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RESEARCH ARTICLE

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Biomarkers of recovery: Characterizing trophic flow following ecological restoration

Nathan B. Spindel[1] | Aaron W. E. Galloway[2] | Julie B. Schram[3] | Gwiisihlgaa Daniel McNeill[4] | SG̱iids Ḵung Vanessa Bellis[4] | Niisii Guujaaw[5] | Jaasaljuus Yakgujanaas[4] | Markus Thompson[6] | Rachele Ferraro[1] | Lynn C. Lee[5] | Daniel K. Okamoto[1,7]

[1]Department of Biological Science, Florida State University, Tallahassee, Florida, USA; [2]Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon, USA; [3]University of Alaska Southeast, Juneau, Alaska, USA; [4]Council of the Haida Nation, Haida Fisheries Program, Skidegate, British Columbia, Canada; [5]Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site, Skidegate, British Columbia, Canada; [6]Thalassia Environmental, Quadra Island, British Columbia, Canada and [7]Department of Integrative Biology, University of California, Berkeley, Berkeley, California, USA

Correspondence
Nathan B. Spindel
Email: natespin@gmail.com

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Abstract

1. Kelp forest degradation is accelerating globally due to marine heatwaves, climate stressors, and persistent overgrazing by sea urchins, creating an urgent need for restoration strategies that rebuild ecosystem function. Yet, how restored kelp subsidies translate into improved food quality and consumer condition, core indicators of trophic recovery, remains poorly quantified.
2. We combined fatty acid biomarkers with a Before–After–Control–Impact Paired Series (BACIPS) experiment to evaluate how targeted urchin removals in Haida Gwaii, British Columbia, altered the nutritional landscape for two ecologically and culturally important grazers: red sea urchins (*Mesocentrotus franciscanus*) and northern abalone (*Haliotis kamtschatkana*).
3. One year after restoration, bull kelp (*Nereocystis luetkeana*) increased ~67-fold in shallow strata, while deep kelp biomass rose from 0 to 9.08 stipes/60 m^2 (±4.52 SE), coinciding with marked increases in kelp-associated fatty acids and improved gonad mass in urchins.
4. In abalone, fatty acid profiles revealed a size-dependent dietary shift in which larger individuals assimilated more kelp, and levels of essential fatty acids increased across both species following kelp recovery.
5. These results provide depth-resolved, field-based evidence that kelp restoration enhances food quality and consumer condition in degraded habitats.
6. *Synthesis and applications*. Fatty acid biomarkers offer a scalable tool for detecting early trophic recovery, identifying high-leverage depth strata for intervention, and evaluating whether restoration actions are rebuilding the ecosystem functions

and fisheries-relevant nutritional pathways that support resilient kelp forest ecosystems.

KEYWORDS
biomarkers, diet tracers, fatty acids, kelp forests, nutritional ecology, restoration, trophic flow, urchin barrens

1 | INTRODUCTION

Kelp forests, one of the most productive and diverse ecosystems on earth (Dayton, 1985), increasingly face compounding threats from climate change and overgrazing. Kelps (i.e., macroalgae in the order Laminariales) span roughly one quarter of the world's coastal habitats and serve as foundation species for many rocky reef ecosystems (Wernberg et al., 2019). By contributing high primary productivity and critical biogenic habitat, kelps form the basis of complex nearshore food webs, increasing secondary productivity and local biodiversity (Smale et al., 2013). Additionally, kelp forests provide valuable ecosystem services for human society including the provision of habitat and food for important fisheries, nutrient cycling, and storm protection (Smale et al., 2013; Wernberg et al., 2019). When sea urchins proliferate, they often graze down macroalgae, resulting in 'sea urchin barrens', and declines in productivity, biodiversity, and fisheries resources (Filbee-Dexter & Scheibling, 2014; Graham, 2004). Owing to urchins' extreme resistance to starvation and physiological resilience (Dolinar & Edwards, 2021; Spindel et al., 2021; Spindel et al., 2026), some urchin barrens can persist for decades or more (Filbee-Dexter & Scheibling, 2014). Unfortunately, the sea urchins dwelling in such food-depauperate environments tend to have depleted gonads (Harrold & Reed, 1985; Kato & Schroeter, 1985; Spindel et al., 2021), rendering them unviable for either human harvest (Claisse et al., 2013) or as prey (Smith, Tomoleoni, et al., 2021). Human interventions to restore kelp forests have the potential to ameliorate these harmful impacts (Claisse et al., 2013) and have increasingly shown promising results (Eger et al., 2022; Grime et al., 2023; Lee et al., 2021). Although several studies report increases in macroalgal abundance resulting from restoration, the degree to which primary consumers incorporate kelp-derived nutrition post-restoration remains poorly quantified in the field using molecular tracers.

Here, we frame trophic recovery as the re-establishment of key food web processes following kelp resurgence. Rather than implying a strict return to historical pre-barrens conditions, we define trophic recovery as increased transfer of kelp-derived energy to primary consumers, improved consumer condition and reproductive investment, and the renewed availability of functional kelp-associated foraging habitat in areas previously dominated by urchin barrens. This process-based framing follows restoration guidelines emphasizing recovery of ecological functions and services relative to appropriate reference conditions, while recognizing that restored systems can stabilize in novel yet functionally robust states.

Understanding how changes in kelp production transfer to consumers is fundamental to kelp forest ecology and conservation. Food availability is among the strongest drivers limiting individual fitness, population dynamics, and community structure (Elliott Smith & Fox, 2021; Harrold & Reed, 1985; Levitan, 1989; Mduma et al., 1999; Okamoto et al., 2012) and may determine the degree to which consumers can absorb stressors like warming (Huey & Kingsolver, 2019). While the importance of kelp as a biogenic habitat-forming species has been relatively well documented (Graham, 2004; Miller et al., 2018), few studies have quantified the use of kelp-derived nutrition by consumers within kelp forests (Elliott Smith & Fox, 2021). Importantly, the stable coexistence of competing consumer species in these ecosystems likely depends on some combination of resource partitioning among different species and within a single species as a function of body size. Such knowledge of the size-specific nature of trophic interactions improves our understanding of the life history of species at risk like abalone and the structure of the community in which it is embedded (Post, 2003). Diet tracer studies have the potential to elucidate the dynamics of such resource partitioning.

Fatty acid-based diet tracing provides an attractive compromise between resolution and technical complexity. This balance is particularly true when assays of wild populations are paired with controlled feeding trials in the laboratory that characterize the modification of dietary fatty acids during the process of tissue building in focal consumers (Galloway & Budge, 2020). Additionally, a fatty acid-based diet tracing approach is well-suited for herbivores like urchins and abalone because macroalgae tend to produce distinct taxa-specific fatty acid signatures (Galloway, Britton-Simmons, et al., 2012), and the method has a demonstrated capacity to detect dietary inputs of different macroalgae in laboratory feeding trials (Raymond et al., 2014; Schram et al., 2018; Spindel et al., 2026). Aquaculture studies have demonstrated that specific fatty acids (e.g. polyunsaturated fatty acids [PUFAs]—fatty acids with two or more double bonds) are essential to the diet of marine consumers because (1) they cannot synthesize certain fatty acids de novo, and (2) they limit physiological functions that shape fitness (Ruiz et al., 2021; Twining et al., 2021). Despite extensive work on other facets of food quality (e.g. energy content, elemental ratios, and bulk macronutrients, such as carbohydrate, protein, and lipid; Campanya-Llovet et al., 2017), relatively few studies have examined, in situ, how fatty acids relate to consumer performance. In this study we use fatty acid signatures as dietary tracers, pairing them with demographic and community surveys, to infer how shifts in primary production propagate to consumers and how consumers partition newly available resources during restoration. We emphasize that this approach is correlative rather than causal: it links variation in fatty acid profiles to observed changes in density, size structure, and community composition, but does not test the functional effects of specific fatty acids on performance. The patterns we document therefore generate hypotheses about fatty acid-mediated mechanisms that should be evaluated with targeted manipulative experiments designed to establish causation.

Here, we deploy a Before-After-Control-Impact Paired Series (BACIPS) of kelp forest restoration via reductions of herbivorous sea urchins from 2018 to present in British Columbia, Canada (Lee et al., 2021). The project, called Chiix̱ uu Tll iinasdll (Skidegate Haida language for 'Nurturing Seafood to Grow'), involved a collaboration among the Council of the Haida Nation, Parks Canada, Fisheries and Oceans Canada, commercial fishers, academia, and research institutes to restore kelp forests from a barrens state along 3-km of coastline in Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site (hereafter Gwaii Haanas) on X̱ aayda Gwaay (Haida Gwaii). In addition to increasing the abundance and diversity of kelp, our research objectives also included: (1) quantifying the degree to which kelp resurgence enhanced the local sea urchin fishery via changes in gonad production, (2) building understanding of how the composition and availability of food resources changed as a function of depth through the process of kelp recovery, and (3) characterizing how changes in the composition and availability of food resources were assimilated by co-occurring grazers including endangered northern abalone, *Haliotis kamtschatkana*, and red sea urchin, *Mesocentrotus franciscanus*.

