechanisms through which the responsible consumers persist in food-poor environments and their role in suppressing productivity recovery remain uncertain. This study examines how food abundance, quality, deprivation, and reintroduction shape plastic energetic traits and nutritional assimilation in an invertebrate herbivore. To evaluate how food composition and quantity affect energetic performance and biomarker composition in herbivore tissues, we analyzed fatty acids in producer and consumer tissues both *in situ* and in laboratory feeding trials. Sea urchins have a history of periodic overgrazing of kelp forests, followed by their extraordinary long-term persistence in the resulting barrens. Despite a two-fold difference in baseline metabolic rates (RMR) between kelp forest and barrens urchins, both consumed algae at equivalent rates in the laboratory. Starvation and feeding of urchins from kelp forests and barrens, respectively, induced reciprocal shifts in RMR and energy reserves over one month. Urchins fed lower-quality diets consumed more calories with lower efficiency in converting food to gonadal tissue. This metabolic resilience could hinder the recovery of kelp, a foundation species critical to nearshore ecosystems.

1. Introduction

Variation in food availability can directly shape the fitness of consumers and associated food web dynamics. Such variation result from, for example, bottom-up changes in primary production (1), shifts in availability of of allochthonous food resources (2), and/or strong consumer pressure (3). Declines in the quantity or quality of available food can reduce rates of reproduction, juvenile survival, growth, and adult survival in many taxa (4-6). A diverse range of animals across trophic levels, taxonomic groups, and ecosystems (7-11) are known to periodically graze down and deplete resource productivity leading to barren landscapes of nutritionally poor, scarce, or low productivity food resources. While many fields of study have focused on how these trophic interactions shape population dynamics, less is known about individual resilience from nutritional deficits. If consumers are to avoid death by starvation, they must

emigrate, switch their diet to alternative foods, and/or cope (12). Among those that cope, it remains unclear how metabolic plasticity and resilience interact with changes in the abundance and quality of food to shape energetic traits and fitness.

Mobile consumer species may respond to reductions in food density or productivity by expanding or shifting their geographic range (13) or reducing activity (14). Consumers may also expand their dietary breadth (15), capitalize on exogenous food subsidies (16), or engage in a last gasp reproductive bout before dying (17). In addition to these behavioral shifts, a wide range of eukaryotes avoid starvation or malnutrition mortality by mobilizing energy reserves for basic functions at the cost of reduced structural growth and/or reproduction (18-21). While heterotrophs likely downregulate cellular metabolic rates under food deprivation (14, 22), the effects of nutritional limitation and resurgence on such metabolic flexibility and the attendant consequences for performance remain poorly studied (12).

Metabolic flexibility influences consumer resilience by setting critical limits on survival and recovery, with responses like metabolic depression enhancing starvation resistance under nutritional stress..The metabolism of an organism consists of processes such as respiration, food intake, tissue building, and gonad production (23). While metabolic rate correlates strongly with specific physiological processes like respiration rate, it is less clear how metabolic rate relates to food intake and gonadal growth (24). For example, while resting metabolic rate (RMR) reflects baseline energetic maintenance, food intake must supply not only energy but also essential nutrients (25). A comprehensive understanding of an organism's metabolic flexibility under food limitation requires a multifaceted understanding of organismal energetics.

Shifts in both resource quantity and quality affect consumer energetics and performance even when caloric intake is sufficient. Macronutrient deficiencies can affect feeding behavior, growth, and longevity in a wide range of organisms (26, 27). Some micronutrients are "essential" in the diets of many consumers For example, highly unsaturated fatty acids (HUFAs).(e.g., docosahexaenoic acid, [DHA]) can be critical biomolecules for successful reproduction , growth, and survival (28, 29). Yet many consumers lack the capacity to synthesize these essential nutrients (30). Compensatory feeding, a phenomenon in which consumers increase per capita consumption of poor-quality food to meet metabolic demands when high-quality food is unavailable, is likely highly consequential for the recovery of overgrazed ecosystems.

Sea urchins are dominant herbivores that in large numbers often graze down highly productive and biodiverse ecosystems (31) to barren low-productivity seascapes which can persist for decades (32). Survival rates of some sea urchins in such barrens has been hypothesized to be high as a result of phenotypic plasticity (33). Recent observations demonstrated a 50% decline in RMR between sea urchins occupying food-rich versus food-poor habitats (22). Understanding how such metabolic depression in food-poor habitats affects the capacity of sea urchins to quickly consume food when it becomes available is crucial for understanding kelp forest recovery. Moreover, the timescale over which animals respond to resurgent food availability and how different foods influence the recovery of reproductive capacity, energy stores, and RMR in consumers is poorly understood (12). We focused on the barren-forming red sea urchin, *Mesocentrotus franciscanus* , because of its important roles in structuring nearshore algal ecosystems, commercial fisheries, and indigenous culture (34). Investigating the plastic responses of barren-forming consumers to changes in the abundance and quality of food is important for understanding how trophic dynamics mediate regional and global drivers of change in productivity.

We addressed two parallel objectives including 1) quantifying feeding rates and metabolic responses following starvation as a function of food quality, and 2) characterizing how habitat and diet affect assimilated FA biomarker profiles as a preliminary step toward drawing accurate inferences of wild diet dynamics. Given the large differences in RMR we observed between barren and kelp forest urchins (22), we hypothesized that feeding rates would initially differ by habitat following the reintroduction of food after starvation. Additionally, we tested three hypotheses for metabolic responses including a) RMR is highly flexible as a function of declines and resurgences in food availability such that starvation results in metabolic depression and feeding results in metabolic recovery, b) this metabolic flexibility correlates with similar shifts in energy stores and reproductive capacity as measured by gonadal mass and lipid

content, and c) calorically rich but nutritionally poor diets require compensatory feeding which yields less efficient physiological recovery following depletion relative to nutritionally-rich diets.

2. Methods

We evaluated the effects of habitat of origin (kelp forest vs. barrens) and experimental diet on both bioenergetics (i.e., metabolism, grazing rate, growth, and gonad production) and FA dietary biomarkers of *M. franciscanus***.** Field assays provided natural ecological context for our laboratory experiment and included measurements of RMR, body size specific gonad mass, and FA biomarker profiles in each habitat. We then subjected individuals from neighboring barrens and kelp forest habitats to a six-week aquarium experiment where we controlled their diets and measured bioenergetic responses and FA biomarker profile outcomes.

