THE UNIVERSITY OF CALIFORNIA, SAN DIEGO

The Conservation and Ecology of Cryptobenthic Fishes on Rocky Reefs in the Gulf of California, Mexico

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Marine Biology

by

Grantly Russell Galland

Committee in Charge:

- Professor Philip Hastings, Chair
- Professor James Leichter
- Professor Richard Norris
- Professor Stuart Sandin
- Professor Jonathan Shurin

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The Dissertation of Grantly Russell Galland is approved, and it is acceptable in quality and form for publication on microfilm and electronically**:**

Chair

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This work is dedicated to my parents, who sacrificed to make sure their children learned and who fostered a sense of curiosity about nature in us from a very young age**.**

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VITA

2004	B.S. University of Georgia
2005-2007	United States Peace Corps Volunteer – Belize
2007-2012	Graduate Researcher, Marine Vertebrate Collection, University of California, San Diego
2009	M.S. University of California, San Diego
2013	Ph.D. University of California, San Diego

PUBLICATIONS

Galland GR, Harrould-Kolieb ER, Herr D (2012). The ocean and climate change policy. *Climate Policy* 12(6):764-771.

Galland GR, Pennebaker SL (2012). A benthic diatom bloom in the Gulf of California, Mexico. *BioInvasion Records* 1(1):65-69.

Aburto-Oropeza A, Erisman BE, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011). Large recovery of fish biomass in a no-take marine reserve. *PLOS One* 6(8):e23601.

Galland GR (2011). Comments on microhabitat specialization and a depth range extension for a chaenopsid tube blenny in the Gulf of California, Mexico. *Bulletin of the Southern California Academy of Sciences* 110(2):52-55.

Galland GR, Aburto-Oropeza O, Hastings PA (2011) Irregular schooling behavior and abandonment of mimicry by the Sabertooth Blenny (Blenniidae) in Cabo Pulmo National Park, Gulf of California, Mexico. *Coral Reefs* 30(1):215.

Erisman BE, Galland GR, Mascareñas-Osorio I, Moxley J, Walker HJ, Aburto-Oropeza O, Hastings PA, Ezcurra E (2011). List of coastal fishes of Islas Marías archipelago, Mexico, with comments on taxonomic composition, biogeography, and abundance. *Zootaxa* 2985:26-40.

Hastings PA, Galland GR (2010). Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae). *Coral Reefs* 29(1):155-164.

Lin H-C, Galland GR (2010). Molecular analysis of *Acanthemblemaria macrospilus* (Teleostei: Chaenopsidae) with description of a new species from the Gulf of California, Mexico. *Zootaxa* 2525:51-62.

Herr D, Galland GR (2009) *The Ocean and Climate Change: Tools and Guidelines for Action*. IUCN US Multilateral Office, Washington, D.C.

García Salgado M, Camarena T, Gold G, Vasquez M, Galland GR, Nava G, Alarcón G, Ceja V (2006). *Baseline of the Status of the Mesoamerican Barrier Reef Systems. Results of the Synoptic Monitoring from 2004 and 2005*. Mesoamerican Barrier Reef Systems Project, Belize City.

ABSTRACT OF THE DISSERTATION

The Conservation and Ecology of Cryptobenthic Fishes on Rocky Reefs in the Gulf of California, Mexico

by

Grantly Russell Galland

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Professor Philip Hastings, Chair

Cryptobenthic fishes are small-bodied, short-lived species that live in near constant contact with the reef surface and generally rely on crypsis as their main means of escaping predation. They constitute an important part of the reef fish community that is often not well understood. For this work, I investigated cryptobenthic fishes in the Gulf of California, Mexico, a basin noted for high productivity, high diversity of fishes, and heterogeneity of local environments. Specifically, I present the results of several studies designed to better understand the role of cryptobenthic fishes in the rocky reef fish community.

In Chapter 1, I place all subsequent results in a local, environmental context by quantifying the temperature variability at several sites across the Gulf. Chapter 2 concentrates on the biogeography of these fishes and details a quantitative analysis of the community dynamics of this group. In Chapter 3, I define the contribution of

cryptobenthic fishes to the wider fish community. In Chapter 4, I use historical samples to examine possible differences between the community structure of these fishes in 2010 and in the 1970s. Finally, in the Appendix, I report several novel natural history observations that I documented while conducting the research reported here. Each of these chapters builds toward a more complete understanding of cryptobenthic fish community ecology, in the Gulf and in general, than has previously been documented.

My results indicate that cryptobenthic fishes are a vital component of the reef fish community and may account for as much as 50% of the total energy requirements of and total species richness of reef fishes at sites in the Gulf. Furthermore, I confirm that the Gulf is, biogeographically, a particularly important region to new world cryptobenthic lineages and that endemism is high among cryptobenthic communities there. Finally, I quantitatively demonstrate, using Canonical Analysis of Principal Coordinates, that this component of the reef fish community was different in 2010 than in the 1970s, in both total and relative abundance, with some species represented by more than a 90% reduction in numbers, while others increased significantly. Prior to this work, the long-term stability of cryptobenthic communities had not been tested. The research presented here provides several new data sets to a growing field and may contribute to the understanding of marine community dynamics.

CHAPTER 1

The Shallow-reef Temperature Variability on Rocky Reefs in the Gulf of California, Mexico

Abstract

As part of a broad scale study to investigate the ecology and biogeography of rocky reef fishes and invertebrates, we quantified the temperature conditions of shallow reefs in the Gulf of California (GOC). We present the data from 43 *in situ* temperature loggers, across more than 5.5 degrees of latitude and 690 km, throughout the GOC. One third of the loggers were deployed at approximately 5 m depth at sites across the GOC, and the remaining instruments were installed at multiple depths at 10 sites around Espíritu Santo Island in the southern GOC off of La Paz Bay. Throughout our study region, the summer and the preceding period of steady increase in average water temperature were the seasons with highest daily temperature variability, and the winter and the preceding period of steady cooling were more stable. Summer maximum temperatures were similar from north to south, but winter minima were more variable and accounted for most of the differences in annual range among sites. High frequency variability differed among sites, and in the case of Espíritu Santo Island varied between the east and west sides of that island. Variability increased with depth at all sites around Espíritu Santo Island, and throughout our data set, there are examples where small depth changes and large latitudinal changes yielded similar magnitude temperature changes. The dynamic oceanography in the GOC creates fast return times for extreme temperature events, and at three of our sites, reef organisms can be expected to experience 5º C cold water anomalies, multiple times per month. Species living on shallow GOC reefs must be tolerant of high frequency temperature variability, at scales not reported in other basins around the

world. Quantifying the temperature environment can be an important tool when studying the ecology and status of reef ecosystems.

Introduction

An organism's fundamental niche is the product of its tolerance to physical variables, while its realized niche is impacted by ecological relationships (e.g., competition, predation) and is more restricted (Hutchinson 1957). Generally speaking, fundamental niches are temporally constant (in the absence of evolution or epigenetic changes to gene expression), while realized niches change based on the relative successes of other community members with overlapping distributions. A species' geographic range can fluctuate both as a function of its ecological interactions and its physiological tolerance (reviewed in Brown et al. 1996; Gaston and Blackburn 2000; Gaston 2009), especially in climatologically or oceanographically dynamic environments (Somero 2012). Therefore, measuring variation in the physical environment is an important tool for studying ecology and biogeography by quantifying the aspects of the physical environment that set the context for ecological interactions.

In the marine environment, most species are characterized by an ability to move great distances, either as larvae, adults, or both (Nybakken 2001). The magnitude and temporal scales of environmental variability at any particular location may influence whether or not a species can immigrate there, establish an ephemeral population, or expand its range to include that new location. Similarly, increased variability or environmental change within a species' range may lead to loss of populations at some sites, causing the range to contract (Somero 2012). Observing these expansions and contractions of species' ranges is especially relevant in shallow water marine ecosystems, which can be highly dynamic with respect to physical environmental variables such as temperature, salinity, and environmental energy (Walther et al. 2002; Belanger et al. 2012). These habitats are dominated by ectothermic animals with little or no ability to regulate their internal body temperatures (Somero 2012), and consistent long-term changes to water temperature have been shown to correlate with shifts in species distribution, both geographically (Perry et al. 2005; Zeidberg and Robison 2007) and in depth (Dulvy et al. 2008). Furthermore, seasonal, decadal, and longer-term changes in temperature may facilitate expansion in range of human-transported invasive species (Peterson 2003), such as the Red Lionfish in the western Atlantic Ocean (Kimball et al. 2004), in addition to those expanding from their native ranges along a continuous path, like the Jumbo Squid in the eastern Pacific Ocean (Zeidberg and Robison 2007).

Marine fishes experience physiological limits associated with minimum and maximum temperature thresholds, and these thresholds can change on evolutionary timescales, with some pairs of sister species exhibiting tolerance to substantially different temperature ranges (Graham 1971). Laboratory-recorded thresholds may not be the best measure of temperature tolerance, however, as temperature is known to affect fish behavior, well within the tolerable range (Biro et al. 2010). These changes are not always consistent and can lead to behavioral "personality" changes – when the magnitude of an individual’s behavioral response is different, relative to other individuals in a group (Biro et al. 2010). As individuals become more or less active, more or less aggressive, and bolder or less so – potentially at different rates of change – their relative ability to capture prey, avoid predation, and dominate conspecifics can change, all as complex functions of environmental temperature (Biro et al. 2010). These behavioral and personality changes may threaten survival of individuals who find themselves outside of the narrower temperature range that is most characteristic of their natural environment (Figueira et al. 2009). Similarly, inter-specific differences in behavioral change may be particularly important with respect to prey capture and predator avoidance. As poleward shifts in distribution are often mentioned as a means for species living near their upper physiological temperature threshold to adapt to ocean warming, it is important to consider how oceanographic variability may lead to sporadic (or regular) low temperatures that alter the behavior, personality, or survivability of species with a tropical affinity.

These issues are especially relevant near transitions between tropical and temperate areas such as the Gulf of California (GOC), Mexico. The GOC is located at the intersection of tropical and temperate zoogeographic provinces in the eastern Pacific (Walker 1960, Rosenblatt 1967) and is also a highly dynamic ocean basin known for its seasonal and higher frequency changes in flow (e.g., currents, eddies, etc.), productivity, and temperature (Alvarez-Borrego 2010). These characteristics, along with its narrow shape and semi-enclosed nature, make the GOC an ideal place to study the effect of the thermal environment on marine organisms. Here, we present a snapshot data set from a large-scale study using *in situ* temperature loggers to describe the seasonal and daily temperature variability on shallow rocky reefs throughout the GOC, and we calculate the return time for extreme daily temperature values that may affect the reef community. The spatial scale of this study, 16 sites across more than 5.5 degrees of latitude and 10 additional sites around one island, is larger than previously attempted in the GOC or elsewhere.

Methods

Study Site

The GOC (Fig. 1.1a) is a long (~1100 km), narrow (~150 km), semi-enclosed basin characterized by dynamic oceanography resulting from its shape, location, and geology (reviewed in Alvarez-Borrego 2010). The North American monsoon blows along the GOC's long axis from the southeast during the summer and from the northwest during the winter (Paden et al. 1991). This switch produces different upwelling patterns for opposing coasts and leads to an annual reversal in the direction of the overall average circulation (Paden et al. 1991). The GOC's narrow shape, however, allows for upwelled water masses at one coast to advect to the other coast before undergoing significant change at the surface (Badan-Dangon et al. 1985; Pegau et al. 2002). The entire GOC is recognized for highly dynamic oceanography, and internal waves have been studied there since at least 1939, using both *in situ* instrumentation and remote sensing (e.g., Munk 1941, Fu and Holt 1984, Badan-Dangon et al. 1991, Filonov and Lavín 2003, etc.). Strong internal waves are generated near the GOC mouth, through interactions with the open Pacific Ocean (Munk 1941), and near the Midriff Islands, as a result of the strong tidal wave interacting with shallow sills between islands there (Fu and Holt 1984, Badan-Dangon et al. 1991, Filonov and Lavín 2003). Internal waves are known to affect the ecology of reefs in other systems (Leichter et al. 1996, 1998), and shallow water organisms in the GOC may experience very different physical environments, depending on their location and the complex interactions between local upwelling, distant upwelling, surface flow from the Pacific, and solar heating.

Observations

As part of a large study to characterize GOC rocky reefs, we conducted *in situ* temperature studies, at two spatial scales, from 2009-2011. In order to characterize the temperature variability on shallow rocky reefs throughout the GOC, we installed Hobo Pro v2 Water Temperature Data Loggers (0.2° accuracy, 0.02° resolution, 5 minute response time) on 16 reef sites over an area stretching from Puerto Refugio at the northern tip of Angel de la Guarda Island in the Midriff Islands to Cerralvo Island south of La Paz Bay (Fig. 1.1a). Sites were chosen based on previously conducted faunal surveys or ongoing semi-regular community monitoring (Table 1.1). At each site, two loggers were installed directly to the rocky reef surface via stainless steel eyebolts. Installation depth was typically 5-6 m, but reef bathymetry and proximity to survey areas required us to install some loggers at slightly shallower sites (Table 1.1). The data loggers recorded temperature at 20-minute intervals, from July 2009 to July

2010.

To measure differences in water temperature at a significantly smaller scale, we installed a second set of data loggers at 12 sites around Espíritu Santo Island (and its associated islets) at the mouth of the La Paz Bay (Fig. 1.1b). While the study sites for the broader GOC study stretched across 690 km and 5.5 degrees of latitude, the sites around Espíritu Santo Island stretched across only 24 km and included locations along the bay side of the island, as well as the side open to the wider GOC (Fig. 1.1b). Furthermore, in order to quantify the effect of depth on temperature at this island, we installed loggers at multiple depths at each site. As in the broader GOC study, we bolted loggers directly to the reef surface, but at the Espíritu Santo Island sites, we installed one logger at each of 5, 10, 15, and 20 m depths, where possible. The rocky reef at some of these sites ends before 20 m depth, limiting the number of installations (Table 1.2). We also recorded distance from shore of each deployment in order to calculate a simple measure of reef slope at each site. All data loggers around Espíritu Santo Island recorded temperature at 20-minute intervals, from November 2009 to May 2011.

Analysis

For each site where two data loggers were recovered, time series were very similar (identical at most time points). In order to obtain a single time series for those locations, we used the mean value at each time point for the two loggers. At some sites, only one of two loggers was recovered or only one logger was installed, and the time series from that logger is considered representative of the site.

Descriptive Statistics: For each temperature series (both spatial scales, every site, every depth), we calculated the daily minimum, maximum, and mean temperatures and used those values to calculate the descriptive statistics (mean, standard deviation, range, minimum, maximum) in daily values for the full time series. In order to remove high frequency variability from the raw data, we also calculated a 31-day centered moving average. Based on a visual survey of the raw data and the moving average that revealed different variability regimes with respect to season, we recalculated several statistics for two seasons: May-October ("summer season") and November-April ("winter season"). We used these values to compare within-island, among-island, and among-depth variability through time.

For five sites around Espíritu Santo Island with loggers installed at 5, 10, and 15 m depth (sites D, F, H, J, and K), we calculated stratification as the difference in the 31-day centered moving average divided by the difference in depth between loggers. In order to determine which parts of the upper water column experience the greatest temperature change with depth, we calculated this value separately for each five meters (5-10 m, 10-15 m, and 15-20 m, where possible).

Time Series Analysis: In order to compare the frequency of temperature variability among sites, we transformed data, using fast Fourier transformation (FFT), and calculated a power spectrum for each time series. To produce smooth spectra, we used Welch's method of averaging replicate spectra calculated from a series of non-overlapping 14-day (1009-data point) sections of the transformed data using the computer program Matlab 7.1. In addition to comparing the peak heights at the diurnal (S1 = solar tide) and approximately semidiurnal (12.4 hour – M2 = lunar tide) frequencies among sites, we compared the area under the power spectrum curves within two frequency bands around the S1 (1/18 to 1/33 cycles per hour) and M2 (1/11 to 1/14 cycles per hour) peaks, after Lerczak 2001. Area was calculated by integrating the power spectral density function across these ranges of frequencies and is the frequency-specific estimate of variance. The square root of this value is the root mean square (rms) temperature amplitude in degrees. We also calculated the rms amplitude for the entire time series by integrating the power spectral density function across the full range of frequencies (1/14 cycles per day to 1/40 cycles per minute).

Temperature Anomalies and Return Times: For each day in each temperature record, we calculated the minimum temperature anomaly as the difference between that day's minimum temperature and the 31-day centered moving average. These values were then used to calculate the estimated median return time for a given extreme event and the estimated magnitude of the most extreme event in a given time period using the methods of Gumbel (1958), Jacocks and Kneile (1975), and Galambos (1987). These methods, applied to ecological data by Denny and Gaines (1990) and Gaines and Denny (1993) and to a temperature time series by Leichter and Miller (1999), involve a four step process to determine the probability that an extreme value, x_i, in a single time interval will be less than or equal to a given value, x:

$$P(x) = \text{Prob}(x_i \leq x). \qquad \text{(Equation 1.1)}$$

To estimate the probability function, $P(x)$, we: 1) divided the data into a series of equal length intervals (1 day); 2) recorded the extreme value in each interval; 3) ranked extreme values by magnitude; and 4) fit a continuous probability function to their cumulative distribution (reviewed in Denny and Gaines 2000). When anomalies are equally distributed, this probability function approaches an asymptotic form:

$$P(x) = \exp -[(\alpha-\beta x)/(\alpha-\beta\varepsilon)]^{1/\beta}, \qquad \text{(Equation 1.2)}$$

with the following qualifications:

if $\beta > 0$, $P = 1$ for $x \geq \alpha/\beta$,

if $\beta < 0$, $P = 0$ for $x \leq \alpha/\beta$.

Estimates of α (the rate of increase of $P(x)$ with the natural logarithm of time), β (which, when divided into α, estimates the maximum achievable extreme value), and ε (the mode value) were found using maximum likelihood, nonlinear curve fitting in the computer program Matlab 7.1 and used to solve $P(x)$. The estimated return time (median number of days between successive extreme occurrences, x), $\tau(x)$, is equal to the inverse of $1-P(x)$:

$\tau(x) = 1/(1-P(x))$. (Equation 1.3)

Results

Seasonal and Spatial Patterns

An example of the raw data is plotted in Fig. 1.2a along with the 31-day centered moving average. This series (site A), while longer than most other series, is representative of the seasonal patterns we observed across the GOC. The warmer summer period, along with the preceding period of general increase in average temperature, is characterized by a high level of variability around the mean (Fig. 1.2b). By comparison, there is a striking lack of variability around the mean during the period of general decrease in average temperature (Fig. 1.2c), and the cooler winter months represent a transition between these two periods. While Fig. 1.2 is representative of the seasonal patterns observed at our other shallow rocky reef sites, the difference in temperature variability between the two seasons is not particularly strong at this southern site. Most of our sites are characterized by an even greater seasonal difference, seen clearly in Fig. 1.3, where the mean within-day range at site 1 (= the first 12 months of site A; Fig. 1.2a) is more similar for the winter and summer seasons than at other sites. That figure also shows a plot of maximum within-day range and the annual range of the full time series. At 8 of 16 sites, more than 40% of the total annual temperature range was observed during a single day, at least once. More than 50% of the total range was observed during a single day at two sites (sites 1 and 15).

A plot of 31-day running means for all of our sites across the GOC shows seasonal patterns on a wide spatial scale (Fig. 1.4). Even while temporal variability in temperature during the summer is significantly higher than during the winter at any given site, winter is the more variable time, when comparing among sites. The largest difference in mean temperature among sites occurs during the winter. General differences in average temperature among sites seem to be driven by the faster rate of change, during both periods of general decrease and increase, observed at cooler (usually more northern) sites (Fig. 1.4). Differences in the unfiltered data, among sites, are also seasonal: the maximum recorded temperature for each site falls in a narrow window of 29°-31° C, while the minimum recorded temperatures fall between 14° and 21° C. These findings corroborate our observation that the cooler sites are those with the largest annual range (Fig. 1.3).

An examination of 31-day mean temperatures for multiple depths at several sites around Espíritu Santo Island reveals a pattern of spatial variability and stratification during the summer season, with greater homogeneity during the winter season (Fig. 1.5). Observable stratification of mean temperatures at any given site during the summer, but not during the winter, follows a similar pattern to the variability for any individual time series, described above. However, spread among sites around the island exhibits the opposite pattern than the one we observed for the wider GOC. Spatial differences among sites (for depths of 5, 10, and 15 m) are greatest during the summer season and nearly absent during the winter season.

Calculations of stratification at five sites around Espíritu Santo Island confirm that the water column over shallow reefs (to 20 m) is relatively well mixed during the winter season and more stratified during the summer season (Fig. 1.6). In general, temperature decreases 0.15 – 0.30º C per meter during the summer months and is constant with depth during the winter months. At most sites, the temperature stratification is stronger within the deeper bins (10-15 m and 15-20 m) than in the shallower bin (5-10 m), though site H seems to follow an opposite pattern (Fig. 1.6a).

Time Series Analysis

Figure 1.7a depicts a power spectrum for the raw data shown in Fig. 1.2. Note the two strong peaks located at frequencies of one cycle per day and approximately two cycles per day, demonstrating that much of the temperature variability within that data set is concentrated at the S1 and M2 frequencies. Peaks to the right of these daily and semidiurnal peaks may represent harmonics of those peaks or they may represent some unidentified internal wave activity.

To contrast with the southern site displayed in Fig. 1.7a, in panels b and c, we display a power spectrum from our most northern site (site 16) and one from a site in the Midriff Islands (site 11). Differences in peak height and width and in overall area under the curve reflect differences in variability among sites. Figure 1.7c, in particular, represents a site that is characterized by a strong semidiurnal peak, an example of a site where tidal influence on temperature variability is strong. Figure 1.7d provides the power spectra from four depths at one site from Espíritu Santo

Island (site F). Analysis of data from this site, representative of other sites at that island, shows the increasing contribution of both the daily and semidiurnal peaks to overall temperature variability with increasing depth. There is also a relative increase of the semidiurnal peak, compared to the daily peak, at deeper depths. Finally, it is interesting to note that the spectrum in panel c (5 m data) more closely aligns with the spectrum in panel d for the 10 m data than for the 5 m data, implying a more variable environment at shallower depths at that site. Throughout our data set, there are several examples of similar instances where small changes in the depth dimension and large changes in the spatial dimension yield similar magnitude changes in variability.

In Fig. 1.7a, the portions of the spectrum inside the two sets of vertical bars, labeled S1 and M2, represent the part of the curve integrated to calculate the variance associated with the daily and approximately semidiurnal peaks, respectively. The rms values for both peaks and for the whole curve are shown in Fig. 1.8a for all sites across the GOC. Values for the total area, the S1 band, and the M2 band for sites at Espíritu Santo Island are plotted in panels b-d. Among 24 sites with temperature records from approximately 5 m depth (wider GOC sites plus Espíritu Santo sites), all but three are characterized by a higher rms temperature amplitude around the S1 peak than around the M2 peak. The three sites where the rms amplitude is higher for the M2 peak are all located in the Midriff Islands region, as is the site with the highest rms amplitude for the total spectrum.

Reviewing only the sites around Espíritu Santo Island (Fig. 1.8b-d), total, S1, and M2 rms amplitude increases with depth at all sites. There are no exceptions in our data set. A Mann-Whitney-U Test of rms amplitude between sides of the island - the west side faces the La Paz Bay (sites A-G) and the east side faces the wider GOC (sites H-L) - reveals significant differences in total and S1 values at 5, 10, and 15 m between sides and a significant difference in M2 values at 5 m ($P < 0.01$ in all tests). In all of these cases, the value is higher for the east side of the island. While we only have 20 m depth data from two sites, the values for the site on the east side are higher than those from the west side for total, S1, and M2 rms amplitudes. These differences are not a result of different reef slopes, as a Mann-Whitney-U Test confirms that the slopes at the east sites are not significantly different from the slopes at the west sites ($P > 0.05$; east sites median = 3.1 m from shore per m increase in depth; west sites median = 3.5 m from shore per m increase in depth).

Return Time

Figure 1.9 displays minimum daily anomaly data from two representative sites (Fig. 1.9a-b), with fitted curves of the form of Equation 2. The graphs in Fig. 1.9c-d are plots of Equation 3, used to estimate return times for anomalies of any magnitude or to estimate the maximum anomaly for any given time period. Using this method, we calculated return times for temperature anomalies of 2-5 degrees for each site across the GOC (Table 1.3) and for every site and depth around Espíritu Santo Island (Table 1.4). The whole-GOC values are given for summer period data only, as summer is the more variable season (discussed above) and the most active time for spawning and recruitment of reef organisms. Return times calculated from winter data for those sites were all greater than 1000 days for anomalies ≥ two degrees, except two sites that had return times of 13 (site 11) and 39 days (site 14) for a two-degree anomaly. These winter findings are consistent with our other observations that the winter period is characterized by minimal high frequency variability.

The Espíritu Santo Island values (Table 1.4) are reported by depth and are not divided by season. While the summer is again the more temporally variable season, the summer data for the 10, 15, and 20 m data sets do not adhere to the assumption of stationarity. The ranked and sorted anomalies did not follow the form of Equation 2 and were therefore not properly fitted by that equation. We suspect that, with more summer data, the ranked and sorted anomalies would begin to take that form. Ranked and sorted anomaly data for the full time series were of the expected form. Estimated return times of extreme events decrease with depth (Table 1.4). In other words, cold anomalies of 2-5 degrees are expected to occur more frequently on deeper reefs. Furthermore, similar to the time series analysis described above, sites along the east side of Espíritu Santo Island are more variable, with shorter return times expected for extreme events than for sites along the west.

The values of α, β, and ε estimated using Equation 2 and the observed data for all time series are reported in Tables 1.3 and 1.4. With these coefficients, estimated return time for anomalies of any magnitude and estimated maximum anomaly for any time period can be calculated for all of our sites using Equation 2.

Discussion

Our study indicates that well-documented oceanographic features in the GOC, such as tidal upwelling, coastal upwelling, and eddy formation, translate into extraordinarily high temperature variability on the shallow rocky reefs along the Baja Peninsula and the islands throughout the western GOC. Through our observation of daily ranges and calculation of estimated return times for extreme events, we found this variability, along with stratification of the shallow water column, to be seasonal, with the summer period generally more variable than the winter period. This seasonal pattern coincides with the northeastward direction of the average GOC winds during the summer months (Paden et al. 1991) that promotes Ekman transport away from the Baja Peninsula and coastal upwelling along the GOC's western boundary (Talley et al. 2011). If coastal upwelling and other higher frequency wind-driven processes are predominately responsible for temperature variability during the summer, we would expect variability to diminish beginning in November when the winds begin to subside (Alvarez-Borrego 2010), followed by a steady decrease in average temperature associated with surface cooling. We see this general pattern for all of our sites. Future research may reveal an opposite pattern along the eastern boundary, where coastal upwelling is expected in the winter period, resulting from the southeastward average wind direction during that time (Paden et al. 1991). Local oceanographic features and local winds are certain to influence these patterns as well.

This observation of a seasonal pattern to temperature variability on shallow reefs is not unique to the GOC and has been observed at several sites around the tropical western Atlantic Ocean (Leichter et al. 2006), at Diego Garcia Atoll in the central Indian Ocean (Sheppard 2009), along southeast Australia (Malcolm et al. 2011), off of central Chile (Kaplan et al. 2003), and in Moorea, French Polynesia (Leichter et al. 2012), among other places. As in our study area, sites around the tropical western Atlantic, in southeast Australia, off of Chile, and around Moorea have the highest temporal variability in temperature during the warming months and are more stable during the cooling months. Sites at Diego Garcia Atoll show the opposite pattern; the cooling period is the more variable time (Sheppard 2009), implying the presence of a well-mixed water column during a period of steady warming and a stratified water column during a period of steady cooling. The causes of those opposite observations at Diego Garcia Atoll are unknown.

Summer maximum temperatures are similar across our study sites, while winter minimums are quite different. Again, the tropical western Atlantic shows a similar pattern, with winter minimum temperatures responsible for most of the differences in annual range among sites (Leichter et al. 2006). In both basins, shallow waters seem to have some maximum temperature between 31 and 32º C that most sites approach, regardless of latitude. Minimum shallow-water temperatures, on the other hand, are affected by both latitude and local oceanographic processes. Interestingly, Barnes et al. (2006) found an opposite pattern for polar waters north of Antarctica. There, winter minimum temperatures are similar across several sites, but summer maximums are higher with decreasing latitude (Barnes et al. 2006); summer temperatures drive variability in annual range. In combination with the differences in magnitude of average temperatures in these regions, differences in seasonal temperature variability may influence physiology of organisms living at these very different latitudes.

The GOC is a dynamic ocean basin. While temperature variability in the GOC shows similar patterns to other basins, such as the tropical western Atlantic, the magnitude of the variability is greater and the likelihood of extreme events is higher in the GOC. The rms temperature amplitude is higher at all of our sites across the wider GOC (3-5 m depth) than all the tropical western Atlantic sites where Leichter et al. (2006) analyzed time series from 10 m depth. Similarly, though return time for extreme events varies across the GOC, some of our sites have shorter expected summer return times for 5º C anomalies at approximately 5 m depth than expected for 2º anomalies in the Florida Keys (Leichter and Miller 1999), one of the most variable parts of the tropical western Atlantic (Leichter et al. 2006). Furthermore, for larger anomalies (4-5º C), three GOC sites at 5 m depth have shorter expected return times than a 30 m depth site in Florida (Leichter and Miller 1999). In some parts of the GOC, very shallow rocky reef organisms experience temperature variability akin to that at 30 m in one of the most dynamic parts of the tropical western Atlantic. Reefs in the GOC experience highly dynamic subtidal thermal conditions.

Among our sites, San Pedro Martir (site 11) has the shortest return times for the most extreme cold water anomalies (Table 1.3) and has the highest rms amplitude for the full time series and the S1 and M2 bands of the power spectrum (Fig. 1.7). San Pedro Martir has the most dynamic temperature conditions at 5 m depth in our study region. That island lies in the east-west center of the GOC and is very close to the latitudinal center as well (Fig. 1.1a). It is also the southernmost island in the Midriff Islands. As a result of its location, San Pedro Martir may experience different oceanographic features from either coast and from the other Midriff Islands. The only three sites where the M2 tide had a higher rms amplitude than the S1 daily variability (Fig. 1.7) are also located in the Midriff Islands (Fig. 1.1a). The Midriffs are recognized as having nearly constant upwelling (Badan-Dangon et al. 1985) and strong internal wave activity (Fu and Holt 1984, Badan-Dangon et al. 1991, Filonov and Lavín 2003), both associated with the tidal wave that strikes a series of shallow sills in that area, driving vertical mixing down to 300 m or more (reviewed in Alvarez-Borrego 2010). Given the particularly dynamic nature of internal waves and the magnitude of vertical movement of water masses in that region, it is not surprising that shallow sites there are some of the most dynamic in the GOC. This consistent daily and tidal mixing does not always coincide with our shortest estimated return times of cold water events, however, as two sites further south (sites 8 and 9) join San Pedro Martir as the sites with highest frequency of cold extremes (relative to their monthly average; Table 1.3).

Spatial differences in frequency of extreme events do not follow a simple geographic pattern, and it is important to consider the local processes that interact with GOC-wide features to shape reef-scale oceanography. Our Espíritu Santo Island sites provide an interesting example of measurable differences on either side of a single island. These observations are not caused by differences in reef slope but may be the result of proximity to deep water or could hint at the presence of higher amplitude internal waves on the east side of the island, facing the wider GOC, than on the west side of the island, facing La Paz Bay. If strong internal waves are associated with summer wind patterns, then they may explain the spread in mean temperature among sites during the summer at Espíritu Santo Island, but not during the winter when the winds show different patterns (Fig. 1.5). Regardless of the underlying cause, the physical environment of the organisms living on these reefs is variable in both time and space, and these meso-scale processes likely affect their biology, as well as the physics that we observe there. For example, subtle differences in variability from one side of an island to the other may lead to differences in the reef community across very short distances, even when the average stratification appears similar.

While there are spatial differences in temperature variability among sites across the GOC and within sites at Espíritu Santo Island, the biggest increase in variability is associated with increased depth. Mobile organisms living at 5 m (“shallow”) at a relatively stable site in the GOC may experience “shallow” Midriff Island-like temperature variability when moving to depths of only 10 m. The same would be true for species that are immobile as adults but that settle at different depths after a larval stage. Small depth differences can yield changes of a similar magnitude to very large horizontal, spatial differences. However, many reef communities are known to exhibit depth zonation with shallow species excluded from deeper reefs (e.g. Lindquist 1985), so successful changes in depth by individuals or by species in systems where depth zonation affects community dynamics may not happen frequently.

High-frequency variability in temperature on rocky reefs of the GOC must have implications for the organisms that live there. These implications likely differ for species with centers of distribution inside the GOC and those with a more tropical affinity. For example, during a long series of tide pool collections in the northern GOC, Thomson and Lehner (1976) demonstrated that cold-water events generally favored endemic fishes, at the expense of some species with a more tropical affinity. The tropical species suffered high mortality, significantly decreasing their relative abundance during especially cold periods. Those tropical species thrived in, and often dominated, the area during much of the study period, but the most extreme cold temperatures reduced their levels of numerical success (Thomson and Lehner 1976). Similar examples may be expected for GOC invertebrates.

A high frequency of cold-water events may also increase the likelihood that fishes undergo behavioral changes associated with temperature. In controlled laboratory experiments, Biro et al. (2009) observed behavior and personality changes in juveniles of an Australian damselfish with only a 2-3º C change in temperature. There are few places in our study area where newly-settled, juveniles would *not* experience 2-3º degree anomalies, multiple times, within their first month post-settlement, with expected 5º anomalies occurring in that time at three sites (Table 1.3). These anomalies may affect juvenile behavior (e.g., through reduced activity), influencing their ability to capture food and escape predation. Settlers of species near the edge of their range, without a long evolutionary history in GOC-like variability, may be unable to survive such frequent changes in temperature, even before physiological thresholds are reached. Transitions into or out of the GOC may involve crossing thresholds in environmental variability that could make dispersal difficult. Even as tropical species experience more frequent warm water events in their native ranges that are physiologically limiting, intermittent cold-water events may prove to be too extreme to facilitate establishment of populations. Here, we show that the GOC, in particular, is a place where cold-water events occur frequently and are particularly strong.

The high frequency and large magnitude of temperature fluctuations we observed have potentially significant implications for the survival of reef organisms in the GOC. They imply that the probability of survival of recently-settled reef organisms may differ between islands, around a single island, and across depths in the GOC. Similarly, established adults may experience radical departures from temperature norms at some sites, especially during the summer months. Given this environmental mosaic, successful GOC species must be highly tolerant of temperature variability or face strong and perhaps somewhat unpredictable selective pressures. Local selection could account in part for the strong genetic structure observed in marine species with dispersive larvae (Marshall et al. 2010), including some in the GOC (e.g., Riginos and Nachman 2001; Riginos 2005; Lin et al. 2009).

Quantifying fine-scale spatial and temporal temperature variability can provide an important tool for studying reef faunas. The dynamic nature of systems like the GOC is evidently not captured by measurements of sea surface temperature alone. In addition, *in situ* time series provide the potential to document the local temperature regime for the entire lifetimes of relatively short-lived, immobile species. For longer-lived species, temperature time series provide a physical data set to complement surveys, faunal collections, and other biological metrics. Wider incorporation of detailed data on environmental variability promises increased insights into our understanding of the factors controlling the fine-scale distribution and abundance of marine species.

