

Contribution of cryptobenthic fishes to estimating community dynamics of sub-tropical reefs

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ABSTRACT: Small, cryptic (cryptobenthic) fishes are an under-surveyed component of reef fish assemblages that can account for a significant amount of diversity, function, and structure of reef fish communities. A complete picture of reef fish dynamics requires an accounting of these species and inclusion of them in analyses of community ecology. We report the results of a large-scale, quantitative study of the rocky reef fish community in the Gulf of California (GOC), where we collected cryptobenthic fishes and surveyed conspicuous fishes to calculate species richness, density, biomass, and community metabolism of the entire fish assemblage. We catalogued 20 764 individuals, representing 112 species in 36 families. Cryptobenthic fishes accounted for more than 40% on average of the species richness per site but were generally unobserved during visual surveys. They also accounted for more than 95% of the total fish abundance and up to 56% of the fish community metabolic requirement, both a likely result of their small body size. The relative contribution of cryptobenthic fishes to the entire quantitatively sampled assemblage differed between the northern and southern GOC, with the north being relatively 'more cryptobenthic' than the south. This study is the first to combine quantitative surveys and collections of the entire fish assemblage in the GOC and is one of the most extensive of its kind for any ocean basin, to date. Our results demonstrate the importance of quantifying all size classes and all functional groups when studying the ecology of diverse vertebrate communities.

KEY WORDS: Cryptobenthic fishes · Rocky reefs · Gulf of California · Community metabolism

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INTRODUCTION

Quantitative studies of ecological communities are a fundamental means for studying the relationships among individuals and among species (Hayek & Buzas 1997) at any one place and are a vital component of macroecology and biogeography studies that explore interactions on a landscape (or broader) scale. Many quantitative studies of nature have advanced our understanding of the population and community ecology of tropical forests (e.g. Janzen 1970, Greig-Smith 1983, Dallmeier et al. 1991), grasslands (e.g. Crocker & Tiver 1948, Tilman 1987, Gibson 2009), marshes (e.g. Nixon & Oviatt 1973, Steever

et al. 1976), intertidal invertebrate communities (e.g. Connell 1961, Dayton 1971), seagrass beds (Hemminga & Duarte 2000, Short & Coles 2001), and other ecosystems.

In the marine environment, quantitative surveys of fishes play an important role in understanding the ecology of these communities and in underpinning strategies of fisheries management and conservation. Without detailed understanding of the number, size, and population structure of marine fishes, it is difficult to manage extractive or non-extractive activities that may alter these populations. However, surprisingly few quantitative studies of reef fishes (e.g. Ackerman & Bellwood 2000) have included both easy to

observe, conspicuous fishes as well as more difficult to observe and difficult to identify fishes, together at the same sites. This shortcoming limits the conclusions that can be drawn about the makeup and function of reef fish assemblages to those species that are easy to visually survey.

On coral and rocky reefs, it is impossible to obtain quantitative samples using towed nets, and researchers in these systems often rely on SCUBA-based, non-extractive surveys to estimate fish densities (e.g. Harmelin-Vivien et al. 1985, Bohnsack & Bannerot 1986, Lang 2003). These methods have worked well in describing many interesting features of reef fish dynamics (Hixon 2011) and in targeted efforts to conserve these communities (e.g. Sala et al. 2002, Sandin et al. 2008, Friedlander et al. 2012). Visual surveys of fishes, however, underestimate or ignore the densities of small, benthic, cryptically colored ('cryptobenthic') species. Depending on the ecological metric of interest, this underestimate may be a significant oversight, as cryptobenthic fishes are abundant (Ackerman & Bellwood 2000, Thomson & Gilligan 2002), diverse (Smith-Vaniz et al. 2006), and may represent a significant portion of reef trophodynamics (Kotrschal 1989, Depczynski & Bellwood 2003, Ackerman & Bellwood 2003, Ackerman et al. 2004) and/or productivity (Allen et al. 1992). Furthermore, small fishes are known to have disproportionately high metabolic rates (Gillooly et al. 2001), so cryptobenthic species may contribute significantly to community metabolism on some reefs (e.g. Ackerman & Bellwood 2000). Finally, many cryptobenthic fishes are microhabitat specialists (e.g. Gonzales-Cabello & Bellwood 2009, Hastings & Galland 2010, Ahmadi et al. 2012, Harborne et al. 2012, Tornabene et al. 2013), so quantitative monitoring of this group may highlight or reveal micro-alterations to coral and rocky reefs (Goatley et al. 2016).

