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

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**Abstract:**

Environmentally mediated transformations of ecological communities can severely affect ecosystem functioning. Coral reef fishes are hypothesized to be particularly 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 (≥ 36ºC maximum water temperature) comprise half as many species and less than a quarter of individuals present in the thermally benign Gulf of Oman, despite equal availability of live coral substrate. This pattern is not primarily driven by intrinsic organismal temperature tolerances. Instead, 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. This, in turn, results in reduced production, transfer, and replenishment of biomass through cryptobenthic fish assemblages. Overall, our results suggest that most cryptobenthic fishes cannot cope with the increasing costs of growth and homeostasis that come with adaptation to rising temperatures. Future reefs may, therefore, lose a critical building block of their characteristic 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 assemblages of species affect rates of critical ecological processes? As escalating human influence on the biosphere depletes and re-shuffles biological communities across ecosystems1,2, answers to these questions are key to our quest to preserve biodiversity and ecosystem services to humanity3,4. There is now consensus that a species’ presence at a given location is mediated by a hierarchical interplay between organismal traits (e.g., temperature tolerance, trophic niches), environmental conditions (e.g., temperature, salinity), and stochastic events (e.g., random walks to extinction, lottery dynamics)5–8. Furthermore, the past three decades have seen growing evidence that both 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 will affect internal physiological processes15, which, if not lethal, will alter organismal energy expenditure16–18. Changes in organismal energy budgets determine the demands on resource acquisition (e.g. feeding rates, prey species) and how resulting energy can be allocated to life-supporting processes (homeostasis), growth, and reproduction19–21. The interaction between these dynamics, which are often investigated through the lens of ecological niches and fitness, are the basis of modern coexistence theory. They are thus critical for our understanding of community assembly dynamics22 and the rate of ecological processes that underpin fluxes of energy and nutrients through ecosystems23. Therefore, integration across levels of biological organization is key if we are to understand the effects global environmental change on our planet’s ecosystems24.

Coral reefs are the most diverse marine ecosystem and their exceptional productivity provides critical services for more than 500 million people worldwide25. Scleractinian corals, the foundations species of tropical reefs, show high thermal sensitivity that, in concert with other stressors, has led to the rapid global decline of coral reef ecosystems26. In the wake of losing coral habitat, communities of the most prominent reef consumers, teleost fishes, are widely reported to decline or shift in composition27–30, which can affect the provision of vital resources to people dependent on reef fisheries31. Nevertheless, recent evidence suggests that many species of fish will be able to cope with or even benefit from the temporary loss live coral habitat31–33. However, as tropical marine ectotherms that are adapted to a relatively narrow thermal environment, reef fishes are also hypothesized to be vulnerable to direct effects of changing water temperatures16,34,35. Consequently, the responses of reef fishes to climate change and their potential to acclimate or adapt to different thermal regimes are studied intensively36–38.

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 if 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 communities to date45. The key to this may lie transgenerational acclimation and adaptation, which can enhance the performance of offspring in higher temperatures through developmental, genetic, or epigenetic pathways38,46. Nevertheless, transgenerational adaptation has only been shown in few selected model species38,46,47 and carries a range of energetic costs that species need to mitigate46,48. Thus, whether this process can truly enhance survival of reef fishes in a competitive, uncontrolled environment, and how species-specific differences in temperature tolerance and adaptational capacity may mediate coexistence in ecological communities remains unresolved.

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 metabolisms, and other physiological challenges resulting from their minute size suggest that cryptobenthics are particularly susceptibility to strong temperature fluctuations41,49,54. Furthermore, due to their limited mobility and close association with the benthos55, behavioral mitigation of temperature extremes through migration is not viable and previous research has shown marked shifts in their community composition following changes in the benthic community30,56. In turn, however, their extremely high generational turnover (up to eight generations per year53,57), along with the prevalence of benthic clutch spawning and parental care in cryptobenthics49, 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 offer uniquely powerful means to detect effects of environmental change on organisms and populations, while promising insights into whether transgenerational plasticity or adaptation offer viable pathways to the persistence of coral reef fishes in warming oceans.