Field collections

We collected individuals using SCUBA from Surge Narrows, British Columbia, (50.22˚N, 125.16 ˚W) from a depth of 2-3 m and 10-12 m relative to mean tide from kelp forest and nearby barrens habitat, respectively (n = 30 per habitat, 60 total; mean test diameter = 69.4 mm ± 1.02 mm SE) in August of 2019. We immediately transported collected individuals in insulated coolers to the Hakai Institute Quadra Island Ecological Observatory (HIQIEO) where we transferred them to flow-through sea tables and allowed them to recover for a period of 48 hours. We collected additional individuals from similar depths for sacrificial sampling to compare habitat-specific gonadal mass allometry and fatty acid composition at Surge Narrows with additional study sites in Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site on Haida Gwaii, including Faraday (52.61° N, 131.49° W) and Murchison (52.60° N, 131.45° W) Islands.

Aquarium setup

We used outdoor sea tables supplied with flow-through treated seawater for the laboratory experiment. Seawater was pumped from a depth of 20 m, filtered at 100 µm a. UV sterilized,. We subdivided each sea table into multiple 17L aquaria (n = 60 aquaria) using plastic bins, each supplied with independent flow-through seawater (flow = 2.20 Lhr^{-1}; turnover = 3.12 d^{-1}) via irrigation plumbing (**figure S1**). Temperature, salinity, and pH were recorded daily (temperature = 13°C ± 1.01°C SE, salinity = 28.85 ppt ± 0.35 ppt SE, pH = 7.61 ± 0.13 SE). We haphazardly assigned individual urchins to solitary chambers in each aquarium following the recovery period

Acclimation and experimental treatments

We minimized relocation stress by allowing the urchins to acclimate to aquarium conditions for 48 hours prior to initiating treatments. We assigned experimental subjects to one of three diet treatments: 1) Monospecific diet (*Nereocystis luetkeana*) , *ad libitum*, 2) Diverse diet (*N. luetkeana, Ulva sp. , Chondracanthus corymbiferus ,* and *Dilsea californica*), *ad libitum*, and 3) Starvation, resulting in a fully-crossed factorial design (n = 10 urchins per habitat-diet treatment combination). These algal taxa have similar caloric content, C:N ratios, and protein content but substantially different concentrations of nutritionally valuable fatty acids (electronic supplemental material; **table S11**). We collected fresh macroalgae for diet treatments from a depth of 3-6 m at nearshore sites around Quadra Island (*N. luetkeana* at Quathiaski Cove 50.04˚N, 125.22 ˚W, *Ulva sp., C. corymbiferus,* and *D. californica* at Wa Wa Kie Beach 50.04˚N, 125.17 ˚W) and transferred collected algae to flow-through sea tables at the HIQIEO. We prevented decomposition of macroalgal tissue by collecting fresh macroalgae immediately prior to and periodically throughout the experiment, only using algae collected within one week. To standardize composition of fresh macroalgal diets we only used thallus tissue which was free of reproductive patches, edges prone to decomposition, and conspicuous epibionts. We maintained experimental treatments for thirty-three days to allow for controlled diets to be assimilated into new urchin biomass.

Energetics

Respirometry

We quantified respiration rate as a proxy for metabolic rate, focusing on resting metabolic rates (RMR). We selected RMR to avoid the confounding effects of specific dynamic action (SDA) (35). To control for SDA, we starved focal subjects for 48 hours prior to respirometry then immediately resumed prescribed feeding after respirometry sessions. We quantified respiration rates using custom-built sealed acrylic chambers (22). To account for the displacement volume of the urchins when calculating respiration rates, we subtracted internal test volume of the urchins (V – calculated from test diameter (D) and height (H) assuming oblate spheroid geometry ($V = 4/3\pi D^2H$)) from the total chamber system volume. We accounted for background oxygen dynamics using an identical empty respiration chamber in the same environmental conditions in parallel with every set of three respiration chambers containing urchins. We conducted reproducible and transparent quality control on oxygen time series data using the R package respR (36).

We standardized RMR with total metabolically active biomass which we measured as ash-free dry mass (AFDM). AFDM represents non-skeletal soft tissue as the difference between dry mass and post-combustion ash mass. We first cracked the test of the urchins and discarded the coelomic fluid, then dried the carcasses for 24 hours at 60 °C in a drying oven, then weighed the dried carcasses. We measured post-combustion ash mass by combusting dried carcasses for six hours at 450 °C in a muffle furnace, then weighed the ashes of each carcass (scale resolution =0.01 mg). To contextualize measurements of RMR made on experimental subjects maintained in the laboratory with natural variation, we also sampled the wild population at the beginning and end of the experiment from the same collection site.

Feeding rate and assimilation efficiency

We measured food consumption and assimilation efficiency using repeated trials spanning from day 7-14 and 23-33 in shaded sea tables to limit macroalgal growth. For each trial, we measured the wet mass of food at the beginning and endpoints, as well as the mass of feces at the endpoints. We standardized wet weight measurements of algae by spinning thallus tissue in a colander for 30 s prior to recording a mass measurement. We approximated algal dry weights for each of the four species of algae by generating species specific linear regressions between wet and dry weights (electronic supplemental material; **figure S3**). We calculated mean feeding rate as the difference in dry weight of algae from the beginning and end of each feeding cycle divided by the amount of time in the feeding cycle (electronic supplemental material; **method S2).**

Gonadal mass and food conversion efficiency

To quantify shifts in gonadal mass in experimental subjects, we calculated the difference between an estimated initial and measured final state. To estimate initial gonadal mass, we used body size and gonadal mass measurements from representative wild individuals in barrens and kelp forest habitats at Surge Narrows to model the effects of habitat and body size on gonadal dry mass. We measured test volume and gonadal dry mass after heating samples at 60 °C for 24 h in a drying oven to correct for variation in water content. We sampled a representative size gradient of benthic stage individuals spanning small through large body sizes at Surge Narrows in the barrens and kelp forest habitats at the beginning of the experiment and combined these measurements with identical measurements taken three months prior (22) (kelp forest habitat: n = 49 individuals, minimum test volume = 26 mL, maximum test volume = 668 mL; barrens habitat: n = 59, minimum test volume = 18 mL, maximum test volume = 452 mL).

