Long term monitoring of coral and fish assemblages (1983-2014) in Tiahura reefs, Moorea, French Polynesia

by

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Abstract. – Coral reefs are one of the most diverse ecosystems on Earth and sustain millions of people worldwide. However, coral reefs are temporally dynamic and fragile systems subject to ever increasing disturbances of anthoropogenic and natural origins. Understanding the patterns and trajectories of changes through time is urgently needed to estimate the resilience of coral reefs. To ascertain these patterns, we depend on the availability of long-term datasets, which are seldom available. In this study, we present the data set which allowed us to analyse the long-term trends of coral and fish assemblages for the island of Moorea (French Polynesia) from 1983 to 2014, a dataset spanning 32 years, comprising two *Acanthaster planci* outbreaks (1987 and 2006) and several hurricanes (1982, 1983, 1991 and 2010), on three permanent monitoring sites (quadrats of 50×2 m^2) located on both fringing and barrier reefs as well as on the outer slope. Coral cover oscillated significantly over time, particularly on the outer slope where it suffered greatly from the effects of *A. planci* outbreaks and hurricanes. Total fish and commercial fish abundances varied significantly across the three habitats. Prior to 2000, both total fish and herbivorous fish abundances increased on the barrier reef while after this time, numbers began to drop significantly along the outer slope. Species richness for total, commercialized and herbivorous fish increased over the sampling period for all three habitats. There were varied responses amongst species to disturbances on the outer slope over the sampling period: while some tended to disappear for a while before reappearing, others showed a peak in abundance in the middle of the sampling period, and still others increased or decreased continuously or were stable over time. Our results support the view that coral reefs are highly dynamic systems and that different functional groups show different temporal trajectories. While disturbance is probably the major driver for coral cover dynamics, its impact is less obvious for fish, possibly due to their mobility and population dynamics which may mask the effect of disturbance.

Résumé. – Suivi à long terme des assemblages de coraux et de poissons (1983-2014) sur le récif de Tiahura, Moorea, Polynésie française.

Les récifs coralliens sont des systèmes dynamiques et diversifiés régulièrement soumis à des perturbations naturelles et anthropiques, sources d'hétérogénéité spatiale et temporelle dans la structure et la dynamique de ces communautés d'organismes que sont, entre autres, les poissons et les coraux. Récemment, il a été démontré que les activités humaines pouvaient modifier les régimes naturels de perturbations des récifs coralliens en transformant les événements ponctuels en perturbations persistantes ou en stress chronique, soit en introduisant de nouveaux types de perturbations, soit en ajoutant ou altérant certaines perturbations naturelles nécessaires au bon maintien de la dynamique inhérente aux récifs. Dans cette étude, nous présentons la base de données qui nous permettra d'analyser les tendances à long-terme des assemblages de poissons et de coraux de l'île de Moorea (Polynésie française) entre 1983 et 2014 sur une période de 32 ans, comprenant deux proliférations d'*Acanthaster planci* (1987 et 2006) et plusieurs cyclones (1982, 1983, 1991 et 2010), sur trois sites de suivi permanents (quadrats de 50×2 m^2) sur les récifs barrière et frangeant ainsi que sur la pente externe. La couverture corallienne présente de fortes oscillations, en particulier sur la pente externe où elle a répondu fortement à la prolifération d'*A. planci* et des cyclones. Les abondances des poissons totaux et des poissons commercialisés montrent des tendances contrastées sur les trois habitats, avec, plus particulièrement, une augmentation sur le récif barrière et une diminution sur la pente externe après 2000. Ces tendances se retrouvent chez les poissons herbivores dans ces deux habitats. La richesse spécifique des poissons totaux, commerciaux et herbivores, augmente de façon continue au cours de la période d'étude dans les trois habitats. Des groupes particuliers d'espèces répondent différemment aux perturbations de la pente externe au cours du suivi : alors que certaines espèces ont tendance à disparaître pendant quelques années avant de réapparaître, d'autres présentent un pic en terme d'abondance en milieu de suivi ; d'autres espèces ont des abondances qui augmentent ou diminuent de façon continue, et d'autres encore montrent des abondances stables. Ceci indique que les récifs coralliens sont des systèmes très dynamiques dans lesquels les perturbations naturelles peuvent affecter les espèces de façon différente. Alors que le régime de perturbations naturelles semble être important pour la dynamique de la couverture corallienne dans certains habitats, cela se retrouve beaucoup moins pour les poissons. Cette atténuation des fluctuations spatiales et temporelles peut être due aux aptitudes de dispersion de nombreuses espèces de poissons, capables de chercher un autre habitat favorable en cas de perturbation de l'habitat corallien d'origine.

There is little doubt that the Earth's biodiversity is experiencing unprecedented decline (Riciardi and Rasmussen, 2000; Sala and Knowlton, 2006; Barnosky *et al*., 2011). This decline is driven by both natural and anthropogenic pressures and today there is great concern that our depleted systems may now lack the ability to perform basic ecological functions necessary to provide services on which all humans depend (Worm *et al*., 2006).

Coral reefs are one of the most diverse ecosystems on Earth (Parravicini *et al.,* 2013). In addition to their biological and ecological importance, coral reefs support major economic and physical functions (food production, tourism, biotechnology development and coastal protection) that sustain people and nations worldwide (Costanza *et al*., 1997). This is particularly true in the Pacific, where coral reefs are the lifeblood for local people and economies for a great number of Pacific Islands and Territories (Wilkinson and Souter, 2008). Unfortunately, the frequency and severity of natural and anthropogenic perturbations on coral reefs globally have greatly increased over the last three decades, leading to unprecedented levels of mortality across reef communities (fish, corals and benthic invertebrates) (e.g. Salvat, 1980; Hughes *et al*., 2005; Wilkinson and Souter, 2008; Burke *et al*., 2011). With the abundance and severity of today threats, there is increasing concern for the future of coral reefs. Recent global analyses indicate that 75% of the world coral reefs are severely threatened by local and global anthropogenic pressures, and it is projected that by 2050, 90% of coral reefs will be at risk (Wilkinson and Souter, 2008; Burke *et al.,* 2011). Within this context, and to ensure the persistence of corals through time, we must drastically improve our collective understanding of reef resilience and their capacity to recover from disturbance (Connell and Sousa, 1983). To do this, we must have access to robust, long-term datasets which are today uncommon for most regions of the world (Bruno and Selig, 2007). A handful of studies have used long-term monitoring data to gain insight into the impacts that disturbances – natural and anthropogenic – are having on coral reefs around the world (Wilkinson and Souter, 2008). In the Caribbean, for example, researchers have documented a dramatic phase shift, from a hard coral-dominated community to one dominated by fleshy algae, in response to disturbance (Hughes, 1994; Hughes *et al.,* 2010).

Over the past few decades, not only research methods have evolved, but so have the disturbances themselves and the ability of reefs to recover (e.g. Connell, 1978; Holling *et al*., 1995; Hughes and Connell, 1999). Reef degradation is a key driver for the loss of critical ecosystem goods and services provided by coral reef fishes (Pratchett *et al*., 2008). Humans play a major role in this degradation, as our impact on natural ecosystems continues to increase over time (Vitousek *et al*., 1997). Human activities alter the natural disturbance regimes of coral reefs by transforming pulse events into persistent disturbances or even chronic stress, through the introduction of new disturbances, or by suppressing or removing disturbances essential for maintaining natural dynamics of coral reefs (e.g. loss of grazing due to overfishing) (Holling and Meffe, 1996). Exacerbating natural disturbance regimes further stresses already compromised coral reef communities, forcing them to respond in new and unpredictable ways (Nystrom *et al*., 2000). A coral reef ecosystem response to natural and human disturbances is referred to as resilience. Ecosystem resilience reflects the ability of a system to experience change, while at the same time retaining its ability to control function and structure, allowing it to remain within a state of coral dominance (Holling *et al*., 1995; Montefalcone *et al*., 2012).