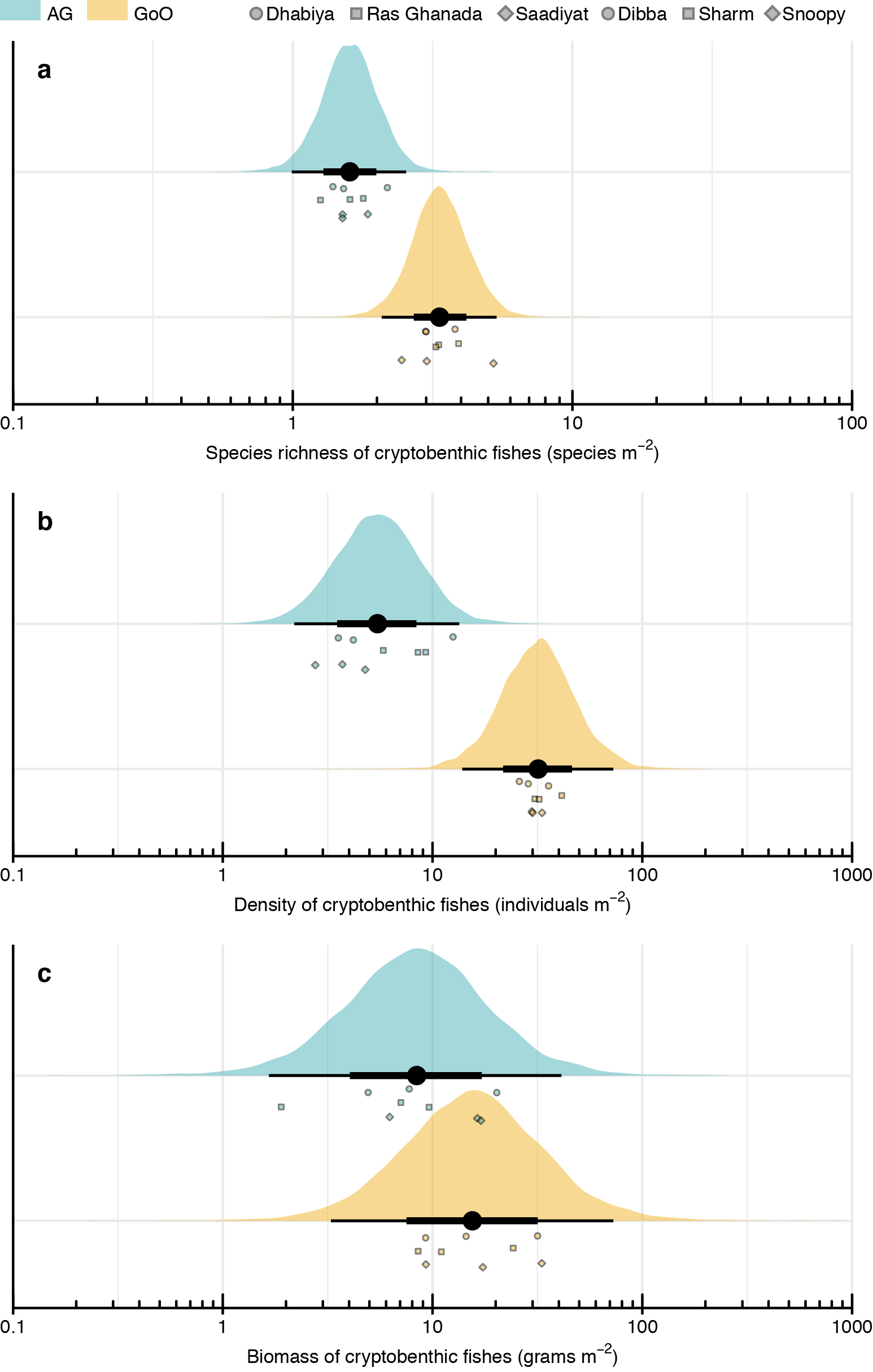
Here, we quantify organismal traits, community assembly, and contributions to ecosystem functioning by cryptobenthic fishes in the world’s hottest coral reef environment, the southeastern Arabian Gulf, and compare the resulting patterns with a spatially proximate, but much more environmentally benign location (the 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 between 16.0º C in the winter months to 36.0º C in the summer59. As such, maximum temperature conditions for reefs along the Arabian Gulf coast of the United Arab Emirates mirror those that are forecast for most tropical coral reefs towards the end of the century60. Nevertheless, despite the 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 differed fundamentally between reefs in the Arabian Gulf and the Gulf of Oman. Reefs in the Gulf of Oman harbored a markedly higher diversity (Bayesian hierarchical model estimate: *GoO β* = 0.73 [0.44, 1.01; lower and upper 95% credible interval]) and density (*GoO* *β* = 1.77 [1.03, 2.58])of cryptobenthic fishes (Fig. 1a,b), but standing biomass estimates were comparable (*GoO* *β* = 0.63 [-0.54, 1.71]; Fig. 1c). Similarly, the composition of cryptobenthic communities varied greatly among the two locations (Fig. 2a), with no overlap among convex hull polygons in the 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: *GoO 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 differ strongly 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 differ substantially between the two locations. Density curves represent predicted values based on 1,000 draws from Bayesian hierarchical linear models testing for differences among 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.

