

Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef

Nicholas A. J. Graham ·
Timothy R. McClanahan · Yves Letourneur ·
René Galzin

Received: 18 January 2006 / Accepted: 25 April 2006 / Published online: 7 July 2006
© Springer Science+Business Media B.V. 2006

Abstract Much of the western Indian Ocean suffered widespread loss of live coral in 1998 and interest is now focussed on the indirect effects of this coral loss on other components of the ecosystem, in particular fishes. However, it is just as important to identify changes in fish assemblages at locations that did not suffer coral mortality to understand local versus regional drivers. We surveyed benthic and fish communities on a reef flat in Mauritius five times between 1994 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore reef locations. The benthic community demonstrates

a clear trend along the coast, likely in response to a dredged water ski lane, but little change through time. Branching *Acropora* colonies dominate much of the live coral and best explain patterns in the fish assemblage ($P < 0.01$). Few changes in overall fish species richness through time were identified, and observed changes were within fishery target families rather than species reliant on live coral. Departure from expected levels of taxonomic distinctness suggests degradation in the community associated with the dredged ski lane. Non-metric multi-dimensional scaling of the fish assemblage demonstrates a similar pattern to that seen in the benthos; greater differences along the coast (Global $R = 0.34$) than through time (Global $R = 0.17$) and no trend between reef positions. SIMPER analysis identified two species of *Stegastes* as the main drivers of trends in the MDS plot and the most dominant of these, *S. lividus*, appears to be reducing species richness of the remaining fish community. The study highlights Mauritius as a regional refugia of thermally-sensitive corals and specialised fish, suggesting a need for careful management.

N. A. J. Graham (✉)
School of Marine Science & Technology, University
of Newcastle, Newcastle-upon-Tyne, NE1 7RU, UK
e-mail: n.a.j.graham@ncl.ac.uk

T. R. McClanahan
Wildlife Conservation Society, Marine Programs,
Bronx, NY 10460, USA

Y. Letourneur
Centre d'Océanologie de Marseille, UMR CNRS,
Université de la Méditerranée, 6540, Campus de
Luminy, Case 901, 13288 Marseille Cedex 09, France

R. Galzin
FRE 2935 CNRS-EPHE, Ecosystèmes Coralliens,
Université de Perpignan, 66860 Perpignan Cedex,
France

Keywords Climate change · Community structure · Reef fishes · Coral bleaching · Mascarene Islands · Tourism · *Stegastes* · Western Indian Ocean

Introduction

Coral reefs globally are suffering increasingly frequent events of thermally induced bleaching and associated mortality (Hoegh-Guldberg 1999; Sheppard 2003). Loss of live coral cover at this scale is expected to affect other components of the ecosystem (Walther et al. 2002), and studies of such impacts are growing in number. Much attention is focussed on likely ramifications for reef-associated fish assemblages. The majority of studies to date have been on the scale of a few months to years and indicate limited community change aside from species directly dependant on live coral or algae for food or shelter (Kokita and Nakazono 2001; Lindahl et al. 2001; Booth and Berretta 2002; Chabanet 2002; McClanahan et al. 2002; Sheppard et al. 2002; Spalding and Jarvis 2002; Sano 2004), whereas the longer term effects may be much greater (Jones et al. 2004; Garpe et al. in press; Graham et al. 2006). This may be due to lag effects associated with changes in physiological condition of fish (Pratchett et al. 2004) and collapse of the physical structure of the reef matrix (Garpe et al. in press; Graham et al. 2006). Understanding such effects and processes will clearly be essential for future use and management of affected reef systems.

When trying to understand the effects of bleaching on fish assemblages, it is just as important to assess change through the same time period at locations that did not suffer badly from bleaching, as it is to study sites where severe mortality occurred. This acts as a control for bleaching effects where other drivers in fish community dynamics can be identified in a region over the same time period. Ecological processes such as variable recruitment (Doherty and Williams 1988; Letourneur et al. 1998; Doherty et al. 2004), predation (Hixon 1991; Graham et al. 2003) or competitive interactions (Robertson 1996; Letourneur 2000; McClanahan 2000a) could be driven by natural processes and influence fish assemblages. They may also be driven by changes in habitat associated with effects such as eutrophication (McCook 1999), sedimentation (Rogers 1990), or fishing (Jennings et al. 1995; McClanahan and Graham 2005), or actions that may cause physical damage to the habitat (Brown et al. 1990;

Adjeroud et al. 1998). Identifying such processes and collecting baseline data at a location that has escaped much of the thermal damage characterised at other sites will provide information for future monitoring and management, particularly when future effects of bleaching at regional scales are expected to be significant (Sheppard 2003).

The warm phase of the El Niño Southern Oscillation (ENSO) event of 1998 resulted in the greatest global bleaching event on record (Hoegh-Guldberg 1999) and was particularly devastating to the western Indian Ocean (WIO) (Goreau et al. 2000) where it interacted with the warm portion of the Indian Ocean dipole (Saji et al. 1999). However, the effects varied greatly, with some locations, such as the Maldives and the inner Seychelles suffering 75–99% mortality, whereas other locations, such as Réunion and South Africa suffering low to negligible damage (Goreau et al. 2000; Obura 2005). Bleaching in Mauritius was also minimal with less than 10% coral cover effected in 1998 (Moothien Pillay et al. 2002; Turner and Klaus 2005), and 24% in 2004 (McClanahan et al. 2005). Post these two events coral cover is still dominated by thermally sensitive genus' such as *Acropora* and overall cover appears to have risen since a broad survey in 1992 (McClanahan et al. 2005).

This study assesses changes in benthic and fish communities on a narrow reef flat in north-west Mauritius that escaped much of the bleaching mortality experienced by other locations in the WIO in 1998. Temporal and spatial trends through a period 1994–2005, thus spanning the 1998, 2003 and 2004 bleaching events, are studied, aiming to identify any change in benthic and fish community structure. Alternative hypotheses are considered and, using a suite of multivariate tools, a case is built for the most plausible explanations for the observed trends.

