

## 1 **Biological Sciences, Ecology**

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

**Authors:** Matthew A. Whalen<sup>1,2,3\*</sup>, Ross D.B. Whippo<sup>3,4</sup>, John J. Stachowicz<sup>5</sup>, Paul H. York<sup>6</sup>, Erin Aiello<sup>7</sup>, Teresa Alcoverro<sup>8,9</sup>, Andrew H. Altieri<sup>10,11</sup>, Lisandro Benedetti-Cecchi<sup>12</sup>, Camilla Bertolini<sup>13</sup>, Midoli Bresch<sup>1</sup>, Fabio Bulleri<sup>12</sup>, Paul E. Carnell<sup>14</sup>, Stéphanie Cimon<sup>15</sup>, Rod M. Connolly<sup>16</sup>, Mathieu Cusson<sup>15</sup>, Meredith S. Diskin<sup>17</sup>, Elrika D'Souza<sup>9</sup>, Augusto A.V. Flores<sup>18</sup>, F. Joel Fodrie<sup>19</sup>, Aaron W.E. Galloway<sup>4</sup>, Leo C. Gaskins<sup>20</sup>, Olivia J. Graham<sup>21</sup>, Torrance C. Hanley<sup>22</sup>, Christopher J. Henderson<sup>23</sup>, Clara M. Hereu<sup>24</sup>, Margot Hessing-Lewis<sup>1,25</sup>, Kevin A. Hovel<sup>26</sup>, Brent B. Hughes<sup>27</sup>, A. Randall Hughes<sup>22</sup>, Kristin M. Hultgren<sup>28</sup>, Holger Jänes<sup>14,29</sup>, Dean S. Janiak<sup>30</sup>, Lane N. Johnston<sup>31</sup>, Pablo Jorgensen<sup>32</sup>, Brendan P. Kelaher<sup>33</sup>, Claudia Kruschel<sup>34</sup>, Brendan S. Lanham<sup>35</sup>, Kun-Seop Lee<sup>36</sup>, Jonathan S. Lefcheck<sup>3</sup>, Enrique Lozano-Álvarez<sup>37</sup>, Peter I. Macreadie<sup>14</sup>, Zachary L. Monteith<sup>1</sup>, Nessa E. O'Connor<sup>13</sup>, Andrew D. Olds<sup>23</sup>, Jennifer K. O'Leary<sup>7,38</sup>, Christopher J. Patrick<sup>39</sup>, Oscar Pino<sup>40</sup>, Alistair G.B. Poore<sup>41</sup>, Michael A. Rasheed<sup>6</sup>, Wendel W. Raymond<sup>42</sup>, Katrin Reiss<sup>43</sup>, O. Kennedy Rhoades<sup>5,30</sup>, Max T. Robinson<sup>44</sup>, Paige G. Ross<sup>45</sup>, Francesca Rossi<sup>46</sup>, Thomas A. Schlacher<sup>23</sup>, Janina Seemann<sup>11</sup>, Brian R. Silliman<sup>20</sup>, Delbert L. Smee<sup>17</sup>, Martin Thiel<sup>40,47,48</sup>, Richard K.F. Unsworth<sup>44</sup>, Brigitta I. van Tussenbroek<sup>37</sup>, Adriana Vergés<sup>41</sup>, Mallarie E. Yeager<sup>26</sup>, Bree K. Yednock<sup>49</sup>, Shelby L. Ziegler<sup>19</sup>, J. Emmett Duffy<sup>3</sup>

**Affiliations:** <sup>1</sup>Hakai Institute, PO Box 309, Heriot Bay, BC V0P 1H0, Canada. <sup>2</sup>Biodiversity Research Centre, University of British Columbia, 2212 Main Mall Vancouver, BC V6T 1Z4, Canada. <sup>3</sup>Tennenbaum Marine Observatories Network, Smithsonian Institution, Edgewater, Maryland 21037 USA. <sup>4</sup>University of Oregon, Oregon Institute of Marine Biology, 63466 Boat Basin Rd., Charleston, OR 97420, USA. <sup>5</sup>Bodega Marine Laboratory, University of California, Davis, 2099 Westside Road, Bodega Bay, CA 94923, USA. <sup>6</sup>James Cook University, Centre for Tropical Water and Aquatic Ecosystem Research, PO Box 6811, Cairns, Qld, Australia. <sup>7</sup>Biology Department, California Polytechnic State University, 1 Grand Avenue, San Luis Obispo, CA 93422 USA. <sup>8</sup>Centre d'Estudis Avançats de Blanes (Spanish National Research Council), Blanes, Girona, Spain. <sup>9</sup>Nature Conservation Foundation, 1311, "Amritha", 12th Main, Opp Kodava Samaj, Vijayanagar 1st Stage, Mysore 570 017, India. <sup>10</sup>Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL 32611, USA. <sup>11</sup>Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama. <sup>12</sup>Department of Biology and CoNISMa, Via Derna 1 I-56126, University of Pisa, Pisa, Italy. <sup>13</sup>Trinity College Dublin, The University of Dublin, College Green, Dublin 2, Ireland. <sup>14</sup>School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Geelong, Victoria 3220, Australia. <sup>15</sup>Département des sciences fondamentales & Québec-Océan, Université du Québec à Chicoutimi, 555, Boulevard de l'Université, Chicoutimi, QC G7H 2B1, Canada. <sup>16</sup>Griffith University, Australian Rivers Institute - Coast & Estuaries, School of Environment and Science. Gold Coast, Queensland 4222, Australia. <sup>17</sup>Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, AL 36528, USA. <sup>18</sup>Centre for Marine Biology, University of São Paulo, <sup>19</sup>Institute of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell St., Morehead City, NC 28557 USA. <sup>20</sup>Nicholas School for