2 | MATERIALS AND METHODS

2.1 | Kelp forest restoration

The details of the collaborative kelp forest restoration project, Chiix̱ uu Tll iinasdll *Nurturing Seafood to Grow*, co-led by Parks Canada and the Council of the Haida Nation, are published in *Ecological Restoration* (Lee et al., 2021) and expanded in Supporting Information (S1.1). This study involved marine invertebrate species that are not subject to institutional animal care and use regulations, and ethical approval from an animal ethics committee was therefore not required. Animals were collected under permits to DKO from the Department of Fisheries and Oceans Canada (permit nos XR 1482019 and XR 1422019).

2.2 | Sea urchin gonad assessment

To estimate how changes in algal food availability translated to shifts in the health and marketability of sea urchins at our study sites, we quantified body size-specific gonad mass of the regionally dominant sea urchin species, *M. franciscanus*, in 2018 and 2019 (Figure 1c). Previous studies have demonstrated that *M. franciscanus* gonad growth is immediately sensitive to food availability (Rogers-Bennett & Okamoto, 2020; Spindel et al. 2026). Divers collected benthic-stage *M. franciscanus* individuals spanning a representative range of body sizes (28–150 mm test diameter), encompassing the full size structure present at our study sites. This range was necessary to quantify size-dependent variation in gonad mass and fatty acid composition, as *M. franciscanus* exhibits strong allometric scaling of reproductive investment. Divers hand-picked urchins on SCUBA near, but outside, the shallow and deep permanent monitoring transects, then immediately transferred them to a nearby floating research camp. We measured test diameters using precision callipers (±0.01 mm), cracked the test, measured drained mass, dissected out one of the five gonads for wet mass, and froze samples of a second gonad for fatty acid analysis (see Section 2.4).

2.3 | Abalone condition assessment

We quantified condition of *Haliotis kamtschatkana* using a mass–volume index that accounts for sex-specific allometry. Divers hand-collected benthic-stage abalone (44–125 mm shell length), a size range selected to balance two constraints: (i) ethical and permitting requirements for non-lethal epipodial biopsy of this threatened species, which preclude sampling of very small juveniles, and (ii) the need to capture size-dependent dietary shifts in *H. kamtschatkana*. This range therefore reflects both regulatory considerations and the biological objective of resolving ontogenetic patterns in fatty acid assimilation. We temporarily retained individuals in flow-through containers to minimize handling stress during non-invasive biometrics and tissue sampling; all were returned to their collection sites after processing. Biometrics included shell length, shell width, overall body height, wet mass, and sex (external visual gonad classification), measured with precision callipers (dimensions) and a digital scale (mass). To approximate body volume, V, we applied the geometric equation for an ellipsoid to our metrics for length (l), width (w), and height (h): $V = \frac{\pi}{6} * l * w * h$. We modelled wet mass with a Bayesian regression (Gamma likelihood, log link) as a function of a log(body volume) × sex interaction (allowing sex-specific scaling) plus a treatment × year × depth × sex interaction; the condition index was defined as the model intercept for each treatment–year–depth–sex combination.

2.4 | Tissue sampling for fatty acid analysis

We used fatty acids as dietary tracers to evaluate how shifts in primary production are assimilated by primary consumers, characterizing contemporaneous fatty acid profiles in producers and consumers at the same study locations and periods, and drawing on a controlled feeding trial (Spindel, 2023). To build a site-specific producer library (Galloway et al., 2015), in 2018, we biopsied as many algal taxa as possible including 4 classes, 13 orders, 22 families, 39 genera, and 47 species, scrubbing conspicuous epibiota from thalli prior to storage; voucher specimens were retained and cryptic taxa were confirmed by DNA barcoding (sensu Gabrielson et al., 2023). Focal consumers were co-occurring but phylogenetically distant grazers: *H. kamtschatkana* and *Mesocentrotus franciscanus*; biomarker sets were defined from the literature (Galloway, Britton-Simmons, et al., 2012; Kelly & Scheibling, 2012) and our algal library. For both producers and consumers, our fatty acid response variables included (i) proportional abundances of individual fatty acids, (ii) aggregated biomarker groups representing kelp-, diatom-, and bacteria-associated fatty acids, and (iii) whole-profile multivariate fatty acid compositions.

To capture potential ontogenetic dietary shifts, consumer sampling spanned sizes (urchins 21–133 mm test diameter; abalone 44–125 mm shell length) and was conducted annually in summer 2018 (pre-restoration) and 2019–2020 (post-restoration) near, but outside, permanent shallow and deep transects at control and restoration sites (urchins: $n = 10–15$ per year × site × depth; after 2018, $n = 15$ per stratum; abalone: $n = 10–27$ per year × site × depth; after 2018, $n \geq 15$ per stratum). For *M. franciscanus*, sampling was lethal and individuals were dissected to obtain gonad tissue for fatty acid profiling. *H. kamtschatkana* is endangered; therefore, fatty acid samples were non-lethal epipodial biopsies, a technique shown to impart negligible stress (Withler et al., 2001). Field sterility was maintained with 70% ethanol between samples. To prevent lipid degradation, tissues were frozen immediately at −20°C in 1.5 mL cryovials and later transferred to −80°C freezers for storage and subsequent lipid extraction and fatty acid composition profiling.

2.5 | Fatty acid extraction and analysis

Our protocols for fatty acid extraction and analysis are published in *Frontiers in Ecology and Evolution* (Schram et al., 2018) and expanded in Supporting Information (S1.2).

2.6 | Statistical analyses

2.6.1 | Univariate

We estimated univariate response variables as functions of predictors using Bayesian regression models. To control for uncertainty in model formulae, we conducted model comparison using approximate leave-one-out (loo) cross-validation and selected model formulae based on weights estimated using stacking (Vehtari et al., 2016; Yao et al., 2018). In cases where including a body size allometric scaling term increased posterior model weights, we accounted for this effect by including the log of body size (test diameter for urchins and shell length for abalone) as a covariate. We compared parameter posteriors directly within selected models. Population-level predictors included a year, treatment (control versus restoration), and depth interaction effect. We estimated model posteriors using Stan (Stan Development Team, 2022, 2024) via the R (R Core Team, 2024) package brms (Bürkner, 2017).

We modelled non-compositional and compositional responses using different likelihood distributions and link functions. Non-compositional responses, such as counts or mass, are independent and unconstrained, whereas compositional responses represent interdependent proportions that sum to one and must be interpreted relative to one another. For non-compositional, continuous, and positive gonad mass responses, we utilized a Gamma distribution and log link function. For compositional fatty acid proportion responses, we implemented a Dirichlet regression. To account for the compositional nature of fatty acid proportions, we modelled a response vector $\mathbf{Y} = (Y_1, Y_2, \ldots, Y_K)$, where each Y_k represents a component fatty acid proportion of the overall profile and the set of component fatty acid proportions sum to one, $\sum_{k=1}^{K} Y_k = 1$, using the Dirichlet distribution, $Y \sim \mathrm{Dirichlet}(\mu, \phi)$. Here, $\mu = (\mu_1, \mu_2, \ldots, \mu_K)$ is the vector of mean parameters, with each component μ_k representing the expected value for the corresponding proportion, and ϕ representing a concentration parameter that controls the variability of the distribution. We used a logit link function to constrain predicted proportions within sensible bounds between zero and one and to respect the compositional nature of the data. We used vague priors relative to the predicted scale of responses (Gelman et al., 2013) detailed in the Supporting Information (S1.3).

We fit our models using 8000 iterations across four chains, discarding the first half of the iterations per chain as a warm-up, resulting in a posterior sample of 16,000 iterations for each response, checking that chains converged using visual inspection. For each parameter estimate, we confirmed that R_{hat}, the potential scale-reduction factor, was less than 1.01 and the minimum effective sample size, n_{eff}, was greater than 1000 (Gelman et al., 2013). To evaluate goodness-of-fit for our models, we evaluated graphical posterior predictive checks, searching for any systematic differences between model simulations and empirical data (Gelman et al., 2013) and estimated Bayesian R^2 values (Gelman et al., 2019).

2.6.2 | Multivariate

We visualized multivariate patterns using ordination and evaluated the significance of predictors using robust distance-based multivariate analysis of variance. We generated non-metric multidimensional scaling ordinations (NMDS) (Clarke, 2006) based on Aitchison dissimilarity for fatty acids, which utilizes a centred log ratio transformation to account for compositionality (Aitchison, 1982), and Bray–Curtis distance for benthic community survey data. NMDS ordinations were fit using the package vegan (Oksanen et al., 2007) in R (R Core Team, 2024). Ordination stress is reported within each NMDS plot. We fit correlation vectors for constituent fatty acids or species, such that vector lengths were scaled by correlation coefficients with respect to NMDS ordination scores for each data point. Fitted vector directions indicated the ordination space towards which the focal fatty acid or species changed most rapidly and had the greatest correlation with the ordination configuration (Oksanen et al., 2023). We ranked the contributions of individual fatty acids to multivariate dissimilarity between groups of interest using a SIMPER analysis (Clarke, 2006) using the package vegan (Oksanen et al., 2007) in R (R Core Team, 2024). To assess significance of predictor variables while accounting for heteroscedasticity and unequal sample sizes, we ran W_d^* tests (Hamidi et al., 2019). We ran post hoc pairwise comparisons using distance-based Welch *t*-tests, T_W^2 (Alekseyenko, 2016), correcting for multiple comparisons using a Bonferroni adjustment.

