

Eastern Pacific reef fish responses to coral recovery following El Niño disturbances

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ABSTRACT: This study examined fluctuations in an eastern Pacific reef fish assemblage as it varied with coral recovery over 30 yr. Concurrent fish and coral monitoring were conducted at Uva Island reef, which lies within the boundaries of Coiba National Park, Panama, in an area that has received virtually no fishing pressure or watershed development over the past 80 yr. Coral and fish monitoring spanned the 1982–1983 and 1997–1998 El Niño disturbances—anomalous warming events that selectively killed reef-building corals. While no fish mortalities were observed during the 1982–1983 El Niño event, live coral cover was reduced to nearly 0% at the study reef. From 1984 to 1990, live coral (*Pocillopora* spp.) cover was extremely low (< 5%), but demonstrated steady recovery to ~35% by 2010. By quantifying disturbance-related, long-term changes in coral reef resources and relating these to fish trophic group responses, several functional relationships emerged. A total of 63 fish taxa were observed, and reef fish density (all taxa combined) remained relatively stable. Multivariate analysis of species abundances revealed a strong overlap between seasons and a clustering of community composition in the years following bleaching. Fish species richness increased significantly as live coral cover rose from near 0 to 15–20% and then demonstrated a decreasing trend to 35% cover. Benthic invertivores showed a significant parabolic increase in density peaking at ~20% live coral cover. A pattern of decline was apparent for the mixed diet feeders guild as coral cover increased, whereas an asymptotic relationship with coral cover emerged for the facultative corallivore guild. No clear patterns in herbivore, piscivore and planktivore abundance were apparent with increasing coral cover. The varying responses of invertivore, corallivore and mixed diet feeders guilds demonstrated strong associations with coral cover, probably reflecting changes in the availability of their respective trophic resources during reef recovery. Thus, variations in coral cover probably influence fish communities through trophic pathways involving invertebrate food sources.

KEY WORDS: Reef fish community responses · El Niño disturbances

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INTRODUCTION

Coral reefs often serve as focal points for a high diversity of fishes. Use of reef resources varies widely, from transient species that move onto reefs intermittently during feeding forays, to species that

are permanent residents as juveniles and/or adults. These fishes depend on reefs for shelter, food, nest sites and numerous other resources (Jones & Syms 1998, Jones & McCormick 2002, Wilson et al. 2006, Pratchett et al. 2009, Montgomery 2011). Major disturbances to coral reefs may cause migrations and

increases in mortality and, therefore, serve as drivers of change in fish community composition and structure. Recent coral reef ecosystem decline is demonstrating a negative impact on coral reef fish communities worldwide (Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008, Graham et al. 2011). On smaller scales, several studies have examined the effects of tropical storms on reef fish communities in Hawaii, USA (Walsh 1983), and Jamaica (Woodley et al. 1981, Kaufman 1983), as well as extensive predation events by the crown-of-thorns sea star *Acanthaster* in Japanese (Sano et al. 1987, Sano 2001) and Australian (Williams 1986) waters. In the eastern Pacific, Grove (1985) reported on the responses of some Galápagos fishes to the severe 1982–1983 El Niño event, which greatly impacted all reef-building corals in the Galápagos Islands (Robinson 1985, Glynn 1990), and Wellington & Victor (1985) examined the effect of El Niño-related coral mortality on reef damselfish populations off Panama.

Globally, reef fish populations have exhibited varied responses to climate change, coral bleaching and mortality during the past 3 decades. Commonly reported responses have ranged from extreme declines in fish community diversity and abundances (Jones et al. 2004, Garpe et al. 2006, Pratchett et al. 2011), local species extinctions (Spalding & Jarvis 2002, Bonin et al. 2009, Wilson et al. 2009), major changes in fish community functional groups (Berumen & Pratchett 2006, Garpe et al. 2006, Wilson et al. 2009) and increased predation (Coker et al. 2009), to no discernible effects (Bellwood et al. 2006, but see Bellwood et al. 2012) and increases in diversity and abundances of some trophic groups (Lindahl et al. 2001, Wilson et al. 2006). These and other responses are reported in the meta-analyses of Wilson et al. (2006) and Pratchett et al. (2011). Three common responses with relevance to the present eastern Pacific study are: (1) declines in fish diversity on species-rich versus depauperate reefs, (2) declines in fish diversity on reefs that experience major versus minor structural habitat loss and (3) the variable nature of the timeframe for recovery following coral mortality.

Disturbance, as it interacts with competition and predation, is recognized as a chief factor in regulating the structure and dynamics of ecosystems (Connell 1978, Pickett & White 1985). Disturbance to coral reefs is particularly relevant in light of significant declines worldwide during the past 3 decades (e.g. Connell 1997, Hoegh-Guldberg et al. 2007, Oliver et al. 2009). In accordance with Connell's (1997) analysis that coral reef recovery is more likely following acute than chronic disturbances, the eastern Pacific

Uva Island reef, Panama, has exhibited consistent and steady recovery of coral cover over a 30 yr period following the transient 1982–1983 El Niño disturbance. This has allowed an assessment of reef fish trophic changes during an extended period of recovery. This poses an interesting question: Are the direction and pattern of trophic group change as coral cover decreases repeated in reverse as coral cover increases?

The 1982–1983 El Niño event that affected eastern Pacific coral reefs resulted in significant reductions of scleractinian corals (50 to 95% overall on numerous coral reefs) and corresponding increases in algal-covered reef substrates (Glynn 1990), changes in densities of epibenthic invertebrates (Glynn 1985, 1988) and an alteration in the population structure of endolithic bioeroders (Scott et al. 1988), leading to significant bioerosion and reduction of reef structural complexity (Eakin 1996, 2001, Reaka-Kudla et al. 1996). These alterations have been observed globally and have important implications for nektonic and crypto-benthic reef fish populations as variations in food availability and shelter may affect community composition, abundance, distribution and diversity (Pratchett et al. 2008, 2009).

The goal of this study was to examine how perturbations in coral cover influence associated reef fish species. Concurrent visual monitoring of live coral cover and fish assemblages at Uva Island reef over a 30 yr time span provided a rare opportunity to examine for patterns of change in fish community composition and structure, ostensibly in response to the steady increase in live coral cover that occurred since the 1982–1983 El Niño disturbance. We examined the temporal trajectories of several components of the Uva Island reef fish community including: (1) species richness (number of different taxa per transect), (2) total fish density (species combined) and (3) densities of each of 6 trophic groups (piscivores, herbivores, planktivores, facultative corallivores, benthic invertivores and mixed diet feeders). Next, we investigated the nature of correlation, if any, between coral cover and each of the above fish community metrics by fitting linear, parabolic and asymptotic regression models. Given that coral cover increased from <2 to ~35% over the study period, it was possible to examine the fish data for consistency with several previously suggested hypotheses. Among these were that corallivore and herbivore densities would be positively and negatively correlated, respectively, with live coral cover, while fish species richness would peak at some intermediate level (McClanahan et al. 2001, Pratchett et al. 2004,

Berumen & Pratchett 2006, Wilson et al. 2009). The opposite responses of coral-dependent fishes and fish herbivores are related to the changing availability of trophic resources, i.e. live coral cover and benthic algae, respectively. Community-wide fish species richness would be expected to increase at some intermediate level of disturbance when diverse resources are available for different trophic guilds. In light of the demonstrated high abundances and persistence of motile cryptofaunal communities in degraded pocilloporid frameworks and rubble (Enochs et al. 2011, Enoch 2012, Enoch & Manzello 2012a,b), we also assessed temporal variations in the densities of mixed diet feeders and benthic invertivore fish guilds.