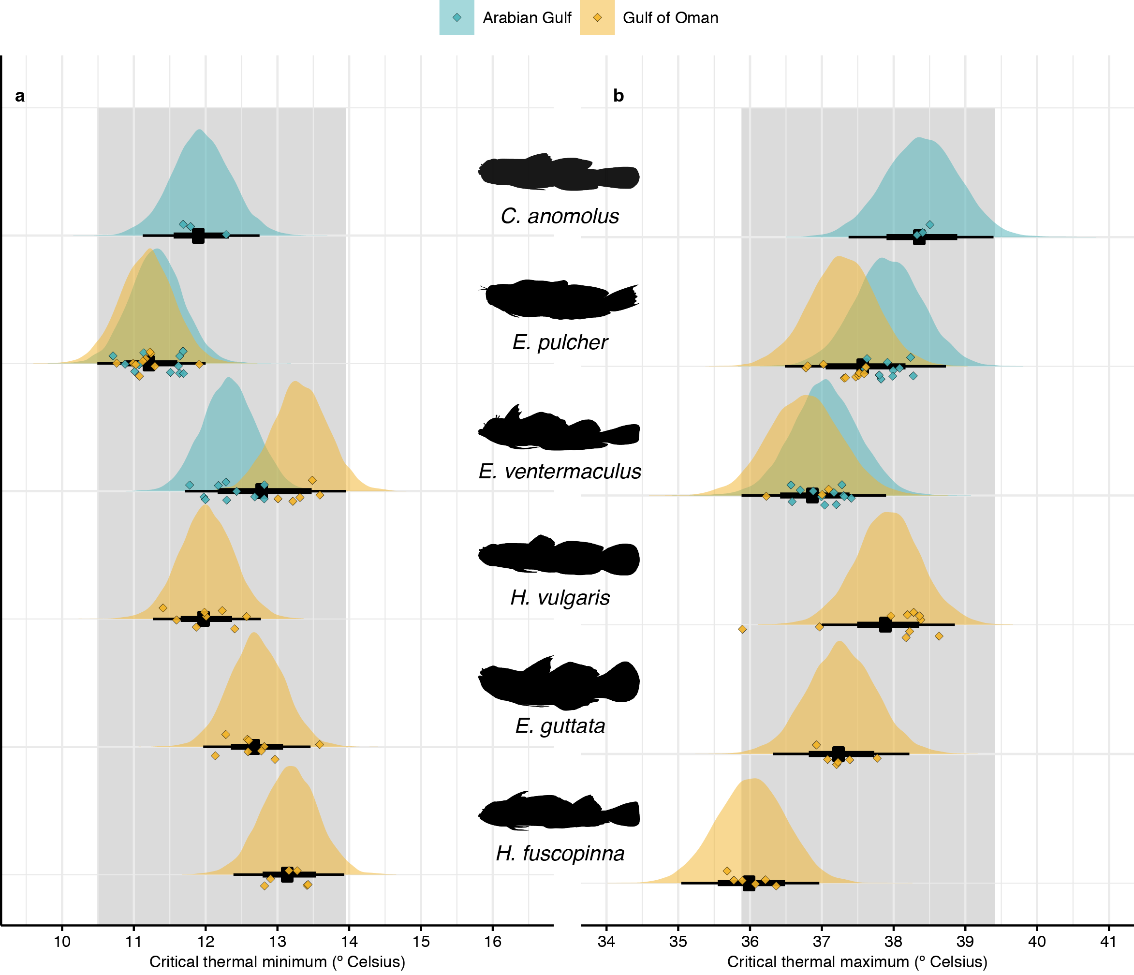
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**Fig. 2 | Community structure of cryptobenthic reef fishes and benthic functional groups in the Arabian Gulf (AG) and Gulf of Oman (GoO).** (**a**)Biplot of a non-metric multidimensional scaling ordination (nMDS) on cryptobenthic fish communities,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

We then tested whether organismal temperature tolerances can explain the absence of species from the Arabian Gulf (albeit being recorded in the northern Arabian Gulf where conditions are more benign61; see Table S1). Despite distinct thermal regimes at the two locations and the drastic differences in cryptobenthic fish assemblages, species-specific critical thermal tolerance limits had poor explanatory power regarding 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 AG 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 (13.3 ± 0.1 ºC). In contrast, the cold-tolerance of *E. ventermaculus* from the Arabian Gulf substantially exceeded that of all three Gulf of Oman populations examined (Table S2), providing evidence for enhanced thermal tolerance *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 AG (Fig. 3a).

Similar to 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 GoO-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 explanation power of thermal tolerance alone.

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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 and 13.3 ºC, but were well below the minimum recorded winter temperature for the southern Arabian Gulf (16.0 ºC). (**b**) Critical thermal maxima ranged between 36.0 and 38.4 ºC, but again were above or equal to the maximum recorded summer temperature in the Arabian Gulf (36.0 ºC). Density curves represent predicted values based on 10,000 draws from Bayesian linear models testing 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 via a molecular approach. Using gut content DNA metabarcoding62, we identified the presence of unique operational taxonomic units (OTUs) and exact sequence variants (ESVs) for sequences amplified using cytochrome oxidase subunit I (COI), which targets metazoan organisms mostly from the kingdom Animalia, and 23S primers, which target autotrophs, respectively, for six species (three of which were unique to the GoO, while the other three occurred in both locations). We then used network theory to determine dietary differences among species and locations.

