Biological Sciences, Ecology

Title: Climate drives the geography of marine consumption by changing predator communities

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Abstract: The global distribution of primary production and consumption by humans (fisheries) are well-documented, but we have no map linking the central ecological process of consumption within food webs to temperature and other ecological drivers. Using standardized assays that span 105 degrees of latitude on 4 continents, we show that rates of bait consumption by generalist predators in shallow marine ecosystems are tightly linked to both temperature and the composition of consumer assemblages. Unexpectedly, rates of consumption peaked at mid-latitudes (25-35°) in both northern and southern hemispheres across both seagrass and unvegetated sediment habitats. This pattern contrasts with terrestrial systems, where biotic interactions reportedly weaken away from the equator, but it parallels an emerging pattern of a subtropical peak in marine biodiversity. The higher consumption at mid-latitudes was closely related to the type of consumers present, which explained rates of consumption better than consumer density, biomass, species diversity, or habitat. Indeed, the apparent effect of temperature on consumption was mostly driven by temperature-associated turnover in consumer community composition. Our findings reinforce the key influence of climate warming on altered species composition and highlight its implications for the functioning of Earth's ecosystems.

Keywords: latitudinal diversity gradient, macroecology, biogeography, trophic processes, climate, seagrass

Significance Statement (max 120 words):

Consumption transfers energy and materials through food chains and fundamentally influences ecosystem productivity. Therefore, mapping the distribution of consumer feeding intensity is key to understanding how environmental changes influences biodiversity, with consequent effects on trophic transfer and top-down impacts through food webs. Our global comparison of standardized bait consumption in shallow coastal habitats finds a previously unrecognized peak in feeding intensity away from the equator that is better explained by the presence of particular consumer families than by latitude or temperature. This study complements recent demonstrations that changes in biodiversity can have similar or larger impacts on ecological processes than those of climate.

Text

Latitudinal diversity gradients have stimulated decades of research, much of it invoking a decline from tropics to poles in rates of key biological processes and species interactions (1–3). General explanations for ecological patterns across latitude, however, remain elusive in part because so many environmental and biological variables change in parallel with latitude. As a result, the connections between ecological patterns and processes at global scales remain controversial (4–6). Our uncertainty has recently been amplified by demonstrations that diversity of many modern and ancient lineages peaks at mid-latitudes rather than at the equator, particularly in the ocean (7, 8).

Temperature is among the environmental factors that vary most consistently with latitude, and is a fundamental driver of biological processes. Metabolic theory mechanistically links environmental temperatures to a suite of biological processes, including metabolism and trophic transfer (9–12). For example, metabolic theory predicts that per capita consumption rates of ectothermic consumers should follow increased metabolic needs and activity, and increase with rising temperature (13). But the traits of consumers, their abundance, and the resources available to them also change with temperature (14, 15), so total consumption rates may be poorly predicted by temperature alone. Separating these effects requires data on geographic variation in consumption.

Our understanding of global variation in top-down processes in marine systems is largely indirect, based on inferences from distributions of organismal traits such as body size (e.g., (2, 16) and on comparisons of primary production, prey abundance, and predator abundance (e.g., (17, 18). The distribution and abundance of species respond to productivity, reproductive rate, migration, mortality, and evolutionary history, all of which are modified by temperature (e.g., (19, 20). But while the spatial distribution of primary production and human predation (fishing) are well-documented (21, 22), we have only sparse empirical measurements of geographic variation in consumption by natural predators, which is needed to predict trophic transfer and prey abundance. Thus, we lack a global map linking the central ecological process of consumption to temperature and other drivers.

We approached this problem by measuring feeding intensity of generalist marine consumers across 42 sites around the globe representing two widespread coastal habitats: seagrass and unvegetated sediments. These critical habitats provide shelter and fuel primary and secondary production (23–25), and seagrass persistence is in turn linked to trophic processes, as mid-level carnivores consume herbivores that can facilitate or damage seagrass (26–30). Therefore, understanding consumption by mid-level predators is key to seagrass conservation and restoration efforts (30).