MATERIALS AND METHODS

Study site

All surveys were conducted at the Uva Island coral reef (7° 48' 46" N, 81° 45' 35" W) in the Pacific Gulf of Chiriquí, Panama. This reef is ~2.5 ha in planar area and is situated in a sheltered, NW-facing embayment (Fig. 1A,B). The principal framework-building corals are ramose, pocilloporid species, mainly *Pocillopora damicornis* and *P. elegans*. The most abundant massive corals are *Gardineroseris planulata*, *Pavona clavus* and *P. varians*, which are most commonly present as large colonies (~0.5 to 1.0 m diameter) on the lower reef slope or along the reef base. Five other zooxanthellate scleractinian corals and the hydrocoral *Millepora intricata* also occur on the reef, but these are relatively unimportant in terms of live surface cover. Further information on reef coral zonation and community structure at Uva Island before the 1982–1983 El Niño event is available in Porter (1972, 1974) and Glynn (1973, 1974a, 1976) and following the 1997–1998 event in Eakin (1996, 2001), Glynn & Maté (1997), Glynn et al. (2001) and Maté (2003).

Coral monitoring

Assessment of coral cover on the study reef began in 1974 (Glynn 1976) and continued to 2010. This was accomplished by fixed chain transect sites (n = 10 transects per survey period, 1974 to 2010) and by sampling fixed 1 m² plots (n = 11 plots per survey period, 1994 to 2010) as well as a single 4 × 5 m² plot (n = 1, with the 20 m² plot subdivided into 20 1 m²

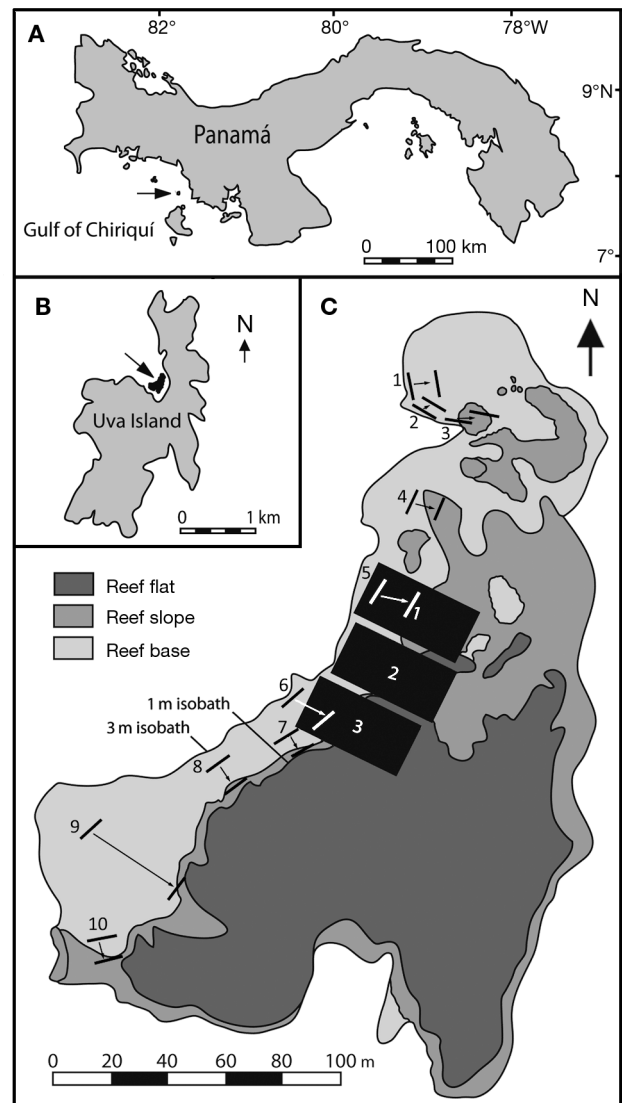


Fig. 1. Uva Island reef, Gulf of Chiriquí, Panama. (A) Arrow indicates Uva Island, Contreras Islands. (B) Arrow indicates Uva Island reef in NW embayment. (C) Disposition of the 3 permanent 20 × 40 m fish transects (black rectangles) in relation to 3 reef zones and depth contours (relative to mean lower low water tidal datum), and locations of twenty 10 m long chain transects. Arrows indicate new upslope chain transect locations in 1985, resulting in 20 total transects. This base map edition was constructed in February 1989 (Eakin 1996)

quadrats, 1984 to 2010). Chain transects were established along the ~350 m long forereef base zone between 3 and 5 m depth, relative to the mean lower low water (MLLW) tidal datum, in the mid-1970s from strictly random site locations determined from an Uva Island reef grid map with numbered axes (Glynn 1976). A second set of 10 fixed transects was located upslope from the reef base in 1985 to monitor denser coral cover at slightly shallower depths fol-

lowing the 1982–1983 mortality event (Fig. 1C). Most benthic sampling was conducted near, but not within the fish transects (see 'Fish monitoring') to minimize diver presence. During each of 20 survey periods, 10 to 20 chain transects were sampled. Coral species live cover and substrate type (e.g. rubble, turf algae, sponges) were enumerated according to the chain links (73 links m^{-1}) resting on these categories. The chain transect sampling was designed to determine the advance or retreat of live coral cover along the deep reef base and slope zones. Coral monitoring was carried out at different times during the 5 to 7 d sampling periods, usually 2 to 3 d before the fish monitoring.

The 1 m^2 plots were located at the northern end of the reef in the reef slope and base zones representative of the fish transect substrate cover. The benthic composition and cover of the 1 m^2 plots were drawn by divers underwater and then digitized using a flat-bed scanner, Adobe Photoshop and ImageJ software. Percent coral cover was determined by dividing the number of pixels representing coral within a quadrat by the total number of pixels in that quadrat. For each year of sampling of the $4 \times 5 \text{ m}^2$ plot, all 20 1 m^2 quadrats were mapped and their composition and cover determined as in the 1 m^2 plots above; these values were averaged to determine the total mean percent coral cover for each survey period. The $4 \times 5 \text{ m}^2$ plot was established by R. H. Richmond in the reef slope zone immediately following the 1982–1983 El Niño event when coral cover on the forereef was reduced to near-zero values. This location was selected to monitor live coral recovery; it is situated at 1 to 2 m depth, between and slightly overlapping fish transects, Transects 1 and 2 (see 'Fish monitoring'). Table S1 in the Supplement at www.int-res.com/articles/suppl/m495p233_supp.pdf summarizes all coral sampling records with information on time of sampling, season and number of samples completed.