Dietary network trees for the COI primer showed strong separations among 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 7 out of 10 individuals of *C. anomolus* from the Arabian Gulf, 8 out of 9 individuals of *E. ventermaculus* from the Arabian Gulf, and one individual of *E. guttata* from the Gulf of Oman. The remaining individuals of the *C. anomolus* and *E. ventermaculus* from the Arabian Gulf clustered with the majority of *E. pulcher* from the Arabian Gulf (5 out of 7), several 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 even stronger separation of locations. All individuals from the Arabian Gulf (except for one *C. anomolus*) were united in a single module (module III) that contained no Gulf of Oman individuals (Fig. 4c,d). While some species separated into distinct modules, location specific differences appeared to greatly supersede taxonomic boundaries. Thus, with the exception of animal prey in *C. anomolus*, populations of species occurring in both locations differed strongly in their used prey resources, while overlapping broadly with other species present in the Gulf of Oman.

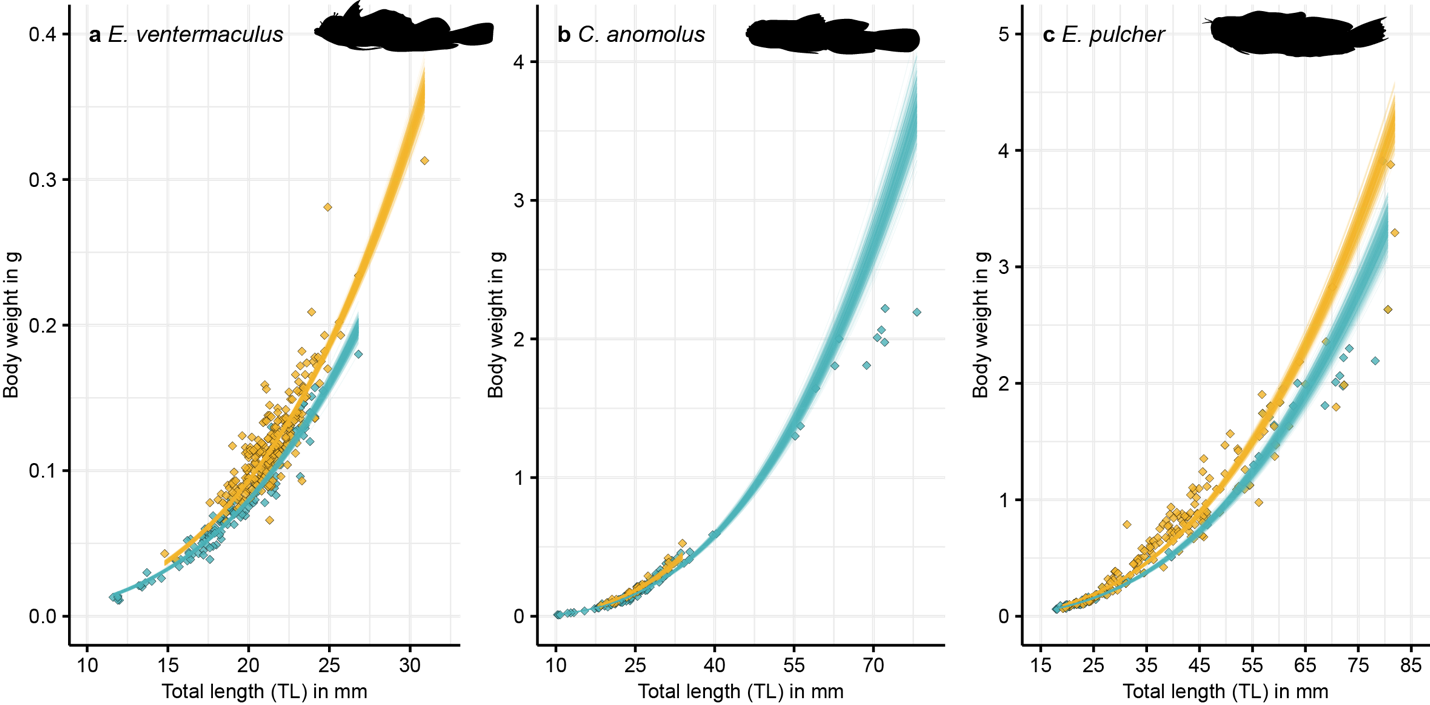
Rarefactions curves of prey diversity in the Gulf of Oman showed that *E. pulcher*, a purportedly herbivorous species63, ingested the widest variety of animal prey species, followed by *E. ventermaculus* (Fig. S1)*.* For both species, Gulf of Oman populations consumed a higher diversity of prey than Arabian Gulf populations. Only *C. anomolus* showed no clear difference for extrapolated values (although diversity was higher for Gulf of Oman populations for the interpolated value), matching the higher similarity between populations in the two locations based on prey identity. For autotroph prey, prey diversity was higher for 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*.

