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Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales

Mehdi Adjeroud[1,a], Yannick Chancerelle[1], Muriel Schrimm[1], Thierry Perez[2], David Lecchini[1], René Galzin[1] and Bernard Salvat[1]

[1] Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), BP 1013, 98729 Papetoai, Moorea, French Polynesia, and École Pratique des Hautes Études, UMR 8046 CNRS, Université de Perpignan, 66860 Perpignan Cedex, France
[2] Centre Océanologique de Marseille, UMR 6540, DIMAR, rue de la batterie des lions, 13007 Marseille, France

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Abstract – Coral reefs in French Polynesia, just like many others throughout the world, have been subjected to several natural disturbances including 15 cyclones, seven major bleaching events, and several *Acanthaster planci* outbreaks since the 1980s. In order to document the effects of these perturbations on coral assemblages, we initiated a long-term monitoring program that extended over both local and regional scales. Coral cover was quantified at 20 sites situated on the outer reef slope of 13 islands. The results from the first decade (1992-2002) are analyzed and the adequacy of our approach is discussed in the context of identifying potential indicators of coral reef health. Among 13 islands in French Polynesia, only two were unaffected by natural disturbances. We found important local and regional variation in the impacts of coral bleaching and cyclones, and three major temporal trends were distinguished: 1) 10 sites where coral cover decreased in relation to the occurrence of major disturbances; 2) nine sites where coral cover increased, despite the occurrence of disturbances affecting seven of them; and 3) a site where no significant variation in coral cover was found. The responses to perturbations were different among coral genera: *Acropora* species were particularly susceptible to bleaching events, whereas physical damages induced by cyclones concerned mainly branching species of *Acropora* and *Pocillopora*. Thus, monitoring surveys could be improved by selecting different and complementary indicators (one on the variation in diversity, one estimating changes in the abundance/cover, and one estimating the potential for recovery), by integrating several spatial scales, and by including at least the most informative species. High frequency recordings of environmental parameters (e.g. sea surface temperature) may be also a complementary tools for identifying causal relationships between changes in coral reef community structure and the factors causing the changes.

Key words: Coral reefs / Temporal variability / Bleaching events / Indicators / Pacific Ocean

Résumé – Evaluation des impacts des perturbations naturelles sur les assemblages de coraux en Polynésie française : résultats de 10 années de suivi à différentes échelles. Comme d'autres récifs à travers le monde, les écosystèmes coralliens de Polynésie française ont subi de nombreuses perturbations naturelles, et depuis les années 1980, 15 cyclones, sept phénomènes de blanchissement et plusieurs explosions démographiques d'*Acanthaster planci*. Afin d'examiner l'impact de ces perturbations sur les assemblages de coraux scléractiniaires, un programme de suivi à long terme a été mis en place, aux échelles locale et régionale. Le recouvrement corallien a été quantifié sur 20 stations localisées sur la pente externe de 13 îles. Nous analysons les résultats obtenus pour la décennie 1992-2002, et nous examinons la pertinence des indicateurs potentiels de l'état de santé des récifs. Sur les 13 îles, deux seulement n'ont subi aucune pertubation. Nos résultats montrent une forte variabilité de l'impact des phénomènes de blanchissement et des cyclones aussi bien à l'échelle locale que régionale. Trois tendances majeures sont observées : 1) diminution du recouvrement corallien pour 10 stations, suite au passage de perturbations successives ; 2) augmentation du recouvrement corallien pour neuf stations, malgré le passage de perturbations pour sept d'entre elles ; 3) stabilité du recouvrement corallien dans une station. Les réponses aux perturbations sont différentes selon les genres de coraux : *Acropora* est le plus sensible aux phénomènes de blanchissement, alors que les dommages physiques causés par les cyclones affectent les formes branchues des genres *Acropora* et *Pocillopora.* Les programmes de suivi pourraient être optimisés *via* la sélection d'indicateurs différents et complémentaires (l'un évaluant la variation de la diversité, l'autre l'évolution de l'abondance et/ou du recouvrement, ou encore le potentiel de recrutement), l'intégration de plusieurs échelles spatiales, et le choix d'espèces informatives. L'enregistrement de facteurs environnementaux (température de l'eau par exemple) se révèle également un outil complémentaire utile pour l'identification des causes des changements observés dans la structure des communautés.

[a] Corresponding author: adjeroud@univ-perp.fr

1 Introduction

Community ecologists have long recognised the important contribution of disturbances to the structure and dynamic of marine communities (Connell 1978; 1997; Sousa 1984; Hughes 1989; 1994; Done 1992a; 1992b; van Woesik 1994; Hughes and Connell 1999). However, they have also pointed out the difficulty of discriminating the relative importance of natural and anthropogenic perturbations in causing the changes in community structure (Brown 1987; Grigg and Dollar 1990; Karlson and Hurd 1993). In coral reef ecosystems, the major natural disturbances experienced by reef communities are cyclones (Rogers 1993; Harmelin-Vivien 1994), coral-bleaching events (Gleason 1993; Hoegh-Guldberg 1999; Wilkinson et al. 1999), long periods of low tides (Eakin and Glynn 1996), dystrophic crisis linked with phytoplankton blooms and associated anoxic conditions (Guzman et al. 1990; Adjeroud et al. 2001; Salvat et al. 2002), outbreaks of predators, particularly the seastar *Acanthaster planci* in the tropical Pacific (Moran 1986; Endean and Cameron 1990), and mass mortalities of keystone species, such as the sea urchin *Diadema antillarum* in the tropical western Atlantic (Lessios et al. 1984; Hughes 1994). The effects of these disturbances depend mainly on the temporal and spatial scales under consideration, the structure of the impacted communities, the life-history characteristics and growth forms of the dominant species, the geomorphology and depth of the reef zone, and on the chronology of the previous disturbances (Witman 1992; Connell et al. 1997; Hughes and Connell 1999). These disturbances may have short-term or immediate direct effects, as well as long-term and indirect effects on population and community structures (Karlson and Hurd 1993; Hughes and Connell 1999).

