Acanthuridae and *Scarinae*: Drivers of the Resilience of a Polynesian Coral Reef

Alizée Martin, Charlotte Moritz, Gilles Siu and René Galzin

Abstract Anthropogenic pressures are increasing and induce more frequent and stronger disturbances on ecosystems especially on coral reefs which is one of the most diverse on Earth. Long-term data series are increasingly needed to understand and evaluate the consequences of such pressures on ecosystems. This 30-years monitoring program allowed a description of the ability of the coral reef of Tiahura (French Polynesia) to recover after two main coral cover declines, due to *Acanthaster planci* outbreaks. The study is divided in two distinct periods framing the drop of coral cover and analyze the reaction of two herbivorous family: *Acanthuridae* and *Scarinae*. First we compared the successive roles they played in the herbivorous community, then we evaluated the changes in species composition that occurred for both *Acanthuridae* and *Scarinae* between these two periods. The long-term study of this coral reef ecosystem provided a valuable study case of the resilience over 30 years.

Keywords Resilience · Long-term analysis · Coral reef · Herbivorous fish · Shift

1 Introduction

The ability of an ecosystem to recover or shift to another state after acute disturbance is still difficult to predict [1–3]. Resilience refers to the capacity of an ecosystem to face disturbance and absorb changes without losing its key functions [4]. This implies a reorganization of ecosystem components before adapting to its surrounding changing environment, which can lead to a redefinition of the communities' structure toward a new stable state. This multi-equilibrium conception of resilience is also called ecological resilience [4–6] and has been studied in many ecosystems [7–10] such as savannahs [9, 11], grasslands [12, 13], forests [14, 15] or

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lakes [7, 16–18]. Coral reefs are also considered as complex systems which experience diverse stable states [19–22] that are mainly characterised by different substrate composition: coral or algal-dominated systems [23, 24].

Coral reefs are one of the most diverse ecosystems on Earth [25] and provide a valuable example for resilience studies in oceans [19, 20, 26–28]. Natural and anthropogenic disturbances have dramatically increased during the last three decades triggering fundamental changes and high rates of mortality in coral reefs ecosystems [29–31]. Seventy five percent of coral reef are currently reported as acutely threatened by anthropogenic pressures and this number should raise to 90% in 2050 [32, 33]. The principal reasons for the degradation of reefs ecosystems are climate change, habitat destruction and overfishing [34–36]. These threats have already been pointed out as responsible for phase shifts in coral reefs ecosystems [31, 34, 37–39], for example from a coral-dominated to a macroalgae-dominated system, as reported in the Caribbean [19, 24, 26]. Such shifts are generated by a perturbation (seastar outbreaks, mortality of sea urchins, cyclones) which induce a development of macroalgae that becomes the dominant substrate, avoiding coral development. In the Caribbean, ecosystems that have gone through this kind of shift exhibit no recovery [40] whereas a recent study establish that 46% of Indo-Pacific reefs do [41].

The coral reef ecosystem of Moorea, a Polynesian island located in the central south Pacific, has been the core of many studies for more than 30 years [42–49]. This island, quite populated compared to other Pacific islands, may be considered as a model island for the study of Indo-Pacific reef resilience. Moorea's coral reef went through many disturbance theses last decades such as coral bleaching, cyclones or Crown-of-thorn seastar *Acanthaster planci* outbreaks [44, 46–50]. *A. planci* is considered as the major enemy of reef-building corals [51] and their outbreaks are one of the most destructive disturbance faced by tropical reefs [52, 53]. Outbreaks occurred in Moorea in 1980, 1981, 1987 and between 2006 and 2010 [44, 46, 48–50]. On the north coast of Moorea, *A. planci* destroyed 35% of the 3000 m^2 of living substrate in 1983 [54] and a maximum density of about 151 $ind.km^{-2}$ was recorded in 2010 [50]. In 2010, cyclone Oli increased the damages due to *A. planci* by breaking and displacing many coral skeletons [50]. Despite all these destructive events, Moorea coral reef successfully avoided shift and showed relatively high resilience. One reason for this may be the important herbivorous biomass that supports Indo-Pacific reefs, three times greater than in Caribbean and mainly due to *Scarinae* (parrot fish), a sub-family of *Labridae*, and *Acanthuridae* (surgeon fish) which have a biomass respectively twice and fourfold higher than in Caribbean [41]. Our study focused on these two families of herbivorous fish that are among the most abundant encountered in coral reefs ecosystems [41, 55].