Here, we report the results of combined visual, non-extractive surveys of conspicuous fishes and quantitative, extractive surveys of cryptobenthic fishes from 17 sites, stretching across more than 5.5° latitude in the Gulf of California (GOC), Mexico. This is a highly productive region (Alvarez-Borrego 2010) particularly important to Mexican fisheries (Cisneros-Mata 2010), and it is a biodiversity hotspot (Roberts et al. 2002) and is known for numerous species of megafauna. The combined study of conspicuous and cryptobenthic fishes contributes to the general understanding of GOC reef structure. Surveys and collections were completed concurrently during an expedition in July 2010 and represent a unique snapshot of the complete reef fish community

at those sites. We report the contribution of the historically undersampled cryptobenthic component to GOC rocky reef fish assemblages and review emergent patterns in richness, density, biomass, and metabolism.

This study is the first to combine quantitative surveys and collections of the rocky reef fish assemblage in the GOC and is the most extensive of its kind for any ocean basin, to date. It provides new insights into the contribution of undersampled fishes to community dynamics and demonstrates the importance of considering all parts of the fish assemblage when studying sub-tropical reefs.

MATERIALS AND METHODS

Study site

Our study sites stretch along the Baja California Peninsula and the GOC, a long (~1000 km), narrow (~150 km), semi-enclosed basin between the Baja Peninsula and continental Mexico (Fig. 1). The GOC has a rich ichthyofauna (Hastings et al. 2010) and is characterized by rocky, rather than coral, reefs (Thomson et al. 2000). The total reef fish fauna of the Gulf includes an estimated 280-plus species (Thomson et al. 2000), and at least 104 of these are cryptobenthic species (Galland 2013).

The northern part of the region is known to include several disjunct populations of temperate fishes from California, USA, that are not present in the southern GOC, and the southern area is known to include tropical species that do not reach the north (Walker 1960, Bernardi et al. 2003). Therefore, we binned sites into 2 sub-regions, after Walker (1960), and hereafter refer to them as 'south' and 'north' (Fig. 1).

Field surveys

To quantitatively describe the conspicuous component of the reef fish assemblage, we conducted area-based visual surveys at each site. Visual surveys followed the methods of Aburto-Oropeza et al. (2011). SCUBA divers swam along 50 m transects, identifying, counting, and estimating the size of all individuals observed within a 5 m wide area (250 m² total area per transect) during 2 passes. Different species were counted during each pass, with mobile species counted during the first pass and territorial/demersal species counted during the second. This methodology prevented individuals from being counted multi-