In this study, we present over 32 years of monitoring data (1983-2014) to describe how coral and fish communities in Moorea, French Polynesia, have evolved through time. This long-term dataset allowed us to document how a coral ecosystem responds to change over a long period of time and how, during these periods of change, reefs maintain functionality and structure. Long-term datasets for coral reefs are seldom seen in the scientific literature. With more than 32 years of continuous data collection, our database is one of the world oldest alongside similar data sets for the Great Barrier Reef in Australia, and for the Caribbean. Today, students and post-doctorate researchers at CRIOBE as Lamy *et al*. (2015) can access the database freely, where they use it regularly to investigate hypotheses pertaining to the resilience of coral reefs in North-West Moorea.

MATERIALS AND METHODS

Study area and disturbance history

Moorea Island (17°30'S, 149°50'W; French Polynesia) is surrounded by a coral reef of 61 km in length and 750 m mean width. The first census of marine organisms in Moorea was conducted in 1971 (Salvat *et al*., 1972). At that time, there were no major recent natural disturbances; prior to this time, the most recent and important hurricane was in 1906, at which time human pressure was almost non-existent (Auzeneau and Darchen, 1983). Since then, indirect and direct human pressures have increased (Aubanel, 1993) and several major natural disturbances have occurred: strong tropical hurricanes in late 1982, early 1983, December 1991 (Wasa) and January 2010 (Oli); huge *Acanthaster planci* (Crown-of-Thorns Starfish – COTS) infestations in 1980, 1981, 1987 and 2006; and coral-bleaching events in March-May 1983, March-April 1987, March-July 1991, March-August 1994, and April-August 2002 (Adjeroud *et al*., 2005). Bleaching events corresponded to periods when sea surface temperatures rose above 29.2°C (i.e. thermal threshold for corals; Hoegh-Guldberg, 1999).

Sampling strategy

After the *Acanthaster planci* outbreaks and hurricanes events in the eighties, a long-term coral and fish monitoring program was implemented in Moorea. Three permanent monitoring sites (50 m × 2 m quadrats) were established on the north-western part of the island (Tiahura sector), two in the lagoon and one on the outer slope (Fig. 1). These three sites corresponded to the reef zones where the diversity and abundance of coral and fish assemblages were the highest (see Galzin, 1985, 1987a, b; Adjeroud, 1997).

To census fish populations, divers swam through each quadrat twice. On the first swim, the diver swam quickly (> 5 m.min^{-1}) and recorded 'transient' fishes, those which were in the vicinity of the quadrat but which consistently fled at the diver approach. On the second swim, the diver swam more slowly (< 1 m.min^{-1}) and recorded sedentary species.

This survey protocol was repeated four times per day for each quadrat, as temporal replicates (vs. spatial replicates) are essential for temporal studies (Galzin, 1987b). Data were collected twice a year from 1987 to 2014, in austral winter and in austral summer. Seasonal averages were then calculated for each year, from data collected during this period. Each species was classified into three functional groups (diet, habitat use, and maximum body size) using published data (Galzin, 1985, 1987a, b; Galzin and Harmelin-Vivien, 2002; Lecchini and Galzin, 2005) in conjunction with our own unpublished observations. A list of the 280 species found in the area, complete with detail on their functional groups, was published in 1997 (Legendre *et al.*). A functional group was defined as a collection of species that show similar traits, regardless of their taxonomic affinities (Steneck and Dethier, 1994).
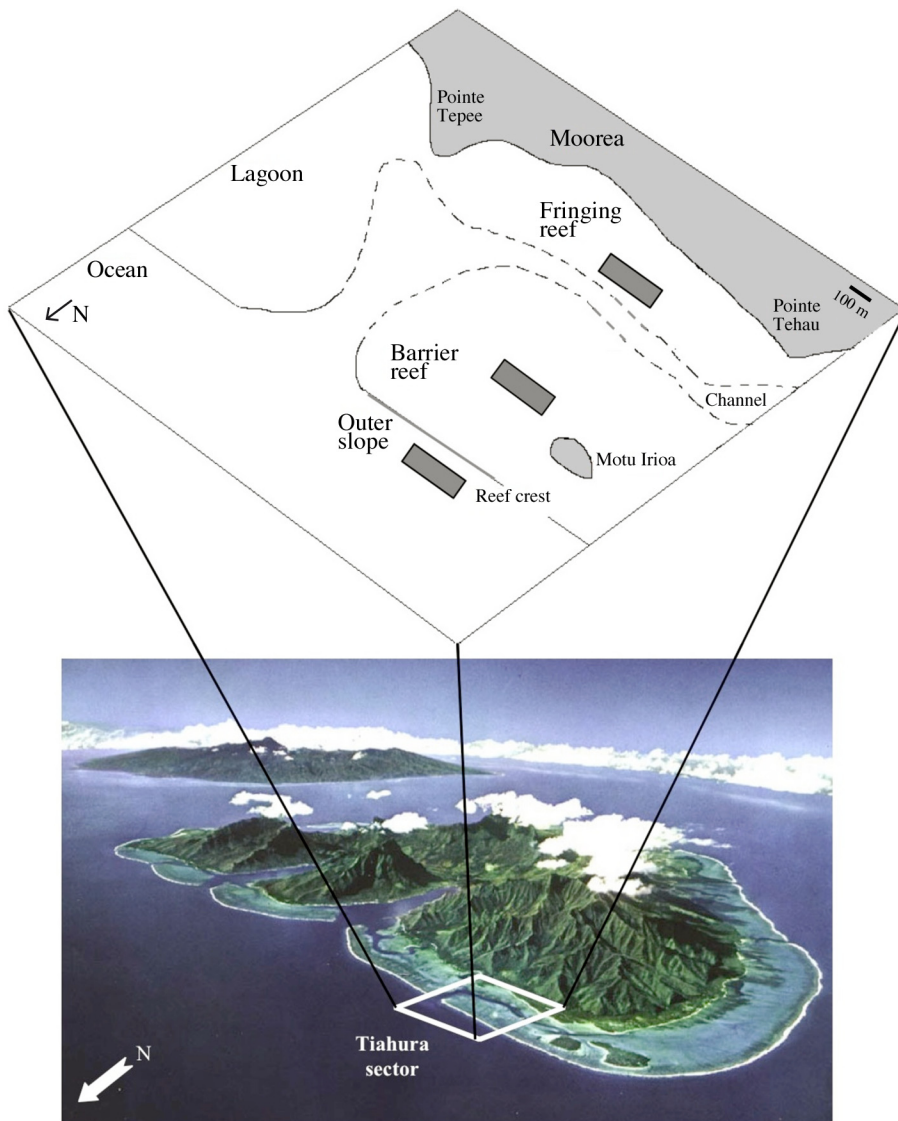

Figure 1. - Location of Tiahura sector in Moorea and layout of the sampling sites (quadrats of 50 × 2 m) in the three habitats (fringing and barrier reefs, outer slope).