Our study monitored the substrate cover and the abundance of herbivorous fish, specifically *Acanthuridae* and *Scarinae*, over more than 30 years. We focused this long term survey on two main *A. planci* outbreak periods, separated by more than 10 years, which provided a comparison of the changes that occurred in the ecosystem over time. Here we compared the abundance and the relative abundance (within the herbivorous fish) of *Acanthuridae* and *Scarinae* between these two

periods to reveal the successive roles they played in the herbivore community. We further aimed to evaluate the changes of community composition that occurred for both *Acanthuridae* and *Scarinae*. Then the analysis of relationship between the two fish families and different substrate allowed us to propose a hypothesis regarding the resilience of Tiahura's coral reef.

2 Materials and Methods

2.1 Study System

Moorea is one of the 118 islands of French Polynesia, located in the Pacific Ocean. Its coral reef extends along 61 km around the island and 750 m from the coast to the fore reef, the oceanic side of the reef crest (Fig. 1). The study site of Tiahura is located on the north-western part of Moorea, and is one of the most heavily studied reefs in the world since 1971 [43, 45, 47, 56, 57]. Three major habitats can be defined in Tiahura: the fringing reef (<2 m depth), the barrier reef (<3 m depth) inside the lagoon and on the reef crest, and the fore reef on the outer slope (<40 m depth). The fore reef of Tiahura, located further from the inhabited coastal areas than the fringing reef, is less impacted by anthropogenic pressures [58] but is regularly exposed to acute natural disturbances such as cyclones or *A. planci* outbreaks [44, 46, 48, 50].

2.2 Data Sampling

Tiahura fore reef was sampled for the first time in 1983, and, from 1987, every year in the context of a long-term monitoring program conducted by the CRIOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement). A permanent fish counting site of 50 × 2 m, located at 12 m depth and parallel to the barrier reef, was surveyed twice a year during wet and dry seasons (in March

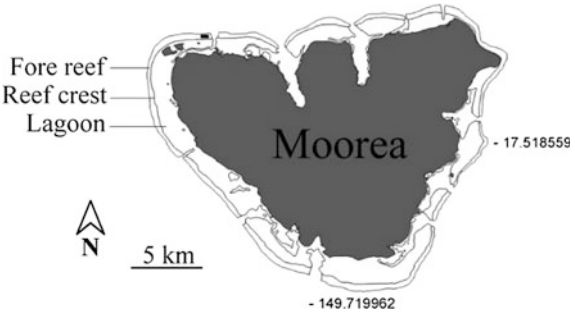


Fig. 1 Map of the study site representing Tiahura location

and September, respectively). Fish were counted and identified to the species level in this corridor by visual census, repeated 4 times in the day. In this study we focused on two families of herbivorous fish: *Acanthuridae* (surgeon fish) and *Scarinae* (parrot fish), sub-family of *Labridae*.

Benthic cover was determined along 3 transects parted along Tiahura's fore reef between 6 and 20 m depth, framing the fish counting site at 12 m depth. Transects were 50 m long and substrate cover was evaluated using the Point Intercept Transect (PIT) method by determining substrate every meter along the transect [59]. Categories of substrate were defined as follows: coral, macroalgae, pavement, CCA (crustose coralline algae), rubble, sand, turf and others. CCA, pavement, rubble and turf cover were grouped as "cropped cover" as they are all substrates possibly grazed by herbivorous fish. This counting was repeated every year since 1987. Percent coral cover collected on the outer slope of Tiahura reef in 1979 [43] and 1983 [54] was retrieved from the publications.