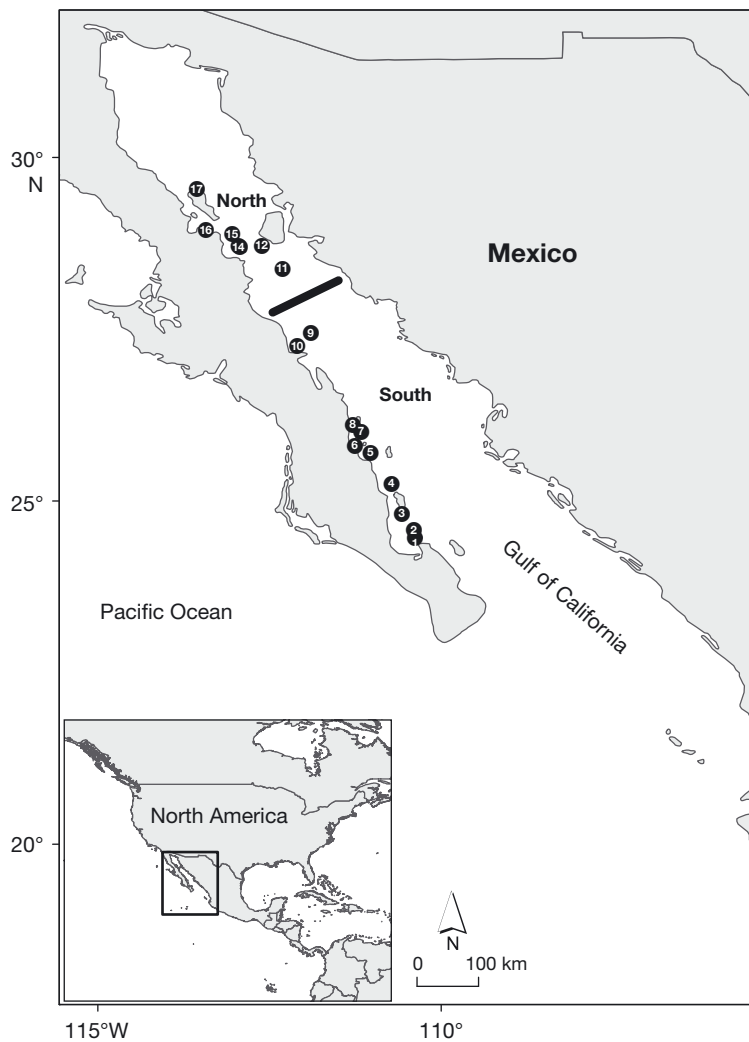


Fig. 1. Gulf of California, Mexico. Numbered circles represent study sites. Site 13 is geographically close to Site 14 and is hidden under the Site 14 circle

ple times and allowed the divers to concentrate their focus on a distinct behavioral group during each pass. At each site, we attempted to conduct at least 4 transects, all at precisely 5 m depth, but weather and reef conditions prevented us from accomplishing this goal at some sites. Therefore, visual counts are compared per transect.

To quantitatively describe the cryptobenthic component of the reef fish assemblage, we conducted area-based extractions at each site. A team of divers erected a barrier net (1.3 m tall, 0.6 cm mesh) around a 10 m² area and released a standardized solution of Prentiss 8.4 % powdered rotenone (1–2 kg, depending on oceanographic conditions), Ivory Ultra liquid dish soap (120 ml per kg of powdered rotenone), and seawater (to form a slurry). Rotenone is widely

considered the most important ichthyocide in marine fish research (Robertson & Smith-Vaniz 2008) and allowed divers to carefully and systematically remove virtually every fish, however small, from inside the barrier net. After rotenone application, divers spent 2 to 4 h collecting all fishes inside the 10 m² area. Generally, one diver patrolled the bottom of the net along the outside to prevent surge or currents from carrying away specimens and to keep away opportunistic predators. A second diver collected all fishes inside the area, actively searching under rocks and within the substrate and vegetation until all fishes were captured. Samples were collected at depths of 1 to 5 m. The areas chosen for collecting were based on detailed field notes obtained from an earlier study that included quantitative rotenone collections of cryptobenthic fishes in the 1970s (Thomson & Gilligan 2002). Specific sites were chosen based on visual inspection of the area to find representative habitat and vegetation cover. Sites were close enough to visual survey transects to be part of the same system but far enough to prevent sampling activities from skewing the survey results—as all surveying and collecting was conducted concurrently. In order to reduce sampling biases, a team of 2 divers conducted all visual surveys, while a second team obtained all rotenone samples.

Collected specimens were either fixed in 10 % formalin or preserved in 95 % ethanol and are archived at the Scripps Institution

of Oceanography Marine Vertebrate Collection in collection numbers SIO 11-85 to SIO 11-102. Individual specimens were weighed to the nearest 0.01 g, and weights were summed by site. Where specimens weighed less than 0.01 g, 2 or more individuals of the same species (of equal length) were weighed together. In this manner, the precise biomass of cryptobenthic fishes was determined for each site.

Data analyses

Biomass of visually surveyed individuals was calculated using the estimated lengths recorded by surveyors in the field and length–weight relationships of the form $W = aL^b$, where W is equal to biomass in

grams, L is equal to length in centimeters, and a and b are constants reported for each species in Fishbase (Froese & Pauly 2015). Weights of all individuals were summed by transect and converted to grams per unit area. Values from the 2 survey techniques were compared to identify the relative contribution of the cryptobenthic and conspicuous fish communities to overall biomass and summed to obtain the total fish biomass per unit area at each site.

Metabolism (measured as routine metabolic rate, RMR), following Gillooly et al. (2001) and Davison et al. (2013), was assumed to be a function of biomass (W) and temperature (T):

$$\text{RMR (J min}^{-1}\text{)} = \text{EXP}(a) \times W^{0.75} \times \text{EXP}[1000c/(273.15 + T)] \quad (1)$$

where a is a mass-independent constant equal to 14.47 and c is a constant associated with the activation energy, equal to -5.020 (Gillooly et al. 2001).

As metabolism scales with a fractional power of biomass, it is higher (per unit mass) in small individuals and was therefore calculated separately for each individual specimen using the measured or derived biomasses and summed by site to obtain whole-community fish metabolism per unit area. Temperatures used in the above equation were derived by averaging temperature taken at each site at 20-min intervals for 30 d prior to surveying the fish assemblage. These temperatures were collected using *in situ* temperature loggers, installed at each site, prior to surveying the fish assemblage (Galland 2013).