Beginning in 1987, corals were surveyed on an annual basis, in summer, along one 50 m transect set up in the middle of each quadrat. The Point Intercept Transect Method was used, with points located at every meter, to estimate coral cover (Loya, 1978). The surface of coral colonies tends to comprise mosaics of living tissue in combination with dead skeletal patches. We assigned the label "live coral colony" when living tissues exceeded 80% and "dead coral colony" when living coral cover was < 80% (Mumby *et al.*, 2001). Following mortality, the calcareous corallite structure of the coral polyp tends to progressively disappear through bioerosion. We assigned this process the label "coral rubble". Data were collected annually from 1983 to 2014 (October).

In order to detect overall trajectory for both coral and fish communities, we employed descriptive statistics and the visual inspection of time-series to describe and infer *a posteriori* potential relationships of the observed trends with major known disturbance events. Linear regression models were fitted to the temporal trajectory of coral percentage cover, total, commercial and herbivorous fish abundance and species richness in the three habitats. Significance was assessed using a Fisher's F test. When linear relationships were not significant (i.e. $p > 0.01$), second-degree polynomial (multiple linear regression) models were fitted to highlight curvilinear trends in the data, and significance was assessed using Fisher's F test.

RESULTS

All coral and fish results

Percentage cover of living corals ranged from 0 to 64.7% (all years and habitats combined) (Fig. 1). It varied between 5.9 and 41.2% on the fringing reef, and between 5.9 and 37.5% on the barrier reef. On the outer slope, cover was generally high (from 23.5 to 62.5%) between 1987 and 2006 (except in 1993), decreased to 12.5% in 2007, and then to zero in 2009. A slight recovery was detectable in 2014 (18.8% coral cover). Total fish abundance over 100 m^2 ranged from 81 to 1115 individuals and total species richness ranged from 37 to 109 (all habitats considered) (Fig. 2). Fish were more abundant and more diverse on the outer slope (from 251 to 1115 individuals and from 67 to 109 species per 100 m^2). The abundance of commercial fish species ranged from 20 to 156 individuals and from 14 to 48 species per 100 m^2 in all habitats. They were also more abundant and more diverse on the outer slope than in the two reef flat habitats. Herbivorous fish abundance varied between 1.8 and 118 individuals per 100 m^2, and their richness
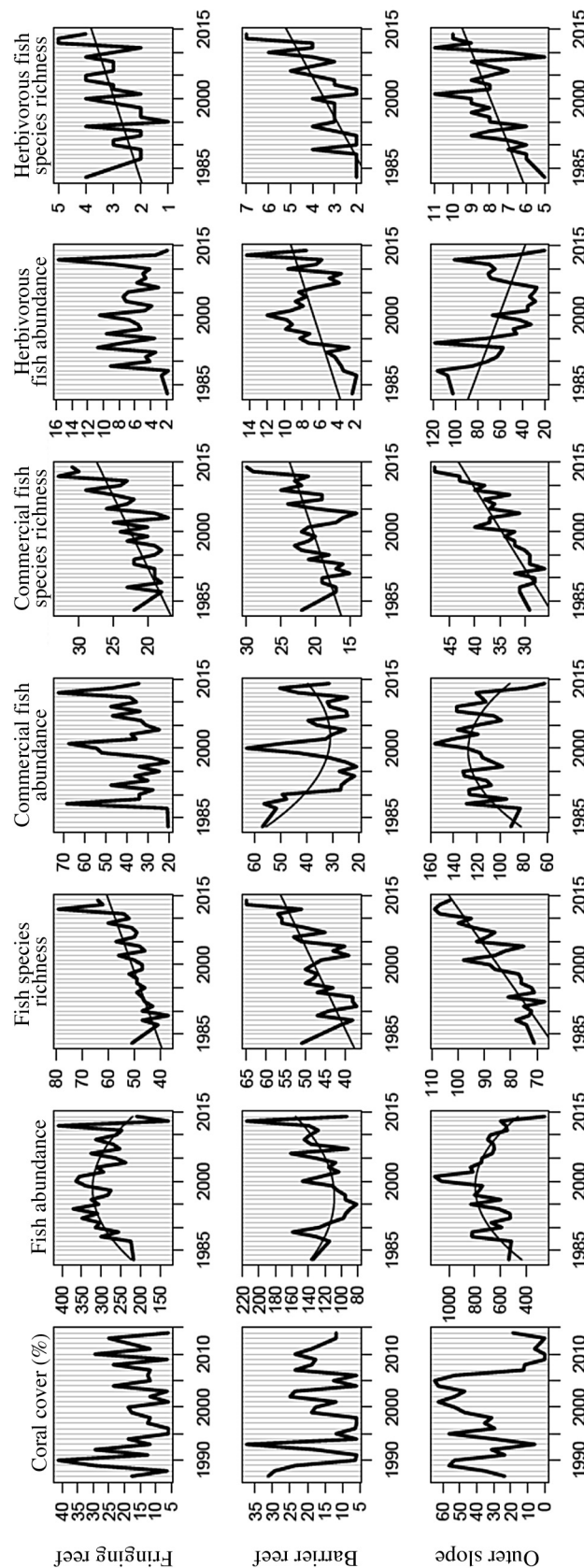

Figure 2. - Coral percentage cover, total, commercial and herbivorous fish abundance and species richness in the three habitats at Tiahura sector in Moorea over their corresponding sampling period. Linear and polynomial (second degree) models are plotted when significant (levels of significance and adjusted R squared are given in Fig. 4 to Fig. 9).
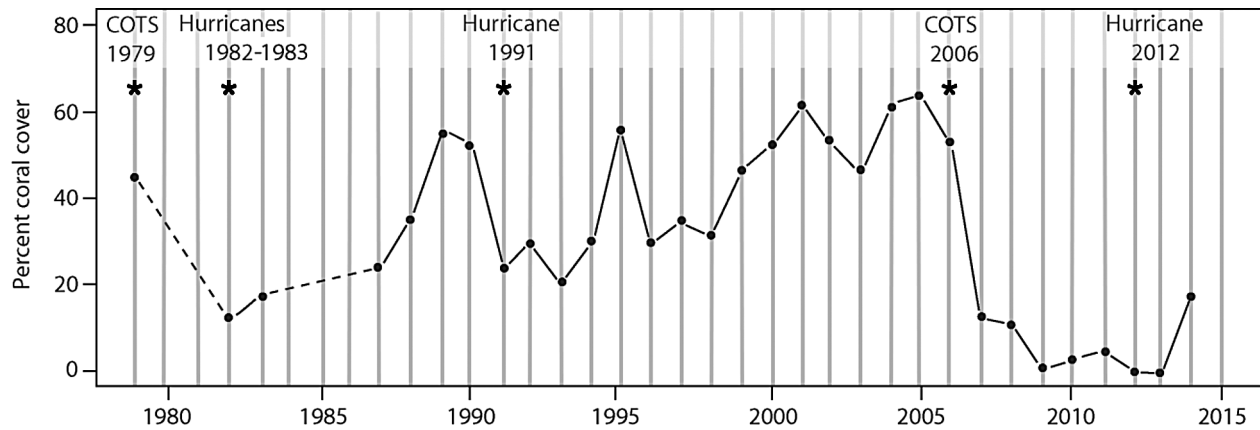
Figure 3. - Temporal dynamics in coral percentage cover on the outer slope of Tiahura sector from 1979 to 2011. Stars denote the five main disturbances that affected the reef over the study period (COTS: *Acanthaster planci* outbreak). Dotted lines correspond to linear interpolation of coral percentage cover.
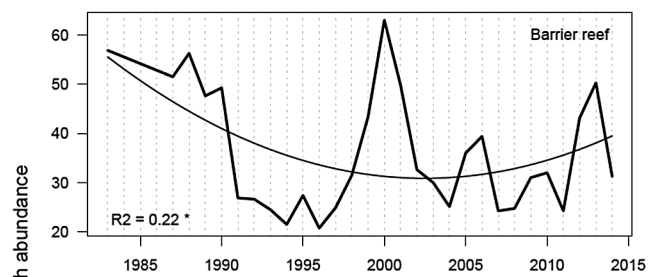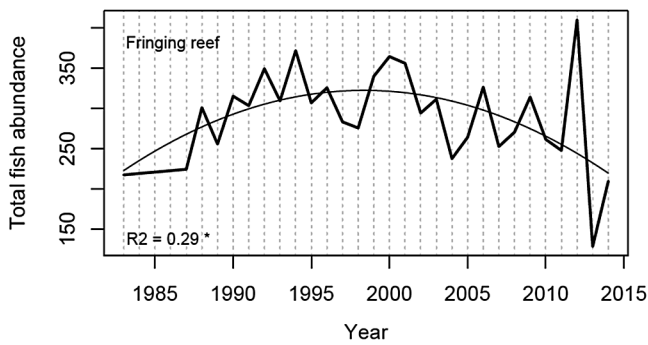