For benthic survey data, we evaluated shifts in community composition across treatments, depths, and time using distance-based redundancy analysis (dbRDA) implemented with the dbrda() function in the vegan R package (Oksanen et al., 2023). For each taxonomic group (kelp, macroinvertebrates, microinvertebrates, fish), we constructed Bray–Curtis dissimilarity matrices from raw abundance data and modelled community structure as a function of Treatment × Period × Depth, conditioning on Site and Plot as random blocking factors to account for spatial nesting. Significance of main effects and interactions was tested via permutation-based ANOVA (anova.cca(), 999 permutations, type III), both sequentially (type I) for model terms and pairwise between groups using permutational tests of between-group dissimilarity. These tests enabled identification of depth-structured and treatment-specific changes in community composition before and after restoration.

3 | RESULTS

3.1 | Restoration context

Manual removal and in situ cracking of sea urchins in fall 2018 and spring 2019 substantially reduced local densities of *M. franciscanus* at treatment sites and the following summer yielded many-fold increases in subtidal kelp densities (Figure 1) along with improved body condition for remaining *M. franciscanus* and co-occurring *H. kamtschatkana* (Figure 3; Lee et al., 2021). Densities of *M. franciscanus* were reduced by ~88%, going from 4.936 individuals/m^2 (±4.38 SE) in summer 2018 pre-restoration surveys to 0.576 individuals/m^2 (±1.22 SE) post-restoration in summer 2019. During the same timeframe, densities remained relatively consistent at the control site (Figure 1). In the post-restoration 2019 summer survey, bull kelp, *Nereocystis luetkeana*, increased by ~6687%, going from 0.83 stipes/60 m^2 (±0.78 SE) to 56.33 stipes/60 m^2 (±32.26 SE; Lee et al., 2021) at the restoration site. One shallow transect at the control site coincidentally had comparable kelp density to the restoration site from July 2019 onward, suggesting generally higher recruitment that summer. However, all other transects at the control site during the same timeframe had at most 2–3 stipes/60 m^2 and mostly no kelp at all (Figures 1d and 2).

3.1.1 | Urchin density and size structure

Following restoration, sea urchin densities declined sharply at the restoration site across all depths, with the most dramatic reductions in shallow waters. For example, at 0–2 m depth, densities dropped more than tenfold—from 6.7 to 0.6 individuals per square metre. In contrast, no meaningful changes were observed at control sites. Alongside these declines, average urchin size also decreased significantly at the restoration site, consistent with the removal of larger individuals. Mean test diameter fell by 37 mm in shallow waters and by 12–16 mm at deeper depths, while control sites saw only modest size changes. These patterns indicate a substantial restoration-driven collapse in both urchin abundance and size structure.

3.1.2 | Abalone density and size structure

Abalone densities showed modest increases at the restoration site across all depths after restoration, particularly at deeper depths where kelp recovery was strongest. Although these changes were not statistically significant across all comparisons, average abalone size increased significantly post-restoration at all depths, with the largest gains (over 4 mm in shell length) observed at mid and deep transects. In contrast, control sites exhibited declines or smaller gains in size.

3.1.3 | Multivariate community responses

Kelp

Bull kelp surged at restoration sites (2018 → 2019: ~6687% increase), and kelp assemblage composition shifted through time ($W_d^* = 1.31$, $p = 0.027$), with deeper restoration transects diverging most; species vectors highlight *Nereocystis* and *Laminaria setchellii* as key drivers. Composition varied with time ('period'—pre vs. post) and depth (permutation test for dbRDA, period: df = 1, $F = 2.21$, $p = 0.003$; depth: df = 2, $F = 2.15$, $p = 0.001$).

Macroinvertebrates (belt transects)

Macroinvertebrate community composition varied significantly with time (pre vs. post), depth, and treatment, including a significant interaction between treatment and time (permutation test for dbRDA, period: df = 1, $F = 8.66$, $p = 0.001$; depth: df = 2, $F = 11.48$, $p = 0.001$; treatment-period: df = 1, $F = 1.93$, $p = 0.048$; treatment-depth: df = 2, $F = 3.41$, $p = 0.001$). These results indicate that restoration effects on community structure were depth-specific and differed between control and restoration sites. Pairwise comparisons confirmed substantial post-restoration divergence in community composition across depths at the restoration site, especially at 2–5 m and 5–10 m, relative to control sites.

Microinvertebrates (quadrats)

Microinvertebrate communities showed significant changes over time and across depth strata (permutation test for dbRDA, period:

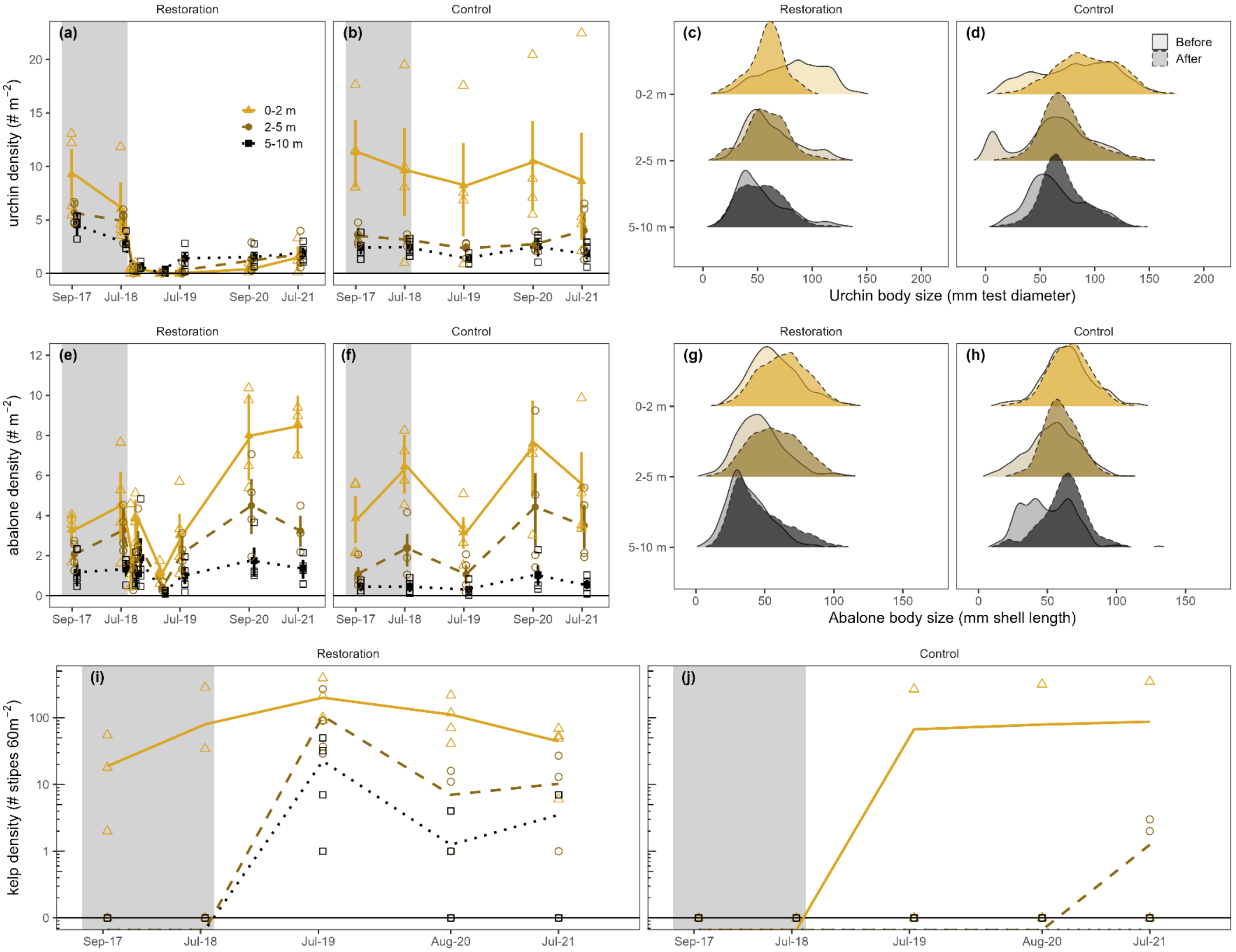

FIGURE 1 Depth-specific density and size structure responses to restoration. (a and b) Time series of the density of *M. franciscanus*. (c and d) Shifts in size structure of *M. franciscanus*. (e and f) Time series of the density of *H. kamtschatkana*. (g and h) Shifts in size structure of *H. kamtschatkana*. (i and j) Time series of the density of kelp. The vertical axis for kelp is on the log scale to capture orders of magnitude shifts in density. For all time series of density, open symbols represent transect-level empirical means for each survey, whereas solid symbols and vertical bars represent bootstrap means and 95% confidence intervals, respectively, for each treatment, depth, and time point. The shaded region of time series plots represents the pre-restoration timeframe (i.e. 'Before'), and the lighter region represents post-restoration timeframe (i.e. 'After'). Ridgeline plots (c, d, g and h) show kernel density estimates of body size for each group, with a smooth 'ridge' (height = relative probability density) stacked along the *y*-axis with slight overlap to enable direct visual comparison of size-frequency distributions across groups.

df = 1, $F = 6.81$, $p = 0.001$; depth: df = 2, $F = 2.46$, $p = 0.003$), but treatment effects were not statistically significant. Pairwise comparisons revealed that most significant differences occurred between time points rather than across treatments.