43 the Environment, Duke University Marine Lab, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA.  
44 <sup>21</sup>Cornell University, Dept. of Ecology and Evolutionary Biology, 215 Tower Rd, Ithaca, NY 14853.  
45 <sup>22</sup>Northeastern University, Marine Science Center, 430 Nahant Road, Nahant, MA 01907, USA. <sup>23</sup>School  
46 of Science and Engineering, University of the Sunshine Coast, Maroochydore QLD 4558, Australia.  
47 <sup>24</sup>Universidad Autónoma de Baja California, Carretera Ensenada, Tijuana 3917, C.P. 22860 Ensenada,  
48 Baja California, Mexico, <sup>25</sup>Institute of the Oceans & Fisheries, 2202 Main Mall, Vancouver, BC V6T  
49 1Z4, Canada. <sup>26</sup>Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego,  
50 CA 92182, USA. <sup>27</sup>Department of Biology, Sonoma State University, 1801 E. Cotati Ave, Rohnert Park,  
51 CA 94954, USA. <sup>28</sup>Department of Biology, Seattle University, 901 12th Ave., Seattle, WA 98122, USA.  
52 <sup>29</sup>Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia, <sup>30</sup>Smithsonian  
53 Marine Station, 701 Seaway Dr, Fort Pierce, FL 34949, USA. <sup>31</sup>School of Marine Sciences and Policy,  
54 University of Delaware, 700 Pilottown Rd., Lewes DE 19958, USA. <sup>32</sup>Geomare, A. C., Paseo del  
55 Pedregal 82, C.P. 22860 Ensenada, Baja California, Mexico. <sup>33</sup>National Marine Science Centre, Southern  
56 Cross University, 2 Bay Drive, Coffs Harbour, NSW 2450, Australia. <sup>34</sup>Department of Ecology,  
57 University of Zadar, Agronomy and Aquaculture M. Pavlinovica 1, 23000 Zadar, Croatia. <sup>35</sup>School of  
58 Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052,  
59 Australia. <sup>36</sup>Department of Biological Sciences, Pusan National University, Busan 46241, Korea.  
60 <sup>37</sup>Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Prolongación  
61 Niños Heroes S/N, Puerto Morelos, Quintana Roo 77580, Mexico. <sup>38</sup>California Sea Grant, 9500 Gilman  
62 Dr., La Jolla, CA 92093-0232, USA <sup>39</sup>Texas A&M University Corpus Christi, HRI 121 Unit 5892, 6300  
63 Ocean Drive, Corpus Christi TX 78412, USA. <sup>40</sup>Facultad Ciencias del Mar, Universidad Católica del  
64 Norte, Coquimbo, Chile. <sup>41</sup>School of Biological, Earth and Environmental Sciences, University of New  
65 South Wales, Sydney, NSW 2052, Australia. <sup>42</sup>University of Alaska Fairbanks Fisheries Division, 17101  
66 Point Lena Loop Rd., Juneau 99801, USA. <sup>43</sup>Faculty for Biosciences and Aquaculture, Nord University,  
67 8049 Bodø, Norway. <sup>44</sup>Seagrass Ecosystem Research Group, College of Science, Swansea University,  
68 Wallace Building, Swansea SA2 8PP, UK. <sup>45</sup>Virginia Institute of Marine Science, PO Box 350,  
69 Wachapreague, VA 23480, USA. <sup>46</sup>CNRS, National Centre for Scientific Research, Université Côte  
70 d'Azur, CNRS, FRE 3729 ECOMERS, Nice 6100, France. <sup>47</sup>Millenium Nucleus Ecology and Sustainable  
71 Management of Oceanic Islands ESMOI, Coquimbo, Chile. <sup>48</sup>Center for Advanced Studies in Arid  
72 Systems, CEAZA, Coquimbo, Chile. <sup>49</sup>South Slough National Estuarine Research Reserve, P.O. Box  
73 5417, Charleston, OR 97420, USA.

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77 **Corresponding Author:**

78 Matthew Adam Whalen

79 Postdoctoral Scholar in Marine Biodiversity

80 Hakai Institute, Smithsonian MarineGEO, University of British Columbia

81 Department of Botany

82 3200-6270 University Blvd.

83 Vancouver, BC, V6T 1Z4, CANADA

84 1-703-909-5732

85 [mawhal@gmail.com](mailto:mawhal@gmail.com)

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

101

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

104

105 **Significance Statement (max 120 words):**

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

115

116 **Text**

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

125

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

135

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

146

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

154

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

169

## 170 **Results and Discussion**

171 Contrary to our expectations, bait consumption peaked away from the equator in both  
172 hemispheres (25-35° North and South), and was consistent between seagrass and sediment  
173 habitats (Fig. 1A), despite slightly higher density, richness, and biomass of consumers in  
174 seagrass (SI Appendix, Fig. S1). Although our sampling near the equator was relatively sparse,  
175 the decline in measured bait consumption at the lowest latitudes was robust in two independent  
176 regions (SI Appendix, Fig. S2). This mid-latitude peak was supported by a hump-shaped  
177 relationship between absolute latitude and consumption (comparison of models with and without  
178 second-order polynomial; quadratic model Akaike weight  $w_{quad} = 0.86$ ). In contrast, satellite-  
179 derived mean annual sea surface temperature decreased monotonically with latitude (SST; Fig.  
180 1C), and the hump-shaped relation of SST to consumption was much stronger than that for  
181 latitude ( $w_{quad} > 0.99$ ). This nonlinear relationship between SST and consumption was also  
182 supported in two independent, well-sampled transects along the Northwest Atlantic ( $w_{quad} =$   
183 0.97) and Southwest Pacific ( $w_{quad} = 0.99$ ; SI Appendix, Fig. S2), strengthening the inference  
184 that the equatorial dip in consumption reflects a response to temperature, rather than some other  
185 correlate of latitude.

186

187 Fish and crabs were the main consumers of bait at all sites, and their taxonomic composition  
188 varied greatly across sites and with temperature (Fig. 2). Because species and genera of coastal  
189 animals differ markedly across ocean basins and hemispheres, we analyzed consumer  
190 composition at the level of taxonomic families, which allowed us to describe gradual shifts in  
191 global consumer biogeography across broad environmental gradients, while maintaining  
192 functional distinction among taxa. We used presence vs. absence rather than abundance data  
193 because we wanted to explore consumer composition and abundance separately. Mean annual  
194 sea surface temperature alone explained 16% of the dissimilarity in fish and crustacean

195 assemblages across sites (canonical analysis coefficient = 0.13,  $P = 0.001$ ). However, a single  
196 unconstrained index of compositional dissimilarity (Principal Components Axis 1 in Fig. 2A)  
197 explained 19.5% of the total variation in consumer composition, and separated cool-water  
198 assemblages from warm assemblages (37). Indeed, this index of consumer composition was a  
199 stronger predictor of bait consumption than water temperature (either measured during the assays  
200 or using mean annual sea surface temperatures; SI Appendix, Fig. S3), latitude, consumer  
201 density and biomass, or estimates of ocean productivity, fishing pressure, or human population  
202 density (Table 1). Consumer density and biomass only became important predictors of  
203 consumption once we reduced the dataset to include only those consumer families whose  
204 presence was associated with increased consumption rates (see Methods, SI Appendix, Table  
205 S1). When viewed as a simple network of causal relationships, the effect of thermal environment  
206 on consumption rate was largely indirect, being mediated by consumer community composition,  
207 and this remained true even when allowing for a nonlinear relationship between consumption  
208 rate and mean annual sea surface temperature (Fig. 3). Roughly three-quarters of the total effect  
209 of thermal environment on bait consumption flowed indirectly through differences in consumer  
210 taxa in different climates.