Over the last three decades, the frequency and severity of these natural perturbations, and particularly coral bleaching events, have greatly increased worldwide, and as a consequence, reef communities have suffered unprecedented levels of mortality (Wilkinson et al. 1999; Hughes et al. 2003; Pandolfi et al. 2003). In this context of increasing degradation of coral reefs, coral reef surveys have become commonplace as a means to document changes in reef communities (i.e. “monitoring”) and the impacts of natural disturbances. Moreover, there has been also a major effort to develop methodologies for detecting changes in reef communities, and to determine reliable indicators of such changes (DeVantier et al. 1998; Hodgson 1999; Dale and Beyeler 2001; Jameson et al. 2001; Diamant and von Westernhagen 2003; Brown et al. 2004; Hallock et al. 2004). Two major types of coral reef monitoring surveys can be distinguished: 1) those that have focused on large scales (regional to global; Aronson et al. 1994; Ninio et al. 2000; Ninio and Meekan 2002), including international monitoring networks such as the global coral reef monitoring network (GCRMN, in Wilkinson 1998), Reef Check (Hodgson 1999; 2000), coral reef assessment and monitoring program (CRAMP) in Hawaii (Brown et al. 2004; Jokiel et al. 2004), or “Commission de l’Océan Indien” (COI; Conand et al. 1999); and 2) those that have examined reef community changes at smaller scales (reef zone or island; Chou et al. 1991; Witman 1992; Bythell et al. 1993; Dollar and Tribble 1993; Andres and Witman 1995; Shulman and Robertson 1996; Zea et al. 1998; Ledesma and Mejia 2002; Chabanet et al. 2002; Edmunds 2002). However, few surveys have documented the effects of natural disturbances on the dynamic of coral assemblages at multiple spatial scales (Done 1992b; Jokiel et al. 2004).

To address this limitation of most coral reef monitoring projects, in 1992 we initiated a monitoring program that includes 13 islands (eight atolls and five high volcanic islands) in four of the five archipelagoes in French Polynesia, with the goal of documenting the effects of natural perturbations on coral assemblages at both local (between sites around an island separated from few meters to kilometers) and regional (between islands and archipelagoes, separated by up to 1880 km) scales. All surveys were conducted on the outer reef slope, since anthropogenic disturbances, such as dredging, construction activities, sewage discharges and runoffs, which may have important impacts on fringing reef communities, have a negligible one on the reef slope of high islands and atolls (Salvat et al. 1979; Augustin et al. 1997). This multi-spatial scale survey complements our knowledge on the temporal variability and local-scale spatial patterns of benthic communities of Moorea (Fagerstrom 1992; Galzin et al. 1993; Adjeroud 1997a; Augustin et al. 1997; Adjeroud et al. 2002).

In the present paper, we explore the results obtained during the first decade 1992-2002 (some preliminary results have been previously published in Salvat 2000, 2002; Salvat et al. 2001), and discuss the adequacy of our approach in the context of recent initiatives to develop methodologies and indicators to assess coral reef health (Jameson et al. 2001; Hallock et al. 2004; Ben-Tzvi et al. 2004). The purpose of reviewing the recent strategies to detect the impacts of natural disturbances on coral reefs is to assist coral reef managers in their decision-making processes, notably in French Polynesia where enforcement of reef management is much needed (Hutchings et al. 1994; Salvat and Aubanel 2002).

2 Materials and methods

2.0.1 Study sites

French Polynesia covers a vast region of the eastern Indo-Pacific province. It comprises five archipelagoes, including 34 high volcanic islands and 84 atolls, which represents a surface area of 4000 km^2 of land. The tides are semi-diurnal, with an amplitude rarely exceeding 40 cm. A total of 15 cyclones that have affected French Polynesia have been reported since the 1980s: in 1981, 1983, 1986, 1988, 1990, 1991, and 1997 (Météo France). During the same period, major bleaching events have occurred: in 1983, 1984, 1987, 1991, 1994, 1998, and 2002 (Salvat 1992; Gleason 1993; Hoegh-Guldberg and Salvat 1995; Augustin et al. 1997; Mumby et al. 2001a,b; Penin and Adjeroud data not pub.). In Moorea, these bleaching events corresponded to periods when sea surface temperatures (SSTs) rose above 29.2 °C (i.e., the thermal threshold; Hoegh-Guldberg and Salvat 1995; Adjeroud et al. 2002). Several *Acanthaster planci* outbreaks also occurred between 1978 and 1984 (Bouchon 1985; Faure 1989), but have not occurred since, possibly because of the seastar-collecting campaigns organized by French Polynesian authorities. An inventory of major natural disturbances that have affected French Polynesian islands is presented (Table 1).