To compare consumption rigorously around the world's coasts, we used a simple, standardized feeding assay, offering small (~1 cm) discs of dried squid mantle as bait. Squid is attractive to many generalist marine predators, including mid-sized fishes and crustaceans, which we surveyed in both seagrass and unvegetated habitats. Importantly, standardizing bait allowed us to estimate consumption rates on a comparable basis while avoiding confounding influences of geographic variation in prey type, prey behavior, and prey defenses. Previous studies (e.g., (31, 32) have shown changes in feeding on standardized prey across latitude, but ours covers nearly the entire latitudinal range of seagrasses on five continents, and multiple ocean basins in both northern and southern hemispheres (our study, 38°S-67°N; seagrass, 45°S-70°N). This allowed us to test the consistency of latitudinal gradients in consumption in two widespread ecosystems, and to begin disentangling the role of correlated drivers. Based on previous studies documenting broad-scale patterns in biodiversity (3, 33, 34), prey defense (2), trophic interactions (5, 35, 36), and metabolism (12), we hypothesized that rates of bait consumption would increase toward the equator.

Results and Discussion

Contrary to our expectations, bait consumption peaked away from the equator in both hemispheres (25-35° North and South), and was consistent between seagrass and sediment habitats (Fig. 1A), despite slightly higher density, richness, and biomass of consumers in seagrass (SI Appendix, Fig. S1). This mid-latitude peak was supported by a hump-shaped relationship between absolute latitude and consumption (comparison of models with and without second-order polynomial; Akaike weight $w_{2vs1} = 0.86$). In contrast, satellite-derived mean annual sea surface temperature decreased monotonically with latitude (SST; Fig. 1C), and the hump-shaped relation of SST to consumption was much stronger than that for latitude ($w_{2vs1} > 0.99$). This nonlinear relationship between SST and consumption was also supported in two independent, well-sampled transects along the Northwest Atlantic ($w_{2vs1} = 0.97$) and Southwest Pacific ($w_{2vs1} = 0.99$; SI Appendix, Fig. S2), strengthening the inference that the equatorial dip in consumption reflects a response to temperature, rather than some other correlate of latitude.

Fishes and crabs were the main consumers of bait at all sites, and their taxonomic composition varied greatly across sites and with temperature (Fig. 2). Because species and genera of coastal animals differ markedly across ocean basins and hemispheres, we analyzed consumer composition at the level of taxonomic families, which allowed us to describe global consumer biogeography using metrics of dissimilarity. We used presence vs. absence rather than abundance data because we wanted to explore the effects of composition and abundance separately. Mean annual sea surface temperature alone explained 16% of the dissimilarity in fish and crustacean assemblages across sites (canonical analysis coefficient = 0.13, P = 0.001). In contrast, a single index of compositional dissimilarity (Principal Components Axis 1 in Fig. 2A) explained 19.5% of the total variation in consumer composition, and separated cool-water assemblages from warm assemblages (37). Indeed, this index of consumer composition was a stronger predictor of bait consumption than water temperature (either measured during the assays or using mean annual sea surface temperatures; SI Appendix, Fig. S3), latitude, consumer density and biomass, or estimates of ocean productivity, fishing pressure, or human population density (Table 1). Consumer density and biomass only became important predictors of consumption once we reduced the dataset to include only those consumer families whose presence was positively associated with increased consumption rates (see Methods, SI Appendix, Table S1). When viewed as a simple network of causal relationships, the effect of thermal environment on consumption rates was largely indirect, being mediated by altered consumer community composition, and this remained true even when allowing for a nonlinear relationship between consumption rate and mean annual sea surface temperature (Fig. 3). Roughly three-quarters of the total effect of thermal environment on bait consumption flowed indirectly from differences in consumer taxa in different climates.