Fish monitoring

Fish species richness and abundances were quantified by snorkeling along the NW (seaward) side of the Uva Island patch reef. During each survey, 3 permanent $20 \times 40 \text{ m}$ transects were sampled with the longest axis oriented in the NW–SE direction, i.e. along the depth gradient and perpendicular to the zonation of forereef corals (Fig. 1). The mean transect width estimate for visual measurement was $\sim 10 \text{ m}$. Substrate type and depth (relative to MLLW tidal datum) in each transect were mapped *in situ* at the

beginning and end of the study. The shallow ends of the transects were located in abundant pocilloporid stands (with scattered reef frame blocks) of relatively high relief; the central sections were dominated by live stands of *Pocillopora* spp. of low relief; the deep ends contained mostly coral rubble with a few isolated patches of massive corals. These substrate zonation patterns characterized the transect areas when sampling was first conducted. Live coral cover returned gradually from near complete loss following the 1982–1983 El Niño to pre-disturbance levels as of March 2010 (Fig. 2). Although the spatial distribution of substrate types differed markedly after nearly 30 yr, coral frameworks and rubble fields predominated at relatively shallow and deep sectors of all transects, respectively. All surveys were conducted at or near high tide. At this time, the shallow ends of the transects were 3 to 4 m deep and their deep ends 5 to 7 m. The spring tidal range in this area is 3.3 m. Surveys were conducted when the lateral visibility was $\geq 10 \text{ m}$. Snorkeling was carried out along the major axis of transects in a straight line pattern to permit a clear view of the transect boundaries (i.e. the NNE and SSW sides). Fish counts were made from the surface by snorkeling slowly, avoiding quick movements or splashing, down the long axis of each transect. Species and abundance of all visible (non-cryptic) individuals $\geq 15 \text{ cm}$ total body length present within the transects were recorded. Whitetip and bull sharks were infrequently observed on the reef but did not enter the transects during the survey periods. Sampling time was standardized at 8 min per transect (per 800 m^2). The sides of adjacent transects were separated by 3 m, and the time interval between successive visual sampling was $\sim 5 \text{ min}$. Fishes were not observed to be attracted to or repelled by the observer.

Trophic group assignments

For the purposes of this study, trophic groups were defined as follows: piscivores, consuming primarily or exclusively living fishes; planktivores, consuming primarily or exclusively plankton; herbivores, consuming primarily benthic algae; facultative corallivores, consuming primarily scleractinian corals; mixed diet feeders, consuming fishes and invertebrates; and benthic invertivores, consuming primarily motile benthic invertebrates.

Assignment of fishes to trophic groups (Table S2 in the Supplement at www.int-res.com/articles/suppl/m495p233_supp.pdf) was determined from feeding

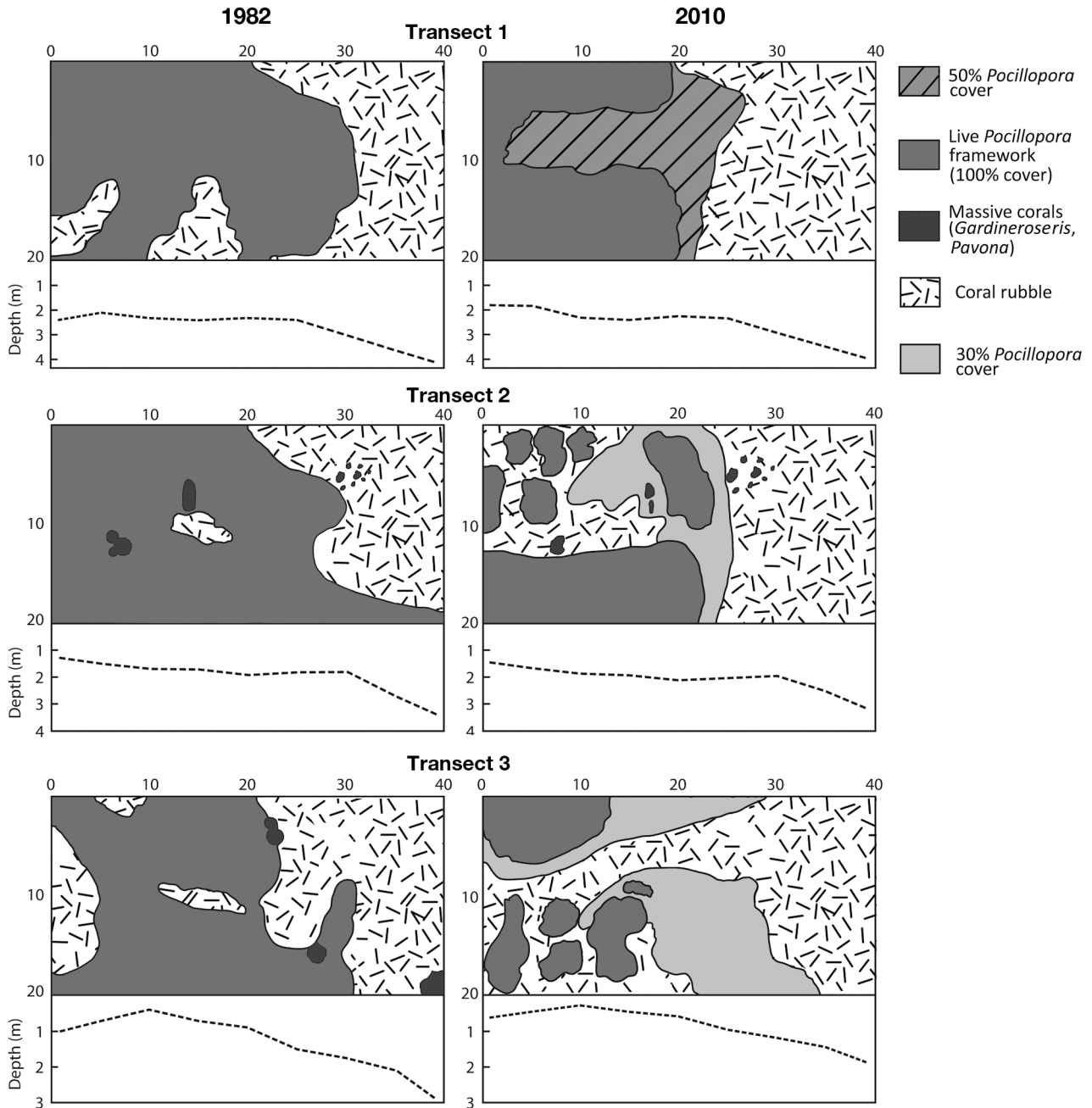


Fig. 2. Planar sketches of substrate cover (top diagram within each panel) and depth profiles (bottom diagram) along the 3 permanent 20 × 40 m fish transects at Uva Island, Panama, in 1982 and 2010

observations and gut analyses conducted on coral reefs in Panama over a 15 yr period and from existing literature. Dedicated feeding observations were made on 2 occasions (20 to 25 June 1975 and 14 to 15 May 1979) on the Uva Island reef with SCUBA in 5 × 5 m study plots located on the reef flat, upper fore-reef slope and reef base. Diurnal feeding activities were recorded continuously for 1 h by an observer at the outside corner of the study plot. Observations

were conducted at high and low water, in the early morning (06:00 to 07:30 h), midday (10:00 to 14:00 h), late afternoon (17:00 to 18:00 h) and at night (19:00 to 21:00 h). At night, a flashlight was used for 10 s at 2 min intervals to illuminate the plot, thereby totaling 5 min (per hour) of intermittent observations. Most species' feeding behaviors were supplemented by many hours of observations in other studies in Panama (e.g. Glynn et al. 1972, Glynn 1974b, 1985).

Data analysis

We constructed a standardized coral cover index (CCI) using generalized linear models (GLMs) following the methods described by Hinton & Maunder (2003) for catch-per-unit-effort standardization. We assumed that while the absolute values of coral cover differed by habitat and measurement method, and sampling methods types probably had different relative efficiencies, each measurement type accurately reflected an underlying overall trend in coral cover over the entire reef. To account for the differing (method specific) measurement efficiencies and the fact that not all methods were employed over the entire time series, an initial GLM model (SAS/STAT 1990) with the factors year, measurement method and interaction was applied. When the interaction term emerged as non-significant ($p > 0.14$, indicating that the different methods and habitats followed a similar trend over time), a main-effects-only model was applied. We then estimated an index of annual coral cover as the least square mean, which adjusts the overall annual coral cover value for the effects of missing method-specific measurements, primarily adjusting the early part of the time series higher to account for the higher relative values collected with the small quadrats. The resulting index cannot be taken as an absolute measure of overall reef coral cover; however, it provides a single relative measure that is useful to track changes over time and employ in correlation analyses.