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Table 1.1. Meta data for sites across the broader Gulf of California

Code	Site	Latitude (ºN)	Longitude (ºW)	Sampling Depth (m)	Mean Temperature (ºC)
1	Gallina	24.4575	110.3833	5	24.66
2	El Embudo	24.5803	110.4000	5	24.36
3	Cerralvo	24.3263	109.9369	5	25.21
4	San Francisquito	24.8207	110.5773	6	24.67
5	Santa Cruz	25.2608	110.7273	5	24.78
6	Monserrate	25.7101	111.0331	5	25.23
7	Carmen	26.0165	111.1686	5	24.46
8	Coronado	26.1174	111.2865	5	23.95
9	San Marcos	27.2563	112.0948	3	23
10	Santa Inez	27.0594	111.9090	3	23.77
11	San Pedro Martir	28.3857	112.3133	5	21.96
12	Las Animas	28.7053	112.9338	5	20.75
13	Partida	28.8867	113.0470	3	21
14	Punta Quemada	28.9504	113.4251	5	20.63
15	Alcatraz	29.1663	113.6068	5	20.4
16	Puerto Refugio	29.5502	113.5474	5	21.51

Table 1.2. Meta data for sites around Espíritu Santo Island outside La Paz Bay. *Mean temperatures reflect the time series from 5 m depth

Code	Site	Latitude (ºN)	Longitude (ºW)	Sampling Depth (m)	Mean Temperature (ºC)*
A	Gallina	24.4650	110.3900	5	23.43
B	El Embudo	24.5801	110.3999	5	23.09
C	ES Southwest	24.4477	110.3840	5, 10	23.37
D	Ballena	24.4793	110.4090	5, 10, 15	23.36
E	ES West	24.5476	110.4150	5, 15	23.39
F	La Tijareta	24.5712	110.4151	5, 10, 15, 20	23.25
G	Los Islotes West	24.5969	110.4020	10	n/a
H	Los Islotes East	24.5985	110.3900	5, 10, 15, 20	23.36
I	ES Northeast	24.5620	110.3670	10, 15	n/a
J	ES Pillar	24.5042	110.3056	5, 10, 15	23.46
K	ES Southeast	24.4650	110.2980	5, 10, 15	23.47
L	Suanee Reef	24.3869	110.3158	7	n/a

Table 1.3. Estimated median, summer return time for extreme temperature anomalies for sites across the Gulf of California. #Site codes reflect those assigned in Table 1.1. * indicates return times > 1000 days

Site Code#	2º C	3º C	4º C	5º C	Coefficient Values		
	Return Times (days)				a	b	e
1	*	*	*	*	0.8773	0.5652	0.2896
2	5	11	25	53	0.8467	-0.1072	0.5349
3	11	30	74	163	0.5877	-0.1504	0.2363
4	8	37	247	*	0.8781	0.1011	0.5086
5	9	27	81	239	0.7741	-0.0331	0.2940
6	6	13	25	47	0.8876	-0.1554	0.1797
7	5	10	17	27	1.1289	-0.1902	-0.0738
8	5	9	14	21	0.6963	-0.4274	0.2141
9	4	10	21	43	0.8506	-0.1119	0.6779
10	6	11	20	34	0.9553	-0.1803	0.1582
11	2	4	8	18	1.6726	0.1249	1.4260
12	8	245	*	*	1.0005	0.2778	0.8301
13	8	105	*	*	1.0765	0.2747	0.6224
14	4	14	88	*	1.3773	0.2386	0.6276
15	3	8	24	101	1.4871	0.1787	0.7453
16	8	23	65	174	0.7503	-0.0582	0.3615

Table 1.4. Estimated median return time for extreme temperature anomalies for all depths at sites around Espíritu Santo Island. #Site codes reflect those assigned in Table 1.2.
* indicates return times > 1000 days

Site Code#	Depth (m)	2º C	3º C	4º C	5º C	Coefficient Values		
		Return Times (days)				a	b	e
A	5	79	338	*	*	0.2725	-0.1654	0.1268
B	5	10	18	29	42	0.3267	-0.4950	0.2305
C	5	28	83	196	400	0.2938	-0.2469	0.2203
C	10	17	37	67	108	0.2834	-0.3978	0.1752
D	5	33	99	239	494	0.3003	-0.2387	0.1657
D	10	13	27	45	69	0.2994	-0.4528	0.1758
D	15	6	9	13	16	0.3390	-0.7436	0.2409
E	5	27	79	182	362	0.3068	-0.2546	0.1803
E	15	7	12	17	24	0.3819	-0.6027	0.2143
F	5	18	42	81	139	0.3271	-0.3378	0.1615
F	10	9	15	23	33	0.3465	-0.5523	0.1981
F	15	6	10	14	19	0.3784	-0.6387	0.2757
F	20	5	8	12	17	0.5142	-0.5718	0.4202
G	10	8	14	21	30	0.3043	-0.5608	0.2860
H	5	8	14	23	33	0.3280	-0.5203	0.2954
H	10	6	10	14	19	0.3089	-0.6484	0.3569
H	15	5	7	10	13	0.3534	-0.7105	0.4178
H	20	4	6	9	13	0.4925	-0.5718	0.5267
I	10	5	8	11	15	0.3599	-0.6828	0.3662
I	15	4	6	8	11	0.4034	-0.7235	0.4655
J	5	9	20	39	68	0.4548	-0.2998	0.3252
J	10	6	11	18	26	0.4247	-0.4773	0.3646
J	15	5	8	13	18	0.4643	-0.5312	0.4145
K	5	12	27	52	91	0.3958	-0.3113	0.2733
K	10	7	14	22	34	0.4150	-0.4417	0.3240
K	15	5	9	14	20	0.4521	-0.5298	0.3712
L	7	17	41	82	146	0.3349	-0.3093	0.2215

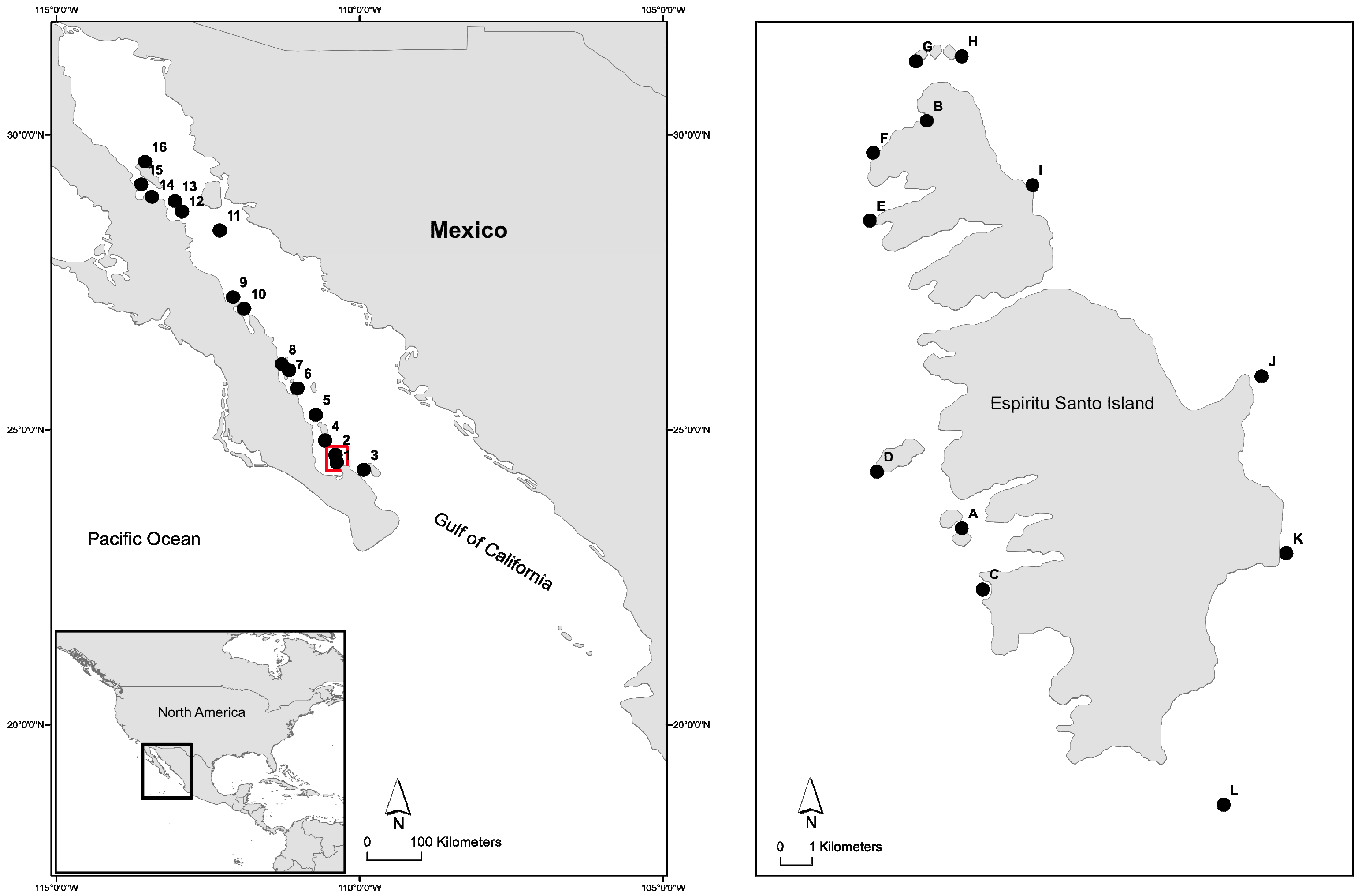

Fig. 1.1. Map of study sites a) across the Gulf of California and b) around Espíritu Santo Island

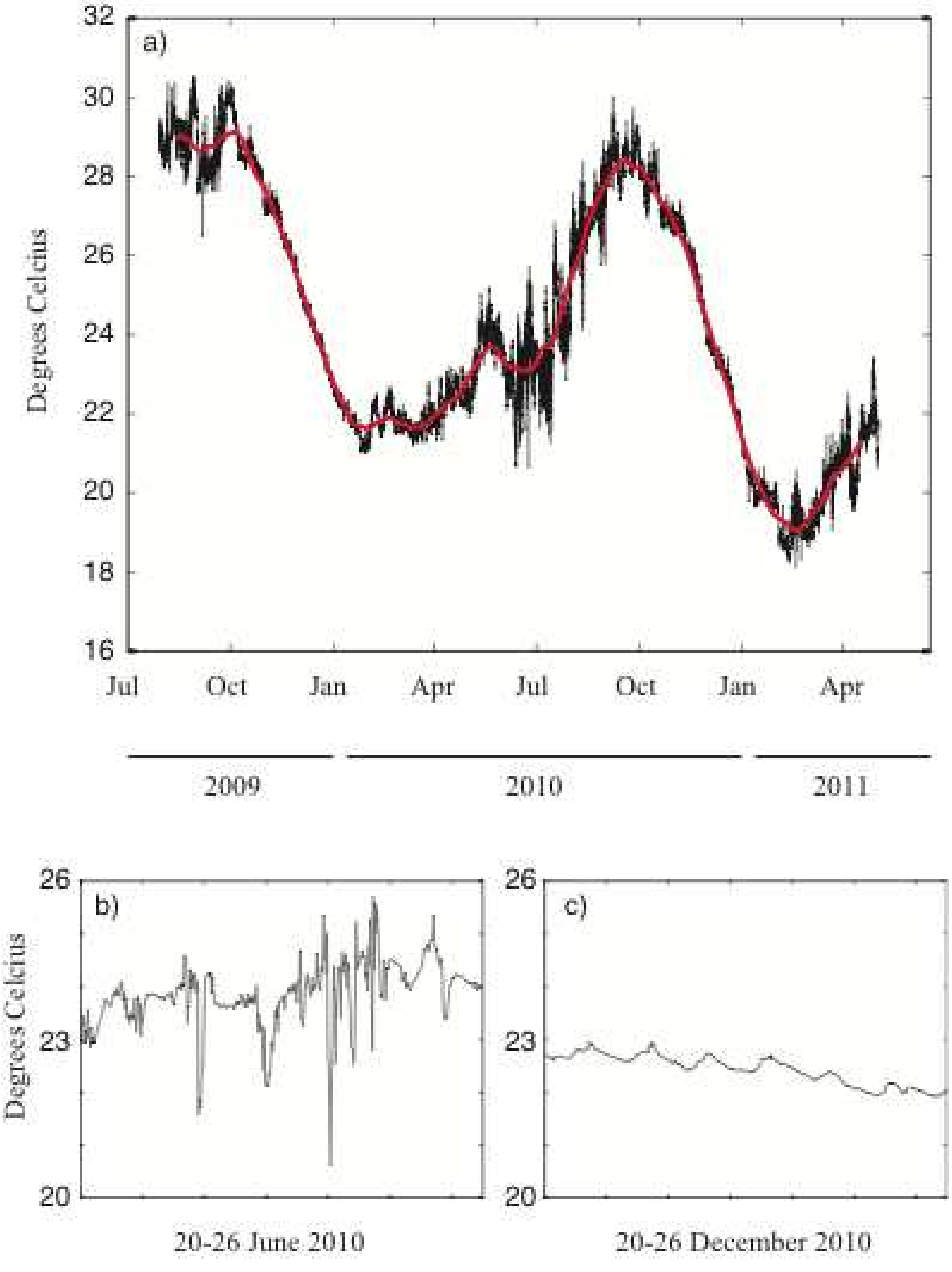

Fig. 1.2. a) Unfiltered temperature time series from a representative site in the southern GOC composed of time series from site 1 (Table 1.1) and site A (Table 1.2), plotted with 31-day centered moving average (red). Below are unfiltered data from one week in b) June and c) December. Note the difference in the vertical axis

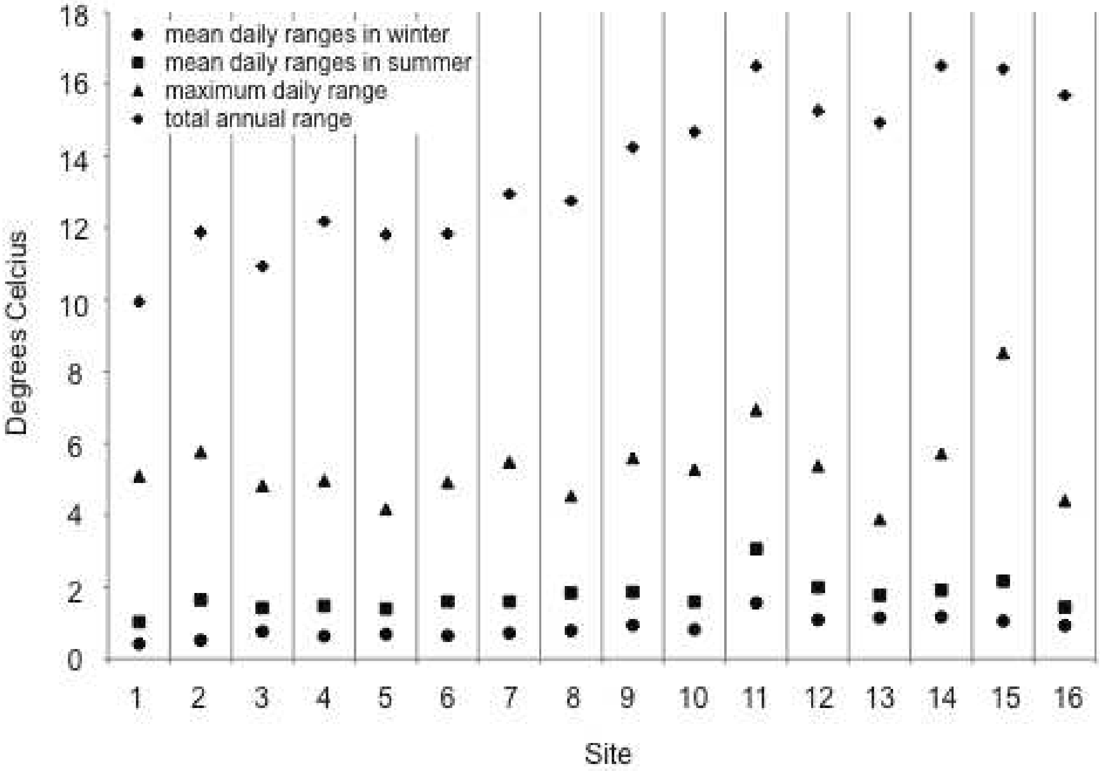

Fig. 1.3. Temperature range at all sites across the Gulf of California. Site codes as in Table 1.1

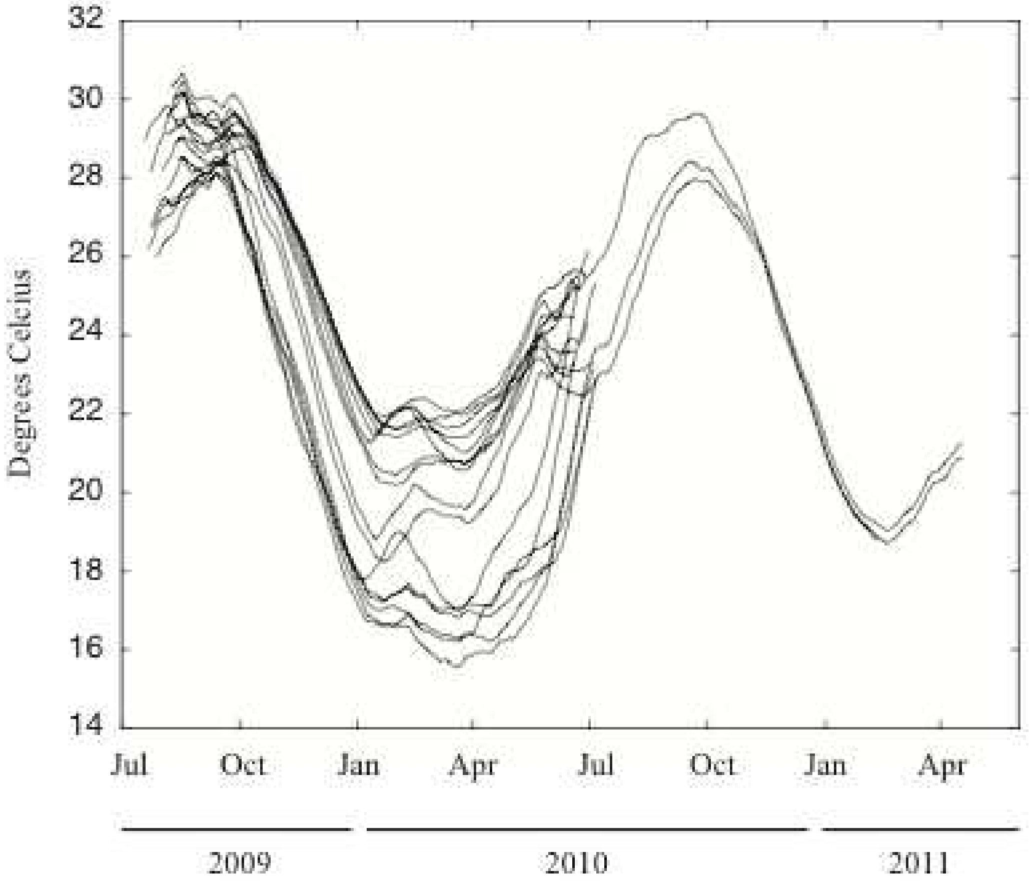

Fig. 1.4. Time series for all sites across the Gulf of California, filtered by 31-day centered moving average

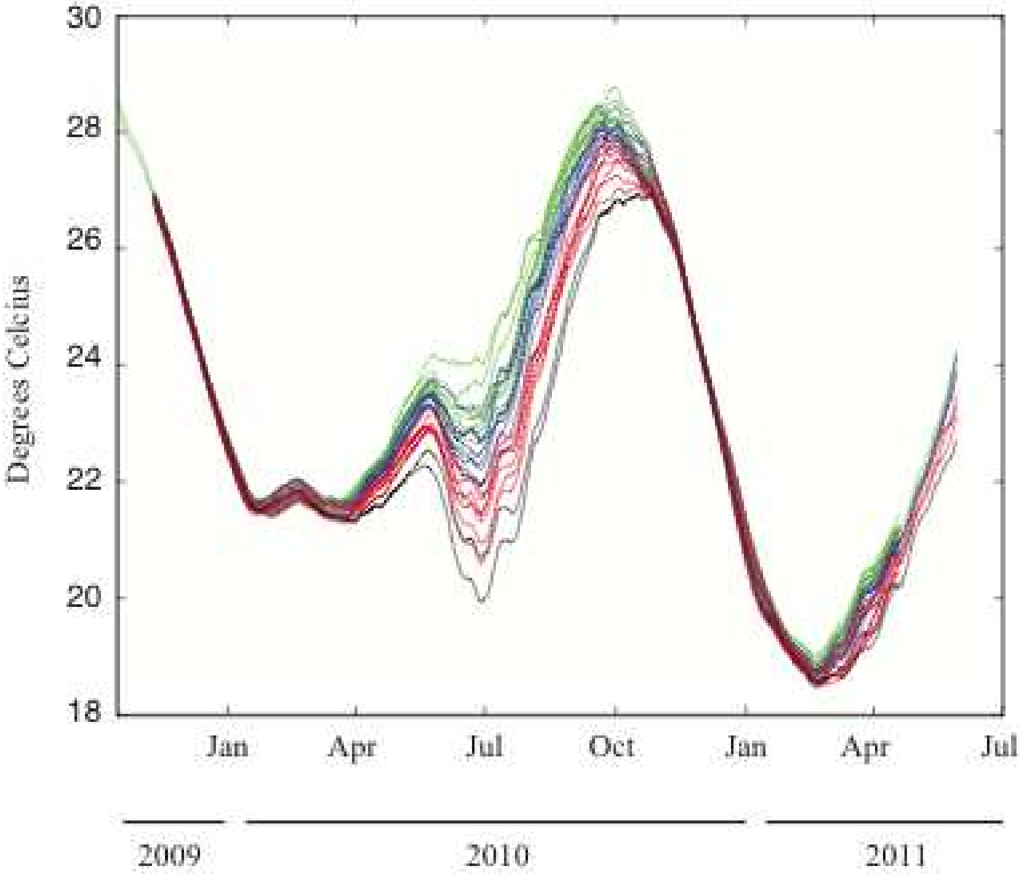

Fig. 1.5. Time series for all sites around Espíritu Santo Island, filtered by 31-day centered moving average. Colors correspond to depth (green = 5 m; blue = 10 m; red = 15 m; black = 20 m). Site codes as in Table 1.2

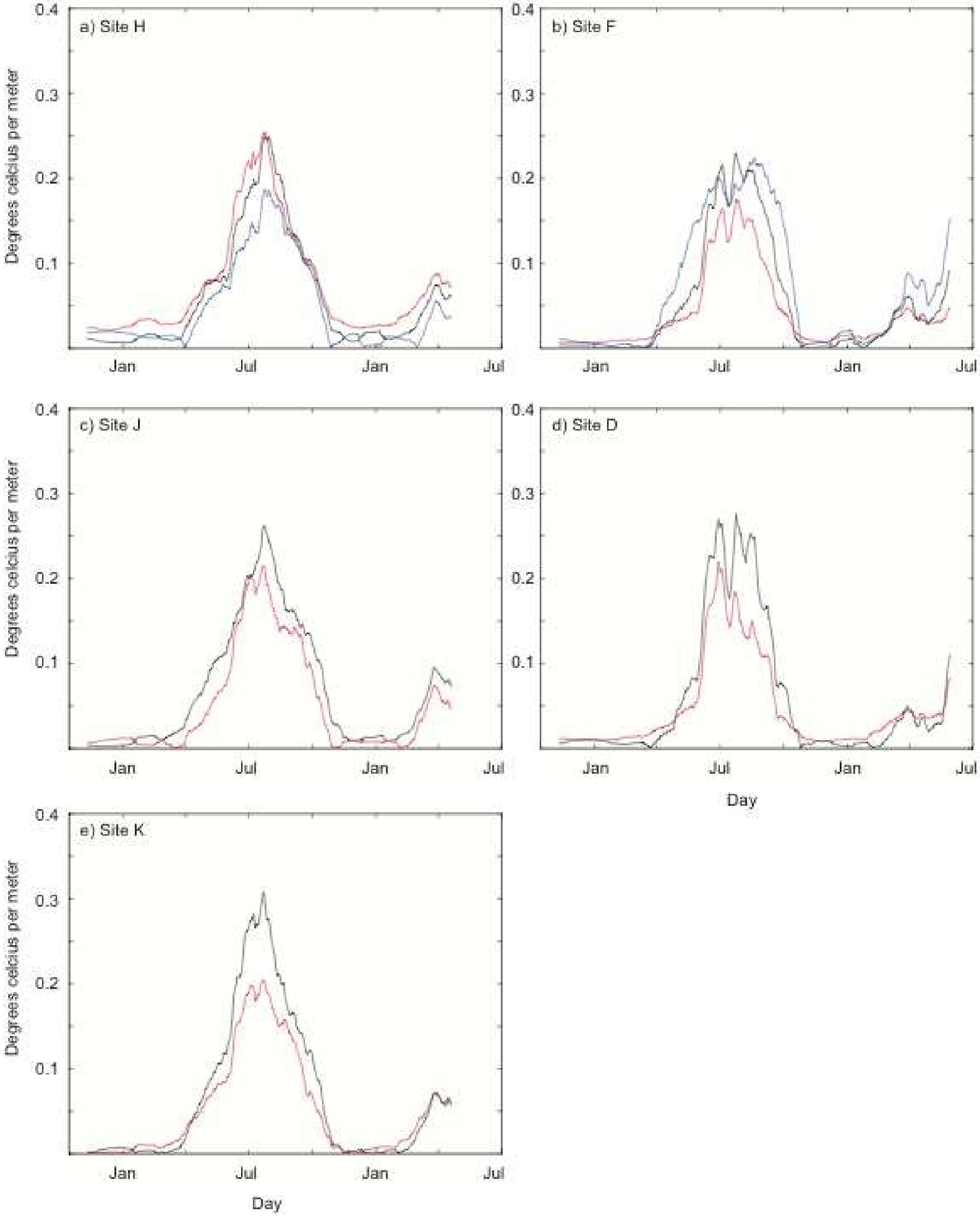

Fig. 1.6. Stratification at 5 sites around Espíritu Santo Island where temperature loggers were installed down to at least 15 m depth, plotted as a function of time. Time series are filtered by 31-day centered moving average. Colors represent bins of the water column (red = 5-10 m; black = 10-15 m; blue = 15-20 m). Panels on left side of graph correspond to sites along the east side of the island, while panels on right side correspond to sites along the west side of the island. Site codes as in Table 1.2

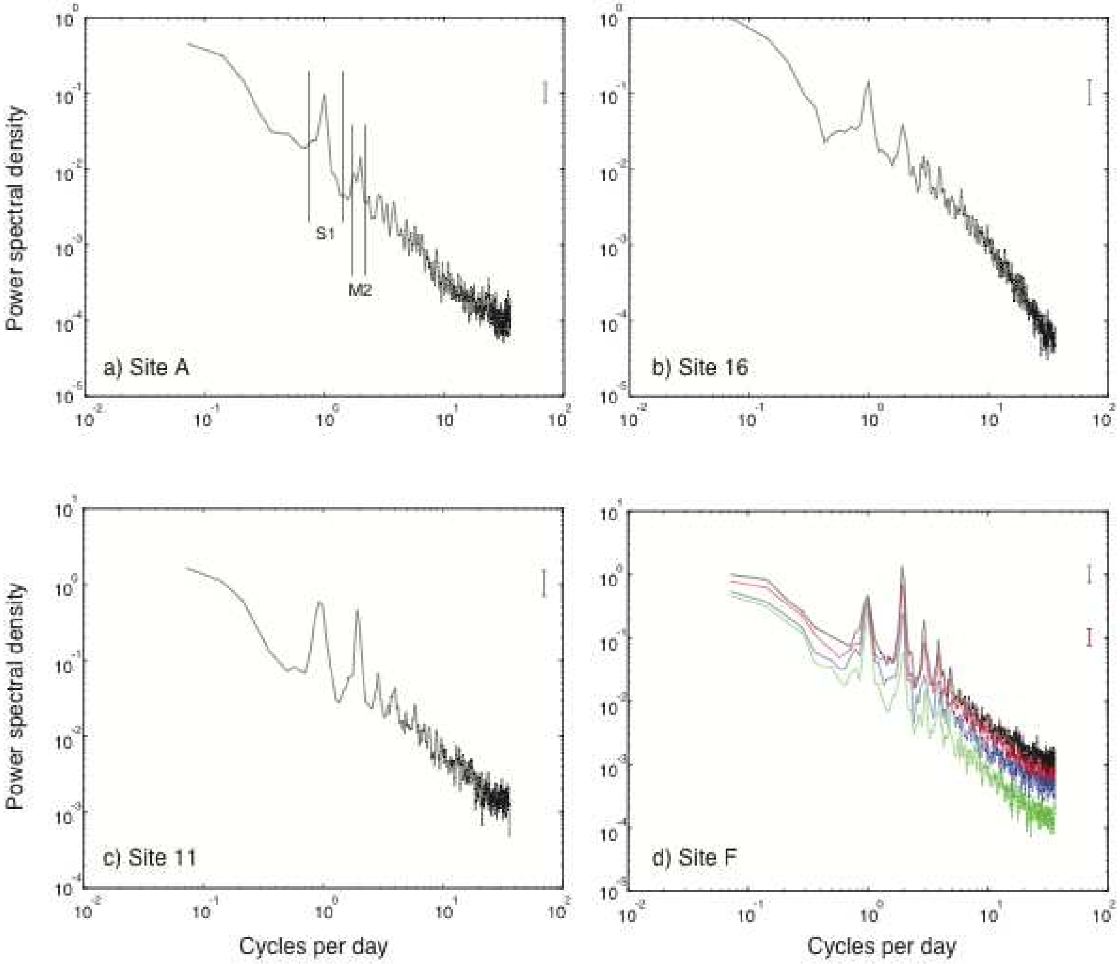

Fig. 1.7. Power spectra for four representative sites around the Gulf of California (a-c) and around Espíritu Santo (a and d). Vertical lines in panel (a) correspond to 1) the daily frequency peak and 2) the approximately semidiurnal peak. Colors in panel (d) represent depth (green = 5 m; blue = 10 m; red = 15 m; black = 20 m). Scale bars in upper right corner of each spectrum represent 95% confidence intervals. Upper scale bar in panel (d) applies to black line (20 m depth), while lower scale bar applies to all other spectra in that panel (5, 10, and 15 m depth). Site codes as in Tables 1.1 and 1.2

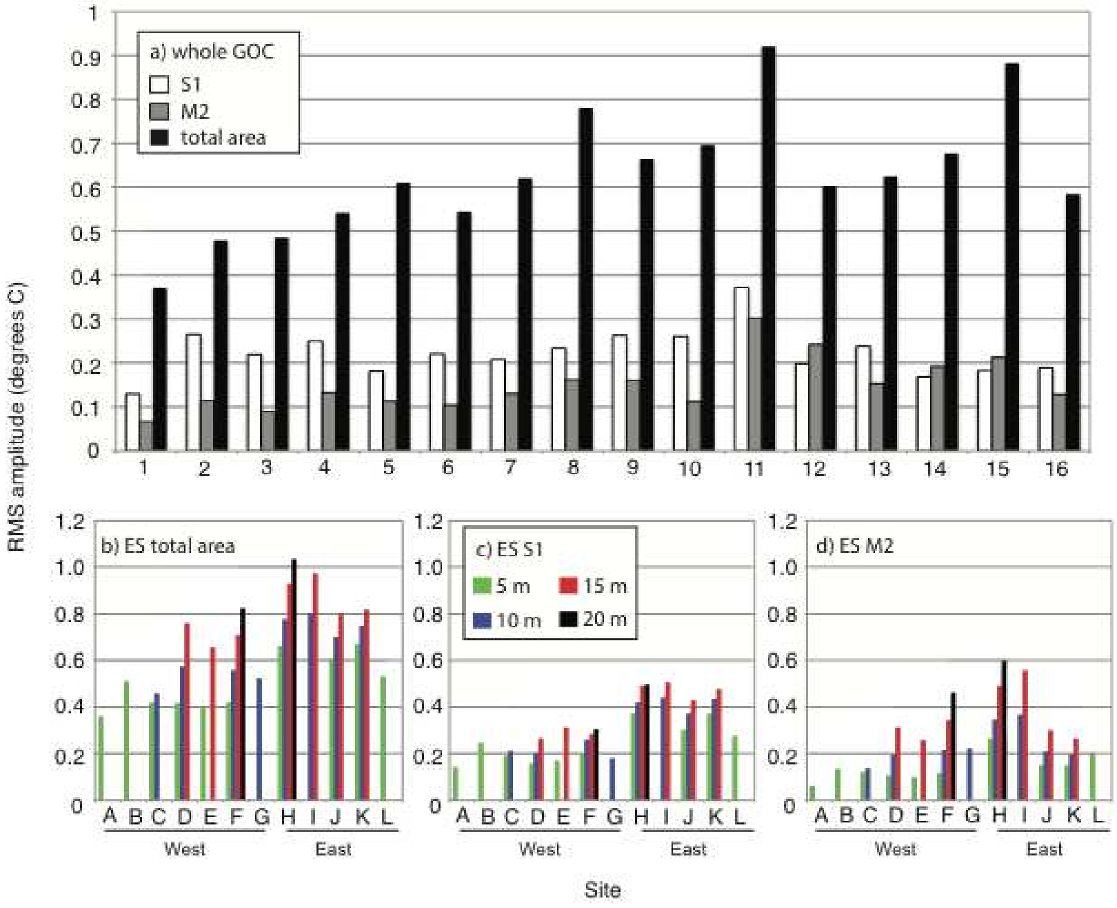

Fig. 1.8. Root mean square temperature amplitude of sites around the Gulf of California (a) and around Espíritu Santo (b-d). Site codes as in Tables 1.1 and 1.2

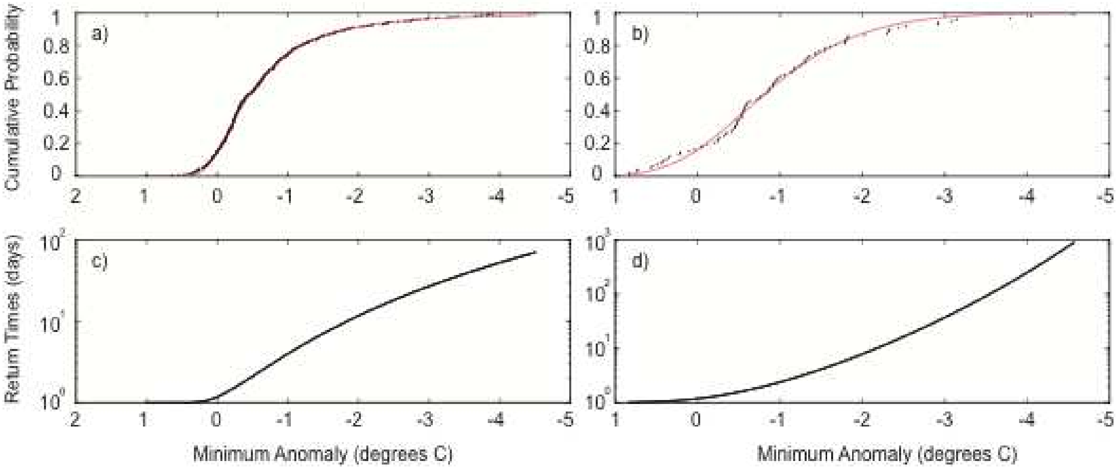

Fig. 1.9. Sorted and ranked minimum anomalies for two representative sites (panels a-b), plotted with line (in red) fitted to the form of Equation 2. Corresponding solutions to Equation 3 for c) panel (a) and d) panel (b) used to estimate return time of extreme temperatures and estimated extreme temperatures during time periods of given length

References

Alvarez-Borrego S (2010). Physical, chemical, and biological oceanography of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Badan-Dangon A, Hendershott M, Lavin MF (1991). Underway doppler current profiles in the Gulf of California. *Eos* 72(209):217-218.

Badan-Dangon A, Koblinsky CJ, Baumgartner T (1985). Spring and summer in the Gulf of California: observations of surface thermal patterns. *Oceanologica Acta* 8(1):13-22.

Barnes DK, Fuentes V, Clarke A, Schloss IR, Wallace MI (2006). Spatial and temporal variation in shallow seawater temperatures around Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography* 53(8):853-865.

Biro PA, Beckmann C, Stamps JA (2010). Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* 277(1678):71-77.

Brown JH, Stevens GC, Kaufman DM (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual review of ecology and systematics* 27:597-623.

Denny MW, Gaines SD (1990). On the prediction of maximal intertidal wave forces. *Limnology and Oceanography*, 35:1-15.

Denny M, Gaines S (2002). *Chance in biology: using probability to explore nature*. Princeton University Press, Princeton.

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* 45(4):1029-1039.

Figueira WF, Biro P, Booth DJ, Valenzuela VC (2009). Performance of tropical fish recruiting to temperate habitats: role of ambient temperature and implications of climate change. *Marine Ecology Progress Series* 384:231-239.

Filonov AE, Lavín MF (2003). Internal tides in the Northern Gulf of California. *Journal of Geophysical Research* 108(C5):3151.

Fu LL, Holt B (1984). Internal waves in the Gulf of California: Observations from a spaceborne radar. *Journal of Geophysical Research* 89(C2):2053-2060.

Gaines SD, Denny MW (1993). The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology* 74:1677-1692.