Materials and methods

Study site and sampling techniques

Mauritius is located in the southwestern Indian Ocean, 200 km east of Réunion Island, and 800 km east of Madagascar, between latitudes

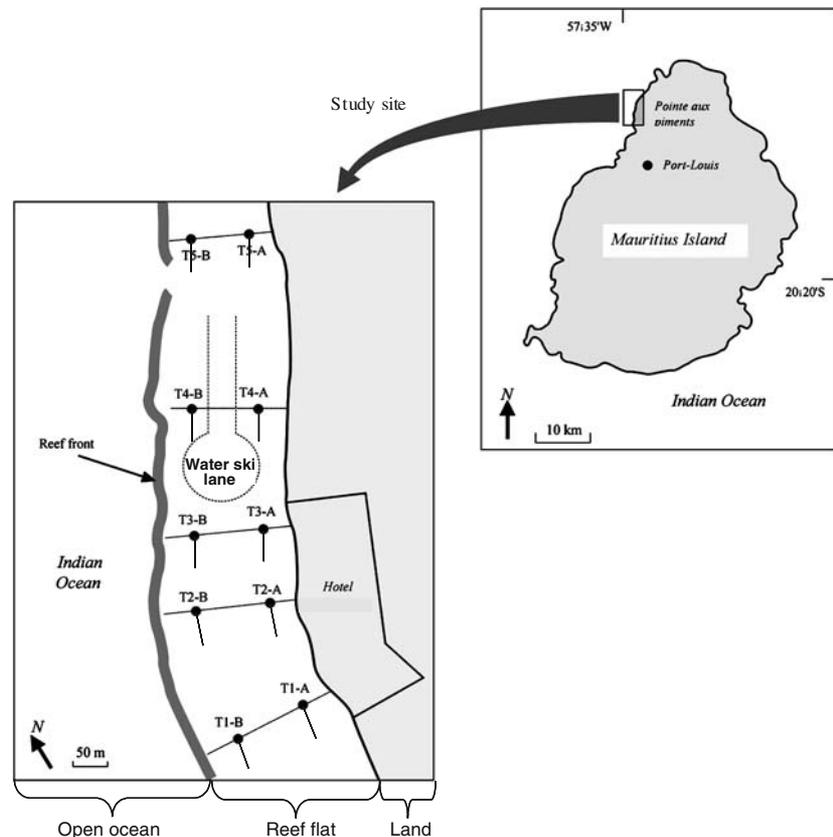
19.58 and 20.31°S, and longitudes 57.18 and 57.46°E. The study was conducted in the north-west coast of the island (Fig. 1), which is sheltered from the dominant southeast trade winds. The study site, Pointe aux Piments, is located 10 km north of the capital, Port-Louis, this part of the coast developed with hotels. The fringing reef, dominated largely by branching *Acropora* corals, is approximately 250 m wide and 1–2 m deep along this section of the coast, and largely used for recreational purposes by hotel guests. Within the study area a dredged water ski lane has been in active use since 1995 (Fig. 1). Fishing pressure around Mauritius is high (~1600 t yr⁻¹ from lagoons and reefs) and is thought to exceed maximum sustainable yields (Turner and Klaus 2005).

Data were collected on benthic and fish communities at ten stations over a 10 year period, where samples were collected in 1994, 1995, 1996, 1997 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore reef locations. Five transects

(T1–T5) perpendicular to the shore, each had a landward (A) and seaward (B) sampling station, where a 50 m transect tape was laid down parallel to the shore in a southerly orientation (Fig. 1). The study site comprised approximately 1 km of shoreline, each transect being separated by 200–350 m. Land sampling stations (A) were located 50 m from the shore, whereas sea stations (B) were ~200 m from the shore.

Full fish censuses were carried out by snorkel along 50*2 m belt transects at each of the ten sampling stations. Fish were identified to the species level (within 29 families) and abundance estimated. The discrete group sampling technique was used, whereby fish in different families and mobility groups were surveyed during different passes of the transect (four in total) to account for varying behaviours (Harmelin-Vivien et al. 1985). This process was repeated 3 times for each station and an average abundance for each species attained. A presence/absence survey was also conducted around each station area during a

Fig. 1 Map of the study site, indicating location in Mauritius, proximity of the ten sampling stations, direction of transects and location of dredged water ski lane. Adapted from Adjeroud et al. 1998



30-min timed swim. Although fish counts were conducted by three different observers over the five sampling years, all observers were highly experienced and observer variation is expected to be minimal (Williams et al. 2006; McClanahan et al. in review). After a fish census was complete the benthos along the same 50 m transect line was quantified using the line intercept method (Loya 1978), whereby the distance of tape occupied by the following substratum categories was quantified: live branching coral, live plating coral, live other coral and dead substratum. These data were converted into percent covers of each category for each of the ten stations surveyed within each year. Data were collected during peak daylight hours. Surveys in 1994, 1996 and 2005 were during the Austral winter, whereas surveys in 1995 and 1997 were during the Austral summer, however analysis of 1994–1997 data indicated little seasonal variation (R. Galzin unpublished data).

Data analysis

Due to the multi-species nature of the data and the design of the survey, the most appropriate analyses were multivariate (Clarke and Warwick 2001a). To assess patterns in benthic data from all stations in all years we used correlation-based principle components analysis. Data were $\log(x + 1)$ transformed to account for some right skewness detected in draftsman's plots and normalised. Eigenvectors were overlaid on the resultant plot to identify direction and contribution of the different variables to the patterns and to identify any correlation between variables. Percent total live coral was also quantified for each transect and landward and seaward sampling stations across the 5-year period. Two-way ANOVA's were used to assess differences through time associated with both trends along and away from the shore. Normality of data was examined with histograms and normal probability plots of the residuals. Homogeneity of variances were tested with Bartlett's test. Where a significant difference was found, Tukey's test identified those samples driving the differences.

Presence/absence fish diversity data from timed swims was pooled to the year level to represent the reef as a whole. Overall species rich-

ness (S) and richness within key families was calculated for each year.

We examined the taxonomic diversity of the fish assemblage for each station and year. Average taxonomic distinctness (AvTD) was calculated by assessing the degree to which species in a sample are taxonomically related, measuring the average path length between every pair of species based on a taxonomic tree (Clarke and Warwick 1998). Variation in taxonomic distinctness (VarTD) was assessed by measuring the evenness to which the taxa were spread across the tree (Clarke and Warwick 2001b). Funnel plots were constructed for both variables with expected mean and 95% confidence limits constructed from a simulation distribution using random subsets of the master taxonomy list (constructed following Helfman et al. (1997)). Any departure from expected values could thus be identified, where low AvTD and low to normal VarTD indicates degraded locations (Clarke and Warwick 2001b). General patterns related to our study design were tested using two-way crossed ANOVAs with the factors year and transect, as these were identified as the key sources of variation by Analysis of Similarities (ANOSIM).