To reduce problems of non-normality and heteroscedasticity, total fish and trophic group density data were \log_e -transformed prior to statistical analyses; coral cover percentages (proportions) were arcsine-transformed following Sokal & Rohlf (1981). Species richness values did not require transformation. Temporal pattern and coral fish correlation analyses were based on mean levels per season–year combination (e.g. dry 2000, wet 2000, dry 2001, etc.). To examine their temporal trajectories, mean species richness, total fish density (species combined) and density values for each guild (expressed per 800 m²) were plotted in chronological sequence. To examine for linear, parabolic or asymptotic relationships between coral cover and each fish community metric, ordinary least squares and nonlinear regression were performed using statistical software (SAS/STAT 1990). The linear, parabolic and asymptotic regression models, respectively, took the form $y = b_0 + b_1x$, $y = b_0 + b_1x + b_2x^2$ and $y = b_0[1 - \exp(x - b_1)]$, where y = fish metric, x = coral cover and b_0 – b_2 are the estimated regression coefficients. Model goodness of fit was first

judged on the basis of its statistical significance ($p < 0.05$), and its R^2 and/or Akaike's information criterion value.

Principal coordinates analysis (PCoA) was used to visualize multivariate community composition. Fish species abundances were averaged across all transects within each season of each year to standardize sampling effort. Data were square-root transformed, and analysis was conducted using a Bray-Curtis similarity matrix. Vectors showing Pearson correlations greater than 0.5 with untransformed species abundances were overlaid onto the Euclidean space of the PCoA plot.

RESULTS

Coral cover

Live coral cover assessed in all 3 sampling areas in 1984, 1 yr after the El Niño bleaching event, ranged from 0 to <1% (Fig. 3A). By 1994 and 1995, *Pocillopora* spp. corals recruited to the sampling areas, and increased to ~20% cover in reef flat and slope zones by 1997. In 2010, 27 yr after the first bleaching and mortality event, pocilloporid cover was ~35%, similar to pre-disturbance abundance values in the forereef slope in the 1970s (Glynn 1976). Nearly all of the coral belonged to *Pocillopora* spp. with <1% contributed by *Porites* and *Pavona*. From 2002 onwards, *Pocillopora* cover was often continuous with vertical growth and reef framework development in certain areas. Even though the 1982–1983 and 1997–1998 El Niño events were of comparable strength (Enfield 2001), only modest coral mortality occurred in the reef flat, slope and base zones during the latter disturbance. The standardized CCI allowed for the aggregation of multiple coral cover measurements into single annual values that collectively are representative of the overall coral cover trend over the period of record. Our index values increased 7-fold over the 27 yr interval sampled (Fig. 3B). Coral rubble increased in all transects, by about 27% overall (Fig. 2, Table 1).

Fish community

A total of 241 fish transects were sampled over the 30 yr monitoring period, 1980 to 2010 (Table S1 in the Supplement). Fishes recorded during this period are listed in rank order of the total number of individuals observed and assigned trophic groups in Table S2 in

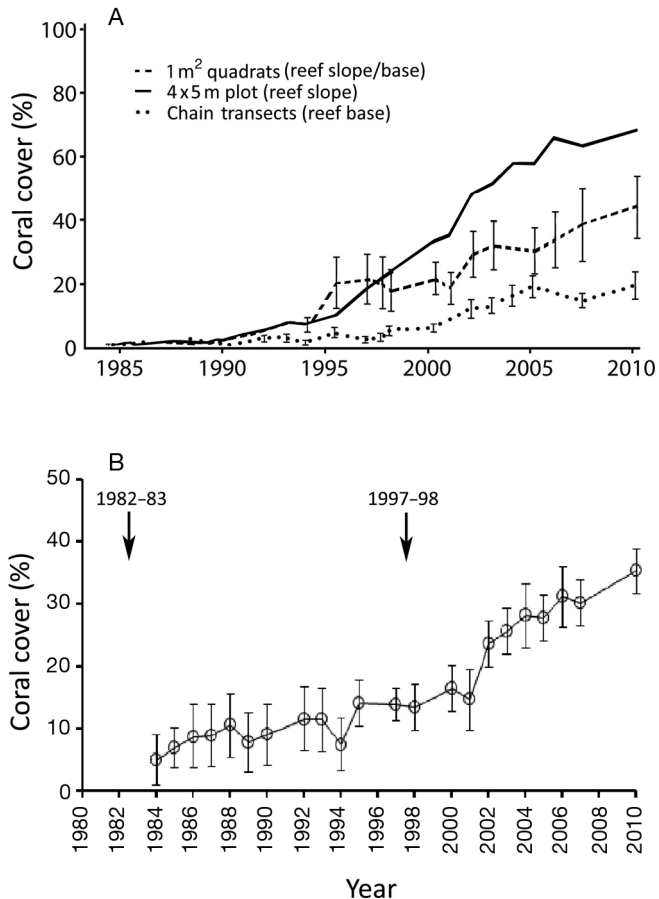


Fig. 3. Variation in live coral cover at the Uva Island reef, Panama, from 1984 to 2010. (A) Cover estimates determined from quadrat sampling in 4×5 m plot (solid line), 1 m^2 quadrats across reef slope and base zones (dashed line) and 10 m long chain transects along reef base (dotted line). (B) Standardized annual coral cover index obtained from data from all 3 sampling methods in (A). Shown are least squares mean and standard error values by applying a general linear model with 'Year' and 'Method' as factors (Hinton & Maunder 2003). Arrows denote El Niño thermal anomaly events

the Supplement. Of the 63 taxa, 58 were identified to species, 3 to genus and 2 to the family level. It is likely that the *Lutjanus* sp. and *Carangidae* sp. taxonomic groups were each represented by more than 1 species. All 22 of the numerically dominant ($n \geq 40$ ind.) taxa were identified to species level. The 2 predominant trophic groups were mixed diet feeders and benthic invertivores, which consisted of 20 member species each (Table 2). Numerically, these 2 groups made up nearly 70% of all individuals observed over the course of the study. Some species ranking high in abundance, e.g. *Lutjanus viridis* and *Paranthias colonus*, typically occurred in large schools that were often absent during sampling peri-

Table 1. Percent coral cover values in fish transects surveyed at Uva Island, Panama, in 1982 and 2010. Coral rubble was encrusted with coralline and filamentous algae; 100% live *Pocillopora* cover was intact framework constructed of interlocking colonies; total live coral cover included *Pocillopora* spp. and massive species (*Gardineroseris planulata*, *Pavona* spp. and *Porites lobata*)

Transect	Live <i>Pocillopora</i> (100, 50, 30%)	Massive coral spp. (%)	Total live coral cover (%)	Coral rubble (%)
1982				
1	66.8, 0, 0	0	66.8	33.2
2	66.3, 0, 0	0.4	66.7	33.3
3	54.0, 0, 0	1.4	55.4	44.6
Mean	62.4, 0, 0	0.6	63.0	37.0
2010				
1	36.8, 21.9, 0	0	58.7	41.3
2	32.4, 0, 14.4	1.3	48.1	51.9
3	20.8, 0, 28.6	0	49.4	50.6
Mean	30.0, 7.3, 14.3	0.3	52.1	47.9

Table 2. Summary of fish trophic group abundances ranked according to the total number of individuals observed over the course of the study

Trophic group	No. of species in group	Species in group (%)	Total no. of ind. observed	Ind. observed (%)
Mixed diet feeders	20	31.8	3888	44.8
Benthic invertivores	20	31.8	2009	23.1
Herbivores	9	14.3	1229	14.2
Facultative corallivores	3	4.8	927	10.7
Piscivores	7	11.1	374	4.3
Planktivores	4	6.4	253	2.9

ods. However, several abundant species, such as *Sufflamen verres*, *Arothron meleagris*, *Holacanthus passer* and *Scarus rubroviolaceus*, were consistently present during all sampling dates over the course of the study. A summary of fish-coral cover correlation results is provided in Table 3.