To visualize differences in community structure among sites and examine whether our study supports previous observations of different rocky reef fish assemblages at sites in the north and south (as concluded by Walker 1960), we analyzed the abundance data (per unit area) using non-metric multidimensional scaling (nMDS; Clarke 1993). A Bray-Curtis dissimilarity matrix was created from the raw data and used in the nMDS, which we limited to 2 dimensions. As we were interested in the cryptobenthic portion's contribution to the whole fish assemblage, we performed this process 3 times, once for each group (cryptobenthic and conspicuous) and once for the combined dataset.

The contribution of the cryptobenthic portion of the fish assemblage was determined by comparing species richness, abundance, biomass, and metabolism of the 2 groups at each site. Biomass, metabolism, and abundance data were converted to values per unit area in order to compare visual and extractive surveys. Species richness was pooled per site. Potential differences in the relative contribution of crypto-

benthic fishes to the community dynamics at sites in the northern and southern sub-regions were tested using a series of t -tests. Data were first subjected to F -tests to test for equivalence of variance between samples. Where variance was equal, Student's t -tests were used to test for differences in means between sub-regions. Where variance was not equal, t -tests for unequal variances were used instead (see Ruxton 2006). To assess differences in just the cryptobenthic and conspicuous portions of the assemblage (separately) between the sub-regions, we followed a similar methodology, with each of the 4 parameters (biomass, metabolism, species richness, and abundance) examined per transect or per extraction plot and tested between sub-regions using Student's t -tests or t -tests for unequal variances.

RESULTS

Across our 17 sites, we collected or surveyed a total of 20764 reef fishes comprising 112 species and 36 families. Four of the species (3 families) were rays or skates, and the remaining 107 species (33 families) were bony fishes. We did not observe any sharks. We collected 40 cryptobenthic species, including gobies (Gobiidae), combtooth blennies (Blenniidae), labrisomid blennies (Labrisomidae), tube blennies (Chaenopsidae), triplefin blennies (Tripterygiidae), clingfishes (Gobiesocidae), scorpionfishes (Scorpaenidae), cardinalfishes (Apogonidae), and viviparous brotulas (Bythitidae). Other families of cryptobenthic fishes (e.g. frogfishes; Antennariidae) were not taken in any sample or observed in surveys of conspicuous fishes, though they are known from the GOC. Seventy-two species are included in the conspicuous group. Though it is difficult to quantify eels (Anguilliformes) or nocturnal fishes (e.g. Holocentridae) with either daytime visual surveys or rotenone collections, we included visual records of individuals in these taxa in the conspicuous group, with the caveat that their densities are likely underestimated. Nineteen of the 72 conspicuous fish species were observed at only one site, while 6 of 40 cryptobenthic fish species were collected only once. Two conspicuous species but no cryptobenthic species were observed or collected at all 17 sites.

The results of the nMDS imply differences in the structure of the rocky reef fish assemblages between the north and south. This is apparent in plots of the results in ordination space for cryptobenthic fishes, conspicuous fishes, and the combined dataset (Fig. 2). There is little overlap between the sites that