Fish assemblages within each station in each year were compared using non-metric multidimensional scaling (MDS) based on Bray–Curtis similarity measures. Species abundance data were square-root transformed to down weight abundant species. Differences between years, transects and reef position (A–B) were tested using ANOSIM, which is a non-parametric permutation procedure. After identification of which transects and years (the 2 significant factors) differed the most (ANOSIM pairwise test output), SIMPER analysis was run on the data matrix. SIMPER decomposes Bray–Curtis dissimilarities between all pairs of samples to identify those species that contribute most to differences (Clarke and Warwick 2001a).

As SIMPER identified *Stegastes lividus* followed by *Stegastes nigricans* as the species contributing most to the significant trends in the MDS plot for both year and transects along the shore, bubble plots were used to overlay relative abundance of both of these species enabling identification of the trends they were contributing

to. As these species are both highly aggressive and territorial (Randall et al. 1997; Letourneur 2000), the influence that their abundance has on species richness of the rest of the fish assemblage was tested using linear regression analysis.

To link the benthic and fish data, bubble plots were used to overlay relative value of benthic variables on the fish species MDS plot. This allowed identification of any trends driven by the benthic variables. The BEST BIO-ENV routine was then run using Spearman rank correlation between benthic Euclidean distance and fish species Bray–Curtis similarity matrices to identify the benthic variable or group of variables that best explained the patterns in the fish species MDS plot (Clarke and Warwick 2001a). The significance of this result was tested using a permutation test.

Results

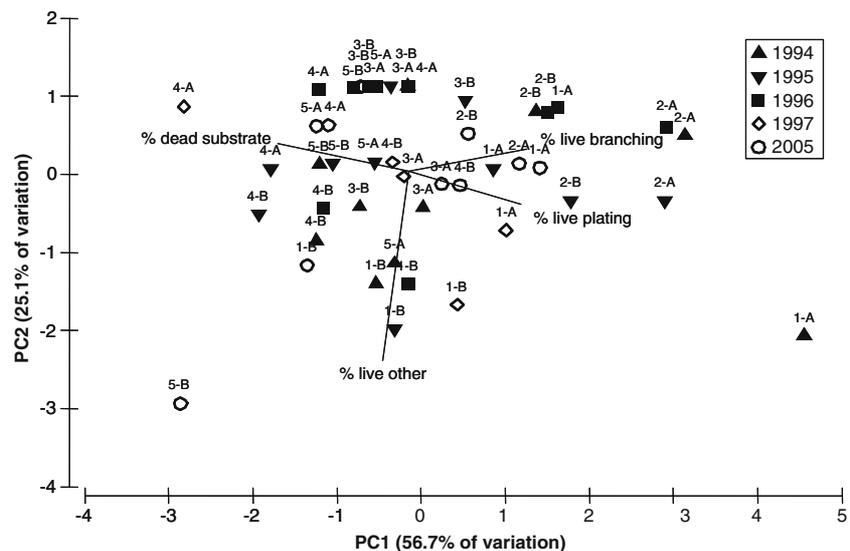
The benthos at this location in Mauritius experienced very little change through the 10-year study period. Principal Components Analysis indicates a trend along the shore line, from Transects 1 and 2 to Transects 4 and 5, but little change with time (Fig. 2). The main factors influencing this pattern along PC1 (~57% of variation) are higher cover of live branching and plating corals towards the

southern end of the study site, or away from the ski lane, and higher cover of dead substratum towards the north (Fig. 2). Percent cover of other live substratum (mainly massive corals) appears to be driving patterns along PC2, however this cover was often low. These trends are further highlighted by looking at overall percent live coral cover. The decline along the coast in a northerly direction is significant ($F_{4,37} = 13.9$, $P < 0.001$), Tukey’s test indicating that T1 differs from T4 and T5, and T2 differs from T3, T4 and T5, whereas no such trend is found through time ($P = 0.70$) (Fig. 3a). The greater cover at near shore locations compared to seaward locations (A–B) in 1994 was not nearly as great in subsequent years, and the overall difference between sites A and B and through time is not significant ($P = 0.15$ and $P = 0.85$) (Fig. 3b).

The timed swim presence/absence surveys demonstrate remarkable stability in overall fish species richness through time (Table 1). Stability is consistent in nearly all the key families involved, including those dependant on live coral such as the chaetodontids. Notable declines in number of species are seen for lethrinids, lutjanids (though both were already in low number) and in particular serranids, all of which are common fishery target species (Table 1).

Conversely, at the level of stations, a number of samples depart negatively from the expected

Fig. 2 Correlation-based Principle Components Analysis of $\log(x + 1)$ transformed and normalised environmental data



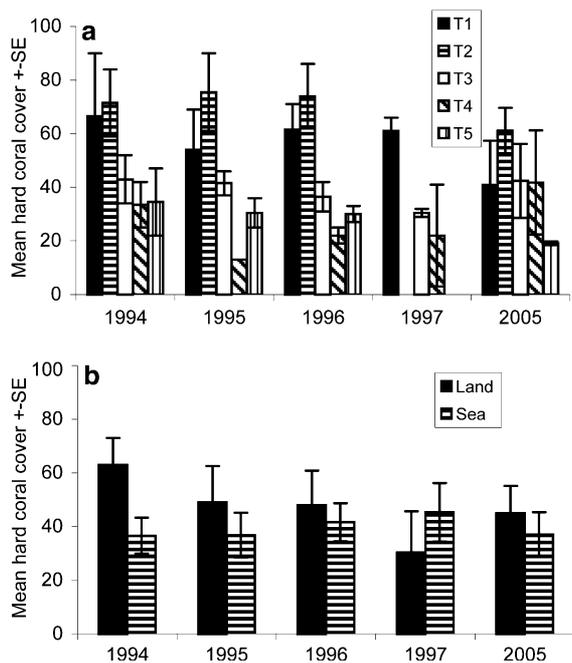


Fig. 3 Percent cover of total live coral in (a) each year by transect and (b) each year by position from the shore

values of AvTD, suggesting some samples may be taxonomically depauperate (Fig. 4a). The only significant decline in the ANOVA model was for the factor year ($F_{4,25} = 3.22$, $P = 0.03$) and Tukey's pairwise comparisons indicate that this was influenced by lower values in 1997 versus 2005 ($P = 0.03$). Much less departure from expected