Total reef fish abundance (i.e. density, all taxa pooled) was relatively stable over the study period (Fig. 4A, Table 3) with mean density ranging from 20 to 50 ind. per transect (800 m^2). Mean species richness (Fig. 4B) ranged between 6 and 9 taxa observed per transect. The temporal trend for species richness was one of gradual increase until about 2001, followed by slow decline over the next 9 yr. While reef fish community densities were relatively stable regardless of coral abundance (Fig. 4C), species richness demonstrated a significant ($p < 0.002$) parabolic relationship with coral cover (Fig. 4D, Table 3). Rela-

Table 3. Regression statistics describing the shape, fit and significance of relationships between fish species richness and abundance (species combined and by trophic group) against coral cover. SSE: sum of squared errors; AIC: Akaike's information criterion; N/A: not applicable

Dependent variable Model	SSE	R ²	p-values	AIC	Best
Fish density (species combined)					
Linear	4.0519	0.0345	0.3737	-30.5523	None
Parabolic	3.5286	0.1592	0.0846	-31.4562	
Asymptotic	4.1776	N/A	N/A	-29.9105	
Species richness					
Linear	38.3871	0.0134	0.5817	16.66715	Parabolic
Parabolic	24.0664	0.3815	0.0015	8.862188	
Asymptotic	35.0222	N/A	N/A	14.74065	
Piscivores					
Linear	3.5273	0.0001	0.9771	-33.4640	None
Parabolic	2.9579	0.1614	0.0517	-35.1606	
Asymptotic	3.4872	N/A	N/A	-33.7039	
Benthic invertivores					
Linear	1.6703	0.2713	0.0155	-49.1625	Parabolic
Parabolic	1.2098	0.4469	0.0004	-53.9358	
Asymptotic	1.4135	N/A	N/A	-52.6675	
Herbivores					
Linear	4.9200	0.0009	0.8861	-26.4755	None
Parabolic	4.4280	0.1313	0.0829	-26.6880	
Asymptotic	4.8961	N/A	N/A	-26.5778	
Facultative corallivores					
Linear	2.1993	0.4099	0.0006	-43.3845	
Parabolic	2.1216	0.4307	0.3792	-42.1396	Linear
Asymptotic	2.1384	N/A	N/A	-43.9738	
Mixed diet feeders					
Linear	13.9736	0.2219	0.0174	-4.55448	
Parabolic	13.4436	0.2515	0.3618	-3.36637	Linear
Asymptotic	17.9597	N/A	N/A	0.715766	
Planktivores					
Linear	7.6224	0.0417	0.5881	-17.2820	
Parabolic	7.6224	0.0513	0.9896	-15.2821	None
Asymptotic	7.7220	N/A	N/A	-17.0094	

tively low mean values of 6 to 8 taxa per transect were observed at low and high coral cover, and maximum richness values of 8 to 10 between 10 and 20% coral cover (Fig. 4D).

Trophic groups

Mean trophic group densities varied widely over time, with trends of increase, decrease or no change depending on the group under scrutiny (Fig. 5). Regression statistics for the relationship between coral cover and density of the different trophic groups are denoted in Table 3. Densities of piscivores, herbivores and planktivores (Fig. 6A–C) appeared uncorrelated with live coral cover; however,

this was not the case for densities of the 3 remaining trophic groups (Fig. 6D–F). Two significant but opposite relationships were observed in the facultative corallivore (Fig. 6F, linear, $p < 0.0006$) and mixed diet feeders (Fig. 6D, linear, $p < 0.018$) trophic groups. Corallivores (predominantly *Arothron meleagris*) increased in density with increasing coral cover, while mixed diet feeders (predominantly *Lutjanus* spp. and *Holacanthus passer*) demonstrated declines in density at high coral abundance. Members of the benthic invertivore group (predominantly the balistid *Sufflamen verres*) demonstrated a highly significant (Fig. 6E, $p < 0.0004$) parabolic increase in density with increasing coral cover. Mean density increased from about 7 ind. at 0% cover and ranged between 12 to 15 ind. from 10 to 35% coral cover.

Species temporal trends

PCoA ordination explained 37.4% of the community variation (Fig. 7). Season was not observed to strongly affect community composition. Clustering was observed for fish communities sampled during 1987 to 1990, correlated with the abundances of *Seriola rivoliana*, *Mulloidichthys dentatus* and *Lutjanus viridis*. Clustering was also observed among communi-

ties sampled during 1991 to 2010, correlated with abundances of *Scarus rubroviolaceus*, *Sufflamen verres*, *Lutjanus argentiventris* and *Arothron meleagris*.

DISCUSSION

Patterns in community diversity

Despite a severe reduction in live coral cover following the 1982–1983 El Niño bleaching event, overall coral fish community densities fluctuated relatively little over the 30 yr sampling period. Species richness, however, increased as live coral cover rose from 0 to ~20% but then fell at yet higher coral cover values. A possible explanation for this pattern is that

Fig. 4. (A) Variation in total fish density (mean number of fishes per 800 m² transect) and (B) species richness (mean number of species per transect) at the Uva Island reef, Panama, from 1980 to 2010. (C) Non-significant linear correlation ($p > 0.05$) between total fish density and coral cover and (D) significant parabolic correlation ($p < 0.002$) between species richness and coral cover. Note that correlations were assessed by regressing \log_e -transformed fish density values against arcsine-transformed coral cover values. In (A) and (C), fish density values are expressed in logarithmic units and in (C) and (D) coral cover is expressed in original (percent cover) units. Solid and dashed lines indicate significant and non-significant relationships, respectively