2.3 Data Analysis

We defined two time windows of 8 years framing the drop and recovery of coral cover due to *A. planci* outbreaks, with the lowest point in 1983 and 2010. Due to the limited extent of our data (no substrate sampling before 1987 and in 2012), the periods were chosen as follows: P1 from 1987 to 1994 and P2 from 2007 to 2015. We analysed fish community and substrate cover using R version 3.2.3 [60] including vegan [61] and stats packages.

A t-test was used to compare the real and relative abundances (i.e. percentage among herbivorous fish) of *Acanthuridae* and *Scarinae* between P1 and P2, choosing a minimum significant p-value of 0.05. To apply this parametric test based on comparison of the means, we first checked the normal distribution of data and the homogeneity of variances. Nonmetric multidimensional scaling (NMDS) was used to visualise the temporal variations in species composition of both families. This ordination based on a Bray-Curtis dissimilarity matrix was represented in two dimensions after checking for the stress value. Bray-Curtis distance is a dissimilarity index based on species abundance which varies between 0 and 1 [62] and is one of the most commonly applied measures to express composition similarity in ecology. To test whether species composition for each family was different between P1 and P2, an analysis of similarity (ANOSIM) based on Bray-Curtis distance using 999 permutations was performed between the two periods, using a minimum significant p-value of 0.05. A similarity percentage analysis (SIMPER) was used to identify the contribution of each species to the change that occurred in communities between P1 and P2 based on Bray-Curtis dissimilarity [63]. We finally analysed the relationships between the abundance of *Acanthuridae* and *Scarinae* and the percentage of macroalgae and cropped cover using linear models (minimum significant

p-value of 0.05). An analysis of variance (aov function) was used to determine whether *Acanthuridae* and *Scarinae* abundance were different with macroalgae and cropped cover. A minimum significant *p*-value of 0.05 was chosen.

3 Results

3.1 Substrate Cover and Species Abundance

Between 1979 and 2015, Tiahura's coral reef faced two main *A. planci* outbreaks, starting in 1980 and 2006 (Fig. 2a). These declines in coral cover were followed by a recovery period: 5 years after the lowest point of P1, coral cover reached 30.0 ± 13.9 and 30.7 ± 19.4% after the lowest point of P2. Macroalgae percentage cover varied between 3.3 ± 5.8% (1994) and 20.6 ± 27.6% (1987) during P1 whereas it varied between 0.7 ± 1.2% (2007) and 8.7 ± 1.2% (2014) during P2 (Fig. 2b). Cropped cover increased during P1 and P2, raising from 37.3 ± 11.6% in 1987 to 67.3 ± 14.0% in 1994 and reaching 92.0 ± 24.0% in 2011. For both periods this increase was due to turf cover (Fig. 2c), but in 2013 an important increase in pavement cover occurred between 2011 (0 ± 0%) and 2015 (36 ± 7.2%). Increase in rubble cover was observed after two cyclones in 1993 (32 ± 12.5%) and 2010 (38 ± 32.2%). *Acanthuridae* remained more abundant than *Scarinae* (Fig. 2d), but their abundance dropped during P2 from 121.6 ± 12.7 (2009) to 72.5 ± 15.6 individuals (2015). On the contrary, *Scarinae* abundance increased during P1 from 15.4 ± 8.7 individuals in 1987 to 48.5 ± 23.1 individuals in 1994 and from 20.5 ± 12.1 individuals in 2007 to 45.8 ± 20.6 individuals in 2015 during P2. Raw abundance of *Acanthuridae* did not change between P1 and P2 ($p = 0.086$) (Fig. 3a), whereas *Scarinae* abundance was significantly higher during P2 (Fig. 3b). However, the mean relative abundance of *Acanthuridae* within herbivorous fish was significantly higher in P1 (32.0 ± 4.2%) than in P2 (25.3 ± 5.6%) (Fig. 3c). Conversely, the relative abundance of *Scarinae* was different ($p < 0.05$) and lower in P1 (8.4 ± 4.9%) than in P2 (12.0 ± 5.8%) (Fig. 3d).