Table 1 Reef fish species richness from presence/absence timed swim data at level of whole assemblage (S) and within selected families

	1994	1995	1996	1997	2005
Total species richness (S)	104	102	110	99	101
Acanthuridae	7	9	8	8	7
Balistidae	2	1	2	1	3
Chaetodontidae	8	9	8	11	10
Holocentridae	3	4	5	4	3
Labridae	19	22	21	24	20
Lethrinidae	3	3	2	2	2
Lutjanidae	1	0	2	0	0
Monacanthidae	4	5	5	3	5
Mullidae	6	5	4	5	7
Pomacentridae	13	13	12	12	14
Scaridae	7	7	9	7	6
Serranidae	7	3	4	4	1
Siganidae	1	1	1	0	1

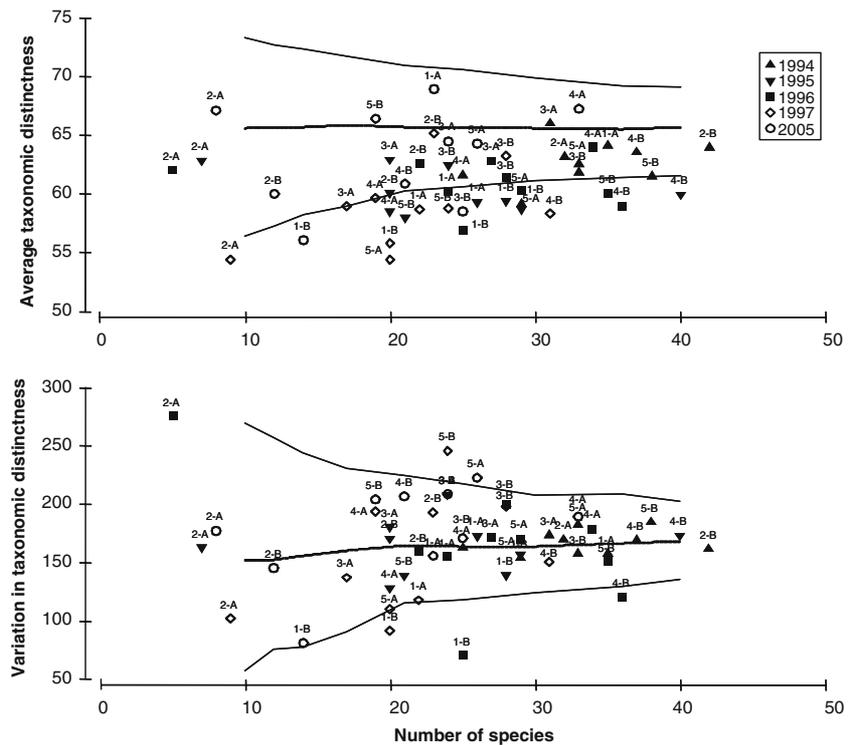
values is noticed for VarTD (Fig. 4b), however a weak significant difference is detected for the factor transect ($F_{4,25} = 2.95$, $P = 0.04$), which is driven by a difference between Transect 1 and 3 ($P = 0.04$).

The fish species MDS plot indicates a very similar pattern to that found in the benthic PCA, some difference in years, but an overall trend along the coast from T1 and T2 to T4 and T5 (Fig. 5a). Samples from T1 and T2 are located in the bottom left side of the plot for all years, with samples from more northerly transects located to the top and right of the plot. This pattern is highlighted by the ANOSIM results, with significant differences for Year and Transect, but not Position on the reef (Table 2). Pairwise testing identified 1994 departing from all other years and 2005 from 1996 and 1997. Pairwise tests for Transect identified T1 departing from T4 and T5, and T2 from T4 (Table 2).

SIMPER analysis, for the 2 years and transects that differed the greatest from one another, highlighted that *Stegastes lividus* followed by *S. nigricans* were contributing by far the greatest to the observed differences (Table 3). Pomacentrids and more mobile scarids, acanthurids and wrasses make up the majority of the remaining species contributing 60% of the differences (Table 3). The trends driven by *S. lividus* and *S. nigricans* are highlighted by the bubble plots (Fig. 5b, c), the former being more dominant in the southerly sites that have greater live coral cover (Fig. 3a), whereas the latter is more dominant in the northerly sites. Furthermore, and likely exacerbating the patterns, is that the abundance of *S. lividus* but not *S. nigricans* is negatively correlated with overall fish species richness, though the trend is not consistently significant between years (Fig. 6).

Bubble plots overlaying percent cover of benthic variables on the fish species MDS further highlight these trends; samples to the bottom left of the plot being dominated more by live branching and plating corals (Fig. 5d, f), whereas samples to the right of the plot have a greater cover of dead substratum (Fig. 5e). Rank correlation of benthic variables to the fish species data indicates that the best single and significant (BioEnv Rho statistic: $P < 0.01$) benthic variable

Fig. 4 Funnel plots of average taxonomic distinctness (a) and variation in taxonomic distinctness (b) of each sampling station (belt transects) within each year with mean and 95% confidence limits from expected values using master taxonomy aggregation file



driving the patterns in the fish data is the percent cover of live branching coral ($r = 0.36$).

Discussion

Coral and fish communities appear to have experienced very little change over 10 years at this location in Mauritius, in contrast to other studied sites in the western Indian Ocean (Lindahl et al. 2001; McClanahan et al. 2002, Sheppard et al. 2002; Graham et al. 2006). Indeed the dominant trend at the study location appears to be along the coast, rather than through time. This suggests that the benthic community has changed very little through the 1998 ENSO event and the more minor 2003 and 2004 bleaching events. Unfortunately, reefs were not sampled between 1997 and 2005, which raises the question as to what happened during this sampling hiatus. The 1998 ENSO event resulted in less than 10% of coral colonies bleaching in Mauritius (Moothien Pillay et al. 2002). The 2003 bleaching event was most evident on the southwest of the island and a cyclone was implicated in the recovery of

bleached corals (Ahamada et al. 2004; Turner and Klaus 2005). In 2004, 24% of corals bleached (McClanahan et al. 2005), however recovery was again high (Ahamada et al. 2004) and coral cover was higher than surveys conducted in 1992 (McClanahan et al. 2005). Although we can not discount the possibility of rapid re-colonisation and recovery of the reef with the predominant fast growing *Acropora* colonies, the above studies and the remarkably similar cover estimates through time suggest a minor influence from bleaching events. Furthermore, *Acropora* is one of the most susceptible genera to thermal stress in the region (McClanahan et al. 2001, 2004) and has experienced large declines in many other locations (Goreau et al. 2000; McClanahan 2000b; McClanahan et al. 2001; Sheppard et al. 2002). Indeed, branching and plating corals now make up less than 1% of the benthos in the inner Seychelles, a decline of over 95% (Graham et al. 2006). Study and protection of this apparent refugia of sensitive, habitat forming corals in Mauritius is important given predictions of further widespread degradation of the region in coming decades (Sheppard 2003).