We quantified food conversion efficiency as a ratio between increase in dry gonadal biomass and total dry food consumption between the beginning and end of the experiment (37). To infer the beginning habitat specific dry gonadal biomass of experimental subjects for a given body size, we used a model fit to data collected from wild sacrificial samples in the beginning of the experiment collected from the same source populations as the experimental subjects. We used an inverse problem approach to estimate food conversion efficiency, combining error in measurement models estimating treatment specific feeding rates

and gonad mass. To estimate treatment specific feeding rates, we fit an error in measurement model to data from replicate feeding trials, combined with an error in measurement model of gonad mass fit to data from wild individuals at the beginning of the experiment and experimental subjects at the end of the experiment.

Total lipid content

We evaluated changes in biomass-specific energy reserves by comparing the lipid content of gonadal tissue in wild individuals of comparable size to experimental subjects at the beginning of the experiment with the lipid content of gonadal tissue of experimental subjects at the end of the experiment. To prevent degradation of lipids, we immediately flash-froze all harvested tissue samples using liquid nitrogen, then transferred frozen samples to -80 °C freezers for storage and later lipid extraction and FA composition profiling (see below). To quantify lipid content of gonadal tissue, we extracted lipids from gonadal tissue biopsies (38): tissue samples were lyophilized for 48 h then homogenized. Following homogenization, lyophilized tissue samples were digested in 2 mL chloroform, then sonicated, vortexed, and centrifuged (3000 rpm for 5 m) twice in a 4:2:1 chloroform:methanol:0.9% NaCl solution. After each of these cycles, the lower chloroform layer containing organic compounds was pipetted out and pooled. Subsamples were collected from this pooled solution for gravimetric analysis of total lipid content (39).

Fatty acid composition

To quantify shifts in FA composition associated with nutritional history and diet, we compared the FA composition of lipids extracted from tissue biopsies collected from individuals in their natural habitat and experimental subjects fed controlled diets of known FA composition. We isolated FAs from the lipid solution extracted from tissue samples. To generate a FA-based dietary resource library, we extracted and characterized FAs from thallus tissue samples harvested from the four species of algae supplied in our diet treatments, avoiding epibiota from algal thallus tissue prior to storage. To quantify shifts in FA composition of gonadal tissues, we estimated the state of gonadal tissue FA composition at the beginning of the experiment using gonadal tissue biopsies from wild individuals of comparable size to experimental subjects collected at the same time and from the same place as the experimental subjects (40) and compared this estimated initial state against biopsies of gonadal tissue collected from dissected experimental subjects at the end of the experiment.

To quantify the FA composition of tissue samples, we isolated and analyzed FAs from extracted lipids, described in (38).

Statistical analyses

Univariate

We estimated the population level effects of body size, habitat of origin, and diet on bioenergetic and FA outcomes using Bayesian regression models. RMR models also included a group-level effect of respiration chamber and tube feet FA models included a group-level effect of individual to account for repeated measures. We used a Gamma likelihood distribution and log link function to model these continuous positive outcomes. We accounted for uncertainty in model structures by approximate leave-one-out cross validation (loo) and stacking weights (41, 42), a method designed to maximize predictive accuracy. To evaluate goodness of fit for our models, we conducted graphical posterior predictive checks, ensuring that model simulations did not systematically differ from empirical data (43) and estimated Bayesian R^2 values(44). We evaluated the sensitivity of parameter estimates and model fits to choices of priors by systematically altering priors and refitting models. Subsequently, we tested hypotheses using Bayes Factors (BF) (45) computed from marginal likelihoods using the R package bridgesampling (46). We contrasted estimated marginal means (EMMs) to explore differences between levels of factors while accounting for interactions and adjustments of covariates, expressed in terms of highest posterior density (HPD) intervals the R package emmeans (47). We estimated model posteriors using Stan(48) via the R(49) package brms(50) with 16,000 iterations across four chains, discarding the first half of the iterations per chain as a warm-up, resulting in a posterior sample of 32,000 iterations for each outcome.

To ensure convergence, we verified that Rhat (the potential scale-reduction factor) was no higher than 1.01 and the minimum effective sample size (n_{eff}) was greater than 1,000 (43).

We estimated starting body size and habitat specific gonadal biomass of experimental subjects using a model fit to data collected from sacrificing individuals at the beginning of the experiment from the same source populations as the experimental subjects. We treated the estimation of gonad mass production and feeding rates as an inverse problem, acknowledging the possibility of measurement errors in both variables and accounting for measurement error explicitly. To do this, we "inverted" our observed data (final gonad mass plus noisy feeding data likely measured with error) to estimate latent gonad production and overall feeding rates. This approach involved a system of two models: one to estimate gonad mass as a function of body size, habitat, diet and an error-prone measurement of feeding rate, and a second to model feeding rate as a function of the same covariates but with its own measurement error term (electronic supplemental material; **method S2**).

Multivariate

We visualized multivariate patterns associated with habitat of origin and diet using non-metric multidimensional scaling ordination (NMDS) and tested for significance of predictors using a multivariate analysis of variance. We accounted for the compositionality of fatty acid data using Aitchison dissimilarity, which implements a centered log ratio transformation (51). NMDS were fit using the package vegan (52) in R (49). Ordination stress and the number of dimensions are reported within each NMDS plot. We fit correlation vectors for constituent fatty acids, such that vector lengths were scaled by correlation coefficients with respect to NMDS ordination scores for each data point. Fitted fatty acid vector directions indicated the ordination space toward which the focal fatty acid changed most rapidly and had the greatest correlation with the ordination configuration (53). We identified fatty acids that contributed most to the observed multivariate separation by habitat using a SIMPER analysis (54). To assess significance of multivariate additive and interaction effects of habitat of origin and diet while accounting for heteroskedasticity and unequal sample sizes, we ran W_d^* (55) tests.

3. Results

Energetics

Resting metabolic rate

RMR increased exponentially as a function of AFDM and depended on both habitat of origin and diet (**figure 1**). RMR rates shifted reciprocally after 33 days in response to feeding and starvation depending on habitat of origin. Kelp forest individuals responded to experimental starvation by depressing RMR to a level comparable with barrens urchins. In contrast, barrens urchins when fed recovered RMR to a level that surpassed even wild kelp forest urchins.