Table 1. Major natural disturbances that have affected French Polynesian islands since the 1980s.

Disturbances	Period	Islands likely affected	Remarks	References
Bleaching events	1983 (March-May)	Reported in Tahiti and Moorea	Moderate event Linked to a sea level depression (Rougerie and Wauthy 1983)	Reported in: Glynn (1984, 1991), Williams and Bunckley-Williams (1990), Salvat (1992), Salvat and Aubanel (2002)
	1984 (March-April)	Reported in Tahiti and Bora Bora	Moderate event	
	1987	Reported in Moorea, Tahiti and Manihi	Moderate event	
	1991 (March-July)	Reported in Moorea, but likely other islands	Major event	Surveyed by: Salvat (1992), Gleason (1993)
	1993 (April-May)	Restricted to some localities around Tahiti	Minor event	Surveyed by: Drollet et al. (1994)
	1994 (March-August)	Reported in Moorea, Tahiti, Tetiaroa and Rangiroa, but likely other islands	Major event	Surveyed by: Fagestrom and Rougerie (1994), Hoegh-Guldberg and Salvat (1995), this survey
	1998 (March-August)	Reported in Aratika, Nengo Nengo, Mataiva, Rangiroa, Tahiti, Takapoto, Tetiaroa and Tikehau, but likely other islands	Major event	Surveyed by: Mumby et al. (2001a; 2001b), this survey
	2002 (April-August)	Reported in Moorea and Raiatea, but likely other islands	Major event	Surveyed by: Carroll et al. (data not pub.), Chancerelle et al. (data not pub.), Penin and Adjeroud (data not pub.), this survey
Cyclones	1981	Thamar (March): Likely no islands affected Fran (March): Austral		
	1983	Nano (January): Marquesas and Tuamotu Orama (February): Tuamotu Reva (March): Tuamotu Veena (April): Tuamotu and East Tahiti William (April): Tuamotu	Major event Major event	Harmelin-Vivien (1985), Laboute (1985), Harmelin-Vivien and Laboute (1986)
	1986	Ima (February): Likely no islands affected Sally (December): South Austral		
	1988	Cilla (March): South Austral		
	1990	Peni (February): South Austral		
	1991	Wasa (December): Society and Austral	Major event	Delesalle et al. (1993)

Table 1. Continued.

Disturbances	Period	Islands likely affected	Remarks	References
	1997	Martin (October): Society, notably Bora Bora and Raiatea		This survey
		Osea (November): Society, notably Bora Bora and Raiatea		
		Pam (December): West Austral		
Acanthaster outbreaks	1980	Reported in Moorea, but likely other islands		Surveyed in: Faure (1989)
	1982			Reported in: Bouchon (1985)
	1984			
Algal blooms / Dystrophic crisis	Undetermined	Taiaro		Reported in: Poli and Salvat (1976), Adjeroud (1997b)
	1983 (April)	Moorea	Linked to a long period of low tide	Galzin (pers. comm.)
	1988	Mataiva		Reported in: Galzin et al. (1989)
	1994 (March)	Hikueru	Mass mortalities in the lagoon	Surveyed in: Adjeroud et al. (2001)
	2001 (December)	Bora Bora	Restricted to the south part of the lagoon	Reported by: Schneider (pers. comm.)

2.0.2 Sampling strategy and data analysis

Our monitoring survey focused on 13 islands, including five high volcanic islands (Bora Bora, Moorea, Raiatea, Tahiti, Tubuai) and eight atolls (Aratika, Marutea Sud, Mataiva, Nengo Nengo, Rangiroa, Takapoto, Tetiaroa, Tikehau), located on four archipelagoes (Fig. 1). A total of 20 sites were situated on these islands. On Moorea and Tahiti, six and three sites were established, respectively, whereas only one site was established on each of the other islands/atolls. On Tahiti, the three sites (Tahiti Wharf, Tahiti Pass, and Tahiti Airport) were separated by approximately 5 km (Fig. 1). In Moorea, four sites were located on the same area and separated by approximately 40 m (Moorea Tiahura 1–2, Moorea Tiahura 3–4, Moorea Tiahura 5–6, and Moorea Tiahura 7–8; Adjeroud et al. 2002). These four sites were separated from the two others sites of the island (Moorea Haapiti, and Moorea Vaipahu) by approximately 10 km) (Fig. 1). This sampling design allowed us to focus on the regional scale (between islands and archipelagoes, separated by 14 to 1880 km), but also to examine the local scale (between sites around an island separated from few meters to 10 km). The monitoring sites were located on the outer reef slope, around 10 m depth, since it is the place of highest diversity and abundance of coral assemblages (Adjeroud 1997a). Moreover, the reef slope has quite similar geomorphological features from one island to another, which allows better inter-island comparisons. The reef slope is also the place where anthropogenic perturbations are less intense, and are thus mainly under the influences of natural events.