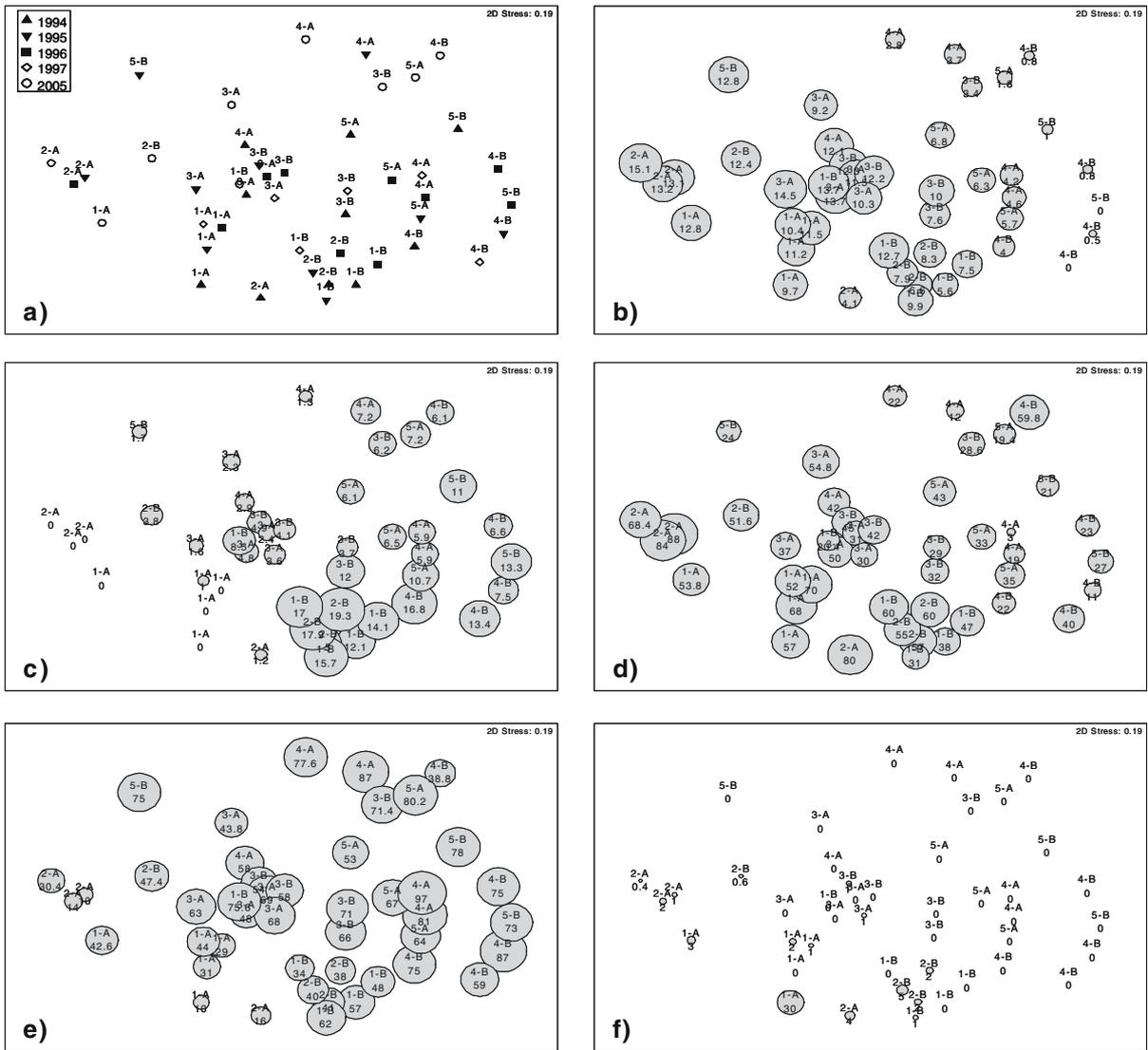


Fig. 5 Non-metric Multi-Dimensional Scaling (MDS) plot of fish assemblages at each of the ten stations (belt transects) within each of the five sample years based on Bray-Curtis similarity measures (**a**). Bubble plots for *Stegastes lividus* (**b**) and *Stegastes nigricans* (**c**) over species MDS sample points indicating patterns driven by their

presence. Abundance at each sample given below station name (scale of bubbles: 0–20). Bubble plots for cover of branching coral (**d**), dead substrate (**e**) and plating coral (**f**) indicating which patterns in the species MDS are driven by these benthic variables. Percent cover at each station given below station name (scale of bubbles: 0–100%)

The observed trend in benthic composition along the coast within the study location is most likely due to the dredged water ski lane that has fragmented the reef flat in this section, likely still results in increased sediment loads and is subject to high recreational use. The disparity between near shore and sea (A–B) stations that was quite apparent and a dominant driver of trends in 1994 (Adjeroud et al. 1998) is not as great on a tem-

poral scale. Given the dominance of the reef flat by fast growing branching *Acropora* corals, it is possible that this may be due to some recovery following completion of the ski lane (1993–1994).