Locations with high consumption rates had consumer assemblages composed largely of invertivores and omnivores that actively forage on or just above the seafloor (SI Appendix, Fig. S3-4). Actively swimming foragers should consume bait faster due to increased encounter rates, all else being equal, and arguably consumption by these foragers might rise more rapidly with temperature than for more sedentary taxa. Video evidence confirmed the association of key families with high consumption. Porgies (family Sparidae), for example, removed bait at every site where they were observed in video footage (SI Appendix, Table S2) and the presence of this family showed the strongest association with consumption rate in our analysis of community composition (Fig. 2B, SI Appendix, Table S1). Many of the actively foraging taxa associated with high consumption rates, including porgies, half-beaks (Hemiramphidae), and grunts (Haemulidae), were rare or absent at the sites closest to the equator (SI Appendix, Fig. S5). The reasons for these differences in consumer composition at low latitudes, and concomitant changes in consumption pressure, may relate to thermal tolerance (38) and remain an open area for future research.

Our finding that feeding intensity peaked at mid-latitudes differs strongly from most previous studies on latitudinal gradients in species interactions (5, 12, 31, 36). Non-linear ecological transitions between warm-temperate and subtropical locations might help explain this result. These regions feature rapid transition between thermal guilds of consumers with cool- vs. warm-water affinities (37) and these biogeographic transitions are correlated with shifts in the relative strength of bottom-up vs. top-down processes that are directly and indirectly related to temperature (17). We find it interesting that all three studies show transitions in similar regions associated with climate: transitions in consumption in this study (~19-22°C SST), transitions of thermal guilds (~21-25°C SST (37)), and transitions in top-down vs. bottom-up control (~17-20°C temperature 0-200m (17)). These comparisons suggest that zones of biogeographic and trophic transitions associated with climate are also areas of transition for consumptive pressure by small mesopredators.

Although our sampling near the equator was sparse, the decline in measured bait consumption at the lowest latitudes was robust in two independent regions. The equatorial decline appears to be related to consumer community composition, as many of the taxa we identified as influential consumers were absent at the lowest and highest latitudes (SI Appendix, Fig. S5). Several possible mechanisms may explain how thermally-driven community shifts could drive the decline in consumption near the equator. First, small mesopredators may be more restricted near the equator in their time or place of foraging if larger enemies are more active there. Alternatively, reduced productivity and increased metabolic demand may disfavor active consumers in the warm oligotrophic waters near the equator. In any case, our results suggest that the thermal environment influences trophic processes by favoring particular consumer taxa (2) in addition to direct physiological effects on individuals (Fig. 3).

The weak and inconsistent differences we found in consumption rates between seagrass vs. unvegetated sediment habitats (SI Appendix, Fig. S6-7) was surprising given decades of research showing that the structure provided by seagrasses and other foundation species can strongly influence predator-prey relationships (39–42). While we found no overall difference in consumer composition between seagrass and unvegetated habitats (permutation test, $P = 0.75$), consumer densities were generally higher inside than outside of seagrass habitat (SI Appendix, Fig. S1). Thus, any protection provided by seagrass structure may have been offset by consumer aggregation in seagrass. Yet the consistency of latitudinal patterns in consumption between the two habitats suggests that environment and consumer biogeography had stronger influences on consumption than local differences in habitat structure at the broad scale of our study.

Our feeding assay used identical bait at all sites to isolate the effect of consumer activity from the behavioral and morphological traits of prey, which vary widely across space. No single bait will attract all predators equally; ours targeted the small to medium-sized generalists that dominate many shallow marine habitats. Thus, the consumption rates that we describe are relative measures of one-half of a predator-prey interaction (i.e., consumption in the absence of prey behavior and other trait variation). Whereas this design cannot completely characterize species interactions, standardization more rigorously estimates how potential consumption varies across the globe. Our assays did not measure top-down control per se, but the kind of information we gathered is critical to understanding trophic interactions, including cascading effects in seagrass ecosystems (30, 43, 44), because it measures the willingness of consumers to eat prey of a certain size. The consistency of our results across ocean basins and hemispheres, along with similar recent findings for pelagic top predators (45), suggests that the mid-latitude peak in marine consumption is indeed general. The importance of particular predator taxa and traits in the geography of consumption we found parallels the outsized role of endothermy in the effectiveness of marine predators (e.g., 54, 55), including in some seagrass meadows (43, 44). We focused on the smaller ectothermic consumers that consume herbivorous invertebrates that can be critical to seagrass persistence (32), but these are potential prey of larger endotherms like fishing birds and small marine mammals, so endothermy might well influence the broader food webs we studied. However, given that many endothermic predators are most abundant and diverse in cooler regions of the world ocean (47), we would expect the distribution of their collective feeding intensity to differ from the pattern we observed.