Galambos J (1987) *The Asymptotic Theory of Extreme Order Statistics* (2nd Edition). Krieger, Malabar.

Gaston KJ, Blackburn TM (2000). *Pattern and process in macroecology*. Blackwell Science, Oxford.

Gaston (2009). Geographic range. In Levin SA (ed.) *The Princeton Guide to Ecology*. Princeton University Press, Princeton.

Graham JB (1971). Temperature tolerances of some closely related tropical Atlantic and Pacific fish species. *Science* 172(3985):861-863.

Gumbel EJ (1958). *Statistics of extremes*. Columbia University Press, New York.

Hutchinson GE (1957). Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology* 22:415–427.

Jacocks JL, Kneile KR (1975). *Statistical prediction of maximum time-variant inlet distortion levels*. Arnold Engineering Development Center Technical Report AD/A-004. National Technical Information Service, US Dept. Commerce, Washington, D.C.

Kaplan DM, Largier JL, Navarrete S, Guiñez R, Castilla JC (2003). Large diurnal temperature fluctuations in the nearshore water column. *Estuarine, Coastal and Shelf Science* 57(3):385-398.

Kimball ME, Miller JM, Whitfield PE, Hare JA (2004). Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Marine Ecology Progress Series* 283:269-278.

Leichter JJ, Wing SR, Miller SL, Denny MW (1996). Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnology and Oceanography* 41(7):1490-1501.

Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR. 1998. Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work. *Marine Ecology Progress Series* 166:83-97.

Leichter JJ, Miller SL (1999). Predicting high-frequency upwelling: spatial and temporal patterns of temperature anomalies on a Florida coral reef. *Continental Shelf Research* 19(7):911-928.

Leichter JJ, Helmuth B, Fischer AM (2006). Variation beneath the surface: quantifying complex thermal environments on coral reefs in the Caribbean, Bahamas and Florida. *Journal of Marine Research* 64(4):563-588.

Leichter JJ, Stokes MD, Hench JL, Witting J, Washburn L (2012). The island-scale internal wave climate of Moorea, French Polynesia. *Journal of Geophysical Research* 117(C6):C06008.

Lerczak JA, Hendershott MC, Winant CD (2001). Coherence between the semidiurnal barotropic tide and internal tidal currents on the southern California shelf and slope. *Journal of Physical Oceanography*.

Lin H-C, Sánchez-Ortiz C, Hastings PA (2009). Colour variation is incongruent with mitochondrial lineages: cryptic speciation and subsequent diversification in a Gulf of California reef fish (Teleostei: Blennioidei). *Molecular ecology* 18(11):2476-2488.

Lindquist DG (1985). Depth zonation, microhabitat, and morphology of three species of *Acanthemblemaria* (Pisces: Blennioidea) in the Guif of California, Mexico. *Marine Ecology* 6(4):329-344.

Malcolm HA, Davies PL, Jordan A, Smith SD (2011). Variation in sea temperature and the East Australian Current in the Solitary Islands region between 2001–2008. *Deep Sea Research Part II: Topical Studies in Oceanography* 58(5):616-627.

Marshall DJ, Monro K, Bode M, Keough MJ, Swearer S (2010). Phenotype–environment mismatches reduce connectivity in the sea. *Ecology Letters* 13(1):128-140.

Munk WH (1941). Internal waves in the Gulf of California. *Journal of Marine Research* 4:81–91.

Nybakken JW (2001). *Marine Biology an Ecological Approach*. Benjamin Cummings, San Francisco.

Paden CA, Abbott MR, Winant CD (1991). Tidal and atmospheric forcing of the upper ocean in the Gulf of California, Part 1: Sea surface temperature variability. *Journal of Geophysical Research* 96(C10):18337-18.

Pegau WS, Boss E, Martínez A (2002). Ocean color observations of eddies during the summer in the Gulf of California. *Geophysical Research Letters* 29(9):1295.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005). Climate change and distribution shifts in marine fishes. *Science* 308(5730):1912-1915.

Peterson AT (2003). Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* 78(4):419-433.

Riginos C (2005). Cryptic vicariance in Gulf of California fishes parallels vicariant patterns found in Baja California mammals and reptiles. *Evolution* 59(12):2678-2690.

Riginos C, Nachman MW (2001). Population subdivision in marine environments: the contributions of biogeography, geographical distance and discontinuous habitat to genetic differentiation in a blennioid fish, *Axoclinus nigricaudus*. *Molecular Ecology* 10(6):1439-1453.

Rosenblatt RH (1967). The zoogeographic relationships of the marine shore fishes of tropical America. *Studies in Tropical Oceanography* 5:579-592.

Sheppard C (2009). Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral reefs* 28(2):399-403.

Somero GN (2012). The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science* 4:39-61.

Talley LD, Pickard GL, Emery WJ, Swift JH (2011). *Descriptive physical oceanography: An introduction* (6th edition). Academic Press, San Diego.

Thomson DA, Lehner CE (1976). Resilience of a rocky intertidal fish community in a physically unstable environment. *Journal of Experimental Marine Biology and Ecology* 22(1):1-29.

Walker BW (1960). The distribution and affinities of the marine fish fauna of the Gulf of California. *Systematic Zoology* 9(3/4):123-133.

Zeidberg LD, Robison BH (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences* 104(31):12948-12950.

CHAPTER 2

Distribution and Abundance of Cryptobenthic Fishes on Rocky Reefs in the Gulf of California, Mexico

Abstract

We report the results of a series of quantitative fish collections from shallow rocky reefs in the Gulf of California (GOC). Using the ichthyocide rotenone and a square barrier net, we collected all cryptobenthic fishes from a 10 m^2 area at 17 sites in July 2010. Of approximately 104 species of cryptobenthic fishes (blennies, gobies, clingfishes, etc.) known to inhabit rocky reefs in the GOC, our samples include 39 species, 26 of which have their centers of distribution (CODs) inside the GOC and 13 that have more tropical CODs. Triplefin blennies are the most abundant family of fishes in our samples, followed by tube blennies, labrisomid blennies, gobies, and others. Density (66 - 446 individuals per 10 m^2) and species richness (12 to 21 species) vary among sites. Species with CODs inside the GOC tend to be more abundant than species with CODs farther south. All but three of the species in our collections have the northern limit of their geographic ranges in the GOC. Therefore, distance to COD and latitudinal range are highly correlated, with species that have small latitudinal ranges living near their COD. Our results support the idea that the GOC is an important biogeographic region for shorefishes in the neotropics and a transition zone between tropical and temperate fauna.

Introduction

Defining the factors that control the distribution and abundance of organisms is a fundamental goal of ecology (Andrewartha and Birch 1954; MacArthur 1972; Brown 1981). Questions on the relationships between range size or center of distribution and local relative abundance or density contribute significantly to the fields of macroecology and biogeography (Brown 1995; Gaston and Blackburn 2000; Gaston 2009; Lomolino et al. 2010). Studying ecological communities with overlapping species of very different range sizes may provide insights into such questions. In the marine environment, "cryptobenthic" fishes are a good model system for studying biogeography as they are characterized by having similarly sized individual home ranges as adults but widely differing species ranges.

Cryptobenthic fishes are those that live in constant or near-constant contact with the benthos, rely on crypsis as their primary means of predator avoidance, and are generally small-bodied (Miller 1979). Many marine families include lineages that fit this general description, including scorpionfishes (Scorpaenidae), frogfishes (Antennariidae), flatfishes (Pleuronectiformes), cusk eels and relatives (Ophidiiformes), gobies (Gobiidae), blennies (Blennioidei), and clingfishes (Gobiesocidae), among others. Cryptobenthic fishes are often abundant but generally poorly studied. As a result of their small size and difficulty in field detection and identification, cryptobenthic fishes on shallow reefs are often overlooked by community ecologists or left out of reef assessments, even as studies have revealed the importance of this group in trophic dynamics (Kotrschal and Thomson 1986; Depczynski and Bellwood 2003), production, and diversity (Allen et al. 1992; Smith-Vaniz et al. 2006). Furthermore, cryptobenthic fishes may be a good model system for studying community structure. They are characterized by variable distributions (among closely related species), their small size and territorial nature often lead to little or no movement as adults, and they may be especially susceptible to fine-scale environmental variability, particularly over short time spans.

We studied the cryptobenthic fishes in the Gulf of California (GOC). The GOC is a long (~1,000 km), narrow (~150 km), semi-enclosed basin characterized by dynamic oceanography resulting from its shape, location, and geology (Alvarez-Borrego 2010). It is a marine biodiversity hotspot (*e.g.*, Roberts et al. 2002) and is an enormously productive region with a diversity of habitats for fishes and other marine life (Brusca et al. 2005; Hastings et al. 2010). A network of shallow, fringing, rocky reefs characterizes much of the near shore environment in the central and southern GOC, specifically along the Baja Peninsula and the many islands throughout (Thomson et al. 2000). The community structure of commercially important and conspicuous fishes is relatively well known on many of these reefs (e.g., Aburto-Oropeza and Balart 2001; Sala et al. 2002, 2004; Aburto-Oropeza et al. 2011), but like most places around the world, the cryptobenthic portion of the reef fish community in the GOC is underrepresented in recent surveys. The systematics of GOC cryptobenthic fishes is well known (e.g., Hubbs 1952; Briggs 1955; Springer 1958; Rosenblatt 1959; Stephens 1963; Thomson et al. 2000), and the ecology of several GOC cryptobenthic species has been examined in recent decades (e.g., Lindquist 1985; Kotrschal and Lindquist 1986; Kotrschal 1989; Hastings 1986, 1991, 1992; Hastings and Galland 2010), but the community structure of this group is less well known. An exception is Thomson and Gilligan (2002), who tested island biogeography theory on these fishes in the GOC in the 1970s.

On rocky reefs of the GOC, the cryptobenthic fish community is dominated by gobies, combtooth blennies (Blenniidae), labrisomid blennies (Labrisomidae), tube blennies (Chaenopsidae), triplefin blennies (Tripterygiidae), brotulas (Bythitidae), scorpionfishes (Scorpaenidae), and clingfishes (Gobiesocidae; Thomson and Gilligan 2002). The cryptobenthic fishes in this region are small (generally less than 6 cm, with a few species reaching ~20 cm) and probably short-lived (Miller 1979; Munday and Jones 1998). Like most reef fishes, GOC cryptobenthic fishes generally have a larval stage (though not always; see Rosenblatt and Taylor 1971; Moller et al. 2005) that leaves the reef and enters the planktonic environment before returning as a fully developed juvenile (Riginos and Victor 2001; Watson 2009). Some species exhibit a second recruitment step, from juvenile to adult microhabitats (e.g., Hastings and Galland 2010), and generally after reaching adulthood, the territorial nature of these fishes leads to very little (if any) movement as adults (e.g., Goncalves and Faria 2009).

Gulf of California cryptobenthic fishes vary greatly in their geographic range sizes. The GOC fish community as a whole is approximately 10% endemic (Hastings et al. 2010), and this percentage may be significantly higher among cryptobenthic species (e.g., 28% of the blennioid species found in the GOC are endemic; Hastings 2009). The remaining species have ranges that extend into southern Mexico or farther into Central America or in a few cases northward toward southern California. Though many fishes have even wider distributions, there are no GOC cryptobenthic fishes with ranges that also include the Caribbean or the western Pacific Ocean. At any site in the GOC, the cryptobenthic fish community typically comprises both GOC endemics and closely related but more widely distributed species, the interactions among which are likely governed by complex ecology.

Here, we present results from a series of quantitative fish collections and describe the cryptobenthic fish community on shallow rocky reefs across more than 5.5 degrees of latitude in the GOC. We specifically address the relative abundance of species with centers of distribution (COD) inside the GOC and those that are more widely distributed along the eastern Pacific.

Methods

From 2009 to 2011, we participated in several natural history expeditions and shorter geographically-focused trips as part of a broader project to study rocky reef fish and invertebrate communities in the GOC and to obtain a snapshot of the current status of its reef ecosystems. During a cruise in July 2010, we visited numerous sites throughout the GOC, observing and collecting cryptobenthic fishes across a wide latitudinal range, stretching from the Midriff Islands to south of La Paz Bay (Fig. 2.1).

The data presented here are the result of a series of 17 quantitative, SCUBA diver-based collections made during the July 2010 expedition. Quantitative collections not only allow us to calculate species' densities but also allow for a more accurate calculation of their relative abundances. At each collection site, we set up a 10 m^2 barrier net – 0.32 cm mesh net, 1.2 m high, weighted at the bottom with heavy gauge chain and suspended at the top by several buoys. General collection areas were chosen based on other complementary research, and specific sites were chosen based on good cryptobenthic fish habitat (= small to large boulders, medium environmental energy, some vegetation, in 1-3 m depth). After removing highly mobile fishes from the area, we dispersed approximately one liter of an ichthyocide consisting of a mixture of rotenone, liquid dish soap (an emulsifying agent), and seawater. Rotenone is a natural chemical produced by some leguminous plants and is a very effective fish poison, widely considered the most important ichthyocide in marine research (Robertson and Smith-Vaniz 2008).

After dispersing the rotenone mixture, we spent two to four hours collecting all fishes inside the 10 m^2 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. The other team member collected all fishes inside the area, actively searching under rocks and within the substrate and vegetation until all fishes were captured.

Specimens were either fixed in 10% formalin or preserved in 95% ethanol. Fixed specimens were later transferred to 50% isopropanol. All specimens, except *Ogilbia* spp., were identified to species. Due to difficulty in identification of juveniles and small adults, all specimens of *Ogilbia* were only identified to genus. Collections are archived at the Scripps Institution of Oceanography Marine Vertebrate Collection in collection numbers SIO 11-85 to SIO 11-102.

For the purposes of this study, we limited our analyses to the cryptobenthic species that are primarily rocky reef residents (as defined by Thomson et al. 2000) and avoided including species that live exclusively over nearby sandy areas. We did, however, include those that inhabit the reef-sand interface and that can be routinely observed maintaining territories on hard reef substrate (e.g., Redlight Goby – *Coryphopterus urospilus*). In Table 2.1, we present a complete list of GOC rocky reef cryptobenthic fishes from published checklists, the primary taxonomic literature, and museum records.

Latitudinal ranges and COD for the species collected during this study were determined from confirmed museum records and from published ranges (e.g., Love et al. 2005). COD was calculated using the midpoint method and represents the middle latitude between the northern and southern range extremes. Species with CODs between 21 and 31 degrees N were considered GOC-centered ("G-C"), while values less than 21 degrees represent species with a more southern affinity ("southern"). Latitudinal range was calculated to distinguish between species with small ranges confined to the GOC and those with wider ranges. A recent review of *Ogilbia* distribution confirms that all species known from our study region are endemic to the GOC and have similar ranges and CODs, so considering that group by genus rather than species does not affect the biogeographic analyses (Moller et al. 2005).

For each species at each site, the relationships between geographic range and abundance were measured by calculating the distance to COD (= the absolute difference between the latitude at the collecting site and the latitude at the COD). These values were examined as individual records and binned by species in order to quantify the relationships between biogeography and density among GOC cryptobenthic fishes.

Linear regression and tests of homogeneity of regressions were utilized to identify possible relationships between species richness and abundance, between abundance and site latitude, and between G-C fishes and southern fishes with respect to site latitude.

Results

During our 2010 collecting efforts, we obtained quantitative collections for 17 locations throughout the islands and peninsular region of the GOC (Fig. 2.1). These locations stretch over approximately 5.5 degrees of latitude and cover a large part of the wider GOC. Of 104 species of cryptobenthic fishes known to occur on GOC rocky reefs (Table 2.1), we collected 39 species, 26 that have CODs inside the GOC and 13 with more southerly distributions. Pooled summary statistics for all sites (e.g., frequency of observation, average abundance, average relative abundance) for each collected species are reported in Table 2.2, and Fig. 2.2a depicts a rank order of abundance of the 39 captured species. The rank order is characterized by clear logarithmic decay, with a few species represented by several individuals and several species represented by few individuals. A view of frequency of observation of those same species (Fig. 2.2b) indicates that species (even the most frequently observed) were not equally distributed among sites and that the most abundant species did not necessarily have the widest distribution across our sites (i.e., the rank order changes). The histogram of number of sites where each species was collected has a peak for those species encountered infrequently in our collections and a peak for species encountered approximately one third of the time (Fig. 2.3a). Like in most studies of abundance and distribution (reviewed in Borregaard and Rahbek 2010), we found a positive relationship between number of sites where species were collected and mean abundance (Fig. 2.3b; $R^2 = 0.52$, $P < 0.0001$, least squares linear regression).

Among the pooled data, the triplefin blennies were the most common family of cryptobenthic fishes (36% of total collected individuals and three of the top four species by abundance), followed by tube blennies (20%), labrisomid blennies (18%), gobies (16%), brotulas (4%), combtooth blennies (2%), scorpionfishes (2%), and clingfishes (<2%). At the site level, the relative abundance of these families varies widely around the mean: triplefin blennies, 37% (±20 percentage points); tube blennies, 16% (±13 pp); labrisomid blennies, 17% (±16 pp); gobies, 16% (±14 pp); brotulas, 5% (±5 pp); combtooth blennies, 2% (±4 pp); scorpionfishes, 4% (±4 pp); and clingfishes, 3% (±7 pp). The high variability in relative abundance of each family can be explained both by variability in true abundance of that family and by differences in the overall community size (Table 2.2). For example, among the triplefin blennies, 83 individuals constituted 19% of the community at Gallina, while approximately the same number (85 individuals) constituted 65% of the community at Santa Cruz (Table 2.3). The same was true among the less abundant families (e.g., the brotulids). Variability in density among sites at the species level was even wider, as a result of heterogeneity in species' distribution and numerical abundance (Table 2.2).

As mentioned above, two thirds (26 of 39) of the species collected during our surveys have CODs inside the GOC and one third (13) have CODs farther south. We collected three species that extend northward to northern Baja California and southern California, but none of these species' distributions have centers north of the GOC. The Bay Blenny's (*Hypsoblennius gentilis*) range is centered on the GOC, and the ranges of the broadly distributed Rainbow Scorpionfish (*Scorpaenodes xyris*) and Bluebanded Goby (*Lythrypnus dalli*) are centered south of the GOC. Among the 39 species we collected, all but these three have the northern limit of their ranges inside the GOC, but eight have southern limits south of the equator. Latitudinal range size varies widely among the species in our samples, from approximately five degrees for the Cortez Barnacle Blenny (*Acanthemblemaria hastingsi*) to at least 48 degrees for the Rainbow Scorpionfish. Each family with more than one collected species has representative species with distributions restricted to the GOC and representatives with relatively larger ranges.

While the ratio of diversity of G-C species to southern species in our samples is 2:1, the total abundance among pooled data is more than 4:1, indicating a disproportionately high abundance of G-C species. This fact is shown clearly in Fig. 2.2a, where most of the highest-ranking species have COD inside the GOC and many of the lowest ranking species are more widely distributed.

While pooling data by species provides an effective summary of the results, a comparison of sites may reveal differences in the cryptobenthic fish community among several locations throughout the GOC (Table 2.3). By pooling the community at each site, total abundance ranged from 66 to 446 individuals per site (= per 10 m^2) and species richness ranged from 12 to 21 species per site (Fig. 2.4). Linear regression revealed a significant positive relationship between species richness and abundance, with richer sites supporting higher densities of cryptobenthic fishes (or denser sites supporting higher numbers of species; $R^2 = 0.57$, $P = 0.0005$). There was not, however, a significant linear relationship between latitude and abundance or species richness, implying that cryptobenthic fish density and diversity are not strongly affected by latitude within the GOC or that other factors confound its effect.

The relationship between collecting latitude and both abundance and species richness of G-C cryptobenthic fishes was not significant, but latitude was significantly negatively correlated with both abundance ($R^2 = 0.25$, $P = 0.0396$) and species richness ($R^2 = 0.42$, $P = 0.0047$) of southern species, implying that this group is more abundant and diverse closer to the southern end of the GOC. A test of homogeneity of regressions of the two groups, however, showed that the negative regression between latitude and southern species abundance could not be distinguished from the lack of relationship with G-C species abundance at an alpha of 0.05 ($t = -1.9482$, $df = 30$, $P = 0.0608$) and that the two groups are best explained as a single data set. Within-group abundance does not account for potential influences of other environmental factors on maximum density at our sites, however, and when the data were normalized by the total abundance at each site, a positive relationship between relative abundance of G-C species and latitude and a negative relationship between relative abundance of southern species and latitude were both significant ($R^2 = 0.64$; $P < 0.0001$), had opposite slopes, and were significantly different ($t = -7.6991$, $df = 30$, $P < 0.001$). These data are shown graphically in Fig. 2.5a. A test of homogeneity of regressions for species richness confirmed a significant difference between the two groups of species, with sites throughout our study area characterized by statistically similar numbers of G-C species, and southern sites characterized by higher numbers of southern species than northern sites ($t = -4.7784$, $df = 30$, $P < 0.0001$).

Consideration of results by family (Fig. 2.5b), rather than geographic distribution, also revealed some interesting trends with latitude. Combtooth blennies ($R^2 = 0.27$, $P = 0.0333$, linear regression), labrisomid blennies ($R^2 = 0.4$, $P = 0.0062$, linear regression), and clingfishes ($R^2 = 0.26$, $P = 0.0365$, linear regression) all showed significant positive relationships between latitude and total abundance. These three groups were more common farther into the GOC, while the other families showed no significant relationship between abundance and latitude. The positive relationships between these three families and latitude seem to be a result of strong positive relationships of only a few species. Within the combtooth blennies, the Bay Blenny increased significantly with latitude, while the other two species that we collected did not. The relationship between latitude and labrisomid blenny abundance was influenced disproportionately by the appearance and relative abundance of the Redrump Blenny (*Xenomedea rhodopyga*), the Redside Blenny (*Malacoctenus hubbsi*), and the Largemouth Blenny (*Labrisomus xanti*) at higher latitudes. Among clingfishes, the Tadpole Clingfish (*Gobiesox pinniger*) was the only species captured at more than two sites, so its presence at the northern collecting sites drove the familial relationship with latitude. The most common family of cryptobenthic fishes on GOC rocky reefs, the triplefin blennies, showed no significant relationship between latitude and abundance in our samples.

Finally, plots of abundance against distance to COD (Fig. 2.6a-c) and latitudinal range (Fig. 2.6d-f) revealed that species near their COD could be highly abundant and that species far from their center of distribution were never very abundant. We had only one record (of Redhead Goby – *Elacatinus puncticulatus*) where a species that was more than 10 degrees from its COD reached at least 20 individuals at a site (only 0.6% of records of fishes farther than 10 degrees from their COD or 2.3% of nonzero records), and there were only seven records of a species reaching 20 individuals at a site that was more than five degrees from its COD (2.7%/11.3%). These additional six records all represented the same species (the Carmine Triplefin – *Axoclinus storeyae*). On the other hand, there were 45 records (representing 14 species and six families) where abundance reached at least 20 individuals for species that were less than five degrees from their COD (11.1%/23.9%). Species near their COD were not always abundant, however, and records where a species was not collected at a site are spread across the entire range of distances to COD (Fig. 2.6a). 74.3% of records representing species more than 10 degrees from their COD, 76.1% of records representing species more than 5 degrees from their COD, and 53.6% of records representing species less than 5 degrees from their COD are equal to zero. In other words, 405 of 663 total records (61.1%) indicate sites where a species was not collected.

In our data set, mean distance to COD and latitudinal range are highly correlated ($R^2 = 0.94$, $P < 0.0001$, linear regression), so we see similar patterns when reviewing abundance against latitudinal range (Fig. 2.6).

Discussion

For over 50 years, the GOC has been known to be an important biogeographic region for shorefishes in the neotropics, particularly because it provides increased subtropical habitat in the otherwise linear tropical eastern Pacific and provides increased area that is not influenced by the cold waters of the California Current (Walker 1960; Rosenblatt 1967; Robertson and Cramer 2009). Its regional importance is particularly evident for the cryptobenthic fishes that inhabit rocky reefs (Hastings 2000, 2009). Among the known species of rocky reef cryptobenthic fishes in the GOC, at least 40% are endemic (Table 2.1) compared with only approximately 10% of the more than 900 fish species known to occur in the GOC in total (Hastings et al. 2010). Given the linear nature of the tropical eastern Pacific coastline, it is likely that the existence of the GOC supports a substantial increase in shorefish diversity over what would otherwise occur in this part of the world, particularly among the cryptobenthic fishes.

Our samples support the hypothesis that the GOC represents a distinctive faunal region between tropical provinces to the south and temperate provinces to the north. Of the 39 species that we collected, all but three have the northern extent of their geographic range inside the GOC. The common shallow cryptobenthic fishes that live in the GOC rarely live north of it, and in some cases they may reach the land barrier of the northern GOC before experiencing physiological limits to their survival. This is also often the case for larger, conspicuous reef fishes, and Rosenblatt (1967) noted that in general, the northern limit of tropical shorefishes in the GOC is as much as five degrees farther north inside the GOC than along the outside of the Baja Peninsula. Therefore, within our results, latitudinal range and distance to COD are highly correlated. Species with CODs inside the GOC are generally restricted to the GOC or a few degrees north or south of it, while species with CODs farther south have necessarily larger latitudinal ranges, resulting from their northern limits falling inside the GOC.

Among the 104 species of cryptobenthic fishes known to inhabit rocky reefs in the GOC, we collected only 39. Even by quantitatively sampling a total of 170 m^2 across 5.5 degrees of latitude, on several islands and at sites along the Baja Peninsula, we collected less than 40% of the known diversity in these groups. Several factors may help to explain this finding. Some species are known only from a few specimens and may be extremely rare or have limited geographic ranges (e.g., Hubbs 1954, Rosenblatt and Taylor 1971), and other species certainly have ranges restricted to the most southern parts of the GOC, where we did not collect (e.g., Briggs 1960, Rosenblatt and Parr 1969, Rosenblatt and Taylor 1971). Furthermore, cryptobenthic fishes can exhibit depth zonation, and though it has only been quantified in a few genera in the GOC (Lindquist 1985, Rosenblatt and Parr 1969), it is likely to apply to other groups as well. All of our collections were restricted to depths less than five meters. Finally, our study area overlaps with the ranges of four species of *Ogilbia*, so our collections may reflect more than one species in that genus.

Species richness in general decreases from south to north in the GOC (Hastings et al. 2010), but our results for shallow, reef fishes reveal a decrease only in numbers of southern species and not in the whole cryptobenthic community. This is not surprising, as the more frequently observed, G-C fishes that we collected often occur throughout the GOC, while the southern species often reach the limits of their distribution in the central GOC (Walker 1960). The northern limits of southern species may be a function of the physical environment (e.g., cooler temperatures at higher latitudes), habitat (e.g., presence/absence of benthic algae and encrusting invertebrates with southern affinities), distance from COD, or some combination of these and other factors.

Latitudinal variation in the abundance of cryptobenthic families inside the GOC may be influenced by wider biogeographic patterns. Among GOC fishes, there are several species that are restricted to the northern GOC but that also live in temperate southern California (Walker 1960; Bernardi et al. 2003). These so-called “northern disjunct” fishes are represented by only one species, the Bay Blenny, in our collections. That species is also the only one that we caught with a COD inside of the GOC that also reaches the outer coast of northern Baja and southern California. As described above, the appearance and numerical abundance of the Bay Blenny at our northern sites drives a relationship between latitude and abundance for the Blenniidae.

The other combtooth blennies that we collected both have CODs far south of the GOC.

Ecology may also influence latitudinal variation at the family level, particularly among cryptobenthic fishes, which are often microhabitat specialists. Many cryptobenthic fishes rely on specific or even unique resources in order to persist. Unlike food specialists (e.g., corallivorous butterflyfishes; Berumen and Pratchet 2008), cryptobenthic fishes are often generalist microcarnivores or detritivores (Fitzhugh and Fleeger 1985; Kotrschal and Thomson 1986; Gee 1989; Depczynski and Bellwood 2003), and their specialization involves their reliance on different microhabitats (Patzner 1999; Depczynski and Bellwood 2004; La Mesa et al. 2006; Goncalves and Faria 2009; Hastings and Galland 2010, Lin and Hastings 2011). Microhabitat specialization reflects, in part, these fishes' reliance on benthic, male-guarded nesting sites for reproduction (Miller 1984; Thresher 1984; Hastings 1992; Hastings and Petersen 2010), unlike many larger-bodied, mobile, reef-associated fishes, which are often broadcast spawners (Thresher 1984) and are less likely to be restricted to specific microhabitats. Among cryptobenthic fishes, the presence of their preferred microhabitats, even under somewhat abnormal environmental conditions, can support apparently viable populations (Galland 2011).

To illustrate this point, consider two more blennioid families. Several species of GOC labrisomids are habitat specialists that prefer weedy macroalgae for cover (e.g, Rosenblatt and Taylor 1971; Thomson et al. 2000; Gonclaves and Faria 2009), while triplefins prefer bare surfaces or patches of short turf algae on large boulders and rely on short, quick movements to the dark underside of these large boulders to escape predation (pers. obs.). Within the Labrisomidae, three species are very common at northern sites and are uncommon or unobserved at southern sites. Though data are not presented here, during general surveys of our sites, we noted that fleshy macroalgae (*Padina* spp., *Sargassum* spp., etc) were a more frequent component of the benthic reef structure at sites in the north. The relative success of labrisomid blennies in that region (Fig. 2.5) may be a result of habitat availability. Triplefins, on the other hand, do not exhibit a linear relationship between latitude and abundance within our collections. This finding may reflect the relative commonness of large boulders and turf algae throughout our study region and the GOC in general. Temperature anomalies may also play a role in structuring cryptobenthic fish communities throughout the GOC (Thomson and Lehner 1976), especially with respect to the variability in the frequency and magnitude of these events among sites (Chapter 1, this volume).

Some of our study sites support higher densities of crypobenthic fishes than others (Fig 2.3a), and some support higher species richness than others (Fig. 2.3b). These differences do not seem to be regional in nature, with each part of the GOC in our study area including a wide range of densities and species richness. Nutrient availability (=productivity), past and present human activity, and presence of intact trophic structure within the wider reef community are all known to impact conspicuous fishes in the GOC (Aburto-Oropeza et al. 2013) and may also affect the cryptobenthic fish density at our sites. Differences in species richness among sites could be a result of inter-species interactions or of microhabitat availability.

The distributions of cryptobenthic fishes in the tropical eastern Pacific support recognition of three faunal provinces: the Cortez, Mexican, and Panamic provinces (*sensu* Hastings 2000, 2009). Robertson and Cramer (2009), however, report that the recognition of these three provinces may be less clear among larger, conspicuous fishes. The latitudinal ranges of GOC cryptobenthic fishes generally fall into three groups: 1) those that are restricted to the Cortez province (range size < 10 degrees); 2) those that are restricted to the Cortez and Mexican provinces (range size < 15 degrees); and 3) those that live in all three provinces (range size > 20 degrees). These three groups appear in plots of abundance versus latitudinal range of the fishes in our samples (Fig. 2.6). The three provinces are separated by gaps in the rocky reef environment in Sinaloa, Mexico and in Central America (Hastings 2000, 2009). The relative ability to disperse across these barriers may determine whether or not a species inhabits multiple provinces and whether or not Panamic fishes extend north into the GOC. Dispersal ability may reflect breeding strategy, with benthic, nest-guarding species restricted to smaller ranges. It may also reflect larval behavior (Brogan 1994). However, among the cryptobenthic species we collected, range size is not tightly correlated with the phylogeny. Several genera include overlapping species, some with restricted ranges and some with much wider ranges (e.g., *Axoclinus*, *Enneanectes*, *Hypsoblennius*, *Elacatinus*, *Tomicodon*), even when these species have similar life history and reproductive strategies. It remains unclear how these differences in range size have arisen.

Our results imply that species near their COD can be abundant or quite rare, while species far from their COD are never very abundant (Fig. 2.6). It would be interesting to determine if the southern species are more abundant nearer their CODs in southern Mexico and Central America than in the GOC or if species restricted to those provinces play a role similar to G-C fishes in possibly restricting their numbers. In other words, are the southern species relatively less abundant because they are near the edge of their ranges or because of other life history characters/ecology? Only through similar quantitative collections in the southern faunal provinces could we begin to find an answer. It is interesting to note, however, that the outlier southern species (i.e., the two most abundant southern species – the Redhead Goby and the Carmine Triplefin) are more abundant in our samples than their congeners that have CODs inside the GOC.

Finally, of the 18 species that we collected with ranges extending south of the GOC, five have CODs inside the GOC and 13 have CODs farther south, implying that it may be easier to disperse into the GOC than out. The seasonal nature of GOC oceanography (reviewed in Alvarez-Borrego 2010) may help to explain this observation. During the late spring and summer, when reef fishes are spawning in the GOC, the average direction of the prevailing currents along the Mexican mainland is from south to north (Alvarez-Borrego 2010). These currents could weaken the passive dispersal of larvae out of the GOC during that time and promote passive dispersal in, though larval dispersal models have not been constructed for that region.

As marine ecosystems continue to change with ongoing human activity, it is important to study overlapping species with different ecological and evolutionary histories. The GOC offers a unique opportunity to study marine species living near the northern limits of their geographic ranges, living near a break between faunal provinces, and moving into and out of a semi-enclosed basin. Cryptobenthic fishes, often characterized by smaller range size and higher prevalence of microhabitat specialization than larger-bodied, more active species, constitute a particularly intriguing system for observing the interactions between species with different range sizes and for studying reef community dynamics. Many questions remain: how do overlapping, ecologically similar congeners develop drastically different range sizes; how does the semi-enclosed nature of the GOC promote or prohibit dispersal into and out of that basin; how do our observations of cryptobenthic fishes compare to those of larger-bodied, more active fishes and other marine organisms; and how do the abundances of species with wider ranges differ across their ranges? The answers to these and more questions will further our understanding of the community dynamics on shallow reefs in the GOC and allow us to apply our results to other systems around the world, particularly in the context of a changing ocean.

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Table 2.1. Cryptobenthic, rocky reef fishes of the Gulf of California*

BYTHITIDAE
Grammonus diagrammus
Ogilbia davidsmithi[a]
Ogilbia nigromarginata[a]
Ogilbia nudiceps[a]
Ogilbia robertsoni[a]
Ogilbia sedorae[a]
Ogilbia ventralis
Ogilbia **species**

OPHIDIIDAE
Petrotyx hopkinsi

BLENNIIDAE
Entomacrodus chiostictus
Hypsoblennius brevipinnis
Hypsoblennius gentilis
Hypsoblennius jenkinsi
Ophioblennius steindachneri

TRIPTERYGIIDAE
Axoclinus nigricaudus
Axoclinus storeyae
Crocodilichthys gracilis
Enneanectes carminalis
Enneanectes reticulatus
Enneanectes species A[b]
Enneanectes species C[b]

LABRISOMIDAE
Cryptotrema seftoni
Dialommus macrocephalus
Exerpes asper
Labrisomus multiporosus
Labrisomus striatus
Labrisomus xanti
Malacoctenus ebisui
Malacoctenus gigas
Malacoctenus hubbsi
Malacoctenus mexicanus
Malacoctenus polyporosus[c]
Malacoctenus tetranemus
Malacoctenus zacae
Malacoctenus zonifer
Paraclinus altivelis
Paraclinus beebei
Paraclinus ditrichus[d]
Paraclinus mexicanus
Paraclinus sini
Paraclinus stephensi[d]
Paraclinus tanygnathus
Starksia cremnobates
Starksia grammilaga
Starksia hoesei
Starksia lepidogaster[e]
Starksia spinipenis
Xenomedea rhodopyga

CHAENOPSIDAE
Acanthemblemaria balanorum
Acanthemblemaria crockeri
Acanthemblemaria hastingsi[f]
Acanthemblemaria macrospilus
Chaenopsis alepidota
Chaenopsis coheni
Cirriemblemaria lucasana
Coralliozetus angelicus
Coralliozetus boehlkei
Coralliozetus micropes
Coralliozetus rosenblatti
Ekemblemaria myersi
Emblemaria hypacanthus
Emblemaria piratica[g]
Emblemaria walkeri
Protemblemaria bicirris
Stathmonotus lugubris
Stathmonotus sinuscalifornici

GOBIIDAE
Aruma histrio
Barbulifer mexicanus
Barbulifer pantherinus
Bathygobius ramosus
Chriolepis cuneata
Chriolepis minutillus
Chriolepis zebra
Chriolepis species A[b]
Chriolepis species B[b]
Coryphopterus urospilus
Elacatinus digueti
Elacatinus limbaughi[h]
Elacatinus puncticulatus
Enypnias seminudus
Gillichthys seta
Gobiosoma chiquita
Gobiosoma nudum
Gobiosoma paradoxum
Gobiosoma species B[b]
Gobulus crescentalis
Gobulus hancocki
Gymneleotris seminudus
Lythrypnus dalli
Lythrypnus pulchellus
Pycnomma semisquamatum

Table 2.1 Continued

GOBIESOCIDAE
Arcos erythrops
Gobiesox adustus
Gobiesox marijeanae[i]
Gobiesox papillifer
Gobiesox pinniger
Gobiesox schultzi
Pherallodiscus funebris
Tomicodon boehlkei
Tomicodon eos
Tomicodon humeralis
Tomicodon myersi
Tomicodon petersii[g]
Tomicodon zebra

SCORPAENIDAE
Scorpaenodes xyris

Notes
*After Thomson et al. 2000. Species added based on other relevant references include: [a]Moller et al. 2005; [b]Robertson 2012; [c]Hastings and Springer 2009; [d]Rosenblatt and Parr 1969; [e]Rosenblatt and Taylor 1971; [f]Lin and Galland 2010; [g]Erisman et al. 2011; [h]Hoese and Reader 2001; [i]Briggs 1960). Species in **bold** were collected during this study.