A close up of a map

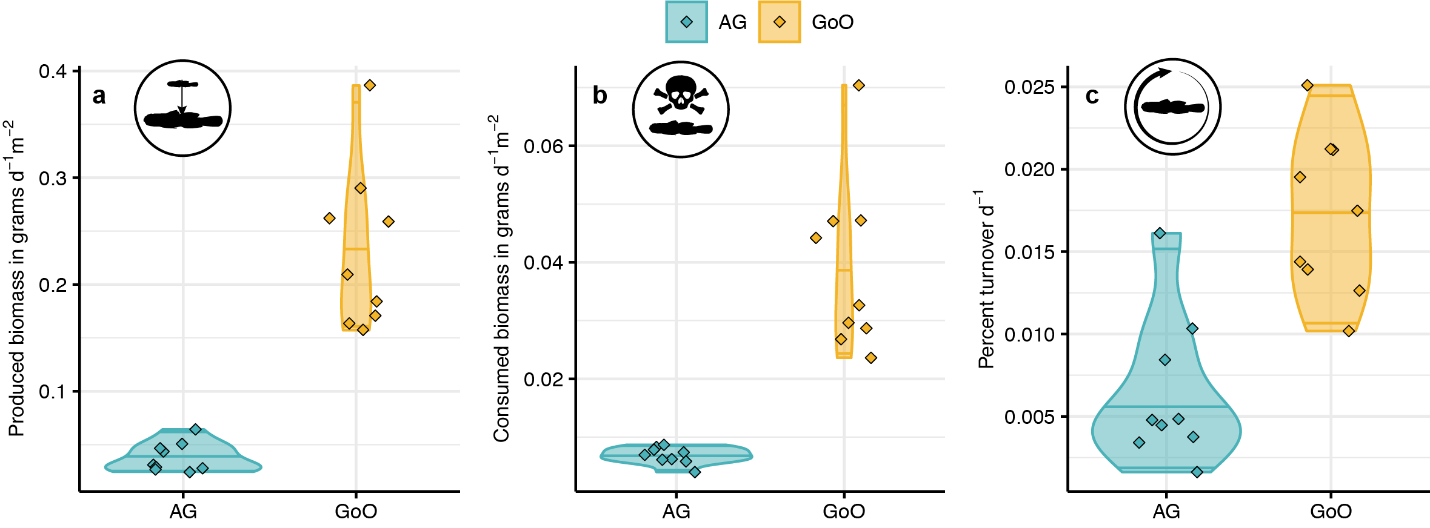
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**Figure 4 | Diet network trees and modularity mosaics showing species-level differences in ingested prey items and individual-based module membership for COI (a,b) and 23S (c,d) primers. (a,c)** Fish silhouettes represent the species as nodes in the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

We examined potential energetic consequences of thermal regimes and resource availability in the two locations by assessing length-weight relationships of three species and by modeling individual-based growth and mortality to estimate community-wide biomass production, consumption, and turnover. The Bayesian linear models testing 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*: *GoO β*= 0.16 [0.13, 0.19], *C. anomolus*: *GoO β*= 0.15 [0.09, 0.21], and *E. pulcher*: *GoO β*= 0.19 [0.14, 0.25]) (Fig. 5). In contrast, no clear differences were evident in the abundances of the three species’ populations across locations (as effect size uncertainties intersected zero), although *E. ventermaculus* (*GoO β*= 0.89 [-1.08, 2.86) and *E. pulcher* (*GoO β*= 3.46 [-0.42, 9.93]) both showed a trend towards lower abundances in the Arabian Gulf, while *C. anomolus* exhibited the opposite tendency (*GoO β*= -0.94 [-3.82, 1.69]). Finally, modeling individual-based growth and mortality for cryptobenthic fish communities at each site revealed drastic 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 AG (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). These results suggest that reefs in the two locations are subject to fundamentally different productivity dynamics at various levels of organization. In the Arabian Gulf, individual fishes accumulate less biomass per mm body size and collectively, cryptobenthic communities produce, provide, and replenish biomass at much lower rates compared to 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).** Eachlines represents a fited draw from 500 iterations based on the posterior parameters from a Bayesian model regressing length against weight (thus delineating uncertainty surrounding the model fit). 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 (i.e. grams of fish tissue grown per day and m2). (**b**) Consumed biomass (i.e. grams of fish tissue perished per day and m2). (**c**) Percent turnover (i.e. 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 sample of cryptobenthic reef fish communities across the six sites (three per site).