Figure 4. - Total fish abundance at Tiahura sector in Moorea for the fringing reef. Second degree polynomial models were fitted to data (*: $0.01 < p \leq 0.05$, **: $0.001 < p \leq 0.01$).
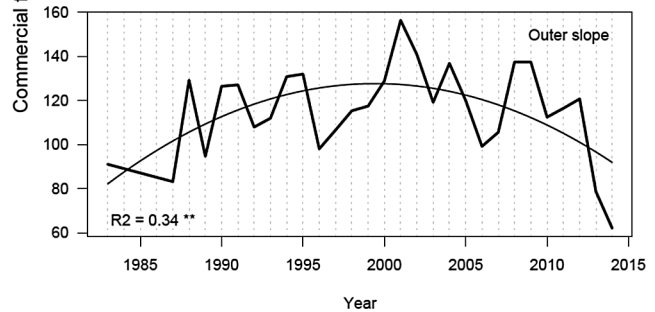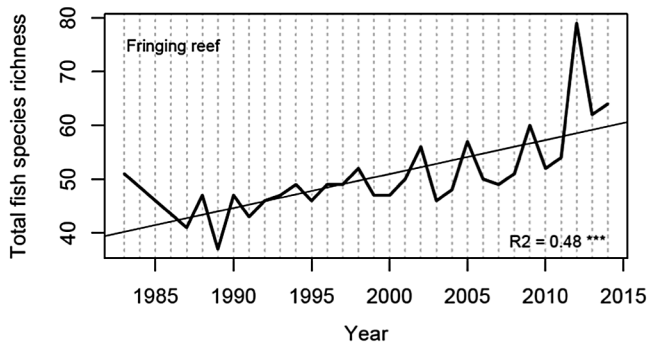

Figure 5. - Total fish species richness at Tiahura sector in Moorea for the fringing reef. Linear models were fitted to data (***: $p \leq 0.001$).

Figure 6. - Commercial fish abundance at Tiahura sector in Moorea for the barrier reef and outer slope. Second-degree polynomial models were fitted to data (*: $0.01 < p \leq 0.05$, **: $0.001 < p \leq 0.01$).

fish events (COTS) in 1979, hurricanes in 1982, 1983, 1991, COTS in 2006, hurricane in 2012 and multiple bleaching events (Bouchon, 1985; Bouchon-Navaro *et al*., 1985; Faure, 1989; Salvat, 1992; Hoegh-Guldberg and Salvat, 1995; Augustin *et al*., 1997; Adjeroud *et al*., 2002, 2005, 2009; Kayal *et al*., 2012).

Fish variations

According to the fitted polynomial model, for fringing reefs and the outer slope, total fish abundance increased until 1999 and decreased thereafter (Figs 2, 4). Conversely, the barrier reef fish abundance decreased until 1997 and then increased. For the three habitats, total fish species richness

between 1 and 11 species. Again, abundance and species richness were higher along the outer slope habitat.

Variation in coral cover on the outer slope

On Tiahura reef, living coral cover on the outer slope showed annual variations over the past 32 years (Fig. 3), due to multiple natural disturbances: crown of thorn star-
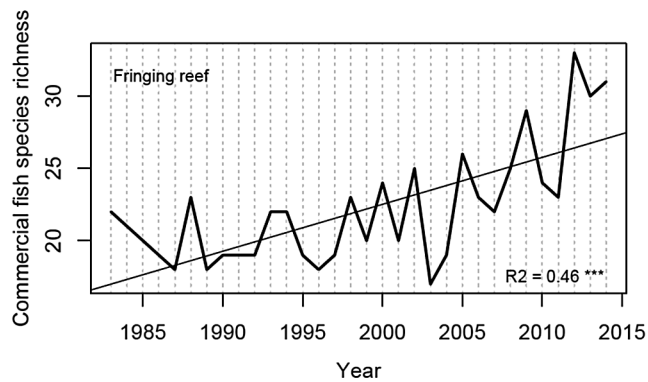
Figure 7. - Commercial fish species richness at Tiahura sector in Moorea for the fringing reef. Linear models were fitted to data (**: 0.001< p≤ 0.01; ***: p ≤ 0.001).
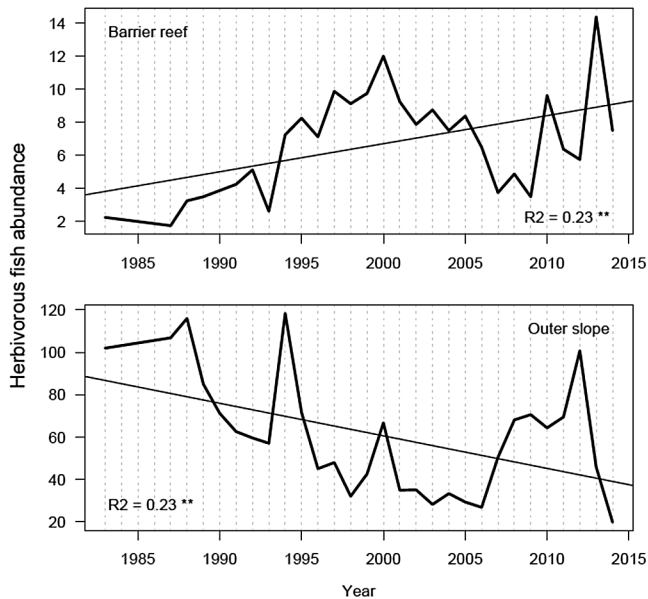

Figure 8. - Herbivorous fish abundance at Tiahura sector in Moorea for the barrier reef and outer slope. Linear models were fitted to data (**: 0.001 < p ≤ 0.01).
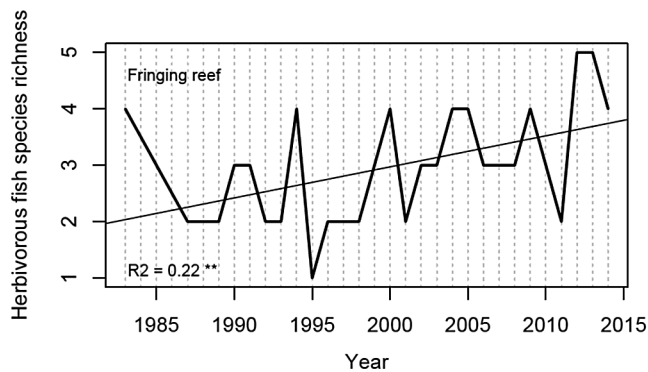

Figure 9. - Herbivorous fish species richness at Tiahura sector in Moorea for the three habitats. Linear models were fitted to data (**: 0.001 < p ≤ 0.01; ***: p ≤ 0.001).

increased regularly over the sampling period (Figs 2, 5). The most pronounced pattern occurred on the outer slope, with 70 species in 1983 and 100 species in 2014.