Changing climate, overfishing, and global species introductions are altering the biogeography of marine life and the composition of communities (48, 49), with wide-ranging effects on ecosystems (50), including in seagrass habitats (51). Shifting biogeography of consumers can alter community and ecosystem structure and processes (52, 53) independent of temperature, as we show here. Simultaneously, warming can directly influence physiology of ectothermic consumers (e.g., metabolic demand, activity; 55). We show that variation in water temperature influences marine trophic process mainly indirectly by changing consumer community composition. The hump-shaped relationship between temperature and consumption we found suggests that predation and trophic transfer may intensify at middle to high latitudes and decline near the equator as the world ocean warms and species continue to shift their ranges. Such shifts in species ranges and biomass distributions could lead to large changes in consumption, with repercussions for community structure and trophic flows through marine food webs. It is already clear that many ectotherms are expanding or contracting their ranges with climate change (55, 56). Our findings suggest that such distributional shifts may affect ecological processes as much or more than those predicted based only on temperature effects on metabolism.

Materials and Methods

We assessed rates of consumption using a simple, standardized field assay (57). We tethered a 1-1.3 cm diameter piece of dried squid mantle with monofilament to a fiberglass garden stake (hereafter, ‘squidpop’), that we inseted into the sediment such that the bait dangled 20-30 cm above the sediment surface in or just above the seagrass canopy. At most sites, we deployed 20-30 squidpops within a seagrass meadow and 20-30 squidpops in nearby unvegetated sediments (SI Appendix, Table S3). We checked the squidpops for presence (1) or absence (0) of bait after one hour and again after 24 hours. Most sites repeated this assay for a total of three deployments in each of the two habitat types, and measured water temperature during each deployment.

To characterize variation in environments across the range of the study, we drew upon several publicly-available datasets with global-scale variables of interest. We accessed sea surface temperature and chlorophyll records using Bio-ORACLE (58), which packages data collected by the Aqua-MODIS satellite. We used mean annual sea surface temperature (SST) because it showed stronger relationships with consumption rate than maximum or minimum annual SST and it summarizes well the differences between thermal conditions across the globe (Fig. 1). Most assays were conducted during the summer, but differences in timing of assays generated variation in *in situ* temperature that altered the rank-order of our estimates of the thermal environments compared to sea surface temperature, making nearby sites appear less similar environmentally (Fig. 3). We used mean annual chlorophyll *a* as a proxy for surface ocean primary productivity across sites. We also accessed data on human population densities from the Gridded Population of the World (59), which we used as a proxy for local human disturbance. Finally, we accessed fishing pressure data from the Sea Around Us project (60) using the R package 'seaaroundus' (61).

At most sites (30 of 42 sites) we also conducted consumer surveys in the areas adjacent to feeding assays. These surveys used hand-pulled seines in seagrass and unvegetated sediment habitats to sample epibenthic consumers (mainly fishes, but also large crustaceans) adjacent to feeding assays. All consumers were identified, counted, and released. The total lengths of the first 25 individual fish of each species were also measured. We used these data to estimate consumer density, size distribution, biomass, and diversity, as well as to generate a species list for each site. Species lists from five additional sites were added using data from video footage and diver transects (FL, India, Italy, Yuca1, Yuca2). Biomass estimates were calculated using length-weight regressions available in Fishbase (62).

For each of the squidpop assays we independently fitted an exponential decay model and estimated consumption rate (bait loss through time) using the slope parameter. We then used the resulting rate estimates as data points in subsequent analysis.