Fish

Fish assemblages showed modest but statistically significant shifts over time, although patterns were not clearly attributable to the restoration treatment. Community composition changed between the pre- and post-restoration periods (permutation test for dbRDA, df = 1, $F = 3.20$, $p = 0.004$), suggesting temporal dynamics—possibly due to broader environmental variability or natural recovery processes. However, there was no significant effect of depth or treatment, nor any evidence of treatment-specific changes over time or depth. Pairwise comparisons showed no consistent patterns of differentiation between restoration and control sites. Overall, fish communities appeared relatively stable over the study period, with weaker and more diffuse responses than those observed in invertebrate assemblages.

3.2 | Consumer body condition

Body condition improved in both grazer taxa at the restoration site (Figure 3). Prior to the urchin reductions, deep transects were urchin barrens occupied by emaciated sea urchins with diminutive gonads. After correcting for body size, gonad mass among remaining deep *M. franciscanus* individuals at the restoration site increased ~89%

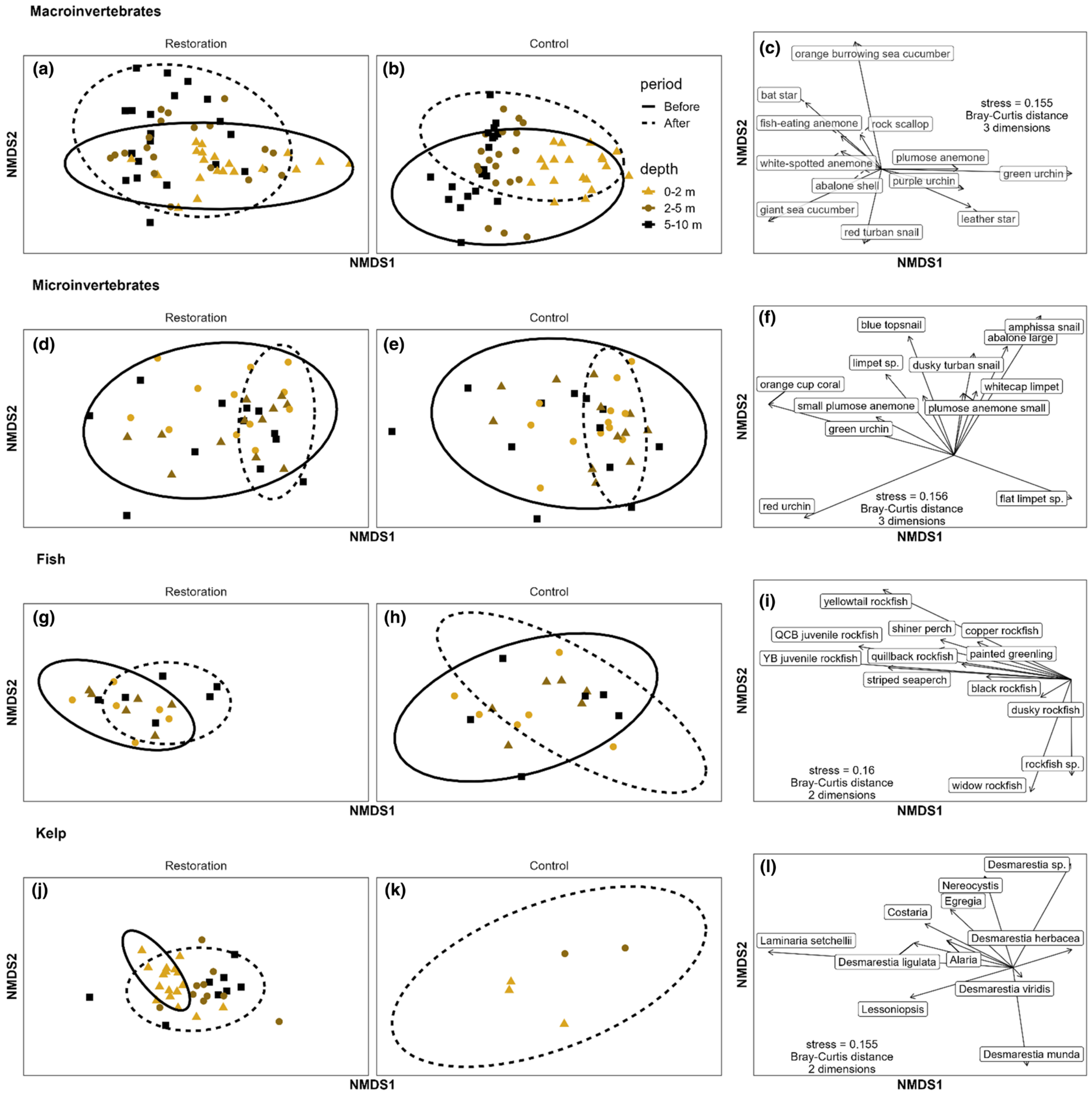

FIGURE 2 Depth-specific multivariate community responses to restoration for (a–c) macroinvertebrates, (d–f) microinvertebrates, (g–i) fish, and (j–l) kelp. Microinvertebrates were sampled using 1 m^2 quadrats whereas all other groups were sampled using belt transects. (k) Note that 95% CI ellipsis for the "Before" period is omitted because at the time, surveys indicated a complete absence of macroalgae at the Control site.

from 2018 pre-restoration to 2019 post-restoration (Figure 3c) coincident with the resurgence of deep kelp at the restoration site. In contrast, gonad mass in shallow urchins remained relatively constant across years at both control and restoration sites (Figure 3a,b). Gonad mass generally increased exponentially with body size (Figure 3a–d). Over the same timeframe, *H. kamtschatkana* body condition index (BCI) generally increased at the restoration site, particularly for females (Figure 3e,g). On average, female BCI at the restoration site increased by 28.4% (95% HPD = 14.8%–45.3%) in shallow individuals and 30.9% (95% HPD = 7.5%–53.8%) in deep individuals. In contrast, female BCI at the control site increased only marginally in shallow individuals and marginally decreased in deep individuals (Figure 3f, h; shallow: 13.4%, 95% HPD = −9.5%–31.5%; deep: −1.7%, 95% HPD = −18.6%–16%).

3.3 | Fatty acid biomarkers

There was strong evidence that restoration reshaped the fatty acid profiles of deep-dwelling consumers, and that these profiles