Although overall species richness of the reef fish assemblage has remained stable through this time period, the richness is fairly low compared to studies in nearby islands such as Réunion (Lettourneur 1996a), Madagascar (Harmelin-Vivien

Table 2 Analysis of Similarity (ANOSIM) outputs for the fish sampling stations

Factor	Global R	Significance	Pairwise test
Year	0.17	$P < 0.01$	1994 diff to all, 2005 diff to 1996 and 1997
Transect	0.34	$P < 0.01$	T1 diff to T4 and T5 T2 diff to T4
Position	0.02	ns	

Global and pairwise test results given for each of the three factors in the design

1989) and Mayotte (Letourneur 1996b; Chabanet 2002). This is likely due to the surveys being restricted to the reef flat and because the reef is narrow along this section of the coast (Adjeroud et al. 1998), although reef flats of a similar width in Réunion had higher species richness (Letourneur 1996a). It could also be due to anthropogenic stress on the system through past dredging of the water ski lane and ongoing effects of fishing and recreational use. Indeed, many samples depart from expected values of taxonomic distinctness, and common fishery target species, in the families Lutjanidae, Lethrinidae and Serranidae, are missing. The years driving the main difference in taxonomic distinctness were 1997 and 2005, with 1997 having lower values. Although coral cover was lowest in this year, the magnitude was small and it is hard to ascribe causation to this trend. Indeed, the stability of species richness from the presence/absence survey within families that often feed on (Chaetodontidae) or dwell in

(Pomacentridae) live coral indicates that these patterns are likely not driven by ENSO effects on the benthos, in contrast to other locations in the region (Spalding and Jarvis 2002; Graham et al. 2006). As samples from all years demonstrated departure from expected values, it is more likely that long-term effects are causing the trends.

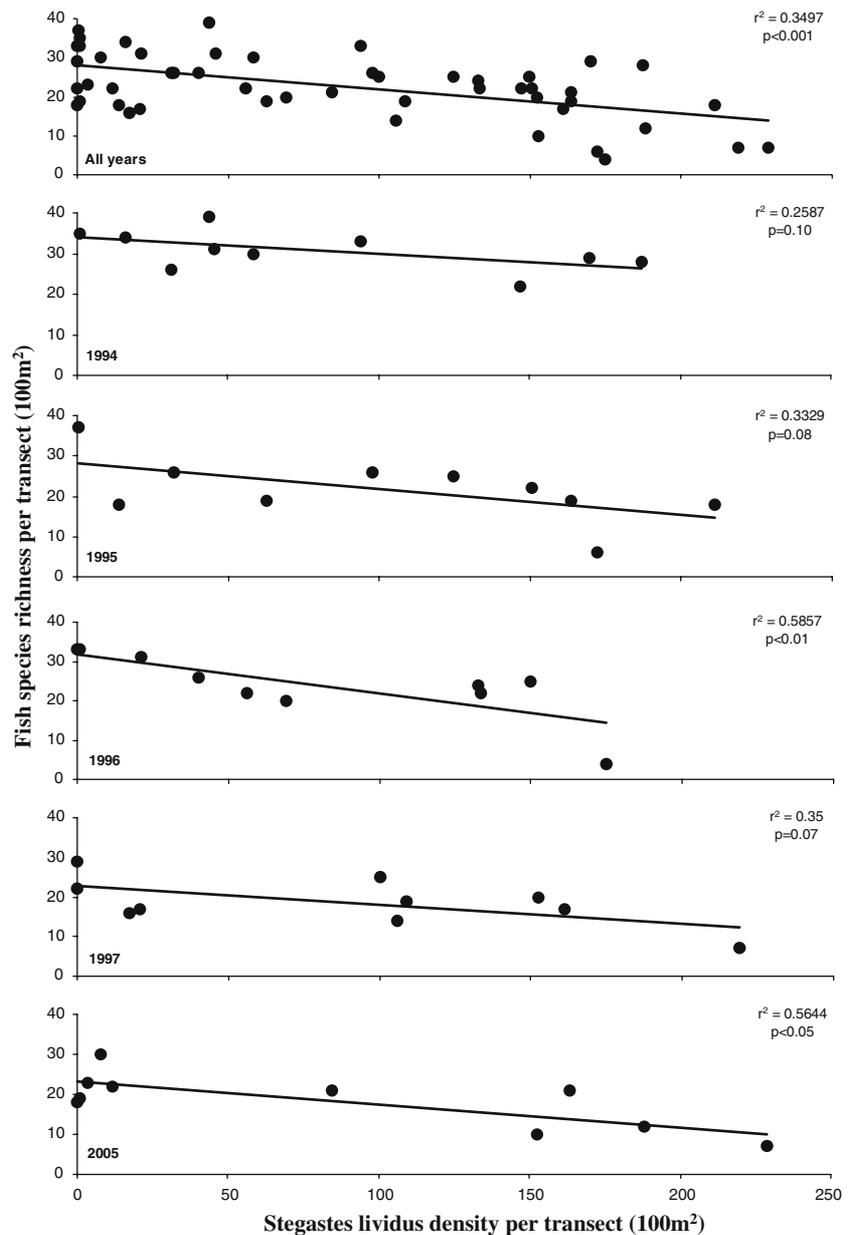
The overall pattern in the fish community from MDS analysis is remarkably similar to that for the benthos, with the greatest differences identified along the coast (Global $R = 0.34$) as apposed to time (Global $R = 0.17$). This lends further support to our conclusion that the ecosystem has remained stable through the ENSO event and other factors are likely responsible for the observed changes. The heavy fishing pressure in Mauritius (Turner and Klaus 2005) and the apparent loss of diversity in key fishery target groups, of which many species are piscivores, may be driving trends related to predation pressure. Studies of predator control on reefs indicate

Table 3 SIMPER outputs for greatest pairwise differences in year and transect identified by ANOSIM

Year (1994 and 2005)		Transect (T1 and T4)	
Species	% Contribution	Species	% Contribution
<i>Stegastes lividus</i>	10.64	<i>Stegastes lividus</i>	12.03
<i>Stegastes nigricans</i>	10.07	<i>Stegastes nigricans</i>	10.84
<i>Dascyllus aruanus</i>	4.77	<i>Scarus psittacus</i>	6.56
<i>Chromis viridis</i>	4.21	<i>Dascyllus aruanus</i>	4.78
<i>Chlorurus sordidus</i>	4.18	<i>Chlorurus sordidus</i>	3.92
<i>Ctenochaetus striatus</i>	4.15	<i>Scarus scaber</i>	3.36
<i>Halichoeres scapularis</i>	2.78	<i>Ctenochaetus striatus</i>	3.26
<i>Stegastes limbatus</i>	2.65	<i>Chromis viridis</i>	3.18
<i>Scarus scaber</i>	2.55	<i>Halichoeres scapularis</i>	2.79
<i>Acanthurus triostegus</i>	2.41	<i>Calotomus spinidens</i>	2.69
<i>Gomphosus caeruleus</i>	2.03	<i>Thalassoma hardwickii</i>	2.36
<i>Zebрасoma scopas</i>	2.02	<i>Stegastes limbatus</i>	1.91
<i>Acanthurus nigrofuscus</i>	1.95	<i>Stethojulis bandanensis</i>	1.76
<i>Stethojulis bandanensis</i>	1.86	<i>Epinephelus merra</i>	1.68
<i>Chrysiptera unimaculata</i>	1.82		
<i>Oxymonacanthus longirostris</i>	1.79		
<i>Parupeneus macronema</i>	1.43		