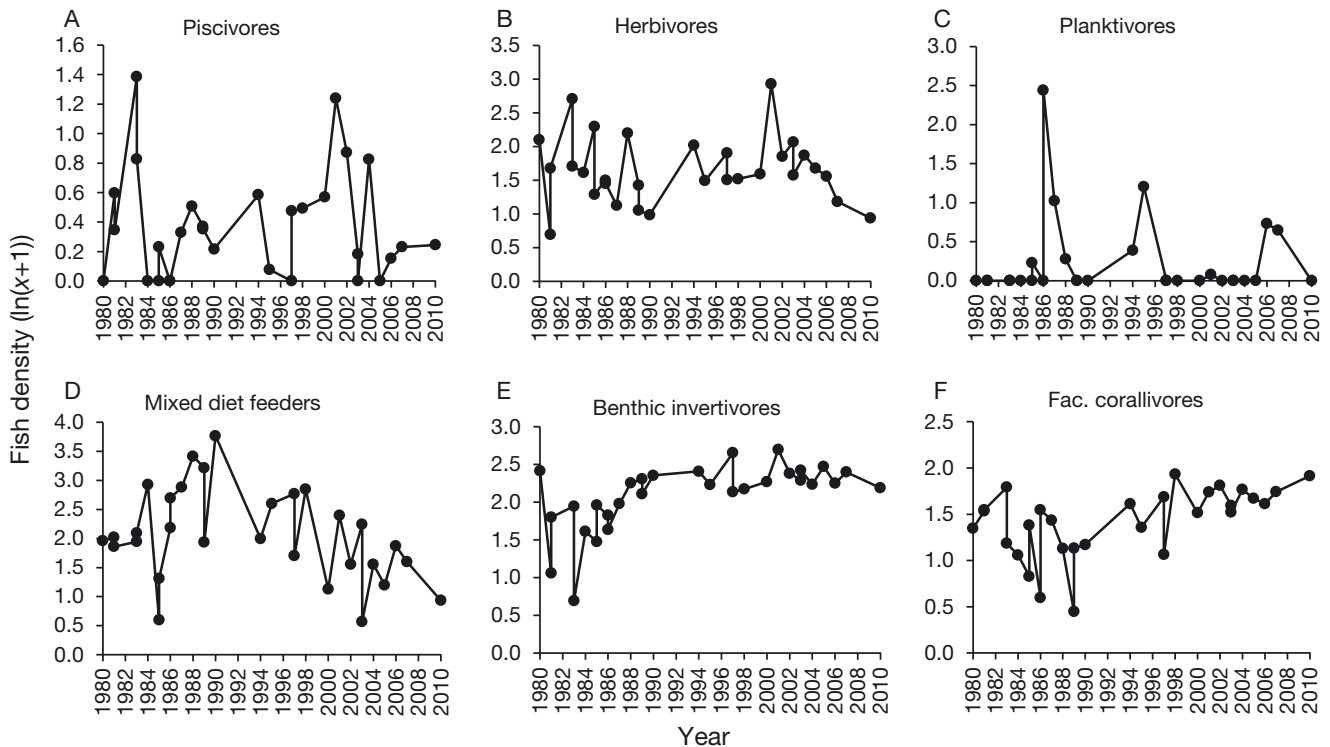
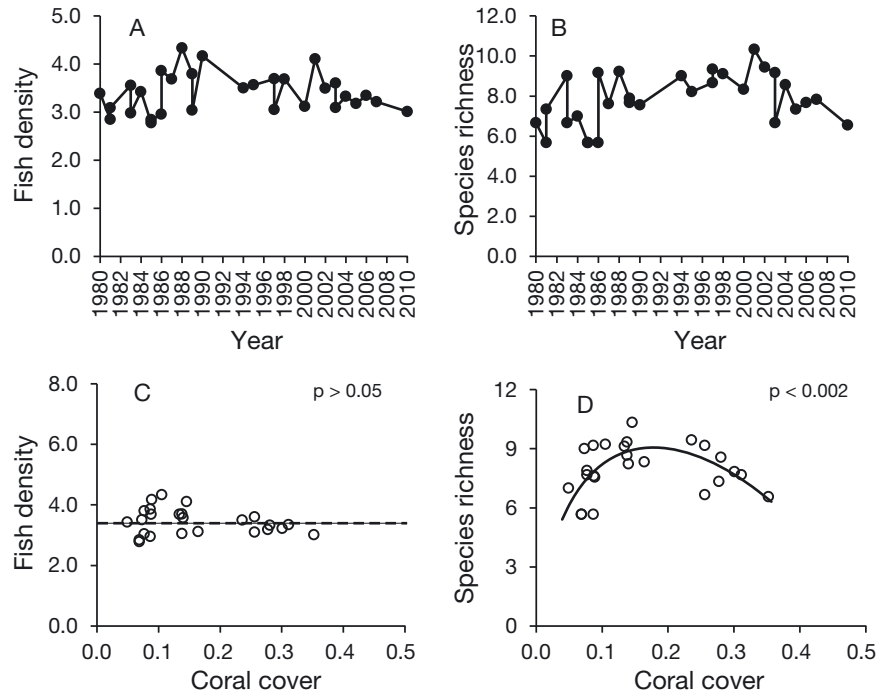


Fig. 5. (A–F) Changes in yearly mean fish trophic group densities from 1980 to 2010. Fish density values are \log_e -transformed. Fac.: facultative

fish diversity directly tracked the diversity of food and shelter resources, e.g. cryptofaunal abundances, coral-associated metazoans, algal turfs, shelter sites (Leviten & Kohn 1980), which also followed this par-

abolic trend. During reef framework degradation following El Niño-induced coral mortality, cryptofaunal community abundances increase and can serve to elevate prey availability for fish consumers (Enochs

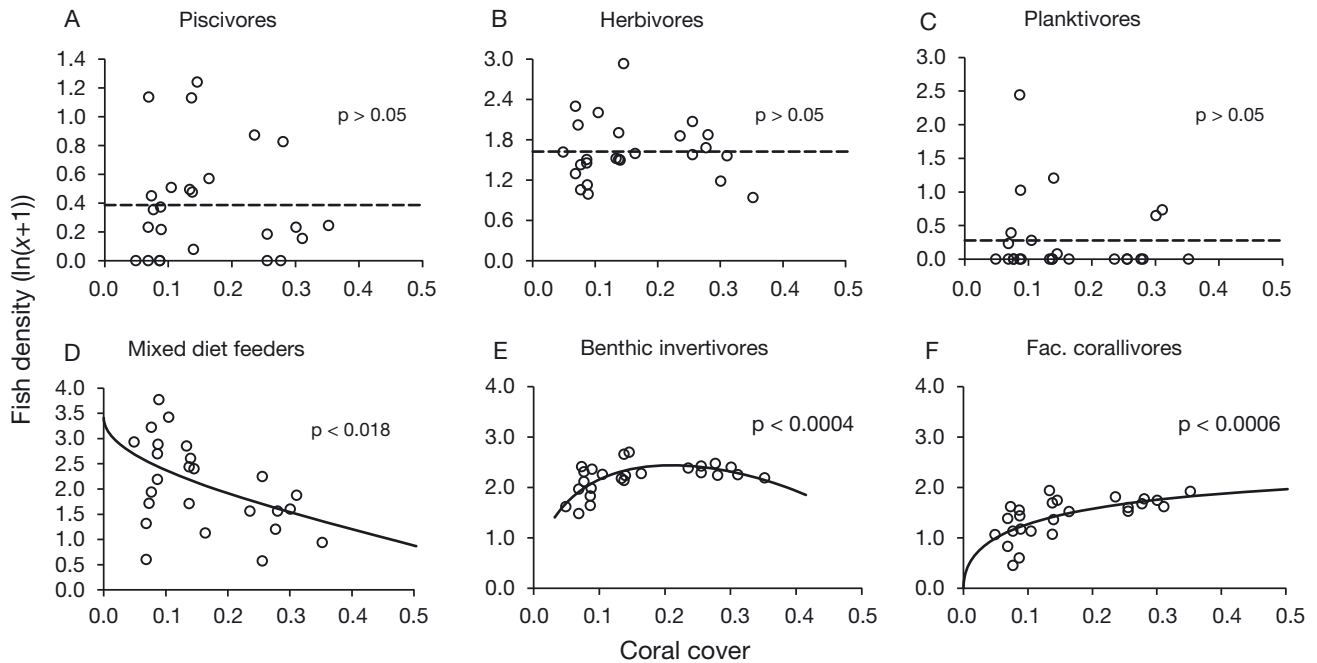


Fig. 6. (A–F) Correlation between fish trophic group density and percent coral cover. Note that correlations were assessed by regressing \log_e -transformed fish density values against arcsine-transformed coral cover values. Fish density values are expressed in logarithmic units, and coral cover is expressed in original (percent cover) units. Solid and dashed lines indicate significant and non-significant relationships, respectively. Fac.: facultative