Table 2.2. Descriptive statistics for 39 captured species during quantitative cryptobenthic fish collections

Species	FoB (%)	Mean abundance (individuals per site; std. dev.)	Maximum abundance (individuals)[a]	Mean relative abundance (%; std. dev.)	Latitudinal Range (degrees)	Center of Distribution (degrees N)
Tripterygiidae[b]	100	78.8 (47)	184	37.4 (20.2)	n/a	n/a
Axoclinus nigricaudus	52.9	4.9 (9.4)	39	2.1 (4.0)	7.54	26.65
Axoclinus storeyae	52.9	19.6 (25)	74	7.9 (9.3)	21.48	17.96
Crocodilichthys gracilis	64.7	20.1 (27.4)	93	10.4 (15.5)	8.24	27
Enneanectes carminalis	5.9	0.2 (0.7)	3	0.1 (0.3)	20.98	17.71
Enneanectes reticulatus	88.2	34.1 (27.6)	94	16.9 (13.3)	7.54	26.65
Blenniidae	70.6	5.1 (8.5)	27	2.2 (3.7)	n/a	n/a
Hypsoblennius brevipinnis	5.9	0.3 (1.2)	5	0.1 (0.3)	40.04	7.93
Hypsoblennius gentilis	35.3	3.8 (8.6)	27	1.7 (3.7)	13.88	29.81
Ophioblennius steindachneri	41.2	1.0 (1.6)	5	0.4 (0.7)	37.23	11.69
Chaenopsidae	94.1	43.4 (54.8)	178	15.0 (12.2)	n/a	n/a
Acanthemblemaria crockeri	82.4	13.1 (24.1)	103	4.3 (5.4)	8.15	26.96
Acanthemblemaria hastingsi	17.6	3.3 (10.6)	45	0.9 (2.5)	5.09	25.42
Cirriemblemaria lucasana	5.9	0.1 (0.2)	1	0.0 (0.2)	6.00	23.63
Coralliozetus angelicus	11.8	0.9 (3.5)	15	0.2 (0.8)	11.42	22.56
Coralliozetus micropes	41.2	3.6 (5.8)	19	1.7 (2.9)	8.16	26.95
Coralliozetus rosenblatti	17.6	0.5 (1.4)	6	0.5 (1.4)	6.69	26.22
Protemblemaria bicirris	23.5	0.6 (1.3)	4	0.3 (0.8)	45.37	8.43
Stathmonotus sinuscalifornici	70.6	21.4 (38.4)	149	7.0 (9.7)	7.43	26.59
Labrisomidae	100	41.0 (51.2)	197	17.3 (16.2)	n/a	n/a
Labrisomus striatus	11.8	0.2 (0.5)	2	0.1 (0.1)	11.18	22.44
Labrisomus xanti	47.1	2.5 (4.3)	14	1.3 (2.3)	12.07	25.32
Malacoctenus hubbsi	52.9	11.6 (13.2)	35	6.5 (7.8)	8.48	27.11
Paraclinus sini	94.1	13.1 (21.7)	90	4.9 (5.4)	8.48	27.11
Starksia spinipenis	17.6	0.5 (1.3)	4	0.2 (0.5)	14.26	23.98
Xenomedea rhodopyga	47.1	13.1 (33.2)	138	4.5 (9.4)	8.24	27

Table 2.2. Continued

Species	FoB (%)	Mean abundance (individuals per site; std. dev.)	Maximum abundance (individuals)[a]	Mean relative abundance (%; std. dev.)	Latitudinal Range (degrees)	Center of Distribution (degrees N)
Gobiidae	94.1	36.3 (43.7)	152	16.5 (14.1)	n/a	n/a
Aruma histrio	41.2	2.7 (4.6)	18	1.7 (3.2)	8.32	27.16
Barbulifer pantherinus	47.1	6.6 (11.8)	43	2.3 (3.5)	7.40	26.60
Chriolepis zebra	58.8	5.5 (7.7)	27	2.8 (3.2)	6.60	26.20
Coryphopterus urospilus	35.3	1.3 (2.2)	8	0.9 (1.4)	31.12	15.56
Elacatinus limbaughi	35.3	0.5 (0.7)	2	0.3 (0.6)	6.45	23.83
Elacatinus puncticulatus	35.3	10.6 (28.8)	123	3.0 (6.7)	32.50	13.25
Gobulus hancocki	5.9	0.2 (0.9)	4	0.1 (0.2)	25.30	15.62
Gymneleotris seminudus	11.8	0.2 (0.5)	2	0.1 (0.3)	31.27	12.64
Lythrypnus dalli	41.2	3.1 (4.5)	13	2.2 (4.1)	42.40	14.20
Lythrypnus pulchellus	17.6	1.3 (3.6)	15	1.1 (3.1)	21.50	18.75
Pycnomma semisquamatum	47.1	4.3 (8.5)	35	2.1 (3.3)	5.36	26.82
Gobiesocidae	52.9	4.0 (7.4)	25	2.9 (6.6)	n/a	n/a
Arcos erythrops	5.9	0.1 (0.2)	1	0.0 (0.1)	12.12	21.91
Gobiesox pinniger	35.3	3.5 (7.2)	25	2.8 (6.4)	8.24	27.00
Tomicodon boehlkei	11.8	0.2 (0.5)	2	0.1 (0.3)	8.44	27.10
Tomicodon myersi	5.9	0.2 (0.9)	4	0.1 (0.2)	25.12	15.53
Bythitidae[d]	88.2	7.8 (5.8)	20	4.9 (5.2)	n/a	n/a
Ogilbia sp.[c]	88.2	7.8 (5.8)	20	4.9 (5.2)	7.00	25.50
Scorpaenidae[d]	82.4	4.7 (4.0)	13	3.7 (4.2)	n/a	n/a
Scorpaenodes xyris	82.4	4.7 (4.0)	13	3.7 (4.2)	48.00	10.00

Notes:
[a] At the species level, maximum abundance also reflects range as each species was absent from at least one site. [b] Family results are based on summed abundances at each site. [c] Due to difficulty in identification of small individuals, all individuals of the *Ogilbia* are considered together. [d] Values for the Bythitidae and the Scorpaenidae reflect the values for the individual species-line results for those families. Species in **bold** have GOC-like centers of distribution.

Table 2.3. Sites where $10m^2$ quantitative collections were completed. S = species richness at site. n = number of individuals at site

Code	Site	Latitude (ºN)	Longitude (ºW)	S	n
1	Gallina	24.457	110.3841	445	21
2	Espíritu Santo	24.5806	110.3996	132	16
3	San Francisquito	24.8198	110.5769	101	14
4	Santa Cruz	25.2588	110.7271	130	13
5	Monserrate	25.7101	111.0331	234	12
6	Danzante	25.8104	111.2612	299	20
7	Carmen	26.0168	111.168	361	21
8	Coronado	26.1174	110.2865	66	13
9	Tortuga	27.4517	111.8988	228	12
10	San Marcos	27.2563	112.0952	436	18
11	San Pedro Martir	28.3863	112.3134	201	11
12	San Esteban	28.7202	112.6119	114	13
13	Las Animas	28.7055	112.9337	165	13
14	Salsipuedes	28.7219	112.9515	151	13
15	Partida	28.887	113.0473	187	14
16	Punta Quemada	28.9503	113.4254	112	13
17	Puerto Refugio	29.5436	113.5575	396	17

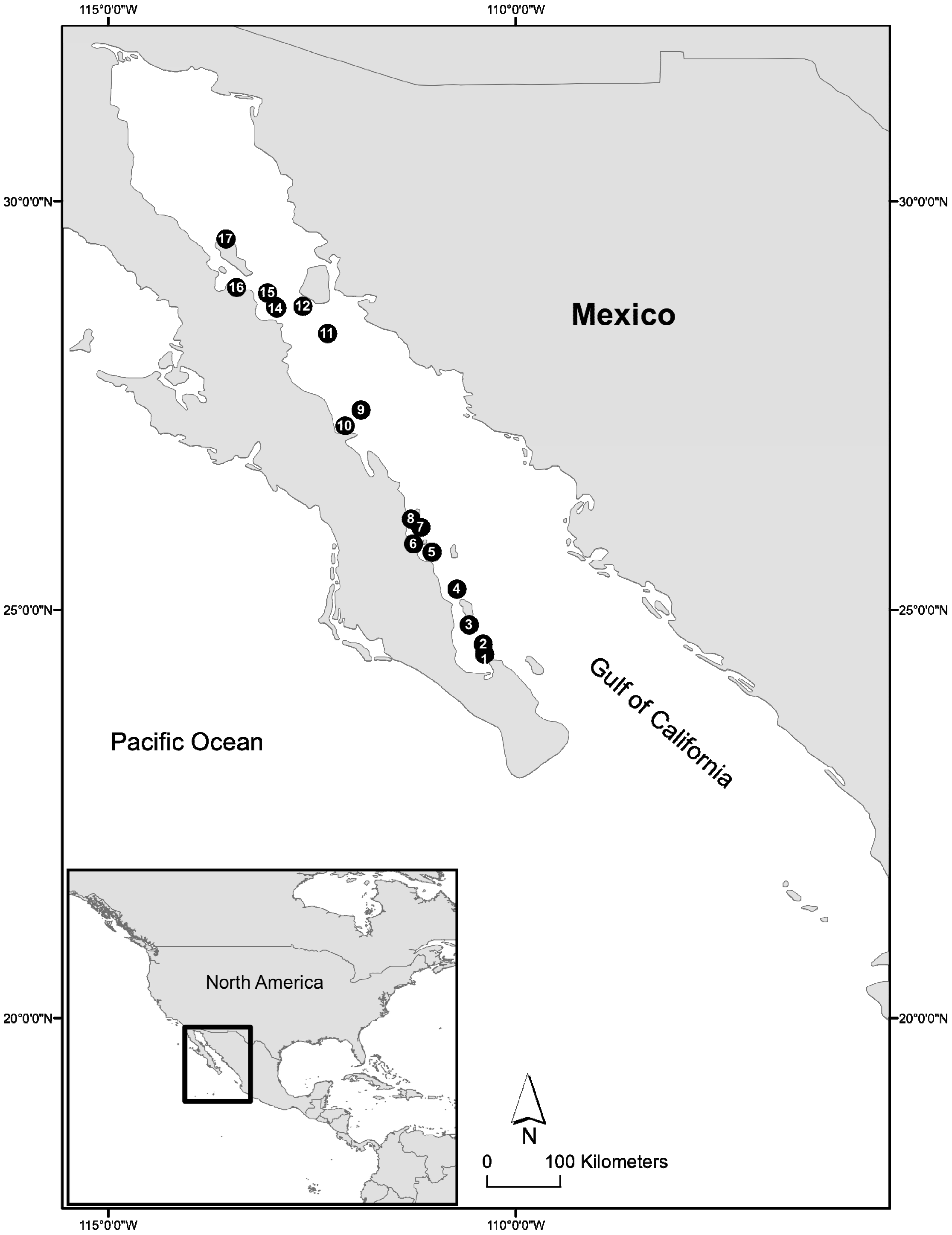

Fig. 2.1. The Gulf of California. Dots represent collection sites. Numbers reflect the site numbers in Table 2.3

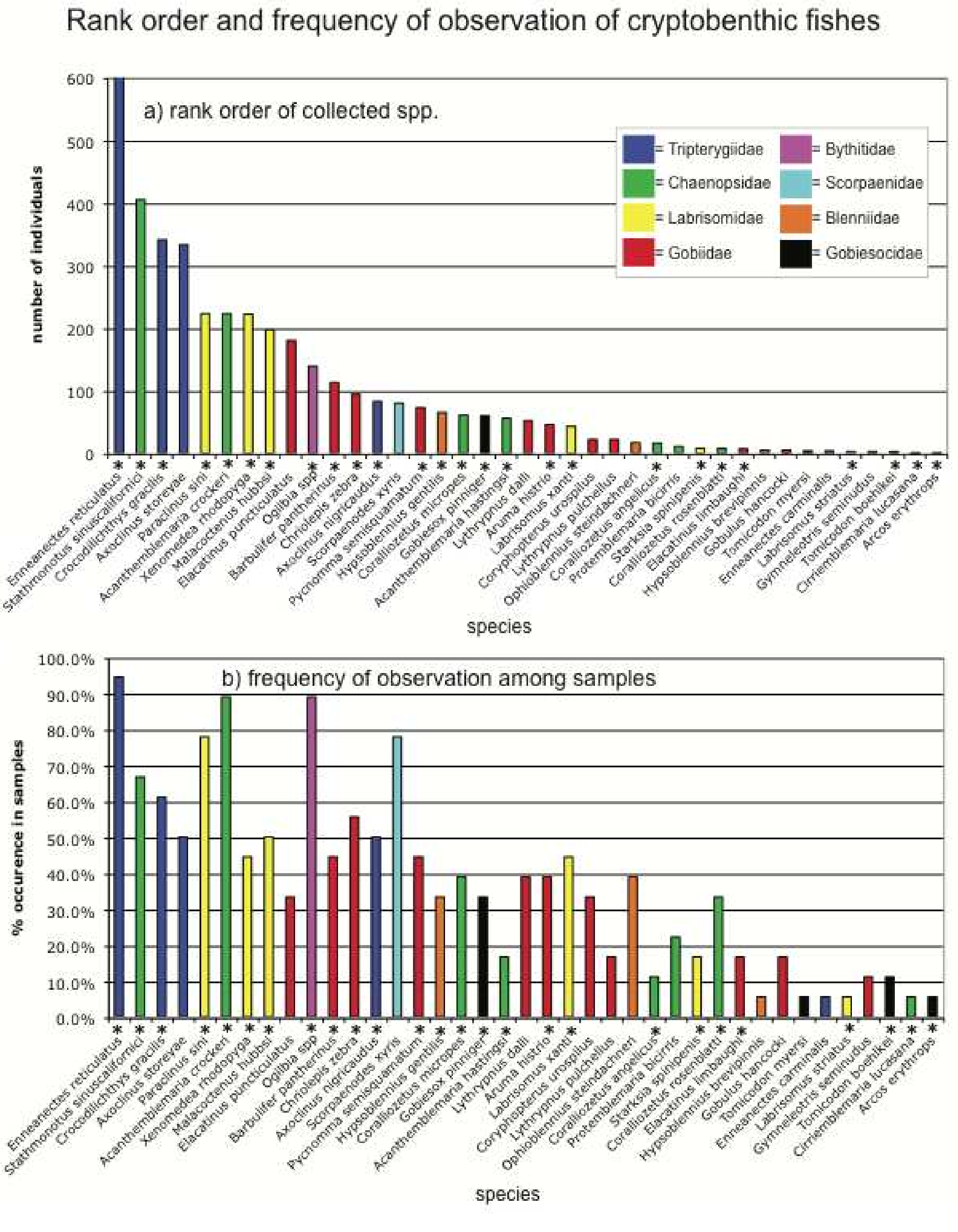

Fig. 2.2. a) rank order (pooled sites) and b) frequency of observation of 39 cryptobenthic fish species collected during this study. Colors represent divisions at the family level. * reflects a species with a GOC-centered distribution

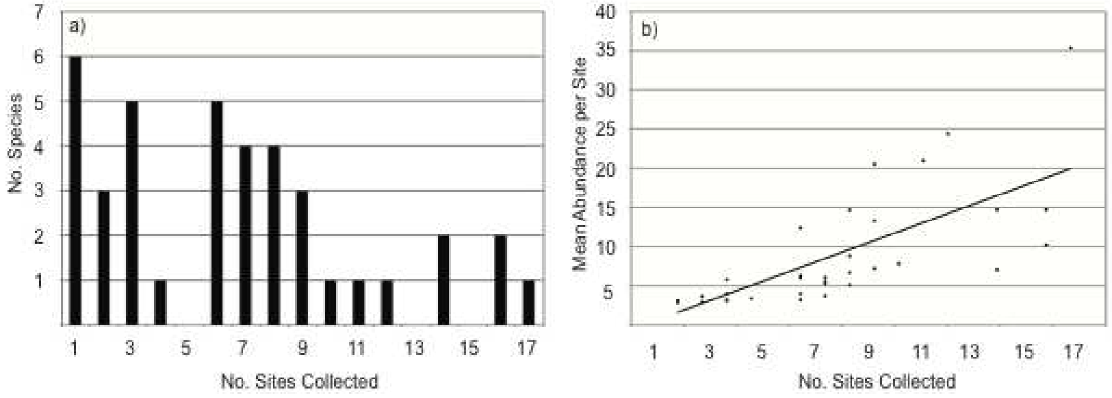

Fig. 2.3. a) histogram of species by number of sites where they were collected and b) mean abundance per site of each species by number of sites where they were collected. Equation of the trend line: mean abundance = 1.2664(number of sites collected) – 2.586

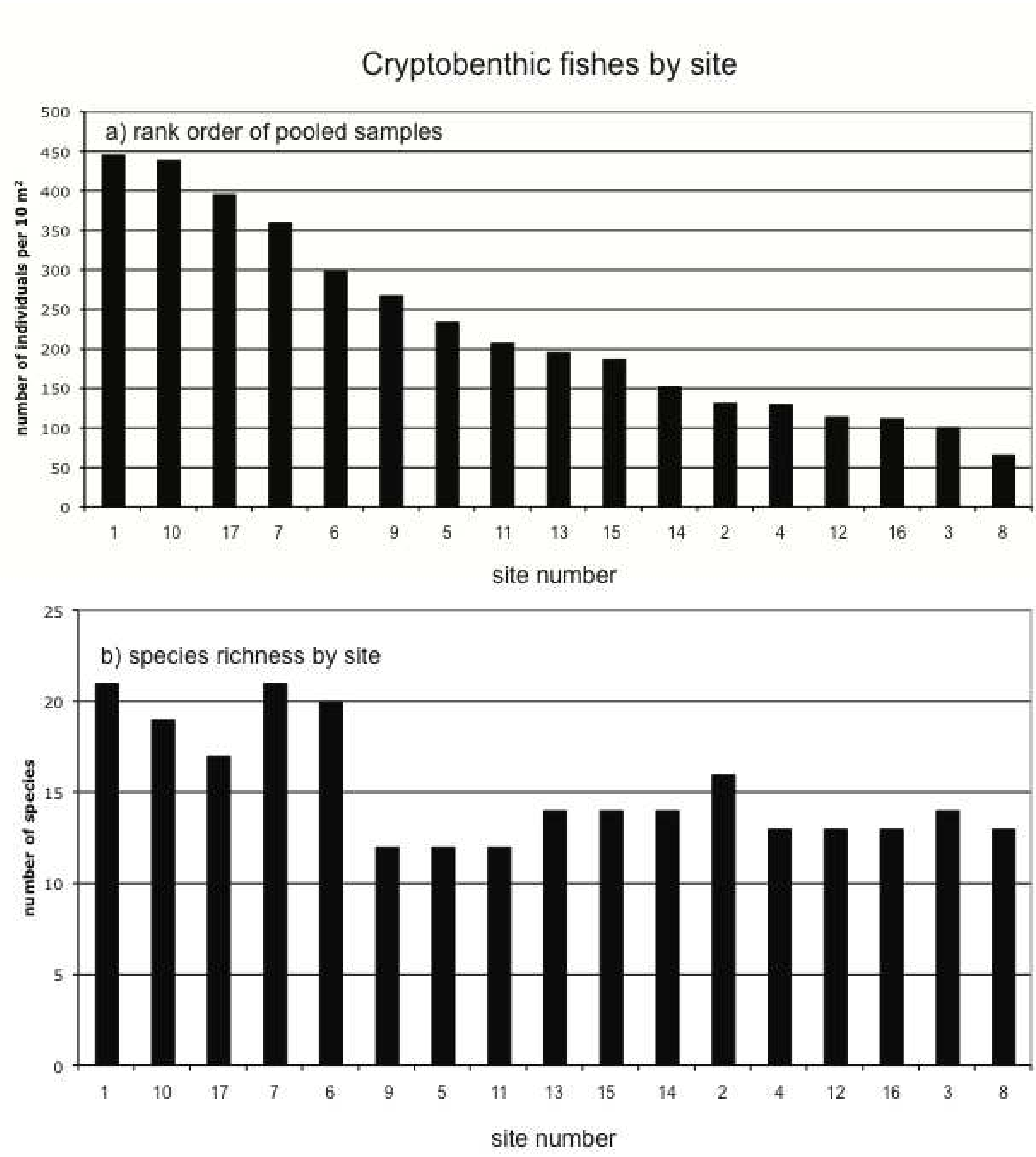

Fig. 2.4. a) rank order (pooled abundance) and b) species richness of 17 collection sites visited during this study. Site numbers reflect those in Table 2.3

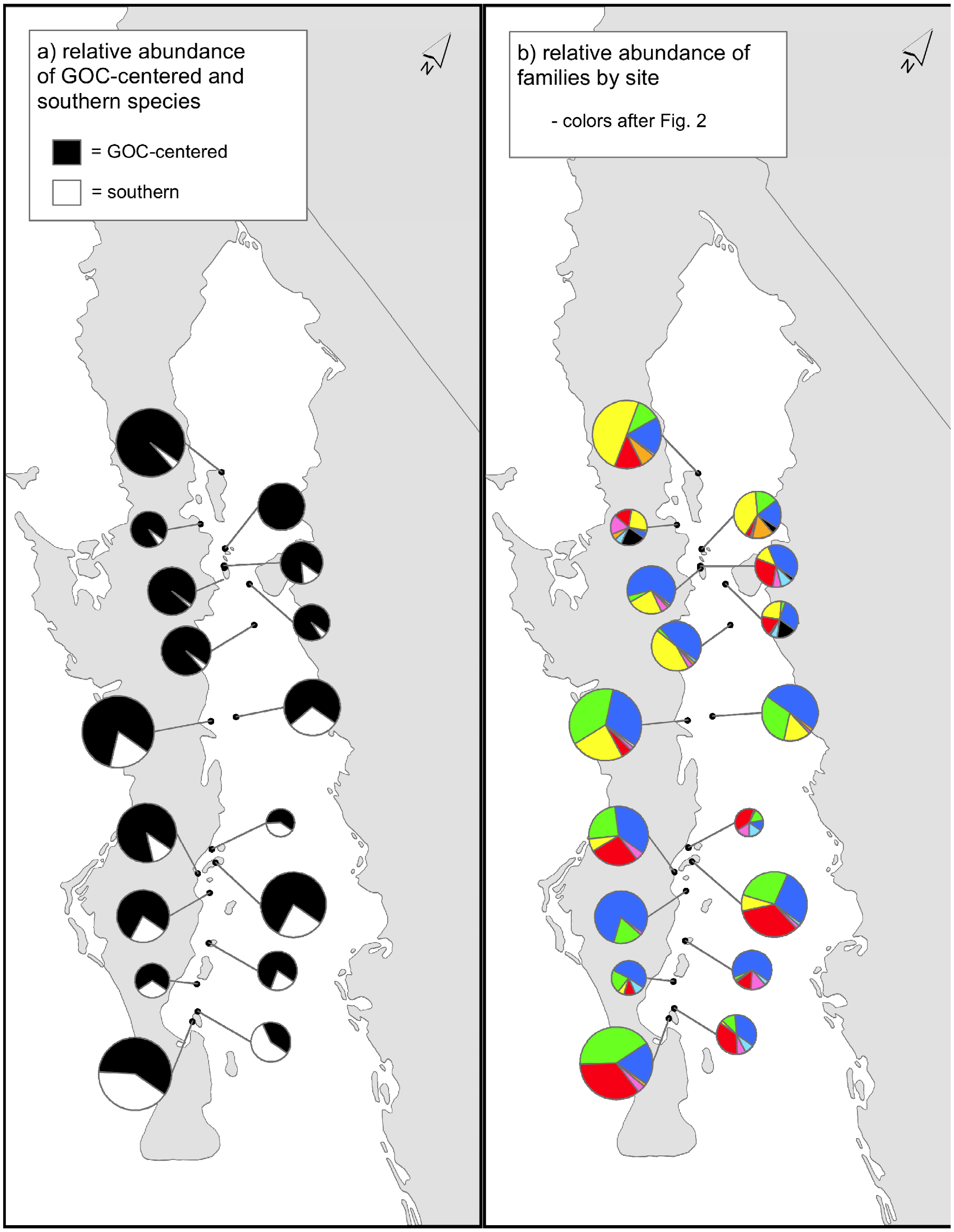

Fig. 2.5. a) relative abundance of endemic and more widely distributed species and b) relative abundance of cryptobenthic families at 17 collection sites. Size of circles reflects relative abundance of total community. Colors in (b) after Fig. 2. Background map is rotated 35 degrees clockwise (see north arrow), and pie graphs are offset for clarity

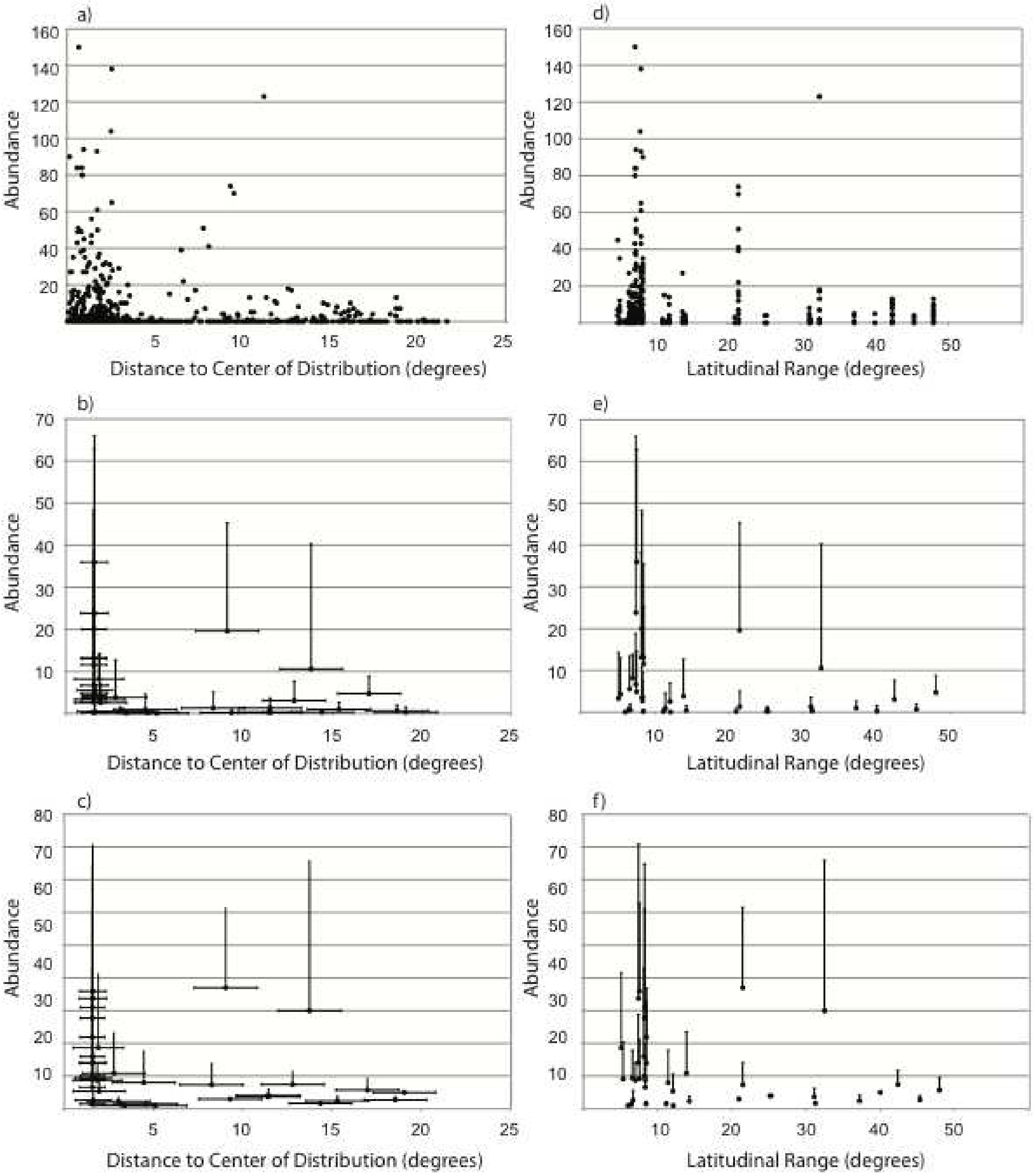

Fig. 2.6. a) individual records of all species collected during the study at all sites (n=663) by distance to center of distribution (COD); b) mean abundance per site of each species by mean distance to COD; c) mean abundance per site where present (nonzero records) of each species by mean distance to COD; d) individual records of all species collected at all sites by latitudinal range; e) mean abundance per site of each species by latitudinal range; f) mean abundance per site where present (nonzero records) of each species by latitudinal range

References

Aburto-Oropeza O, Balart EF (2001). Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. *Marine Ecology* 22(4):283-305.

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011). Large recovery of fish biomass in a no-take marine reserve. *PloS One* 6(8):e23601.

Aburto-Oropeza O, Sánchez A, Mascareñas-Osorio I, Sánchez C, Calderon M, Moxley J, Erisman B, Ezcurra E (2013). Linking fish biomass, geomorphology, and community assemblages to assess the health of reefs in the Gulf of California. In review.

Allen LG, Bouvier LS, Jensen RE (1992). Abundance, diversity, and seasonality of cryptic fishes and their contribution to a temperate reef fish assemblage off Santa Catalina Island, California. *Bulletin of the Southern California Academy of Sciences* 91(2):55-69.

Alvarez-Borrego S (2010). Physical, chemical, and biological oceanography of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Andrewartha HG, Birch LC (1954). *The distribution and abundance of animals.* The University of Chicago Press, Chicago.

Bernardi G, Findley L, Rocha-Olivares A (2003). Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57(7):1599-1609.

Berumen ML, Pratchett MS (2008). Trade-offs associated with dietary specialization in corallivorous butterflyfishes (Chaetodontidae: Chaetodon). *Behavioral Ecology and Sociobiology* 62(6):989-994.

Borregaard MK, Rahbek C (2010). Causality of the relationship between geographic distribution and species abundance. *The Quarterly Review of Biology* 85(1):3-25.

Briggs JC (1960). A new clingfish of the genus *Gobiesox* from the Tres Marías Islands. *Copeia* 1960(3):215-217.

Briggs JC (1955). A monograph of the clingfishes (Order Xenopterygii). *Stanford Ichthyological Bulletin* 6.

Brogan MW (1994). Distribution and retention of larval fishes near reefs in the Gulf of California. *Marine Ecology Progress Series* 115:1-13.

Brown JH (1981). Two decades of homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist* 21(4):877-888.

Brown JH (1995). *Macroecology*. University of Chicago Press, Chicago.

Brusca RC, Findley LT, Hastings PA, Hendrickx ME, Cosio JT, van der Heiden AM (2005). Macrofaunal diversity in the Gulf of California. *Biodiversity, Ecosystems, and Conservation in Northern Mexico* 179.

Depczynski M, Bellwood DR (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* 256:183-191.

Depczynski M, Bellwood DR (2004). Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Marine Biology* 145(3):455-463.

Fitzhugh GR, Fleeger JW (1985). Goby (Pisces: Gobiidae) interactions with meiofauna and small macrofauna. *Bulletin of Marine Science* 36(3):436-444.

Galland GR (2011). Comments on microhabitat specialization and a depth range extension for a chaenopsid tube blenny in the Gulf of California, Mexico. *Bulletin of the Southern California Academy of Sciences* 110(2):52-55.

Gaston KJ (2009). Geographic range. In Levin SA (ed.) *The Princeton Guide to Ecology*. Princeton University Press, Princeton.

Gaston KJ, Blackburn TM (2000). *Pattern and process in macroecology*. Blackwell Science, Oxford.

Gee JM (1989). An ecological and economic review of meiofauna as food for fish. *Zoological Journal of the Linnean Society* 96(3):243-261.

Goncalves EJ, Faria C (2009). Patterns of microhabitat utilisation in blennies. In Patzner RA, Goncalves EJ, Hastings PA, Kapoor BG (eds.) *The Biology of Blennies*. Science Publishers, Enfield.

Hastings PA (1986). Habitat selection, sex ratio and sexual selection in *Coralliozetus angelica* (Blennioidea: Chaenopsidae). In Uyeno T, Arai R, Taniuchi T, Matsuura K (eds.) *Indo-Pacific fish biology*. Ichthyological Society of Japan, Tokyo.

Hastings PA (1988). Female choice and male reproductive success in the angel blenny, *Coralliozetus angelica* (Teleostei: Chaenopsidae). *Animal Behaviour* 36(1):115-124.

Hastings PA (1992). Nest-site size as a short-term constraint on the reproductive success of paternal fishes. *Environmental biology of fishes* 34(2):213-218.

Hastings PA (2000). Biogeography of the Tropical Eastern Pacific: distribution and phylogeny of chaenopsid fishes. *Zoological Journal of the Linnean Society* 128(3):319-335.

Hastings PA (2009). Biogeography of new world blennies. In Patzner RA, Goncalves EJ, Hastings PA, Kapoor BG (eds.) *The Biology of Blennies*. Science Publishers, Enfield.

Hastings PA, Findley LT, Van der Heiden AM (2010). Fishes of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Hastings PA, Galland GR (2010). Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae). *Coral reefs* 29(1):155-164.

Hastings PA, Peterson CW (2010). Parental care, oviposition sites, and mating systems of blennioid fishes. In Cole KS (ed.) *Reproduction and sexuality in marine fishes. Patterns and processes*. University of California Press, Berkely.

Hubbs C (1952). A contribution to the classification of the blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. *Stanford Ichthyological Bulletin* 4(2):41-165.

Hubbs C (1954). Additional records of clinid fishes, with the description of a new species of *Cryptotrema* from the Gulf of California. *Copeia* 1954(1):17-19.

Kotrschal K (1989). Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological roles. *Environmental Biology of Fishes* 24(3):199-218.

Kotrschal K, Lindquist DG (1986). The feeding apparatus in four Pacific tube blennies (Teleostei: Chaenopsidae). *Marine Ecology* 7(3):241-253.

Kotrschal K, Thomson DA (1986). Feeding patterns in eastern tropical Pacific blennioid fishes (Teleostei: Tripterygiidae, Labrisomidae, Chaenopsidae, Blenniidae). *Oecologia* 70(3):367-378.

La Mesa GL, Muccio SD, Vacchi M (2006). Structure of a Mediterranean cryptobenthic fish community and its relationships with habitat characteristics. *Marine Biology* 149(2):149-167.

Lin H-C, Hastings PA (2011). Evolution of a neotropical marine fish lineage (subfamily Chaenopsinae, Suborder Blennioidei) based on phylogenetic analysis of combined molecular and morphological data. *Molecular Phylogenetics and Evolution* 60(2):236-248.

Lindquist DG (1985). Depth zonation, microhabitat, and morphology of three species of *Acanthemblemaria* (Pisces: Blennioidea) in the Gulf of California, Mexico. *Marine Ecology* 6(4):329-344.

Lomolino MV, Riddle BR, Whittaker RJ, Brown JH (2010). *Biogeography, fourth edition*. Sinauer Associates, Sunderland.

MacArthur RH (1972). *Geographical ecology. Patterns in the distribution of species*. Princeton University Press, Princeton.

Miller PJ (1979). Adaptiveness and implications of small size in teleosts. *Symposia of the Zoological Society of London* 44:263-306.