We predicted individual consumption rates in linear mixed effects models using a variety of potential abiotic and biotic drivers, and compared models using Akaike Information Criterion corrected for small sample size calculated using the R package 'bbmle' (63). We also explored a variety of polynomial terms and LOESS curves to investigate possibilities of non-linear relationships between temperature and consumption, although for model comparison we only included linear terms. We restricted the data used in model comparison to the 27 sites for which we had the full complement of explanatory variables. For simplicity, and because our analysis was largely exploratory using a large set of candidate explanatory variables, we compared models with individual predictor variables only. All mixed models were fitted using maximum likelihood in the package 'lme4' in R (64).

When estimating consumer species (alpha) diversity, we used both species richness and Hurlbert's probability of interspecific encounter as effective numbers of species (65). We also wanted to investigate changes in consumer community composition across sites (beta diversity), but given the scale of our analysis and the large biogeographic gradients we captured, comparing composition in terms of species identity was not possible. Species level overlap was low among sites, especially across ocean basins and hemispheres, so we chose to compare composition (presence-absence) at the level of families across sites using Raup-Crick dissimilarities. While this metric has been used to investigate small spatial scale differences in species composition within regions (66), we use it here to investigate global among-site turnover of consumers at higher taxonomic levels. In order to visualize and quantify major axes of community variation, we used Principal Coordinates Analysis (PCoA) to ordinate consumer communities based on their dissimilarities, and then assess how these dissimilarities related to the thermal environment and consumption rate. We used a combination of unconstrained (PCoA) and constrained (Canonical Analysis of Principal Coordinates) techniques in this analysis. Unconstrained ordination reduces dimensionality of the dataset by finding orthogonal axes of decreasing variation in the dataset, while constrained ordination uses a regression-based approach to define a set of axes of interest a priori based on explanatory variables (67). We used the resultant axes from unconstrained ordination (PCoA) as explanatory variables in the models described above because the unconstrained ordination does not require a priori assumptions about which factors are important. We also assessed relationships between consumer community composition and thermal environment by constraining the first ordination axis to SST or *in situ* temperature. Multivariate analyses were performed using the R package 'vegan' (68).

In order to identify which consumer families were positively and negatively associated with consumption intensity across sites, we constrained the first axis of the ordination to align with our estimates of consumption rate. Then we selected families that mapped onto the positive side of this axis as candidate taxa driving spatial variation in consumption rate, and calculated the density and biomass of these consumers at sites with seining data (27 of 42 sites). Finally, we compared the results from multivariate analysis to direct observations of squidpop attacks and bait removal from video footage captured at 14 sites (SI Appendix Table S2).

To explore which predator traits might explain feeding intensity in our assays, we scored six traits for each taxon in our dataset (416 morphospecies in 103 taxonomic families). Four traits were derived from Fishbase (feeding habit, lateral body shape; (69) and Reef Life Survey (trophic group, water column usage; (70). A fifth binomial trait scored whether each taxon is an actively swimming forager or tends towards ambush or sit-and-wait behavior, either on the benthos or in the water column. We applied the most common value of this trait to all taxa in each family, but we acknowledge that variation in foraging activity can occur within families. Traits missing in these databases were filled using expert opinion of co-authors and available trait information from related taxa. A sixth continuous trait describing body size as the average total length of each taxon (carapace width for crabs) was calculated from our seining data. Whereas published total length estimates are available for many taxa, we opted to use length estimates from our own dataset because many taxa only utilize seagrass and other nearshore habitats for part of their development, when they may differ greatly from the species' maximum size. Using the R package 'FD' (71) we calculated community-level weighted means of trait values to derive estimates of average conditions for each of the six individual traits in each site and habitat combination in the dataset, and we calculated a variety of functional diversity metrics (functional richness, functional dispersion, functional evenness, functional diversity, and Rao's

Q) following published methods (71–73). For all consumer functional diversity metrics and all community-level weighted means except body size we used presence-absence data instead of weighting by relative abundance so that we could include sites with seining and video data. We did weight mean consumer body size estimates by relative abundance because we only had size estimates from seine sampling. Weighting by abundance did not qualitatively change the results. We regressed each functional diversity metric and each community-level weighted mean trait against consumption rate individually using the linear mixed effects models described above.

