**Title:** Energetic requirements of extreme temperatures reduce biodiversity and functioning in cryptobenthic coral reef fish communities

**Authors:** Simon J. Brandl1,2,3\*, Jacob L. Johansen4,5\*, Jordan M. Casey2,3, Luke Tornabene6, Renato A. Morais7,8, John A. Burt5

\* indicates shared first authorship

**Corresponding author:** Simon J. Brandl, [simonjbrandl@gmail.com](mailto:simonjbrandl@gmail.com)

**Affiliations:**

1 Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

2 PSL Université Paris: CNRS-EPHE-UPVD USR3278 CRIOBE, Université de Perpignan, Perpignan, France

3 Laboratoire d’Excellence “CORAIL,” Perpignan, France

4 Hawai’i Institute of Marine Biology, University of Hawai’i at Manoa, Kane’ohe, HI, USA

5 Marine Biology Laboratory, Centre for Genomics and Systems Biology, New York University Abu Dhabi, Abu Dhabi, United Arab Emirates

6 School of Aquatic and Fishery Sciences and the Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA

7 ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

8 College of Science and Engineering, James Cook University, Townsville, QLD, Australia

**Abstract:**

Environmentally mediated transformations of ecological communities can influence ecosystem functioning. Coral reef fishes are hypothesized to be vulnerable to changing temperatures, but cascading effects of organismal tolerances on the assembly and functioning of reef fish communities are largely unknown. Here, we show that cryptobenthic reef fish assemblages in the southern Arabian Gulf, which reaches a maximum water temperature of greater than 36ºC, are comprised of half as many species and less than a quarter of individuals present in the thermally benign nearby Gulf of Oman, despite equal availability of live coral substrate. This pattern is not primarily driven by intrinsic organismal temperature tolerances. Rather, shifts in resource use and declining body condition in Arabian Gulf populations indicate significant energetic costs of adjusting to higher temperatures, which may prohibit the persistence of many small-bodied species. In turn, this results in the reduced production, transfer, and replenishment of biomass through cryptobenthic fish assemblages. Our results suggest that many cryptobenthic fishes cannot cope with the increasing costs of growth and homeostasis in response to rising temperatures. Consequently, future reefs may lose cryptobenthic fishes, a critical building block of their fast-paced dynamics, independent of live coral loss.

**Introduction:**

Why do some species occur in a given location while similar taxa are missing? And how do resulting species assemblages affect rates of critical ecological processes? As escalating human impacts on the biosphere deplete and re-shuffle biological communities across ecosystems1,2, answers to these questions are key to our quest to preserve biodiversity and ecosystem services to humanity3,4.

A species’ presence at a given location is mediated by a hierarchical interplay between organismal traits (e.g., temperature tolerance, trophic niche), environmental conditions (e.g., temperature, salinity), and stochastic events (e.g., random walks to extinction, lottery dynamics)5–8. Furthermore, the identity and diversity of species and their traits affect rates of ecosystem functioning, including processes that are critical to human well-being, such as primary or secondary productivity9–11. However, by modifying abiotic conditions, species’ niches, and biotic interactions, global stressors such as climate change can interfere with these dynamics through numerous pathways12–14.

At the organismal level, changes in environmental factors, such as temperature, affect internal physiological processes15, which, if not lethal, will alter organismal energy expenditure16–18. Changes in organismal energy budgets subsequently drive resource acquisition (e.g. feeding rates, prey species) and how resulting energy is allocated to life-supporting processes (homeostasis), growth, and reproduction19–21. The interaction between these dynamics, which are often investigated through the lens of ecological niche and fitness, are the basis of modern coexistence theory. Thus, they are critical for our understanding of community assembly dynamics22 and the rate of ecological processes that underpin energy and nutrient fluxes through ecosystems23. Therefore, integration across levels of biological organization is crucial to understand the effects global environmental change on our planet’s ecosystems24.

Coral reefs are the most diverse marine ecosystem, and their productivity provides vital services for more than 500 million people worldwide25. Scleractinian corals, the foundation species of tropical reefs, show high thermal sensitivity that has led to the rapid global decline of coral reef ecosystems26. In wake of losing coral habitat, communities of the most prominent reef consumers, teleost fishes, decline or shift in composition27–30, which can affect the provision of resources to people dependent on reef fisheries31. Nevertheless, recent evidence suggests that many species of fishes will be able to cope with or even benefit from the temporary loss of live coral31–33. However, as tropical marine ectotherms adapted to a relatively narrow thermal environment, reef fishes may also be vulnerable to the direct effects of changing water temperatures16,34,35. Consequently, the responses of reef fishes to climate change and their potential to adapt to different thermal regimes are intensively studied36–38.

Despite marked differences in species-specific tolerances to higher temperatures39–43, most reef fish species tested to date suffer from non-lethal44 adverse physiological, developmental, or behavioral responses when exposed to temperatures outside of their normal range, which suggests long-term deleterious effects on reef fish populations in the wild36. However, few cases of direct temperature-mediated population declines have been documented for *in situ* reef fish communities45. This may be explained by transgenerational acclimation and adaptation, which can enhance the performance of offspring in higher temperatures through developmental, genetic, or epigenetic pathways38,46. However, transgenerational adaptation has only been shown in a few model species38,46,47 and carries a range of energetic costs that species must mitigate46,48. Therefore, it is unresolved whether this process can truly enhance survival of reef fishes in a competitive, uncontrolled environment and how species-specific temperature tolerance differences may mediate coexistence in ecological communities.

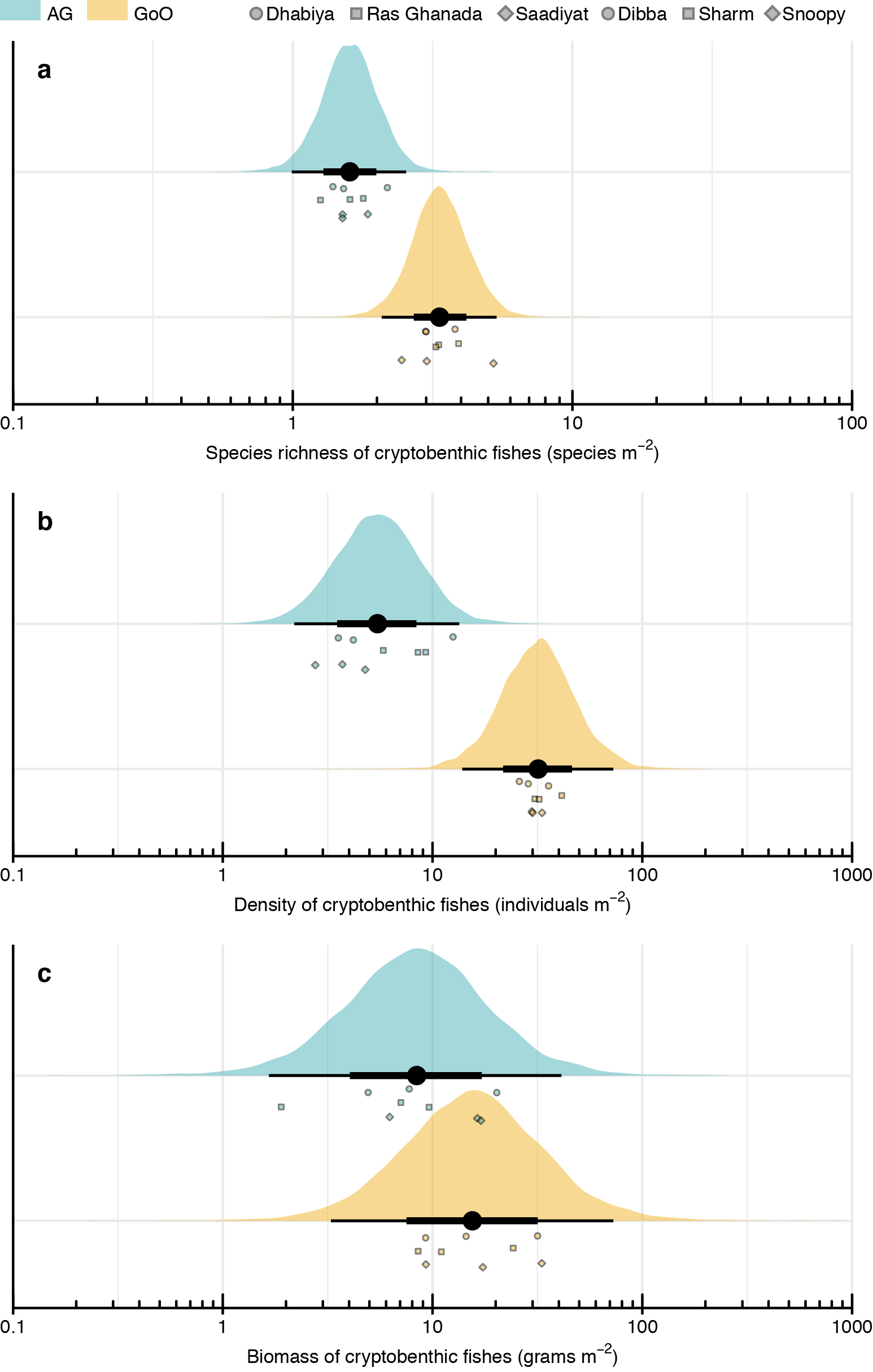
Cryptobenthic fishes are the smallest of all reef fishes, rarely exceeding 50mm in body size49. They account for almost half of all reef fish species and are numerically abundant and ubiquitous on reefs worldwide49–52. Due to their small body size, these fishes have evolved a unique life history strategy of rapid growth, high mortality, and continuous larval replenishment, which plays an important part in coral reef trophodynamics53. Their small body size and associated life-history also promise exceptional traceability concerning the effects of, and responses to, increasing temperatures49. Limited gill surface area, unfavorable mass to surface ratios, high mass-specific metabolism, and other physiological challenges resulting from their minute size suggest that cryptobenthics are particularly susceptible to temperature fluctuations41,49,54. Further, due to their limited mobility and close association with the benthos55, mitigation of temperature extremes through migration is not viable and marked community composition shifts follow changes in the benthic community structure30,56. However, their extremely high generational turnover (up to eight generations per year53,57), along with the prevalence of benthic clutch spawning and parental care49, may make them ideally suited for transgenerational adaptation to changing conditions36. In fact, an extremely fast evolutionary clock has been implicated as a driver for rapid speciation in cryptobenthic fishes58, which may permit similarly fast microevolutionary changes (i.e. rapid adaption). Thus, cryptobenthic fishes may be well-suited to detect the impact of environmental change on organisms and populations, with promising insights into whether transgenerational plasticity or adaptation can provide pathways to the persistence of coral reef fishes in warming oceans.