Model selection based on loo stacking weights favored a formula including an allometric biomass scaling term (log-AFDM), habitat, diet, and all interactions at the population level plus a group-level chamber effect over similar candidate formulae (electronic supplemental material; **table S1**). Comparing models based on BF indicated decisive evidence to support three core hypotheses: that treatment effects depended on 1) log-AFDM (model 1: log-AFDM, habitat, diet, and interactions; model 2: habitat, diet, and interactions; $BF_{1,2} > 100$), 2) habitat (model 1: log-AFDM, habitat, diet, and interactions; model 2: log-AFDM, diet, and interactions; $BF_{1,2} > 100$), and 3) diet (model 1: log-AFDM, habitat, diet, and interactions; model 2: log-AFDM, habitat, and interactions; $BF_{1,2} > 100$). After controlling for biomass, wild kelp forest urchins had 97.8% faster RMR (ratio = 1.978, 95% HPD: 1.613-2.380) than wild barrens urchins (electronic supplemental material, **figure S4**). After 33 days of experimental starvation, kelp forest urchin respiration decreased while barrens urchin RMR stayed relatively constant. At this endpoint, credible intervals for the difference by habitat of origin overlap zero (ratio = 1.135, 95% HPD: 0.749-1.525). In reciprocal fashion, after 33 days of ad libitum algal diet, barrens urchin RMR increased such that credible intervals for the difference by habitat of origin overlap zero (ratio = 1.058, 95% HPD: 0.691-1.430; ratio = 0.985, 95% HPD: 0.661-1.342, for monospecific and diverse diets, respectively). Barrens

urchins that were fed a monospecific diet had 318.2% faster RMR (ratio = 3.182, 95% HPD: 2.355-4.073) than in their natural habitat, and 328.0% faster RMR (ratio = 3.280, 95% HPD: 2.199-4.431) than experimentally starved individuals. Kelp forest urchins that were starved had 44% slower RMR (ratio = 0.560, 95% HPD: 0.404-0.731) than in their natural habitat. In contrast, kelp forest urchins that were fed a monospecific diet had 306.0% faster RMR(ratio = 3.060, 95% HPD: 2.040-4.177) than experimentally starved individuals. The effects of a monospecific versus diverse algal diet on RMR were largely indistinguishable from one another, regardless of habitat of origin. After 33 days of ad libitum algal diet, credible intervals for the difference in treatment effects between monospecific and diverse diets overlap zero both for kelp forest urchins (ratio = 0.872, 95% HPD: 0.586-1.179) and barrens urchins (ratio = 0.937, 95% HPD: 0.610-1.272).

Feeding rate

After 33 days, diet was the strongest predictor of per capita consumption (**figure 2**). Model selection for repeated measures of feeding rates based on loo stacking weights, regardless of units (algal biomass, calories, or PUFA), favored a model with an allometric scaling term (log-test volume), diet, and a diet-date interaction at the population level plus a group-level individual effect (electronic supplemental material; **tables S2, S3, S4**). At the beginning of the experiment, algal biomass and caloric intake was independent of habitat of origin and diet, but after 33 days was lower for individuals fed a diverse diet. Conversely, PUFA intake was higher at the beginning of the experiment for individuals fed a diverse diet, but PUFA intake converged for all treatments by the end of the experiment. Comparing models based on BF, we found no evidence to support the hypothesis that body size substantially altered treatment effects (model 1: log-test volume, diet, timepoint, and diet-timepoint interaction; model 2: diet, timepoint, and diet-timepoint interaction; $BF_{1,2} < 1$). We also found no evidence to support the hypothesis that habitat of origin substantially altered treatment effects (model 1: diet, timepoint, and diet-timepoint interaction; model 2: habitat, diet, timepoint, and diet-timepoint interaction; $BF_{1,2} < 1$). In contrast, we found decisive evidence for the hypothesis that diet shaped per capita consumption (model 1: diet, timepoint, and diet-timepoint interaction; model 2: timepoint; $BF_{1,2} > 100$). Based on these results, we subsequently analyzed a model with diet, feeding trial timepoint, and a diet-timepoint interaction as population-level effects plus a group level effect of individual. In terms of algal biomass consumption, by the end of the experiment, individuals fed a diverse mixed diet had a 44.7% lower per capita feeding rate than those fed a monospecific diet (ratio = 0.553, 95% HPD: 0.425-0.690). In contrast, at the beginning of the experiment, credible intervals for the difference in per capita consumption between diets overlap zero (ratio = 1.017, 95% HPD: 0.784-1.240).

Assimilation efficiency

Assimilation efficiency was generally consistent across treatments. Model selection based on loo stacking weights for repeated measures of assimilation efficiency favored a model with additive effects of allometric scaling (log-test volume), habitat, and diet at the population level plus a group-level individual effect (electronic supplemental material; **table S5**). However, subsequent model comparisons based on BF did not provide substantial evidence that these population level effects shaped assimilation efficiency. There was no evidence to support the hypothesis that body size shaped treatment outcomes (model 1: log-test volume, habitat, diet, and time point; model 2: habitat, diet, and time point; $BF_{1,2} < 1$). Nor was there evidence that habitat (model 1: habitat, diet, and time point; model 2: diet and time point; $BF_{1,2} < 1$) or diet (model 1: diet and time point; model 2: time point; $BF_{1,2} < 1$) was determinant. Moreover, the effect of time point merits only a bare mention (model 1: time point; model 2: null; $BF_{1,2} = 1.05$). Assimilation efficiency was marginally higher after 33 days of treatment exposure than it was at the beginning of the experiment, but credible intervals for the difference between these time points overlap zero (odds ratio = 1.16, 95% HPD 0.86-1.45).

Gonad mass and lipid content

For a given body size, kelp forest urchins had consistently higher gonadal mass and lipid content than barrens urchins, yet these metrics responded to experimentally imposed diets in qualitatively similar

fashion regardless of habitat of origin (**figure 3a,** electronic supplementary material; **figure S5).** Gonad mass increased exponentially as a function of body size at Faraday, Murchison, and Quadra Island (electronic supplementary material; **figure S6**). The relationship between lipid content and body size was less consistent (electronic supplementary material; **figure S7**). Animals from both habitats exhibited increases in gonadal mass and lipid content when fed ad libitum, regardless of whether they were fed a monospecific or diverse diet. Starvation consistently resulted in decreased gonadal mass and lipid content, regardless of habitat of origin.