Between 1992 and 1997, the sites were surveyed every one to four years, whereas from 1997 they were surveyed at least once every two years. Each study site consists of two permanent stainless stakes separated by 20 m. During the surveys, a stainless cable was stretched between the two stakes, and 20 metal markers were used to mark the position of 1 m^2 quadrat that was subdivided into 81 squares with string. A photograph of the quadrat was taken at each position with a Nikonos V Body camera equiped with a Nikkor 15 mm lens, a SB 104 flash and a Fuji Velvia film fine-grained low-sensibility photographic (ASA 50). On the films, dead and living coral colonies were distinguished at the generic level. Living coral cover values were obtained by the ratio of the number of points (rope cross) under which a living colony was identified to the total number of points (81) in the quadrat. Coral cover values between years were compared using a t test (Scherrer 1984). Trends in temporal variability were analyzed using a Principal Component Analysis (PCA). The analysis was done with cover values (raw data were log $(x + 1)$ transformed) of the six dominant coral genera obtained at the 20 sites during the study period (1992-2002). In the biplot, successive surveys for each site were linked in order to visualize the extent and characteristics of the temporal variability. Trends in temporal variability of coral cover of the six major genera were then compared among the 20 sites.

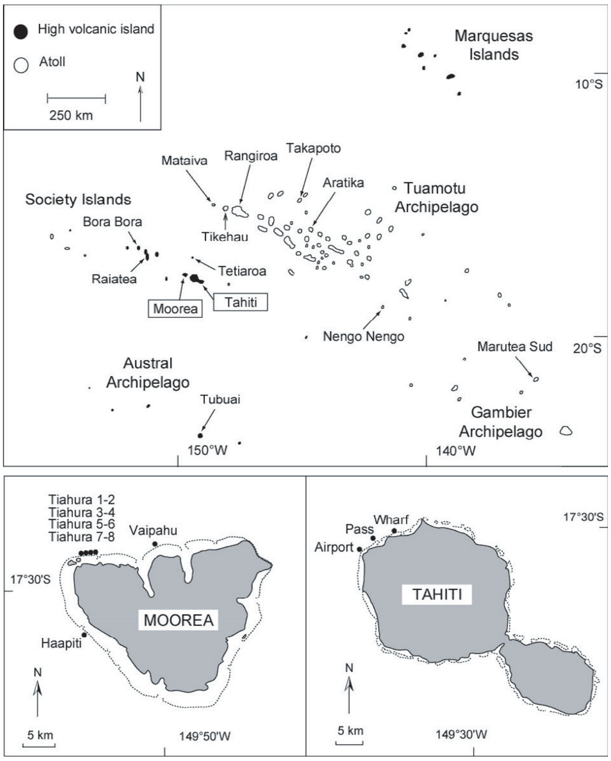

Fig. 1. Location of the 13 French Polynesian islands (eight atolls and five volcanic high islands) surveyed in the present monitoring program. On Moorea and Tahiti, respectively six and three sites were established, whereas only one site was disposed on the other islands/atolls. In Moorea, the four sites in Tiahura (Moorea Tiahura 1–2, Moorea Tiahura 3–4, Moorea Tiahura 5–6, and Moorea Tiahura 7–8) were separated by approximately 40 m.

3 Results

Table 2 presents coral cover values obtained between 1992 and 2002 at the 20 sites surveyed on the 13 islands. Coral cover ranged from 2.2% (Raiatea 2000) to 57.9% (Tahiti Wharf 2001), but there was high variation among sites on different islands, and significant but less pronounced variation among sites of the same island (Moorea and Tahiti).

For most of the sites, a significant temporal variability was found among successive surveys. Three major temporal trends were distinguished: 1) sites where coral cover decreased over the course of the study: Aratika, Mataiva, Moorea Vaipahu, Nengo Nengo, Raiatea, Tahiti Airport, Tahiti Pass, Takapoto, Tetiaroa, Tikehau; 2) sites where coral cover increased: Bora Bora, Marutea Sud, Moorea Tiahura 1–2, Moorea Tiahura 3–4, Moorea Tiahura 5–6, Moorea Tiahura 7–8, Moorea Haapiti, Tahiti Wharf, Tubuai; and 3) a site, Rangiroa, where no significant variation among successive surveys was observed.

For the first category, the sharp decrease in coral cover always was associated with the occurrence of major natural disturbances. The 1998 bleaching event was probably responsible of the decrease in coral cover observed in Aratika, Mataiva, Nengo Nengo, Tahiti Airport, Tahiti Pass, Takapoto and Tikehau. Cyclones caused by the 1997-1998 El Niño Southern Oscillation event could be also associated with the coral decline recorded at Mataiva, Raiatea and Tikehau. However, several sites that were impacted by one of these natural perturbations showed no signs of coral cover decrease, but instead, some sites showed a trend of increase during this period (Bora Bora, Moorea Tiahura 1–2, Moorea Tiahura 3–4, Moorea Tiahura 5–6, Moorea Tiahura 7–8, Moorea Haapiti, Tahiti Wharf). For sites where no major perturbations were reported (Tubuai, Marutea Sud), coral cover increased.

Since the responses to natural perturbations can be different among coral genera, we examined the variability of cover values for the six dominant coral genera. We focused on two sites that were subjected to different stresses: Aratika was affected by the 1998 bleaching event, whereas Raiatea was impacted by two successive cyclones in 1997 (Martin in October, and Osea in November). In Aratika, surveys made before (August 1997) and after (June 1999) the event showed that coral cover clearly decreased for *Acropora* (4.3% in 1997, 0.5% in 1999) and *Pavona* (0.6% in 1997, 0.1% in 1999), whereas the decrease was less pronounced for other genera (Fig. 2). In Raiatea, the highest decrease in coral cover was found for *Acropora* (3.5% in 1994, 0.4% in 1998) and *Pocillopora* (2.0% in 1994, 0.6% in 1998), and to a lesser degree for *Montipora* (0.6% in 1994, 0.2% in 1998; Fig. 2). In contrast, the two other genera observed at this site, *Pavona* and *Porites* (massive growth forms), showed a slight increase in cover between successive surveys.