211  
212 Locations with high consumption rates had consumer assemblages composed largely of  
213 invertivores and omnivores that actively forage on or just above the seafloor (SI Appendix, Fig.  
214 S3-4). Actively swimming foragers should consume bait faster due to increased encounter rates,  
215 all else being equal, and arguably consumption by these foragers might rise more rapidly with  
216 temperature than for more sedentary taxa. Video evidence confirmed the association of key  
217 families with high consumption. Porgies (family Sparidae), for example, removed bait at every  
218 site where they were observed in video footage (SI Appendix, Table S2) and the presence of this  
219 family showed the strongest association with consumption rate in our analysis of community  
220 composition (Fig. 2B, SI Appendix, Table S1).

221  
222 The equatorial decline in bait consumption appears to be related to consumer community  
223 composition, as many of the actively foraging taxa associated with high consumption rates,  
224 including porgies, half-beaks (Hemiramphidae), and grunts (Haemulidae), were rare or absent at  
225 the sites closest to the equator (SI Appendix, Fig. S5). Some of these consumer families (e.g.,  
226 porgies) are known from low latitude waters but were not recorded in our surveys (38). It is  
227 possible that larger enemies reduce mesopredator abundance or restrict their foraging (39, 40) to  
228 a greater extent at low latitudes, but we do not have any direct evidence to support this  
229 hypothesis. Similarly, human harvest or other activities could have restricted the abundance of  
230 these key consumers, but we know of no reason to expect this to be more intense at low latitudes,  
231 as many of the middle and high latitude sites in this study are heavily influenced human  
232 activities, including overfishing (41). Alternatively, environmental tolerances could limit  
233 consumer access or abundance in shallow seagrass habitats at low latitude (42). There is  
234 currently little evidence to evaluate these explanations.

235  
236 Our finding that feeding intensity peaked at mid-latitudes differs strongly from most previous  
237 studies on latitudinal gradients in species interactions (5, 12, 31, 36). Non-linear ecological  
238 transitions between warm-temperate and subtropical locations might help explain this result.  
239 These regions feature rapid transition between thermal guilds of consumers with cool- vs. warm-  
240 water affinities (37) and these biogeographic transitions are correlated with shifts in the relative  
241 strength of bottom-up vs. top-down processes that are directly and indirectly related to  
242 temperature (17). We find it interesting that such transitions co-occur in similar climatic regions:  
243 transitions in consumption from this study (~19-22°C SST), transitions in dominant fish guilds  
244 (~21-25°C SST; 37), and transitions in top-down vs. bottom-up control (~17-20°C temperature  
245 0-200m; 17). These comparisons suggest that zones of biogeographic and trophic transitions  
246 associated with climate are also areas of transition for consumptive pressure by small  
247 mesopredators.

248  
249 The weak and inconsistent differences we found in consumption rates between seagrass vs.  
250 unvegetated sediment habitats (SI Appendix, Fig. S6-7) was surprising given decades of research  
251 showing that the structure provided by seagrasses and other foundation species can strongly  
252 influence predator-prey relationships (43–46). While we found no overall difference in consumer  
253 composition between seagrass and unvegetated habitats (permutation test,  $P = 0.75$ ), consumer  
254 densities were generally higher inside than outside of seagrass habitat (SI Appendix, Fig. S1).  
255 Thus, any protection provided by seagrass structure may have been offset by consumer  
256 aggregation in seagrass. Yet the consistency of latitudinal patterns in consumption between the  
257 two habitats suggests that broad-scale environment and consumer biogeography had stronger  
258 influences on consumption than local differences in habitat structure.

259  
260 Our feeding assay used identical bait at all sites to isolate the effect of consumer activity from  
261 the behavioral and morphological traits of prey, which vary widely across space. No single bait  
262 will attract all predators equally; ours targeted the small to medium-sized generalists that  
263 dominate many shallow marine habitats. Thus, the consumption rates that we describe are  
264 relative measures of one-half of a predator-prey interaction (i.e., consumption in the absence of  
265 prey behavior and other trait variation). Whereas this design cannot completely characterize  
266 species interactions, standardization more rigorously estimates how potential consumption varies  
267 across the globe. Our assays did not measure top-down control per se, but the kind of  
268 information we gathered is critical to understanding trophic interactions, including cascading  
269 effects in seagrass ecosystems (30, 47, 48), because it measures the willingness of consumers to  
270 eat prey of a certain size. The consistency of our results across ocean basins and hemispheres,  
271 along with similar recent findings for pelagic top predators (49), suggests that the mid-latitude  
272 peak in marine consumption is indeed general. The importance of particular predator taxa and  
273 traits in the geography of consumption we found parallels the outsized role of endothermy in the  
274 effectiveness of marine predators (e.g., 50, 51), including in some seagrass meadows (47, 48).

275 We focused on the smaller ectothermic consumers that consume herbivorous invertebrates that  
276 can be critical to seagrass persistence (32), but these are potential prey of larger endotherms like  
277 fishing birds and small marine mammals, so endothermy might well influence the broader food  
278 webs we studied. However, given that many endothermic predators are most abundant and  
279 diverse in cooler regions of the world ocean (51), we would expect the distribution of their  
280 collective feeding intensity to differ from the pattern we observed.

281  
282 Changing climate, overfishing, and global species introductions are altering the biogeography of  
283 marine life and the composition of communities (52, 53), with wide-ranging effects on  
284 ecosystems (54), including in seagrass habitats (55). Shifting biogeography of consumers can  
285 alter community and ecosystem structure and processes (56, 57) independent of temperature, as  
286 we show here. Simultaneously, warming can directly influence physiology of ectothermic  
287 consumers (e.g., metabolic demand, activity; 58). We show that variation in water temperature  
288 influences marine trophic process mainly indirectly by changing consumer community  
289 composition. The hump-shaped relationship between temperature and consumption we found  
290 suggests that predation and trophic transfer may intensify at middle to high latitudes and decline  
291 near the equator as the world ocean warms and species continue to shift their ranges. Such shifts  
292 in species ranges and biomass distributions could lead to large changes in consumption, with  
293 repercussions for community structure and trophic flows through marine food webs. It is already  
294 clear that many ectotherms are expanding or contracting their ranges with climate change (59,  
295 60). Our findings suggest that such distributional shifts may affect ecological processes as much  
296 or more than those predicted based only on temperature effects on metabolism.