Miller PJ (1984). The tokology of gobioid fishes. In Potts GW, Wootton RJ (eds.) *Fish reproduction: strategies and tactics*. Academic Press, London.

Møller PR, Nielsen JG, Schwarzhans W (2005). Review of the American Dinematichthyini (Teleostei: Bythitidae). Part II. *Ogilbia*. *Journal of Ichthyology and Aquatic Biology* 10(4):133-208.

Munday PL, Jones GP (1998). The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review* 36:373-411.

Patzner RA (1999). Habitat utilization and depth distribution of small cryptobenthic fishes (Blenniidae, Gobiesocidae, Gobiidae, Tripterygiidae) in Ibiza (western Mediterranean Sea). *Environmental biology of fishes* 55(3):207-214.

Riginos C, Victor BC (2001). Larval spatial distributions and other early life–history characteristics predict genetic differentiation in eastern Pacific blennioid fishes. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268(1479):1931-1936.

Roberts CM, McClean CJ, Veron JE, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002).

Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295(5558):1280-1284.

Robertson DR, Cramer KL (2009). Shore fishes and biogeographic subdivisions of the Tropical Eastern Pacific. *Marine Ecology Progress Series* 380:1-17.

Robertson DR, Smith-Vaniz WF (2008). Rotenone: An essential but demonized tool for assessing marine fish diversity. *Bioscience* 58(2):165-170.

Rosenblatt RH (1959). *A revisionary study of the blennioid fish family Tripterygiidae*. Ph.D. Dissertation, University of California, Los Angeles.

Rosenblatt RH (1967). The zoogeographic relationships of the marine shore fishes of tropical America. *Studies in Tropical Oceanography* 5:579-592.

Rosenblatt RH, Parr TD (1969). The Pacific species of the clinid fish genus *Paraclinus*. *Copeia*, 1969(1):1-20.

Rosenblatt RH, Taylor Jr LR (1971). The Pacific species of the clinid fish tribe *Starksiini*. *Pacific Science*, 25(3):436-463.

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002). A general model for designing networks of marine reserves. *Science* 298(5600):1991-1993.

Sala E, Aburto-Oropeza O, Reza M, Paredes G, López-Lemus LG (2004). Fishing down coastal food webs in the Gulf of California. *Fisheries* 29(3):19-25.

Smith-Vaniz WF, Jelks HL, Rocha LA (2006). Relevance of cryptic fishes in biodiversity assessments: a case study at Buck Island Reef National Monument, St. Croix. *Bulletin of Marine Science* 79(1):17-48.

Springer VG (1958). *Systematics and zoogeography of the clinid fishes of the subtribe Labrisomini Hubbs*. Publication of the Institute of Marine Science, University of Texas 5:417-492.

Stephens JS (1963). *A revised classification of the blennioid fishes of the American family Chaenopsidae*. University of California Publication in Zoology 68.

Thomson DA, Gilligan MR (2002). Rocky-shore fishes. In Case TJ, Cody ML, Ezcurra E (eds.) *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford.

Thomson DA, Lehner CE (1976). Resilience of a rocky intertidal fish community in a physically unstable environment. *Journal of Experimental Marine Biology and Ecology* 22(1):1-29.

Thomson DA, Findley LT, Kerstitch AN (2000). *Reef fishes of the Sea of Cortez: The rocky-shore fishes of the Gulf of California*. University of Texas Press, Austin.

Thresher RE (1984). *Reproduction in reef fishes*. TFH Publications, Neptune City.

Walker BW (1960). The distribution and affinities of the marine fish fauna of the Gulf of California. *Systematic Zoology* 9(3/4):123-133.

Watson W (2009). Larval development in blennies. In Patzner RA, Goncalves EJ, Hastings PA, Kapoor BG (eds.) *The Biology of Blennies*. Science Publishers, Enfield.

CHAPTER 3

The Contribution of Cryptobenthic Species to Community Ecology in a Marine Fish Community

Abstract

We report the results of a large-scale, quantitative study of the rocky reef fish community in the Gulf of California (GOC), Mexico. In July 2010, we visited 17 sites in the GOC where we collected small fishes and visually surveyed conspicuous fishes in order to calculate densities representative of the whole fish community on GOC reefs. We counted or collected 28,880 individuals, representing 107 species in 36 families. Small, cryptic (cryptobenthic) fishes accounted for one third of the total species richness and were not observed during visual surveys. Those species also accounted for more than 95% of the total fish abundance and as much as 40% of sub-region-scale metabolic requirements of the fish community. At one site, more than 50% of the community metabolism resulted from the presence of a dense cryptobenthic fish assemblage. Density-body size relationships of the complete fish community were negatively linear (in log-log space), with small individuals/species exponentially more abundant than larger individuals/species, but the slopes of these relationships were lower than predicted by the ‘energetic equivalence rule.’ We found no statistical relationship between abundance or biomass of cryptobenthic and conspicuous fishes.

Introduction

Quantitative studies of ecological communities are a fundamental means for understanding the relationships among individuals and among species (Hayek and Buzas 1997). Many quantitative studies of nature involve species that are sessile (or nearly sessile) as adults, and these studies have contributed significantly to population and community ecology of tropical forests (e.g., Janzen 1970; Greig-Smith 1983; Dallmeier et al. 1991), grasslands (e.g., Crocker and Tiver 1948; Tilman 1987; Gibson 2009), marsh grasses (e.g., Nixon and Oviatt 1973, Steever et al. 1976), intertidal invertebrate communities (e.g., Connell 1961; Dayton 1971), sea grasses (Hemminga and Duarte 2000; Short et al. 2001), and other ecosystems. However, obtaining quantitative numbers of mobile species is more difficult, though methods have been derived to somewhat accurately estimate densities of animals in many of those same systems.

In the marine environment, quantitative samples of fishes play an important role in fisheries management, conservation, and ecology. Unlike soft bottom (otter trawls) and mid-water systems (Isaacs-Kidd mid-water trawls or Oozeki trawls), it is difficult or nearly impossible to quantify rocky-, coral-, or algal-reef fishes using net sampling. Researchers in these systems often rely on non-extractive, SCUBA-based surveys to obtain fish densities (e.g., Harmelin-Vivien et al. 1985; Bohnsack and Bannerot 1986; Lang 2003), and these methods have worked well in describing many interesting features of reef fish dynamics and conservation (e.g., Sala et al. 2002; Sandin et al. 2008). SCUBA surveys of fish densities, however, typically require divers to swim along a predetermined distance during a predefined time, counting, identifying, and estimating the size of all fishes present along a transect. This method underestimates the densities of small, cryptically-colored (“cryptobenthic”) species. Cryptobenthic fishes are often overlooked and consequently undervalued in these analyses. Depending on the ecological metric of interest, this undervaluation may be a significant oversight, as cryptobenthic fishes are abundant (Ackerman and Bellwood 2000; Thomson and Gilligan 2002; Chapter 2, this volume), diverse (Allen et al. 1991; Smith-Vaniz et al. 2006), and may represent a significant portion of reef trophodynamics (Kotrschal 1989; Depzcynski and Bellwood 2003; Ackerman and Bellwood 2003; Ackerman et al. 2004).

In order to study the cryptobenthic species living on reefs, extractive collecting is often employed, and rotenone is widely considered the most important ichthyocide in marine fish research (Robertson and Smith-Vaniz 2008). While historical rotenone stations were often qualitative, in recent years, ecologists have begun quantitatively collecting small fishes at rotenone stations, with the help of barrier nets enclosing known areas (e.g., Ackerman and Bellwood 2000; Thomson and Gilligan 2002; Willis 2001; Smith-Vaniz et al. 2006; Chapter 2, this volume). However, though rotenone is not strongly selective among marine fishes, mobile species can often avoid the chemical or avoid capture, and rotenone stations necessarily cover small areas. For these reasons, rotenone samples are selective against large fishes, diminishing our ability to make generalizations about reef-scale, fish ecology from these alone.

Surprisingly, few studies have considered a combination of visually-derived densities and quantitative rotenone stations to study community ecology of both conspicuous and cryptobenthic fishes together at a site. A primary exception is a series of papers written based on visual surveys and rotenone collections at Orpheus Island, Great Barrier Reef (Ackerman and Belwood 2000, 2003; Ackerman et al.

2004). Ackerman and colleagues studied the community ecology of the entire reef fish assemblage there (Ackerman and Bellwood 2000) and specifically examined density-body size relationships among reef fishes in order to test Damuth's (1981) hypothesis that individuals (or species) in small size classes are exponentially more abundant than those in larger size classes and therefore that the two groups utilize a similar amount of the reef's total energy (Ackerman and Bellwood 2003; Ackerman et al. 2004). Those authors had mixed results, with fishes binned by species showing a negative relationship between log density and log biomass that had lower slope than predicted (Ackerman and Bellwood 2003), while individuals binned by size class, regardless of species, showed a negative relationship closer to predictions when all but the smallest size classes were considered (Ackerman et al. 2004). For reef fishes, the Orpheus Island collections/surveys represent one of the most complete data sets of quantitative fish densities and sizes, and to date, the generality of the findings of Ackerman and his colleagues have not been tested in other locations or on algal or rocky reefs.

Here, we report the results of a combination of quantitative rotenone collections and visual surveys for 16 islands and one peninsular site, stretching across more than 5.5 degrees of latitude in the Gulf of California (GOC), Mexico. Surveys and collections were completed concurrently during an expedition in July 2010 and represent a snapshot of the complete reef fish community at those sites. In addition to reviewing any GOC patterns in diversity, biomass, and metabolism through a quantitative study of the whole fish community for the first time, we repeat some of

Ackerman and colleagues' analyses for a distinct fauna in a rocky reef system and speculate on the role of local oceanography in impacting reef metabolism and energy use.

Methods

Study Site

In order to characterize the rocky reef community at locations throughout the GOC, we embarked on an expedition to 17 island and peninsular sites (Fig. 3.1). The GOC is a long (~1,000 km), narrow (~150 km), semi-enclosed basin, along a northwest-southeast axis between the Baja Peninsula and continental Mexico. This region is highly productive, particularly important to Mexican fisheries in a national context (Cisneros-Mata 2010), and is a biodiversity hotspot (Roberts et al. 2002) known for numerous species of megafauna. The GOC is relatively rich in ichthyofauna (Hastings et al. 2010) and is characterized by rocky, rather than coral reefs (Thomson et al. 2000), though at least 18 species of hermatypic corals have geographic ranges that include the GOC (Brusca and Hendrickx 2010). At least 104 species of crytobenthic fishes are known to inhabit the rocky reefs of the GOC, but no more than 25 to 30 are typically observed at one site (Chapter 2, this volume).

In order to examine diversity, abundance, biomass, and metabolism of reef fishes in the GOC, we binned sites into three sub-regions based on biogeographic patterns of the fauna. The northern sites in our study region are known to include several disjunct populations of temperate fishes from California, USA that are not present in the southern GOC (Walker 1960; Bernardi et al. 2003). Our southern sites include species from southern Mexico and Central America that do not reach our northern sites (Walker 1960; Chapter 2, this volume). Sites in the central GOC have some species from each of these groups and seem to represent a transition zone (Sala et al. 2002; Chapter 2, this volume). Therefore, we binned sites into subdivisions, hereafter referred to as “south,” “central,” and “north” (Fig. 3.1). Our central and south sub-regions are both included in the central GOC by Walker (1960).

Field Observations

To quantitatively describe the complete reef fish community, we utilized a combination of area-based visual surveys and quantitative rotenone collections at each site. Visual surveys followed the methods of Aburto-Oropeza et al. (2011) and involved SCUBA divers swimming multiple passes along 50 m transects, identifying, counting, and estimating the size of all individuals observed within a five meter wide area (250 m^2 total area per transect). Different behavioral groups were counted during each pass, with larger, highly mobile species counted during the first pass and smaller, demersal species counted during subsequent passes (Aburto-Oropeza et al. 2011). This methodology prevented individuals from being counted multiple times. At all sites but one, we completed four transects.

Collections

The methods used to obtain quantitative rotenone collections are described in Chapter 2 (this volume). A team of divers erected a barrier net around a 10 m^2 area and released a slurry of powdered rotenone, seawater, and liquid dish soap in order to collect every cryptobenthic fish at the site. Rotenone samples were collected at depths of one to five meters. Comparing the effectiveness of extractive collections and visual surveys was not a goal of our study, and divers actively chased away conspicuous fishes before releasing the rotenone mixture. Any larger, mobile fishes that were captured were not included in the analyses.

In order to reduce sampling biases, a team of two divers conducted all visual surveys, while a second team obtained all rotenone samples.

Analysis

For our purposes, we defined cryptobenthic fishes as any species of goby (Gobiidae), blenny (Blennioidei), clingfish (Gobiesocidae), scorpionfish (Scorpaenidae), or cusk eel (Ophidiiformes) and considered only species from those groups, with the addition of cardinalfishes (Apogonidae), in analyses of the rotenone collections. Juveniles or adults of conspicuous species captured in rotenone collections were not considered in analyses. Similarly, cryptobenthic fishes were not included in analyses of visual surveys. Furthermore, it is difficult to quantify eels (Anguilliformes) or nocturnal fishes (e.g., Holocentridae) with either visual surveys or rotenone collections, but we included visual records of conspicuous individuals in these groups with the caveat that they may underestimate density.

Individual collected fishes were weighed to 0.01 g, and weights were summed by site. Where specimens weighed less than 0.01 g, two or more individuals of the same species (of equal length) were weighed together. In this manner, precise biomass was calculated for each site and converted to grams per unit area. 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 and Pauly 2012). Weights of all individuals were summed by transect and converted to grams per unit area. Values from the two 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, following Gillooly et al. 2001 and Davison et al. 2013, was assumed to be a function of biomass (W) and temperature (T),

$$\text{Routine Metabolic Rate (J/min)} = \text{EXP}(a) * W^{0.75} * \text{EXP}(1000c/(273.15 + T)),$$

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. As metabolism scales with a fractional power of biomass, it is higher (per unit mass) in small individuals and was calculated separately for each individual fish using the above measured or derived biomass and summed by site to obtain whole-community, fish metabolism per unit area.

Temperatures used were means of the 30 days prior to collecting/surveying at each site and were calculated using data reported Chapter 1 (this volume). At the time of collection, average temperatures were similar across all study sites (26 to 30 degrees C; Chapter 1, this volume).

To identify any potential linear relationships between cryptobenthic fishes and conspicuous fishes, we calculated a simple least-squares regression between the biomass/abundance of the cryptobenthic group and the conspicuous group.

Following Ackerman and Bellwood (2003) and Ackerman et al. (2004), we plotted log mean density by log mean biomass for every species in each sub-region and log mean density for all individuals binned into eight log biomass groups in order to test for density-body size relationships. Least-squares regression lines were used to determine whether or not there is a linear relationship between these two parameters (in log-log space).

Finally, we compared sites using a “healthiness score,” calculated by Aburto-Oropeza et al. (2013) for each island or peninsular site in our study area. Scores were calculated using visual surveys of the reef fauna at sites across the GOC (including the 17 reported here) from 2009 (Aburto-Oropeza et al. 2013). As the scores included 51 parameters based on visual transects of conspicuous fishes and invertebrates, we avoid autocorrelation by only examining potential relationships between these scores and cryptobenthic fishes.

Results

Across our 17 sites, we collected or surveyed a total of 20,880 reef fishes comprising 107 species from 36 families. Four of the species (three families) were rays or skates, and the remaining 103 species (33 families) were bony fishes. We did not observe or collect any sharks. Thirty-five species represent families defined above as cryptobenthic and 72 species are included in our conspicuous group. Results vary by sub-region, with the south (8 sites) represented by 92 species, while the approximately equally surveyed north (7 sites) included only 69 species. The central sub-region (two sites) was under-surveyed relative to the north and south, and species richness (48 species) is consequently lower. The central sub-region was defined to remove a transition zone between north and south and to allow the approximately equal effort undertaken in the north and south to be compared more directly. Only one species (2.1% of the richness) was collected or observed only in the central GOC. Conversely, 27 species (29%) occurred only in the south, and 14 species (20.3%) occurred only in the north. In both our northern and southern sub-regions, the cryptobenthic fishes comprised approximately 35% of the total species richness.

We captured or observed six temperate California species previously determined to have disjunct populations in the northern GOC (Table 3.1). Not surprisingly, all six species were observed in our northern sub-region. Interestingly, however, one species was also collected at a central site, and another species (the Bluebanded Goby – *Lythrypnus dalli*) was collected at several sites in the south.

Abundance, biomass, and metabolism were all calculated per unit area and can be compared by sub-region. The south and central GOC were characterized by higher biomass and metabolism than the north, and the central sites had much higher densities of fishes than the rest of our study area, primarily as a result of the dense cryptobenthic fish community at the two sites there (Table 3.2). The contribution of cryptobenthic fishes to these community metrics varied by sub-region (Fig. 3.2) and by site (Fig. 3.3), with percent total abundance generally > percent total species richness > percent total metabolism > percent total biomass at most sites. Figure 3.3 highlights, in particular, the overwhelmingly high abundance of cryptobenthic fishes (relative to conspicuous species) on GOC rocky reefs.

In plots of mean log density by mean log biomass of each species, all sub-regions had the expected negative relationship between size and density, with small species being exponentially denser than larger species (Fig. 3.4). We found similar results when comparing densities of individuals binned by log biomass, independent of species (Fig. 3.5). These negative relationships are linear and significant (Table 3.3).

The cryptobenthic fish group and the conspicuous fish group do not covary in space at our sites. We found no statistical relationship between the abundance or biomass of these two groups ($R^2 < 0.11$ in both cases, $P > 0.05$). Similarly, our analyses of cryptobenthic abundance and biomass were also unrelated to the healthiness scores reported by Aburto-Oropeza et al. (2013; $R^2 < 0.22$ in both cases; $P > 0.05$).

Discussion

General patterns of GOC reef fish abundance and distribution

Our data set is derived from the most complete, quantitative survey of GOC reef fishes available to date. Our results quantitatively confirm that shallow rocky reefs in the lower GOC are characterized by higher species richness than those in the upper GOC, following the same general pattern found for the more than 900 total fish species observed in the GOC (Sala et al. 2002; Hastings et al. 2010). Sites in the north, however, may experience more seasonal turnover among the shallow water reef fishes as a result of seasonal changes to the marine environment there (Thomson and Lehner 1976). There are at least 19 species of temperate, California fishes with populations in the northern GOC (Present 1987; Bernardi et al. 2003). During July 2010, we observed six of them. It is possible that shallow reefs may have fish communities characterized by more species and higher abundances of these temperate fishes in the cooler months and a higher prevalence of fishes with a tropical affinity in the warmer months. We do not expect a similar turnover in the community for our more oceanographically stable (Chapter 1, this volume), southern sites. Quantitative surveys of reef fishes in our study area during the cooler period are not currently available.

We did not observe any sharks during our study. This is notable, as several of the most intact reef-fish communities around the world are characterized by relatively large numbers of (and in some cases dominance by) predatory sharks, affecting the relative distribution of biomass and other community ecology metrics within the food web (e.g., Sandin et al. 2008; Friedlander et al. 2012). Our surveys were conducted at depths of only five meters, so large numbers of sharks may not be expected at even the relatively undisturbed sites, but our lack of a single individual during our surveys and unpublished surveys at 20 m depth indicate that, with few spatial exceptions, sharks are now extremely rare per unit area in the GOC, a likely consequence of overfishing (Applegate et al. 1993). This apparently missing component of the reef fish community may affect our conclusions, by significantly reducing the biomass, metabolism, etc. in the largest size classes.

During the 2010 expedition and similar expeditions, we surveyed fishes at 20 m depth in addition to the surveys and collections reported here. We do not report the results of those efforts because we do not have complementary quantitative cryptobenthic fish collections. While we know that abundance and biomass of conspicuous fishes generally increase from five to 20 m depth (unpublished data), we cannot be sure if the cryptobenthic group changes in a similar or opposite manner or does not change at all. Furthermore, while there are few differences in the conspicuous species pool at those two depths (unpublished data), most cryptobenthic species are microhabitat specialists and some are restricted to the uppermost depth zones on GOC reefs (e.g., Briggs 1955; Lindquist 1985; Thomson et al. 2000; Galland 2011). Therefore, reefs at 20 m depth may have a very different pool of cryptobenthic species than at five meters, precluding further speculation.

Density-body size relationships

As in the reef fish community at Orpheus Island, Great Barrier Reef (Ackerman and Bellwood 2002), our analysis of density and biomass of GOC reef fishes revealed a negative, linear relationship, with small species denser than large species in each sub-region (Fig. 3.4; Table 3.3). The slopes of the regression lines are steeper than that reported for Orpheus Island (slope = -0.45 +/-0.10, $R^2 = 0.28$), indicating a greater difference between densities of small and large species in the GOC than there.

Binning individuals into eight size classes, independent of species, revealed a similar negative relationship between density and biomass (Fig. 3.5; Table 3.3). Our analysis for GOC fishes differs from a similar analysis of Orpheus Island fishes (Ackerman et al. 2004) in two primary ways. First, there is a significant, linear relationship between density and biomass across the entire reef fish community in all three sub-regions of the GOC. At Orpheus Island, Ackerman et al. (2004) did not find a linear relationship between these two metrics when they included the smallest fishes. Only after removing size classes smaller than the mode was the relationship linear. They hypothesized that the smallest individuals on the reef there may not have access to the same energetic resources as the larger size classes or that physiological (e.g., body size:gonad size ratios) or ecological (e.g., interactions with invertebrates of similar body size) limitations may cap densities of the smallest fishes (Ackerman et al. 2004). Following that discussion, our results imply that small reef fishes in the GOC do not experience (or somehow overcome) the same energetic, physiological, or ecological limitations to abundance.

The second difference between the Orpheus Island and GOC reef fish communities is the slope of the regression line when the smallest size classes are removed. Following Ackerman et al. (2004), we reevaluated relationships between biomass and density after removing all size classes smaller than the mode (Fig. 3.5; Table 3.3). In doing so, the linear relationship becomes steeper and tighter in all sub-regions. However, even these modified slopes are not as steep as that reported for Orpheus Island (-0.77 +/- 0.28). The slope for Orpheus Island fishes of intermediate to large sizes is not statistically different than the slope predicted by the 'energy equivalence rule' (-0.75; Ackerman et al. 2004). That rule states that when the slope of the regression between log biomass and log density is -0.75, each size class removes the same amount of energy from the environment (because metabolism increases with biomass to a power of 0.75; Damuth 1981). Ackerman et al. (2004) showed that to be true for Orpheus Island fishes in intermediate to large size classes. We cannot make a similar claim for GOC fishes. In the GOC, the midsized fishes (those near the mode) are relatively less dense than predicted by Damuth (1981) and shown by Ackerman et al. (2004) for Orpheus Island fishes.

Metabolism

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), small fishes use 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 metabolism can be quite high (Fig. 3.2). This is especially evident in the northern sub-region, where the cryptobenthic fishes account for fully 40% of the energy intake by reef fishes. This is a significant amount of energy for a portion of the community that is rarely included in reef surveys and, for that matter, rarely observed. At the site level, we found the cryptobenthic fishes to account for more than half of the total fish metabolism at one site. Furthermore, total reef fish production may be even more highly influenced by the cryptobenthic group because our calculation of reef fish metabolism is a snapshot and does not account for growth and turnover rates. As many of these species are short-lived (Miller 1979), with several living no more than one or two years, the turnover in the cryptobenthic fish community may be high and account for more fish production than slower growing, large species. This assumption has yet to be tested in cryptobenthic fishes, however, and may be complicated by the disproportionately high percentage of growth that many cryptobenthic species undergo while living as planktonic larvae (Stephens et al. 1970). Furthermore, the quantity of cryptobenthic fish production that is available to species in the conspicuous fish group, including commercially important species, is unknown, as the role of cryptobenthic fishes in GOC food webs is poorly understood.

Fish metabolism is not simply a function of biomass, but it is also a function of temperature (Gillooly et al. 2001). While examining metabolism at one time point for several sites/sub-regions is interesting in that it provides a means to compare locations, it is important to remember that even if biomass is in a steady state (however improbable), metabolism 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 (Chapter 1, this volume). During the summer, mean temperatures are similar from site to site, but winter temperatures can be very different depending on location in the GOC. During winter conditions, fishes at warm sites in the south utilize more energy per unit biomass than cooler sites in the north, or put another way, given a fixed amount of available environmental energy, cooler sites could maintain higher stocks of standing biomass. Productivity and temperature are often inversely related as a result of upwelling (Alvarez-Borrego 2010) and could align to promote much higher biomass at cold, productive sites. Interestingly, the biomass per unit area in the northern sub-region (the coolest and most productive part of the GOC) is much lower than in the central and southern GOC (Table 3.2). This finding may reflect potential differences in fishing pressure among sub-regions.

To demonstrate potential differences in the mean metabolism resulting from temperature change across our study area, we report a time series of metabolism for the year preceding fieldwork at sites in each of our sub-regions (Fig. 3.6). In order to derive these curves, we assumed that biomass is in a steady state and that our snapshot is representative of the biomass at any time point at our sites and utilized 31-day, centered moving average temperatures reported in Chapter 1 (this volume) to calculate metabolism for each day. Throughout the year, metabolism per unit biomass may change sharply, and at different rates and magnitudes, depending on location in the GOC, as a result of the local oceanography. Therefore, sites with widely different community metabolism per unit area during one season may have similar energy requirements during another season (Fig. 3.6). We know, however, that densities of short-lived cryptobenthic fishes fluctuate throughout the year (e.g., Thomson and Lehner 1976; Hastings and Galland 2010), so biomass is probably not in a steady state, and the relative contribution of cryptobenthic species to community metabolism is likely to change, seasonally.

Studying disturbed systems

We found no statistical relationship between healthiness scores (determined, in part, from conspicuous fish abundance/biomass; Aburto-Oropeza et al. 2013) and the biomass or abundance of the cryptobenthic species group. This finding may be a result of the uniformly low scores that were calculated for our sites. According to those authors, all of the sites researched for this study are at the lower end of the spectrum for GOC reef health (Aburto-Oropeza et al. 2013). The ‘healthiest’ sites in the GOC are found inside strictly-protected marine reserves where we did not quantitatively collect small fishes. We know that the community structure of conspicuous fishes and invertebrates is quite different at those highest scoring sites (Aburto-Oropeza et al. 2011, 2013), and it would be interesting to know if there are similar or opposite differences in the cryptobenthic group there. The lack of a clear relationship between cryptobenthic fishes and the healthiness scores at our 17 sites may be a result of the fact that all of our sites are among the lowest scoring in the GOC.

Much of our understanding of reef fish ecology is based on the careful study of disturbed ecosystems, and this situation may lead to incomplete findings and misconceptions about community structure in nature. 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. For example, a quantitative study of cryptobenthic fishes (in addition to visual surveys) in the Northern Line Islands, across the gradient of human impacts reported by Sandin et al. (2008), would be vitally important to our understanding of interactions among cryptobenthic reef fishes under different degrees of human influence. Quantitative sampling at the top-predator-dominated, unfished reefs of the outer islands there would allow for examination of community metabolism, production, and density-size relationships among nearly pristine communities. We suspect that metrics of community ecology would differ across the gradient and could bring into question the application of rules, such as the ‘energy equivalence rule,’ to disturbed systems like those examined here. Correcting for disturbance may also clarify differences between our results and those for Orpheus Island discussed above. In general, results of studies undertaken in disturbed ecosystems may not accurately reflect community ecology of pristine systems. Preserving places where ecologists can study intact communities is one more advantage of establishing marine reserves. In the GOC, that place is Cabo Pulmo National Park (Aburto-Oropeza et al. 2011; Galland et al. 2011).

Conclusions

This is one of the few studies to quantitatively measure the contribution of cryptobenthic fishes to the reef fish community density, species richness, biomass, and metabolism and the only such study for the GOC. Our results demonstrate the importance of whole-community assessments and the need to consider all size categories in evaluations of community ecology among marine vertebrates. By continuing 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 in reef ecosystems.

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IGERT 0333444. Chapter 3, in part, is currently being prepared for submission for publication of the material with O Aburto-Oropeza, BE Erisman, and PA Hastings who helped organize field expeditions and provided many valuable comments and suggestions on the text.

Table 3.1. Temperate California species with populations in the northern Gulf of California that we quantitatively observed in the present study

Species	Sub-region observed	Method of observation
Hypsoblennius gentilis	north/central	quantitative collection
Lythrypnus dalli	north/south	quantitative collection
Anisotremus davidsonii	north	visual survey
Halichoeres semicinctus	north	visual survey
Hermosilla azurea	north	visual survey
Paralabrax maculatofasciatus	north	visual survey

Table 3.2. Mean density, biomass, and metabolism of reef fishes in the Gulf of California

	Density (ind/m^2)		Biomass (g/m^2)		Metabolism (J/min/m^2)	
Sub-region	Crypto	Conspicuous	Crypto	Conspicuous	Crypto	Conspicuous
South	22.7	1.2	6.6	169.5	0.6	3.7
Central	37.0	1.4	18.3	163.5	1.3	3.3
North	20.1	0.6	15.7	94.1	1.2	1.8

Table 3.3. Least-squares regression between log mean biomass and log mean density of individuals binned by species or into size classes

	All data		
By Species	Slope (+/- 95% CI)	R^2	P
South	-0.58 (+/- 0.1)	0.62	< 0.0001
Central	-0.56 (+/- 0.15)	0.57	<0.0001
North	-0.80 (+/-0.2)	0.47	<0.0001

	All data			Excluding size classes smaller than mode		
By Size	Slope (+/- 95% CI)	R^2	P	Slope (+/- 95% CI)	R^2	P
South	-0.36 (+/-0.16)	0.83	0.0017	-0.45 (+/-0.15)	0.92	0.0006
Central	-0.41 (+/-0.16)	0.86	0.0008	-0.57 (+/-0.14)	0.97	0.0003
North	-0.32 (+/-0.29)	0.55	0.0363	-0.63(+/-0.17)	0.96	0.0005

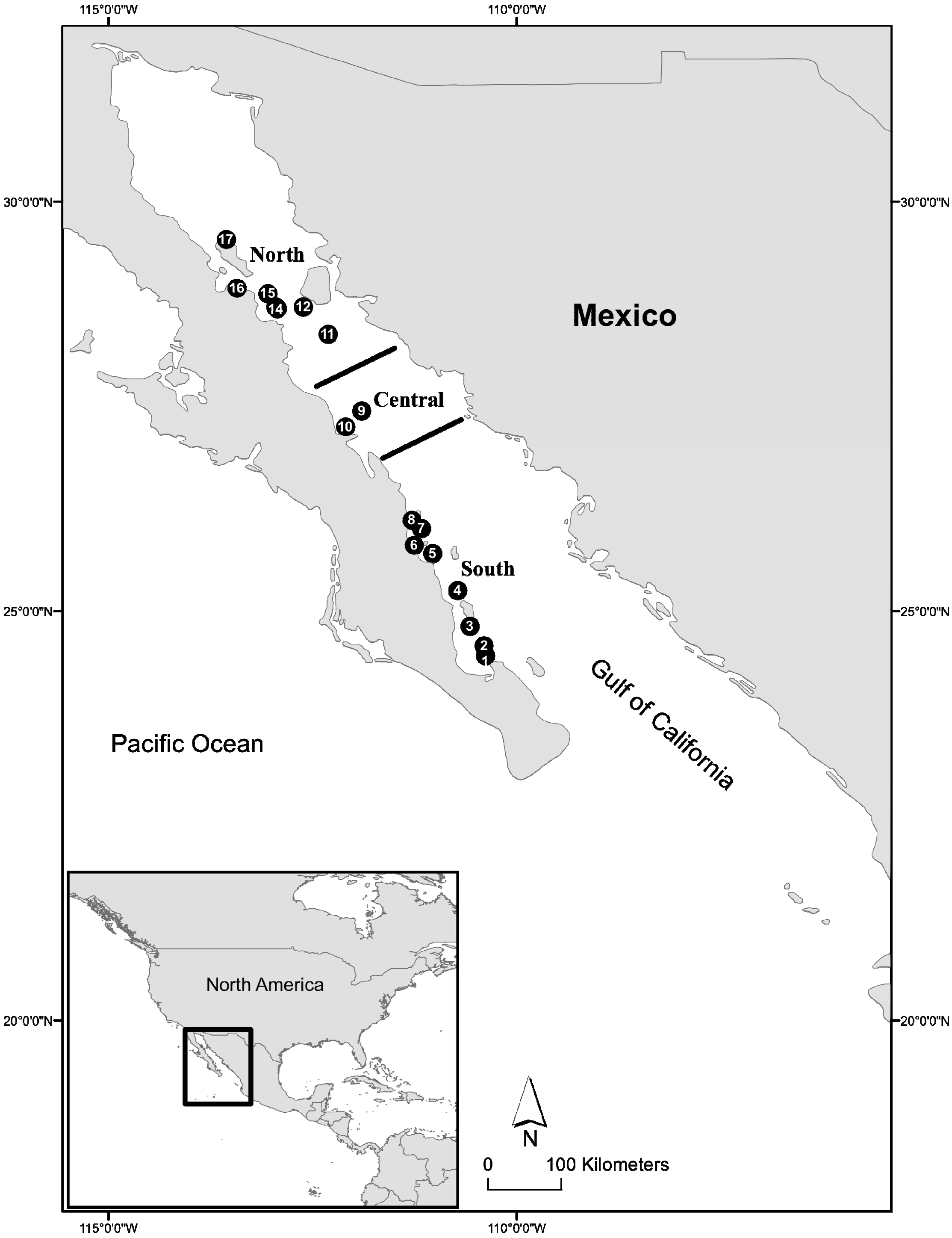

Fig. 3.1. The Gulf of California, Mexico. Numbered dots represent study sites

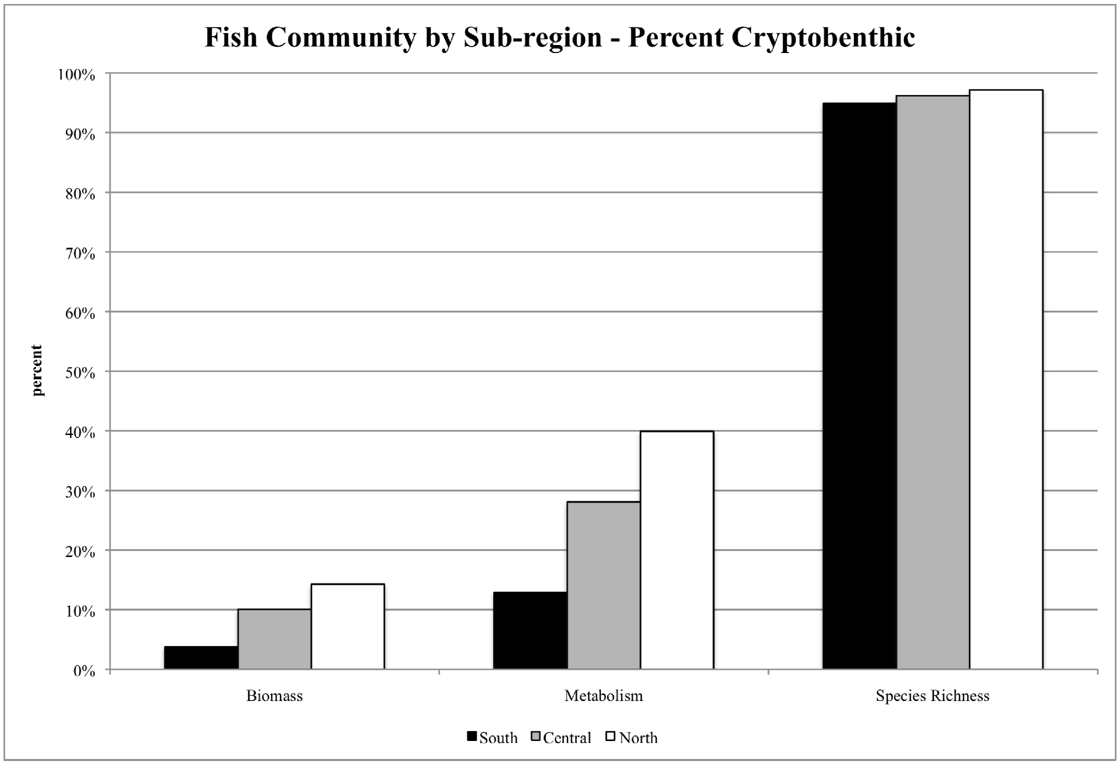

Fig. 3.2. The relative contribution of cryptobenthic fishes (sampled via extractive collection) to the reef fish community at three sub-regions