Trends in temporal variability of coral cover of the six major genera among the 20 sites were analyzed using a PCA. The cumulative percentage of variance of the first two axes of the PCA was 59.32%. Axis 1 (38.43%) was positively correlated to all six coral genera, whereas axis 2 (20.89%) was positively correlated to *Pocillopora* and *Porites*, and negatively to *Montastrea* (Table 3). These correlations explained, for example, the position of Marutea (high coral cover, notably for *Acropora* and *Montastrea*), Bora Bora (high coverages of *Pocillopora*), or Tubuai (low coverage values, particularly for *Pocillopora* and *Porites*) sites on the biplot of the PCA (Fig. 3). The biplot also showed that the patterns in temporal variability of coral cover of the six major genera were clearly different among the 20 sites (Fig. 3). A relatively high variation was found at Aratika, Mataiva, Nengo Nengo and Raiatea, whereas this temporal variability was less pronounced in Bora Bora, Marutea Sud, Rangiroa, Takapoto, or Tubuai (Fig. 3a). In Moorea, the pattern of temporal variability was relatively similar among the four sites located at Tiahura (Moorea Tiahura 1–2, Moorea Tiahura 3–4, Moorea Tiahura 5–6, Moorea Tiahura 7–8), whereas Moorea Vaipahu and Moorea Haapiti showed distinct patterns (Fig. 3b). In Tahiti, patterns of temporal variability of the six major genera were different among the three sites (Tahiti Airport, Tahiti Pass, Tahiti Wharf; Fig. 3c).

4 Discussion

4.1 Impact of natural perturbations on French Polynesian coral reefs

During the 10 year period of this survey (1992-2002), French Polynesian reefs were subjected to three major coral

Table 2. Mean coral cover values (%) obtained during the period 1992-2002 at the 20 sites disposed on the 13 islands of the monitoring survey. Standard errors are given in brackets. *: values significantly different from previous survey at the same site (*t* test, $p < 0.05$). Dates of surveys are indicated in italics.

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Aratika						27.7 (2.5) *5 Aug.*		19.6 (1.7)* *22 June*		24.1 (2.1)* *21 Sept.*	
Bora Bora							32.6 (2.2) *1 Sept.*		40.7 (19)* *4 March*		46.3 (2.0)* *19 Feb.*
Marutea Sud			36.9 (1.5) *1 Aug.*			49.1 (1.9)* *21 May*		54.1 (2.2) *14 Sept.*		54.0 (2.8) *27 Sept.*	
Mataiva	24.8 (1.7) *1 Sept.*		24.6 (2.9) *19 July*					4.6 (0.6)* *12 Feb.*		11.0 (1.5)* *4 May*	
Moorea Tiahura						33.0 (2.6) *7 Nov.*		34.5 (2.8) *14 April*		45.4 (2.5)* *15 June*	
Moorea Tiahura 3–4						31.8 (3.2) *6 Nov.*	34.0 (2.0) *12 Aug.*	32.9 (1.5) *24 April*		40.7 (2.5) *15 June*	
Moorea Tiahura 5–6						27.5 (2.8) *7 Nov.*		26.5 (2.6) *14 April*		34.1 (2.9)* *15 June*	
Moorea Tiahura 7–8						34.9 (2.6) *14 Nov.*		39.6 (2.7) *14 April*		48.2 (2.1)* *15 June*	
Moorea Vaipahu		16.1 (1.5) *14 March*	24.9 (2.1)* *8 May*			29.3 (2.6) *5 Nov.*	33.2 (3.3) *10 Aug.*		42.8 (3.5)* *7 June*		35.3 (2.0) *14 Sept.*
Moorea Haapiti				12.7 (1.6) *15 Nov.*			31.3 (1.7)* *9 Sept.*		35.7 (1.6)* *4 March*		37.4 (1.8) *18 Dec.*
Nengo Nengo			15.1 (1.2) *29 July*			22.9 (1.4)* *26 Dec.*			16.8 (1.3)* *28 Nov.*		24.8 (1.8)* *29 Aug.*
Raiatea			8.3 (1.1) *27 May*				2.7 (1.1)* *7 Jan.*		2.2 (0.8) *5 April*		13.0 (1.3)* *11 Dec.*
Rangiroa			29.0 (3.3) *21 June*				31.7 (1.5) *3 Sept.*		27.5 (3.4) *23 June*		26.5 (3.9) *13 June*
Tahiti Airport		13.8 (1.8) *15 Oct.*	19.0 (2.1)* *9 May*		31.1 (2.5)* *2 Dec.*	44.0 (4.7)* *18 Dec.*		36.9 (4.4)* *22 April*		38.8 (3.8) *9 Aug.*	
Tahiti Wharf					39.0 (2.4) *3 Dec.*	45.1 (2.8) *18 Dec.*		48.6 (1.7) *30 April*		57.9 (2.4)* *29 March*	
Tahiti Pass					52.7 (2.4) *4 Dec.*	56.7 (2.1) *19 Dec.*		36.8 (2.5)* *30 April*		40.4 (3.0) *9 Aug.*	
Takapoto			19.4 (2.9) *9 July*				12.1 (1.7)* *4 Aug.*		25.8 (2.1)* *8 Dec.*		28.9 (1.9)* *27 Nov.*
Tetiaroa			48.6 (6.8) *23 May*			38.0 (4.5) *9 Dec.*		30.8 (4.8)* *28 January*		31.4 (4.9) *24 Oct.*	
Tikehau			39.6 (2.0) *19 June*				4.1 (0.5)* *5 Sept.*		5.3 (0.8) *21 July*		12.8 (1.2)* *11 June*
Tubuai						11.1 (2.1) *28 Oct.*		9.6 (1.8) *29 Dec.*		13.2 (2.5)* *20 Dec.*	