**Discussion:**

As rapid environmental change sweeps across the Earth’s ecosystems, understanding the processes that underpin local community structure and ecosystem functioning within a regional species pool has gained renewed urgency. Coral reefs generally afford relatively benign environmental conditions, but anthropogenically-mediated climate change is pushing water temperatures on reefs to new extremes. 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 dramatically 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 did not appear to be the main driver of species presence/absence in the Arabian Gulf. Rather, stark 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 intrinsic metabolisms. Physiological differences, coupled with dramatically divergent community structure, have far reaching consequences for ecosystem scale fluxes of energy and nutrients, as even generous estimates of cryptobenthic reef fish productivity in the Arabian Gulf are an order of magnitude lower than in the nearby Gulf of Oman. Our results indicate that reef fish assemblages on future coral reefs are shaped by a multidimensional energetic filtering mechanism that may severely decrease the rate of bottom-up productivity and turnover on reefs, ultimately resulting 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 tolerances of species from the relatively cool Gulf of Oman align with previous results on critical thermal tolerances in cryptobenthics42, and may reflect the need to mediate short-term temperature extremes in shallow waters when behavioral mitigation (i.e., movement) is limited49,55. This would suggest that colonization of reefs in the extremely hot southeastern Arabian Gulf would be feasible for all species. In fact, the swift generational turnover of cryptobenthic fishes53,57 should allow for transgenerational thermal plasticity (as seen in the two tested species with populations in both locations), which should further facilitate persistence in the southeastern Arabian Gulf even in light of its relatively short geological history65. In addition, despite being separated by the relatively narrow Strait of Hormuz, no hard biogeographic boundary appears to be in place that would drive the absence of so many species from our samples. Indeed, 26 out of 29 (89.7%) cryptobenthic fish species from the Gulf of Oman that were absent from the southeastern Arabian Gulf are recorded from the cooler Arabian Gulf regions of Saudi Arabia and Kuwait (Table S1)61,66,67. Thus, neither intrinsic tolerances to short-term temperature extremes nor biogeographic history appear to drive the observed depletion of cryptobenthic communities on the most thermally extreme coral reefs.

Instead, it appears that existence on these reefs is mediated by the latent demands of thermal regimes on individual’s energy budgets and the inability of small bodied fishes to compensate for these demands. Transgenerational acclimation or adaptation to increasing temperatures has been shown to occur in a limited suite of model reef fish species47,68, but 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 tested species (Fig. 5). Thus, although shifts in transgenerational temperature tolerance permits survival and adequate performance of selected reef fish species in controlled laboratory conditions38,46, such shifts in tolerance may not be viable in a natural environment that imposes a range of energetic trade-offs and challenges on individuals and populations69.

Reduced prey diversity and differing composition may further exacerbate the energetic dilemma of consumer species like cryptobenthics that face increasing energy demands under elevated temperatures15,17. Our molecular dietary analysis revealed a different and narrower range of both primary and secondary prey resources ingested by individuals from the Arabian Gulf (with *C. anomolus* being the least pronounced species), with more interspecific overlap in the Gulf of Oman than intraspecific overlap across locations. While we cannot definitely say whether the dietary differences shown here (Fig. 4) also reflect differences in diet quality (i.e., prey with poor nutrient content), evidence from recent work shows that large reef fish species exhibit unusual diets dominated by nutritiously poor benthic invertebrates in the Arabian Gulf72. Moreover, the single cryptobenthic species to show only moderately distinct prey composition across locations and higher primary prey richness in the Arabian Gulf, *Coryogalops anomolus*, was also the only species more abundant and larger in the Arabian Gulf, with a weaker (albeit still clear) reduction in body condition compared to *E. pulcher* and *E. ventermaculus*. The genus *Coryogalops*, however, differs from most of the taxa that dominate cryptobenthic communities in both the Arabian Gulf and Gulf of Oman (e.g. *Ecsenius, Eviota,* *Enneapterygius*, etc.), in that it belongs to a clade containing many non-reef associated species from comparatively extreme habitats73,74. Specifically, the genus *Coryogalops* is more commonly associated with tidepools and other extremely shallow environments exposed to substantially fluctuating temperatures and salinity, where they may be forced to rely on a cryptic, sedentary lifestyle with relatively low energetic costs75,76. Thus, the persistence of *C. anomolus* in the southeastern Arabian Gulf may reflect preadaptation to more extreme environments afforded by its phylogenetic history of belonging to a lineage of non-reef, extreme habitat specialists.

Persistence in thermally extreme environments is energetically costly77 and elevated temperatures, in particular, 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 costs of growth with a restricted suite of different resources. For a group of vertebrates that already has high energetic demands per gram of body mass while exhibiting rapid growth49, this may represent an energetic double jeopardy that cannot be borne by species with intrinsically high energy demands, especially since further decreases in body size (a universal physiological response to warmer temperatures18,70) are nearly impossible for the smallest species of cryptobenthics (e.g., *Eviota*, *Trimma*). In other words, 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. Our findings, therefore, provide key evidence from highly-vulnerable tropical ectotherms in natural settings for the consequences of predicted climate change effects on routine organismal performance (the plastic metabolic floor) 78,79 and their ramifications for species persistence and community assembly80.