Here, we quantify cryptobenthic community assembly, species-specific organismal traits, and contribution to ecosystem functioning in the world’s hottest coral reef environment, the southeastern Arabian Gulf, and we compare the resulting patterns with the spatially proximate, but more environmentally benign, Gulf of Oman. Specifically, the goal of our study was to 1) describe cryptobenthic fish assemblages across the two locations, 2) identify organismal traits that permit or preclude existence in the Arabian Gulf, and 3) determine the consequences of these results for the production, provision, and renewal of cryptobenthic fish biomass24.

**Results:**

Reefs in the shallow southern Arabian Gulf range from 16.0º C in the winter months to 36.0º C in the summer59. As such, maximum temperatures on reefs along the Arabian Gulf coast of the United Arab Emirates mirror forecasted temperatures for most tropical coral reefs in the end of the century60. Despite the seemingly unfavorable conditions for tropical reef building corals, corals have persisted in this region for approximately 15,000 years, with the modern coastline harboring coral reef structures for circa 6,000 years60. Therefore, the Arabian Gulf represents an exceptional natural laboratory to examine the capacity of reef organisms to cope with unfavorable conditions and how this influences the diversity and dynamics that underpin modern coral reefs.

Cryptobenthic reef fish assemblages markedly differed between the Arabian Gulf and the Gulf of Oman. Reefs in the Gulf of Oman harbored a higher diversity (Bayesian hierarchical model estimate: *Gulf of Oman: β* = 0.73 [0.44, 1.01; lower and upper 95% credible interval]) and density (*Gulf of Oman:* *β* = 1.77 [1.03, 2.58])of cryptobenthic fishes (Fig. 1a,b), but standing biomass estimates were comparable (*Gulf of Oman:* *β* = 0.63 [-0.54, 1.71]; Fig. 1c). Similarly, the composition of cryptobenthic communities greatly varied between the two locations (Fig. 2a), with no overlap among convex hull polygons in the non-metric multidimensional scaling (nMDS) ordination and a strong effect of *Location* in the PERMANOVA on the site-by-species dissimilarity matrix (*Location*: *df* = 1, *F* = 13.58, *P* = 0.001, *R2* = 0.46). There were 29 unique species in the Gulf of Oman, 13 unique species in the Arabian Gulf, and 16 species shared among the two locations. In contrast to the cryptobenthic fish community, there were no differences in coral cover (Bayesian hierarchical model: *Gulf of Oman: β* = 0.02 [-1.30, 1.42]) nor overall benthic community structure as revealed by a PERMANOVA (*Location*: *df* = 1, *F* = 1.63, *P* = 0.187, *R2* = 0.09; Fig. 2b). Thus, despite broadly comparable benthic conditions and no differences in live coral cover, the cryptobenthic fish assemblages strongly differed between the two locations.

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**Fig. 1 | Community structure of cryptobenthic reef fish communities in the Arabian Gulf (AG) and Gulf of Oman (GoO).** (**a**) Species richness and (**b**) density of cryptobenthic reef fishes was markedly higher on reefs in the GoO, while (**c**) biomass did not substantially differ between the two locations. Density curves represent predicted values based on 1,000 draws from Bayesian hierarchical linear models testing for differences between locations, while black caterpillar plots represent their means, 50%, and 95% credible intervals. Circles, squares, and diamonds represent raw values from the respective sites in each location, jittered on the y-axis.

A close up of a yellow wall

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**Fig. 2 | Community structure of cryptobenthic reef fishes and benthic functional groups in the Arabian Gulf (AG) and Gulf of Oman (GoO).** (**a**)Biplot of a non-metric multidimensional scaling (nMDS) ordination on cryptobenthic fish communities, with the arrows indicating the position and strength of the seven most important species. (**b**) Biplot of an nMDS on benthic functional groups, with the influence of all groups indicated with arrows. Convex hull polygons delineate the two locations. Each point represents a sample station at a particular site, with the shape size in (**b**) scaled by percent live coral cover.

We then tested whether organismal temperature tolerance can explain the absence of species from the Arabian Gulf (despite being recorded in the northern Arabian Gulf where conditions are more benign61; see Table S1). Notwithstanding distinct thermal regimes at the two locations and the drastic differences in cryptobenthic fish assemblages, species-specific critical thermal tolerance limits did not explain the absence of three common Gulf of Oman species in the Arabian Gulf. In terms of critical thermal minima (ctmin), all species, regardless of origin, tolerated the minimum winter temperature of the UAE Arabian Gulf at 16.0 ºC. Among individuals sampled from the Gulf of Oman population, *Ecsenius pulcher* had the greatest tolerance to cold (ctmin = 11.3 ± 0.1 ºC), while *Enneapterygius ventermaculus* had the least tolerance (13.3 ± 0.1 ºC). In contrast, the cold-tolerance of *E. ventermaculus* in the Arabian Gulf substantially exceeded all three examined Gulf of Oman populations (Table S2), which provides evidence for enhanced thermal tolerance in *E. ventermaculus* from the Arabian Gulf.Although there were considerable species-specific differences in the critical thermal minimum, mean cold tolerances of all Gulf of Oman species fell within the 95% credible bounds of the species present in the Arabian Gulf (Fig. 3a).

Similar to the ctmin, the mean critical thermal maximum tolerance limits (ctmax) of all species, regardless of origin, equaled or surpassed the maximum summer temperatures recorded in the Arabian Gulf (36.0 ºC). *Helcogramma fuscopinna* (a Gulf of Oman species) had the lowest heat tolerance at 36.0 ± 0.11 ºC, while *Coryogalops anomolus* from the Arabian Gulf had the greatest heat tolerance (38.4 ± 0.06 ºC). While there were no population differences in heat tolerance for *E. ventermaculus*, the Arabian Gulf population of *E. pulcher* showed considerably greater heat tolerance than their Gulf of Oman counterparts, providing evidence for enhanced thermal tolerance in a second Arabian Gulf species. Similar to ctmin, despite considerable interspecific differences (Table S3), mean predicted maximum posterior heat tolerances of all species restricted to the Gulf of Oman were within the 95% credible intervals of the species present in the Arabian Gulf (Fig. 3b) suggesting limited explanatory power of thermal tolerance.

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**Fig. 3 | Critical thermal tolerance limits of cryptobenthic fish species from the Arabian Gulf and Gulf of Oman.** (**a**) Critical thermal minima ranged between 11.9 ºC and 13.3 ºC, but they were well below the minimum recorded winter temperature for the southern Arabian Gulf (16.0 ºC). (**b**) Critical thermal maxima ranged between 36.0 ºC and 38.4 ºC, but they were above or equal to the maximum recorded summer temperature in the Arabian Gulf (36.0 ºC). Density curves represent fitted values based on 10,000 draws from Bayesian linear models that test for differences among all populations, while black caterpillar plots represent their means, 50%, and 95% credible intervals. Diamonds represent raw values, jittered on the y-axis. Grey boxes delineate the range of the 95% credible intervals obtained for the three species present in the Arabian Gulf.