297

## 298 **Materials and Methods**

299 We assessed rates of consumption using a simple, standardized field assay (61). We tethered a 1-  
300 1.3 cm diameter piece of dried squid mantle with monofilament to a fiberglass garden stake  
301 (hereafter, 'squidpop'), that we inseted into the sediment such that the bait dangled 20-30 cm  
302 above the sediment surface in or just above the seagrass canopy. At most sites, we deployed 20-  
303 30 squidpops within a seagrass meadow and 20-30 squidpops in nearby unvegetated sediments  
304 (SI Appendix, Table S3). We checked the squidpops for presence (1) or absence (0) of bait after  
305 one hour and again after 24 hours. Most sites repeated this assay for a total of three deployments  
306 in each of the two habitat types, and measured water temperature during each deployment.

307

308 To characterize variation in environments across the range of the study, we drew upon several  
309 publicly-available datasets with global-scale variables of interest. We accessed sea surface  
310 temperature and chlorophyll records using Bio-ORACLE (62), which packages data collected by  
311 the Aqua-MODIS satellite. We used mean annual sea surface temperature (SST) because it  
312 showed stronger relationships with consumption rate than maximum or minimum annual SST  
313 and it summarizes well the differences between thermal conditions across the globe (Fig. 1).  
314 Most assays were conducted during the summer, but differences in timing of assays generated



315 variation in *in situ* temperature that altered the rank-order of our estimates of the thermal  
316 environments compared to sea surface temperature, making nearby sites appear less similar  
317 environmentally (Fig. 3). We used mean annual chlorophyll *a* as a proxy for surface ocean  
318 primary productivity across sites. We also accessed data on human population densities from the  
319 Gridded Population of the World (63), which we used as a proxy for local human disturbance.  
320 Finally, we accessed fishing pressure data from the Sea Around Us project (64) using the R  
321 package ‘searoundus’ (65).

322

323 At most sites (30 of 42 sites) we also conducted consumer surveys in the areas adjacent to  
324 feeding assays. These surveys used hand-pulled seines in seagrass and unvegetated sediment  
325 habitats to sample epibenthic consumers (mainly fishes, but also large crustaceans) adjacent to  
326 feeding assays. All consumers were identified, counted, and released. The total lengths of the  
327 first 25 individual fish of each species were also measured. We used these data to estimate  
328 consumer density, size distribution, biomass, and diversity, as well as to generate a species list  
329 for each site. Species lists from five additional sites were added using data from video footage  
330 and diver transects (FL, India, Italy, Yuca1, Yuca2; SI Appendix Movie S1). Biomass estimates  
331 were calculated using length-weight regressions available in Fishbase (66).

332

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

336

337 We predicted individual consumption rates in generalized linear mixed effects models (logit link,  
338 random intercepts for sites) using a variety of potential abiotic and biotic drivers, and compared  
339 models using Akaike Information Criterion corrected for small sample size calculated using the  
340 R package ‘bbmle’ (67). We also explored a variety of polynomial terms and LOESS curves to  
341 investigate possibilities of non-linear relationships between temperature and consumption,  
342 although for model comparison we only included linear terms. We restricted the data used in  
343 model comparison to the 27 sites for which we had the full complement of explanatory variables.  
344 For simplicity, and because our analysis was largely exploratory using a large set of candidate  
345 explanatory variables, we compared models with individual predictor variables only. All mixed  
346 models were fitted using maximum likelihood in the package ‘lme4’ in R (68).

347

348 When estimating consumer species (alpha) diversity, we used both species richness and  
349 Hurlbert’s probability of interspecific encounter as effective numbers of species (69). We also  
350 wanted to investigate changes in consumer community composition across sites (beta diversity),  
351 but given the scale of our analysis and the large biogeographic gradients we captured, comparing  
352 composition in terms of species identity was not possible. Species level overlap was low among  
353 sites, especially across ocean basins and hemispheres, so we chose to compare composition  
354 (presence-absence) at the level of families across sites using Raup-Crick dissimilarities. While

355 this metric has been used to investigate small spatial scale differences in species composition  
356 within regions (70), we use it here to investigate global among-site turnover of consumers at  
357 higher taxonomic levels. In order to visualize and quantify major axes of community variation,  
358 we used Principal Coordinates Analysis (PCoA) to ordinate consumer communities based on  
359 their dissimilarities, and then assess how these dissimilarities related to the thermal environment  
360 and consumption rate. We used a combination of unconstrained (PCoA) and constrained  
361 (Canonical Analysis of Principal Coordinates) techniques in this analysis. Unconstrained  
362 ordination reduces dimensionality of the dataset by finding orthogonal axes of decreasing  
363 variation in the dataset, while constrained ordination uses a regression-based approach to define  
364 a set of axes of interest a priori based on explanatory variables (71). We used the resultant axes  
365 from unconstrained ordination (PCoA) as explanatory variables in the models described above  
366 because the unconstrained ordination does not require a priori assumptions about which factors  
367 are important. We also assessed relationships between consumer community composition and  
368 thermal environment by constraining the first ordination axis to SST or *in situ* temperature.  
369 Multivariate analyses were performed using the R package ‘vegan’ (72).

370

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

378

379 To explore which predator traits might explain feeding intensity in our assays, we scored six  
380 traits for each taxon in our dataset (416 morphospecies in 103 taxonomic families). Four traits  
381 were derived from Fishbase (feeding habit, lateral body shape; 73) and Reef Life Survey (trophic  
382 group, water column usage; 74). A fifth binomial trait scored whether each taxon is an actively  
383 swimming forager or tends towards ambush or sit-and-wait behavior, either on the benthos or in  
384 the water column. We applied the most common value of this trait to all taxa in each family, but  
385 we acknowledge that variation in foraging activity can occur within families. Traits missing in  
386 these databases were filled using expert opinion of co-authors and available trait information  
387 from related taxa. A sixth continuous trait describing body size as the average total length of  
388 each taxon (carapace width for crabs) was calculated from our seining data. Whereas published  
389 total length estimates are available for many taxa, we opted to use length estimates from our own  
390 dataset because many taxa only utilize seagrass and other nearshore habitats for part of their  
391 development, when they may differ greatly from the species’ maximum size. Using the R  
392 package ‘FD’ (75) we calculated community-level weighted means of trait values to derive  
393 estimates of average conditions for each of the six individual traits in each site and habitat  
394 combination in the dataset, and we calculated a variety of functional diversity metrics (functional

395 richness, functional dispersion, functional evenness, functional diversity, and Rao's Q) following  
396 published methods (75–77). For all consumer functional diversity metrics and all community-  
397 level weighted means except body size we used presence-absence data instead of weighting by  
398 relative abundance so that we could include sites with seining and video data. We did weight  
399 mean consumer body size estimates by relative abundance because we only had size estimates  
400 from seine sampling. Weighting by abundance did not qualitatively change the results. We  
401 regressed each functional diversity metric and each community-level weighted mean trait against  
402 consumption rate individually using the linear mixed effects models described above.