3.2 Community Structure Variations

The NMDS revealed changes in community structure for both *Acanthuridae* and *Scarinae* between P1 and P2 (Fig. 4). The major change was captured by the first dimension of the NMDS (NMDS 1). For both families, a drastic change in community occurred in 2009, 2 years after the beginning of period P2, and when coral cover was almost the lowest (Fig. 2a). Two different communities could be distinguished with the ANOSIM between P1 and P2 for both *Acanthuridae* ($R = 0.6172$, $p < 0.05$) and *Scarinae* ($R = 0.7309$, $p < 0.05$). SIMPER analysis

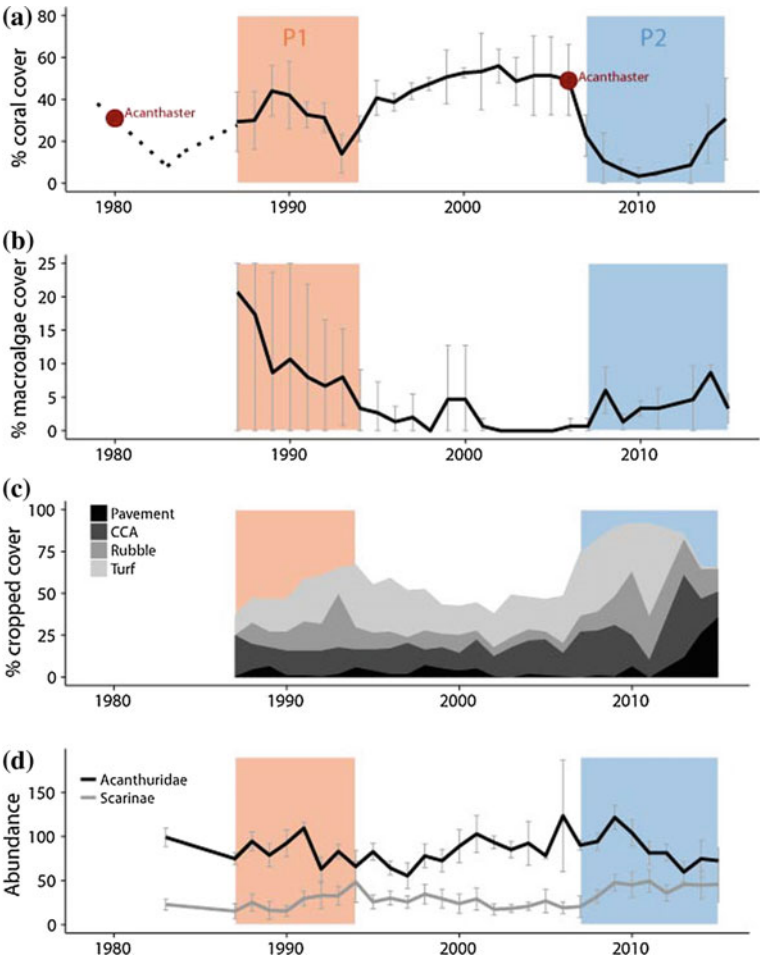


Fig. 2 Percentage of **a** coral cover, **b** macroalgae cover, **c** cropped cover, including different categories and **d** abundance of *Acanthuridae* and *Scarinae*. Periods P1 and P2 are represented in *orange* and *blue* respectively. Onset dates of outbreaks are represented by a *red point* (see color figure online)

singled out *Ctenochaetus striatus* (average = 0.25 ± 0.14), *Acanthurus nigricans* (average = 0.09 ± 0.06), and *Acanthurus nigrofuscus* (average = 0.07 ± 0.06) as the three major species responsible for the *Acanthuridae* community change between P1 and P2. For the *Scarinae*, *Chlorurus sordidus* (average = 0.20 ± 0.09), *Scarus psittacus* (average = 0.05 ± 0.04) and *Scarus oviceps* (average = 0.05 ± 0.03) were singled out. All these species showed a decrease in abundance during P2. The analysis of species composition of each family revealed that there were more species but with fewer individuals each during P2 for both *Acanthuridae* and *Scarinae*. *Acanthuridae* were mainly composed of *Ctenochaetus*