Commercial fish abundance showed contrasting patterns on the barrier reef and on the outer slope (Figs 2, 6). While it decreased until 2003 on the barrier reef (with a strong dip in 2000), it increased until 2000 on the outer slope. No significant trend could be observed on the fringing reef. Commercial fish species richness increased steadily over the sampling period across the three habitats (Figs 2, 7).

Herbivorous fish species abundance increased slowly on the barrier reef but decreased on the outer slope during the study period (Figs 2, 8). No significant trend could be observed on the fringing reef (not represented). The species richness of herbivorous fish continuously increased between 1983 and 2014 in all three habitats, with a strong decline on the fringing reef in 1995, on the barrier reef in 2001-2002 and on the outer slope in 2009 (Figs 2, 9).

**Species profiles on the outer slope**

On the outer slope, five distinct profiles were identified to describe the abundance dynamics of several fish species (Fig. 10). Within this study, we narrowed our focus to a single habitat as we wanted focus to remain on the richness and potential of the database itself and not on a detailed analysis of the data. This database clearly shows a number of large and important patterns of change within Moorea's reef communities and future students of CRIOBE will examine these changes in greater detail.

DISCUSSION

With the current rapid global change arising from intricate climatic and anthropogenic factors and causing abrupt changes in biological communities, ecologists are increasingly aware that they have limited knowledge of the processes affecting communities over time (McLean and May, 2007). This is partly due to the limited availability of accurate long-term data (i.e. community-wise) with sufficient geographical extent, specifically with respect to the marine environment. Accordingly, the IPCC (Intergovernmental Panel on Climate Change) Fourth Assessment Report (2007) noted 28,586 significant long-term monitoring programs in terrestrial systems, but only 85 from marine and freshwater systems. Long-term monitoring can provide answers to, among others, two key questions concerning the temporal components of biodiversity: (1) what is the underlying level of temporal turnover in a community, and (2) is biodiversity changing relative to this turnover (e.g. due to anthropogenic impacts or in response to an experimental treatments)? Long-term monitoring allows scientists, conservationists and, in our case, reef managers concerned with maintaining

Pomachromis.fuscidorsalis - Outer slope
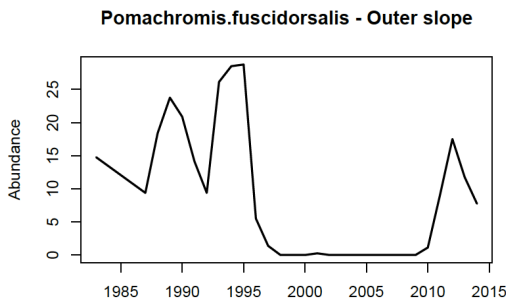
Pomachromis fuscidoraslis **profile**. These species were usually very abundant during the 1980's. They then disapeared for one to 20 years before showing out again. The species typical of this profile were Chaetodons (*Chaetodon ulietensis*, *C. unimaculatus*, *C. quadrimaculatus*), Cirrhitidae (*Nemateleotris magnifica* and *Paracirrhites hemistictus*), Mullidae (*Parupeneus multifasciatus*), Holocentridae (*Sargocentron caudimaculatum* and *S. microstoma*), and Scaridae (*Scarus rubroviolaceus* and *Cetoscarus ocelattus*).

Cephalopholis.argus - Outer slope
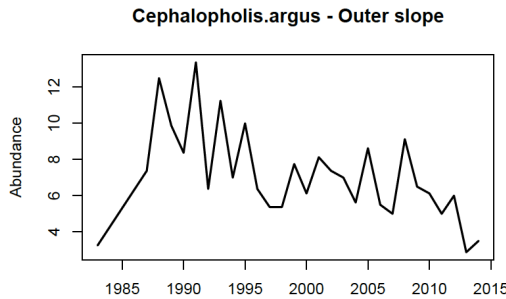
Cephalopholis argus **profile**. Fish abundance of these species decreased slowly from 1983. This profile concerned: Pomacentridae (*Abudefduf sexfasciatus* and *Chromis xanthura*), Acanthuridae (*Acanthurus nigricans* and *Ctenochaetus striatus*), Labridae (*Cirrhilabrus scottorum*, *Coris gaimard*, *Halichoeres melasmapomus*, *Hemigymnus fasciatus*, *Labroides dimidiatus*), Scaridae (*Chlorurus sordidus* and *Scarus oviceps*), Lethrinidae (*Lethrinus xanthochilus*), and Lutjanidae (*Lutjanus kasmira*).

Dascyllus.flavicaudus - Outer slope
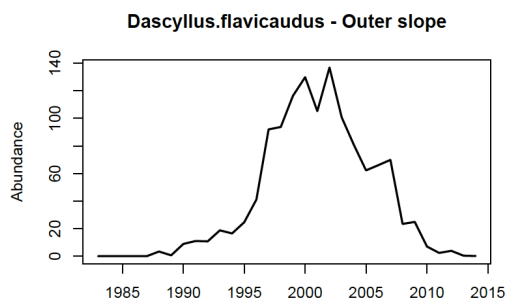
Dascyllus flavicaudus **profile**. Species in this profile were scarce at the beginning of the sampling period, but reached high abundances in the 1990's and 2000's, before decreasing again. These species were: Pomacentridae (*Chromis agilis*, *C. margaritifer* and *Plectroglyphidodon johnstonianus*), Acanthuridae (*Acanthurus nigricauda*, *A. nigrofuscus*, *Ctenochaetus flavicauda* and *Naso lituratus*), Labridae (*Cheilinus oxycephalus*, *Epibulus insidiator*, *Gomphosus varius*, *Labroides bicolor*, *Oxycheilinus unifasciatus*), Scaridae (*Calotomus carolinus* and *Scarus longipinnis*), Chaetodontidae (*Chaetodon ornatissimus*, *C. pelewensis*, *C. reticulatus*, *Forcipiger longirostris*), Balistidae (*Aluterus scriptus*, *Balistapus undulatus*, *Melichthys vidua*, *Odonus niger*), Pomacanthidae (*Centropyge loriculus*, *Hemitaurichthys polylepis*), Lethrinidae (*Aphareus furca*, *Gnathodentex aureolinatus*), Aulostomidae (*Aulostomus chinensis*), Caracanthidae (*Caracanthus maculatus*), Serranidae (*Cephalopholis urodeta*), Carangidae (*Elegatis bipinnulata*), and Cirrhitidae (*Paracirrhites fosrteri*).