403

404 We tested whether consumer composition mediated the influence of mean annual SST on  
405 consumption rates using the package 'mediation' in R (78). Because we found support for a  
406 hump-shaped relationship between SST and consumption rate, we tested whether consumer  
407 composition mediated the non-linear relationship between temperature and consumption rate  
408 (using 33 of 42 sites with all three variables). We modeled the relationships using 1) smooth  
409 terms for SST on consumption rate and a linear term for composition (PCoA1) on consumption  
410 rate in a generalized additive model (GAM; logit link function; R package 'mgcv' 79) and 2) a  
411 general linear model for SST on composition. We report the standardized linear regression  
412 coefficients, estimated degrees of freedom for smoothed GAM terms (and associated chi-square  
413 statistic), estimates of the mediation effect and direct effect, and the proportion of the direct  
414 effect of SST mediated by composition for the second mediation analysis, along with 95%  
415 confidence intervals around estimates of the direct effect, mediation effect, and the proportion  
416 mediated. All models in mediation analysis used data that were averaged at the level of habitats  
417 within sites, which is the lowest level of pairwise comparisons we can make between squidpop  
418 assays and consumer composition.

419

420 All analyses were performed in R version 3.5.3 (80). Data and analyses for this project are  
421 available at <https://doi.org/10.5281/zenodo.3998836>.

422

## 423 **References**

- 424 1. T. Dobzhansky, Evolution in the tropics. *Am. Sci.* **38**, 208–221 (1950).
- 425 2. G. J. Vermeij, *Evolution and Escalation: An Ecological History of Life* (Princeton  
426 University Press, 1993).
- 427 3. A. Z. Krug, D. Jablonski, J. W. Valentine, K. Roy, Generation of Earth's first-order  
428 biodiversity pattern. *Astrobiology* **9**, 113–124 (2009).
- 429 4. S. A. Levin, The problem of pattern and scale in ecology: the Robert H. MacArthur Award  
430 Lecture. *Ecology* **73**, 1943–1967 (1992).
- 431 5. D. W. Schemske, G. G. Mittelbach, H. V. Cornell, J. M. Sobel, K. Roy, Is there a latitudinal  
432 gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.* **40**, 245–269  
433 (2009).

- 434 6. A. T. Moles, S. P. Bonser, A. G. B. Poore, I. R. Wallis, W. J. Foley, Assessing the evidence  
435 for latitudinal gradients in plant defence and herbivory. *Funct. Ecol.* **25**, 380–388 (2011).
- 436 7. M. G. Powell, V. P. Beresford, B. A. Colaianne, The latitudinal position of peak marine  
437 diversity in living and fossil biotas: latitudinal position of peak marine diversity. *J.*  
438 *Biogeogr.* **39**, 1687–1694 (2012).
- 439 8. C. Chaudhary, H. Saeedi, M. J. Costello, Bimodality of latitudinal gradients in marine  
440 species richness. *Trends Ecol. Evol.* **31**, 670–676 (2016).
- 441 9. J. F. Gillooly, J. H. Brown, West, Geoffrey B., V. M. Savage, Charnov, Eric L., Effects of  
442 size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2001).
- 443 10. J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, G. B. West, Toward a metabolic  
444 theory of ecology. *Ecology* **85**, 1771–1789 (2004).
- 445 11. G. G. Mittelbach, *et al.*, Evolution and the latitudinal diversity gradient: speciation,  
446 extinction and biogeography. *Ecol. Lett.* **10**, 315–331 (2007).
- 447 12. J. R. Schramski, A. I. Dell, J. M. Grady, R. M. Sibly, J. H. Brown, Metabolic theory  
448 predicts whole-ecosystem properties. *Proc. Natl. Acad. Sci.* **112**, 2617–2622 (2015).
- 449 13. M. I. O’Connor, B. Gilbert, C. J. Brown, Theoretical predictions for how temperature  
450 affects the dynamics of interacting herbivores and plants. *Am. Nat.* **178**, 626–638 (2011).
- 451 14. M. I. O’Connor, M. F. Piehler, D. M. Leech, A. Anton, J. F. Bruno, Warming and resource  
452 availability shift food web structure and metabolism. *PLoS Biol.* **7**, e1000178 (2009).
- 453 15. A. I. Dell, S. Pawar, V. M. Savage, Temperature dependence of trophic interactions are  
454 driven by asymmetry of species responses and foraging strategy. *J. Anim. Ecol.* **83**, 70–84  
455 (2014).
- 456 16. M. B. J. Harfoot, *et al.*, Emergent global patterns of ecosystem structure and function from  
457 a mechanistic general ecosystem model. *PLOS Biol.* **12**, e1001841 (2014).
- 458 17. D. G. Boyce, K. T. Frank, B. Worm, W. C. Leggett, Spatial patterns and predictors of  
459 trophic control in marine ecosystems. *Ecol. Lett.* **18**, 1001–1011 (2015).
- 460 18. P. D. van Denderen, M. Lindegren, B. R. MacKenzie, R. A. Watson, K. H. Andersen,  
461 Global patterns in marine predatory fish. *Nat. Ecol. Evol.* **2**, 65–70 (2018).
- 462 19. J. R. Bernhardt, J. M. Sunday, P. L. Thompson, M. I. O’Connor, Nonlinear averaging of  
463 thermal experience predicts population growth rates in a thermally variable environment.  
464 *Proc. R. Soc. B Biol. Sci.* **285**, 10 (2018).
- 465 20. D. Pauly, On the interrelationships between natural mortality, growth parameters, and mean  
466 environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* **39**, 175–192 (1980).