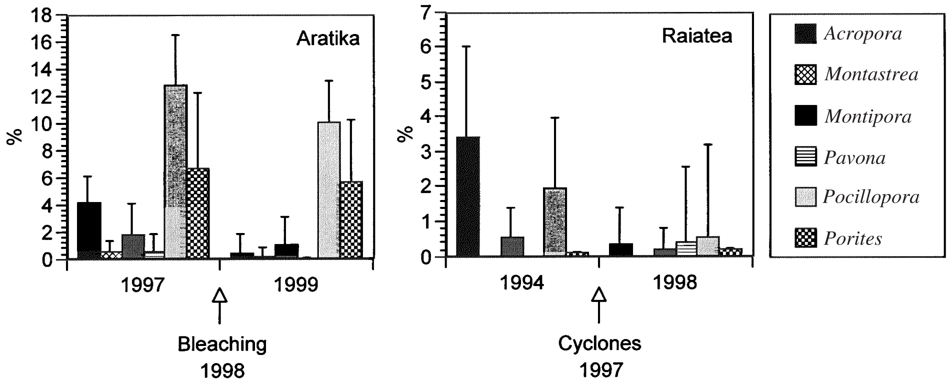

Fig. 2. Variation of living coral cover of the six major coral genera in Aratika, which was affected by a bleaching event in 1998, and in Raiatea, which was affected by two successive cyclones in 1997 (Martin in October and Osea in November).

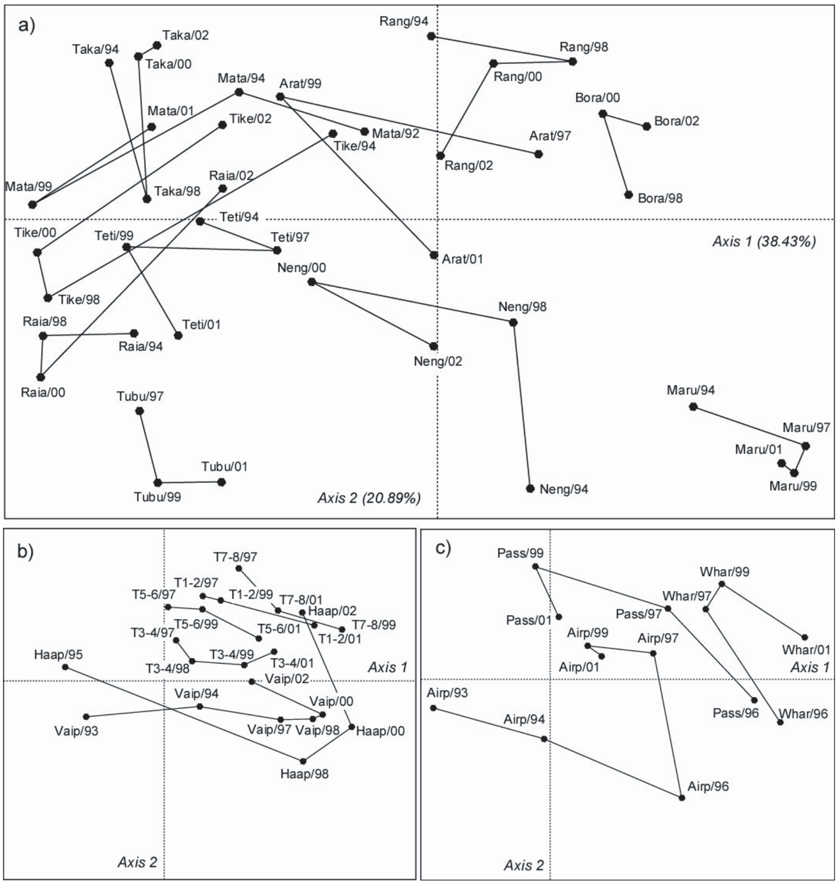

Fig. 3. Plots of the principal component analysis (PCA) performed on the cover values of the six major genera obtained at the 20 sites during the study period (1992-2002). The percentage of variance of the first two axes are given. Successive surveys for each site were linked in order to visualize the extent and characteristics of the temporal variability. The six sites around Moorea (b), and the three sites around Tahiti (c) were plotted on separate figures to ease legibility.

bleaching events (1994, 1998, 2002) and three cyclones (1997) that were generated by El Niño Southern Oscillation events. Among the 13 islands selected in our survey, only two, Marutea Sud and Tubuai, were not affected by one of these disturbances. If we add major disturbances recorded before the beginning of this survey, it is a total of seven bleaching events, 15 cyclones, and several *Acanthaster planci* outbreaks that have affected French Polynesian coral reefs since the 1980s. As for many other coral reefs worldwide, this increasing frequency of disturbances is a major concern for coral reef health, and several models predict that this trend will continue in the coming decades, largely as a result of the effects of global warming (Hoegh-Guldberg 1999; 2002; Wilkinson et al. 1999; Hughes et al. 2003; Pandolfi et al. 2003).