Scarus.psittacus - Outer slope
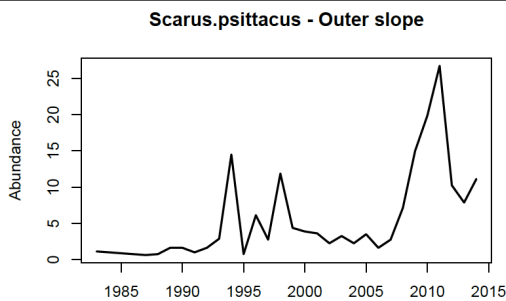
Scarus psittacus **profile**. These species showed increasing abundances along the sampling period. Within this profile can be found: other Scaridae (*Scarus globiceps*, *Chlorurus frontalis* and *C. microrhinos*), Pomacentridae (*Chromis acares* and *Plectroglyphidodon lacrymatus*), Cirrithidae (*Cirrhilabrus exquisitus* and *Parracirrhites arcatus*), Labridae (*Halichoeres claudia*, *Labroides rubrolabiatus*, *Macropharyngodon meleagris*, *Pseudocheilinus evanidus*, *P. hexataenia*, *P. tetrataenia*, *P. atavai*), Holocentridae (*Myripristis berndti* and *M. kuntee*, *Sargocentron caudimaculatum* and *S. microstoma*), Acanthuridae (*Acanthurus pyroferus*), Pomacanthidae (*Canthigaster solandri*), and Blenniidae (*Plagiotremus tapeinosoma*).

Dascyllus.trimaculatus - Outer slope
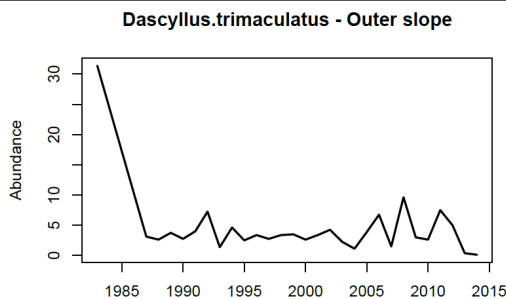
Dascyllus trimaculatus **profile**. These species were found to have nearly constant abundances over the sampling period. In this profile were: another Pomacentridae (*Chromis iomelas*), Labridae (*Halichoeres hortulanus*, *Hemigymnus fasciatus*, *Pseudocheilinus octotaenia*, *Stethojulis bandanensis*), Acanthuridae (*Acanthurus thompsoni*, *Naso brevirostris*, *N. hexacanthus*), Scaridae (*Scarus altipinnis*, *S. forsteni*, *S. niger* and *S. rubroviolaceus*),

Figure 10. - Different fish abundance dynamic profiles between 1983 and 2014 on the outer slope at Tiahura sector in Moorea.

biodiversity, to better understand two main attributes of an ecosystem with respect to external drivers: (1) resistance, the amount of external force a system can absorb without a qualitative change; and (2), resilience, the tendency of a system to return to its previous state after a disturbance (e.g. Nystrom and Folke, 2001; Roff and Mumby, 2012). Our long-term monitoring program in Moorea allowed us to highlight the trajectory of change for coral and fish communities from 1983 to 2014 (32 years).

Effects of natural and human disturbances on coral and fish assemblages

The coral ecosystem in Moorea was first studied in 1971 (Salvat *et al.*, 1972) and a monitoring program for both coral and fish assemblages began in 1983. During this period (1983-2014), three major coral-bleaching events, two crown of thorns starfish events and two tropical storms occurred in Moorea. These disturbances have always affected coral, algae and fish assemblages, but their impacts varied greatly in space (lagoon *vs.* outer slope) and time (see Fig. 2). For example, the December 1991 hurricane reduced fish abundance on the outer slope (748 fish in October 1991 vs. 531 fish in April 1992), but not in the lagoon (278 fish in October 1991 vs. 445 fish in April 1992). The 1991 bleaching event reduced the live coral cover on the outer slope (29 live coral colonies recorded along the transect in 1990 vs. 19 in 1991), while the live coral cover increased on the outer slope after the 1994 bleaching event (6 live coral colonies in 1993 *vs.* 16 in 1994). Yet, the magnitude of the bleaching event (i.e. the proportion of bleached colonies) and the order of susceptibility of coral genera were similar in 1991 and 1994 (Adjeroud *et al.*, 2002*)*, whereas mortality at the end of the event was greatly reduced in 1994, explaining why the coral cover did not decrease between 1994 and 1995. One possible explanation is that most of the colonies present in 1994 were those that survived the 1991 event or were young recruits derived from those colonies. We can assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events (Hoegh-Guldberg, 1999).

Disturbances can be detrimental to individual reef organisms, and recovery depends largely on the type of disturbance (i.e. its intensity and duration) and on the history of the reef (i.e. the chronology of disturbances). After each disturbance, new substratum becomes available, which creates opportunity for new growth and expansion of older colonies to occur, a scenario commonly observed on the outer slope in Moorea (i.e. decrease of encrusting algae cover over many years has favoured an increase of live coral cover, which has most likely driven an increase of fish abundance from 1987 to 2004). Disturbances enhance species diversity and stimulate the development of community structure and dynamics of coral reef organisms. Human derived dis-

turbances are generating additional stress on coral reef ecosystems, which can alter the temporal and spatial scales of natural disturbance regimes, which in turn may affect a reef potential for recovery following disturbance (Hoegh-Guldberg, 1999). The human population in Moorea, increased nearly fifteenfold from 1971 to 2014 (from 1034 to 15,500 inhabitants) and hotel capacity has increased five times from 125 rooms in 1971 to 620 rooms in 2014. This increase in human pressure on the Moorea lagoon, combined with natural disturbances, could generate compounded perturbations unfamiliar to coral organisms, leading to unpredictable synergistic effects and ecological surprises (i.e. disappearance of macro-algae and relative stability of live coral cover over time in the Moorea lagoon).

Ecosystem resilience

The concept of ecosystem resilience, or the capacity of complex systems to absorb disturbance, reorganise, and adapt to change (see review of Nystrom *et al.*, 2000), is central in our study. A reef capacity to buffer itself in response to disturbance is determined by characteristics such as genetic variability, the number of species involved in ecological processes on different hierarchical levels, functional groups of species, and the variability of habitats (e.g. Done *et al.*, 1996; Chapin *et al.*, 2000).

In the Moorea lagoon, we did not detect the classic shift from coral-dominated to algae-dominated communities. Macroalgae disappeared after the 1994 bleaching event. This shift in habitat assemblage is probably responsible for the changes in the composition of the associated fish communities. Coral reef fishes are thought to be relatively robust to population fluctuations because their dispersive larval phase enables declines in abundance at one location to be replenished by recruitment from other parts of the population (Sale, 1991). However, as the spatial scale of disturbance to coral reefs increases, population connectivity is no longer sufficient to buffer local populations against persistent declines. Thus, since 1994-1995, the abundance and species richness of fish decreased in the Moorea lagoon resulting in a shift within functional groups (decrease of herbivorous and planktivorous fish living inside coral colonies and of the 0-15 cm size class). Species composition was different between 1987 and 2014 with an increase in Labridae (small carnivores) in favour of a decrease in Acanthuridae (herbivores). The loss of habitat diversity has then been detrimental to fish assemblages in Moorea lagoon. Habitat loss is often a major factor driving population decline and extinction of both terrestrial and marine species (Vitousek *et al.*, 1997; Hughes *et al.*, 2005). Predicting the risk of species extinctions from this type of habitat degradation is one of the most challenging and urgent tasks faced by ecologists (Thomas *et al.*, 2004). The question we now want to answer is when will lagoonal fish assemblages in Moorea decrease in abundance

and species richness, and will this result in a change within functional groups?