- 467 21. C. B. Field, Primary production of the biosphere: integrating terrestrial and oceanic  
468 components. *Science* **281**, 237–240 (1998).
- 469 22. R. A. Watson, *et al.*, Global marine yield halved as fishing intensity redoubles. *Fish Fish.*  
470 **14**, 493–503 (2013).
- 471 23. J. Cebrian, Patterns in the fate of production in plant communities. *Am. Nat.* **154**, 449  
472 (1999).
- 473 24. S. L. Williams, K. L. Heck, Jr., “Seagrass Community Ecology” in *Marine Community*  
474 *Ecology*, M. D. Bertness, S. D. Gaines, M. E. Hay, Eds. (Sinauer, 2001), pp. 317–337.
- 475 25. M. Sievers, *et al.*, The role of vegetated coastal wetlands for marine megafauna  
476 conservation. *Trends Ecol. Evol.* **34**, 807–817 (2019).
- 477 26. J. F. Valentine, J. E. Duffy, “The Central Role of Grazing in Seagrass Ecology” in  
478 *Seagrasses: Biology, Ecology and Conservation*, A. W. D. Larkum, R. J. Orth, C. M.  
479 Duarte, Eds. (Springer Netherlands, 2006), pp. 463–501.
- 480 27. J. E. Duffy, J. P. Richardson, K. E. France, Ecosystem consequences of diversity depend on  
481 food chain length in estuarine vegetation. *Ecol. Lett.* **8**, 301–309 (2005).
- 482 28. S. P. Baden, A. Emanuelsson, L. Pihl, C.-J. Svensson, P. Åberg, Shift in seagrass food web  
483 structure over decades is linked to overfishing. *Mar. Ecol. Prog. Ser.* **451**, 61–73 (2012).
- 484 29. P. L. Reynolds, J. P. Richardson, J. E. Duffy, Field experimental evidence that grazers  
485 mediate transition between microalgal and seagrass dominance. *Limnol. Oceanogr.* **59**,  
486 1053–1064 (2014).
- 487 30. J. E. Duffy, A. R. Hughes, P.-O. Moksnes, “Ecology of Seagrass Communities” in *Marine*  
488 *Community Ecology and Conservation*, 2nd Edition, M. D. Bertness, J. F. Bruno, B. R.  
489 Silliman, J. J. Stachowicz, Eds. (Sinauer Associates Inc., 2013), pp. 271–297.
- 490 31. P. L. Reynolds, *et al.*, Latitude, temperature, and habitat complexity predict predation  
491 pressure in eelgrass beds across the Northern Hemisphere. *Ecology* **99**, 29–35 (2018).
- 492 32. C. A. Musri, *et al.*, Variation in consumer pressure along 2500 km in a major upwelling  
493 system: crab predators are more important at higher latitudes. *Mar. Biol.* **166** (2019).
- 494 33. P. D. Mannion, P. Upchurch, R. B. J. Benson, A. Goswami, The latitudinal biodiversity  
495 gradient through deep time. *Trends Ecol. Evol.* **29**, 42–50 (2014).
- 496 34. B. Worm, D. P. Tittensor, *A Theory of Global Biodiversity* (Princeton University Press,  
497 2018) <https://doi.org/10.2307/j.ctt1zkjz6q> (September 19, 2019).
- 498 35. A. L. Freestone, R. W. Osman, G. M. Ruiz, M. E. Torchin, Stronger predation in the tropics  
499 shapes species richness patterns in marine communities. *Ecology* **92**, 983–993 (2011).

- 500 36. T. Roslin, *et al.*, Higher predation risk for insect prey at low latitudes and elevations.  
501 *Science* **356**, 742–744 (2017).
- 502 37. R. D. Stuart-Smith, G. J. Edgar, N. S. Barrett, S. J. Kininmonth, A. E. Bates, Thermal  
503 biases and vulnerability to warming in the world’s marine fauna. *Nature* (2015)  
504 <https://doi.org/10.1038/nature16144> (May 10, 2018).
- 505 38. K. E. Carpenter, Ed., “The Living Marine Resources of the Western Central Atlantic.  
506 Volume 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine  
507 mammals” in *FAO Species Identification Guide for Fishery Purposes and American Society*  
508 *of Ichthyologists and Herpetologists Special Publication No.5*, (FAO, 2002), pp. 1375–  
509 2127.
- 510 39. F. Micheli, C. H. Peterson, Estuarine Vegetated Habitats as Corridors for Predator  
511 Movements. *Conserv. Biol.* **13**, 869–881 (1999).
- 512 40. E. M. P. Madin, *et al.*, Multi-Trophic Species Interactions Shape Seascape-Scale Coral Reef  
513 Vegetation Patterns. *Front. Ecol. Evol.* **7** (2019).
- 514 41. B. K. Eriksson, *et al.*, Effects of altered offshore food webs on coastal ecosystems  
515 emphasize the need for cross-ecosystem management. *AMBIO* **40**, 786 (2011).
- 516 42. J. M. Sunday, A. E. Bates, N. K. Dulvy, Global analysis of thermal tolerance and latitude in  
517 ectotherms. *Proc. R. Soc. Lond. B Biol. Sci.*, 1823–1830 (2011).
- 518 43. K. A. Hovel, R. N. Lipcius, Habitat fragmentation in a seagrass landscape: patch size and  
519 complexity control blue crab survival. *Ecology* **82**, 1814–1829 (2001).
- 520 44. R. J. Orth, K. L. Heck, Jr., J. van Montfrans, Faunal communities in seagrass beds: a review  
521 of the influence of plant structure and prey characteristics on predator-prey relationships.  
522 *Estuaries* **7**, 339–350 (1984).
- 523 45. K. L. Main, Predator avoidance in seagrass meadows: prey behavior, microhabitat  
524 selection, and cryptic coloration. *Ecology* **68**, 170–180 (1987).
- 525 46. J. Mattila, *et al.*, Increased habitat structure does not always provide increased refuge from  
526 predation. *Mar. Ecol. Prog. Ser.* **361**, 15–20 (2008).
- 527 47. B. B. Hughes, *et al.*, Recovery of a top predator mediates negative eutrophic effects on  
528 seagrass. *Proc. Natl. Acad. Sci.* **110**, 15313–15318 (2013).
- 529 48. A. C. Huang, M. Essak, M. I. O’Connor, Top–down control by great blue herons *Ardea*  
530 *herodias* regulates seagrass-associated epifauna. *Oikos* **124**, 1492–1501 (2015).
- 531 49. M. Roesti, *et al.*, Pelagic fish predation is stronger at temperate latitudes than near the  
532 equator. *Nat. Commun.* **11**, 1–7 (2020).