To further examine potential drivers of cryptobenthic community structure, we quantified species’ diets in the two locations with gut content DNA metabarcoding62, targeting the cytochrome *c* oxidase subunit I (COI), which amplifies eukaryotes, and 23S rRNA gene regions, which amplifies autotrophs. Across all fishes, the COI primers yielded a total of 547 unique OTUs, while the 23S primers yielded 3,009 unique ESVs. Dietary network trees for the COI marker showed strong separations between the Arabian Gulf and Gulf of Oman populations (Fig. 4). The COI network contained five distinct modules (modularity = 0.472). 92.3% of individuals from the Arabian Gulf were distributed across two modules that contained few Gulf of Oman individuals. Module V contained seven out of ten individuals of *C. anomolus* from the Arabian Gulf, 8 out of 9 individuals of *E. ventermaculus* from the Arabian Gulf, and one *E. guttata* from the Gulf of Oman. The remaining individuals of *C. anomolus* and *E. ventermaculus* from the Arabian Gulf clustered with *E. pulcher* from the Arabian Gulf (five out of seven), four Gulf of Oman individuals of *C. anomolus*, and a single *H. vulgaris* in module II (Fig. 4a,b). The 23S primer also revealed five modules (modularity = 0.359) but showed an even stronger regional separation. All individuals from the Arabian Gulf (except for one *C. anomolus*) were united in a single module (module III), which contained no Gulf of Oman individuals (Fig. 4c,d). While some species separated into distinct modules, location specific differences superseded taxonomic boundaries. With the exception of *C. anomolus*, species occurring in both locations had strongly dietary differences, while broadly overlapping with other species in the Gulf of Oman.

Prey diversity rarefaction curves in the Gulf of Oman showed that *E. pulcher*, a purportedly herbivorous species63, ingested the widest variety of animal prey species (COI marker), followed by *E. ventermaculus* (Fig. S1)*.* For both species, Gulf of Oman populations consumed a higher diversity of prey items than Arabian Gulf populations. Only *C. anomolus* showed no clear difference in extrapolated values (although diversity was higher for Gulf of Oman populations for the interpolated value). For autotroph prey items (23S marker), prey diversity was higher in Gulf of Oman populations of *E. pulcher* and *E. ventermaculus*, while the opposite was evident for *C. anomolus*. Overall, Gulf of Oman populations of *E. ventermaculus* exhibited the highest autotroph prey diversity, followed by Arabian Gulf populations of *C. anomolus*.

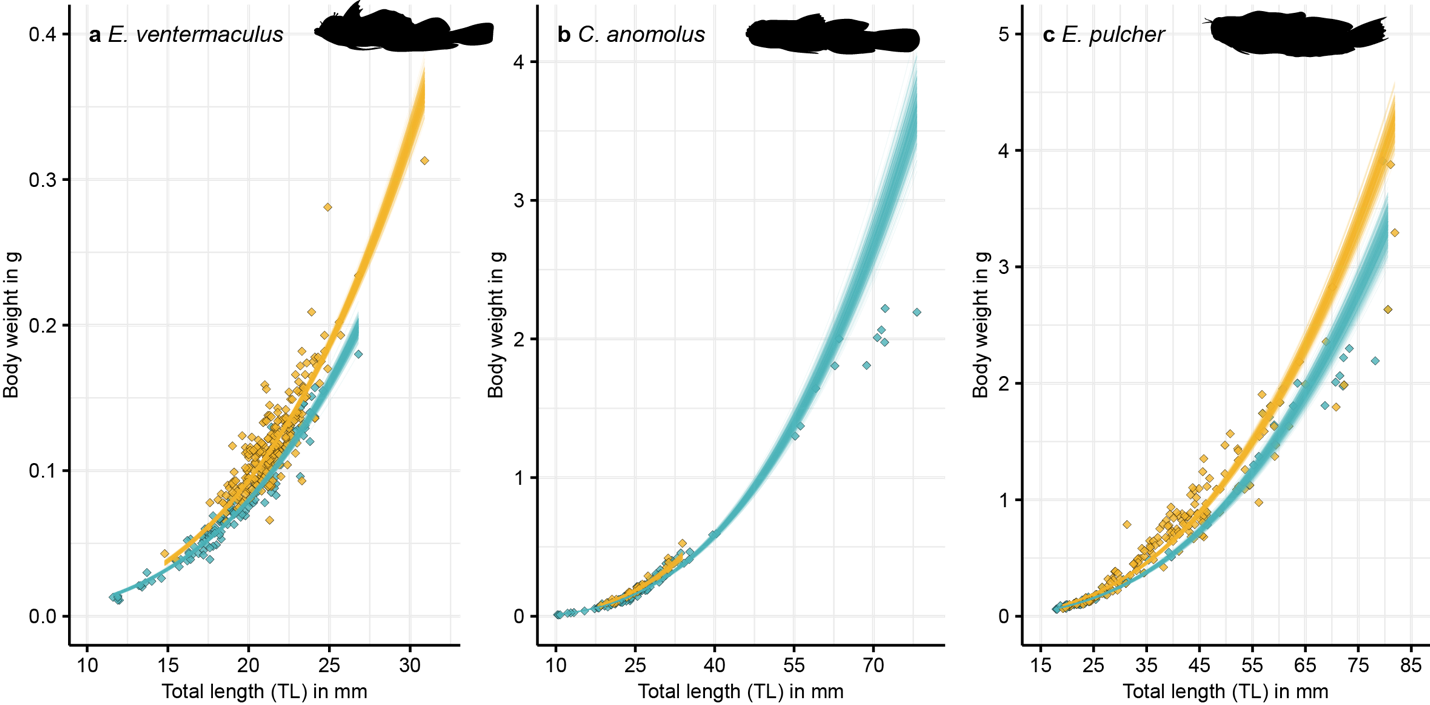
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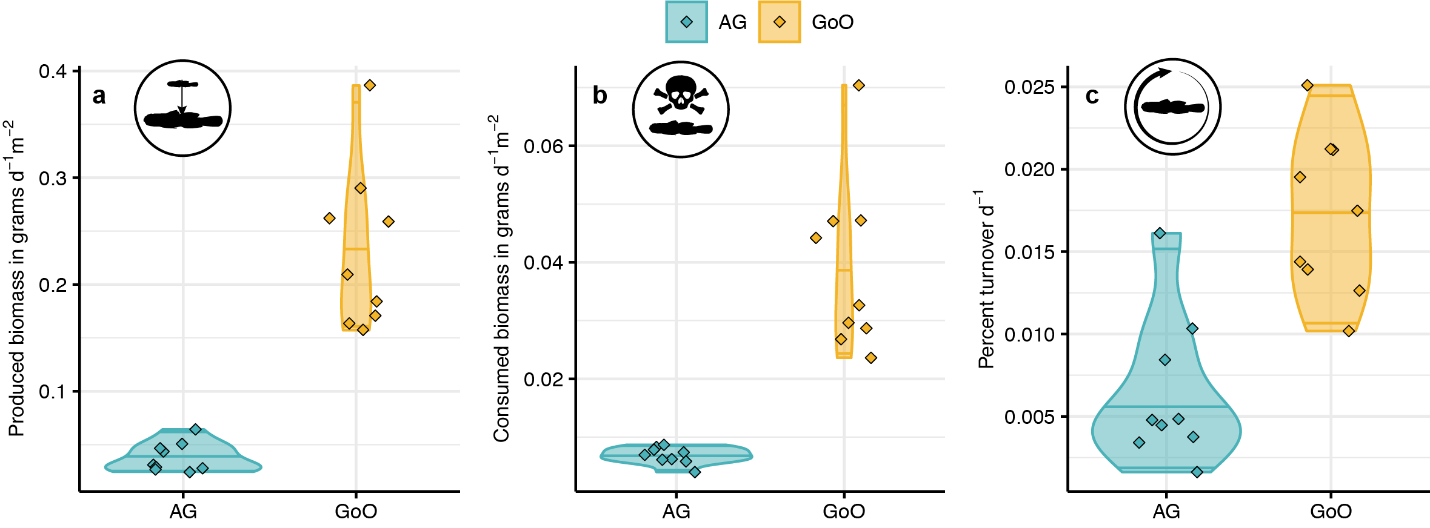
**Figure 4 | Diet network trees and modularity mosaics showing species-level differences in ingested prey items and individual-based module membership for COI (a,b) and 23S (c,d) markers. (a,c)** Fish silhouettes represent the species as nodes in the network tree. Blue symbols are OTUs (COI) or ESVs (23S) found only in populations from the Arabian Gulf, gold symbols are from the Gulf of Oman populations, and grey symbols are shared between the two locations. **(b,d)** Results of the modularity analysis with modules (I-V) as columns and individuals within each species as columns. Colored squares indicate membership in a given module.

We further examined the potential energetic consequences of thermal regimes and resource availability in the two locations by assessing length-weight relationships of the three co-occurring species and by modeling individual-based growth and mortality to estimate community-wide biomass production, consumption, and turnover. The Bayesian linear models that test the effects of total length (*TL*) and *Location* on *Weight* showed clear effects of *Location* across all species, with Gulf of Oman populations consistently having higher weights for a given body length (*E. ventermaculus*: *Gulf of Oman: β*= 0.16 [0.13, 0.19], *C. anomolus*: *Gulf of Oman: β*= 0.15 [0.09, 0.21], and *E. pulcher*: *Gulf of Oman: β*= 0.19 [0.14, 0.25]) (Fig. 5). In contrast, no clear differences emerged between the abundances of the three species’ populations across locations (effect size uncertainties intersected zero), although *E. ventermaculus* (*Gulf of Oman: β*= 0.89 [-1.08, 2.86) and *E. pulcher* (*Gulf of Oman: β*= 3.46 [-0.42, 9.93]) showed a trend toward lower abundances in the Arabian Gulf, while *C. anomolus* exhibited the opposite trend (*Gulf of Oman: β*= -0.94 [-3.82, 1.69]).