We tested whether consumer composition mediated the influence of mean annual SST on consumption rates using the package ‘mediation’ in R (74). Because we found support for a hump-shaped relationship between SST and consumption rate, we tested whether consumer composition mediated the non-linear relationship between temperature and consumption rate (using 33 of 42 sites with all three variables). We modeled the relationships using 1) smooth terms for SST on consumption rate and a linear term for composition (PCoA1) on consumption rate in a generalized additive model (GAM; logit link function; R package ‘mgcv’ (75)) and 2) a general linear model for SST on composition. We report the standardized linear regression coefficients, estimated degrees of freedom for smoothed GAM terms (and associated chi-square statistic), estimates of the mediation effect and direct effect, and the proportion of the direct effect of SST mediated by composition for the second mediation analysis, along with 95% confidence intervals around estimates of the direct effect, mediation effect, and the proportion mediated. All models in mediation analysis used data that were averaged at the level of habitats within sites, which is the lowest level of pairwise comparisons we can make between squidpop assays and consumer composition.

All analyses were performed in R version 3.5.2 (76). Data and analyses for this project are available at https://github.com/mawhal/Bitemap_Whalen.

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Figures

Figure 1. Distributions of bait consumption by generalist marine predators and temperature across the 42 sites in this study. A) Consumption rate of tethered dried squid bait peaks at mid-latitudes in both hemispheres. Point color represents habitat, and lines show independent quadratic GLMs fitted for each habitat type in each hemisphere. B) Map of study sites. C) Latitudinal pattern of mean annual sea surface temperature (SST).

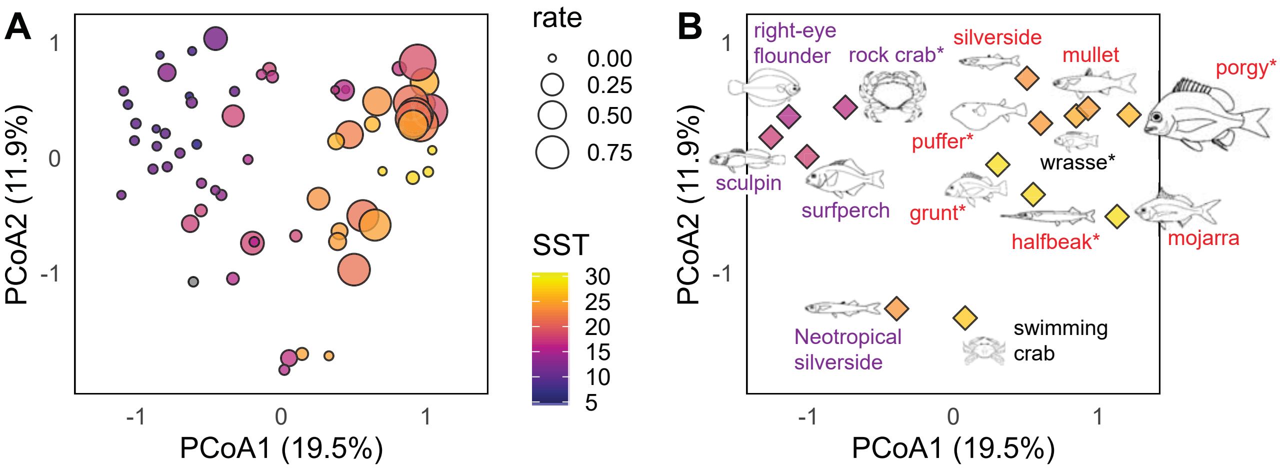
Figure 2. The composition of consumer assemblages reflects global gradients in environmental temperatures and consumption rate. A) Principal coordinates analysis, where locations of symbols reflect compositional differences among sites and habitats based on family-level presence-absence data. Symbol color represents mean annual sea surface temperature (°C), and symbol size corresponds to bait consumption rate. B) The same ordination showing scores for consumer families driving differences in composition and consumption rate among sites. Symbol color represents average in situ temperature at sites where the predator family was observed label color represents positive (red), negative (purple), or non-significant (black) correlations with consumption rate, and body length (width for crabs) is proportional to the magnitude of the correlation. Asterisks denote families that were seen feeding on bait in video footage.