The evident 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 pathways and phenomena82–85. Among these pathways, benthic productivity86 and its assimilation and transfer through cryptobenthic reef fishes and their unique demographic dynamics 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 small-bodied vectors of energy and nutrients to larger consumers may be substantially stymied in warming waters. Alarmingly, yearly estimates of productivity 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 demonstrated in our study (but not considered in the model), and the influence of seasonality on daily averages of biomass production. Specifically, previous studies in the Arabian Gulf have shown variability in large reef fish abundance across seasons, suggesting that these fishes seek out more benign conditions during extreme conditions in the summer and winter87,88. For cryptobenthics, mediation via migration is highly improbable, leaving little choice but to either adjust basic life-supporting processes to survive (i.e., decreased activity, somatic growth, or reproductive investment), or to bridge seasonal adversity through generational turnover and ontogenetic differences in physiology or habitat occupation89. Either strategy is likely to further stunt the yearly estimates of productivity, suggesting that differences in ecosystem functioning among the two systems may be more extreme than revealed from our model.

Reefs in the Gulf of Oman used for comparison in this study may be particularly productive environments due to seasonal upwelling90, and indeed, our estimates of cryptobenthic productivity substantially exceed 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 we acquired for the Arabian Gulf compares poorly with the same GBR-reef. Notably, the GBR-reef had undergone a sequence of severe disturbances91, which greatly reduced space availability and shelter for small bodied fishes; yet, it also retained a diverse assemblage of cryptobenthic fish species able to satisfy their energetic demands due to benign temperature profiles29. Reefs in the Arabian Gulf, at the time of our survey, had also undergone periods of extensive bleaching in previous years92–95, which may have negatively affected the diversity and abundance of cryptobenthic fishes compared to less disturbed and more resilient reefs in the Gulf of Oman27,96,97. However, the observed lack of differences in live coral cover and overall benthic community structure between locations also suggests that, beyond few specialist species92,98, loss of live coral habitat may not be a primary agent of richness and abundance changes small reef fish populations and ecosystem productivity30,32,92. Instead, our results cast a new light on the imminent threats to cryptobenthic reef fishes and their critical role for coral reef functioning: similar to reef corals, which are highly susceptible to extreme temperatures26, many of the world’s smallest marine ectotherms may struggle to compensate for increasing costs of growth and homeostasis as they try to adapt to changing temperatures on the world’s coral reefs. 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. Whether these patterns are driven by similar mechanisms as proposed herein (e.g., energetic filtering on large fish species) or instead relate more to decreased productivity at lower trophic levels remains unresolved. Yet, in light of the hypothesized importance of small vertebrate consumers in food webs globally101 and the unique ecological role of cryptobenthics for reef fish trophic dynamics53, the apparent effects of elevated temperature on cryptobenthic fish assemblages may considerably hamper ecosystem functioning 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. We studied cryptobenthic fish communities across six distinct coral reefs in two distinct locations that differ dramatically in their yearly temperature fluctuations. The reefs we sampled 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 ≥ 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) generally lie within normal coral reef temperature profiles throughout the year, ranging between approximately 32.0 ºC and 22.0 ºC. All fieldwork was performed in April and May 2018.

*Field sampling*

Cryptobenthic fishes are small (generally <50mm), bottom-dwelling reef fishes across 17 families that frequently live deep within the reef framework49. However, due to their high growth rates, rapid mortality, and larval replenishment dynamics, cryptobenthics are a critical component of coral reef trophic dynamics, often supplying a large proportion of consumable biomass to larger fish species53. We sampled six distinct reefs (hereafter *Site*)in the southeastern Gulf and northwestern Gulf of Oman (three 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 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 (usually 2-3 mins), we removed the tarpaulin and started to gently peel back the net while collecting all fishes found within the sampled area with tweezers. We searched the entire area, including caves and crevices until five minutes were spent by all divers without collecting any additional fishes. We placed all fishes into ziplock-bags, brought them to the surface, euthanized them with a clove-oil overdose, and immediately placed them into and ice-water slurry until preservation. At the end of each day, all specimens were brought to the laboratory at New York University Abu Dhabi or to room #211 at the Radisson Blu hotel in Fujairah, where they were kept on ice until processing. For each sampled clove-oil station, we also took five photographs of the benthos to quantify benthic community structure. Specifically, we haphazardly placed a 20×20cm PVC-quadrate onto the outcrop within the area of our sample and took a close-up photograph of the benthos within the frame of the quadrat.

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 spraybottles of clove-oil ethanol solution, a dipnet, and ziplock bags, searched the reef for individuals of cryptobenthic fishes across three (Arabian Gulf: *Coryogalops anomolus*, *Ecsenius pulcher*, and *Enneapterygius ventermaculus*) and six (Gulf of Oman: *Coryogalops anomolus*, *Ecsenius pulcher*, and *Enneapterygius ventermaculus* plus *Eviota guttata*, *Helcogramma fuscopinna*, and *Hetereleotris vulgaris*) species. Upon locating an individual or identifying a suitable microhabitat in which a fish was suspected, the diver carefully 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, fish were brought to the seawater laboratory facilities at NYUAD in Abu Dhabi. 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 establish protocol that involves photographing, identifying, recording, measuring, weighing and preserving each specimen50. To photograph the fishes, we placed each individual in a small phototank 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 its conspecifics. A subset of the samples was then shipped to the University of Washington under export permit #XXX, where they are now cataloged, while the rest were retained and archived at NYUAD.