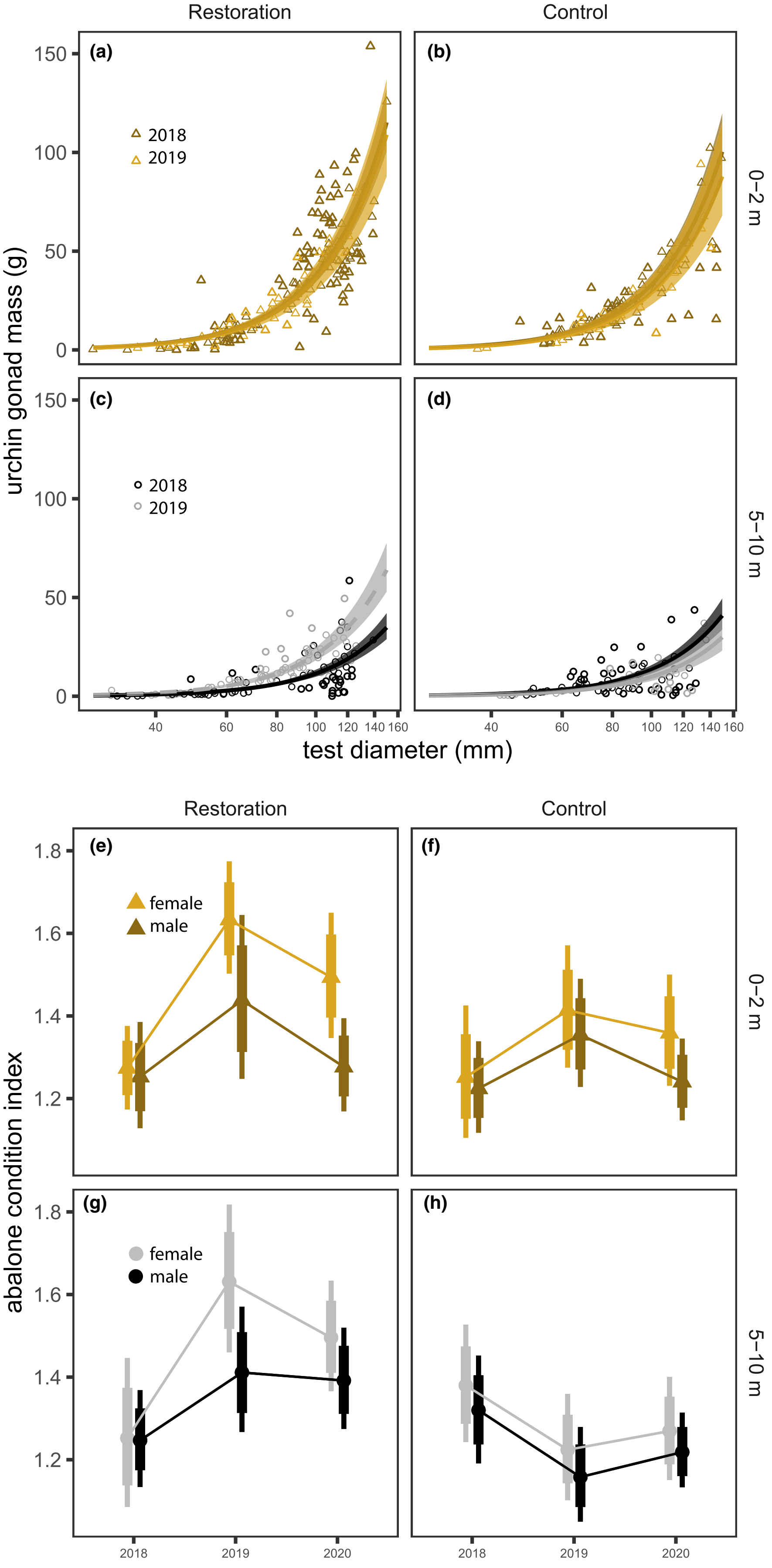

FIGURE 3 Depth-specific body condition responses to restoration. (a–d) Body size-specific gonad mass of *M. franciscanus* by treatment and depth. The horizontal axis is on the log scale to highlight that modelling the relationship between gonad mass and body size was more accurately modelled allometrically as a power function, as opposed to isometrically as a linear function. Lines and shaded ribbons represent conditional modelled means and 95% credible intervals, respectively. Open symbols represent data points. Dashed lines represent instances with significant year over year differences in body size-specific gonad mass for a given depth. (e–h) Condition index for *H. kamtschatkana*. representing the ratio of body wet mass to volume as a function of sex, depth, and treatment, pre- and post-restoration after accounting for body size. Points represent conditional modelled means and thin and thick vertical bars represent 95%, and 80% credible intervals, respectively.

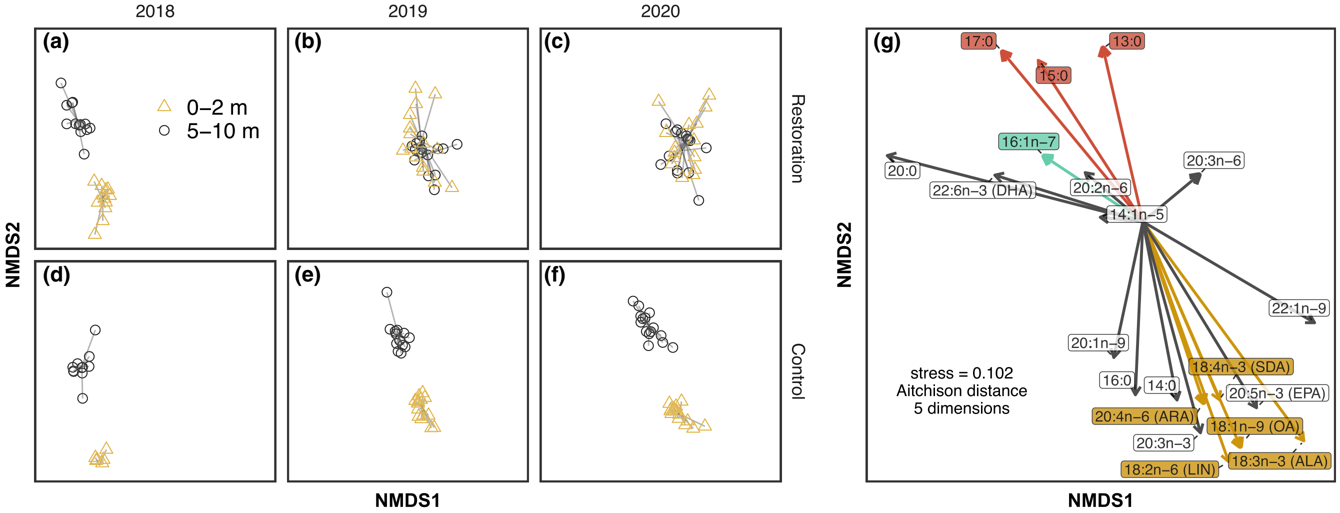

FIGURE 4 (a–f) Time series of multivariate fatty acid profile shifts in *M. franciscanus* gonads reveal a convergence in composition at the restoration site contrasting with persistent depth separation at the control site. Points represent measured profiles comprised of 34 fatty acids, where open black circles represent shallow and open gold triangles represent deep samples. (g) Vectors illustrating the contributions of the top twenty most influential (SIMPER) constituent fatty acids driving multivariate dissimilarity between depth strata. Specific vectors are highlighted in colour to emphasize the contribution of key classes of biomarkers to dissimilarity: Kelp (gold), bacteria (red), and diatoms (aquamarine).

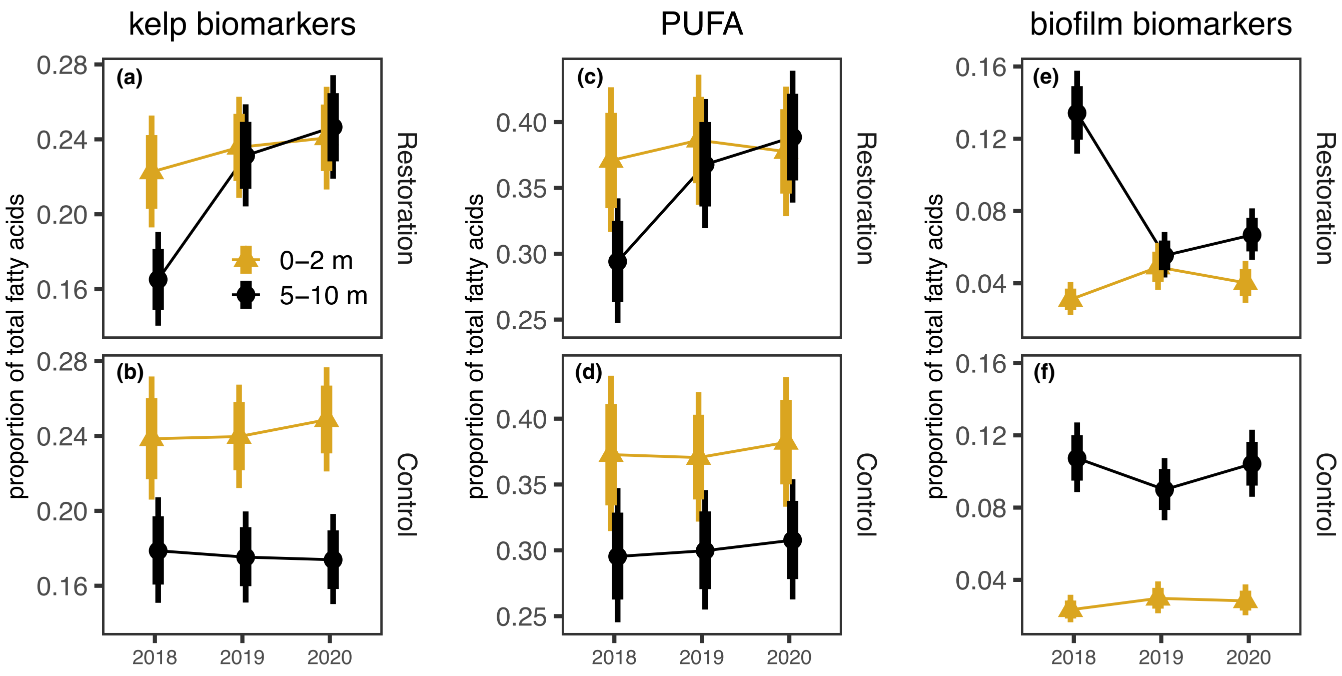

FIGURE 5 Time series of select fatty acid biomarkers in *M. franciscanus* gonad tissue reveal a convergence in composition at the restoration site resulting from an increase in kelp biomarkers and PUFA accompanied by a decrease in biofilm biomarkers, contrasting with persistent depth separation at the control site. Black indicates deep and gold indicates shallow samples. (a and b) Kelp biomarkers, (c and d) kelp biomarkers plus other nutritionally valuable polyunsaturated fatty acids (PUFA—fatty acids with two or more double bonds), and (e and f) biofilm biomarkers following kelp restoration. Points represent biomass corrected conditional modelled means and thin and thick vertical bars represent 95%, and 80% credible intervals, respectively.