In contrast, the outer slope assemblage in Moorea demonstrated ecosystem resilience. Despite frequent disturbances, ecosystem development on the outer slope has followed the same trend since 1987 with respect to coral cover, fish abundance and functional diversity. Functional diversity, the presence of multiple species that fill similar ecological roles, may potentially provide alternative ways of maintaining key ecosystem functionality in the face of change (e.g. Walker *et al*., 1999; Chapin *et al*., 2000). The 1994 bleaching event caused a decrease in abundance of Labridae and Acanthuridae. This decrease was immediately counterbalanced by an increase of Pomacentridae, a family which shares similar ecological role. Thus, the impact of bleaching in 1994 is only detectable within the composition of fish families due to a high functional diversity of the fish assemblage on the outer slope. Ecosystem stability depends on the ability of a system to support its individuals or functional groups as they respond in multiple ways to disturbance. Indeed, a loss of diversity within or among functional groups can lead to simplification of coral reef habitats, reduce functional plasticity and decrease the ability to buffer disturbances (McClanahan and Muthiga, 1998; Kinzie, 1999; Wilkinson, 1999).

The trend we have observed for Moorea is much different from what scientists have observed in Caribbean. Here, coral reefs have experienced an extreme transition over the past two to three decades, from hard coral dominated communities to communities now dominated by fleshy algae, likely due to the loss of diversity within the functional group of herbivores, and resulting in reduced resilience (Hughes, 1994). Frequent natural and human derived disturbances have precipitated this phase shift, as these reefs are now forced to adapt quickly between periods of recovering and decline (Gardner *et al*., 2003; Jones *et al*., 2004; Hughes *et al*., 2005). Today, Moorea outer reef slope continues to be dominated by hard corals (where hard corals continue to out compete encrusting algae) and has an increasing abundance of fish. However, to maintain this trend and learning from experiences in the Caribbean, we must preserve the diversity within fish functional groups. If the functional diversity decreases, the system may become more susceptible to disturbances, and may become less resilient than it was in the past (1987-2014). A new bleaching or hurricane event, even moderate in duration and intensity, has the potential to trigger a phase shift towards algal dominance and will result in the loss of essential ecosystem services.

CONCLUSION

The analysis of inter-annual variability in coral and fish assemblages in Tiahura reefs in Moorea Island, French Poly-

nesia, showed the dynamic interplay between disturbance and resilience and the way humans modify them (lagoon *vs*. outer slope monitoring sites). Disturbance alters the seascape, contributes to ecosystem reorganisation, and builds adaptive capacity. To sustain the positive effects of disturbances, ecosystem resilience must be maintained as it has been on the outer slope coral and fish assemblages in Moorea. Lacking this resilience, a reef ability to recover is compromised and the likelihood of phase shift increases, as we observed in Moorea lagoon assemblages. Disturbance and resilience are thus critical for coral reef conservation. Ecosystem resilience not only protects a system by acting as a buffer to disturbance, but it creates opportunity for a reef to reorganise, renew, evolve, and grow after disturbance (Gunderson, 2000).

REFERENCES

ADJEROUD M., 1997. - Factors influencing spatial patterns on coral reefs around Moorea, French Polynesia. *Mar. Ecol. Progr. Ser.,* 159: 105-119.

ADJEROUD M., AUGUSTIN D., GALZIN R. & SALVAT B., 2002. - Natural disturbances and the interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia. *Mar. Ecol. Progr. Ser.,* 237: 121-131.

ADJEROUD M., CHANCERELLE Y., SCHRIMM M., PEREZ T., LECCHINI D., GALZIN R. & SALVAT B., 2005. - Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. *Aquat. Living Resour.,* 18: 111-123.

ADJEROUD M., MICHONNEAU F., EDMUNDS P.J., CHANCERELLE Y., LISON DE LOMA T., PENIN L., THIBAUD J., VIDAL DUPIOL J., SALVAT B. & GALZIN R., 2009. - Recurrent disturbances, recovery trajectories and resilience of coral assemblages on a south central pacific reef. *Coral Reefs,* 28: 775-780.

AUBANEL A., 1993. - Valeurs socio-économiques du milieu corallien récifal et de ses ressources. Application à une île océanique du Pacifique sud: Moorea, archipel de la Société. PhD., 320 p. Univ. de Bordeaux III, France.

AUGUSTIN D., GALZIN R., LEGENDRE P. & SALVAT B., 1997. - Variations interannuelles des peuplements récifaux du récif barrière de Tiahura (île de Moorea, Polynésie française). *Oceanol. Acta,* 20(5): 743-756.

AUZENEAU S. & DARCHEN J., 1983. - Autour de la saison 1982-1983, des perturbations tropicales en Polynésie française. *Météorol. Mar.,* 120: 15-39.

BARNOSKY A.D., MATZKE N., TOMIYA S. *et al*. [12 authors], 2011. - Has the Earth's sixth mass extinction already arrived? *Nature,* 471: 51-7.

BOUCHON C., 1985. - Quantitative study of scleractinian coral communities of Tiahura reef (Moorea Island, French Polynesia). *Proc. 5th Int. Coral Reef Congr.,* 6: 279-284.

BOUCHON-NAVARO Y., BOUCHON C. & HARMELIN-VIVIEN M., 1985. - Impact of coral degradation on a Chaetodontidae fish assemblage (Moorea, French Polynesia). *Proc. 5th Int. Coral Reef Congr.,* 5: 427-432.

BRUNO J.F. & SELIG E.R., 2007. - Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *Plos ONE,* 2(8): e711.

BURKE L., REYTAR K., SPALDING M. & PERRY A., 2011. - Reef at Risk Revisited. Washington, DC, USA: World Resources Institute. Available at: www.wri.org/publication/reefs-risk-revisited.

CHAPIN F.S., ZAVALETA E.S., EVINER V.T. et al. [12 authors], 2000. - Consequences of changing biodiversity. *Nature,* 405: 234-242.

CONNELL J.H., 1978. - Diversity in tropical rain forests and coral reefs. *Science,* 199: 1302-1310.

CONNELL J.H. & SOUSA W.P., 1983. - On the evidence needed to judge ecological stability or persistence. *Am. Nat.,* 121: 789-824.

COSTANZA R., d'ARGE R., de GROOT R. *et al.* [13 authors], 1997. - The value of the world's ecosystem services and natural capital. *Nature,* 387: 253-260.

DONE T.J., OGDEN J.C., WIEBE W.J. & ROSEN B.R., 1996. - Biodiversity and ecosystem function of coral reefs. *In:* Functional Roles of Biodiversity: a Global Perspective (Mooney J.H., Cushman E., Medina E., Sala O.E. & Schulze E.D., eds). New York: Wiley-Blackwell: 393-429.

FAURE G., 1989. - Degradation of coral reefs at Moorea Island (French Polynesia) by *Acanthaster planci. J. Coast. Res.,* 5(1): 295-305.

GALZIN R., 1985. - Variations spatio-temporelles des peuplements, dynamique des populations de trois espèces dominantes des lagons nord de Moorea, évaluation de la production ichtyologique d'un secteur récifo-lagonaire. PhD., 195 p. Univ. Montpellier, France.