Finally, modeling individual-based growth and mortality for cryptobenthic fish communities at each site revealed strong differences in the ecological dynamics that underpin ecosystem functioning in the Arabian Gulf and Gulf of Oman (Fig. 6). Biomass production was almost one order of magnitude higher on reefs in the Gulf of Oman (0.231 ± 0.025 [mean ± SE] g d-1 m-2) compared to the Arabian Gulf (0.038 ± 0.014 g d-1 m-2), while production of consumed biomass was more than five times higher (0.039 ± 0.015 vs. 0.007 ± 0.001 g d-1 m-2). Percent turnover per day was also higher in the Gulf of Oman (0.017 ± 0.005) compared to the Arabian Gulf (0.006 ± 0.005). Therefore, these reefs are subjected to different productivity dynamics at various levels of organization. In the Arabian Gulf, individual fishes accumulate less biomass per millimeter of body size and collectively, cryptobenthic communities produce, provide, and replenish biomass at much lower rates than Gulf of Oman communities.

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**Figure 5 | Relationships between total length (TL) and body weight in populations of *Enneapterygius ventermaculus* (a), *Coryogalops anomolus* (b), and *Ecsenius pulcher* (c) in the Arabian Gulf (blue) and Gulf of Oman (gold).** Eachline represents a fitted draw from 500 iterations based on the posterior parameters from a Bayesian model regressing length against weight (thus showing model fit uncertainty). Diamonds represent raw values for individual fishes.



**Figure 6 | Model estimated biomass production, consumption, and turnover in cryptobenthic fish assemblages across the two locations.** (**a**) Produced biomass (grams of fish tissue grown per day and m2). (**b**) Consumed biomass (grams of fish tissue perished per day and m2). (**c**) Percent turnover (renewal of produced and consumed biomass per day). Violin plots and lines represent medians and variance estimates (95% quartiles) for the three metrics across the two locations. Diamonds represent values for each sampled cryptobenthic reef fish community across the six sites (three per site).

**Discussion:**

As rapid environmental change sweeps across the Earth’s ecosystems, garnering an understanding of the processes that underpin local community structure and ecosystem functioning is urgent. Here, we show that reefs exposed to the world’s most extreme temperature regime in the southeastern Arabian Gulf harbor a community of cryptobenthic fishes with reduced diversity, abundance, and body condition compared to reefs with more moderate temperatures in the nearby Gulf of Oman, despite similarities in live coral cover and benthic community structure. While species present at both locations exhibited improved thermal tolerances to the Arabian Gulf conditions, species-specific temperature tolerances were not the main driver of species presence/absence in the Arabian Gulf. Rather, intraspecific dietary differences (Fig. 4) alongside poor body condition in Arabian Gulf populations (Fig. 5) suggest that physiological changes in response to the conditions in the Arabian Gulf harbor energetic costs that can only be borne by species with low metabolic rates. Physiological differences, coupled with divergent community structure, have far reaching consequences for ecosystem-scale energy and nutrient fluxes; even generous estimates of cryptobenthic reef fish productivity in the Arabian Gulf are an order of magnitude lower than the Gulf of Oman. Our results indicate that reef fish assemblages on future coral reefs are shaped by multidimensional filtering, which may decrease the rate of bottom-up productivity and turnover on reefs and result in less productive, slower-paced reefs.

As the smallest and shortest lived marine vertebrates, cryptobenthic fishes should be particularly traceable concerning the effect of, and response to, extreme temperatures49. Yet, critical thermal tolerances of all tested species from both locations were equal or greater than maximum summer temperatures in the most extreme southeastern Arabian Gulf42,44,64. The high intrinsic tolerance of species from the relatively cool Gulf of Oman aligns with previous results on critical thermal tolerances in cryptobenthics42, which emphasize these fishes’ needs to mediate short-term temperature extremes in shallow waters when movement is limited49,55. This, however, suggests that the colonization of reefs in the extremely hot southeastern Arabian Gulf is feasible for all species and the swift generational turnover of cryptobenthic fishes53,57 should allow for transgenerational thermal plasticity to facilitate persistence in the southeastern Arabian Gulf despite its short geological history65. Notably, despite being separated by the relatively narrow Strait of Hormuz, no hard biogeographic boundary is in place that drives the absence of so many species in the Arabian Gulf. Indeed, 26 out of 29 (89.7%) cryptobenthic fish species from the Gulf of Oman that were absent from the southeastern Arabian Gulf have been recorded in the cooler Arabian Gulf regions of Saudi Arabia and Kuwait (Table S1)61,66,67. Thus, neither thermal tolerances, short-term temperature extremes, or biogeographic history drive the observed depletion of cryptobenthic communities in the most thermally extreme coral reefs.

Instead, temperature-driven demands on an individual’s energetic budget and the inability of small-bodied fishes to meet these demands appears to mediate existence on these extreme reefs. Transgenerational acclimation or adaptation of fishes to increasing temperatures can come with substantial energetic costs38,46,68 that are reflected in reduced body condition69–71. These costs are evident in the lower mass per unit body length of Arabian Gulf populations in the three examined species (Fig. 5). Thus, although shifts in transgenerational temperature tolerance permits survival and adequate performance in controlled laboratory conditions38,46, shifts in tolerance may not be viable in a natural environment that imposes a range of energetic trade-offs and challenges69.

Reduced prey diversity and differing composition may further exacerbate the energetic dilemma of cryptobenthics that face increasing energy demands under elevated temperatures15,17. Gut content metabarcoding revealed a different and narrower range of both primary and secondary prey resources ingested by individuals from the Arabian Gulf, with more interspecific overlap in the Gulf of Oman than intraspecific overlap between locations. While we cannot definitively say whether the dietary differences shown here reflect differences in diet quality (i.e., prey with poor nutrient content), evidence from recent work shows that large reef fish species have unusual diets dominated by nutritiously poor benthic invertebrates in the Arabian Gulf72. Moreover, the single cryptobenthic species to show weakly distinct prey composition between locations and higher primary prey richness in the Arabian Gulf, *Coryogalops anomolus*, was also the only species that was more abundant and larger in the Arabian Gulf, with a weaker reduction in body condition compared to *E. pulcher* and *E. ventermaculus*. The genus *Coryogalops*, however, differs from most other genera that dominate cryptobenthic communities in both the Arabian Gulf and Gulf of Oman (e.g. *Ecsenius, Eviota,* *Enneapterygius*, etc.). *Coryogalops* belongs to a clade that contains many non-reef associated species from comparatively extreme habitats73,74, such as tidepools and other shallow environments exposed to fluctuating temperatures and salinity where they rely on a cryptic, sedentary lifestyle with low energetic costs75,76. Thus, the persistence of *C. anomolus* in the southeastern Arabian Gulf may reflect a preadaptation to extreme environments afforded by its history of belonging to a lineage of non-reef, extreme habitat specialists.

Persistence in thermally extreme environments has high energetic costs77, and elevated temperatures can increase the cost of growth and homeostasis in fishes18. Collectively, our evidence suggests that to exist in the Arabian Gulf, cryptobenthic fishes need to satisfy elevated metabolic demands and growth costs with a restricted suite of resources. For a group of vertebrates with already high energetic demands per gram of body mass and rapid growth49, this may represent an energetic double jeopardy since further decreases in body size (a universal physiological response to warmer temperatures18,70) are nearly impossible for many cryptobenthics. Species-specific capacities to cope with routine energetic costs of thermally-driven metabolic adjustments in the southeastern Arabian Gulf, rather than the direct effects of temperature *per se* or its effect on benthic community structure (cf.64), appear to underpin the reduced diversity and abundance of cryptobenthic fishes on these extreme reefs. Therefore, our findings provide evidence from highly-vulnerable, tropical ectotherms in a natural setting for the consequences of forecasted climate change effects on organismal performance78,79 and their ramifications for species persistence and community assembly80.

The energetic filtering effect of the Arabian Gulf provides a sobering perspective on coral reef ecosystem functioning in a warming ocean. Coral reefs are some of the most productive marine ecosystems81 that are sustained through a variety of energetic pathways82–85. Among these pathways, benthic productivity86 and its assimilation and transfer through cryptobenthic reef fishes represents an important bottom-up flux of energy and nutrients to higher trophic levels53. The dramatic differences in biomass production, transfer, and turnover between cryptobenthic fish communities in the Arabian Gulf and Gulf of Oman suggest that the role of cryptobenthics as vectors of energy and nutrients to larger consumers may be stymied in warming waters. In fact, yearly productivity estimates in the Arabian Gulf may be even lower than our model suggests due to the decreased individual-level production of biomass per unit body size and the influence of seasonality on biomass production. Furthermore, previous studies in the Arabian Gulf have shown variable abudances of large reef fishes across seasons, suggesting that these fishes seek more benign conditions during extreme conditions in the summer and winter87,88. For cryptobenthics, mediation via migration is improbable, so they either have to adapt to survive (e.g., decreased activity, somatic growth, or reproductive investment), or bridge seasonal adversity with generational turnover and ontogenetic differences in physiology or habitat occupation89. Either strategy is likely to further stunt yearly estimates of productivity, suggesting that differences in ecosystem functioning between the two regions may be more extreme than predicted by our model.