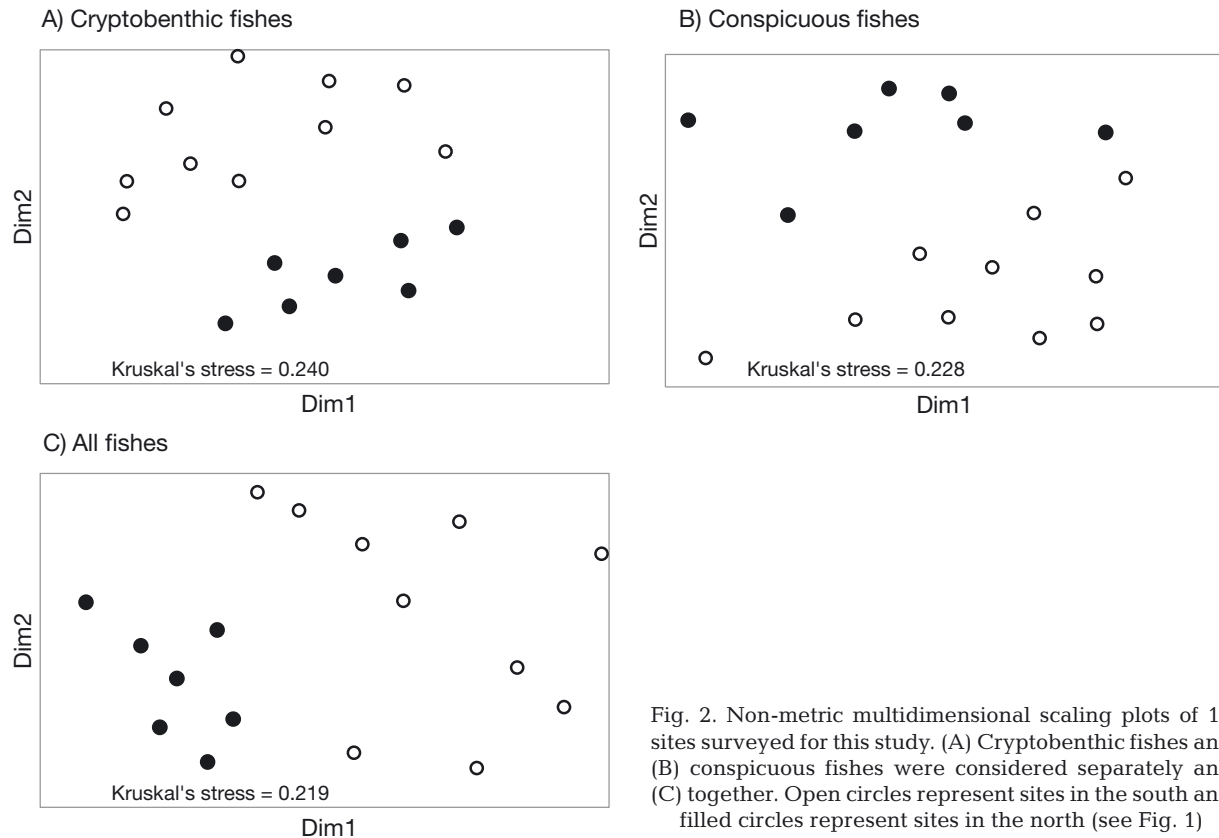


Fig. 2. Non-metric multidimensional scaling plots of 17 sites surveyed for this study. (A) Cryptobenthic fishes and (B) conspicuous fishes were considered separately and (C) together. Open circles represent sites in the south and filled circles represent sites in the north (see Fig. 1)

we assigned to our northern and southern groups, with the northern sites forming fairly tight clusters for cryptobenthic fishes and the combined dataset, in particular. We note, however, the relatively high Kruskal's stress values for each plot (Fig. 2).

Species richness varied by sub-region, with the south (10 sites) represented by 96 total species, while the north (7 sites) included only 69 species. A total of 31.3% of the species observed in the south occurred only there, and 21.7% of the species observed in the north were absent from the south. GOC-wide, triplefin blennies were the most common cryptobenthic family (35% of total collected individuals and 3 of the top 4 species by abundance), followed by tube blennies (20%), labrisomid blennies (18%), gobies (16%), and others (11% combined).

The percent contribution of cryptobenthic fishes to the examined community metrics varied by sub-region as well, with this group contributing more heavily to the biomass (Student's *t*-test, $t = 4.81$, $df = 15$, $p < 0.001$), metabolism (Student's *t*-test, $t = 5.64$, $df = 15$, $p < 0.0001$), and abundance (*t*-test for unequal variances, $t = 2.52$, $df = 12.41$, $p = 0.027$) of the observed fish assemblage in the north than in the south. The contribution of the cryptobenthic group to species richness was the same between sub-regions

(Student's *t*-test, $t = 0.93$, $df = 15$, $p = 0.367$). At the site level, cryptobenthic fishes accounted for 85–99% of community abundance, 24–66% of species richness, 9–56% of community metabolism, and 2–24% of community biomass (Fig. 3).

In our comparison of each portion of the rocky reef fish assemblages in the northern and southern sub-regions, we found measurable differences in some metrics (Table 1). The species richness, abundance, biomass, and metabolic requirements of the conspicuous fishes were higher in the south than in the north. The biomass and metabolic requirements of the cryptobenthic fishes were higher in the north than in the south. Neither the species richness nor abundance of the cryptobenthic fishes was statistically different between sub-regions.