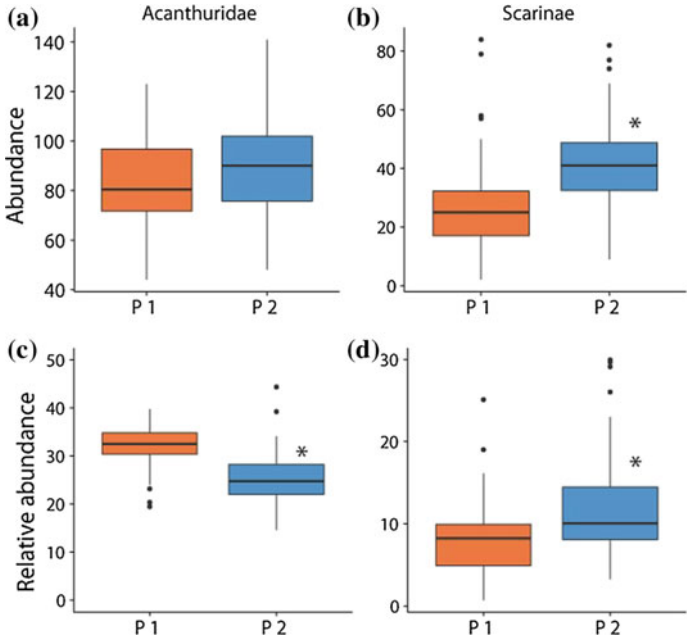


Fig. 3 Boxplot of the abundance of **a** *Acanthuridae* and **b** *Scarinae* and of their relative abundance **c**, **d** for periods P1 and P2. Relative abundance is abundance of a given family within the abundance of all herbivores. Error bars are 95% confidence limits. Significantly different boxplot are identified by a *black star*

striatus during P1, with a mean of 7 species, whereas there were around 13 different and rare species during P2 with no dominating species. The same patterns were observed for *Scarinae*, dominated by *Chlorurus sordidus* during P1 and comprising a mean of 6 species, and comprising 13 species with less individuals during P2.

3.3 Relationship Between Abundance of Acanthuridae and Scarinae and Macroalgae and Turf Cover

The ANOVA showed that *Scarinae* abundance was different with different values of macroalgae ($p < 0.05$) and cropped cover ($p < 0.05$) (Table 1) whereas *Acanthuridae* abundance was related to any of them. The relationships between *Acanthuridae* and *Scarinae* abundance and substrate cover showed opposite patterns. While *Acanthuridae* tended to become more abundant with increasing macroalgae cover during P1 (Fig. 5a), *Scarinae* abundance decreased with macroalgae cover ($p < 0.05$) (Fig. 5c). The opposite trend was observed during P2: *Acanthuridae* were negatively correlated with the percentage of macroalgae cover ($p < 0.05$),