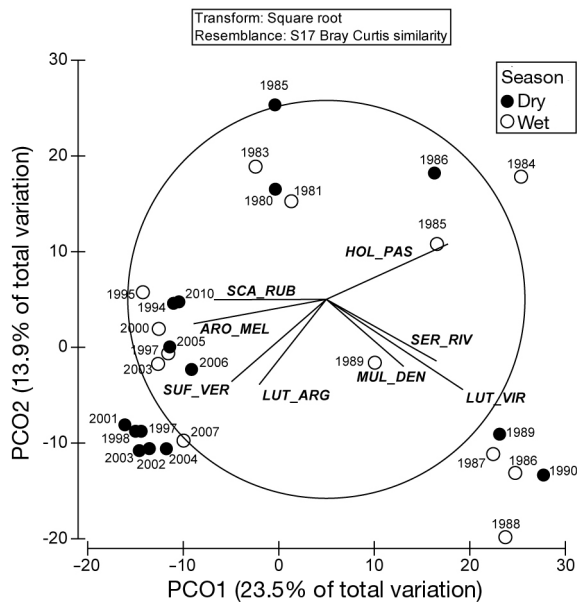


Fig. 7. Principal coordinates analysis showing the community composition of fishes at the Uva Island reef, Panama. Sampling year indicated next to each data point. Vectors show Pearson correlations with untransformed abundances of the associated species. *SCA-RUB*: *Scarus rubroviolaceus*; *HOL-PAS*: *Holacanthus passer*; *SER-RIV*: *Seriola rivoliana*; *LUT-VIR*: *Lutjanus viridis*; *MUL-DEN*: *Mulloidichthys dentatus*; *LUT-ARG*: *Lutjanus argentiventris*; *SUF-VER*: *Sufflamen verres*; *ARO-MEL*: *Arothron meleagris*. Length of each vector is proportional to the degree of correlation, with perfect correlation (1.0) denoted by a line that reaches the encompassing circle

& Manzello 2012a,b). Motile cryptic invertebrates (e.g. polyclad flatworms, polychaete annelids, crustaceans, molluscs and echinoderms; Glynn 2008, Enochs & Manzello 2012a), and cryptic fishes (e.g. apogonids, grammistids, blenniids, muraenids; Glynn 2006) attain maximum abundances in highly degraded reef frameworks and coral rubble habitats (Enochs & Manzello 2012b). These potential prey are more accessible to excavating macropredators, such as turtles, reef sharks, balistids, labrids, tetraodontids and carangids (Glynn 2008) in degraded and unstable substrates of lower porosity compared with intact reef frameworks (Enochs et al. 2011). The species-rich motile cryptofauna may also persist long after coral mortality (Enochs 2012), providing a constant food source during coral reef recovery.

In the case of the Uva Island study reef, forereef coral recovery began slowly in 1984 and progressed gradually to ~35% over a 27 yr period. An increasing biomass of trophic resources became available as live pocilloporid cover increased (Enochs & Hockensmith 2009) and, importantly, elevated calcification and the generation of carbonate skeletal materials that contribute to degraded rubble habitats.

An assessment of reef fish diversity on the Great Barrier Reef demonstrated maximum species richness with disturbance-related declines in coral cover from 40 to 60% to ~20% (Wilson et al. 2009). These

declines in coral cover also had a trophic underpinning but did not involve changes in the abundances of invertebrate prey and their fish predators as observed at the Uva Island reef site. In Australia, the greatest contribution to fish community species richness were the retention and increases in herbivorous species that fed on the epilithic algal matrix on degraded reef substrates. In Panama, the mixed diet feeder and benthic invertivore trophic guilds were the predominant contributors to fish community species richness. Thus, the large numbers of species in these guilds, combined contributing 63.6% to community composition, and their retention during coral loss are critical in sustaining reef fish community diversity in Panama. Losses of live coral cover in both studies were accompanied by declines in corallivore abundances. This had a greater effect in Australia, where obligate coral feeders comprised numerically 12.7% of the fish community (Wilson et al. 2009), whereas in Panama facultative corallivores made up only 4.8% of the reef fish community (Table 2).

Trophic group abundances

Marked changes in fish species composition, abundance and richness were generally lacking in this long-term study, which spanned 3 decades and 2 extreme disturbance events. Detailed analyses, however, revealed significant changes in fish densities of particular trophic groups as they relate to several essential resources associated with the coral habitat under investigation. Numerous studies have shown that obligate corallivores generally emigrate or die within weeks of the disappearance of their coral prey (e.g. Shibuno et al. 1999, 2002, Kokita & Nakazono 2001, Spalding & Jarvis 2002, Sano 2004). This has been demonstrated for species in the families Gobiidae, Pomacentridae, Monacanthidae and Chaetodontidae. The facultative corallivore *Arothron meleagris* (guineafowl puffer) showed relatively low abundances soon after coral cover loss but then increased in abundance to 20% live coral cover and remained at 4 to 5 ind. per transect for several years. This increase was presumably due to a recovering food source, which at the Uva Island reef was *Pocillopora* spp. (Glynn 2008). It is likely that the low abundances were influenced in part by the movement of puffers off the reef to communities of *Psammocora stellata*, a prey species they also consume (Guzmán & Robertson 1989). As *A. meleagris* is territorial, population densities do not exceed 50 to 60 ind. ha⁻¹. Even with these relatively low densities, however, the

feeding behavior of *A. meleagris* results in extensive colony breakage and non-consumption that can promote coral community recovery through asexual propagation (Guzmán & López 1991).

The linear decline in mixed diet feeder densities with increasing coral cover could have resulted from a greater sheltering effect of potential prey (Jones et al. 2004). As live pocilloporid cover increased higher than 50%, colonies began to fuse, forming interlocking frameworks and increased topographic complexity, thus creating shelter sites for motile invertebrates and small fishes. In addition, none of the mixed diet feeder species were ever observed excavating pocilloporid frameworks. Unlike the time-lag response in reef fish abundances observed in the Indian Ocean, which was brought about by significant declines in the structural complexity and shelter sites for fish recruits (Graham et al. 2011), this hypothesized effect does not seem likely on the Uva Island reef. Topographic complexity at the Uva Island reef site varied greatly among zones but did not show a significant overall decline (Eakin 2001). At the Uva Island reef, variations in fish abundances are more likely due to trophic interactions and not loss of structure. Immediately following the 1982–1983 El Niño event, high rates of bioerosion were observed on the Uva Island reef—declining a few years later along with sea urchin abundances (Glynn 1988, Eakin 1996, 2001). Many of the coral frameworks were left dead but remained largely intact. A large part of coral recovery occurred on the summits of dead reef frames.