DISCUSSION

General distribution patterns of shallow reef fishes in the GOC

The contribution of cryptobenthic fishes to reef fish dynamics has only rarely been studied through systematic pairing of visual and extractive surveys

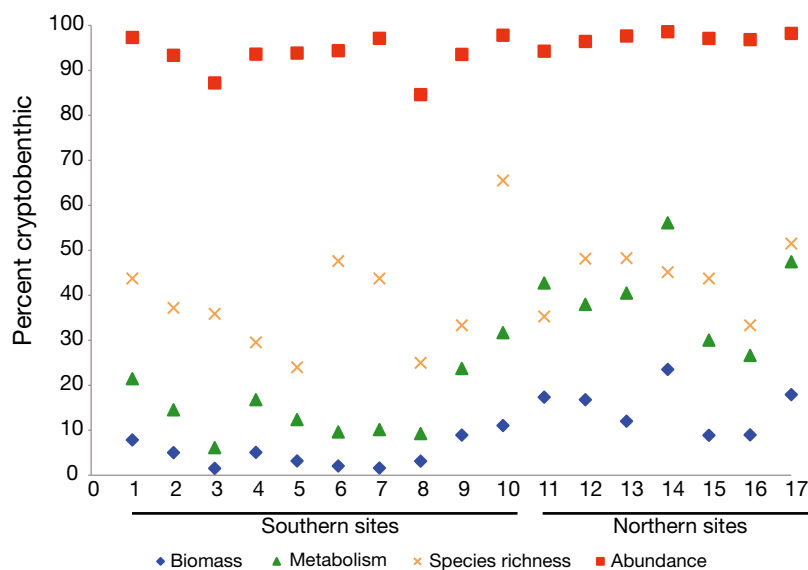


Fig. 3. Relative contribution of cryptobenthic fishes to biomass, metabolism, species richness, and abundance of the reef fish community at 17 study sites. Site numbers refer to Fig. 1

(e.g. Allen et al. 1992, Ackerman & Bellwood 2000), and those instances have been restricted to small geographic areas (single islands) in tropical Australia and temperate California, USA. The cryptobenthic fish assemblage in the GOC is one of the best studied such assemblages in the world, with long histories of study by several Mexican and American institutions. Previous studies, however, have not quantitatively considered the conspicuous assemblage.

Though cryptobenthic fishes are often missed or totally ignored in quantitative visual surveys, they are a major component of the reef fish assemblage in

the GOC that should not be overlooked. These fishes account for 9 of 10 individuals and as much as 20% of the biomass and 50% of the community metabolic requirement at the site level. We collected less than 40% of the known cryptobenthic fish species on rocky reefs in the GOC (see Galland 2013 for a complete list of species)—likely as a result of the extreme rarity, depth partitioning, and limited geographic range of some species. Still, the diversity of these fishes that we collected is nearly equivalent to that of the conspicuous fishes that we surveyed. Though the direct contribution of cryptobenthic fishes to reef food webs is not well understood, there is evidence that marine systems with higher diversity are more resilient to human perturbations (e.g. Jackson et al. 2001, Lotze et al. 2006).

Without quantitative study of these small-bodied species, half of the common fish species on rocky reefs in the GOC may be missed.

nMDS supports conclusions by much earlier work (e.g. Walker 1960) that there is a difference in the dynamics of the rocky reef fish assemblage between the 2 sub-regions that we pre-defined. This is the case for the cryptobenthic and conspicuous groups of species, both individually and combined. Likely contributing to this finding is the presence of several 'northern disjunct' populations of species found more commonly along the west coast of the Baja California peninsula and southern California (Walker 1960, Present 1987, Bernardi et al. 2003). Among crypto-

Table 1. Comparisons of mean ($\pm 95\%$ CI) species richness, abundance, biomass, and metabolism of conspicuous and cryptobenthic fishes between 2 sub-regions of the Gulf of California (see Fig. 1). Conspicuous transects covered 250 m² while cryptobenthic plots covered only 10 m². Mean cryptobenthic abundance and metabolism were compared using Student's *t*-tests. All other means were compared using *t*-tests for unequal variance (see Ruxton 2006)