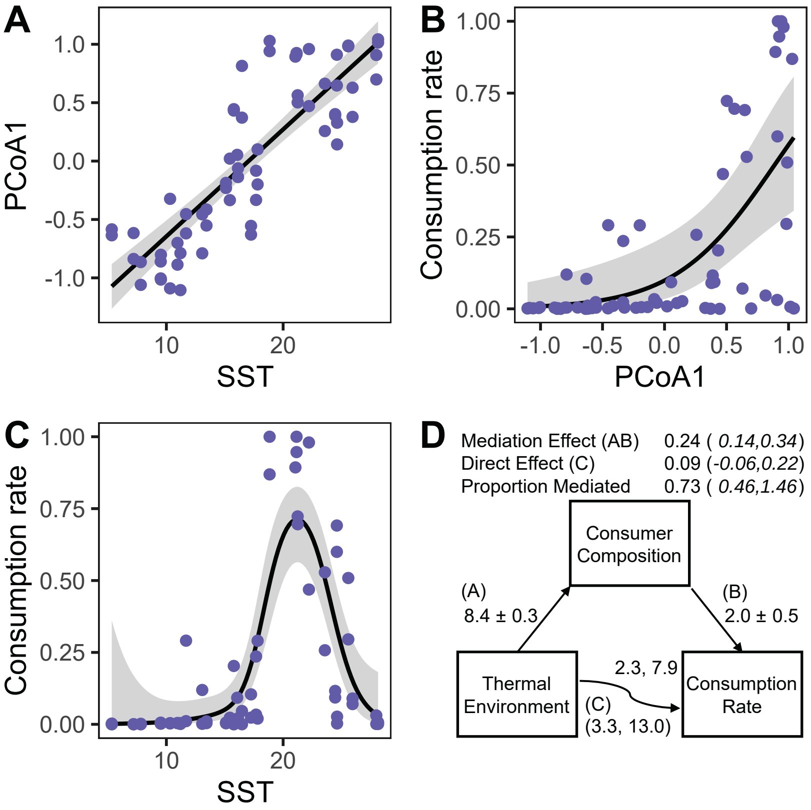
Figure 3. Predator composition mediates the effect of thermal environment on consumption rates. (A-C) Bivariate relationships between consumer composition (PCoA1, Fig. 2A), thermal environment (SST) and consumption rate. Lines show predictions from models used in mediation analysis (A, linear regression; B, logistic regression; C, generalized additive modeling). D) Paths represent causal hypotheses about relationships. Numbers next to paths leading to and from consumer composition are standardized regression coefficients and standard errors. Numbers above and below the path from thermal environment to consumption rate are estimated degrees of freedom and chi-square values for the smooth term in the presence and absence of mediation, respectively. Numbers above the path diagram are estimates of the direct and indirect (mediation) effects with 95% bootstrapped confidence intervals.

Tables

Table 1. Comparison of generalized linear mixed effects models predicting bait consumption by generalist marine consumers in two shallow marine habitats worldwide. Model comparison used Akaike Information Criterion corrected for small sample size. GLMs used logit link with random intercepts for sites. Taxonomic Composition refers to the first axis from the PCoA of consumer assemblages (Fig. 2). Selected Abundance and Biomass refer to density or biomass of fish and decapod families selected with constrained ordination (Fig. 2B, SI Appendix, Table S1). Productivity refers to remotely-sensed mean annual chlorophyll *a*. Habitat categorically relates seagrass and unvegetated habitats within sites. Abundance, biomass, and human population density were $\log_{10}$-transformed. Body size, Trophic Group, Lateral Body Shape, and Water Column Use are community-weighted mean trait values per site and habitat. We also provide marginal pseudo-R^2 values for comparison of fixed effects. For this model comparison we only included data from sites with the full complement of predictors (27 of 42 sites).