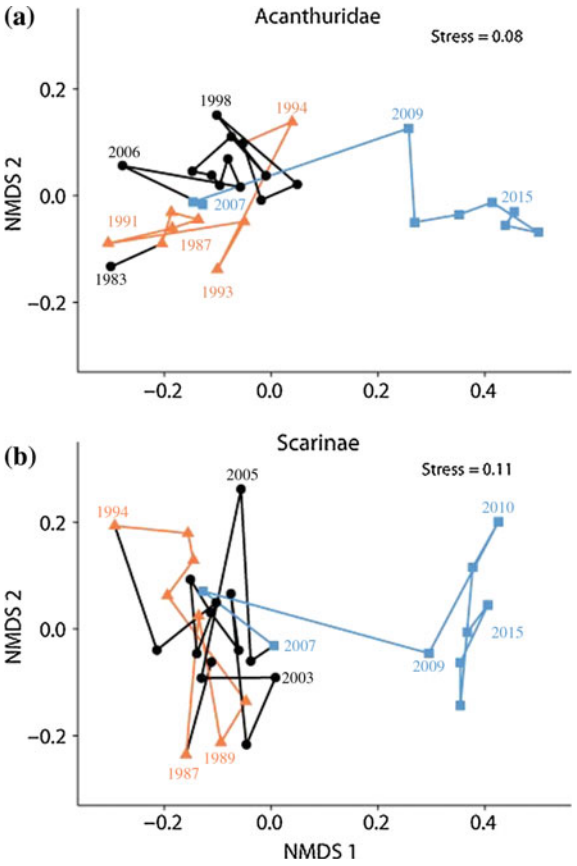


Fig. 4 Temporal non-metric multidimensional scaling of the **a** *Acanthuridae* and **b** *Scarinae* communities. Periods P1 and P2 are indicated by *orange* and *blue dots*, respectively. Stress corresponds to the disagreement between 2-D configuration and predicted values from the regression (see color figure online)

Table 1 Results of linear models (Fig. 5), Bold *p*-values are significant

		Algae		Turf	
		P1	P2	P1	P2
Acanthuridae	p	0.2911	**<0.05**	0.3698	**<0.05**
	R^2	0.004969	0.15	−0.005545	0.1531
Scarinae	p	**<0.05**	0.3017	**<0.05**	0.2604
	R^2	0.3152	0.003361	0.5904	0.01009

whereas *Scarinae* tended to be positively correlated with it. Opposite patterns were observed for the relationship between fish and cropped cover: *Scarinae* percentage increased with cropped cover during P1 ($p < 0.05$), tended to increase during P2 (Fig. 5d), and *Acanthuridae* percentage tended to decrease during P1 but increased during P2 ($p < 0.05$) (Fig. 5d).