	South	North	<i>t</i>	df	<i>p</i>
Conspicuous fishes					
Species richness (spp. transect ⁻¹)	15.8 (± 1.7)	10.2 (± 0.9)	5.94	54.27	<0.0001
Abundance (ind. transect ⁻¹)	336 (± 68)	151 (± 49)	4.4	61.67	<0.0001
Biomass (g transect ⁻¹)	44257 (± 9544)	23646 (± 4101)	4.03	47.19	<0.001
Metabolism (J min ⁻¹ transect ⁻¹)	963 (± 280)	471 (± 83)	4.45	45.54	<0.0001
Cryptobenthic fishes					
Species richness (species plot ⁻¹)	16.1 (± 2.7)	13.9 (± 1.5)	1.68	12.82	0.12
Abundance (ind. plot ⁻¹)	256 (± 102)	201 (± 90)	0.87	15	0.4
Biomass (g plot ⁻¹)	89 (± 42)	157 (± 89)	2.42	13.67	0.03
Metabolism (J min ⁻¹ plot ⁻¹)	7 (± 3)	12 (± 5)	2.32	15	0.03

benthic species, another factor is the higher density of larger-bodied labrisomid blennies in the north, and smaller-bodied tube blennies and gobies in the south (Galland 2013).

The cryptobenthic fishes do not contribute equally to the overall community dynamics of the quantitatively sampled assemblages in the north and south. Though the overall richness and density of cryptobenthic species is similar between the sub-regions, differences in the species composition contribute to the biomass and community metabolism of cryptobenthic fishes being higher in the north than the south. These differences, coupled with our observation that the abundance, species richness, biomass, and metabolism of conspicuous fishes is lower in the north than the south, lead to a situation where the whole quantitatively sampled, rocky reef fish assemblage is relatively 'more cryptobenthic' in the northern sub-region and 'less cryptobenthic' in the southern sub-region.

Our observation that shallow rocky reef fish assemblages (combined conspicuous and cryptobenthic) in the southern GOC are characterized by higher species richness than those in the northern GOC follows the same general pattern found for the more than 900 total fish species observed in the GOC (Walker 1960, Hastings et al. 2010). This difference is primarily the result of a richer assemblage of conspicuous fishes in the south, as the species richness of cryptobenthic fishes is similar between sub-regions. However, sites in the north may experience more seasonal turnover among the shallow water reef fishes as a result of the temperature variability in that region (e.g. Thomson & Lehner 1976), and 'northern disjunct' species are likely to be more common in the fall or spring, as opposed to July, when we visited the region. Surveys during other seasons may highlight patterns different to those we have measured here.

Comments on the contribution of cryptobenthic fishes to community metabolism

Fish biomass is often used as a primary metric in studies of reef health (Harmelin-Vivien et al. 1985, Bohnsack & Bannerot 1986, Lang 2003, Sandin et al. 2008, Aburto-Oropeza et al. 2011, Friedlander et al. 2012). However, in recent years, metabolism has been proposed as a means of quantifying flow of energy and materials through ecosystems and linking ecology at multiple scales—from individuals to landscapes (Gillooly et al. 2001, Brown et al. 2004). As fish metabolism is generally assumed to increase

with biomass to a power of 0.75 (Gillooly et al. 2001, Davison et al. 2013), small fishes use (require) more total energy per unit biomass than large fishes. In the GOC, cryptobenthic fishes are much more abundant and much smaller than more conspicuous species, so even given their relatively small contribution to total reef fish biomass, their metabolic requirements can be quite high. This is especially evident in the northern sub-region, where the cryptobenthic fishes account for fully 40% of the energy use by reef fishes. This is a significant amount of energy given that this portion of the community is rarely included in reef surveys and, for that matter, rarely observed. Furthermore, total reef fish production may be even more highly influenced by the cryptobenthic group as our calculation of reef fish metabolism is a snapshot and does not account for their high growth rates. As many of these species are short-lived (Miller 1979), with several living no more than 1 or 2 yr, the turnover in the cryptobenthic fish community is high and may account for more production than slower growing, large species (Allen et al. 1992).

This is not the first study to consider the metabolic requirements of small fishes. Ackerman & Bellwood (2000) reported oxygen consumption for all size classes at several sites around Orpheus Island, Great Barrier Reef, Australia. They concluded that fishes less than 50 mm in length may be responsible for more than 25% of the community metabolic requirement and that fishes less than 100 mm in length may utilize over 57% of the community metabolism at a site, remarkably consistent with our site that had the highest proportion of community metabolism attributed to the cryptobenthic species group (Site 14, 56%). Most of the individuals in the smallest size classes at Orpheus Island were cryptobenthic species that were undersampled during visual surveys and better sampled using quantitative, extractive methods (Ackerman & Bellwood 2000). In a study of a very different fish assemblage (the mesopelagic zone of the California Current), Davison et al. (2013) determined that small individuals (those weighing less than 1 g) accounted for more than 40% of the carbon export to the deep sea (a function of oxygen consumption and vertical movement in their model), despite the presence of some much larger individuals. Their specimens were collected using quantitative net sampling (Davison et al. 2013).