The reefs in the Gulf of Oman in this study may be particularly productive environments due to seasonal upwelling90, and indeed, our estimates of cryptobenthic productivity exceeded estimates for a degraded but species-rich reef on the Australian Great Barrier Reef (GBR) (2.31 vs. 0.64 g ha-1d-1)91. In contrast, even the optimistic estimate of 0.38 g ha-1d-1 for the Arabian Gulf poorly compared with the same GBR-reef. Notably, the study site on the GBR had undergone a sequence of severe disturbances91, which greatly reduced space availability and shelter for small-bodied fishes; yet, it retained a diverse assemblage of cryptobenthic fish species that were able to satisfy their energetic demands due to benign temperature profiles29. At the time of our survey, reefs in the Arabian Gulf, had also undergone extensive bleaching in previous years92–95, which may have negatively affected the diversity and abundance of cryptobenthic fishes compared to the less disturbed reefs in the Gulf of Oman27,96,97. However, lack of difference in benthic community structure between regions suggests that, beyond a few specialist cryptobenthic species92,98, the loss of live coral cover may not substantially alter small reef fish richness and abundance and overarching ecosystem productivity in the short-term30,32,92.

Our results showcase the imminent threats to cryptobenthic reef fishes and their critical role for coral reef functioning: similar to corals, which are highly susceptible to extreme temperatures26, many of the world’s smallest marine ectotherms may struggle to compensate for increasing growth costs as they attempt to adapt to changing temperatures. As a consequence, heterotrophic productivity, energy transfer, and replenishment of biomass at the bottom of the fish food chain may decrease severely under climate change18. Analogous to cryptobenthics, large reef fish communities are less diverse and abundant in the Arabian Gulf compared to nearby locations with more moderate temperatures99,100. It remains unresolved whether these patterns are driven by similar mechanisms as proposed herein (e.g., energetic filtering on large fish species) or relate to decreased productivity at lower trophic levels. Yet, in light of the hypothesized importance of small vertebrate consumers in global food webs101 and the unique ecological role of cryptobenthics in coral reef trophic dynamics53, the effects of elevated temperature on cryptobenthic fish assemblages may considerably hamper ecosystem functioning on future coral reefs.

**Methods:**

All field and laboratory work was performed under permit #XXX and ethics approval #XXX, granted by New York University Abu Dhabi (NYUAD). We studied cryptobenthic fish communities across six distinct coral reefs in two distinct locations that differ dramatically in yearly temperature fluctuations. Samples reefs in the Arabian Gulf (Dhabiya: 24.36383º, 54.10121º; Ras Ghanada: 24.84743º, 54.69235º; Saadiyat: 24.65771º, 54.48691º) are some of the most extreme reefs in the world in terms of the annual temperature gradient, with summer maximum temperatures reaching up to or above 36.0 ºC, while winter minimum temperatures fall to 16.0 ºC. In contrast, sampled reefs in the Gulf of Oman (Dibba Rock: ﻿25.55378º, 56.35694º; Sharm Rock: ﻿25.48229º, 56.36695º; Snoopy Rock: ﻿25.49210º, 56.36401º) lie within more typical coral reef temperature profiles throughout the year, ranging from 32.0 ºC to 22.0 ºC. All fieldwork was performed in April and May of 2018.

*Field sampling*

We sampled six distinct reefs (hereafter *site*)in the southeastern Arabian Gulf and northwestern Gulf of Oman (three sites per location). At each site, we sampled three distinct reef outcrops for cryptobenthic reef fishes using enclosed clove oil stations50,102, covering an average of 4.63 ± 0.38 and 4.73 ± 0.16 m2 in the Arabian Gulf and Gulf of Oman, respectively, for a total of 18 community samples. For each station, we covered a reef outcrop with a fine-mesh, bell-shaped net (2.74 m in diameter), weighted by a chain on the bottom. We then covered the same area with an impermeable bell-shaped tarpaulin, also weighted by a chain on the bottom. Then, three to four divers inoculated the area under the net with two liters of clove-oil:ethanol solution (1:5) using collapsible spray bottles (clove bud oil: Jedwards International, Inc., Braintree, MA, USA). Upon emptying the entire solution and a short wait period to allow the clove oil to disperse and take effect (approximately 2-3 mins), we removed the tarpaulin and gently peeled back the net while collecting all fishes found within the inoculated area with tweezers. We searched the entire area, including inside caves and crevices until five minutes passed without a single diver collecting any additional fish. We placed all fishes into Ziplock bags, brought them to the surface, euthanized them with a clove-oil overdose, and immediately placed them into an ice-water slurry until processing and preservation. At the end of each day, all specimens were brought to the laboratory at NYUAD or to room #211 at the Radisson Blu hotel in Fujairah. To quantify benthic community structure, we used a haphazardly placed a 20×20cm PVC-quadrat to frame and take five photographs of the benthos at each sampled clove-oil outcrop.

In addition to the quantitative samples obtained from the clove-oil stations, we collected individuals for thermal tolerance trials using roving diver collections. Specifically, two divers, each equipped with spray bottles of clove-oil:ethanol solution, a dipnet, and Ziplock bags, searched the reef cryptobenthic fishes across three species in the Arabian Gulf (*Coryogalops anomolus*, *Ecsenius pulcher*, and *Enneapterygius ventermaculus*) and six species in the Gulf of Oman (*C. anomolus*, *E. pulcher*, and *E. ventermaculus* plus *Eviota guttata*, *Helcogramma fuscopinna*, and *Hetereleotris vulgaris*). Upon locating an individual or identifying a suitable microhabitat in which a fish was suspected, the diver applied the clove-oil solution until the fish showed signs of anesthesia. At the earliest opportunity, we caught the fish with a dipnet and placed it into a ziplock bag. Upon completion of the dive, all fishes were placed in small holding tanks equipped with air stones and periodically replenished with fresh seawater. Upon completion of all collections, fishes were brought to the seawater laboratory facilities at NYUAD. All roving diver collections were performed at Dhabiya Reef (Arabian Gulf) and Snoopy Rock (Gulf of Oman).

*Laboratory processing*

For samples obtained from the enclosed clove-oil stations, we followed an established protocol that involved photographing, identifying, recording, measuring, weighing and preserving each specimen50. To photograph the fishes, we placed each individual in a small photo tank and used a Nikon D300 DSLR camera with an AF-S Micro Nikkor 60mm macro lens (f/2.8G ED; Nikon Inc., Melville, NY, USA) against a black or white background. We measured each individual to the nearest 0.1mm using digital calipers and weighed the individual (wet weight) to the nearest 0.001 grams on a precision jewelry scale. We preserved all individuals in 95% ethanol, either separately or in lots with conspecifics. A subset of the samples was then shipped to the University of Washington under export permit #XXX, where they were cataloged, while the rest were retained and archived at NYUAD.

*Benthic photo analysis*

For the benthic photographs, we created a grid with 16 equally spaced points which we superimposed on every photograph. We then categorized the benthos at each of the points into functional groups, including barnacles, bleached corals, crustose coralline algae, dead coral, hydroids, branching, encrusting, foliose, and massive live coral, mollusks, bare rock, soft sediment, sponges, algal turf, and sea urchins. Whenever no visual identification was possible (due to obstruction, shading, or blurriness), we categorized the point as “unidentifiable” (n = 69 out of 1,440).

*Critical thermal maximum and minimum trials*

We examined individual temperature tolerances by using critical thermal maximum (CTmax) and minimum (CTmin) trials103. We transported all fishes caught during roving diver collections to the wet laboratory facilities at NYUAD and housed them for at least 24 hours in large holding tanks. Trials took place from the 9th to 13th of Mayof 2018. For the trials, a haphazardly selected subset of individuals was moved from the holding tanks into separate chambers filled with seawater at ambient temperature and salinity. Then, after providing individuals with a 15-minute settlement period, we incrementally decreased (CTmin) or increased (CTmax) the water temperature within the chambers while keeping all other parameters constant. Specifically, we lowered or increased the temperature by 0.3ºC every minute103 while keeping all fishes under constant observation. Critical endpoints were classified as loss of equilibrium or uncontrolled swimming without a righting response for two seconds or more103. When individuals reached their critical endpoints, they were immediately removed, euthanized using a clove-oil overdose, measured, weighed, and photographed. In total, we processed 60 individuals across six species for CTmax trials, and 62 individuals across the same species for CTmin trials.

*Gut content DNA metabarcoding*

We processed a subset of individuals across six species (*A. adenensis*, *C. anomolus*, *E. pulcher*, *E. guttata*, *E. ventermaculus*, and *H. vulgaris*) for gut content DNA metabarcoding at the University of Washington. We haphazardly selected ten, ten, and seven (due to limited sample availability) individuals of *C. anomolus*, *E. ventermaculus*, and *E. pulcher*, respectively, from the Arabian Gulf, and ten individuals each (with the exception of *E. pulcher*, for which we selected eleven individuals) of *C. anomolus*, *E. ventermaculus, A. adenensis*, *E. guttata,* and *H. vulgaris* from the Gulf of Oman. Then, under sterile conditions, we dissected out the entire alimentary tract and removed all other organs (e.g. liver, gonads) under a Zeiss V20 SteREO dissecting microscope using micro-surgery tools. We placed the entire gut into an extraction tube and performed DNA extractions with a DNeasy PowerSoil Pro DNA Isolation Kit (Qiagen, Hilden, Germany). We stored all DNA extracts at 4ºC until further processing.