changed as a function of body size in *H. kamtschatkana*. In general, fatty acid profiles transformed at the restoration site from a barrens type to a kelp forest type after restoration efforts (Figures 3–6), with much of the dissimilarity driven largely by two classes of fatty acids, kelp biomarkers and biofilm (i.e., bacteria and diatom) biomarkers (Kelly & Scheibling, 2012). There was a significant three-way interaction effect of year, treatment, and depth on multivariate fatty acid profiles in *M. franciscanus* gonad

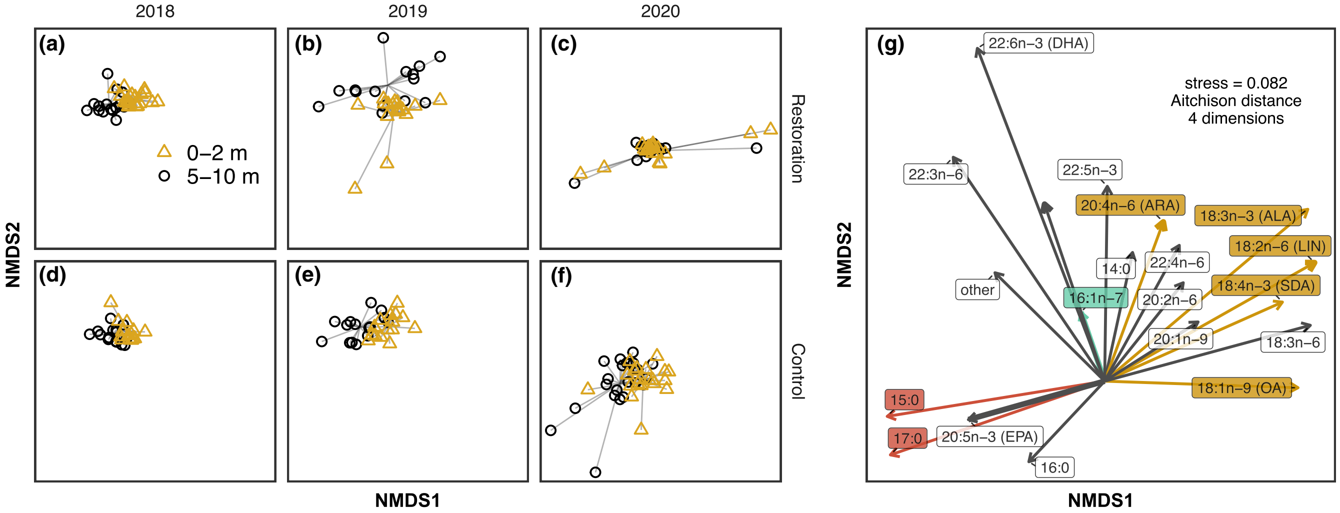

FIGURE 6 (a–f) Time series of multivariate FA profile shifts in *H. kamtschatkana* epipodia tissue as a function of depth and treatment show consistent depth-stratified differences in composition at both restoration and control sites. Points represent measured data points comprised of 34 fatty acids, where open black circles represent shallow and open gold triangles represent deep samples. (g) Vectors illustrating the contributions of the top twenty most influential (SIMPER) constituent fatty acids driving multivariate dissimilarity between depth strata. Specific vectors are highlighted in colour to emphasize the contribution of key classes of biomarkers to dissimilarity: Kelp (gold), bacteria (red), and diatoms (aquamarine).

($n = 166$, $W_d^* = 20.388$, $p = 0.001$) and *H. kamtschatkana* epipodia tissues ($n = 212$, $W_d^* = 29.527$, $p = 0.001$).

3.3.1 | *Mesocentrotus franciscanus* (gonad tissue)

Profiles of deep versus shallow individuals at the restoration site differed in 2018 pre-restoration ($T_w^2 = 16.742$, W_d^* $p = 0.001$, $n_{deep} = 13$, $n_{shallow} = 12$), but not post-restoration (2020: $T_w^2 = 1.918$, W_d^* $p = 0.264$, $n_{deep} = 15$, $n_{shallow} = 15$). In contrast, individuals at the control site differed by depth across all years (W_d^* $p \leq 0.001$). Neither the restoration nor the control sites differed year-over-year in shallow habitats (restoration 2019–2020: $T_w^2 = 0.942$, W_d^* $p = 0.576$; control 2019–2020: $T_w^2 = 0.781$, W_d^* $p = 0.767$).

The summed proportions of kelp biomarker fatty acids (oleic acid [OA], alpha-linolenic acid [ALA], alpha-linoleic acid [LIN], stearidonic acid [SDA], arachidonic acid [ARA], and vaccenic acid) increased by ~27% along deep transects in the first year post-restoration at the restoration site and sustained this level the following year (Figure 4a). In contrast, the proportions of kelp biomarkers did not change significantly at the control site over the same period (Figure 4b). The proportion of nutritionally valuable PUFAs in deep urchins at the restoration site increased to levels comparable with shallow urchins post-restoration (Figure 4c), whereas this proportion was consistently lower in deep individuals relative to shallow individuals at the control site (Figure 4d).

At the control site, individuals from deep, barren habitat had higher proportions of biofilm fatty acid biomarkers (Figure 4). The proportions of odd-chain fatty acids 13:0, 15:0, and 17:0 (bacterial), and 16:1n-7 (diatomaceous) were consistently higher in deep versus shallow habitats at the control site. In contrast, deep-dwelling urchins at the restoration site initially had higher proportions of these fatty acids than their shallow counterparts in 2018, but these proportions decreased to a level comparable to shallow urchins in 2019 post-restoration and remained at similar proportions the following year.

3.3.2 | *Haliotis kamtschatkana* (epipodia tissue)

After controlling for the strong effect of body size, kelp biomarkers consistently increased in deep habitats at the restoration site post-restoration (Figures 6 and 7). The proportion of biofilm biomarkers in *H. kamtschatkana* epipodia decreased as a function of increasing body size with higher proportions in small deep-dwelling individuals (Figure 7c). Conversely, the proportion of kelp biomarkers increased as a function of body size with consistently higher proportions in shallow-dwelling individuals for all but the largest body sizes recorded (Figure 7d). The proportion of kelp biomarkers increased in epipodia tissue from 20% to 25% along deep transects the first year post-restoration at the restoration site, then again from 25% to 29% the following year (Figure7a). Additionally, individuals along deep transects at the restoration site had ~9.2% higher kelp biomarker proportions than at the control site at similar depth in the first year post-restoration, and ~8.9% higher the following year (Figure 7a,b).

4 | DISCUSSION

Overgrazing threatens kelp forests worldwide, particularly in the context of rapid global change. Although urchin culls often restore

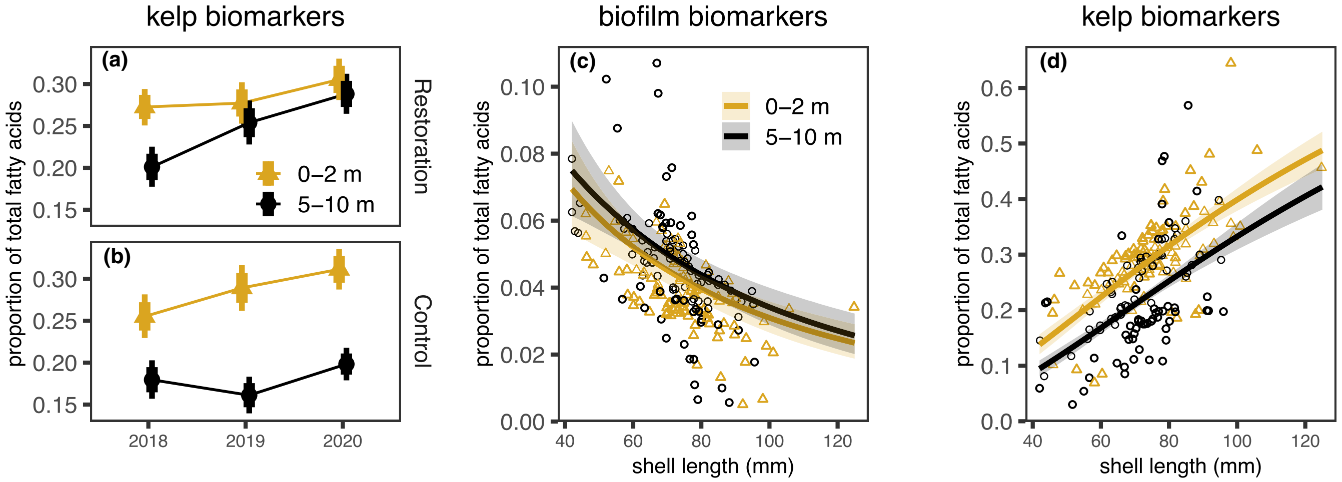

FIGURE 7 (a and b) Time series of kelp biomarkers in *H. kamtschatkana* epipodia tissue as a function of depth and treatment. Points and thin and thick vertical bars represent conditional modelled means, 95%, and 80% credible intervals, respectively. (c and d) Relationship between body size and assimilation of (c) biofilm versus (d) kelp biomarkers. Lines and faded ribbons represent conditional modelled means and 95% HPD, respectively. Faded points represent empirical data points. Horizontal axis is on the log scale to spread data more evenly and improve the visibility of overall trends.