Species that contributed 60% of the overall difference are listed in descending order of most contribution

Fig. 6 Regressions of *Stegastes lividus* density against fish species richness per station (belt transects) overall and for each year separately. R^2 and regression analysis results given on plots



trends both at the level of single species (Graham et al. 2003), aggregated by size class (Dulvy et al. 2004), and evidence suggesting there is a direct relationship between gape size of the predator and size of prey (Mumby et al. 2006). Recruitment has also been shown to drive variation in fish assemblages on reefs (Doherty and Williams 1988), particularly following mass-events (Lettourneur et al. 1998). Given the time between surveys and the narrow spatial scale over which the study has been conducted, variable recruit-

ment could influence the small temporal patterns detected, but is unlikely to be driving the larger trends along the coast. Given that the availability of habitat types has not altered a great deal, competition for resources among fish species may be expected to have remained stable through this time period. However changes in certain dominant species, such as *Stegastes*, could well be causing changes in the rest of the assemblage.

The coastline adjacent to the study site has experienced rapid development for tourism in the

last 10–15 years, and this is likely exerting stress on the reef ecosystem. Along the 1-km stretch of coast, two large hotel complexes actively use the reef for water sports activities. High use of reefs for snorkelling and diving can have detrimental effects (Hawkins et al. 1999; Zakai and Chadwick-Furman 2002). In this case, however, the greatest effect is likely to be from the dredged water ski lane through the middle of the reef flat. Increased pollution, sedimentation and changes in current regimes are all likely to be effecting both the coral and fish assemblages, and may be partly responsible for the changes through time. However, the greatest effects of the ski lane appear to be along the coast in the survey area.

Both the benthic and fish communities display the strongest patterns along the coast from Transects 1 and 2 to Transects 4 and 5, with greater live coral to the south end of the study site away from the dredged area. Branching coral is likely to be causing the observed patterns in the fish assemblages given that it was best at predicting the patterns in the fish assemblage structure and because it provides important three-dimensional structure (Bellwood et al. 2004). Furthermore, this habitat is critical at the early life history stage when fish settle from the plankton; 65% settling directly into live coral (Jones et al. 2004).

The two species of *Stegastes* were influencing the greatest difference along the coast and through time in the MDS plots. Although the preferred habitat of both species' is branching coral (Randall et al. 1997), it appears that *Stegastes lividus* is dominating the area of the reef where branching coral is most abundant. This may be explained by *S. lividus* growing to a larger maximum size than *S. nigricans* (Randall et al. 1997); size of individual correlating to size of territory and dominance over more favourable habitats in this genera (Robertson 1996; Letourneur 2000). If the relationship between *S. lividus* abundance and overall fish species richness is causal, this one species of small reef fish appears to be accounting for a large portion of the variation in fish species richness; benthic variables and *Stegastes nigricans* demonstrating no measurable control. Although the competitive dominance of larger species of *Stegastes* over abundance of

other *Stegastes* species in the same area has been identified (Robertson 1996), and the influence of territorial pomacentrids on behaviour and foraging of individual species of other reef fish is well documented (e.g. Jones 2005), we believe this influence on the species richness of an entire fish community has not been demonstrated before.

Dominance of space by branching coral and *Stegastes lividus* is clearly contributing to the patterns in the MDS plot, but not necessarily in the direction one may expect from previous positive relationships between coral cover and fish species richness (e.g. Bell and Galzin 1984). Areas of high cover of live branching coral in Mauritius are dominated by large numbers of *S. lividus* and their territorial behaviour may actually reduce species richness, such that the relationship between coral cover and fish species richness is negative. Consequently, mono-specific stands of branching coral are resulting in an ecosystem more susceptible to competitive dominance by fewer species (Almany 2004). Indeed, dominance of a reef by one main taxa of coral will not necessarily promote high species diversity, rather a range of different taxa and habitat types is expected to provide more niches and a more diverse ecosystem (Almany 2004). This will be particularly true for small-bodied species of reef fish that are closely reliant on habitat for shelter and food and are often specialised (Munday and Jones 1998).

The western Indian Ocean has suffered the greatest effects from coral bleaching in the Indo-Pacific (Goreau et al. 2000) and future bleaching is predicted to result in the 'extinction' of these reefs in coming decades (Sheppard 2003). However, various locations in the southern western Indian Ocean, including Mauritius, currently seem to be a refuge from coral bleaching, demonstrating "protection" from serious thermal stress (Obura 2005) and host high coverage of thermally sensitive corals that still support specialist fish species. This study has demonstrated minimal community change through time on a coral reef in Mauritius, and identified other factors likely to be driving trends. Such data and future monitoring in these areas of bleaching refugia will be important to understand natural variation in fish communities and associated management implications.

Acknowledgements This work was funded by the Leverhulme Trust, Eppley Foundation, the Marine Science for Management Program (MASMA) of the Western Indian Ocean Marine Science Association and the Fisheries Society of the British Isles. Many thanks to Hotel Victoria, in particular Hervé Doboscq for field support. We are grateful to Mehdi Adjeroūd, Gilbert Poli, Bernard Salvat, Michel Porcher and Nyawira Muthiga for assistance with field studies. We thank the Mauritius Institute of Oceanography and Director, Dr. Bhikajee, for permission to undertake the work.