A
Seagrass
Unvegetated
Latitude
60
45
30
15
0
−15
−30
0.00
0.25
0.50
0.75
1.00
Consumption rate (hr^{-1})
B
AK
BC
WA2
WA
OR
CA4
CA3
CA2
CA
Baja
QC
DE
MA
VA
VA2
NC
NC2
TX
FL
Yuca1
Yuca2
Belize
Panama
Brazil
Chile
Norway
Ireland
Wales
France
Italy
Croatia
Korea
India
QLD1
QLD2
QLD3
QLD4
NSW1
NSW2
NSW3
NSW4
VIC
C
10
20
30
Mean annual SST (°C)
Latitude


A
PCoA2 (11.9%)
PCoA1 (19.5%)
1
0
-1
-1
0
1
rate
0.00
0.25
0.50
0.75
SST
30
25
20
15
10
5
B
PCoA2 (11.9%)
PCoA1 (19.5%)
1
-1
-1
0
1
right-eye flounder
rock crab*
silverside
mullet
porgy*
puffer*
wrasse*
sculpin
surfperch
grunt*
halfbeak*
mojarra
Neotropical silverside
swimming crab


A
PCoA1
1.0
0.5
0.0
-0.5
-1.0
10
20
SST
B
Consumption rate
1.00
0.75
0.50
0.25
0.00
-1.0
-0.5
0.0
0.5
1.0
PCoA1
C
Consumption rate
1.00
0.75
0.50
0.25
0.00
10
20
SST
D
Mediation Effect (AB) 0.24 (0.14,0.34)
Direct Effect (C) 0.09 (-0.06,0.22)
Proportion Mediated 0.73 (0.46,1.46)
Consumer Composition
(A)
8.4 ± 0.3
(B)
2.0 ± 0.5
Thermal Environment
2.3, 7.9
(C)
(3.3, 13.0)
Consumption Rate

Predictor	**AICc**	**dAICc**	**k**	**weight**	**pseudo-R^2**
Taxonomic Composition	70.3	0	3	0.932	0.51
Selected Abundance	77.0	6.7	3	0.033	0.39
(Sea Surface Temperature)^2	79.2	8.9	4	0.011	0.66
Selected Biomass	79.6	9.3	3	0.009	0.38
Functional Richness	79.9	9.5	3	0.008	0.26
Sea Surface Temperature	80.5	10.2	3	0.006	0.39
in situ Temperature	82.8	12.5	3	0.002	0.31
Productivity	90.5	20.2	3	<0.001	0.12
Proportion of Active Foragers	90.5	20.2	3	<0.001	0.10
Body size	90.6	20.3	3	<0.001	0.10
Consumer Species Richness	90.8	20.5	3	<0.001	0.05
Functional Evenness	91.4	21.1	3	<0.001	0.04
Intercept-Only	92.0	21.7	2	<0.001	0
Trophic Group	92.1	21.8	6	<0.001	0.27
Functional Group Richness	92.2	21.9	3	<0.001	0.04
Feeding Type	92.4	22.1	3	<0.001	0.15
Habitat	93.1	22.8	3	<0.001	0.01
Lateral Body Shape	93.1	22.8	6	<0.001	0.23
Total Biomass	93.2	22.9	3	<0.001	0.02
Effective Number of Species	93.2	22.9	3	<0.001	0.01
Total Abundance	93.3	23.0	3	<0.001	0.02
Fishing Pressure	93.6	23.3	3	<0.001	0.02
Water Column Use	93.7	23.4	6	<0.001	0.20
Human Population Density	94.0	23.7	3	<0.001	<0.01
Rao Q	94.0	23.7	3	<0.001	<0.01
Functional Dispersion	94.0	23.7	3	<0.001	<0.01