We processed a subset of individuals (as dictated by sample-availability and sequencing costs) in six species (*Antennablennius adenensis*, *C. anomolus*, *E. pulcher*, *E. guttata*, *E. ventermaculus*, and *H. vulgaris*) for gut content DNA metabarcoding by removing the entire alimentary tract under sterile conditions at the University of Washington. Specifically, we haphazardly selected ten, ten, and seven individuals of *C. anomolus*, *E. ventermaculus*, and *E. pulcher*, respectively, from the Arabian Gulf, and ten specimens each (with the exception of *E. pulcher*, for which we selected eleven) of *C. anomolus*, *E. ventermaculus, Antennablennius species A*, *E. guttata,* and *H. vulgaris* from the Gulf of Oman. Then, we dissected out the 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 filled with C1-buffer from the Qiagen DNEasy PowerSoil DNA extraction kit. After every specimen, we sterilized the work platform and tools using a series of baths consisting of dish soap solution, 10% sodium hypochlorite:water solution, and Milli-Q UV-sterilized water. Upon completion of twenty samples, we immediately proceeded to perform DNA-extractions from the dissected gut samples. All DNA extractions were performed according to the protocol outlined in62. We stored all DNA samples at 4ºC until aliquoting them into 96-well plates for library preparation and amplification.

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).

*Gut content DNA metabarcoding*

All DNA samples were sent to Jonah Ventures (Boulder, CO) for post-extraction processing.

*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 between May 9th and May 13th 2018. For the trials, a haphazardly selected subset of individuals was moved from the holding tanks into separate chambers filled with seawater at ambient temperatures 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 criticial 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.

*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) and then computing available surface area under the assumption that outcrops represent hemispherical constructs (*SA* = 4*πr*2/2). Then, 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 a fixed effect of *Location* (*Arabian Gulf vs. Gulf of Oman*) and a 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* package104. 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 our 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 ordination on 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. 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 did not perform the SIMPER routine due to the lower number of categories and scaled the size of the dots representing unique samples by their 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 to have 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 among pairwise levels using post-hoc contrasts (Tables S2 and S3). Models were run with a Gaussian error distribution and the same specifications as previous models (e.g., burnin, iterations, priors, etc.). As previously, we took 1,000 draws from the posterior parameters to predict posterior distributions and 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*, *E. ventermaculus*) and ran separate models for each species testing 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 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 overdispersed when run under a Poisson distribution. To validate our 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 the composition of prey items in the guts of the examined fishes using a network theory approach on both the COI and 23S primer results105. We first created a presence-absence matrix of ESVs/OTUs 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 different purposes. First, to create a dietary network tree, we transformed this matrix into a data frame that contained each ESV/OTU 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/populations, which we plotted using the Fruchterman-Reingold algorithm. Second, to examine the community structure within the network, we first omitted all prey items (i.e., ESVs/OTUs) 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 measure106. We used Beckett’s community detection algorithm107, which we re-iterated 20 times for each primer dataset. We then used the convergent output from the 20 iterations to determine the module membership of each individual in our network and plotted membership in a mosaic plot.

Furthermore, we investigated the diversity of prey items in each species’ population for both the 23S and COI primer results via a rarefaction analysis on the species richness of prey items given the number of sequences in each species to account for quantitative differences in prey tissues and sequencing depth. Specifically, we rarefied species richness estimates for each species/population to an endpoint defined by the maximum sequences in any population (for 23S and COI, respectively) using 100 bootstraps and 50 knots along the x-axis108. We then visualized the rarefaction curves for each species and population separately, marking inter- and extrapolated estimates on the graph.

Finally, we used previously established methods91,109,110 to model 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). 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 has 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] ratio111) by also including consumed biomass (consumed biomass/standing biomass)109. As such, the turnover metric approximates the rate at which particles flow through the system, either via incorporation into fish body mass or via their release to other consumers through mortality.

To perform the modeling, we first accrued information on 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 relationship[s. 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 Gorwth Model (VBGM)110. By subtracting the observed size of fishes (as obtained from our samples) from the weight obtained by the same fish after one day using the modeling procedure, we calculated the expected biomass production by said individual. We estimated daily mortality rates by calculating species-level mortality risk coefficients via VBGM parameters and SST109,112 and then adjusted the risk based on relationships between mortality and body size113. Using these coefficients, we obtained a daily probability of survival 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 visualization was performed in *R* (version 3.6.1) using the *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 that underly the results presented in this paper 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* and *GO* 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 sequences for six species in the Arabian Gulf (blue) and Gulf of Oman (gold).** OTU curves (a) mark the diversity of unique prey taxa for each species and population as obtained from gut content DNA metabarcoding using COI primers, while ESV curves (b) show the diversity of unique prey taxa for 23S primers. 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.