All DNA samples were sent to Jonah Ventures (Boulder, Colorado, USA) for two-step PCRs, library preparation, and sequencing. We targeted two universal gene regions: the mitochondrial cytochrome c oxidase subunit I (COI) for metabarcoding metazoan biodiversity and the chloroplast 23S rRNA for metabarcoding algae. For the COI gene, we selected the m1COIintF forward primer104 and jgHCO2198 reverse primer105. For the 23S gene, we selected the p23SrV\_f1 and Diam23Sr1 23S primers106–108. All COI and 23S primers contained a 5’ adaptor sequence to facilitate indexing and sequencing. The PCR reactions for both COI and 23S genes were run at a volume of 25 μl according to the Promega PCR Master Mix guidelines (Promega catalog #M5133, Madison, Wisconsin, USA): 12.5 μl Master Mix, 0.5 μM of each primer, 1 μl gDNA, and 10.5 μl DNase/Rnase-free water. For COI, PCR amplification was run with the following conditions: initial denaturation at 94 °C for 2 minutes, followed by 45 cycles of 15 seconds at 94 °C, 30 seconds at 50 °C, 1 minute at 72 °C, and a final elongation at 72 °C for 10 minutes. For 23S, DNA was PCR-amplified under the following conditions: initial denaturation at 94 °C for 3 minutes, followed by 40 cycles of 30 seconds at 94 °C, 45 seconds at 55 °C, 1 minute at 72 °C, and a final elongation at 72 °C for 10 minutes. After PCR amplification, each reaction was visually inspected with a 2% agarose gel to determine amplicon size and PCR efficiency.

All remaining library preparation and sequencing protocols apply to both the COI and 23S genes. Clean-ups were performed by incubating amplicons with Exo1/SAP for 30 minutes at 37 °C, followed by inactivation at 95 °C for 5 minutes, then the products were stored at -20 °C. Next, a second indexing PCR was performed to bind a unique 12-nucleotide index sequence. The PCR reaction included Promega Master mix, 0.5 μM of each primer, and 2 μl of template DNA. The PCR was performed with the following conditions: initial denaturation at 95 °C for 3 minutes, followed by 8 cycles of 95 °C for 30 seconds, 55 °C for 30 seconds, and 72 °C for 30 seconds. Each reaction was visually inspected with a 2% agarose gel to ensure successful amplification.

25 μl of each indexed amplicon was cleaned and normalized with the SequalPrep Normalization Kit (Life Technologies, Carlsbad, California, USA) according to the manufacturer’s protocol. For sample pooling, 5 μl of each sample was added together. Finally, library pools were sent to the Genohub service provider (Austin, Texas, USA). Prior to sequencing, quality control measures were performed, including bead cleaning with Agencourt AMPure XP beads (Beckman Coulter, Brea, California, USA) to remove <200 bp amplicons, sample quantification with a Qubit Fluorometer (Invitrogen, Carlsbad, California, USA), and amplicon average size analysis with an Agilent TapeStation 4200 (Agilent, Santa Clara, California, USA). Finally, sequencing was performed on an Illumina HiSeq using the HiSeq Rapid SBS Kit v2, 500-cycles (Illumina, San Diego, California, USA).

*Sequence bioinformatics*

For the COI sequences, a joint QIIME109 and UPARSE110 pipeline was employed for bioinformatic processing. Sequences were demultiplexed and initial quality filtering was performed with QIIME v1.9.1. Primer sequences were trimmed with Cutadapt v1.18111, then forward and reverse reads were pair-end merged with USEARCH v11.0.667112. Quality filtering was then performed in accordance with the UPARSE pipeline. Sequences were clustered into operational taxonomic units (OTUs) at 99% similarity, and the OTU table was generated by mapping quality-filtered reads back to the OTU seeds. Taxonomy was assigned by recording the top basic local alignment search tool (BLASTn113) hit when query coverage and percent identity exceeded 95% and 80%, respectively. GenBank was used as the reference database. When OTU taxonomic assignments did not meet these criteria, taxonomy was removed and recorded as “NA.” Finally, we removed all self-hits from the OUT-dataset, which we identified by matching the highest sequence reads of each species to its individuals, as well as unambiguous (>97% identity match) assignments to species not found in the area (specifically *Oncorhynchus nerka*).

For the 23S sequences, raw sequences were processed with the JAMP pipeline (<https://github.com/VascoElbrecht/JAMP>). After demultiplexing, forward and reverse reads were pair-end merged with USEARCH v11.0.667112. Primers were trimmed from both ends using Cutadapt v1.18111 and quality filtering was conducted with expected error filtering, as implemented through USEARCH114. Reads affected by sequencing and PCR error were removed using the UNOISE algorithm115. Exact sequence variants (ESV) were then compiled into an ESV table, which included read counts for each sample. Taxonomy was assigned to each ESV by mapping them against a 23S database from Silva116, specifying zero deviations to ensure mapping accuracy. Consensus taxonomy was generated from the hit tables, first considering 100% matches, then decreasing by 1% until hits were available for each ESV. Taxonomy that was present in at least 90% of the hits was reported; otherwise, an “NA” was assigned when several different taxa matched the ESV. For error reduction due to misidentified taxa, the bracket was increased to 2% when matches of 97% and higher were present, but no family-level or lower taxonomy was assigned.

*Data analyses and modeling*

To analyze the community variables, we first calculated the surface area (*SA*) for each sampled outcropfrom the curved surface length (*CSL*) by deriving the sampled outcrop’s radius *r* (*r* = 2\*CSL/2π), then computing available surface area under the assumption that outcrops represent hemispherical constructs (*SA* = 4*πr*2/2). We calculated the sum of individuals, species, and their respective body weight for each station to obtain abundance, diversity, and biomass estimates, which we converted to density estimates by dividing them by the sampled surface area. Using these estimates, we performed three Bayesian hierarchical models, each on the natural logarithm of the response variables (density, species density, and biomass per m2). Models were specified to include the fixed effect of *Location* (*Arabian Gulf vs. Gulf of Oman*) and the random effect of *Site* (*Dhabiya*, *Ras Ghanada*, *Saadiyat*, *Dibba Rock*, *Sharm Rock*, *Snoopy Rock*) and were run with a Gaussian error distribution. For each model, we ran four chains with 4,000 post burn-in samples, and we validated chain convergence visually. We used the default, non-informative priors set by the *brm* function in the *brms* package117. Then, we used the model parameters to predict distributions based on 1,000 draws from the posterior and plotted the distributions, their mean and confidence bands, and the raw data for each site to evaluate model fit.

To examine cryptobenthic fish community composition across the two locations, we created a species-by-sample matrix indicating the abundance of each species in a given sample. We then performed a non-metric multidimensional scaling (nMDS) ordination with the Bray-Curtis dissimilarity matrix of the data in two dimensions (stress = 0.101). We performed a permutational analysis of variance (PERMANOVA) on the same distance matrix (using 999 permutations) and extracted the most influential species using the similarity of percentages (SIMPER) routine. We constructed convex hull polygons for the two locations (as determined by the location of each sample) and plotted them in a biplot with the seven most influential species (average contribution > 0.025) superimposed. For benthic community composition, we followed a similar process. After our initial categorization, we first combined live coral categories into “branching” and “other” and omitted all categories with fewer than three records (bleached coral and hydroids) from the data. We also excluded the “unidentifiable” category (<5% of points). We then calculated the proportional contribution of each category to the benthos in a given sampled outcrop and arranged the data into a sample-by-category matrix and performed another nMDS analysis as per above. We also performed a PERMANOVA and visualized the data in the same way as described above, but we did not perform the SIMPER routine due to the lower number of categories. Further, we scaled the size of the symbols to represent the percent of live coral cover. Finally, we statistically compared live coral cover among the two locations using a Bayesian hierarchical model. We logit-transformed proportional *LiveCoralCover* and specified *Location* as a fixed effect, with *Site* specified as a random effect. Model and chain specifications were programmed as described above.

To compare intrinsic temperature tolerances, as derived from CTmin and CTmax trials, we ran two separate Bayesian linear models. For both models, we specified an effect of *Population* (i.e., separate levels for each species and their respective Arabian Gulf and Gulf of Oman populations) on the critical thermal limit of individuals and examined differences between pairwise levels using post-hoc contrasts (Tables S2 and S3). Models were run with a Gaussian error distribution and the same specifications as the previous models (e.g., burnin, iterations, priors, etc.). We took 1,000 draws from the posterior parameters to draw fitted posterior distributions as well as their mean and confidence bands and plotted them alongside the raw data. Furthermore, to examine location-specific differences in length-weight relationships and species-specific abundances, we isolated individuals from three species (*C. anomolus*, *E. pulcher*, and *E. ventermaculus*) and ran separate models for each species to test the effects of total length (*TL*) and *Location* on *Weight*, with both *Weight* and *TL* being log-transformed and the effect of location (with a random effect of *Site*) on abundance. We used a Gaussian error distribution for the first set of models since the data were continuous and approximately normally distributed. We used a negative binomial error distribution for the second set of models since data were non-negative integers and over-dispersed when run under a Poisson distribution. To validate the model performance, we used the posterior parameters to predict values across a sequence of 100 evenly spaced values within the sampled size range of the two populations. We performed this 500 times and plotted each predicted model fit alongside the raw data. Models were run with the same prior and chain specifications as above.