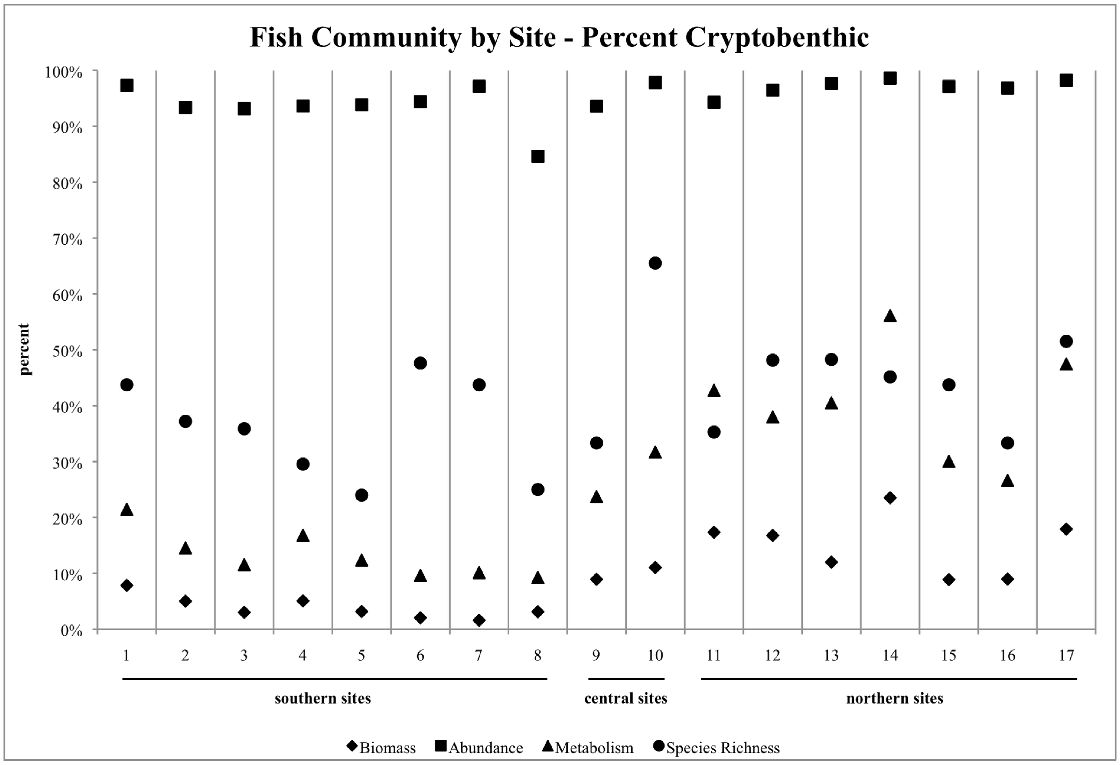

Fig. 3.3. The relative contribution of cryptobenthic fishes (sampled via extractive collection) to the reef fish community at 17 sites. Site numbers refer to Fig. 3.1

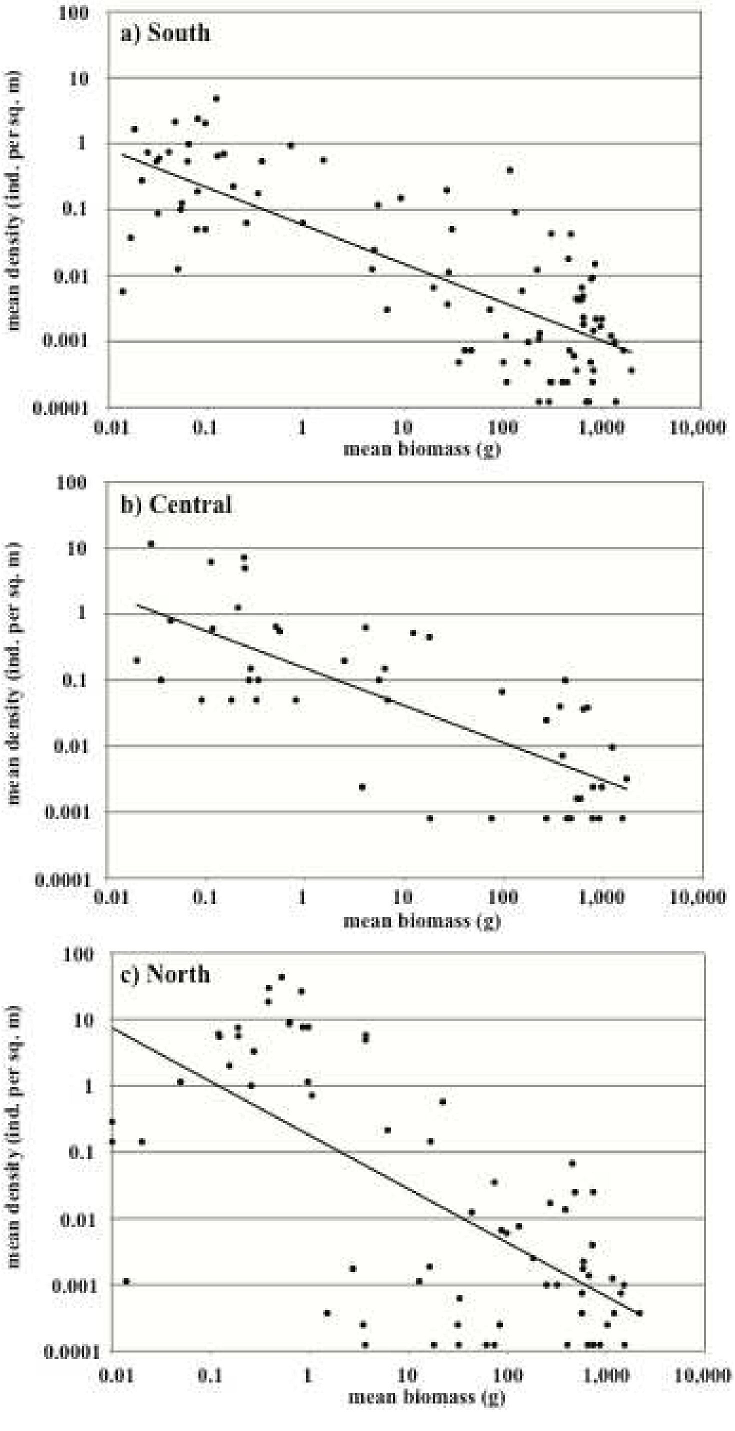

Fig. 3.4. Log mean biomass versus log mean density of each species observed or collected in each sub-region. Trend lines determined from least-squares, linear regression

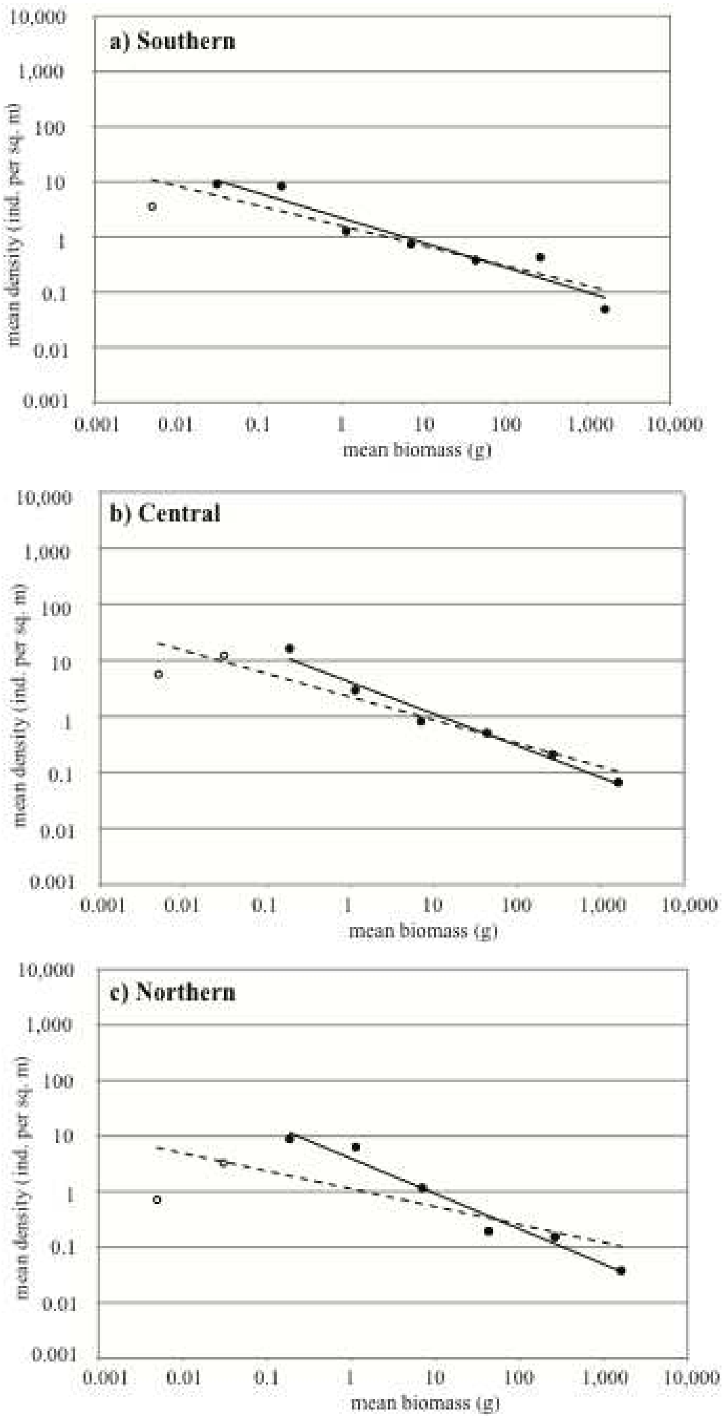

Fig. 3.5. Log mean biomass versus log mean density of Gulf of California reef fishes, binned by size, independent of species. Open circles reflect size classes smaller than the mode. Dashed trend lines determined from least-squares, linear regression of all size classes. Solid trend lines determined from least-squares, linear regression of data excluding size classes smaller than the mode

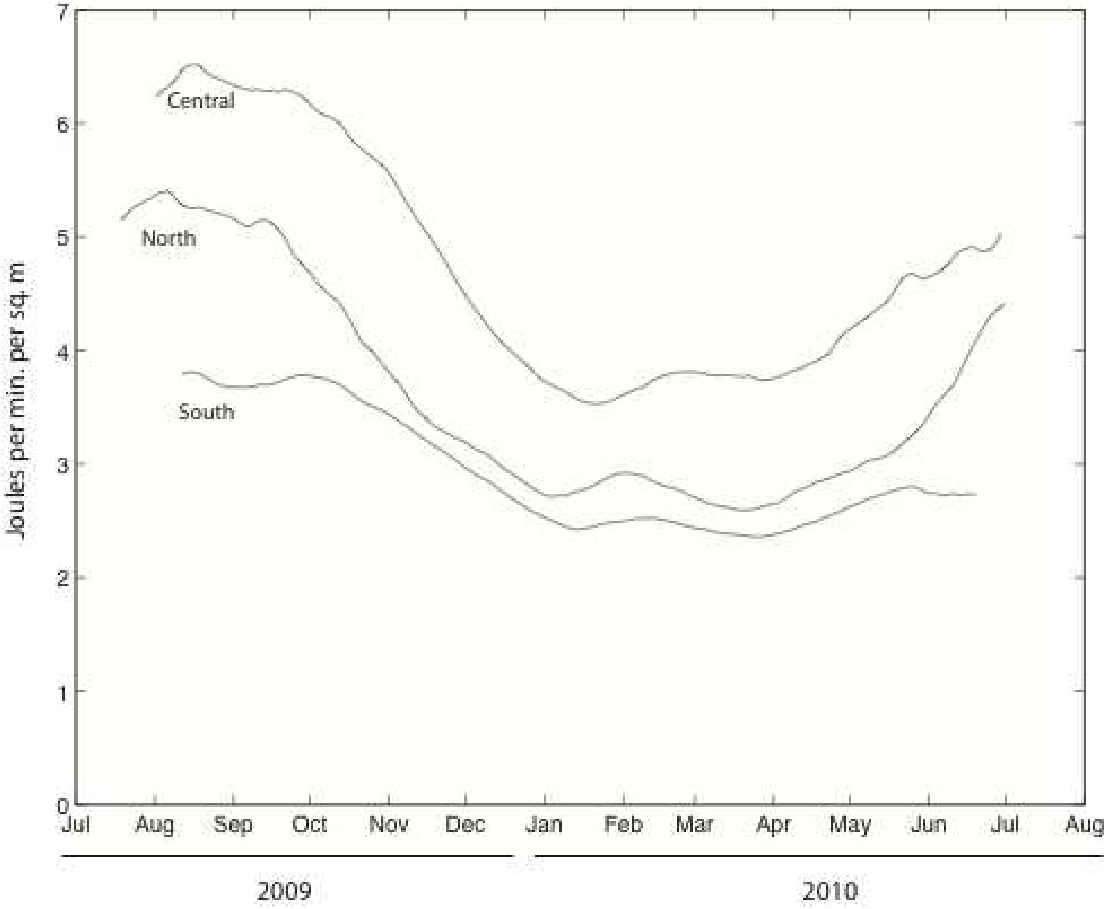

Fig. 3.6. Metabolism at sites in each of the three sub-regions, calculated using Equation 1 with an assumed steady state of biomass and 31-day centered moving average temperatures reported in Chapter 1, this volume

References

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011). Large recovery of fish biomass in a no-take marine reserve. *PloS One* 6(8):e23601.

Aburto-Oropeza O, Sánchez A, Mascareñas-Osorio I, Sánchez C, Calderon M, Moxley J, Erisman B, Ezcurra E (2013). Linking fish biomass, geomorphology, and community assemblages to assess the health of reefs in the Gulf of California. In review.

Ackerman JL, Bellwood DR (2000). Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series* 206:227-237.

Ackerman JL, Bellwood DR (2003). The contribution of small individuals to density-body size relationships. *Oecologia* 136(1):137-140.

Ackerman J, Bellwood D, Brown J (2004). The contribution of small individuals to density-body size relationships: examination of energetic equivalence in reef fishes. *Oecologia* 139(4):568-571.

Allen LG, Bouvier LS, Jensen RE (1992). Abundance, diversity, and seasonality of cryptic fishes and their contribution to a temperate reef fish assemblage off Santa Catalina Island, California. *Bulletin of the Southern California Academy of Sciences* 91(2):55-69.

Alvarez-Borrego S (2010). Physical, chemical, and biological oceanography of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Applegate SP, Soltelo-Macias F, Espinosa-Arrubarrena L (1993). An overview of Mexican shark fisheries, with suggestions for shark conservation in Mexico. In: Branstetter, S. (Ed.), *Conservation Biology of Elasmobranchs*. NOAA Technical Report. NMFS 115:31–37.

Bernardi G, Findley L, Rocha-Olivares A (2003). Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57(7):1599-1609.

Bohnsack JA, Bannerot SP (1986). A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report. NMFS 41:1-15.

Briggs JC (1955). A monograph of the clingfishes (Order Xenopterygii). *Stanford Ichthyological Bulletin* 6.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004). Toward a metabolic theory of ecology. *Ecology* 85(7):1771-1789.

Brusca RC, Hendrickx ME (2010). Invertebrate biodiversity and conservation in the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Cisneros-Mata MA (2010). The importance of fisheries in the Gulf of California and ecosystem-based sustainable co-management for conservation. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Connell JH (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42(4):710-723.

Crocker RL, Tiver NS (1948). Survey methods in grassland ecology. *Grass and Forage Science* 3(1):1-26.

Dallmeier F, Foster RB, Romano CB, Rice R, Kabel M. (1991) *User's guide to the Beni Biosphere Reserve biodiversity plots 01 and 02, Bolivia*. Smithsonian Institution, Washington, D.C.

Damuth J (1981). Population density and body size in mammals. *Nature* 290:699-700.

Davison PC, Checkly DM, Koslow JA, Barlow J (2013). Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. In review.

Dayton PK (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41(4):351-389.

Depczynski M, Bellwood DR (2003). The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* 256:183-191.

Friedlander AM, Zgliczynski BJ, Ballesteros E, Aburto-Oropeza O, Bolaños A, Sala E (2012). The shallow-water fish assemblage of Isla del Coco National Park, Costa Rica: structure and patterns in an isolated, predator-dominated ecosystem. *Revista de Biología Tropical* 60:321-338.

Froese R, Pauly D (eds.) (2012). FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2012).

Galland GR (2011). Comments on microhabitat specialization and a depth range extension for a chaenopsid tube blenny in the Gulf of California, Mexico. *Bulletin of the Southern California Academy of Sciences* 110(2):52-55.

Galland GR, Aburto-Oropeza O, Hastings PA (2011). Irregular schooling behavior and abandonment of mimicry by the Sabertooth Blenny (Blenniidae) in Cabo Pulmo National Park, Gulf of California, Mexico. *Coral Reefs* 30(1):215.

Gibson DJ (2009). *Grasses and grassland ecology*. Oxford University Press, Oxford.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001). Effects of size and temperature on metabolic rate. *Science* 293(5538), 2248-2251.

Greig-Smith P (1983). *Quantitative plant ecology* (Vol. 9). University of California Press, Berkley.

Harmelin-Vivien ML, Harmelin JG, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabe G, Blanc F, Chevalier R, Duclerc J, Lasserre G (1985). Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. *Revue d'écologie* 40(4):467-539.

Hastings PA, Findley LT, Van der Heiden AM (2010). Fishes of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Hastings PA, Galland GR (2010). Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae). *Coral reefs* 29(1):155-164.

Hayek LC, Buzas MA (1997). *Surveying natural populations*. Columbia University Press, New York.

Hemminga MA, Duarte CM (2000). *Seagrass ecology*. Cambridge University Press, Cambridge.

Janzen DH (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104(940):501-528.

Kotrschal K (1989). Trophic ecomorphology in eastern Pacific blennioid fishes: character transformation of oral jaws and associated change of their biological roles. *Environmental Biology of Fishes* 24(3):199-218.

Lang JC (ed.) (2003) Status of coral reefs in the western Atlantic: results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. *Atoll Research Bulletin* 496, Smithsonian Institution, Washington, D.C.

Lindquist DG (1985). Depth zonation, microhabitat, and morphology of three species of *Acanthemblemaria* (Pisces: Blennioidea) in the Gulf of California, Mexico. *Marine Ecology* 6(4):329-344.

Miller PJ (1979). Adaptiveness and implications of small size in teleosts. *Symposia of the Zoological Society of London* 44:263-306.

Nixon SW, Oviatt CA (1973). Ecology of a New England salt marsh. *Ecological Monographs* 43(4):463-498.

Present TM (1987). Genetic differentiation of disjunct Gulf of California and Pacific outer coast populations of *Hypsoblennius jenkinsi*. *Copeia* 1987:1010-1024.

Roberts CM, McClean CJ, Veron JE, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295(5558):1280-1284.

Robertson DR, Smith-Vaniz WF (2008). Rotenone: An essential but demonized tool for assessing marine fish diversity. *Bioscience* 58(2):165-170.

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002). A general model for designing networks of marine reserves. *Science* 298(5600):1991-1993.

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay, M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008). Baselines and degradation of coral reefs in the northern Line Islands. *PLoS One* 3(2):e1548.

Short FT, Coles RG (eds.) (2001). *Global seagrass research methods.* Elsevier, Amsterdam.

Smith-Vaniz WF, Jelks HL, Rocha LA (2006). Relevance of cryptic fishes in biodiversity assessments: a case study at Buck Island Reef National Monument, St. Croix. *Bulletin of Marine Science* 79(1), 17-48.

Steever EZ, Warren RS, Niering WA (1976). Tidal energy subsidy and standing crop production of *Spartina alterniflora*. *Estuarine and Coastal Marine Science* 4(4):473-478.

Stephens Jr JS, Johnson RK, Key GS, McCosker JE (1970). The comparative ecology of three sympatric species of California blennies of the genus *Hypsoblennius* Gill (Teleostomi, Blenniidae). *Ecological monographs,* 40(2):213-233.

Thomson DA, Findley LT, Kerstitch AN (2000). *Reef fishes of the Sea of Cortez: The rocky-shore fishes of the Gulf of California*. University of Texas Press, Austin.

Thomson DA, Gilligan MR (2002). Rocky-shore fishes. In Case TJ, Cody ML, Ezcurra E (eds.) *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford.

Thomson DA, Lehner CE (1976). Resilience of a rocky intertidal fish community in a physically unstable environment. *Journal of Experimental Marine Biology and Ecology* 22(1):1-29.

Tilman D (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological monographs* 57(3):189-214.

Walker BW (1960). The distribution and affinities of the marine fish fauna of the Gulf of California. *Systematic Zoology* 9(3/4):123-133.

Willis TJ (2001). Visual census methods underestimate density and diversity of cryptic reef fishes. *Journal of Fish Biology* 59(5):1408-1411.

CHAPTER 4

Dramatic Changes in an Unexploited Marine Fish Assemblage

Abstract

We report the results of a study designed to understand the environmental parameters that regulate cryptobenthic fish communities in the Gulf of California, Mexico and to examine potential differences in the community in the 1970s and in 2010. Using several data sets published throughout this volume and elsewhere, we built a correlation matrix, in order to identify parameters predictive of numerical success in cryptobenthic families living on rocky reefs. In general, northern sites, with higher benthic algal cover and colder temperatures, support higher densities of labrisomid blennies, combtooth blennies, and clingfishes than southern sites that are warmer and have lower benthic algal cover. Those southern sites support higher densities of tube blennies and gobies. Density of larger, conspicuous fishes generally did not correlate with cryptobenthic density. In 2010, we quantitatively re-sampled several sites that were previously sampled in the 1970s and dramatic differences in total and relative abundances of cryptobenthic fishes between these two samples. The overall community in 2010 exhibited densities approximately half as high as in the 1970s, on average, with some families represented by as little as 11% of the densities previously recorded. Some taxa, however, increased in total abundance. Environmental or anthropogenic changes that may have led to the differences in cryptobenthic fish densities in these two data sets are explored.

Introduction

Humanity's longest and closest relationship with the marine environment is that of exploitation. People have physically removed marine organisms from the ocean since long before the advent of agriculture (Erlandson and Fitzpatrick 2006), and the prehistoric colonization of entire continents perhaps followed the coast and the ample coastal resources available to early hunters or gatherers (Erlandson et al. 2007). Throughout this long history, there are countless examples of instances when people overharvested these living marine resources, and in today's ocean, fishing constitutes a major exertion of ecological and evolutionary pressure on fish communities, either through direct exploitation (reviewed in Helfman 2007) or through incidental bycatch of non-target species (see Crowder and Murawski 1998).

Even given the seemingly ubiquitous nature of fishing in the marine environment, there are many marine fish species that are not targeted or captured as bycatch in any fishery. Unfished species, however, may still be affected by fishing, for example through trophic cascades - alterations of food webs resulting from removal of one or more species (Helfman 2007) - and major trophic cascades have been observed in the north Atlantic (e.g., Steneck et al. 2004), the Chesapeake Bay (Myers et al. 2007), the northeast Pacific (e.g., Estes et al. 2004), and the Black Sea (Daskalov et al. 2007), among other basins. However, there are likely examples of species that do not experience direct or indirect effects of fishing. These species offer marine ecologists an opportunity to study community and population ecology in assemblages or communities that are somewhat buffered from the effects of fishing.

Some marine fish populations are heavily affected by natural climatic or seasonal cycles (e.g., sardine-anchovy cycles in the California Current; Chavez et al. 2003), or from local resource availability (e.g., number of suitable breeding sites; Hastings and Galland 2010), or both (e.g., when natural cycles influence availability of suitable recruitment habitat; Aburto-Oropeza et al. 2007). Parsing out the relative influence of natural and anthropogenic pressures on marine fish populations can be difficult, especially in cases where anthropogenic pressures are indirect (e.g., in the case of a trophic cascade). Identifying and studying unfished assemblages is important to our understanding of community dynamics in marine ecosystems. Here, we present the results of an analysis of the unfished portion of the fish community on rocky reefs in the Gulf of California (GOC), Mexico. To begin to understand the oceanographic and ecological factors that shape an unfished marine assemblage, we compared the densities of 45 species at 17 sites across the GOC and tested the absolute densities and relative abundances of these species against a variety of physical and biological parameters. We also utilized natural history collections to place our findings in a historical perspective by comparing densities of the same unfished species in 2010 and at the same sites 35 years earlier.

Methods

Study Site

The GOC is a long, narrow ocean basin located between the Baja Peninsula and continental Mexico in the tropical, eastern Pacific Ocean. Two notable geographic features of the GOC are its narrow shape and its approximately north-south orientation (Fig. 4.1). These features lead to the obvious observation that distance to the GOC mouth and latitude occur along similar axes and also allow for oceanographic features along the GOC's eastern boundary to affect sites at the western boundary and vice versa (Badan-Dangon et al. 1985; Pegau et al. 2002). Throughout the central and southern GOC, the shoreline is characterized by fringing, rocky reefs (Thomson et al. 2000) that provide habitat for a diverse community and high abundance of fishes. The GOC is a very productive basin (reviewed in Alvarez-Borrego 2010) and accounts for half of Mexico's total fisheries production (Cisneros-Mata 2010). Many reefs in the GOC have been fished heavily for at least the last 40 years, with a significant increase in fishing activity occurring in the 1980s (Sala et al. 2004).

Reefs in the GOC also support a diverse and abundant community of cryptobenthic fishes, numerically dominated by triplefin blennies, tube blennies, other blennies, gobies, clingfishes, cusk eels, and scorpionfishes (Thomson and Gilligan 2002; Chapter 2, this volume). The species in these groups are generally small (weighing less than a few grams; Chapter 3, this volume) and are not targeted by fishers. Furthermore, the benthic geology of GOC rocky reefs prevents trawling, and the primary capture methods utilized by fishers are spearfishing (often supported by surface supplied air) and hook and line fishing, two methods with little to no bycatch of small, cryptic species.

Finally, cryptic fishes in the GOC are not targeted for the live-fish, aquarium trade (Aburto-Oropeza and Sánchez 2000). For all of these reasons, we confidently assume that few to no small, cryptic fishes are directly removed from rocky reefs in the GOC by humans.

Oceanography, Ecology, and Cryptobenthic Fishes

In order to identify factors that may play a role in regulating the cryptobenthic fish community in the GOC, we reanalyzed previously reported densities of cryptobenthic fishes (binned by family) at 17 islands and peninsular sites (Chapter 2, this volume) with several additional data sets that describe either the physical environment or ecological relationships of other assemblages within the rocky reef ecosystem. Cryptobenthic fishes were quantitatively collected from an area of 10 m^2 at each site, with the aid of a block net, using the ichthyocide rotenone (Chapter 2, this volume). The additional data sets are the results of previously published work (Table 4.1), with the exception of percent algal cover, which is reported for the first time here.

We were particularly interested in measuring benthic algal cover because many cryptobenthic fishes are microhabitat specialists (Patzner 1999; La Mesa et al. 2006; Goncalves and Faria 2009; Lin and Hastings 2011), and based on our and others' observations, we suspected that some GOC fishes (specifically labrisomid blennies and the Gulf Worm Blenny, *Stathmonotus sinuscalifornici*) specialize on macroalgae (Thomson et al. 2000), while other groups (e.g., triplefin blennies and tube blennies) do not. The Gulf Worm Blenny is a non-tube-dwelling blennioid with unclear taxonomic relationships (Hastings and Springer 1994; Lin 2010) and is considered individually, here. Percent algal cover was estimated from photoquadrats. At each site, we set up a 10 m^2 plot to quantitatively collect cryptobenthic fishes and to study the benthos. Using a pvc camera frame, we photographed the benthos at nine equally spaced locations within the study plot. Quadrats were 0.35 m^2. Images were later analyzed in the computer program PhotoGrid 1.0, where the substrate was described at 50 stratified random points per image. For the purposes of this study, each point was assigned to one of three categories: fleshy macroalgae, branching coralline algae, or other. Percent cover was calculated as the percentage of points assigned to each category.

To test for statistical relationships among the physical and ecological parameters reported in Table 4.1, we constructed a simple correlation matrix in the computer program Matlab 7.1. We calculated the Spearman’s rank correlation coefficient for each pair of variables, and the resulting matrix highlights areas with evidence of correlation (at $\alpha = 0.05$) within the cryptobenthic fish assemblage and between that assemblage and our environmental parameters at 17 sites across the central and southern GOC.

A Historical Perspective on Cryptobenthic Fishes

Using samples archived in natural history collections, it is possible to obtain an additional time point of densities and relative abundances of cryptobenthic fishes in the GOC. Twelve of the 17 sites introduced above were selected to match sites that were quantitatively sampled in the 1970s for a mainland-island biogeography study (Thomson and Gilligan 2002). After communicating with the authors of that study, and with the help of their original field notes, we returned to 12 of their sites and resampled the cryptic fish community (Chapter 2, this volume). In most cases, we are confident that our sites were within tens of meters or less from the original collecting sites, with the caveat that we qualitatively chose places in the immediate area with high relief and some algal cover, in order to obtain the densest, most speciose collections. To ensure comparability, we utilized similar collecting methods and specifically obtained permission to use the same collecting agent (rotenone), which had been prohibited in Mexico between the two surveys. Specimens from these studies are archived at the Scripps Institution of Oceanography Marine Vertebrate Collection and the University of Arizona Fish Collection.

We compared the cryptobenthic fish assemblages at these two time points by binning across all sites to examine GOC-wide differences and by comparing relative abundances of families at each site in order to ascertain what, if any, families are more or less abundant in each data set. Based on our initial examination of the two data sets, we also conducted a multivariate analysis to explore whether or not the two time points differ, statistically, in community composition and to explore whether or not the combined data set exhibits regionalization within the GOC, independent of time. In order to do so, we used several tools available in Fathom Toolbox (Jones 2012) for the computer program Matlab. We started by applying a square root transformation to the raw densities of all 45 species in the combined data set, in order to diminish the statistical influence of the largest events (an event = number of individuals of one species at one site). We then did a pairwise comparison of the 24 combined sites by Bray-Curtis dissimilarity (Bray and Curtis 1957) and utilized the resulting dissimilarity matrix to conduct a Canonical Analysis of Principal Coordinates (CAP; Anderson and Willis 2003). CAP allowed us to reduce the number of dimensions from 45 (= the number of species in the combined data sets) to *m* number of principal coordinate axes, reducing the likelihood that the analysis is overparameterized (i.e., that the explanatory variables outnumber the observations). The optimal *m* was chosen by running the analysis multiple times, each time adding a principal coordinate axis, and choosing the value of *m* that returns the highest percentage of site assignments to the correct group of interest (i.e., the 1970s vs. 2010 or north vs. central vs. south; Anderson and Willis 2003). After analysis, leave-one-out cross validation was incorporated to check the ability of the CAP to correctly identify the proper group. Four principal coordinate axes constituted the optimal *m* in both analyses, as these axes explained 68.5% of the variation in the Bray-Curtis dissimilarity matrix for each analysis and led to correct group assignment for 91.67% (by time) and 87.5% (by sub-region) of the sites.

Results

Oceanography, Ecology, and Cryptobenthic Fishes

Our correlation analysis revealed several significant correlations between oceanographic and ecological parameters on GOC rocky reefs (Table 4.2). The approximately north-south orientation of the GOC ensured that latitude was a significant correlate with both physical and biological parameters (Fig. 4.1), including average annual temperature (-), percent macroalgal cover (+), percent branching coralline algal cover (+), density (-) and species richness (-) of conspicuous fishes, densities of labrisomid blennies (+), tube blennies (-), and clingfishes (+), relative endemism of cryptobenthic fishes (+), and oceanographic productivity (not tested here). Though the relationship across all sites was not significant, our northern sites were also the most variable with respect to temperature (Chapter 1, this volume). It is difficult to determine which of these parameters have the most effect (if any) on the density of the cryptobenthic fish community as a whole or divided by family. However, northern, cooler sites with high macroalgal cover supported larger densities of labrisomid blennies, combtooth blennies, and clingfishes than southern, warmer, low macroalgal cover sites, which had more tube blennies. Triplefin blennies, gobies, brotulas, and scorpionfishes did not significantly correlate with latitude or any of these covarying parameters (Table 4.2).

Focusing on cryptobenthic fishes and benthic cover, fleshy macroalgal cover was positively correlated with density of labrisomid blennies and with density of combtooth blennies, which include the few cryptobenthic fishes that are herbivorous. Branching coralline algae was positively correlated with density of both labrisomid blennies and clingfishes. The other cryptobenthic fish families were not correlated with algal cover of either type. This is particularly notable for the Gulf Worm Blenny, which we hypothesized would have a positive relationship with branching coralline algae based on our field observations. The lack of correlation among our 17 sites fails to reject a null hypothesis of no relationship.

High density and biomass of conspicuous fishes correlated negatively with clingfish density but did not have a statistical relationship with the other groups of cryptobenthic fishes. Similarly, correlation analysis of cryptobenthic fish densities with the “healthiness scores,” calculated, in part, from surveys of conspicuous fishes at these sites (Aburto-Oropeza et al. 2013), did not reveal a statistical relationship with any cryptobenthic family.

Finally, the only negative, statistically significant correlations among cryptobenthic families all included associations with scorpionfishes (here represented by one species *Scorpaenodes xyris*). That species was negatively correlated with triplefin blenny, Gulf Worm Blenny, labrisomid blenny, and clingfish densities (Table 4.2), implying that there may be differences in microhabitat requirements or agonistic relationships between scorpionfishes and these other groups.

A Historical Perspective on Cryptobenthic Fishes

Twelve sites sampled in 2010 were selected to resample sites originally studied in the 1970s, and there were several differences between these two data sets. The most obvious difference was the total abundance of individuals collected. When binning all sites, there were 56.2% fewer fishes in the 2010 collections than in the 1970s collections. Eleven of the twelve sites had fewer fishes in 2010, ranging from a decrease of 93.4% to 6.5%, and one site had 6.2% more fishes. The mean percent difference was -47.4% (standard deviation = 32.3 percentage points). The difference between the two time points was not consistent across all families, with clingfishes (-89.6%), combtooth blennies (-74.3%), labrisomid blennies (-72.3%), scorpionfishes (-58.3%), triplefin blennies (-58%), and tube blennies (-44.6%) all decreasing substantially, while brotulas (+8.4%) gobies (+86.3%), and the Gulf Worm Blenny (+500%) increased in total (and relative) abundance. Among the pooled data, a list of the 15 most abundant species also differed substantially between the two time points, as did their densities (Table 4.3). Relative abundance of cryptobenthic families also varied among sites and between time points at individual sites. The general trend of elevated relative abundance of the Gulf Worm Blenny, gobies, and brotulas observed in the pooled data was somewhat consistent at the site level as well (Table 4.4).

The multivariate CAP analysis of the dissimilarity matrix constructed for the combined 24 sites (representing twelve 1970s sites and twelve 2010 sites) supported the hypothesis that the two time points represent statistically distinct groups (Fig. 4.2). The analysis yielded a single canonical axis with a squared canonical correlation of 0.73 and a significant test statistic (P = 0.001 for the trace statistic with 999 permutations). Leave-one-out cross validation confirmed that the canonical axis could reliably identify the decade of collection 91.67% of the time. The analysis also identified the 11 species that most strongly pulled sites one way or the other along the canonical axis (Fig. 4.2). As expected based on our observations of differences in relative abundance above, four gobies and the Gulf Worm Blenny (along with a tube blenny) pulled sites toward the 2010 group, while a clingfish, a triplefin blenny, two tube blennies, and a labrisomid blenny pulled sites toward the 1970s group (Fig. 4.2).

CAP analysis of geographic sub-regions (south, central, and north), independent of collection year, supported a hypothesis that there are geographic differences in the cryptobenthic fish community in the GOC (Fig. 4.3). The analysis yielded two canonical axes with squared correlations of 0.73 and 0.59 and significant test statistics (P = 0.001 for the trace statistic and P = 0.003 for the greatest root statistic with 999 permutations). Leave-one-out cross validation confirmed that the canonical axis could reliably identify the region of collection 87.5% of the time. Again, the species that most strongly pull sites toward one group or another were identified and plotted in the canonical space (Fig. 4.3).