An increase in the abundance of benthic invertivores over the post-El Niño 10 yr period (1984 to 1994) corresponded closely with the recovery of *Pocillopora* and the increasing availability of coral-associated prey (Enochs 2012). Pocilloporid corals are host to a high abundance and biomass of potential invertebrate prey (Stella et al. 2011, Enochs 2012). As about half of all known coral-associated invertebrates have an obligate association with their coral hosts, it is clear that coral loss would deplete an important trophic resource. Both facultative and obligate invertebrates associated with live coral undergo sudden high mortality with the bleaching and death of their hosts (Glynn et al. 1985, Caley et al. 2001, Baker et al. 2008). This mortality is due to the loss of host-generated trophic resources (mucus, coral tissue, zooxanthellae, interalialia), the emigration of invertebrates from corals (Castro 1978) and their increasing susceptibility to predation in bleached colonies (Coker et al. 2009). This study has demonstrated that the Uva Island fish invertivore guild begins to recover when live corals reach ~10% cover,

suggesting the re-establishment of the coral-associated trophic resource.

As the great majority of studies have reported on the changes of fish assemblages in response to coral decline, here we considered the responses of the 3 trophic groups that demonstrated significant changes during increasing coral cover. On the Uva Island reef, the mixed diet feeder guild exhibited decreasing fish densities with increasing coral cover. This trend was also recognized in reverse on several Indo-Pacific coral reefs, i.e. with decreasing coral cover, some fish trophic groups increased in abundance (Wilson et al. 2006, 2009). The Indo-Pacific trophic groups included epilithic algal matrix feeders and invertivores, which showed increases in abundance on reefs with low coral cover and minimal structural degradation. As in Panama, this positive response was probably attributable to a greater availability and diversity of trophic resources. Benthic invertivores and facultative corallivores demonstrated increasing abundances at higher coral cover and, conversely, declines as live coral decreased. The parabolic relationship with benthic invertivores, with an apparent decline in density at coral cover values exceeding 30%, was probably due to a lower proportion of reef substrate that could be excavated by balistids, labrids, tetraodontids and mullids in search of motile cryptic metazoan prey (Enochs 2012, Enoch & Manzello 2012a,b). Fishes in these families were frequently observed over rubble-dominated substrates with scattered live pocilloporid colonies. Facultative corallivores were most frequently observed over continuous patches of live coral.

Multivariate analysis of community structure

PCoA indicated a gradual, chronological shift in fish species composition and structure over the period of record (Fig. 7). For the most part, sampling events grouped into 1 of 3 clusters: 1980 to 1986, 1987 to 1990 or 1994 to 2010. Correlated with the community shift from the earliest to intermediate years were increases in the mixed diet feeder *Lutjanus viridis*, the piscivore *Seriola rivoliana* and the benthic invertivore *Mulloidichthys dentatus*. These 3 species are transient carnivores, and perhaps their frequent occurrence was associated with improved feeding opportunities under conditions of relatively low structural complexity. Correlated with the shift from the intermediate years to the latest were increases in 4 species: *Sufflamen verres* (benthic invertivore), *Arothron meleagris* (facultative coralli-

vore), *Lutjanus argentiventris* (mixed diet feeder) and *Scarus rubroviolaceus* (herbivore). Increasing abundances of the corallivore and invertivore follow the expected trophic group responses during coral recovery; however, the mixed diet feeder and herbivore demonstrated unexpected increases in abundance. This perhaps is a reflection of response diversity or varied species feeding behaviors within particular trophic groups of broadly similar ecological function (Pratchett et al. 2011). Also associated with the intermediate-to-later-years shift was a decrease in the abundance of *Holacanthus passer* (mixed diet feeder).

Although the Uva Island reef is subject to wet and dry seasonal conditions, the non-upwelling thermal environment is relatively constant, dissolved inorganic nutrients are in low concentration and organic production is low year round (D'Croz & O'Dea 2007). These conditions are probably in large part responsible for the absence of a conspicuous seasonal signal in the reef fish community.

CONCLUSIONS

On the Uva Island reef, the high abundance of fish carnivores and steady increase in coral cover since the severe 1982–1983 El Niño mortality event is in accordance with the regional trend reported by Edgar et al. (2011), namely highly protected marine areas (MPAs) possess a high abundance of carnivorous fishes, low densities of macroinvertebrates and high coral cover. This relationship was observed across the eastern tropical Pacific corridor at several sites from the Galápagos Islands to Costa Rica and Panama, including Uva Island in the Contreras Islands group. The high abundance of known fish predators of the corallivore *Acanthaster* (Glynn 1984) and the bioeroder *Diadema* (Eakin 2001) probably diminished the impact of these macroinvertebrates on coral recovery at Uva Island.

Globally, numerous coral reefs are in a dramatic state of decline (e.g. Gardner et al. 2003, Hoegh-Guldberg et al. 2007, Baker et al. 2008, Alvarez-Filip et al. 2009, Eakin et al. 2009). Many of these reefs are in varying stages of erosion, with significant loss of framework structures due to bioerosion and low coral recruitment (Glynn 2003, Graham et al. 2006, Riegl 2007). This has led to noticeable declines in topographic complexity with accompanying negative effects on fish communities (Wilson et al. 2006). The Uva Island reef in Panama demonstrated high rates of erosion, principally by echinoids, in the few years im-

mediately following El Niño-induced coral mortality. With the decline of echinoid abundances in the mid-1990s to the present (Eakin 2001, Wellington & Glynn 2007) most pre-1983 framework structures remained intact with rapid recruitment and growth of *Pocillopora* corals. This reef recovery has probably contributed to the relative stability of the Uva Island reef fish communities. The availability of off-reef resources may also have helped stabilize the overall abundance of reef fishes. Guzmán et al. (2008) have noted the widespread occurrence of non-reefal high diversity coral communities and associated fish assemblages as potentially important source populations in the conservation of coral reefs in the eastern Pacific. In further support of such a refuge effect, Benfield et al. (2008) reported that coral communities in the Pearl Islands, Panama exhibited more diverse and species-rich reef fish assemblages than coral reefs.

It is of interest to consider a crucial question posed by Pratchett et al. (2011): Are coral reefs with depauperate coral and fish assemblages more vulnerable to acute disturbances than reefs that exhibit high species richness? Relative to levels of coral loss, these workers found that declines in fish diversity were greatest in species-rich regions. An ordering of greatest to least impacts was from coral reefs in the Indo-Australian Archipelago to the western and central Indian Ocean, central Pacific and lastly Caribbean reefs. In terms of coral and reef fish species richness, the eastern Pacific Uva Island reef, with about 10 and 60 species, respectively, is one of the world's most depauperate reefs. Considering the observed disturbance-related changes at Uva Island with coral losses of 85%, and 0% change in fish community species richness, it is seen that this response is more akin to Caribbean fish faunas. This result stems in large part from the absence of specialist, coral-dependent fishes on the Uva Island reef.

This study is unique in that it examines the longest-running reef fish survey ever conducted in eastern Pacific waters. By virtue of its long duration, several patterns suggestive of cause-and-effect relationships between fishes and coral-associated resources (i.e. food and shelter) were revealed. That is, an important pathway by which coral bleaching alters reef fish trophic guilds is through the availability of invertebrate prey. Clearly, additional fish and coral monitoring at this site and others in the region are warranted to test for consistency in patterns within and among eastern Pacific reefs. Long-term manipulative studies are also needed, however, to test the correlative relationships that have emerged here and to identify more precisely the nature and magnitude of resource

dependency among reef-associated fishes. This will be important for advancing our understanding of how natural and anthropogenic factors will interact to shape reef fish communities in future decades.

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