We examined prey item ingestion of the examined fishes using a network theory approach for both the COI and 23S markers118. We first created a presence-absence matrix of OTUs/ESVs across fish individuals in all species and their populations, creating a bipartite dietary network based on prey presence or absence. We used this matrix for two reasons. First, to create a dietary network tree, we transformed this matrix into a data frame that contained each OTU/ESV and its linkage to the fish individual in two columns, which we then summarized by each species and population. This created a list of symbolic edges in the network across the two columns, linking each prey item to a species/population, which we plotted using the Fruchterman-Reingold algorithm. Second, to examine the community structure within the network, we omitted all prey items with only a single occurrence across the dataset since the full dataset identified the majority of individuals as unique modules. This step reduced the COI dataset from 1,357 to 1,046 unique predator-prey interactions and the 23S dataset from 7,872 to 5,698 predator-prey interactions. We then sought to identify modules within the network using Newman’s modularity measure119. We used Beckett’s community detection algorithm120, which we re-iterated 20 times for each dataset. We then used the convergent output from the 20 iterations to determine the module membership of each individual in our network, and we plotted module membership in a mosaic plot.

Furthermore, for the COI and 23S markers, we investigated the diversity of prey items ingested by each species’ population by producing interpolated and extrapolated rarefaction curves, which showcase sequencing depth by plotting prey item species richness by the total number of sequences detected for each species. We ran rarefaction analyses by rarefying species richness estimates for each species or population to an endpoint defined by the maximum sequences in any population using 100 bootstraps and 50 knots along the x-axis121.

Finally, modelled growth and mortality dynamics in cryptobenthic fish assemblages from the two locations, ultimately yielding a standing biomass estimate and three rate-based metrics that serve as indicators of energy and nutrient fluxes, and thus, ecosystem functioning24: produced biomass (in g d-1m-2), consumed biomass (in g d-1m-2), and total turnover (percent d-1)91,122,123. Produced biomass represents the amount of fish tissue accumulated by an assemblage (in this case, a cryptobenthic fish assemblage collected in a given sample), thus considering only the growth that will occur on any given day (based on yearly averages). Consumed biomass, in turn, represents the amount of fish tissue that perished based on our estimates of fish mortality. In this pathway, the energy and nutrients produced by fishes are provided to other consumers or decomposers via predation or detritivory. Finally, total turnover expands on the classic estimate of turnover (the production/standing biomass [P/B] ratio124) by also including consumed biomass (consumed biomass/standing biomass)122. As such, the turnover metric approximates the rate at which particles flow through the system, either via incorporation into fish biomass or release to other consumers through mortality.

For the modeling, we first accrued species-specific information on maximum lengths and a range of coarse ecological traits (pertaining to diet, sociality, habitat association, and prevailing mean sea surface temperatures [SST]) from the literature for each species present in our samples. We also extracted length-weight relationships at the family-level, since not all species in our samples were common enough to construct robust length-weight relationships. We then used these data to calculate species-specific growth coefficients (Kmax) to the specified maximum size and modeled individual weight gain based on changes in fish size per day under a Von Bertalanffy Growth Model (VBGM)123. By subtracting the observed fish size (as obtained from our samples) from the weight obtained by the same fish after one day (from the model), we calculated the expected biomass production by that individual. We estimated daily mortality rates by calculating species-level mortality risk coefficients via VBGM parameters and SST122,125, and then we adjusted the risk based on relationships between mortality and body size126. Using these coefficients, we obtained a daily survival probability for a given individual in the dataset. By combining this probability with weight gains as obtained from the previous step, we were able to generate the expected loss of biomass due to natural mortality at the individual level. Finally, we summed the individual-level estimates of weight, growth, and mortality for each sample to obtain community-level values of standing biomass, produced biomass, and consumed biomass, which we used to calculate total turnover as the combined quotients of produced and consumed biomass and standing biomass.

All data preparation, analyses, and visualizations were performed in *R* (version 3.6.1) using *tidyverse*, *vegan*, *brms*, *iNEXT*, *igraph*, *tidybayes*, *modelr*, *ggpubr*, *ggrepel*, *scales*, *geomnet*, *xgboost*, and *GGally*. All graphs were made using the *Trimma lantana* color palette in the package *fishualize*. Growth modeling was performed using a beta version of the package *rfishprod*. All data and code are provided in the supplemental material of the paper and will be made publicly accessible with publication of the article.  
  
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Supplemental Material:

**Table S1: Presence, abundance, and previous records of species sampled in the present study.** Each row represents a species, with columns *AG* (Arabian Gulf) and *GO* (Gulf of Oman) indicating the abundance of the species in our samples. Column *R* indicates whether the species has been previously recorded in other parts of the Arabian Gulf (\* = yes, – = no). References for previous records are provided.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| ***Family*** | ***Species*** | ***AG*** | ***GO*** | ***R*** | ***Reference*** |
| Apogonidae | *Apogon coccineus* | 6 | 10 | \* | present |
| Apogonidae | *Apogonichthyoides taeniatus* | 2 | 0 | \* | present |
| Apogonidae | *Cheilodipterus novemstriatus* | 2 | 9 | \* | present |
| Apogonidae | *Cheilodipterus persicus* | 0 | 1 | \* | Krupp & Müller 1994 |
| Apogonidae | *Fowleria variegata* | 5 | 1 | \* | present |
| Apogonidae | *Ostorhinchus cyanosoma* | 0 | 15 | \* | Krupp & Müller 1994 |
| Apogonidae | *Ostorhinchus fleurieu* | 0 | 30 | \* | Eagderi et al. 2019 |
| Batrachoididae | *Colletteichthys occidentalis* | 6 | 0 | \* | present |
| Blenniidae | *Antennablennius adenensis* | 0 | 54 | \* | Bishop 2003 |
| Blenniidae | *Ecsenius pulcher* | 8 | 97 | \* | present |
| Blenniidae | *Laiphognathus multimaculatus* | 1 | 0 | \* | present |
| Bythitidae | *Dinematichthys iluocoeteoides* | 5 | 0 | \* | present |
| Gobiidae | *Asterropteryx semipunctata* | 0 | 2 | \* | Krupp & Müller 1994 |
| Gobiidae | *Callogobius bifasciatus* | 2 | 0 | \* | present |
| Gobiidae | *Callogobius speA* | 0 | 3 | \* | Eagderi et al. 2019 |
| Gobiidae | *Coryogalops anomalus* | 65 | 33 | \* | present |
| Gobiidae | *Eviota guttata* | 0 | 69 | \* | Krupp & Müller 1994 |
| Gobiidae | *Eviota punyit* | 0 | 12 | \* | Krupp & Müller 19941 |
| Gobiidae | *Favonigobius melanobranchus* | 1 | 0 | \* | present |
| Gobiidae | *Fusigobius inframaculatus* | 0 | 3 | \* | Eagderi et al. 2019 |
| Gobiidae | *Gnatholepis caudimaculata* | 0 | 14 | \* | Eagderi et al. 2019 |
| Gobiidae | *Gobiodon reticulatus* | 0 | 2 | \* | Bishop 2003 |
| Gobiidae | *Hetereleotris vulgaris* | 0 | 405 | \* | Eagderi et al. 2019 |
| Gobiidae | *Istigobius decoratus* | 0 | 15 | \* | Eagderi et al. 2019 |
| Gobiidae | *Priolepis cincta* | 0 | 4 | \* | Winterbottom & Burridge 1992 |
| Gobiidae | *Priolepis randalli* | 0 | 2 | \* | Winterbottom & Burridge 1993 |
| Gobiidae | *Priolepis semidoliata* | 0 | 10 | – | NA |
| Gobiidae | *Trimma corallinum* | 0 | 11 | \* | Eagderi et al. 20192 |
| Muraenidae | *Gymnothorax speA* | 0 | 12 | \* | Eagderi et al. 20193 |
| Ostraciidae | *Ostracion cubicus* | 0 | 3 | \* | Eagderi et al. 2019 |
| Pomacanthidae | *Pomacanthus maculosus* | 7 | 0 | \* | present |
| Pomacentridae | *Chromis flavaxilla* | 0 | 19 | \* | Bishop 2003 |
| Pomacentridae | *Chromis xanthopterygius* | 0 | 3 | \* | Bishop 2003 |
| Pomacentridae | *Neopomacentrus cyanomos* | 0 | 38 | \* | Bishop 2003 |
| Pomacentridae | *Neopomacentrus miryae* | 0 | 38 | – | NA |
| Pomacentridae | *Neopomacentrus sindensis* | 0 | 6 | \* | Bishop 2003 |
| Pomacentridae | *Pomacentrus aquilus* | 3 | 0 | \* | present |
| Pomacentridae | *Pomacentrus leptus* | 0 | 5 | \* | Bishop 2003 |
| Pomacentridae | *Pomacentrus trichrourus* | 5 | 0 | \* | present |
| Pseudochromidae | *Pseudochromis aldabraensis* | 0 | 4 | \* | Bishop 2003 |
| Pseudochromidae | *Pseudochromis linda* | 1 | 0 | \* | present |
| Pseudochromidae | *Pseudochromis nigrovittatus* | 2 | 1 | \* | present |
| Pseudochromidae | *Pseudochromis persicus* | 1 | 0 | \* | present |
| Serranidae | *Cephalopholis hemistiktos* | 2 | 2 | \* | present |
| Syngnathidae | *Corythoichthys flavofasciata* | 0 | 5 | \* | Froese & Pauly 2019 |
| Syngnathidae | *Doryrhamphus excisus* | 0 | 3 | \* | Bishop 2003 |
| Tripterygiidae | *Enneapterygius ventermaculus* | 131 | 262 | \* | present |
| Tripterygiidae | *Helcogramma fuscopinna* | 0 | 134 | – | NA |