kelp biomass, how those gains move through food webs to resident consumers has largely been inferred rather than measured in situ. We combine fatty acid diet tracing with depth-resolved demographic and multivariate community analyses to show kelp assimilation by consumers, strongest in deeper habitats. These diet shifts coincide with urchin declines, abalone growth, and benthic community reassembly. This provides mechanistic evidence linking kelp recovery to consumer and community outcomes, yielding actionable guidance for restoration design and evaluation. We interpret these patterns within a functional definition of trophic recovery, where restoration success reflects the renewed flow of kelp-derived energy through consumers and the reoccupation of previously barren depths as productive foraging habitat, rather than a strict return to historical community states. Because kelp forests underpin fisheries production, cultural harvest, and coastal food security, trophic recovery following restoration has direct implications for the ecosystem services these habitats provide.

In this study, we demonstrate that kelp forest restoration via urchin culling led to increased kelp abundance and expanded habitat availability, particularly in deeper zones that were previously dominated by urchin barrens (Figure 1). In turn, primary consumers in these areas showed marked changes in tissue fatty acid composition: both *M. franciscanus* and *H. kamtschatkana* exhibited elevated assimilation of kelp-derived biomarkers, especially polyunsaturated fatty acids (PUFAs), coinciding with improvements in body condition (Figure 3). These results provide field-based evidence that restored kelp biomass contributes directly to consumer nutrition through trophic transfer, and that these benefits extend beyond shallow core kelp zones into deeper, previously depauperate areas. Trophic recovery manifests not simply as kelp regrowth but as measurable improvements in consumer nutrition, condition, and refuge habitat availability. These functional indicators recovered rapidly and in a depth-structured manner, illustrating how food web processes respond to restoration even when community structure has not fully returned to historical baselines. Our results lead to three key conclusions detailed below:

First, kelp restoration can improve not only the abundance but also the nutritional quality of food resources for benthic consumers. In *M. franciscanus*, fatty acid biomarkers and gonad condition suggest restored kelp availability enhances the biochemical composition of roe to levels comparable with those from healthy shallow kelp forests. This has potential relevance for roe-based fisheries management, where improving both the yield and market value of urchins may align with ecological goals of overgrazing control. While our study did not directly measure starvation tolerance, our results together with kelp restoration experiments elsewhere indicate that *M. franciscanus* can regain near-normal gonad biomass within less than a year once high-quality kelp becomes available, even after prolonged food limitation (Grime et al., 2023; Okamoto, 2014; Spindel, 2023; Spindel et al., 2021). By comparison, other benthic herbivores and echinoderms often show slow or incomplete recovery following energetic collapse. For example, *Diadema antillarum* populations have remained far below pre-die-off densities for decades after mass mortality in the Caribbean (Lessios, 2016), and red abalone reproductive indices decline sharply under chronic food limitation and warming, contributing to multi-year fishery closures in northern California (Rogers-Bennett et al., 2010). This implies that post-restoration urchin densities should be carefully managed to balance ecological recovery with fishery access. Future research should aim to quantify target urchin densities that allow for sustainable kelp regrowth while supporting viable harvests. Moreover, these improvements in gonad quality are directly relevant to commercial and Indigenous roe fisheries, where product value depends on both yield and nutritional composition. By increasing access to PUFA-rich kelp, restoration can enhance marketability and fishery viability while simultaneously reducing grazing pressure on recovering kelp beds. This alignment between ecological and economic outcomes highlights the dual benefits of targeted urchin removals.

Second, our results support and extend previous evidence of ontogenetic dietary shifts in North American abalone. Prior laboratory and field studies have shown that juvenile pinto abalone primarily consume benthic diatoms, microalgae, and bacterial biofilms while larger individuals incorporate increasing amounts of drift and attached macroalgae into their diets, particularly kelps such as *Macrocystis pyrifera* and *Nereocystis luetkeana* (Breen, 1980; Sloan & Breen, 1988; Won et al., 2010). Our study adds a novel field-based fatty acid perspective to this body of work by demonstrating that tissue fatty acid composition varies with abalone body size, with larger individuals exhibiting greater assimilation of nutritious kelp-derived fatty acids and reduced biofilm-associated fatty acids (Figure 7). For *H. kamtschatkana*, improvements in food quality at depth may support higher reproductive output, with direct implications for conservation aquaculture, restoration of culturally important fisheries, and long-term population recovery under the Species at Risk Act. Access to deeper, more stable kelp habitats may also reduce vulnerability to thermal stress, predation, and illegal harvest, offering substantial co-benefits for coastal communities that depend on this species.

Third, restoration efforts that expand the vertical extent of kelp forests may generate additional ecological benefits by subsidizing food availability and creating spatial refugia for vulnerable benthic species. For *H. kamtschatkana* in particular, the presence of deeper kelp can improve access to both food and shelter in habitats less impacted by predation, human harvest, and warming surface waters. These broader spatial and nutritional benefits strengthen the case for sea urchin reduction as a restoration tool, not only for promoting kelp recovery but for supporting multi-species resilience in coastal ecosystems. The strong nutritional and physiological responses we observed at depth indicate that these zones may serve as high-leverage targets for accelerating trophic recovery. Re-establishing kelp in deeper barrens could yield disproportionately large ecological benefits by expanding high-quality foraging habitat into areas that have historically functioned as energy bottlenecks. These depth-specific gains suggest that restoration efforts prioritizing deep strata can maximize early functional recovery even when shallow kelp zones are less responsive. Similar dynamics are likely in other urchin-dominated kelp systems where deep barrens have persisted for decades. Global syntheses and regional case studies show that targeted urchin removals can rapidly restore kelp biomass and associated communities in temperate reefs from California, New Zealand, Tasmania, and northern Europe, particularly when efforts are sustained and strategically located in persistent barrens (Christie et al., 2024; Eger et al., 2022, 2024; Miller et al., 2023; Miller & Shears, 2023). Our depth-focused results therefore complement broader reviews of kelp restoration, which emphasize sea urchin control and spatially explicit planning as key ingredients for scaling recovery of kelp forest structure, trophic function, and ecosystem services across regions.

The observed increases in consumer body condition following restoration reflect not only improved food availability but also species-specific physiological responses to restored kelp access. In *M. franciscanus*, these responses are consistent with known forms of metabolic plasticity that allow individuals to persist under food scarcity and recover rapidly when conditions improve. Unlike tropical taxa that reduce body size to lower metabolic demand (e.g. *Diadema antillarum*; Levitan, 1989), *M. franciscanus* appears to rely on plasticity in energy allocation, exhibiting variable investment in gonadal reserves and modulated resting metabolic rates (Dolinar & Edwards, 2021; Okamoto, 2014; Spindel, 2023; Spindel et al., 2021). Our data show that following targeted urchin reductions and a resurgence of kelp in deeper habitats, gonad mass in *M. franciscanus* increased by 89%, after accounting for body size, within a single year (Figure 3). This rapid physiological rebound aligns with findings from both field and laboratory studies (e.g. Grime et al., 2023) and underscores that remnant urchin populations can quickly capitalize on enhanced food availability. From a restoration monitoring perspective, this suggests that recovery of trophic function and consumer condition may occur on relatively short timescales, particularly in areas where overgrazing had most severely suppressed macroalgal production.

These responses were especially pronounced in deeper habitats (20–30 m), which historically supported persistent kelp beds but had remained locked in long-lived urchin barrens. Because kelp productivity is naturally lower at depth due to light limitation, any restoration-driven increases in kelp availability represent a disproportionately large improvement in food quality relative to pre-restoration conditions. Herbivore densities at depth are also typically lower and more resource-limited, making consumer fatty acid profiles highly sensitive to restored kelp access. These mechanisms align with evidence from other kelp systems showing that deeper zones often exhibit stronger demographic (Dayton et al., 1992; Filbee-Dexter & Scheibling, 2014; Krumhansl et al., 2016; Ling et al., 2015) and biochemical (Barbosa et al., 2020; Koch et al., 2016; Shalders et al., 2023) responses when released from chronic grazing pressure.

While fatty acid profiles provide powerful integrative indicators of consumer nutrition, they also carry important limitations for interpreting dietary assimilation. Tissue FA composition reflects both diet and species-specific metabolic modification, meaning that some dietary biomarkers may be selectively retained, transformed, or diluted. Temporal lags between ingestion and tissue turnover can obscure short-term diet changes, and environmental stressors, such as temperature, energetic demands, or reproductive state may shift FA composition independently of diet. For these reasons, our findings represent strong correlative evidence of trophic linkage rather than direct estimates of assimilation rate.