Model selection for gonad mass based on loo stacking weights indicated the strongest support for a model with additive effects of allometric scaling (log-test volume), habitat, and diet at the population level (electronic supplementary material; **table S6**). The same selection process favored a model for lipid content with all these predictors plus all interactions (electronic supplementary material; **table S7**). Gonad mass model comparison based on BF provide decisive evidence in support of the hypothesis that treatment outcomes depended on body size (model 1: log-test volume, habitat, and diet; model 2: habitat and diet; $BF_{1,2} > 100$), habitat of origin (model 1: log-test volume, habitat, and diet; model 2: log-test volume and diet; $BF_{1,2} > 100$), and diet (model 1: log-test volume, habitat, and diet; model 2: log-test volume and habitat; $BF_{1,2} > 100$). For lipid content, model comparisons based on BF indicated no support for a hypothetical body size effect on treatment outcomes (model 1: log-test volume, habitat, diet, and all interactions; model 2: habitat, diet, and interactions; $BF_{1,2} < 1$). The evidence in support of the hypothesis that habitat of origin shape treatment outcomes is not worth more than a bare mention (model 1: habitat, diet, and interactions; model 2: diet only; $BF_{1,2} = 1.607$). However, we find strong evidence that diet drove treatment outcomes (model 1: habitat, diet, and interactions; model 2: habitat only; $BF_{1,2} = 29.096$).

In their natural habitats, kelp forest urchins had 89% higher body size-specific gonad mass (ratio = 1.89, 95% HPD = 1.34-2.46) and 37% lower biomass specific lipid content (ratio = 1.37, 95% HPD = 1.03-1.74) relative to barrens urchins. Experimentally starved kelp forest urchins had 38.7% lower gonadal biomass (ratio = 0.66, 95% HPD = 0.40-0.84) and 26.6% lower gonadal lipid content (ratio = 0.734, 95% HPD = 0.55-0.93) than kelp forest urchins in their natural habitat. Similarly, experimentally starved barrens urchins had 33.6% lower gonadal biomass (ratio = 0.66, 95% HPD = 0.45-0.91) and 43.5% lower biomass specific lipid content (ratio = 0.57, 95% HPD = 0.37-0.77) than barrens urchins in their natural habitat. Kelp forest urchins fed controlled diets did not exhibit substantial differences in gonad mass or lipid content in the laboratory relative to those in their natural habitats; credible intervals for the difference in outcomes overlap zero for all diet contrasts. However, barrens urchins fed controlled diets had 47.4% (ratio = 1.47, 95% HPD = 1.00-1.97) and 38.2% (ratio = 1.38, 95% HPD = 0.95-1.87) higher gonadal biomass and 53.1% (ratio = 1.53, 95% HPD = 1.09-2.01) and 62.7% (ratio = 1.63, 95% HPD = 1.07-2.23) higher gonadal lipid content with a monospecific and diverse diet, respectively, relative to urchins in their natural habitat.

Food conversion efficiency

For a given body size, urchins fed a diverse diet had nearly three times higher FCE relative to a monospecific diet, regardless of habitat of origin (**figure 3b**; ratio = 2.81, 95% HPD = 1.91-3.81). Model selection based on loo stacking weights strongly favored a model with additive effects of allometric scaling (log-test volume) and diet (electronic supplementary material; **table S8**). Comparing models based on BF indicated that the hypothetical effect of body size on treatment outcomes is not worth more than a bare mention (model 1: log-test volume and diet; model 2: diet; $BF_{1,2} = 1.19$). However, we found decisive evidence that diet shaped treatment outcomes (model 1: log-test volume and diet; model 2: log-test volume; $BF_{1,2} > 100$).

Fatty acid composition

Urchins in their natural habitat at Faraday, Murchison, and Quadra Islands had distinct and consistent fatty acid (FA) profiles depending on their habitat of origin and these profiles were sensitive to experimental diets and starvation. These trends were consistent for two tissue types including gonads (**figure 4 & 5;** electronic supplemental material **figure S7**) and tube feet (electronic supplemental

material; **figure S8**). Analysis using SIMPER indicated that specific FAs correlated strongly with habitat of origin and diet (**figure 4**). Within this subset of the FA profile, we analyzed two groups of FAs which are well established dietary biomarkers. First, kelp biomarkers include oleic acid, linoleic acid, stearidonic acid, and alpha-linolenic acid, all of which are essential precursors for the synthesis of docosahexaenoic acid (DHA) (56). Second, biofilm biomarkers include odd-chain FA (OCFA), which are generally bacterial metabolites (57), and the diatom biomarker, palmitoleic acid (58). Kelp forest urchins in their natural habitat had consistently higher kelp biomarker and lower biofilm biomarker concentrations relative to nearby barrens urchins. Regardless of habitat of origin, experimental subjects fed controlled macroalgal diets resulted in increased concentrations of kelp biomarkers. Biofilm biomarker concentrations were similar among experimentally starved urchins and barrens urchins in their natural habitat. However, for kelp forest urchins, biofilm biomarker concentrations were more than twice as high in experimentally starved individuals than in their natural habitat (ratio = 2.50, 95% HPD = 1.66-3.37).

In gonad tissue, FA profiles differed significantly by habitat of origin (W_d^*=11.18, p = 0.001, nrep = 999), diet (W_d^*=10.70, p = 0.001, nrep = 999), and habitat-diet interaction (W_d^*=18.00, p = 0.001, nrep = 999). Model selection based on loo stacking weights favored a kelp biomarker model with additive effects of allometric scaling (log-test volume), habitat, and diet (electronic supplementary material; **table S9**). A similar model with the addition of a habitat-diet interaction was favored for biofilm biomarkers (electronic supplementary material; **table S10**). Subsequent BF analyses provided no evidence in support of the hypothesis that body size affected kelp biomarker outcomes (model 1: log-test volume, habitat, and diet; model 2: habitat and diet; $BF_{1,2} < 1$) and negligible evidence in terms of biofilm biomarker outcomes (model 1: log-test volume, habitat, diet, and interaction; model 2: habitat, diet, and interaction; $BF_{1,2}$ = 3.2). However, we found decisive evidence to support the hypothesis that habitat (model 1: habitat, and diet; model 2: diet; $BF_{1,2} > 100$) and diet (model 1: habitat and diet; model 2: habitat; $BF_{1,2} > 100$) both shaped kelp biomarker outcomes. Similarly, we found strong evidence for a hypothetical habitat effect (model 1: habitat, diet, and interaction; model 2: diet; $BF_{1,2}$ = 59.4) and decisive evidence for a diet effect (model 1: habitat, diet, and interaction; model 2: habitat; $BF_{1,2} > 100$) on biofilm biomarker outcomes. Kelp biomarker concentrations were generally 27.5% higher (ratio = 1.28, 95% HPD = 1.07-1.48) in urchins fed a monospecific diet and 45.5% higher (ratio = 1.46, 95% HPD = 1.22-1.70) in urchins fed a diverse diet relative to urchins in their natural habitats. Credible intervals for the difference in biofilm biomarker concentrations between barrens urchins in their natural habitat and experimentally starved urchins overlap zero. For more details on trophic modification and assimilation of FAs, refer to electronic supplemental material.