GALZIN R., 1987a. - Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Mar. Ecol. Progr. Ser.,* 41: 129-136.

GALZIN R., 1987b. - Structure of fish communities of French Polynesian coral reefs. II. Temporal scales. *Mar. Ecol. Progr. Ser.,* 41: 137-145.

GALZIN R. & HARMELIN-VIVIEN M., 2002. - Écologie des poissons des récifs coralliens. *Océanis,* 26(3): 465-495.

GARDNER T.A., COTE I.M., GILL J.A., GRANT A. & WATKINSON A.R., 2003. - Long term region wide declines in Caribbean corals. *Science,* 301: 958-960.

GUNDERSON L.H., 2000. - Ecological resilience: in theory and application. *Ann. Rev. Ecol. Syst.,* 31: 425-439.

HOEGH-GULDBERG O., 1999. - Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Resour.,* 8: 839-866.

HOEGH-GULDBERG O. & SALVAT B., 1995. - Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Mar. Ecol. Progr. Ser.,* 121: 181-190.

HOLLING C.S. & MEFFE G.K., 1996. - Command and control and the pathology of natural resource management. *Conserv. Biol.,* 10: 328-337.

HOLLING C.S., SCHINDLER D.W., WALKER B.W. & ROUGHGARDEN J., 1995. - Biodiversity in the functioning of ecosystems: an ecological synthesis. *In:* Biodiversity Loss, Ecological and Economical Issues (Perrings C.A., Maler K.G., Folke C., Holling C.S. & Jansson B.O., eds). Cambridge Univ. Press: 44-83.

HUGHES T.P., 1994. - Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science,* 265: 1547-1551.

HUGHES T.P. & CONNELL J.H., 1999. - Multiple stressors on coral reefs: a long-term perspective. *Limnol. Oceanogr.,* 44: 932-940.

HUGHES T.P, BELLWOOD D.R., FOLKE C., STENECK R.S. & WILSON J., 2005. - New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.,* 20: 380-360.

HUGHES T.P., GRAHAM N.A.J., JACKSON J.B.C., MUMBY P.J. & STENECK R.S., 2010. - Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.,* 25(11): 633-642.

JONES G.P., McCORMICK M.I., SRINIVASAN M. & EAGLE J.V., 2004. - Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA,* 101: 8251-8253.

KAYAL M., VERCELLONI J., LISON DE LOMA T. *et al.* [11 authors], 2012. - Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals and cascading effect on reef fish and benthic communities. *Plos ONE,* 7(10): e47363.

KINZIE R.A., 1999. - Sex, symbiosis and coral reef communities. *Am. Zool.,* 39: 80-91.

LAMY T., GALZIN R., KULBICKI M., LISON DE LOMA T. & CLAUDET J., 2015. - Three decades of recurrent declines and recoveries in coral cover belie ongoing change in fish assemblages. *Coral reefs,* published online: 1-10. doi:10.1007/s00338-015-1371-2.

LECCHINI D. & GALZIN R., 2005. - Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Mar. Biol.,* 147: 47-58.

LEGENDRE P., GALZIN R. & HARMELIN-VIVIEN M., 1997. - Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology,* 78(2) : 547-562.

LOYA Y., 1978. - Plotless and transect methods. *In:* Coral Reefs: Research Methods (Stoddard D.R. & Johannes R.E., eds). Paris: UNESCO: 197-217.

McCLANAHAN T.R. & MUTHIGA N.A., 1998. - An ecological shift in a remote coral reef atoll of Belize over 25 years. *Environ. Conserv.,* 25: 122-130.

McLEAN A.R. & MAY R.M., 2007. – Introduction. *In:* Theoretical Ecology, 3rd edit. (May R.M. & McLean A.R., eds). Oxford: Oxford Univ. Press: 1-6.

MONTEFALCONE M., PARRAVICINI V. & BIANCHI C.N., 2012. - Quantification of coastal ecosystem resilience. *In:* Treatise on Estuarine and Coastal Science, Vol. 10 (Wolanski E. & McLusky D.S., eds), pp. 49-70. Academic Press.

MUMBY P.J., CHISHOLM J.R.M., EDWARDS A.J., CLARK C.D., ROARK E.B., ANDREFOUET S. & JAUBERT J., 2001. - Unprecedented bleaching-induced mortality in *Porites* spp. At Rangiroa Atoll, French Polynesia. *Mar. Biol.,* 139: 183-189.

NYSTROM M. & FOLKE C., 2001. - Spatial resilience of coral reefs. *Ecosystems,* 4: 406-417.

NYSTROM M., FOLKE C. & MOBERG F., 2000. - Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.,* 15: 413-417.

PARRAVICINI V., KULBICKI M., BELLWOOD D.R. *et al*. [11 authors], 2013. - Global patterns and predictors of tropical reef fish species richness. *Ecography*, 36: 1254-1262.

PRATCHETT M., MUNDAY P., WILSON K., JONES G.P. & MCCLANAHAN T.R., 2008. - Effects of climate-induced coral bleaching on coral reef fishes, ecological and economic consequences. *Oceanogr. Mar. Biol. Ann. Rev.,* 46: 251-296.

RICIARDI A. & RASMUSSEN J.B., 2000. - Extinction rates of North American freshwater fauna. *Conserv. Biol*., 13: 1220-1222.

ROFF G. & MUMBY P.J., 2012. - Global disparity in the resilience of coral reefs. *Trends Ecol. Evol*., 27: 404-413.

SALA E. & KNOWLTON N., 2006. - Global Marine Biodiversity Trends. *Ann. Rev. Environ. Resour.,* 31: 93-122.

SALE P.F., 1991. - Reef fish communities: open non-equilibrium systems. *In:* The Ecology of Fishes on Coral Reefs (Sale P.F., ed.). Academic Press, San Diego: 564-578.

SALVAT B., 1980. - Death for the coral reefs. *Oryx,* 15: 341–344.

SALVAT B., 1992. - Blanchissement et mortalité des scléractiniaires sur les récifs de Moorea (archipel de la Société) en 1991. *C.R. Acad. Sci*., 314(2): 105-111.

SALVAT B., RICHARD G., SALVAT F., BERIGAUD R., ANTOINE L., BERIGAUD M.C. & PLESSIS Y., 1972. - Moorea-Tiahura : étude des peuplements du lagon et du récif. Rapport EPHE: 1-104.

STENECK R.S. & DETHIER M.N., 1994. - A functional group approach to the structure of algal-dominated communities. *Oikos*, 69: 476-498.

THOMAS C.D., CAMERON A. & GREEN R., 2004. - Extinction risk from climate change. *Nature*, 427: 145-148.

VITOUSEK P.M., MOONEY H.A., LUBCHENCO J. & MELILLO J.M., 1997. - Human domination of earth's ecosystems. *Science*, 277: 494-499.

WALKER B., KINZIG A. & LANGRIDGE J., 1999. - Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2: 95-113.

WILKINSON C.R., 1999. - Global and local threats to coral reef functioning and existence: review and predictions. *Mar. Freshw. Resour.*, 50: 867-878.

WILKINSON C.R. & SOUTER D., 2008. - Status of Caribbean coral reefs after bleaching and hurricanes in 2005. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville: 1-148.

WORM B., BARBIER E.B., BEAUMONT N. *et al*. [14 authors], 2006 - Impacts of biodiversity loss on ocean ecosystem services. *Science,* 314: 787-790.