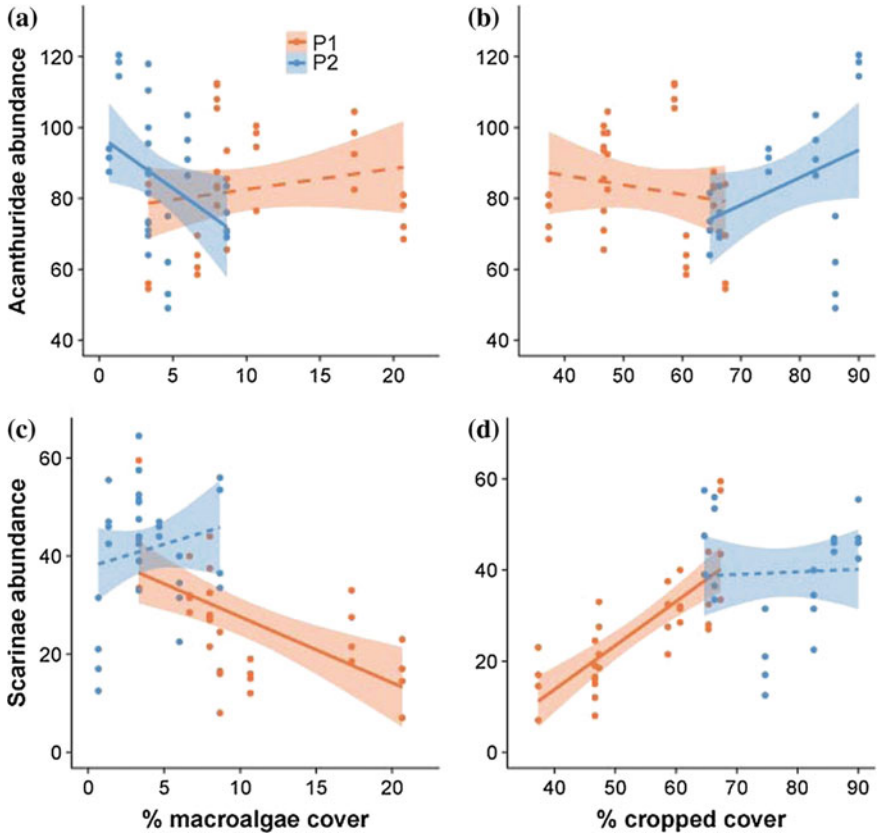


Fig. 5 Relationship between the abundance of *Acanthuridae* and *Scarinae* and the percentage of macroalgae and cropped cover. Linear models are plotted with 95% confidence intervals. *Dotted lines* represent non-significant relationships

4 Discussion

4.1 Herbivory and Resilience

Changes that Tiahura's coral reef went through may be perceived from the perspective of ecological resilience: *A. planci* outbreaks that occurred in 1980 and 2006 might have led to ecosystem re-organization. The notion of ecological resilience refers to a multi-equilibrium system due to changes of the environment [19, 20, 26] inducing a reorganization of the system that experiences different states. In Tiahura, this reorganization led to two different states: herbivorous fish, usually known to promote reef recovery [3, 64–67], were dominated by *Acanthuridae* during both period, but *Scarinae* importance increased during P2. In numerous studies changes between different trophic levels were expounded (e.g. [68–70]),

whereas our study showed transition within the herbivorous fish community. Whether other changes between different trophic levels occurred in the coral reef of Tiahura remains to be assessed.

4.2 Comparison with Shifting Systems

Many studies were carried out on coral reefs phase shifts from coral to macroalgae-dominated systems in the Caribbean [19, 24, 26], more than twice as much as in the Indo-Pacific [41]. Even though some shifts occurred in Indo-Pacific coral ecosystems [20, 27], an analysis of long-term studies showed that declines without ensuing recovery occurred in 57% of studied cases in Caribbean and in only 27% in Indo-Pacific [40]. Our study supports these results since the Indo-Pacific coral reef of Tiahura showed a long-term resilience, without shifting to algae-dominated state for more than three decades. Some hypothesis were suggested to explain this major difference between Caribbean and Indo-Pacific reefs. One of them is the high herbivore diversity supported by Indo-Pacific reefs compared to Caribbean ones. For example *Acanthuridae* counts 88 species in the Indo-Pacific and only 4 in the Caribbean where Naso genus, consumer of macroalgae, does not occur [41].

4.3 Species Richness Increase

Increasing fish diversity may imply a complexification of coral reef ecosystem which is then more adapted to buffer disturbances [3, 24] and hence increase the resilience of the system [71]. Although an increase in species richness can be observed just after a disturbance, resulting from new species attracted by new available resources or free habitats [72], species richness in Tiahura expanded over 30 years and beyond many disturbances. The increase of species richness of both *Acanthuridae* and *Scarinae* was not likely to be an observer bias (increasing scientific expertise) since only three different observers monitored the fish communities, but could be a real diversification of these two herbivorous families. Although climate change has been predicted to conduce to species extirpation [73] as it has already been observed [74], local increase in fish species richness was observed in Tiahura and in other parts of the world [75, 76]. Usually, a loss of coral cover that exceeds 20% induces a decline in species richness of fish communities [77]. In Tiahura, strong coral cover loss did not affect species richness of the main herbivorous families, and this may be one of the key components of its high resilience.