- 533 50. Y. Y. Watanabe, K. J. Goldman, J. E. Caselle, D. D. Chapman, Y. P. Papastamatiou,  
534 Comparative analyses of animal-tracking data reveal ecological significance of endothermy  
535 in fishes. *Proc. Natl. Acad. Sci.* **112**, 6104–6109 (2015).
- 536 51. J. M. Grady, *et al.*, Metabolic asymmetry and the global diversity of marine predators.  
537 *Science* **363**, eaat4220 (2019).
- 538 52. M. L. Pinsky, B. Worm, M. J. Fogarty, J. L. Sarmiento, S. A. Levin, Marine taxa track local  
539 climate velocities. *Science* **341**, 1239–1242 (2013).
- 540 53. D. J. McCauley, *et al.*, Marine defaunation: Animal loss in the global ocean. *Science* **347**,  
541 1255641 (2015).
- 542 54. J. A. Estes, *et al.*, Trophic downgrading of planet earth. *Science* **333**, 301–306 (2011).
- 543 55. G. A. Hyndes, *et al.*, Accelerating tropicalization and the transformation of temperate  
544 seagrass meadows. *BioScience* **66**, 938–948 (2016).
- 545 56. L. D. Zeidberg, B. H. Robison, Invasive range expansion by the Humboldt squid, *Dosidicus*  
546 *gigas*, in the eastern North Pacific. *Proc. Natl. Acad. Sci.* **104**, 12948–12950 (2007).
- 547 57. I. M. Côté, S. J. Green, M. A. Hixon, Predatory fish invaders: Insights from Indo-Pacific  
548 lionfish in the western Atlantic and Caribbean. *Biol. Conserv.* **164**, 50–61 (2013).
- 549 58. B. J. Sinclair, *et al.*, Can we predict ectotherm responses to climate change using thermal  
550 performance curves and body temperatures? *Ecol. Lett.* **19**, 1372–1385 (2016).
- 551 59. R. D. Sagarin, J. P. Barry, S. E. Gilman, C. H. Baxter, Climate-related change in an  
552 intertidal community over short and long time scales. *Ecol. Monogr.* **69**, 465–490 (1999).
- 553 60. E. Sanford, J. L. Sones, M. García-Reyes, J. H. R. Goddard, J. L. Largier, Widespread  
554 shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves.  
555 *Sci. Rep.* **9**, 4216 (2019).
- 556 61. J. E. Duffy, S. L. Ziegler, J. E. Campbell, P. M. Bippus, J. S. Lefcheck, Squidpops: a simple  
557 tool to crowdsource a global map of marine predation intensity. *PLOS ONE* **10**, e0142994  
558 (2015).
- 559 62. L. Tyberghein, *et al.*, Bio-ORACLE: a global environmental dataset for marine species  
560 distribution modelling: Bio-ORACLE marine environmental data rasters. *Glob. Ecol.*  
561 *Biogeogr.* **21**, 272–281 (2012).
- 562 63. Center for International Earth Science Information Network - CIESIN - Columbia  
563 University, Gridded Population of the World, Version 4 (GPWv4): Population Density,  
564 Revision 10 (2017).
- 565 64. D. Pauly, D. Zeller, Eds., Sea Around Us Concepts, Design and Data (searoundus.org)  
566 (2015).

- 567 65. S. Chamberlain, R. S. Reis, *searoundus: Sea Around Us API Wrapper* (2017).
- 568 66. R. Froese, D. Pauly, Fishbase. *World Wide Web Electron. Publ.* (2019).
- 569 67. B. M. Bolker, R. D. C. Team, *bbmle: Tools for General Maximum Likelihood Estimation*  
570 (2017).
- 571 68. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using  
572 lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
- 573 69. J. M. Chase, T. M. Knight, Scale-dependent effect sizes of ecological drivers on  
574 biodiversity: why standardised sampling is not enough. *Ecol. Lett.* **16**, 17–26 (2013).
- 575 70. J. M. Chase, N. J. B. Kraft, K. G. Smith, M. Vellend, B. D. Inouye, Using null models to  
576 disentangle variation in community dissimilarity from variation in  $\alpha$ -diversity. *Ecosphere* **2**,  
577 art24 (2011).
- 578 71. M. J. Anderson, T. J. Willis, Canonical Analysis of Principal Coordinates: a useful method  
579 of constrained ordination for ecology. *Ecology* **84**, 511–525 (2003).
- 580 72. J. Oksanen, *et al.*, *vegan: Community Ecology Package* (2018).
- 581 73. C. Boettiger, D. T. Lang, P. Wainwright, rfishbase: exploring, manipulating and visualizing  
582 FishBase data from R. *J. Fish Biol.* (2012).
- 583 74. R. D. Stuart-Smith, *et al.*, Integrating abundance and functional traits reveals new global  
584 hotspots of fish diversity. *Nature* **501**, 539–542 (2013).
- 585 75. E. Laliberté, P. Legendre, A distance-based framework for measuring functional diversity  
586 from multiple traits. *Ecology* **91**, 299–305 (2010).
- 587 76. S. Villéger, N. W. H. Mason, D. Mouillot, New multidimensional functional diversity  
588 indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301 (2008).
- 589 77. Z. Botta-Dukát, Rao’s quadratic entropy as a measure of functional diversity based on  
590 multiple traits. *J. Veg. Sci.* **16**, 533–540 (2005).
- 591 78. D. Tingley, T. Yamamoto, K. Hirose, L. Keele, K. Imai, mediation: R Package for Causal  
592 Mediation Analysis. *J. Stat. Softw.* **59**, 1–38 (2014).
- 593 79. S. N. Wood, Fast stable restricted maximum likelihood and marginal likelihood estimation  
594 of semiparametric generalized linear models. *J. R. Stat. Soc. B* **73**, 3–36 (2011).
- 595 80. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation  
596 for Statistical Computing, 2019).

597  
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599



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607 RDBW, PHY, and MAW curated the data, MAW performed the formal analyses and  
608 visualization, MAW and JED wrote the original draft, MAW, JJS, and JED wrote the final draft,  
609 all authors contributed to field investigations and to reviewing and editing the manuscript. This is  
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612 **Figures**