1identified as *E. sebreei*

2synonymous with *T. winterbottomi*

3genus level

**Table S2 | Contrasts between levels of the explanatory variable for the model testing CTmin differences in cryptobenthic reef fishes.** Population columns highlight the contrast estimated in the model, whereas the estimate and its confidence intervals indicate estimated differences.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Population I** | **Population II** | **Estimate** | **LCI** | **UCI** |
| *C. anomolus.AG* | *E. pulcher.AG* | *0.613* | *0.173* | *1.069* |
| *C. anomolus.AG* | *E. ventermaculus.AG* | *-0.400* | *-0.851* | *0.054* |
| *C. anomolus.AG* | *E. pulcher.GoO* | *0.747* | *0.316* | *1.211* |
| *C. anomolus.AG* | *E. ventermaculus.GoO* | *-1.391* | *-1.887* | *-0.888* |
| *C. anomolus.AG* | *E. guttata.GoO* | *-0.784* | *-1.241* | *-0.317* |
| *C. anomolus.AG* | *H. fuscopinna.GoO* | *-1.235* | *-1.736* | *-0.754* |
| *C. anomolus.AG* | *H. vulgaris.GoO* | *-0.080* | *-0.549* | *0.384* |
| *E. pulcher.AG* | *E. ventermaculus.AG* | *-1.011* | *-1.313* | *-0.709* |
| *E. pulcher.AG* | *E. pulcher.GoO* | *0.137* | *-0.165* | *0.446* |
| *E. pulcher.AG* | *E. ventermaculus.GoO* | *-2.003* | *-2.402* | *-1.641* |
| *E. pulcher.AG* | *E. guttata.GoO* | *-1.394* | *-1.704* | *-1.076* |
| *E. pulcher.AG* | *H. fuscopinna.GoO* | *-1.847* | *-2.206* | *-1.489* |
| *E. pulcher.AG* | *H. vulgaris.GoO* | *-0.694* | *-1.010* | *-0.358* |
| *E. ventermaculus.AG* | *E. pulcher.GoO* | *1.149* | *0.847* | *1.459* |
| *E. ventermaculus.AG* | *E. ventermaculus.GoO* | *-0.990* | *-1.382* | *-0.610* |
| *E. ventermaculus.AG* | *E. guttata.GoO* | *-0.381* | *-0.706* | *-0.065* |
| *E. ventermaculus.AG* | *H. fuscopinna.GoO* | *-0.836* | *-1.201* | *-0.475* |
| *E. ventermaculus.AG* | *H. vulgaris.GoO* | *0.318* | *-0.016* | *0.648* |
| *E. pulcher.GoO* | *E. ventermaculus.GoO* | *-2.138* | *-2.526* | *-1.766* |
| *E. pulcher.GoO* | *E. guttata.GoO* | *-1.530* | *-1.843* | *-1.213* |
| *E. pulcher.GoO* | *H. fuscopinna.GoO* | *-1.985* | *-2.341* | *-1.615* |
| *E. pulcher.GoO* | *H. vulgaris.GoO* | *-0.832* | *-1.174* | *-0.519* |
| *E. ventermaculus.GoO* | *E. guttata.GoO* | *0.607* | *0.231* | *1.018* |
| *E. ventermaculus.GoO* | *H. fuscopinna.GoO* | *0.152* | *-0.260* | *0.582* |
| *E. ventermaculus.GoO* | *H. vulgaris.GoO* | *1.307* | *0.895* | *1.691* |
| *E. guttata.GoO* | *H. fuscopinna.GoO* | *-0.453* | *-0.822* | *-0.088* |
| *E. guttata.GoO* | *H. vulgaris.GoO* | *0.700* | *0.360* | *1.041* |
| *H. fuscopinna.GoO* | *H. vulgaris.GoO* | *1.153* | *0.799* | *1.543* |

**Table S3 | Contrasts between levels of the explanatory variable for the model testing CTmax differences in cryptobenthic reef fishes.** Population columns highlight the contrast estimated in the model, whereas the estimate and its confidence intervals indicate estimated differences.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Population I** | **Population II** | **Estimate** | **LCI** | **UCI** |
| *C. anomolus.AG* | *E. pulcher.AG* | *0.486* | *-0.079* | *1.054* |
| *C. anomolus.AG* | *E. ventermaculus.AG* | *1.360* | *0.808* | *1.949* |
| *C. anomolus.AG* | *E. pulcher.GoO* | *1.114* | *0.581* | *1.726* |
| *C. anomolus.AG* | *E. ventermaculus.GoO* | *1.633* | *0.939* | *2.342* |
| *C. anomolus.AG* | *E. guttata.GoO* | *1.143* | *0.534* | *1.759* |
| *C. anomolus.AG* | *H. fuscopinna.GoO* | *2.392* | *1.758* | *2.992* |
| *C. anomolus.AG* | *H. vulgaris.GoO* | *0.492* | *-0.061* | *1.078* |
| *E. pulcher.AG* | *E. ventermaculus.AG* | *0.879* | *0.509* | *1.252* |
| *E. pulcher.AG* | *E. pulcher.GoO* | *0.636* | *0.244* | *1.016* |
| *E. pulcher.AG* | *E. ventermaculus.GoO* | *1.159* | *0.624* | *1.737* |
| *E. pulcher.AG* | *E. guttata.GoO* | *0.656* | *0.227* | *1.134* |
| *E. pulcher.AG* | *H. fuscoguttata.GoO* | *1.905* | *1.463* | *2.341* |
| *E. pulcher.AG* | *H. vulgaris.GoO* | *0.011* | *-0.368* | *0.417* |
| *E. ventermaculus.AG* | *E. pulcher.GoO* | *-0.245* | *-0.640* | *0.118* |
| *E. ventermaculus.AG* | *E. ventermaculus.GoO* | *0.277* | *-0.260* | *0.815* |
| *E. ventermaculus.AG* | *E. guttata.GoO* | *-0.225* | *-0.680* | *0.212* |
| *E. ventermaculus.AG* | *H. fuscopinna.GoO* | *1.024* | *0.578* | *1.449* |
| *E. ventermaculus.AG* | *H. vulgaris.GoO* | *-0.878* | *-1.265* | *-0.508* |
| *E. pulcher.GoO* | *E. ventermaculus.GoO* | *0.519* | *-0.0290* | *1.073* |
| *E. pulcher.GoO* | *E. guttata.GoO* | *0.020* | *-0.426* | *0.494* |
| *E. pulcher.GoO* | *H. fuscopinna.GoO* | *1.274* | *0.839* | *1.726* |
| *E. pulcher.GoO* | *H. vulgaris.GoO* | *-0.628* | *-1.037* | *-0.253* |
| *E. ventermaculus.GoO* | *E. guttata.GoO* | *-0.502* | *-1.125* | *0.106* |
| *E. ventermaculus.GoO* | *H. fuscopinna.GoO* | *0.750* | *0.130* | *1.344* |
| *E. ventermaculus.GoO* | *H. vulgaris.GoO* | *-1.148* | *-1.710* | *-0.584* |
| *E. guttata.GoO* | *H. fuscopinna.GoO* | *1.252* | *0.735* | *1.778* |
| *E. guttata.GoO* | *H. vulgaris.GoO* | *-0.647* | *-1.094* | *-0.148* |
| *H. fuscopinna.GoO* | *H. vulgaris.GoO* | *-1.906* | *-2.363* | *-1.449* |

**A close up of a map

Description automatically generated**

**Figure S1 | Rarefaction curves of OTU and ESV richness across total sequences for six species in the Arabian Gulf (blue) and Gulf of Oman (gold).** OTU curves (a) indicate the diversity of prey items for each species and population as obtained from gut content DNA metabarcoding with the COI marker, while ESV curves (b) show the diversity of prey items obtained with the 23S marker. Solid lines indicate interpolated richness, while dashed lines indicate extrapolated richness (to the maximum number of sequences across species). Shaded ribbons indicate 95% confidence intervals of extrapolations.