4.4 Changes in Community Composition

Herbivorous fish can be classified into two functional groups: grazers and browsers [78] and grazers are subdivided into different types: scrapers, excavators and detritivores [79]. *Scarinae* are mainly scrapers or excavators that let large grazing scars in the substrate, removing both hard substratum and algal recruit developing on it [79]. Such a feeding mode could explain the low percentage of macroalgae during P2 as their increasing abundance would have removed many algal recruits and then prevented macroalgae development during this period. This is the main hypothesis that could explain the relationship between *Scarinae* and macroalgae since *Scarinae* are mainly grazers and only *Calotomus carolinus* is considered as browser and thus feed on macroalgae. Two species of *Acanthuridae* (*Naso lituratus* and *Naso unicornis*) may feed on macroalgae on the outer slope, but their abundance stayed really low even when macroalgae developed during P1. Hence the opposite patterns of *Acanthuridae* and *Scarinae* related to substrate cover were not due to their diet since they are both mainly grazers feeding on cropped cover. Nonetheless, the abundance of *Scarinae* presented a threshold when cropped cover reached 60%, which may confirm the results of [80] who have found that herbivorous fish and specifically *Scarinae* are able to maintain 40–60% of reef substratum in cropped state. To explain the shift between the role played by *Acanthuridae* and *Scarinae*, we can consider that if dominant species decline under changing conditions then minor species are able to substitute for them, which maintain ecosystem function over time [81]. In Tiahura, *Scarinae* were considered as a minor species in the nineties (P1) but then played a crucial role when *Acanthuridae* decreased around 2009 (P2). However, both states were dominated by cropped cover but the first one had higher percentage of macroalgae. This slight change in substrate cover may have attracted different families of herbivores and thus explain the different controls by *Acanthuridae* then *Scarinae*. The increasing importance of *Scarinae* may also have been due to fish recruitment that was not affected by *A. planci* outbreaks since juveniles settled in the lagoon, less impacted by the seastar. Growing *Scarinae* could then benefit from new available food, such as turf developing on the outer slope [82]. All these hypothesis assume that *A. planci* outbreaks triggered changes in the herbivorous fish community, and within both *Acanthuridae* and *Scarinae* communities. This post-disturbance reorganization allowed a quicker recovery of the coral ecosystem, as suggested by [83].

4.5 Implication of Different Herbivores

Acanthuridae, *Scarinae* and sea urchins are the major herbivores that control algal development in coral reefs [84, 85]. However, urchins were not taken into account in this study since they encountered an important wave of mortality in 1983–1984 reported by Caribbean studies [86, 87] which have concerned the Indo-Pacific since

2000 [88] and thus may distort the dataset. Urchins, *Acanthuridae* and *Scarinae* are competing for benthic algae [89], which means that the mortality wave of sea urchins could have let an available gap for the development of herbivorous fish in the eighties. On the other hand, such a mortality may have led to a reduction of the herbivory power which could have decreased the resilience capacity of the ecosystem. In the Caribbean, the presence of both sea urchins (*Diadema antillarum*) and parrot fish maintained the system in a coral-dominated state, without urchins, the system turned to macroalgae-dominated state [90]. In our case, it remains complex to assess whether the presence of both *Acanthuridae* and *Scarinae* was necessary to maintain resilience over time, and whether urchins were significantly involved in controlling algal development. Nevertheless we can assume that, at least, these two herbivorous families have been involved in the preservation of the coral reef of Tiahura from a shift toward a macroalgae dominated state, as it has been reported in the Red Sea [55].

5 Conclusion

The coral reef of Tiahura persisted over more than 30 years and underwent many disturbances without shifting toward a macro-algal ecosystem. *Acanthuridae* in the nineties and *Scarinae* around 2010 have played a crucial role in maintaining a low rate of algal cover, and this was made possible by the changes that occurred within communities. It follows that reef fish community of Tiahura was highly resistant to natural disturbances, as it has been observed around the whole island [48, 49]. Nevertheless we did not take into account the implication of human pressure in our study although Moorea hosts more than 16.000 habitants and face many anthropogenic disturbances (tourism, overfishing, habitat destruction) which undoubtedly affect the ecosystems [34–36]. The long-term analysis of the reef ecosystem of Tiahura provided us a valuable case of the expression of coral reef resilience, and the impact of the marine protected area established in 2004 at Tiahura should be further studied in order to evaluate whether the limitation of human activities could have improved this resilience.

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