Metabolism in ectotherms is not simply a function of biomass; it is also a function of environmental temperature (Gillooly et al. 2001). While examining metabolism at one time point for several sites provides a means to compare locations, it is interesting

to consider that even if biomass is in a steady state (however improbable), metabolic requirements in the marine environment can be expected to change with the local oceanography. At our study sites, temperature is known to vary widely, both temporally and spatially (Galland 2013). For illustrative purposes, we present a theoretical time series of metabolism for the year preceding fieldwork at one site in each of our sub-regions (Fig. 4). In order to derive these curves, we assumed that biomass is in a steady state for the entire year and utilized 31-d centered moving average temperatures (collected by *in situ* temperature loggers) to calculate metabolism for each day. Throughout the year, assemblage-scale metabolic requirements may change sharply, and at different rates and magnitudes, simply as a result of local temperature variability. Therefore, sites with widely different community metabolic requirements per unit area during one season may have similar energy requirements during another season (e.g. Fig. 4). These illustrations are heavily impacted by the high densities of small-bodied cryptobenthic fishes observed throughout the GOC, particularly in the north.

Conclusions

This is one of the few studies to quantitatively measure the contribution of cryptobenthic fishes to species richness, density, biomass, and metabolism of whole reef fish assemblages, and the only such study

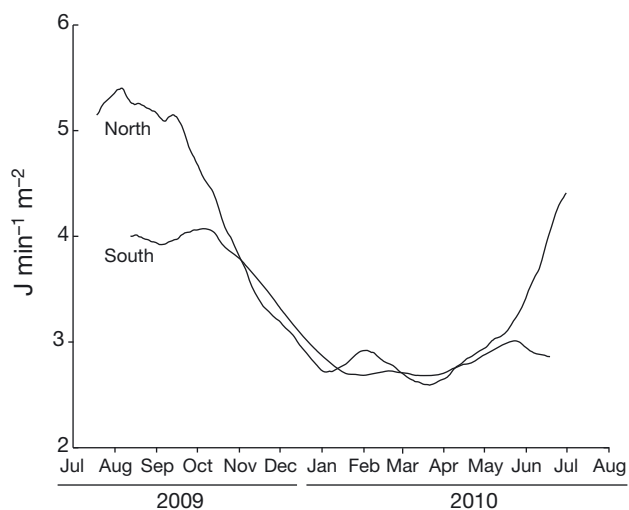


Fig. 4. Estimated community metabolism at individual sites in each of the 2 sub-regions (see Fig. 1), calculated using Eq. (1) with an assumed steady state of biomass and 31-d centered moving average temperatures recorded with *in situ* temperature loggers (Galland 2013)

for the GOC. Our results support the relevance of whole-community assessments and the need to consider all size categories in evaluations of community ecology among marine vertebrates. Many of the places around the world that are generally accepted as having the most intact reef fish communities (e.g. northern Line Islands, Sandin et al. 2008; Cabo Pulmo, GOC, Aburto-Oropeza et al. 2011; Cocos Island, Friedlander et al. 2012) have been quantitatively studied only for conspicuous fishes. Quantitative study of the cryptobenthic fishes in those systems would contribute to our understanding of ecological dynamics in relatively intact assemblages. If the general ratios of cryptobenthic to conspicuous fishes that we measured in the GOC are somewhat consistent across systems, then the density and diversity of reef fish assemblages in those systems may be considerably higher than reported. Community metabolism may change, and even biomass may increase in some cases. Such surveys in these remote places with intact fish communities may also provide results that look significantly different than those that we present here. The GOC has been heavily fished for decades (Applegate et al. 1993, Sala et al. 2004), and the indirect impact of fishing on cryptobenthic fishes is not well understood (but see Ahmadi et al. 2012).

The relationships between cryptobenthic and conspicuous fishes are likely complex. Estimates of species richness and fish density both increase considerably when cryptobenthic fishes are included in surveys. In some cases, the community metabolic requirements also increase significantly, despite the comparably minuscule percentage of total biomass contributed by this group of fishes. By continuing complete reef surveys of this nature, in the GOC and elsewhere, we can continue testing macroecological rules with marine fishes and investigate seasonal, spatial, and anthropogenic differences among reef ecosystems.

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