4. Discussion

Classic models of consumer resource dynamics expect consumer populations will collapse following overgrazing potentially allowing resources to recover. Yet if consumers are able to depress energetic demands in the absence of food, but rebound when food becomes abundant, such phenomena are likely to inhibit such cyclic dynamics and facilitate persistent barren states. Our results demonstrate metabolic resilience of the dominant nearshore grazer, *M. franciscanus* with strong consequences for grazing effects in nearshore ecosystems. While starvation induces metabolic depression, individuals presented with food can quickly recover to feed at consistent rates regardless of whether it has a history of metabolic depression (**figures 1 and 2**). This contrasts with a common simplifying assumption in metabolic theory (59) of tight coupling between RMR and food intake. In this study, emaciated individuals were capable of nearly complete recovery of gonadal mass in just over one month when supplied ample food. Moreover, recovery was more efficient with a diverse diet (**figure 3**), supporting the hypothesis that consumers balance the intake of complementary nutrients (60) rather than selecting singular substitutable food resources based on energy density (61).

436 ***(a) Ecological implications***

437 Metabolic plasticity and resilience among sea urchins have serious implications for the
438 productivity of kelp forests. We show that metabolic depression in *M. franciscanus* does not inhibit food
439 intake. On the contrary, metabolically depressed, and emaciated *M. franciscanus* individuals from barrens
440 immediately resumed feeding at full consumptive capacity when food became available to them in the
441 laboratory. Not only can *M. franciscanus* resist starvation mortality, persisting in a hypometabolic state in
442 barrens for decades (32), but they likely reanimate with voracious grazing capacity whenever they
443 encounter any recovering macroalgae, perpetuating the barrens state. When fed, these barrens individuals
444 recovered their RMR from a metabolically depressed state to a level equivalent to kelp forest individuals
445 over one month**.** These results are consistent with recent research on another barrens forming sea urchin,
446 *Strongylocentrotus purpuratus*, that found reciprocal declines and recovery following starvation and
447 feeding, respectively, in both RMR and gonadal mass over a period of seven weeks (62, 63). Such
448 resilience in consumptive capacity, RMR, and gonadal mass likely allows multiple starvation-resistant
449 grazer taxa to suppress growth and survival of primary producer recruitment pulses and convert those
450 metabolic gains to increased reproductive capacity (22).

451 Compensatory feeding to offset nutrient deficiencies could also contribute to the hysteresis
452 observed in degraded ecosystems (e.g., (11))**.** For example, once space is cleared by the initial formation
453 of a sea urchin barren, good macroalgal colonizers such as the annual *N. luetkeana* could be expected to
454 dominate early succession algal recruitment and represent a large proportion of macroalgal food
455 availability for grazers. This less nutritious macroalgal food combined with high densities of *M.*
456 *franciscanus* could lead to large-scale compensatory feeding that would again clear substrate and allow
457 for the cycle to repeat. Conversely, late succession, diverse kelps and other algae likely satisfy
458 complementary nutrient demands for primary consumers, thereby potentially reducing metabolic demands
459 on per capita consumption and reducing the likelihood of overgrazing.

460 Nutritional quality likely also shapes the efficiency with which grazers convert food to gonadal
461 tissue and thus reproductive potential. Although the final gonadal mass of experimental subjects was diet
462 independent, those fed a diverse diet rich in PUFA achieved the same gonadal yield with fewer calories.
463 Such efficiency gains support the hypothesis that the different components of the diverse diet provided
464 complementary nutrients (sensu (64)). Similarly, *Daphnia* growth rate tends to positively correlate with
465 phytoplankton biodiversity in the diet, especially when phytoplankton taxa have high PUFA content (65).
466 *S. purpuratus* also showed strong diet-specific differences in per capita consumption for monospecific
467 versus diverse diets (40). The authors concluded that a diverse diet did not yield increased performance
468 because they observed little effect on somatic and gonadal growth. However, as we found in this study,
469 individuals achieved equivalent gonadal yield while consuming less of a diverse diet relative to a
470 monospecific diet. A more recent study on *Daphnia* reported that food quality alone can account for as
471 much as a 128% difference in RMR between low- and high-quality diets and that a high-quality diet rich
472 in nutritionally valuable fatty acids produced a lower RMR and higher growth rate response, which the
473 authors attributed to reduced demands for biosynthesis of essential compounds (29). Although we found
474 *M. franciscanus* had slightly lower RMR when fed a diverse diet that included macroalgae with higher
475 concentrations of nutritionally valuable fatty acids relative to a monospecific diet of *N. luetkeana*, the
476 effect size was much smaller. We can likely attribute this difference in effect size to the difference
477 between carefully formulated artificial diets versus the naturally occurring wild macroalgae offered in the
478 present study.

479 ***(b) Fatty acid biomarkers and the importance of biofilms in food-poor habitats***

480 A major question in dietary tracing research is whether markers used reflect the intended
481 inference. Our results confirm that *M. franciscanus* assimilates consistent habitat-specific FA profiles and
482 that changes in FA profiles reflect both starvation and algal diet composition (**figure 4 & 5;** electronic
483 supplemental material **figure S7 & S8**). Additionally, we demonstrate a link between elevated biofilm
484 biomarkers, starvation, and barren habitats. Our results build upon previous studies on the assimilation
485 histories of fatty acids in sea urchins (38, 66), adding novel contrasts between individuals with differing

nutritional histories, and linking starvation with consistent shifts in FA composition. This result complements recent findings that the gut microbiomes of *M. franciscanus* and *S. purpuratus* differ by habitat, with higher microbial diversity in barrens than conspecifics in nearby kelp forests (67). That study found that bacteria in the genus *Achromobacter*, a microbe composed of nutritious protein (68), was abundant in the *M. franciscanus* gut microbiome, but not in their food. Moreover, Campylobacteraceae, a family which predictive metagenomics suggest metabolizes lipids, amino acids, and carbohydrates (69), dominated the gut microbiome in *M. franciscanus*.