Fatty acid profiles also revealed species- and size-specific differences in dietary assimilation for *H. kamtschatkana*, a more mobile grazer that competes with urchins for macroalgal resources. In this species, we found a size-dependent dietary shift: smaller individuals assimilated more biofilm-derived fatty acids, while larger individuals incorporated more kelp-derived lipids (Figure 7). This pattern supports and extends previous evidence of ontogenetic diet shifts in abalone (Breen, 1980; Won et al., 2010), and suggests that access to high-quality kelp is particularly important for larger, reproductive individuals. Importantly, our benthic surveys showed that restoration expanded macroalgal cover in deeper habitats where larger abalone were more abundant and where body condition also improved post-restoration. These findings imply that kelp restoration not only increases food quality but may also shift the spatial distribution of suitable foraging habitat into deeper, more stable zones. The observed shifts in abalone fatty acid profiles similarly indicate trophic recovery, with larger individuals regaining access to high-quality kelp-derived nutrition and expanding into deeper, newly productive habitats.

This spatial shift has critical implications for the conservation of *H. kamtschatkana*. In the absence of kelp, larger abalone may be forced into shallower waters in search of food, where they face increased risks from predation, harvesting, and thermal stress (Lee et al., 2016; Rogers-Bennett & Catton, 2022). Unlike sea urchins, which exhibit higher tolerance to warming, acidification, and starvation (Byrne et al., 2011; Spindel et al., 2021; Uthicke et al., 2016), abalone may be more physiologically constrained due to their narrower dietary requirements and lower metabolic flexibility. Climate-driven kelp declines in northern California, for example, pushed red abalone into shallows where increased exposure led to both ecological collapse and fishery mismanagement (Rogers-Bennett & Catton, 2022). Our findings suggest that strategic kelp restoration, particularly in deeper subtidal zones, can mitigate these risks by improving food quality and extending access to lower risk habitat for vulnerable grazers. For *H. kamtschatkana*, this may be especially important for female breeders, whose reproductive output is strongly tied to nutritional condition. More broadly, we anticipate that other macroalgal grazers may similarly benefit from expanded access to deeper kelp, though further empirical work is needed to test this across trophic guilds and ecosystem types.

Our BACIPS study helps clarify how gains in kelp biomass from targeted restoration efforts propagate through food webs to influence grazer physiology, trophic ecology, and habitat use. In particular, we show that increases in kelp abundance were associated with improved body condition and biochemical profiles in *M. franciscanus* and *H. kamtschatkana*, especially in deeper habitats that had previously been barren. These results provide mechanistic insight into the pathways by which kelp recovery reorganizes benthic communities, and how the benefits of restoration may differentially accrue to consumers depending on their mobility, body size, and trophic flexibility. We focused on two ecologically and culturally important taxa, but many other consumers may respond similarly, or idiosyncratically, to kelp restoration. Expanding these approaches across functional groups and trophic levels will be critical to developing general principles for monitoring food web recovery following restoration in coastal ecosystems. Together, these patterns highlight that trophic recovery proceeds through restoration of energy pathways and consumer performance, outcomes that may precede or differ from historical community compositions but nonetheless represent meaningful ecological recovery. Depth-stratified monitoring is therefore essential for detecting and interpreting early trophic recovery. Because biochemical responses to restored kelp access were strongest in deeper habitats, sampling consumer fatty acid profiles along depth gradients can help managers identify where recovery is progressing fastest and where additional intervention might be needed. Incorporating depth explicitly into monitoring frameworks can also improve adaptive restoration design by revealing which zones contribute most to the re-establishment of energy flow. Incorporating trophic indicators such as fatty acid biomarkers into monitoring programmes can also help managers anticipate the return of fishery-relevant traits before population metrics respond. This provides a practical decision-support tool for guiding restoration investments, fishery openings, and community-based stewardship efforts.

From a monitoring perspective, FA biomarkers offer a practical and sensitive indicator of trophic recovery. Because consumer FA signatures integrate diet over weeks to months, they can reveal early nutritional responses to kelp restoration before demographic changes become detectable. Increases in essential fatty acids (e.g. SDA, ARA, long-chain PUFA precursors) provide a direct measure of improved food quality, while repeated sampling of sentinel herbivores across depth strata can track the spatial progression of restored energy flow. These biomarker-based indicators represent a relatively low-cost, scalable tool for managers seeking to evaluate the functional effectiveness of kelp restoration across years and sites.

Our findings have broad relevance for temperate reef ecosystems worldwide where kelp forests have been degraded by unchecked herbivore populations. The use of fatty acid biomarkers and consumer condition indices offers a transferable, field-applicable approach for detecting trophic recovery following restoration interventions. Similar urchin overgrazing dynamics and restoration efforts are underway in regions, such as California, New Zealand, Tasmania, and Japan, where targeted urchin removals aim to promote kelp resilience (Eger et al., 2022). By demonstrating depth-resolved trophic responses to kelp restoration, our study provides both conceptual and methodological insights that can inform global efforts to recover kelp forest food webs. While our study spans 4 years of post-restoration monitoring (2017–2021), ongoing surveys in Haida Gwaii continue to track the persistence of kelp recovery and consumer responses. Long-term data are critical to evaluate the stability and resilience of restored ecosystems, especially in the face of climate variability and shifting grazer dynamics. We emphasize the need for restoration monitoring programmes to incorporate not only structural metrics (e.g. kelp cover, species abundance), but also ecosystem-based indicators, such as trophic tracers, body condition indices, and community composition. While our analyses focused on well-established fatty acid biomarkers with clear ecological interpretation, we acknowledge that other fatty acids may offer additional insights, and future studies could explore their sources and functional significance in greater detail. These integrative approaches can better capture the functional outcomes of restoration and guide adaptive management over decadal timescales. More broadly, the trophic pathways documented here connect kelp restoration to ecosystem services that directly benefit people. Enhanced kelp availability and improved consumer nutritional condition can support commercial and subsistence fisheries, strengthen cultural harvest practices, and increase local food provisioning. As kelp forests also contribute to shoreline protection, carbon cycling, and biodiversity maintenance, trophic recovery reflects not only ecological change but improvements in the social–ecological resilience of nearshore communities.

5 | CONCLUSION

While multiple stressors, including marine heatwaves, contribute to kelp loss worldwide, chronic sea urchin overgrazing remains a major impediment to kelp recovery, leading to persistent barrens and associated declines in ecological function and ecosystem services. Failure to recover from such degradation has cascading negative impacts on nearshore ecosystems and the critical services they provide (Graham, 2004; Rogers-Bennett & Catton, 2019). This phenomenon has been exacerbated by recent climatic trends (Smale, 2020; Smith, Burrows, et al., 2021) and the extirpations of key predators (Burt et al., 2018; Estes & Palmisano, 1974; Watson & Estes, 2011) that otherwise regulate sea urchin populations. Targeted sea urchin reduction is emerging as an effective technique for increasing the abundance of kelp (Lee et al., 2021; Miller et al., 2022) and enhancing the fishery value of resident taxa (Grime et al., 2023). Such intervention may best be applied as part of a multifaceted ecological restoration strategy involving, in addition, promoting the recovery of natural predators, marine protected areas, and conservation aquaculture (Eger et al., 2022; Miller et al., 2022). This study demonstrates the value of pairing observational ecological surveys with diet tracing using molecular techniques when, as is often the case (Nakazawa, 2015), consumers shift their diet throughout ontogeny and organize their habitat associations and interactions with conspecifics and other taxa accordingly.

AUTHOR CONTRIBUTIONS

Nathan B. Spindel, Aaron W. E. Galloway, Lynn C. Lee, and Daniel K. Okamoto conceived the ideas and designed methodology; Nathan B. Spindel, Aaron W. E. Galloway, Julie B. Schram, Gwiisihlgaa Daniel McNeill, SG̱iids Ḵung Vanessa Bellis, Niisii Guujaaw, Jaasaljuus Yakgujanaas, Markus Thompson, Rachele Ferraro, Lynn C. Lee, Daniel K. Okamoto collected the data; Nathan B. Spindel and Daniel K. Okamoto analysed the data; Nathan B. Spindel led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our international collaboration includes authors based in Haida Gwaii where the study was carried out. These local experts engaged with the research and study design throughout the process.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sqv9s4njd (Spindel, Galloway, Schram, McNeill, Bellis, Guujaaw, Yakgujanaas, Thompson, et al., 2026). Code available from Zenodo: https://doi.org/10.5281/zenodo.18407196 (Spindel, 2026).

ORCID

Nathan B. Spindel https://orcid.org/0000-0002-4853-7427
Aaron W. E. Galloway https://orcid.org/0000-0001-7826-299X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Detailed description of kelp forest restoration methods, fatty acid extraction and analysis protocols, and statistical model specifications supporting the investigation of trophic flow following ecological restoration.

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