References

- Adjeroūd M, Letourneur Y, Porcher M, Salvat B (1998) Factors influencing spatial distribution of fish communities on a fringing reef at Mauritius, S.W. Indian Ocean. *Environ Biol Fishes* 53:169–182
- Ahamada S, Bijoux J, Bigot L, Cauvin B, Koonjul M, Maharavo J, Meurier S, Moine-Picard M, Quod J-P, Pierre-Louis R (2004) Status of the coral reefs of the south west Indian Ocean island states. In: Wilkinson C (ed) Status of coral reefs of the world: 2004. Australian Institute of Marine Science, Townsville, pp 189–212
- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Bell JD, Galzin R (1984) Influence of live coral cover on coral reef fish communities. *Mar Ecol Prog Ser* 15:265–274
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. *Mar Ecol Prog Ser* 245:205–212
- Brown BE, Letissier MDA, Scoffin TP, Tudhope AW (1990) Evaluation of the environmental-impact of dredging on intertidal coral reefs at Ko-Phuket, Thailand, using ecological and physiological-parameters. *Mar Ecol Prog Ser* 65:273–281
- Chabanet P (2002) Coral reef fish communities of Mayotte (western Indian ocean) two years after the impact of the 1998 bleaching event. *Mar Freshwater Res* 53:107–113
- Clarke KR, Warwick RM 1998. A taxonomic distinctness index and its statistical properties. *J App Ecol* 35:523–531
- Clarke KR, Warwick RM (2001a) Change in marine communities: an approach to statistical analysis and interpretation, (2nd edn). PRIMER-E Ltd, Plymouth
- Clarke KR, Warwick RM (2001b) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar Ecol Prog Ser* 216:265–278
- Doherty PJ, Williams DM (1988) The replenishment of coral-reef fish populations. *Oceanogr Mar Biol Ann Rev* 26:487–551
- Doherty PJ, Dufour V, Galzin R, Hixon M, Meekan M, Planes S (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology* 85:2422–2428
- Dulvy NK, Polunin NVC, Mill AC, Graham NAJ (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can J Fish Aquat Sci* 61:466–475
- Garpe KC, Yahya SAS, Lindahl U, Ohman MC (in press) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar Ecol Prog Ser*
- Goreau T, McClanahan T, Hayes R, Strong A (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conserv Biol* 14:5–15
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200–208
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci USA* 103:8425–8429
- Harmelin-Vivien ML (1989) Reef fish community structure: an Indo-Pacific comparison. In: Harmelin-Vivien ML, Bourlière F (eds) Vertebrates in complex systems. Springer-Verlag, Berlin, pp 21–60
- Harmelin-Vivien M, 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. *Rev Ecol (terre Vie)* 40:467–539
- Hawkins JP, Roberts CM, Van't Hof T, de Meyer K, Tratalos J, Aldam C (1999) Effects of recreational scuba diving on Caribbean coral and fish communities. *Conserv Biol* 13:888–897
- Helfman GS, Colette BB, Facey DE (1997) The diversity of fishes. Blackwell Science, Oxford, UK, pp 528
- Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 475–508
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshwater Res* 50:839–866
- Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14:225–235
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Jones KMM (2005) The effect of territorial damselfish (family Pomacentridae) on the space use and behaviour of the coral reef fish, *Halichoeres bivittatus* (Bloch, 1791) (famile Labridae). *J Exp Mar Biol Ecol* 324:99–111
- Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. *Coral Reefs* 20:155–158

- Letourneur Y (1996a) Dynamics of fish communities on Reunion fringing reefs, Indian Ocean 1. Patterns of spatial distribution. *J Exp Mar Biol Ecol* 195:1–30
- Letourneur Y (1996b) Réponses des peuplements et populations de poissons aux réserves marines. Le cas de l'île de Mayotte, Océan Indien occidental. *Ecoscience* 3:442–450
- Letourneur Y (2000) Spatial and temporal variability in territoriality of a tropical benthic damselfish on a coral reef (Réunion Island). *Environ Biol Fish* 57:377–391
- Letourneur Y, Chabanet P, Vigliola L, Harmelin-Vivien M (1998) Mass settlement and post-settlement mortality of *Epinephelus merra* (Pisces: Serranidae) on Réunion coral reefs. *Mar Biol Assess UK* 78:307–319
- Lindahl U, Ohman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. *Mar Pollut Bull* 42:127–131
- Loya Y (1978) Plotless and transect methods. In: Stoddart DR, Johannes RE (eds) *Coral research methods*. UNESCO, Paris, pp 197–217
- McClanahan TR (2000a) Recovery of the coral reef key-stone predator, *Balistapus undulatus*, in East African marine parks. *Biol Conserv* 94:191–198
- McClanahan TR (2000b) Bleaching damage and recovery potential of Maldivian coral reefs. *Mar Pollut Bull* 40:587–597
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380–391
- McClanahan T, Maina J, Pet-Soede L (2002) Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. *Ambio* 31:543–550
- McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Mar Poll Bull* 48:327–335
- McClanahan TR, Graham NAJ (2005) Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Mar Ecol Prog Ser* 294:241–248
- McClanahan TR, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. *Mar Ecol Prog Ser* 298:131–142
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357–367
- Moothien Pillay R, Terashima H, Kawasaki H (2002) The extent and intensity of the 1998 mass bleaching event on the reefs of Mauritius, Indian Ocean. *Galaxea* 4:43–52
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Munday PL, Jones GP (1998) The ecological implications of small body size among coral-reef fishes. *Ocean Mar Biol Ann Rev* 36:373–411
- Obura DO (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuary Coast Shelf Sci* 63:353–372
- Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* 23:352–356
- Randall JE, Allen GR, Steene RC (1997) *The complete divers' & fishermen's guide to fishes of the Great Barrier Reef and Coral Sea*. Crawford House Publishing, Bathurst, Australia
- Robertson DR (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77:885–899
- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Mar Ecol Prog Ser* 62:185–202
- Saji NH, Goswami BN, Vinayachandran PN, Yamagata TA (1999) A dipole mode in the tropical Indian Ocean. *Nature* 401:360–363
- Sano M (2004) Short-term effects of a mass coral bleaching event on a reef fish assemblage at Iriomote Island, Japan. *Fish Sci* 70:41–46
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* 425:294–297
- Sheppard CRC, Spalding M, Bradshaw C, Wilson S (2002) Erosion vs. recovery of coral reefs after 1998 El Niño: Chagos reefs, Indian Ocean. *Ambio* 31:40–48
- Spalding MD, Jarvis GE (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Mar Poll Bull* 44:309–321
- Turner J, Klaus R (2005) Coral reefs of the Mascarenes, Western Indian Ocean. *Phil Trans R Soc A* 363:229–250
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Williams ID, Walsh WJ, Tissot BN, Hallacher LE (2006) Impact of observers' experience level on counts of fishes in underwater visual surveys. *Mar Ecol Prog Ser* 310:185–191
- Zakai D, Chadwick-Furman NE (2002) Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. *Biol Cons* 105:179–187