(c) Conservation implications

The critical ecosystem services provided by foundation species are increasingly threatened by climatic drivers (70) which can be exacerbated by overgrazing. We demonstrate that urchins persisting in barrens can wait to capitalize on resurgent productivity in short order. Therefore, remarkable urchin metabolic resilience may reduce the resilience of macroalgal forests following barren formation. Within their thermal tolerance window, many kelp forest declines are attributed to overgrazing by sea urchins (11). Such declines reduce ecosystem services provided by kelp forests including provision of fisheries, support for nutrient cycling, shoreline protection, and many cultural benefits (71, 72). While global demand for sea urchins as fishery species is estimated in the range of 60,000-70,000 metric tons annually (73), the product (gonads) is only marketable when individuals consume sufficient food such that nutritive phagocytes of the gonads have accumulated peak mass with correspondingly high levels of lipid reserves, protein, and carbohydrates just before gametogenic differentiation (74). Malnourished individuals in barrens have no commercial value. However, our results suggest that a restoration approach involving urchin removal by humans and/or by recolonization of predators including sea otters (75) and sunflower sea stars (76) may reduce resource competition for urchins that recolonize the restoration site, ultimately enhancing local seafood yield (see Miller et al (77) for a global review of urchin removal efforts geared toward macroalgal restoration). Additionally, harvesting *M. franciscanus* from barrens then enhancing their roe via aquaculture (78) may be a viable complementary strategy for achieving dual objectives of yielding a marketable seafood and restoring degraded kelp forests.

Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

Declaration of AI use

We have not used AI-assisted technologies in creating this article.

Conflict of interest declaration

We declare we have no competing interests.

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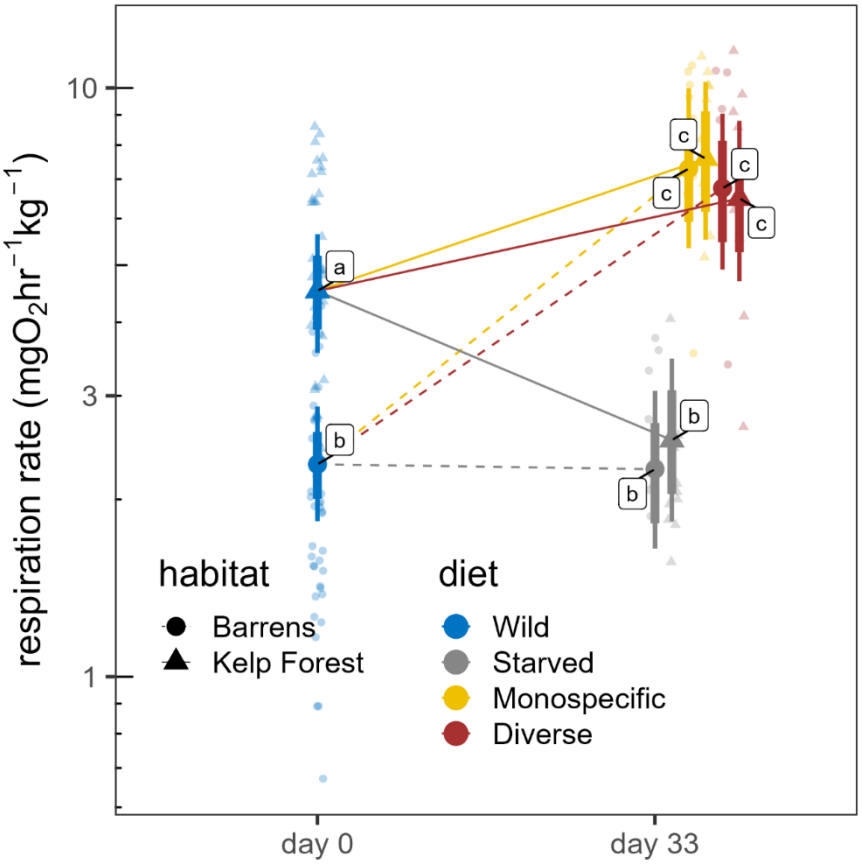

Figure 1. Shifts in resting metabolic rate associated with habitat of origin and diet. Smaller faded symbols represent measured data points, larger solid symbols represent modeled mean values, and thin and thick vertical bars represent 95% and 80% credible intervals, respectively. Lettered labels next to modeled means indicate statistically homogenous groups.

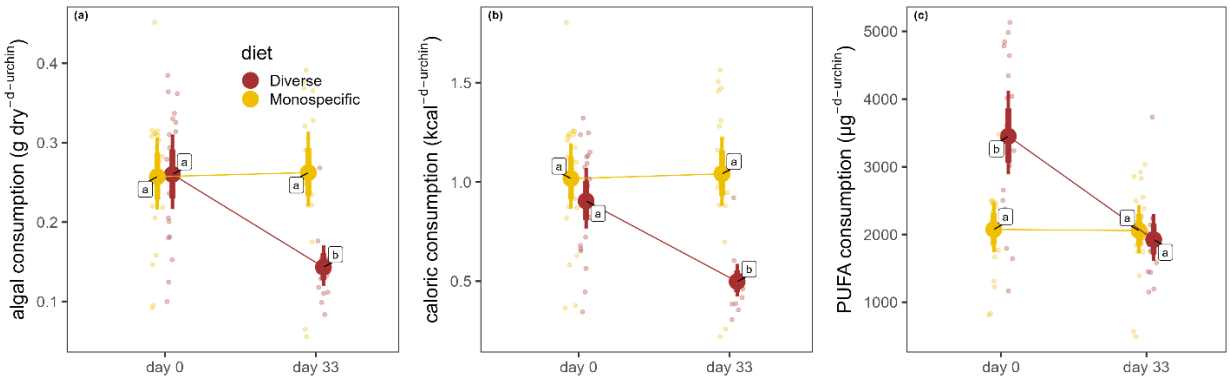

Figure 2. Effects of diet on per capita consumption as a function of time, after controlling for habitat of origin, in terms of (a) algal biomass, (b) calories, and (c) nutritionally valuable polyunsaturated fatty acids (PUFA – fatty acids with two or more double bonds). Smaller faded symbols represent measured data points, larger solid symbols represent modeled mean values, and thin and thick vertical bars represent 95% and 80% credible intervals, respectively. Lettered labels next to modeled means indicate statistically homogenous groups.