Discussion

Our results reveal several interesting correlations between environmental parameters and cryptobenthic fish densities. Correlation analysis alone does not allow us to predict the community composition of cryptobenthic fishes on GOC rocky reefs but instead reveals possible univariate relationships between individual environmental factors and the abundance of cryptobenthic families. Based on a survey of these univariate relationships, it seems likely that parameters varying with latitude (e.g., mean annual temperature, benthic algal cover, distance into the GOC) may be good predictors of success for some groups of cryptobenthic fishes, including labrisomid blennies, combtooth blennies, and clingfishes (Table 4.2). Conversely, none of the environmental parameters tested (Table 4.1) seem likely to successfully predict the population size of the other cryptobenthic groups, including the most abundant family on GOC rocky reefs, the triplefin blennies (chapter 2, this volume). We believe that the preferred habitat (bare boulders or turf algae) of triplefin blennies is common to all sites (pers. obs.) and is not strongly influenced by latitude or its covarying parameters. The same may be true for brotulas and scorpionfishes. Some gobies (see Thomson et al. 2000) and all tube blennies (e.g., Hastings and Galland; Lin and Hastings 2011), however, are certainly microhabitat specialists, and in these cases, they specialize on biogenic microhabitats, such as urchin holes, vacated worm tubes, or dead barnacles. In some places, these specialists are known to be limited by shelter density (i.e., the density of their hosts' tests; Hastings and Galland 2010) and can maintain viable populations under abnormal conditions when their preferred microhabitat is available (e.g., at greater than normal depths; Galland 2011). Species in these groups specialize on different microhabitats, and we did not test for correlations between individual species abundance and relevant environmental parameters (e.g., presence of their preferred shelters), so the underlying causes of the lack of correlation between latitude and family-level density of these specialists remain unclear.

Our results also show dramatic, statistically significant differences between the cryptobenthic fish community in 2010 (Chapter 2, this volume) and in the 1970s (Thomson and Gilligan 2002). These differences are readily apparent with a cursory survey of the data – there are half as many individuals at each site, on average, and the relative abundances of the cryptobenthic families are noticeably different in the two data sets. CAP analysis revealed that the abundance and composition of the community differ significantly between the two time points (Fig. 4.2) and lead to correct group (i.e., sample decade) identification of a site more than 90% of the time. That analysis also confirmed that species in the families with higher relative abundances in 2010 are those that pull sites toward the 2010 group along the canonical axis (Fig. 4.2). Reanalysis by sub-region, independent of time, revealed some geographic structure among sites. Given the statistical significance of correlation coefficients between latitude and densities at the family level (discussed above), some regionalization was expected.

What environmental factors underlie these differences in community structure? Because only two quantitative time points were available, we do not suggest that differences between the 1970s and 2010 data sets represent a trend. The simplest explanation for differences in total abundance is a difference in collecting effort or season. However, both studies occurred in July, specifically attempted to achieve quantitative samples of cryptobenthic fishes from 10 m^2, and included individuals of extremely small size (down to less than 10 mm long and weighing less than 0.01 g). If densities were in fact consistent at each site, the 2010 samples would have had to erroneously cover half the area, on average, of the 1970s sites and in one case, one tenth the area (i.e. 90% fewer fishes were collected in 2010). Furthermore, the differences in densities are not consistent among taxa, with several families represented by far fewer individuals in 2010 and two groups represented by far more individuals in 2010. In the case of the Gulf Worm Blenny, there were six times as many individuals in the 2010 collections. In fact, after examination of regional natural history collections, we are confident that the 2010 samples included the three largest collections of that endemic GOC species in any museum, regardless of sampling area size (Hastings and Springer 1994). While collecting effort may impact reported densities, it is unlikely to account for all of the differences between the 1970s and 2010 samples. Furthermore, given the short generation time of cryptobenthic fishes (one to two years; Miller 1979), there should be no impact of the 1970s collections on the 2010 samples.

It is possible that small-scale, spatial differences in habitat sampled led to both differences in total and relative abundance of cryptobenthic fishes between the two study periods. In 2010, we returned to the same sites sampled in the 1970s, but it is unlikely that we sampled the exact same 10 m^2, and small spatial differences may have resulted in significant differences in microhabitat (e.g., differences in number of boulders or algal cover). A recent multivariate analysis of the cryptobenthic fish assemblage at several sites around an island in the Caribbean concluded that different habitats, from the shoreline to the fore-reef, yielded different assemblages (Harborne et al. 2012). However, in both the 1970s and 2010 GOC studies, samples were obtained from rocky reefs, adjacent to the shoreline, in less than three meters depth and are more similar than the different habitats sampled by Harborne et al. (2012).

We do not have detailed habitat data to accompany the original samples, but we may be able to use our spatial correlations among 2010 sites as a proxy. Consider GOC labrisomid blennies, most of which are macroalgae specialists (Thomson et al.

2000), and which were positively correlated with both fleshy macroalgal cover and branching coralline algal cover in 2010 (Fig. 4.1; Table 4.2). Total abundance of this family was 72.3% lower in the pooled 2010 samples than in the pooled 1970s samples. If the majority of this loss occurred at southern sites where macroalgal cover was minimal or absent, then that lack of macroalgae may be a contributing reason. In fact, 52% of the total reduction in labrisomid blenny abundance occurred at 5 (of 12 total) sites with less than 20% total macroalgal cover. That group of sites included one site with an increase in labrisomid density. If we consider only fleshy macroalgae, 60% of the reduction from the 1970s to 2010 occurred at 8 sites with less than 20% cover in 2010 (including the only two sites with an increase in labrisomid density). Macroalgal cover, while positively correlated with labrisomid density in 2010, may not provide insight into the observed overall lower densities in the 2010 as compared to the 1970s samples.

Human activity may also affect relative and total abundances of cryptobenthic fishes. Fishing pressure has increased dramatically since the 1970s, with more fishers, fishing more reefs, with more gear (Sala et al. 2004), and currently, approximately 50,000 artisanal fishers work from 25,000 small vessels in GOC waters (many concentrating on reefs; Cisneros-Mata 2010). While we are confident that these fisheries do not directly remove cryptobenthic fishes, it is likely that removing much of the top predator biomass (Sala et al. 2004) could change the GOC ecology in such a way that the cryptobenthic fishes are affected. Concurrently, the number of permanent, human residents in the GOC watershed and domestic and international visitors to the GOC, along with a variety of associated environmental pressures, has increased significantly (Carvahal et al. 2004). Furthermore, the GOC is not immune to the anthropogenic changes to the global ocean (e.g., in temperature, pH, nutrients) experienced during the last several decades. Any of these human-induced regional and global changes to marine ecosystems may affect the cryptobenthic fish community.

Populations of marine fishes fluctuate over seasonal to decadal (or longer) time scales and are affected by oceanographic variability, local resource availability, and human activity. These changes can be expected to be particularly strong for short-lived, microhabitat specialists. With only two quantitative time points, we do not have the data to fully evaluate the underlying causes of the differences that we observed during this study. However, these differences could represent inter-annual variability or points along a moderate to long-term trajectory, and they may be driven by inherent environmental variation or may result, in part or in total, from human-induced changes in GOC ecosystems.

In recent years, there has been increased interest in the study of community ecology of cryptobenthic fishes (Allen et al. 1992; Munday and Jones 1998; Ackerman and Bellwood 2000, 2003; Thomson and Gilligan 2002; Ackerman et al. 2004; Harborne et al. 2012; chapters 2 and 3, this volume), but most studies have not considered long-term stability of the ecological relationships within this component of the fish community. Our results from this and related studies (other chapters in this volume) show high variation among cryptobenthic fishes in the GOC, in both space and time. This variability is particularly interesting, precisely because this portion of the rocky reef community is not fished, purposely or incidentally. Our observations are intriguing, whether they imply that this assemblage experiences a 50% difference in total abundance and dramatic changes in relative abundance naturally or that these differences reflect true changes within a heavily impacted basin. By broadening our results to include qualitative time points, we may be able to separate inherent environmental variability from anthropogenic impacts in this semi-enclosed basin.

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Table 4.1. Parameters identified as potential drivers of cryptobenthic (CB) fish community structure and utilized in the correlation analysis, with abbreviations and data sources

Parameter Category	Parameter	Abbreviation	Data Source
Geographic	Latitude	Lat	
Cryptobenthic	CB fish abundance	n	Chapter 2, this volume
Cryptobenthic	CB fish species richness	S	Chapter 2, this volume
Cryptobenthic	Percent endemic (by abundance) of CB fishes	End	Chapter 2, this volume
Cryptobenthic	Percent widely dispersed (by abundance) of CB	Wide	Chapter 2, this volume
Cryptobenthic	Triplefin blenny density	Trip	Chapter 2, this volume
Cryptobenthic	Tube blenny density	Tube	Chapter 2, this volume
Cryptobenthic	Gulf Worm Blenny density	WB	Chapter 2, this volume
Cryptobenthic	Labrisomid blenny density	Lab	Chapter 2, this volume
Cryptobenthic	Combtooth blenny density	Comb	Chapter 2, this volume
Cryptobenthic	Goby density	Gob	Chapter 2, this volume
Cryptobenthic	Brotula density (Bythitidae)	Brot	Chapter 2, this volume
Cryptobenthic	Scorpionfish density	Scorp	Chapter 2, this volume
Cryptobenthic	Clingfish density	Cling	Chapter 2, this volume
Conspicuous	Conspicuous fish biomass	Consp b	Chapter 3, this volume
Conspicuous	Conspicuous fish density	Consp n	Chapter 3, this volume
Conspicuous	Conspicuous fish species richness	Consp S	Chapter 3, this volume
Habitat	Percent fleshy macroalgal cover	Macro	present study
Habitat	Percent branching coralline algal cover	Cor	present study
Physical	Mean temperature (for 30 days prior to sampling)	T-30	Chapter 1, this volume
Physical	Mean temperature (annual)	T-365	Chapter 1, this volume
Physical	Return time (days) for 2° temperature anomaly	2°	Chapter 1, this volume
Physical	Return time (days) for 3° temperature anomaly	3°	Chapter 1, this volume
Physical	Return time (days) for 4° temperature anomaly	4°	Chapter 1, this volume
Physical	Return time (days) for 5° temperature anomaly	5°	Chapter 1, this volume
Health Score	“Healthiness” score	Health	Aburto-Oropeza et al. 2013

Table 4.2. Matrix of Spearman's rank correlation coefficients between parameters listed in Table 4.1

	Lat	n	S	End	Wide	Trip	Tube	WB	Lab	Gob	Brot	Comb	Scorp	Cling	Consp b	Consp n	Consp S	Macro	Cor
Lat	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
n	-0.07	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
S	-0.22	**0.51**	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
End	**0.80**	0.06	-0.12	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wide	**-0.80**	-0.06	0.12	**-1.00**	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trip	-0.26	**0.69**	0.05	-0.01	0.01	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
Tube 1	**-0.50**	**0.54**	**0.58**	-0.21	0.21	0.33	1.00	-	-	-	-	-	-	-	-	-	-	-	-
Stath	0.00	**0.52**	0.40	-0.06	0.06	0.37	0.29	1.00	-	-	-	-	-	-	-	-	-	-	-
Lab	**0.66**	0.47	0.16	**0.69**	**-0.69**	0.22	-0.07	0.38	1.00	-	-	-	-	-	-	-	-	-	-
Gob	-0.23	0.31	**0.80**	-0.32	0.32	-0.21	0.43	0.15	-0.18	1.00	-	-	-	-	-	-	-	-	-
Brot	-0.20	-0.06	0.12	-0.13	0.13	-0.05	-0.15	-0.38	-0.37	0.27	1.00	-	-	-	-	-	-	-	-
Comb	0.45	0.43	0.16	0.43	-0.43	-0.01	-0.02	0.12	**0.62**	-0.05	0.10	1.00	-	-	-	-	-	-	-
Scorp	-0.20	**-0.68**	-0.05	-0.38	0.38	**-0.56**	-0.34	**-0.58**	**-0.55**	0.24	0.29	**-0.58**	1.00	-	-	-	-	-	-
Cling	**0.68**	0.04	0.04	0.47	-0.47	-0.39	-0.33	-0.03	0.41	0.02	-0.03	**0.59**	-0.16	1.00	-	-	-	-	-
Consp b	-0.39	0.12	-0.05	-0.47	0.47	0.24	0.23	0.32	-0.35	0.17	0.30	-0.21	-0.09	-0.44	1.00	-	-	-	-
Consp n	**-0.50**	0.26	0.07	**-0.52**	**0.52**	0.32	0.35	0.40	-0.36	0.27	0.28	-0.25	-0.13	**-0.52**	**0.96**	1.00	-	-	-
Consp S	**-0.62**	-0.24	-0.18	**-0.64**	**0.64**	-0.07	0.22	-0.19	**-0.74**	0.07	0.34	-0.36	0.24	**-0.55**	**0.58**	**0.60**	1.00	-	-
Macro	**0.59**	-0.01	-0.18	**0.58**	**-0.58**	-0.14	-0.09	-0.10	**0.68**	-0.43	-0.42	**0.59**	-0.31	0.38	-0.44	**-0.57**	-0.46	1.00	-
Cor	**0.73**	0.30	0.03	**0.59**	**-0.59**	0.20	-0.38	0.35	**0.73**	-0.19	-0.29	0.37	-0.40	**0.54**	-0.47	-0.48	**-0.76**	0.36	1.00
T-30	-0.10	0.34	-0.13	0.04	-0.04	0.48	0.17	0.17	0.19	-0.05	-0.02	-0.03	-0.33	-0.46	0.40	0.45	0.18	-0.11	-0.07
T-365	**-0.84**	0.04	-0.01	-0.69	0.69	0.34	0.47	-0.05	**-0.62**	0.17	-0.11	**-0.65**	0.20	**-0.68**	0.38	0.53	**0.64**	**-0.75**	-0.76
2°	-0.31	0.09	0.26	-0.07	0.07	0.00	0.39	0.05	-0.22	0.13	-0.02	0.11	-0.28	0.16	-0.41	-0.29	0.10	-0.23	-0.13
3°	-0.09	0.07	0.26	0.15	-0.15	-0.09	0.27	-0.03	0.00	-0.04	0.05	0.36	-0.33	0.51	-0.57	-0.54	-0.18	0.06	0.11
4°	0.00	-0.02	0.21	0.21	-0.21	-0.20	0.15	-0.06	0.03	-0.10	0.08	0.42	-0.29	**0.60**	**-0.56**	**-0.59**	-0.24	0.16	0.16
5°	0.02	-0.14	0.17	0.18	-0.18	-0.31	0.07	-0.13	0.01	-0.08	0.12	0.40	-0.16	**0.61**	-0.51	**-0.59**	-0.23	0.19	0.12
Health	0.35	0.03	-0.09	0.47	-0.47	-0.03	-0.08	-0.44	0.18	0.03	0.02	-0.07	0.04	0.17	-0.40	-0.39	-0.14	0.09	0.30

Notes

Abbreviations after Table 4.1. Correlation coefficients in **bold** show evidence of correlation at α = 0.05.

Table 4.3. The 15 most common species (family abbreviation) and their mean number per site for the 1970s data set and for the 2010 data set

1970s Collections		2010 Collections	
Species	Mean No./Site	Species	Mean No./Site
Axoclinus nigricaudus (T)	91	*Enneanectes reticulates* (T)	41
Acanthemblemaria crockeri (C)	68	*Stathmonotus sinuscalifornici* (WB)	32
Malacoctenus hubbsi (L)	56	*Axoclinus storeyae* (T)	24
Enneanectes reticulates (T)	53	*Crocodilichthys gracilis* (T)	17
Tomicodon boehlkei (Cl)	43	*Acanthemblemaria crockery* (C)	16
Xenomedea rhodopyga (L)	43	*Paraclinus sini* (L)	16
Crocodilichthys gracilis (T)	40	*Elacatinus puncticulatus* (G)	13
Coralliozetus micropes (C)	26	*Malacoctenus hubbsi* (L)	12
Axoclinus storeyae (T)	24	*Ogilbia* spp. (B)	9
Paraclinus sini (L)	18	*Xenomedea rhodopyga* (L)	7
Labrisomus xanti (L)	16	*Chriolepis zebra* (G)	6
Ophioblennius steindachneri (Bl)	15	*Barbulifer pantherinus* (G)	6
Scorpaenodes xyris (S)	9	*Axoclinus nigricaudus* (T)	6
Ogilbia spp. (B)	8	*Pycnomma semisquamatum* (G)	5
Aruma histrio (G)	8	*Acanthemblemaria hastingsi* (C)	4

Notes

Family abbreviations: T = triplefin blenny; C = tube blenny; L = labrisomid blenny; Cl = clingfish; B = brotula; Bl = combooth blenny; G = goby; S = scorpionfish; WB = Worm Blenny

Table 4.4. Density (ind./10 m^2) of cryptobenthic fish families in the 1970s and 2010 data sets. Each row represents a site

Trip		Tube		Stath		Lab		Comb		Gob		Brot		Scorp		Cling	
1970s	2010	1970s	2010	1970s	2010	1970s	2010	1970s	2010	1970s	2010	1970s	2010	1970s	2010	1970s	2010
154	83	104	179	0	177	61	2	8	6	43	152	1	15	0	3	49	4
316	184	139	41	0	40	463	1	73	0	22	2	5	4	2	1	103	0
325	109	255	73	0	35	132	38	8	1	8	80	5	14	3	1	9	0
117	101	113	97	2	17	51	80	1	0	81	120	2	7	0	6	18	0
443	8	303	10	0	4	111	6	30	0	10	27	31	10	2	10	72	0
135	133	37	84	8	0	68	84	25	5	16	0	7	4	8	0	17	1
135	137	50	163	19	13	203	150	56	5	23	21	12	7	31	1	6	1
277	96	79	5	2	5	130	0	7	4	12	1	5	7	46	4	5	0
175	34	41	4	10	3	71	1	2	0	2	20	8	2	0	7	178	20
142	38	27	30	4	9	28	21	2	27	3	7	3	3	1	0	87	8
88	6	11	2	0	2	293	0	4	6	14	18	0	20	0	7	0	25
200	124	43	8	10	7	80	1	6	3	7	1	16	10	10	3	34	1

Notes

Abbreviations after Table 4.1.

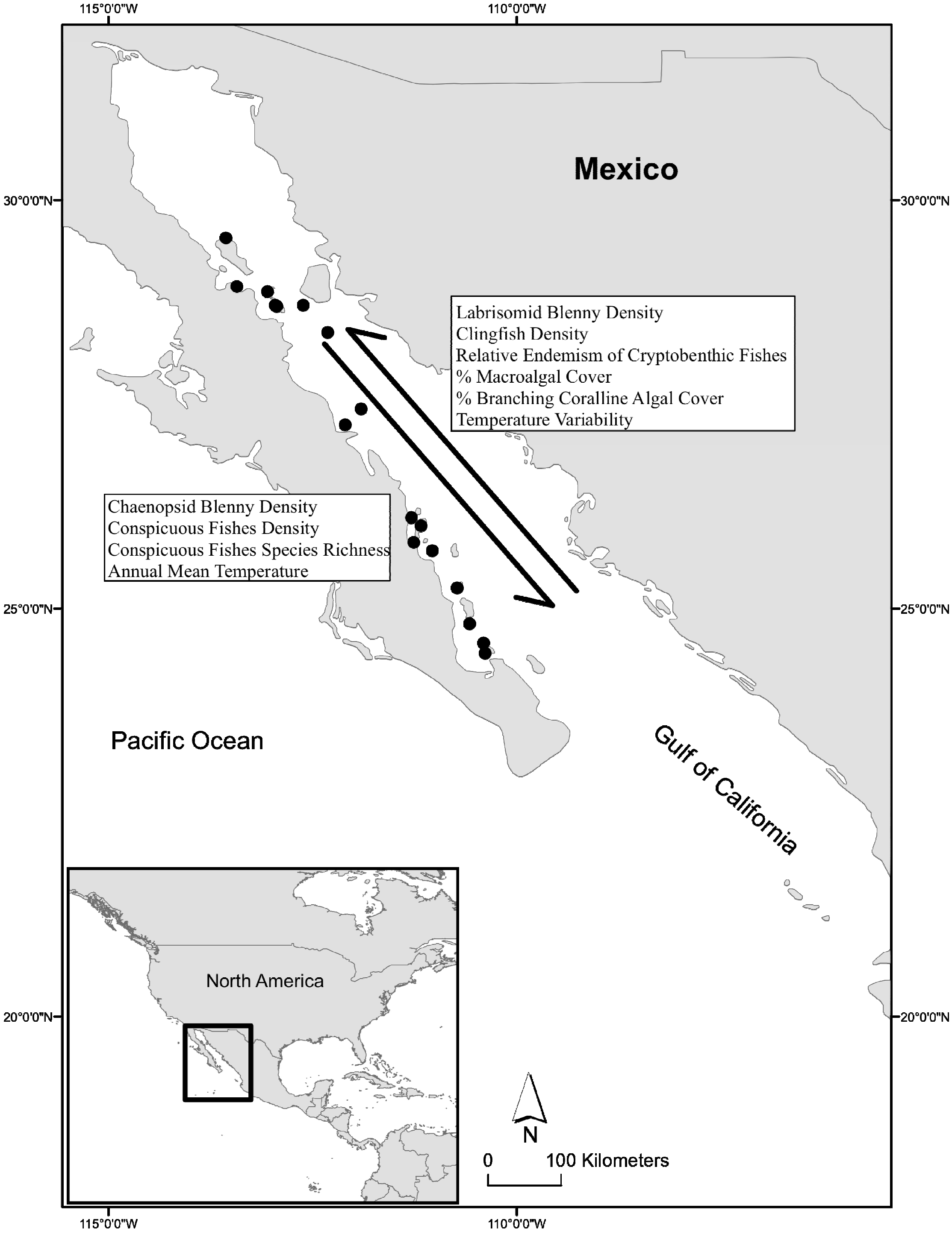

Fig. 4.1. The Gulf of California. Dots represent study sites. Boxes represent environmental parameters that are significantly correlated with latitude

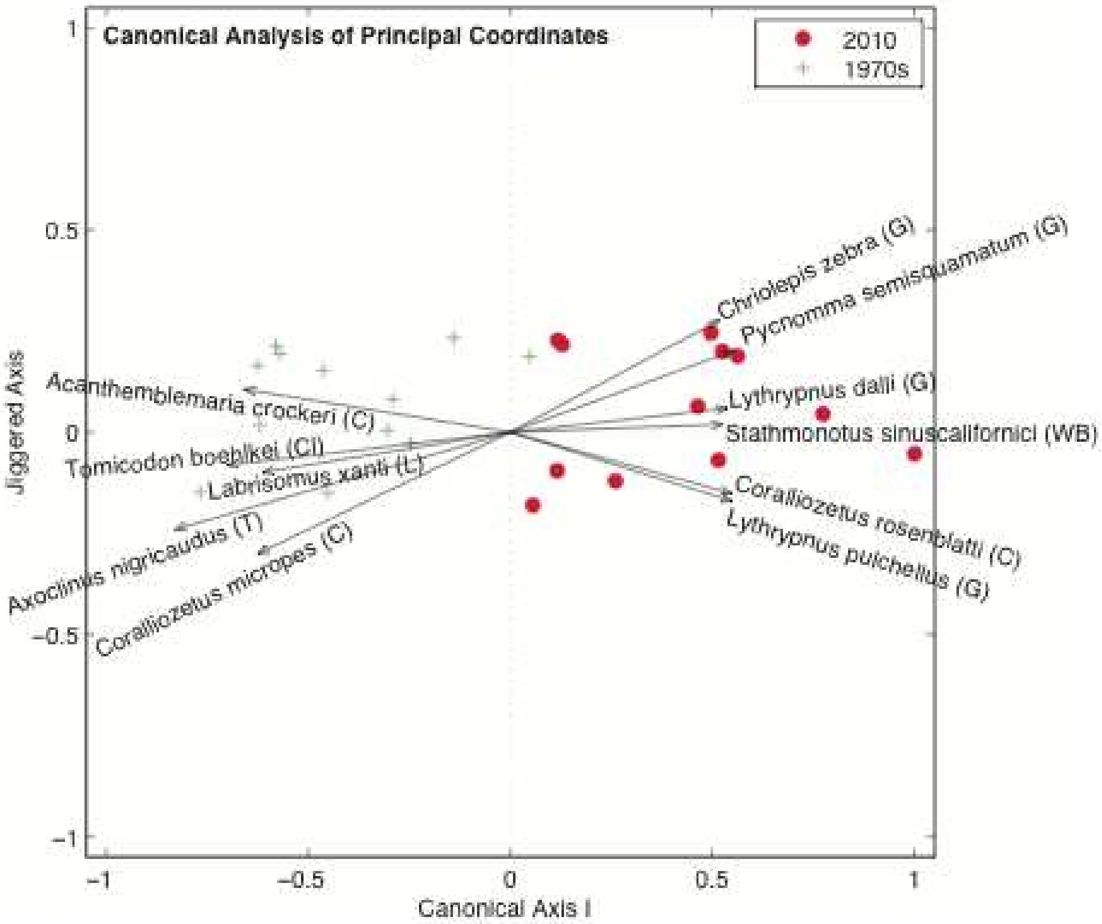

Fig. 4.2. Plot of study sites, divided by decade of study (i.e., 1970s vs. 2010), in canonical space, with the most important species driving their position shown with vectors. Family abbreviations (in parentheses) reflect those in Table 4.3

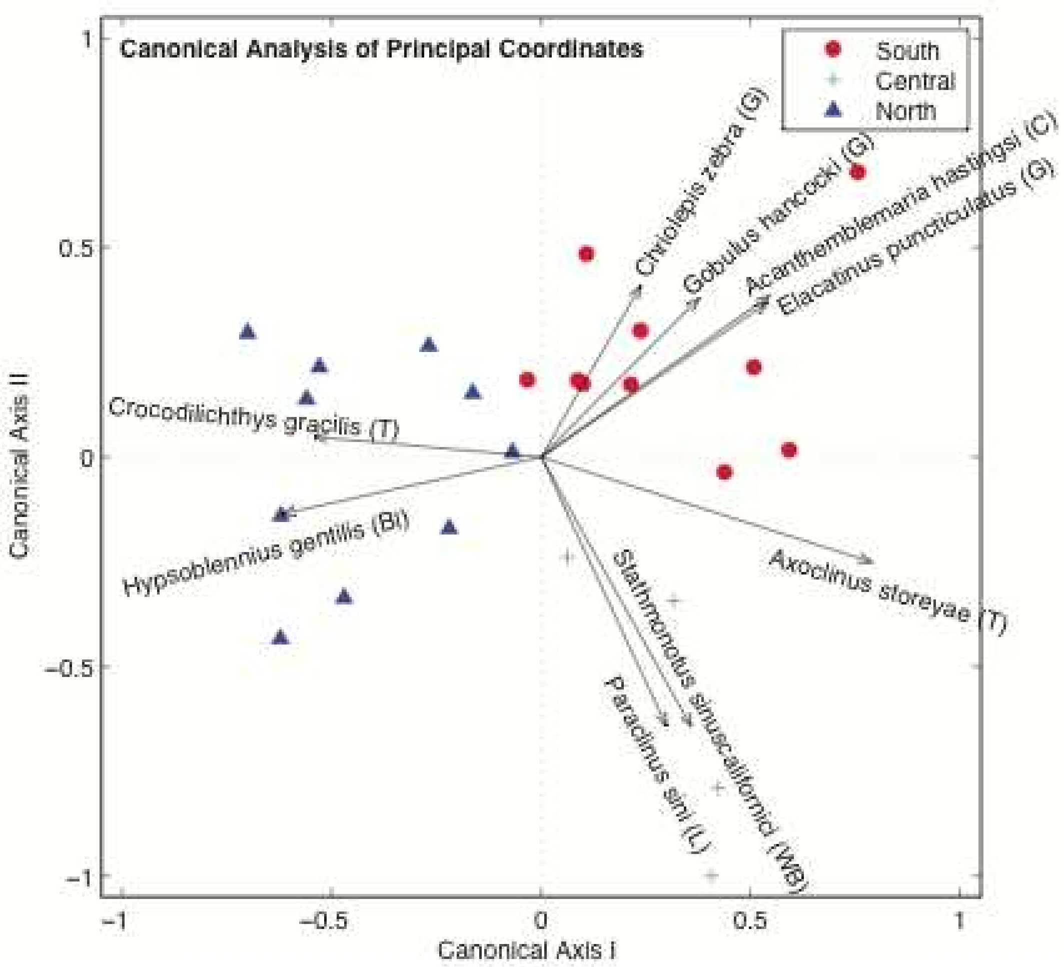

Fig. 4.3. Plot of study sites, divided by sub-region (i.e., south vs. central vs. north), in canonical space, with the most important species driving their position shown with vectors. Family abbreviations (in parentheses) reflect those in Table 4.3

References

Aburto-Oropeza O, Sala E, Paredes G, Mendoza A, Ballesteros E (2007). Predictability of reef fish recruitment in a highly variable nursery habitat. *Ecology* 88(9):2220-2228.

Aburto-Oropeza O, Sánchez CA (2000). *Recursos arrecifales del Golfo de California: estrategias de manejo para las especies marinas de ornato*. Universidad Autónoma de Baja California Sur, La Paz.

Aburto-Oropeza O, Sánchez A, Mascareñas-Osorio I, Sánchez C, Calderon M, Moxley J, Erisman B, Ezcurra E (2013). Linking fish biomass, geomorphology, and community assemblages to assess the health of reefs in the Gulf of California. In review.

Ackerman JL, Bellwood DR (2000). Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series* 206:227-237.

Ackerman JL, Bellwood DR (2003). The contribution of small individuals to density-body size relationships. *Oecologia* 136(1):137-140.

Ackerman J, Bellwood D, Brown J (2004). The contribution of small individuals to density-body size relationships: examination of energetic equivalence in reef fishes. *Oecologia* 139(4):568-571.

Allen LG, Bouvier LS, Jensen RE (1992). Abundance, diversity, and seasonality of cryptic fishes and their contribution to a temperate reef fish assemblage off Santa Catalina Island, California. *Bulletin of the Southern California Academy of Sciences* 91(2):55-69.

Alvarez-Borrego S (2010). Physical, chemical, and biological oceanography of the Gulf of California. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Anderson MJ, Willis TJ (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84(2):511-525.

Badan-Dangon A, Koblinsky CJ, Baumgartner T (1985). Spring and summer in the Gulf of California: observations of surface thermal patterns. *Oceanologica Acta* 8(1):13-22.

Bray JR, Curtis JT (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27(4):325-349.

Carvahal MA, Ezcurra E, Robles A (2004). The Gulf of California: natural resource concerns and the pursuit of a vision. In Glover LK, Earles S (eds.) *Defying Ocean's End*. *An agenda for action*. Island Press, Washington, D.C.

Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen M (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299(5604):217-221.

Cisneros-Mata MA (2010). The importance of fisheries in the Gulf of California and ecosystem-based sustainable co-management for conservation. In Brusca RC (ed.) *The Gulf of California Biodiversity and Conservation*. The University of Arizona Press, Tucson.

Crowder LB, Murawski SA (1998). Fisheries bycatch: implications for management. *Fisheries* 23(6):8-17.

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences* 104(25):10518-10523.

Erlandson JM, Fitzpatrick SM (2006). Oceans, islands, and coasts: Current perspectives on the role of the sea in human prehistory. *Journal of Island & Coastal Archaeology* 1(1):5-32.

Erlandson JM, Moss ML, Des Lauriers M (2008). Life on the edge: early maritime cultures of the Pacific Coast of North America. *Quaternary Science Reviews* 27(23):2232-2245.

Estes JA, Danner EM, Doak DF, Konar B, Springer AM, Steinberg PD, Tinker MT, Williams TM (2004). Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Science* 74(3):621-638.

Galland GR (2011). Comments on microhabitat specialization and a depth range extension for a chaenopsid tube blenny in the Gulf of California, Mexico. *Bulletin of the Southern California Academy of Sciences* 110(2):52-55.

Goncalves EJ, Faria C (2009). Patterns of microhabitat utilisation in blennies. In Patzner RA, Goncalves EJ, Hastings PA, Kapoor BG (eds.) *The Biology of Blennies*. Science Publishers, Enfield.

Harborne AR, Jelks HL, Smith-Vaniz WF, Rocha LA (2012). Abiotic and biotic controls of cryptobenthic fish assemblages across a Caribbean seascape. *Coral Reefs* 31(4):1-14.

Hastings PA, Galland GR (2010). Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae). *Coral reefs* 29(1):155-164.

Hastings PA, Springer VG (1994). Review of *Stathmonotus*, with redefinition and phylogenetic analysis of the Chaenopsidae (Teleostei: Blennioidei). *Smithsonian Contributions to Zoology* 558.

Helfman GS (2007). *Fish Conservation. A guide to understanding and restoring global aquatic biodiversity and fishery resources*. Island Press, Washington, D.C.

Jones DL (2012). The Fathom Toolbox for Matlab: multivariate ecological and oceanographic data analysis. College of Marine Science, University of South Florida, St. Petersburg. Available from: http://seas.marine.usf.edu/~djones/

La Mesa GL, Muccio SD, Vacchi M (2006). Structure of a Mediterranean cryptobenthic fish community and its relationships with habitat characteristics. *Marine Biology* 149(2):149-167.

Lin H-C (2010). *Evolution of the suborder Blennioidei: phylogeny and phylogeography of a shallow water fish clade*. Ph.D. dissertation, University of California, San Diego.

Lin H-C, Hastings PA (2011). Evolution of a neotropical marine fish lineage (subfamily Chaenopsinae, Suborder Blennioidei) based on phylogenetic analysis of combined molecular and morphological data. *Molecular Phylogenetics and Evolution* 60(2):236-248.

Miller PJ (1979). Adaptiveness and implications of small size in teleosts. *Symposia of the Zoological Society of London* 44:263-306.

Munday PL, Jones GP (1998). The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review* 36:373-411.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315(5820):1846-1850.

Patzner RA (1999). Habitat utilization and depth distribution of small cryptobenthic fishes (Blenniidae, Gobiesocidae, Gobiidae, Tripterygiidae) in Ibiza (western Mediterranean Sea). *Environmental biology of fishes* 55(3):207-214.

Pegau WS, Boss E, Martínez A (2002). Ocean color observations of eddies during the summer in the Gulf of California. *Geophysical Research Letters* 29(9):1295.

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002). A general model for designing networks of marine reserves. *Science* 298(5600):1991-1993.

Sala E, Aburto-Oropeza O, Reza M, Paredes G, López-Lemus LG (2004). Fishing down coastal food webs in the Gulf of California. *Fisheries* 29(3):19-25.

Steneck RS, Vavrinec J, Leland AV (2004). Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems* 7(4):323-332.

Thomson DA, Findley LT, Kerstitch AN (2000). *Reef fishes of the Sea of Cortez: The rocky-shore fishes of the Gulf of California*. University of Texas Press, Austin.

Thomson DA, Gilligan MR (2002). Rocky-shore fishes. In Case TJ, Cody ML, Ezcurra E (eds.) *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford.

APPENDIX

Novel natural history observations

Introduction

The study of conservation and ecology of any ecosystem or group of species often involves a deep understanding of the behaviors and life history traits of the component species. With this understanding and with the hours of observing nature inherent in ecological study, it is possible to identify quirks or abnormalities in an organism's behavior, in community structure, or in ecosystem function. Reporting these observations is relevant to several fields of study, including behavioral ecology, conservation biology, biogeography, etc.

A1 - Irregular schooling behavior and abandonment of mimicry by the Sabertooth Blenny (Blenniidae) in Cabo Pulmo National Park, Gulf of California, Mexico

Plagiotremus azaleus (the Sabertooth Blenny; Fig. A.1a) is an obligate scale-eating blenny (Hobson 1968) endemic to and widespread in the Tropical Eastern Pacific. Like many members of Tribe Nemophini (Blenniidae), *P. azaleus* typically relies on mimicry to gain access to potential prey fishes (Smith-Vaniz 1976). Throughout its range, the model of this aggressive mimic is the initial phase of the *Thalassoma lucasanum* (the Cortez Rainbow Wrasse). At several sites throughout the Gulf of California, we have observed *P. azaleus* in its typical mimic capacity, resembling its model in both appearance and behavior. On these reefs, *P. azaleus* is significantly outnumbered by *T. lucasanam*, with an average of more than 160 wrasses per blenny (2009 belt transect survey data). Distinguishing between the two is not difficult, as the blennies are more slender and utilize anguilliform rather than labriform swimming, as in the wrasses. This typical difference in densities is not surprising given the necessary prevalence of the model and scarcity of the mimic in evolutionarily stable aggressive mimicry systems.