Table 3. Correlations of variables (six dominant coral genera) with first two ordination axes of the PCA performed on the coral cover values obtained at the 20 sites during the study period (1992-2002).

Variables	Axis 1	Axis 2
Acropora	0.67	−0.33
Montastrea	0.49	−0.66
Montipora	0.57	−0.21
Pavona	0.52	0.02
Pocillopora	0.50	0.59
Porites	0.48	0.50

Our results show that the impacts of a natural disturbance such as bleaching events or cyclones may be largely variable among different sites around an island, and among islands within a region. This local and regional variability of the impacts of disturbances complements the variability reported on other reefs around the world (Edmunds and Bruno 1996; Hughes and Connell 1999; Edmunds 2002; Kramer and Kramer 2002; Ninio and Meekan 2002). An interannual survey of reef communities at Tiahura, Moorea, showed that the mortality of coral colonies following a bleaching event was decreasing with successive events, even if the latter have the same intensity (Adjeroud et al. 2002). This spatial and temporal variability of the impacts observed at several scales during the present and previous surveys may reflect an acclimation and/or adaptation of local populations. In fact, coral colonies and/or their endosymbiotic zooxanthellae may be phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events (Rowan et al. 1997; Hoegh-Guldberg 1999; Kinzie III et al. 2001; Coles and Brown 2003).

The results of our long-term monitoring program also show that the impacts of bleaching events and cyclones differ between coral genera, perhaps in relation to their life-history traits. The decline in coral cover attributed to bleaching events was particularly evident for *Acropora* species, a genus that is particularly susceptible to increasing SSTs (Salvat 1992; Gleason 1993; Hoegh-Guldberg and Salvat 1995; Fujioka 1999; Sugihara et al. 1999; Obura 2001). For cyclones, the physical damages concerned mainly branching species of *Acropora* and *Pocillopora*, has occurred on many other coral reefs (Randall and Eldredge 1977; Highsmith et al. 1980; Grigg 1995). In contrast, massive species such as *Porites* apparently were not affected by either of these disturbances, at least in term of coral cover (Salvat 1992; Gleason 1993; Hoegh-Guldberg and Salvat 1995; Fujioka 1999). Thus, the spatio-temporal variability of the impacts of a perturbation is also dependent, at least in part, on the species composition of coral assemblages.

4.2 Strategies for monitoring coral reef health and perturbation impacts

Our large-scale monitoring survey was initiated to detect the impacts of natural perturbations, particularly cyclones and bleaching events, on coral assemblages in French Polynesia. After a decade in which several major disturbances were recorded, it is timely to examine the adequacy and effectiveness of our approach in the context of the recent effort to define sampling strategies and indicators of reef degradation following disturbances (Jameson et al. 2001; Diamant and von Westernhagen 2003; Hallock et al. 2004). Concerning the sampling strategy, our results clearly demonstrate the importance of integrating multiple scales in monitoring programs, as suggested by previous reports (Edmunds and Bruno 1996; Edmunds 2002; Miller et al. 2002; Ninio and Meekan 2002). A possible way to take into account the local-scale variability is to select several sampling sites around each island, thus defining a hierarchical sampling design. High resolution images from satellite or airborne remote sensing could be also relevant for detecting this kilometer-wide variation, but these techniques generally are restricted to shallow and clear waters (Ammenberg et al. 2002; Andréfouët et al. 2002; Yamano and Tamura 2002; Yamano et al. 2002; Mumby et al. 2004). An interesting perspective is also the recent method of the photo-tow developped by Chancerelle (unpublished data). This method allows the collection of coral cover data over large distances, thereby providing a quantitative analysis of the impact of disturbances at the island scale, as it was successfully done for the effects of bleaching on the reefs of Moorea (Chancerelle et al. unpublished data).

The results of our monitoring program provide clear evidence of selective mortality among coral species under natural disturbances. Species of *Acropora* and *Pocillopora* clearly are the most sensitive to bleaching events and cyclones. Morevover, other reports showed that these two genera are also particularly sensitive to *Acanthaster planci* predation (Moran 1986; Faure 1989). Thus, it appears necessary to include and to focus on the dynamic of these two genera in monitoring programs on the impacts of natural disturbances.

Several descriptors recently have been proposed as indicators for the detection of the impacts of natural disturbances. Ideally, an effective indicator has to be relevant to the specified assessment objectives, easy to measure and interpret, and must also be sensitive to environmental effects. Additionally, it should have a high information content, and must be able to discriminate human-induced changes from natural variation (Grigg and Dollar 1990; Dale and Beyeler 2001). Clearly, the development of such standardized and reliably indicators is a difficult task, partly because the degradation of coral reef ecosystems and the subsequent mortality of reef organisms can be the consequence of one or several environmental factors, that can covary, and may act in synergy.