613

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

619

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

630

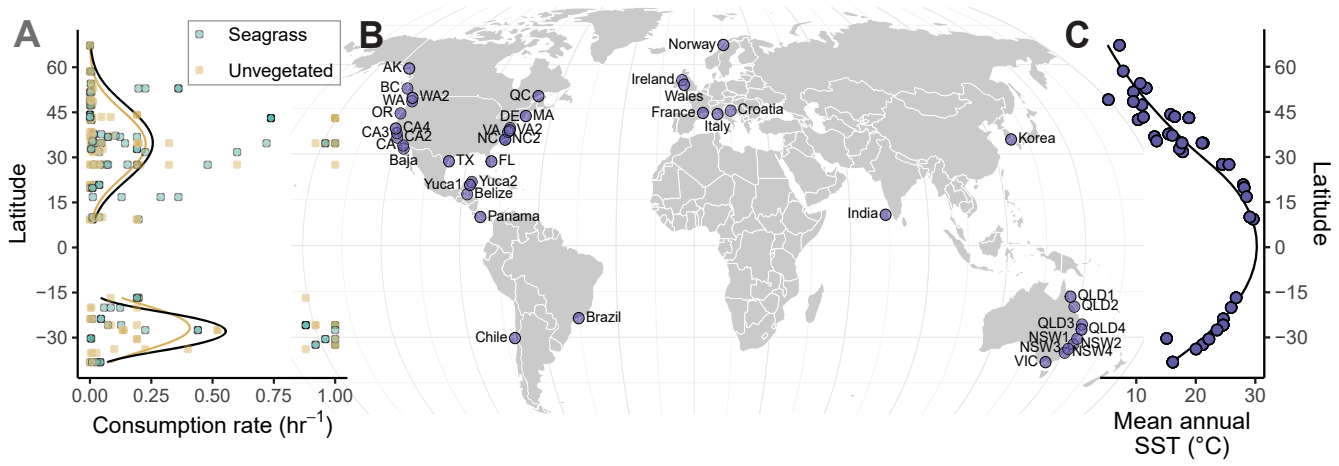
631 Figure 3. Predator composition mediates the effect of thermal environment on consumption rates.  
632 (A-C) Bivariate relationships between consumer composition (PCoA1, Fig. 2A), thermal  
633 environment (SST) and consumption rate. Lines show predictions from models used in  
634 mediation analysis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

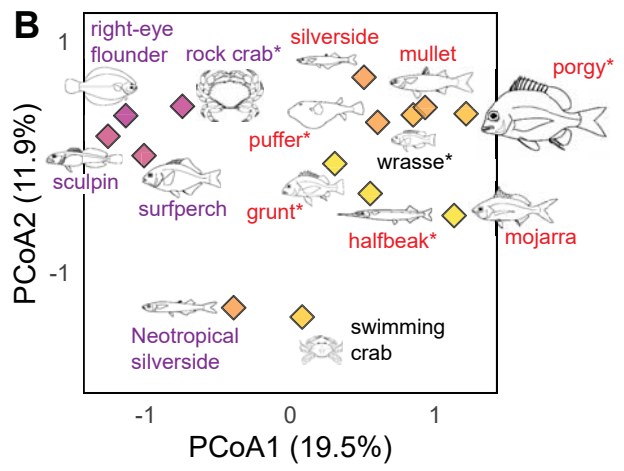
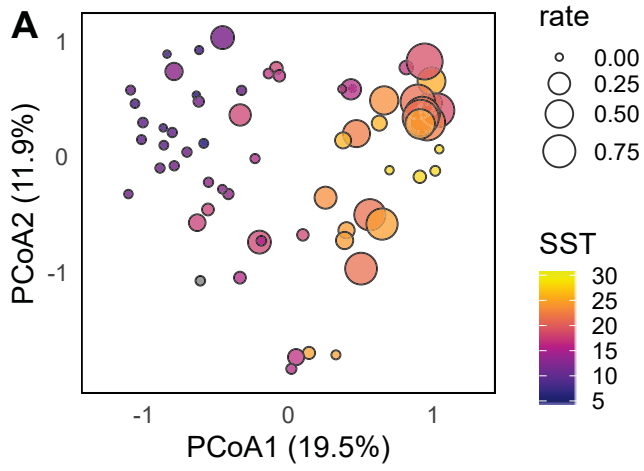
641

642 **Tables**

643

644 Table 1. Comparison of generalized linear mixed effects models predicting bait consumption by  
645 generalist consumers in two shallow marine habitats





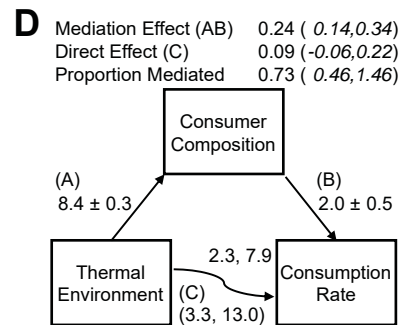
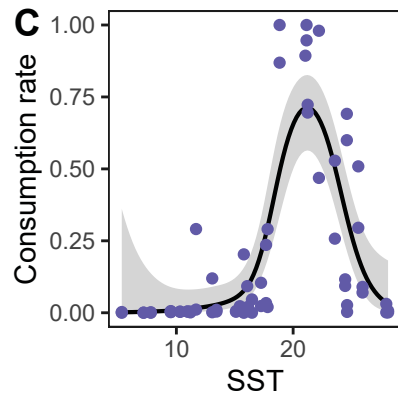
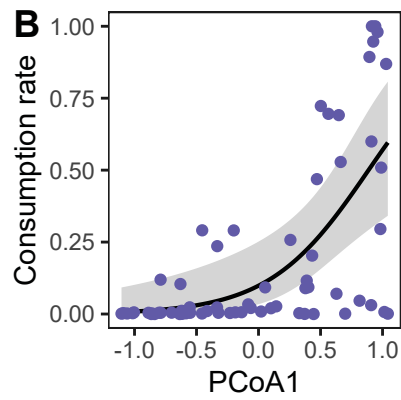
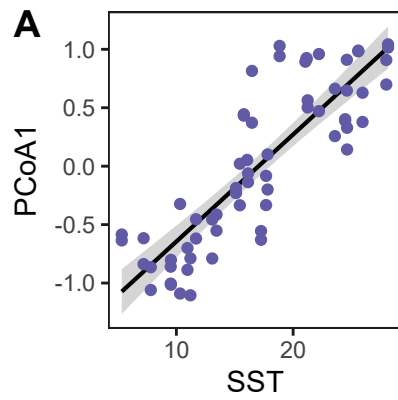


Table 1. Comparison of generalized linear mixed effects models predicting bait consumption by generalist consumers in two shallow marine habitats

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

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 through constrained ordination (Fig. 2B, SI Appendix, Table S1). Productivity refers to remotely-sensed mean annual chlorophyll *a*. Habitat categorically relates seagrass and unvegetated habitats. Abundance, biomass, and human population density were log<sub>10</sub>-transformed. Body size, Trophic Group, Lateral Body Shape, and Water Column Use are community-weighted mean trait values by site and habitat. We provide marginal pseudo- $R^2$  values for comparison of fixed effects. For model comparison we only included data from sites with the full complement of predictors (27 of 42 sites).