In summer 2010 at reef sites in Cabo Pulmo National Park (CPNP), we observed several aggregations of *P. azaleus* ranging in number from 10-20 individuals and one group of well over 100 blennies (Fig. A.1b). In contrast to our observations elsewhere, these blennies greatly outnumbered *T. lucasanum*, did not school with it, and did not display the dark coloration typical of individuals engaged in mimicry (Fig. A.1). Instead, blennies from these groups aggressively attacked large fishes, including *Mycteroperca rosacea* (Leopard Grouper) and *Lutjanus novemfaciatus* (Dog Snappers) in such large numbers and with such ferocity that they affected the behaviors and movements of these much larger fishes, displacing them from the area.

How a species that typically relies on mimicry can maintain such high local abundances without resembling its model is paradoxical. CPNP has been closed to fishing for 15 years and has some of the highest densities of reef fishes in the tropical eastern Pacific (2009 belt transect data). Perhaps these local abundances of potential prey allow for the large numbers of *P. azaleus* that we observed, even when they seemingly no longer utiliza mimicry to gain access to food resources.

A2 – A Benthic Diatom Bloom in the Gulf of California, Mexico

Introduction

Benthic invertebrate and algal blooms, often the result of a biological invasion, can be harmful to the shallow marine environment and often involve a single species spatially dominating an ecosystem (e.g., Griffiths et al. 1991; Meinesz *et al.* 1993; Watson and Estes 2011). In some cases, these blooms may represent an alternate stable state, reaching levels that are detrimental to competitors or to associated species that rely on the characteristics of the natural environmental state. In the shallow, coastal marine environment, invertebrate and algal blooms are often a result of accidental human transport of exotic species (Carlton 1996; Ruiz et al. 1997; Ruiz et al. 2000) and can be costly and very difficult to reverse (though reversal is possible in some cases; e.g., Anderson 2005). Furthermore, these events occur most frequently in areas of high human population, travel, or commerce (Ruiz *et al.* 1997), ecosystems that are already highly impacted by human presence (Lotze *et al.* 2006).

In the summers of 2009 and 2010, during expeditions around the Gulf of California (GOC), Mexico to systematically survey both conspicuous and cryptic reef fishes and invertebrates (Fig. A.2; Aburto-Oropeza et al. 2001), we observed a benthic algal bloom, seemingly invasive in nature, at the relatively remote (though fished) Isla San Esteban, in the Midriff Islands, Central GOC. Here we report on those observations and the results of our preliminary study of the alga.

Study Site and Context

The GOC is a semi-enclosed basin, located between the Baja California peninsula and the Mexican mainland, approximately 1300 km long by 100-150 km wide (Fig. A.2). The Midriff Islands are located in the central GOC, between 28 degrees and 30 degrees N and constitute one of the more productive marine ecosystems in the world (Brusca 2010). That region is characterized by consistent tidal (Paden *et al.* 1991) and coastal (Badan-Dangon *et al.* 1985) upwelling that support high surface productivity and large communities of seabirds, marine mammals, pelagic and reef fishes, and artisanal fishers. Isla San Esteban is nearly equidistant to the Baja Peninsula and the Mexican mainland (Fig. A.2) and is approximately 40-70 km from the nearest permanent settlements. However, even given its relative remoteness, Isla San Esteban is fished by communities in Bahía de Kino on the Mexican mainland and Bahía de San Francisquito and El Barril on the Baja Peninsula (Moreno-Báez *et al.* 2010).

During expeditions in July 2009 and July 2010, we visited 28 sites at islands throughout the central and southern GOC and along remote areas of the Baja Peninsula, including ten sites in the Midriff Islands region. Sites stretched from the Midriff Islands to Cabo Pulmo National Park near the tip of the Baja Peninsula and covered more than six degrees of latitude (Fig. A.2).

Methods

At each island/peninsular area, we set up a 10 m^2 area to study the benthos and the benthic fish community. Sites were chosen based on appropriate benthic fish habitat, were consistent (3-5 m deep, rocky reef, dominated by boulders of all sizes) across the GOC, and were representative of the reefs in each area. Using a pvc camera frame and SCUBA gear, we photographed the benthos at nine nonrandom locations within the study area (three regularly spaced rows of three regularly spaced photos). Photoquadrats from the 2009 expedition are 0.25 m^2, and those from 2010 are 0.35 m^2.

In the lab, all images were analyzed in PhotoGrid 1.0, where the substrate was described at fifty stratified random points per image. For the purposes of this study, each point was given a value of 1 (= diatom mat) or 0 (= no diatom mat), and percent cover was calculated for all images.

After the opportunistic discovery of the algal bloom at Isla San Esteban in both 2009 and 2010, we collected samples that were preserved in the field in 10% formalin or 90% ethanol and others that were returned to the lab without preservation (in seawater). In the lab, filamentous material and supernatant (viscous liquid secreted by the filamentous material) were extracted from the non-preserved (seawater) sample and prepared for further analysis. The material was washed once with tap water to remove excess salt, plated on a microscope slide, and viewed using scanning electron microscopy (SEM). Preserved samples are stored at Scripps Institution of Oceanography, La Jolla, CA, USA.

Results and Discussion

Analysis of samples via SEM confirmed that the blooming species is a diatom, *Biddulphia biddulphiana* (J.E. Smith) Boyer, 1900 (Fig. A.3). This centric diatom forms chains that may attach to benthic substrates and is also often found in the phytoplankton (Round *et al.* 1990). As with many coastal species that have planktonic stages (and can be easily transported by the shipping industry), it is difficult to know the natural home range of *B. biddulphiana*; however, algal checklists from North and South America and from Western Europe include the species, implying a wide current distribution (see Guiry and Guiry 2012). In their in-depth study of the planktonic diatoms of the GOC, Moreno *et al.* (1996) report its presence at some locations in the GOC, but to date there have been no similarly systematic surveys of benthic diatoms in that region. Our observations of *B. biddulphiana* at Isla San Esteban seemingly constitute a first report of a benthic bloom of this nature in the GOC.

In 2009, we observed the benthic *B. biddulphiana* bloom only on the rocky reefs of Isla San Esteban (Fig. A.2). According to our PhotoGrid 1.0 analysis, it covered an average of 31% of the area of each photoquadrat at that time (*e.g.*, Fig. A.4) and was attached to all substrates, including a demonstrated ability to overgrow colonies of *Porites californica* Verrill, 1868, one of the few species of stony corals that survives in that region (*e.g.*, Fig. A.4 inset). It was not observed at any of our other sites that year. In 2010, we measured a non-significant increase in average percent cover at Isla San Esteban (37%; Man-Whitney P>0.05) and observed the same diatom on the shallow rocky reefs of two nearby islands in the Midriff Islands group: Isla Salsipuedes and Isla Las Animas (Fig. A.2). In that year at Isla Salsipuedes, *B. biddulphiana* covered an average of 11% of the photoquadrats, and at Isla Las Animas, it was not observed inside any quadrat but was noted during a general survey of the area.

SEM analysis revealed several individuals of much smaller diatom species living on *B. biddulphiana* cells (Fig. A.3). This relationship between *B. biddulphiana* and smaller epiphytic diatoms has been previously described by Tiffany and Lange (2002) in San Diego, CA, USA. Those authors described their San Diego site at 20-24 m depth as containing “vast carpets of diatoms on the seafloor” and identified several species attached to *B. biddulphiana* cells (Tiffany and Lange 2002). The high densities that we observed are analogous to the “vast carpets” reported there. The potential advantages or costs to the host cells and the possible facilitation of a carpet-forming, benthic lifestyle by this symbiosis should be explored in greater detail.

This study is the first to describe a dense benthic bloom of *B. biddulphiana* in the GOC. Its ability to attach to most surfaces and overgrow other benthic species, including stony corals, along with the apparent trend of increased density of coverage at Isla San Esteban, was noticeably affecting the habitat and could be affecting the survival of other sessile benthic organisms and benthos-associated fishes and invertebrates. For example, we observed several individuals of tube-dwelling fishes struggling to feed and court females through patches of the *B. biddulphiana* carpet. Furthermore, if Isla San Esteban was ground zero for this bloom, the fact that our 2010 surveys revealed new patches of *B. biddulphiana* at two of the nearest islands may indicate its ability to spread or a wider expansion of the environmental conditions that favor its growth.

Notably, in July 2011, we received information from a credible source that the *B. biddulphiana* bloom is gone (T.A. Pfister pers. comm.). During a research expedition in June 2011 to the Midriff Islands, no *B. biddulphiana* patches were observed at any of the sites that we discuss here. While that expedition did not include quantitative, photographic surveys of the benthic environment, we received no reports of opportunistic observations of the diatom. Furthermore, the 2011 expedition included one researcher (T.A. Pfister) who also participated in our 2009 expedition, when the bloom was first discovered, and who has 25 years of experience diving in the Midriff Islands without ever observing a bloom like the one in 2009-2010.

Unlike in the case of benthic blooms of undoubtedly exotic species, we were unable to determine the cause of the bloom and subsequent bust of *B. biddulphiana* at these sites. The environmental factors that could lead to these observations should be investigated further. The high productivity and high oceanographic variability characteristic of the Midriff Islands could play a role, but the specific variables that led to this phenomenon are unknown. Consistent monitoring and experimental study of the interactions among the species in the benthic community there could help reveal these variables and allow researchers and managers to predict/prevent future blooms that potentially negatively affect the benthic fish and invertebrate communities.

A3 - Comments on Microhabitat Specialization and a Depth Range Extension for a Chaenopsid Tube Blenny in the Gulf of California, Mexico

Acanthemblemaria balanorum Brock (Clubhead Blenny; Fig. A.5) is a chaenopsid tube blenny endemic to the Tropical Eastern Pacific. Adults of this species, as all members of the Chaenopsidae, inhabit vacated invertebrate tubes or tests (Stephens 1963; Lindquist 1985). In the case of *A. balanorum*, the shelter of choice is the vacated test of *Megabalanus* Hoek barnacles, a genus characterized in the tropical eastern Pacific by a complex of species (Henry and McClaughlin 1986) that typically live in the upper 10 m on shallow rocky reefs (Brusca and Hendrickx 2008). In the Gulf of California (GOC), Mexico, *A. balanorum* overlaps in distribution with two congeners, *A. crockeri* Beebe and Tee-Van and *A. hastingsi* Lin and Galland, and these species are known to exhibit depth partitioning, with *A. balanorum* inhabiting relatively shallower depths, *A. crockeri* inhabiting relatively deeper depths, and *A. hastingsi* overlapping near the edges of the depth ranges of the other two species at intermediate depths (Lindquist 1985). A detailed study of the relationships among these three congeners in the southern GOC (Lindquist 1985) reported that *A. balanorum* inhabits shelters (=barnacles) down to approximately 7 m depth. Guides to the fishes of the region (e.g., Allen and Robertson 1994; Humann and DeLoach 2004) report a similar depth range.

In November 2010, I observed and collected several individuals of *A. balanorum* at a depth of 21 m at the base of a pinnacle off the south end of Maria Cleofas, the southernmost point in the Islas Marias archipelago, southern GOC. These individuals, like all individuals of this species that I have observed, inhabited vacant barnacles (*Megabalanus*). This observation represents a significant depth range extension for this normally shallow subtidal fish (and may also represent an extension for the barnacle; Brusca and Hendrickx 2008). This ability of a microhabitat specialist to colonize abnormal macrohabitats (in this case much deeper than normal waters) when its microhabitat (=barnacles) is available supports a hypothesis that these specialists are resource (=shelter) limited. Similar shelter limitation has already been experimentally demonstrated in the GOC congener, *A. crockeri*, which increases in average density with shelter addition (Hastings and Galland 2010).

I observed additional evidence that *A. balanorum* is a shelter-limited microhabitat specialist in July 2009 at Las Animas, a small island and a series of small pinnacles in the central GOC. That site proved to be ideal *A. balanorum* habitat, with several large boulders completely covered by broad, very dense *Megabalanus* fields down to 5 m depth. Within these barnacle fields, I observed large numbers of *A. balanorum*, more densely distributed than any other chaenopsid population reported to date (e.g. in Lindquist 1985; Clarke 1996; Thomson and Gilligan 2002; P.A. Hastings, pers. comm.). During an opportunistic survey of the area, I placed a 0.25 m^2 quadrat on five randomly selected areas on the top of a large, flat boulder at 5 m depth in order to survey chaenopsids and ascertain densities. Numbers of *A. balanorum* ranged (mean +/- SD) from 8 – 28 (20.4 +/- 8.6) individuals per 0.25 m^2. These high densities may reflect the very high barnacle densities at this site, though it is difficult to quantify available shelters, as it is not immediately obvious what a chaenopsid considers to be a sufficient shelter.

To date, no experiments have been designed to determine what a second limiting factor is for these or similar shelter-dwelling microhabitat specialists, but it is quite possibly an issue of territory size. Males of *Acanthemblemaria* and several other chaeonpsid genera actively court females, which, upon choosing a suitable male, enter the male’s shelter and deposit eggs (Hastings 1986; Hastings 1988; Hastings and Peterson 2011). The males guard the eggs and may simultaneously protect clutches from multiple females (Hastings 1986; Hastings 1988; Hastings and Peterson 2011). Under these conditions, males compete for female choice and for the most desirable shelters (Hastings 1988; Hastings 1992). The high densities of *A. balanorum* observed at Las Animas could lead to agonistic interactions that secondarily limit the population size (or density) of this species.

In order to begin quantifying the distance between occupied barnacle shelters at the densely populated Las Animas site, I randomly chose an individual *A. balanorum* and measured the distance to its nearest neighbor. I then measured the distance to that individual’s nearest neighbor and repeated the process until I reached ten total individuals. On average (SD), these ten individuals were only 4.4 cm (1.6) from their nearest neighbor. Upon collecting the specimens, I obtained sex and standard length (SL) for each individual and determined that they were, on average (SD), 28.9 mm SL (3.8) and were all sexually mature adults. In fact, to the best of my knowledge, juvenile habitat preference in this species is unknown. The male to female sex ratio was 7:3, indicating the ability of several adult males to live in close proximity to one another and to mature females, which were somewhat evenly dispersed among the males, within this set of ten individuals (numbers one, three, and eight out of ten; 5, 2.5, and 5 cm from their nearest neighbors, respectively). The presence of some shelters inhabited by less competitive chaenopsid species, *Coralliozetus angelicus* (Böhlke and Meade) and *Protemblemaria bicirrus*

(Hildebrand), increases the overall chaenopsid density, and the availability of some uninhabited shelters perhaps implies that the community at that site is approaching some maximum. It is difficult, however, to determine whether or not empty barnacles represent a choice to avoid high densities, a preference for other more highly desirable shelters, or some additional factor.

While the preliminary evidence presented here supports a hypothesis that these microhabitat specialists are first limited by the presence of their preferred shelter and then by some other factor (possibly territoriality) that prevents higher densities, even with greater shelter availability, it is necessary to design and implement experiments to test this and similar hypotheses empirically. Species like *A. balanorum* that rely on biologically derived microhabitats may be able to utilize a wider range of macrohabitats as their "hosts" move to new areas. In the case of the depth range extension at Maria Cleofas, the ability of *Megabalanus* barnacles to survive down to at least 21 m at this site allows a species that specializes on its empty tests to do the same, and this ability is not unique to *A. balanorum*. A blenniid (*Hypsoblennius brevipinnis* Günther) and another chaenopsid (*A. macrospilus* Brock) were observed and collected at the Maria Cleofas site, inhabiting barnacle tests. *Hypsoblennius brevipinnis* is also a microhabitat specialist, its preferred shelter is also *Megabalanus*, and it is typically confined to the upper 3-4 m of the subtidal zone (Allen and Robertson 1994; Humann and DeLoach 2004; though it may be known from as deep as 10 m; De la Cruz Agüero et al. 1997). Like in *A. balanorum,* this observation represents a significant depth range extension for this specialist and an interesting finding for the Blenniidae, which are characterized by few species reaching depths greater than approximately 25 m (Springer and Smith-Vaniz 1970). *Acanthemblemaria macrospilus*, sister to the more northern *A. hastingsi* discussed above (see Lin and Galland 2010), shares its ability to utilize multiple microhabitat shelters (Lindquist 1985) and typically lives to depths of 15-18 m (Allen and Robertson 1994). Observation of individuals at a depth of 21 m may represent a minor change in depth range, but its flexibility in shelter choice probably allows it to occupy a greater diversity of habitats than *A. balanorum*. Further research into the intra- and inter-specific relationships within this group of species that utilize (and potentially compete for) similar microhabitats will reveal more of the processes at play in determining the makeup of this assemblage and may provide further insight into the relative advantages and disadvantages of microhabitat specialization.

All specimens of all species discussed here were collected using quinaldine and are archived at the Scripps Institution of Oceanography Marine Vertebrate Collection (Las Animas collection number = SIO 09-261; Maria Cleofas collection number = SIO 10-132).

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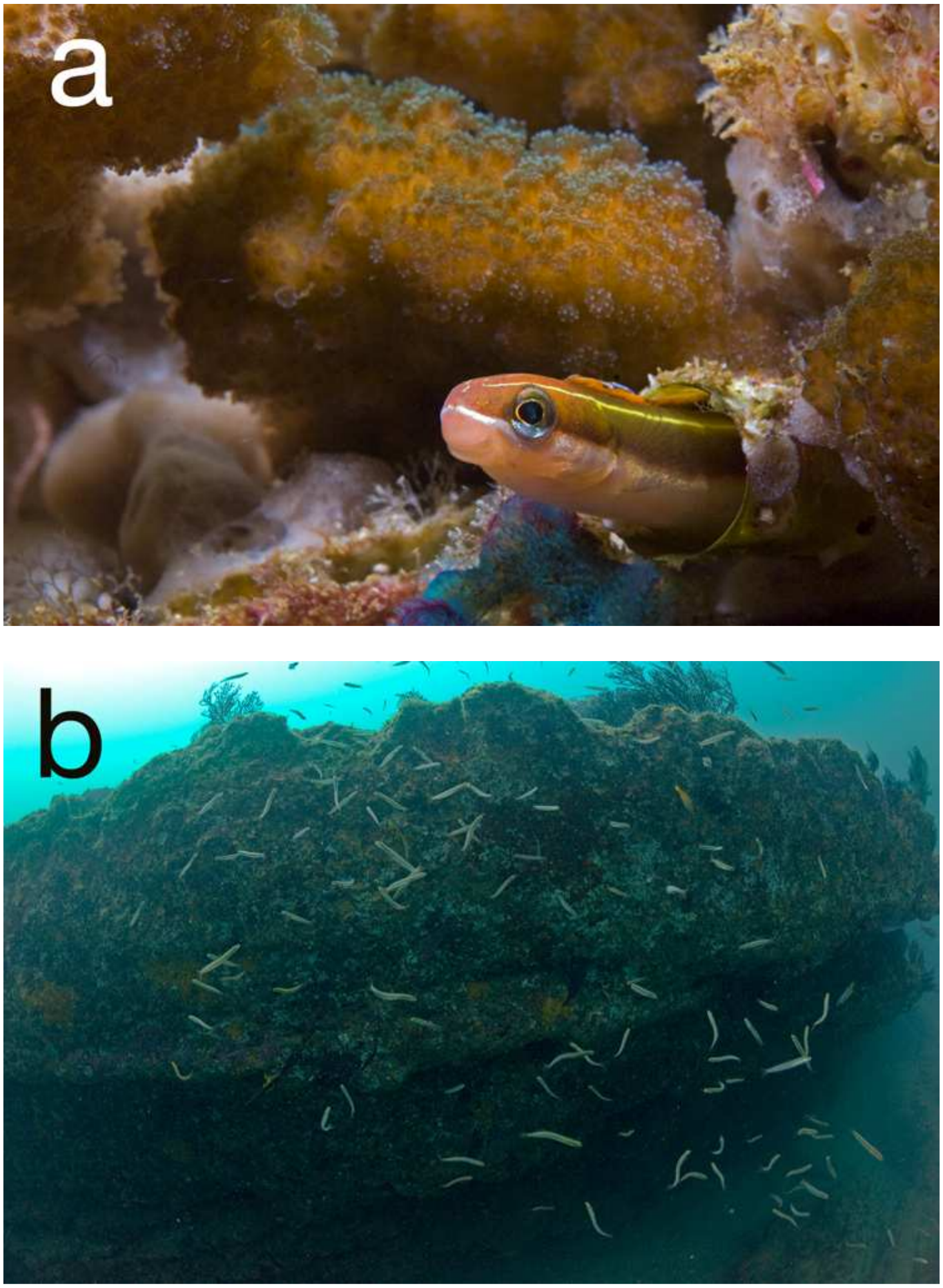

Fig. A.1. *Plagiotremus azaleus*: a) in a vacated invertebrate tube and b) schooling in an aggregation of over 100 individuals. Note the light coloration atypical of individuals of this species engaged in mimicry. Photos courtesy of O. Aburto-Oropeza

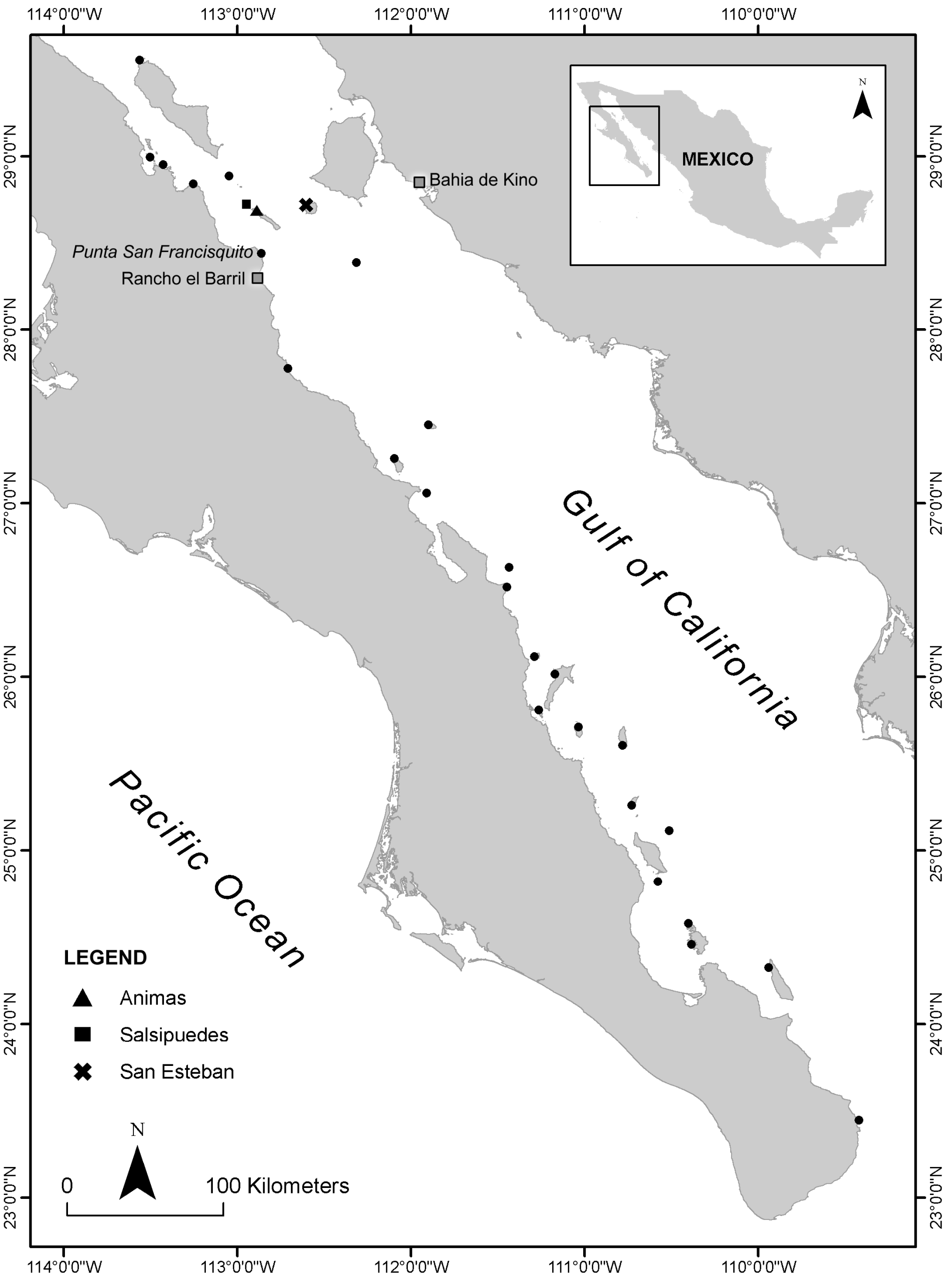

Fig. A.2. Map of sites surveyed in 2009-2010. x marks Isla San Esteban, “ground zero” for the diatom bloom; dots represent sites surveyed in 2009-2010 that did not have evidence of the diatom’s presence. El Barril, San Francisquito, and Kino Bay are communities with fishers who exploit the reefs of the Midriff Islands

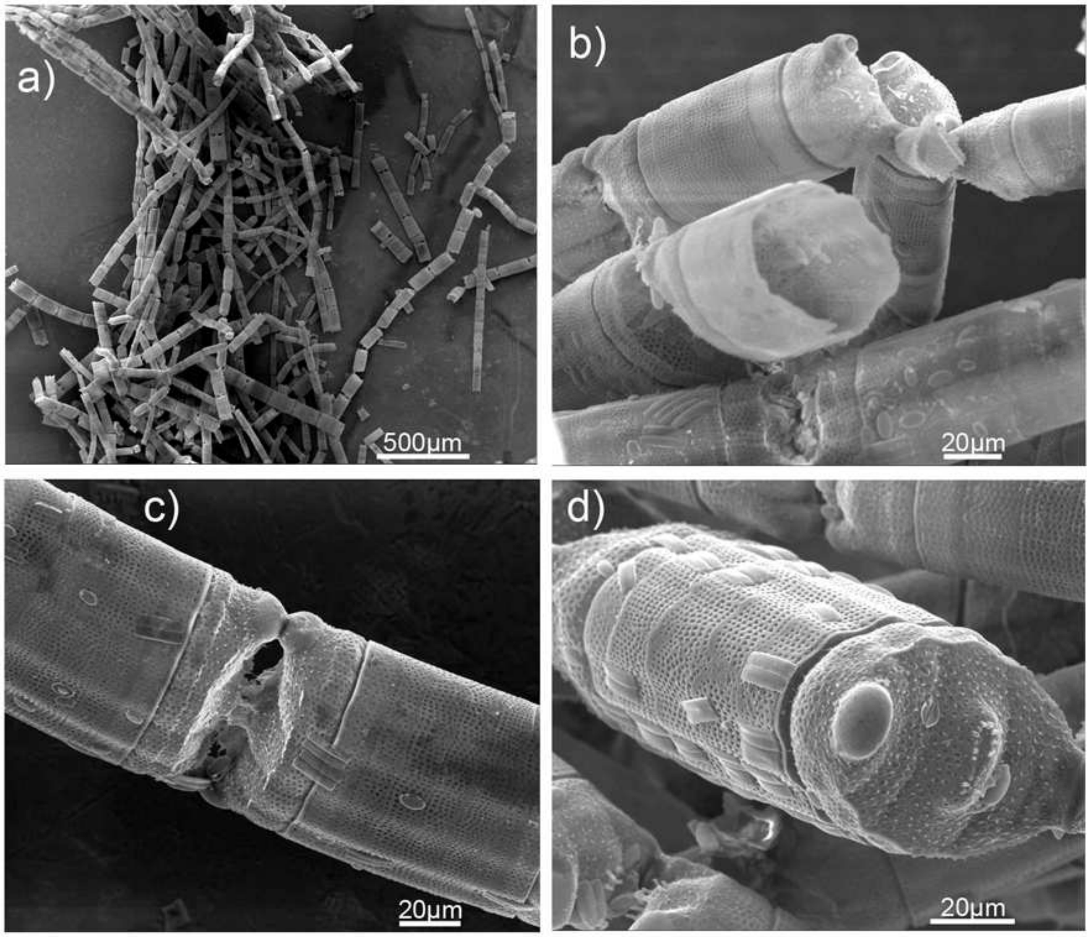

Fig. A.3. Scanning Electron Microscope images of *Biddulphia biddulphiana* collected from the bloom at Isla San Esteban and used for identification. A) shows several cells of the chain-forming diatom, and B)-D) show close-up shots of individual cells with associated, epiphytic diatoms attached at several locations along the cells' tests

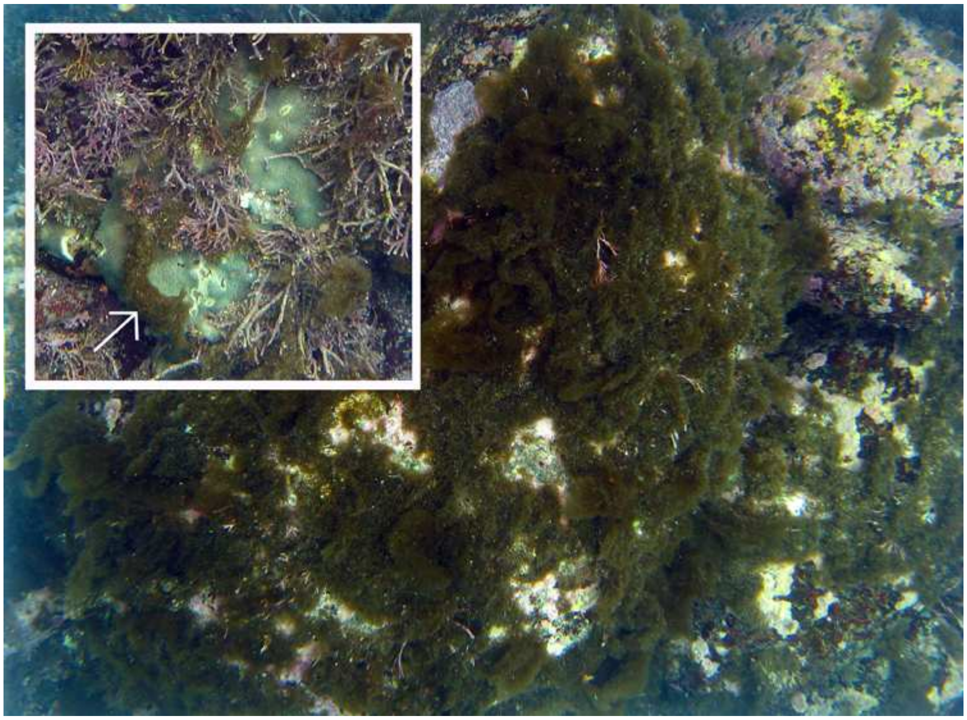

Fig. A.4. Photograph of the *Biddulphia biddulphiana* bloom at Isla San Esteban. Inset shows overgrowth of the stony coral *Porites californica*. Photos courtesy of J. Lund

Fig. A.5. *Acanthemblemaria balanorum* in shelter at Las Animas in the central Gulf of California, Mexico. Photo taken in July 2009 at 5 m depth during nearest neighbor surveys. Photo courtesy of J. Lund

References

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Ororio I, Sala E, Ezcurra E (2011). Large recovery of fish biomass in a no-take marine reserve. *PLOS One* 6(8):e23601.

Allen GR, Robertson DR (1994). *Fishes of the Tropical Eastern Pacific*. Crawford House Press, Bathurst.

Anderson LWJ (2005). California's reaction to *Caulerpa taxifolia*: a model for invasive species rapid response. *Biological Invasions* 7:1003-1016.

Badan-Dangon A, Koblinsky CJ, Baumgartner T (1985). Spring and summer in the Gulf of California: observations of surface thermal patterns. *Oceanologica Acta* 8(1):13-22.

Brusca RC (ed.) (2010). *The Gulf of California biodiversity and conservation*. The University of Arizona Press, Tucson.

Brusca RC, Hendrickx M (2008). The Gulf of California invertebrate database: the invertebrate portion of the macrofauna golfo database. www.desertmuseum.org/center/seaofcortez/database.php

Carlton JT (1996). Pattern, process, and prediction in marine invasion ecology. *Biological Conservation* 78:97-1066.

Clarke RD (1996). Population shifts in two competing fish species on a degraded coral reef. *Marine Ecology Progress Series* 137:51-58.

De la Cruz Aguero J, Martínez MA, Cota Gómez VM, De la Cruz Aguero G (1997). Catalogo de los peces marinos de Baja California Sur. IPN-CICIMAR, La Paz, Mexico.

Griffiths RW, Schloesser DW, Leach JH, Kovalak WP (1991) Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences* 48(8):1381-1388.

Guiry MD, Guiry GM (2012) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 12 January 2012

Hastings PA (1986). Habitat selection, sex ratio and sexual selection in *Coralliozetus angelica* (Blennioidea: Chaenopsidae). In Uyeno T, Arai R, Taniuchi T, Matsuura K (eds.) *Indo-Pacific fish biology*. Ichthyological Society of Japan, Tokyo.

Hastings PA (1988). Correlates of male reproductive success in the browncheek blenny, *Acanthemblemaria crockeri* (Blennioidea: Chaenopsidae). *Behavioral Ecology and Sociobiology* 22:95-102.

Hastings PA (1992). Nest-site size as a short-term constraint on the reproductive success of paternal fishes. *Environmental Biology of Fishes* 34:213-218.

Hastings PA, Galland GR (2010). Ontogeny of microhabitat use and two-step recruitment in a specialist reef fish, the Browncheek Blenny (Chaenopsidae). *Coral Reefs* 29:155-164.

Hastings PA, Peterson CW (2010). Parental care, oviposition sites, and mating systems of blennioid fishes. In Cole KS (ed.) *Reproduction and sexuality in marine fishes. Patterns and processes*. University of California Press, Berkely.

Henry DP, McClaughlin PA 1(986). The recent species of *Megabalanus* (Cirripedia: Balanomorpha) with special emphasis on *Balanus tintinnabulum* (Linnaeus) *sensu lato*. *Zoologische Verhandelingen* 235:1-60.

Hobson ES (1968). Predatory behavior of some shore fishes in the Gulf of California. Research Report 73, Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service.

Humann P, DeLoach N (2004). *Reef Fish Identification. Baja to Panama*. New World Publications, Jacksonville.

Lin H-C, Galland GR (2010). Molecular analysis of *Acanthemblemaria macrospilus* (Teleostei: Chaenopsidae) with description of a new species from the Gulf of California, Mexico. *Zootaxa* 2525:51-62.

Lindquist DG (1985). Depth zonation, microhabitat, and morphology of three species of *Acanthemblemaria* (Pices: Blennioidea) in the Gulf of California, Mexico. *P.S.Z.N.I.:Marine Ecology* 6(4):329-344.

Lotze HK, Lenihan HS, Borque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kiry MX, Peterson CH, Jackson JBC (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806-1809.

Meinesz A, de Vaugelas J, Hesse B, Mari X (1993). Spread of the introduced tropical green alga *Caulerpa taxifolia* in northern Mediterranean waters. *Journal of Applied Phycology* 5:141-147.

Moreno JL, Licea S, Santoyo H (1996). *Diatomeas del Golfo de California*. Universidad Autonoma de Baja California Sur, La Paz.

Moreno-Báez M, Orr BJ, Cudney-Bueno R, Shaw WW (2010). Using fishers' local knowledge to aid management at regional scales: spatial distribution of small-scale fisheries in the northern Gulf of California, Mexico. *Bulletin of Marine Science* 86(2):339-353.

Paden CA, Abbott MR, Winant CD (1991). Tidal and atmospheric forcing of the upper ocean in the Gulf of California: 1) sea surface temperature variability. *Journal of Geophysical Research* 96(C10):18337-18359.

Round FE, Crawford RM, Mann DG (1990). *The diatoms. Biology and Morphology of the genera.* Cambridge University Press, Cambridge.

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997). Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37:621-632.

Ruiz GM, Fotonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31:481-531.

Smith-Vaniz WF (1976) *The Saber-toothed Blennies, Tribe Nemophini (Pisces: Blenniidae). Monograph 19.* Academy of Natural Sciences of Philadelphia, Philadelphia.

Springer VG, Smith-Vaniz WF (1970). *Blennius antholops*, new deep-water fish, from the Gulf of Guinea, with comments on the bathymetric distribution of the family Blennidae. Proceedings of the Biological Society of Washington 83(20):215–220.

Stephens JS (1963). *A revised classification of the blennioid fishes of the American family Chaenopsidae*. University of California Publication in Zoology 68.

Thomson DA, Gilligan MR (2002). Rocky-shore fishes. In Case TJ, Cody ML, Ezcurra E (eds.) *A new island biogeography of the Sea of Cortés*. Oxford University Press, Oxford.

Tiffany MA, Lange CB (2002). Diatoms provide attachment sites for other diatoms: a natural history of epiphytism from southern California. *Phycologia* 41(2):116-124.

Watson J, Estes JA (2011) Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs* 81(2):215-239.