Most of the indicators currently available to detect the effects of natural disturbances on coral reefs concern scleractinian corals, which are particularly sensitive to environnemental disturbances (Adjeroud et al. 2002). In the past, the most commonly used descriptors to detect coral reef degradation were species richness and diversity indexes, density/abundance of colonies, and living/dead coral coverages. In recent years, several coral descriptors were proposed to be used as indicators of reef health (Table 4). Other authors have also proposed multimetric indexes, such as the Molecular Biomarker System (Downs et al. 2000; Woodley et al. 2002), the rarity and coral indexes (DeVantier et al. 1998), the coral vitality indices (Gomez et al. 1994; Ginsburg et al. 1996), the

Table 4. Major coral descriptors that have recently been proposed as indicators of coral reef health and perturbation impacts.

Potential indicators	References
Growth of adult colonies or transplants	Cortes and Risk 1985; Brown 1988; Guzman et al. 1994; Naim et al. 2001
Skeletal density	Atkinson et al. 1995; Steven and Broadbent 1997
Partial mortality	Ginsburg et al. 2001; Bouchon et al. 2004
Tissu regeneration potential	Meesters and Bak 1993
Depth of skeleton occupied by coral tissue	Barnes and Lough 1992
Acid-insoluble, metals and phosphorus contents in skeleton	Dodge et al. 1984; Hanna and Muir 1990; Edinger et al. 2000
Stable isotopes of nitrogen	Mendes et al. 1997; Heikoop et al. 2000
Size-frequency distribution	Bak and Meesters 1998; 1999; Meesters et al. 2001
Fecundity of coral colonies	Ward and Harrison 2000
Recruitment rates	Hunte and Wittenberg 1992; Miller and Barimo 2002
Coprostanol concentrations	Risk et al. 1994
RNA/DNA	Meesters et al. 2002
Lipid content	Harriott 1993
Stress protein expressions (heat shock proteins and ubiquitine)	Black et al. 1995; Fang et al. 1997; Sharp et al. 1997; Tom et al. 1999; Rossi and Snyder 2001
Protein concentrations and the free amino-acid pool	Kendall et al. 1985
Coral diseases	Santavy and Peters 1997; Porter et al. 2001; Santavy et al. 2001; Nugues 2002
Loss of zooxanthellae	Jones 1997

biodiversity value (Done 1995), the coral reef health index (Hodgson 1999), and the Deterioration Index (Ben-Tzvi et al. 2004). These multimetric indicators are supposed to be more sensitive since they may respond to several stresses. However, the effectiveness and reliability of some of these potential indicators were severely critiqued (in Brown 1988; Brown et al. 1990; Edinger et al. 2000). Moreover, several of these indicators are difficult to incorporate into long-term monitoring programs, since they generally involve expensive equipements and laborious laboratory analyses, and need technical expertise to be interpreted.

Despite the fact that corals are the key component of the reef ecosystem, measuring the effects of disturbances on other target reef communities may offer complementary information to assess changes in coral reef community structure, especially of the cascading effects that follow a major disturbance. For example, surveys of temporal trends of the coral/macroalgae or coral/clionid cover (Schönberg 2001; Schönberg and Wilkinson 2001; Bouchon et al. 2004), bioeroder organisms (Holmes 1997), or disease incidence and virulence of some marine invertebrates (Harvell et al. 1999), may provide complementary indication of reef health. Mortality rates and changes in benthic and fish assemblages following natural disturbances may also be indicative of the intensity of the impacts (Kaufman 1983; Williams 1986; Chabanet et al. 1995; Lewis 1998; Lindahl et al. 2001).

The critical analysis of the available information and our results lead us to think that monitoring surveys could be improved by selecting different and complementary indicators, as suggested by several authors (Dale and Beyeler 2001; Hallock et al. 2004; Niemi and McDonald 2004). In order to detect the impacts of natural disturbances on coral assemblages, we propose to integrate three types of coral indicators: one that gives information of the variation in diversity (the generic richness, which avoid the identification difficulties, is sufficiently informative), one estimating changes in the abundance/coverage, and one estimating the potential for recovery following the disturbance (for example, by studying the density of recruits/juveniles; Pearson 1981; Connell et al. 1997; McClanahan 2000; Ridgway and Hoegh-Guldberg 2002; Ben-Tzvi et al. 2004).

5 Conclusion

Despite the recent efforts to identify and select indicators of reef health, it is clear that there is much to be done before standardized and reliably indicators of the impacts of natural disturbances on coral reef health are developed (see Dale and Beyeler 2001; Jameson et al. 2001). There is a critical need for additional physiological and observation studies to identify indicators species of certain type of perturbations (Jameson et al. 2001). Measuring molecular parameters appears difficult within the framework of a monitoring program, and yet there is also an urgent need to develop reliable technologies to quickly determine the coral physiological status.

However, "classical" monitoring surveys may provide usefull information on the impacts of natural perturbations on reef communities. These surveys could be largely improved, by clearly integrating several spatial scales, by selecting at least the most informative species, and by focussing on three main types of indicators: diversity, abundance/coverage, and recruitment/recovery patterns. These monitoring programs should be also associated with high frequency recordings of environmental parameters (such as SSTs), as a complementary tools for identifying causal relationships. However, the type of monitoring programs that could be initiated is largely dependent of practical constraints such as the available expertise, logistic and fundings (Brown et al. 2004; Niemi and McDonald 2004).

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