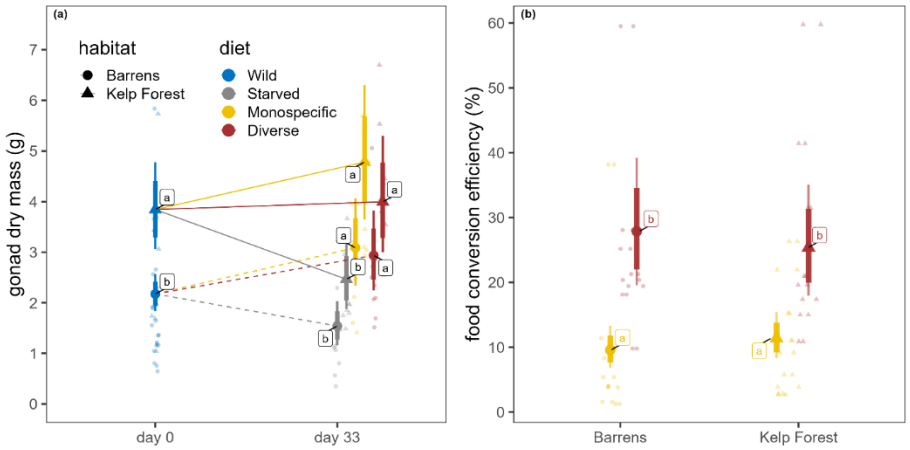

Figure 3. Effects of habitat and diet on (a) gonad mass and (b) food conversion efficiency. Smaller faded symbols represent measured data points, larger solid symbols represent modeled mean values, and thin and thick vertical bars represent 95% and 80% credible intervals, respectively. Lettered labels next to modeled means indicate statistically homogenous groups.

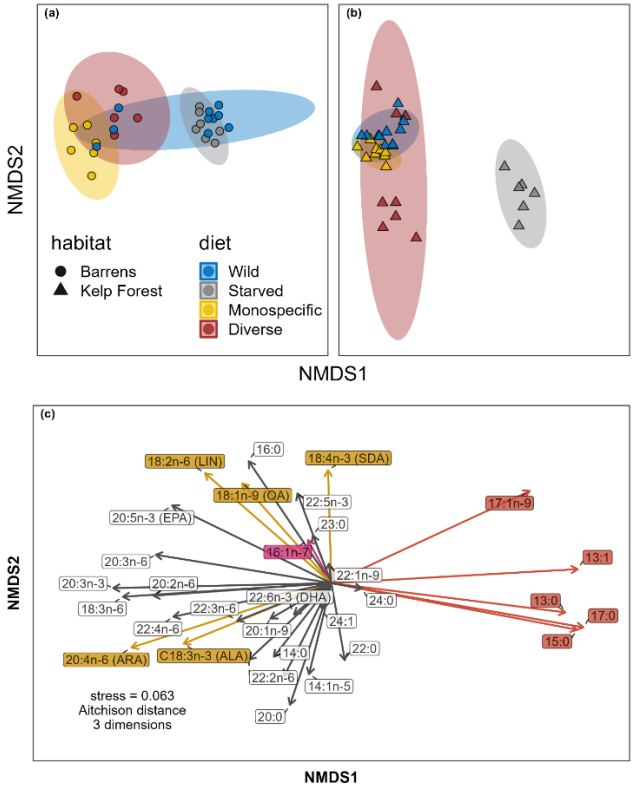

Figure 4. Shifts in gonadal fatty acid (FA) composition as a function of habitat of origin and diet. (a & b) Icons represent individual profiles and ellipses indicate 95% confidence intervals. (c) Arrows indicate correlation vectors for constituent fatty acids, with FAs representing kelp biomarkers, biofilm biomarkers, and diatoms colored in gold, red, and aquamarine, respectively.

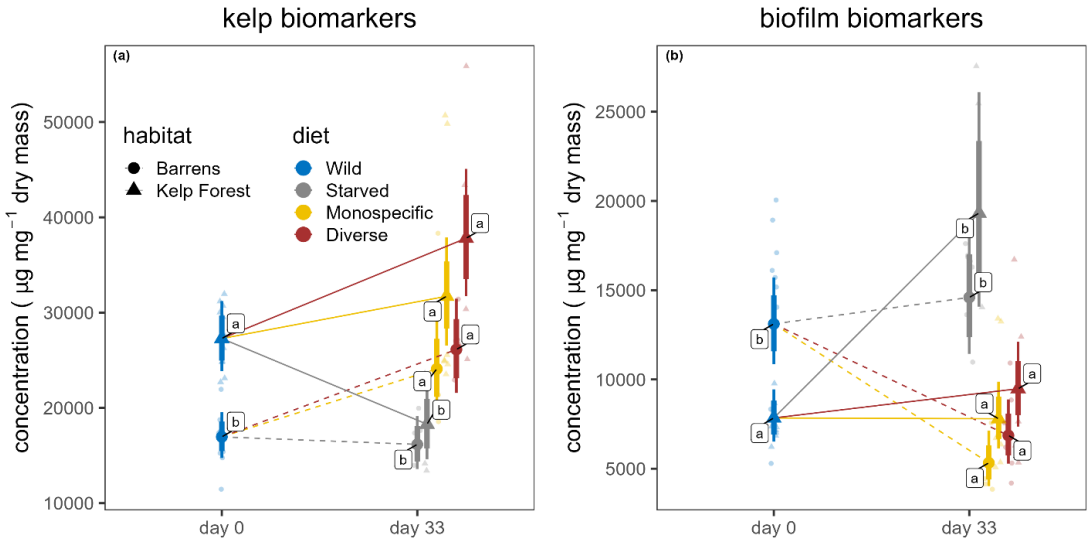

Figure 5 Effects of habitat of origin and diet on gonadal concentrations of (*a*) kelp biomarkers, and (*b*) biofilm biomarkers. Smaller faded symbols represent measured data points, larger solid symbols represent modeled mean values, and thin and thick vertical bars represent 95% and 80% credible intervals, respectively. Lettered labels next to modeled means indicate statistically homogenous groups.

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