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Shifting dominance among Scarid species on reefs representing a gradient of fishing pressure

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Abstract – The present paper analyzes data collected between 2001 and 2002 on 81 reef fish species targeted by fishers at 5 sites in the Kingdom of Tonga (South Pacific). We first ranked the sites with respect to fishing pressure using two independent methods: (i) Tongan demography and reef surfaces available for fishing, and (ii) the differential effects of fishing on the whole set of 81 species grouped by their life history traits (LHT). We then focused on Parrotfish (Scaridae), which are heavily targeted in coral reef fisheries. We used the identified gradient of fishing pressure to study the effect of fishing on the community structure and test the hypothesis of "shifting dominance" amongst the 20 Scarid species present in the surveys. In addition to the classical effect of decreasing fish size in a family strongly targeted by fishers, the shifting dominance phenomenon includes a decrease in the abundance of the large-bodied and highly targeted species, favouring their replacement by smaller-bodied species from the same family, which are less impacted by fishing. In a context of interspecific competition amongst Scarids, the stress of fishing appears as a factor favouring the replacement of species with large maximum size, and LHT promoting low resilience, by smaller species with the opposite attributes. The discussion focuses on the various processes that can explain the shifting dominance phenomenon. The total density of resilient species, which increased along the gradient of increasing fishing pressure, can be used as an indicator of the over-exploitation of fish communities for reef fisheries management.

Key words: Fishing pressure / Coral reef fish assemblages / Reef fisheries indicator / Shifting dominance / Scarid fish / Pacific Ocean.

Résumé – Inversion de dominance chez les espèces de Scaridae peuplant des récifs, soumis à un gradient de pression de pêche. Cet article analyse des données collectées entre 2001 et 2002 sur 81 espèces de poissons de récifs composant la ressource de 5 pêcheries coralliennes du Royaume de Tonga (Pacifique Sud). Nous avons tout d'abord procédé à un classement des sites, par pression de pêche croissante, en utilisant deux approches indépendantes reposant respectivement sur (i) une relation entre la démographie des habitants de l'archipel et les surfaces de récifs valorisables par la pêche et (ii) les effets différentiels de la pêche sur les 81 espèces-cibles regroupées selon leurs traits de vie (TDV). Nous avons ensuite focalisé l'étude sur les poissons-perroquets (Scaridae) qui sont une cible privilégiée des pêcheries des récifs coralliens. Nous avons utilisé le gradient de pression de pêche pour étudier les effets de la pêche et tester l'hypothèse d'inversion de dominance dans la famille des Scaridae. En marge de l'effet classique de diminution de la taille moyenne des poissons au sein d'une famille ciblée par la pêche, ce phénomène repose sur une diminution de la densité des poissons-perroquets de grande taille (absolue), ciblés en priorité par les pêcheurs, auxquels se substituent des espèces de plus petite taille (absolue), qui sont moins affectées par la pêche. Dans un contexte de compétition interspécifique au sein de la famille des Scaridae, le stress lié à la pêche apparaît comme un facteur favorisant le remplacement des espèces de plus grande taille qui possèdent des TDV favorisant une faible résilience, par des espèces présentant les attributs inverses. La discussion met l'accent sur les processus pouvant expliquer le phénomène d'inversion de dominance. La densité des espèces résilientes qui augmente en fonction de la pression de pêche pourrait être utilisée comme un indicateur du degré de surexploitation des communautés de poissons de récif à des fins de gestion des pêcheries récifales.

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1 Introduction

Coral reef ecosystems are known for their extremely high species diversity. This makes the study of their functioning at the community level particularly difficult. This objective becomes even more challenging when external stresses are affecting the complex processes of species interactions; among these processes, competition and predation play critical roles. Fishing is an external stressor for the community; we can distinguish between its direct and indirect effects on the community structure. Direct effects have been well documented; the reduction in abundance of carnivorous species is the most detectable effect of fishing pressure on multi-species communities (Russ 1991; Jennings and Lock 1996; McClanahan and Mangi 2001; Pet Soede et al. 2001). Indirect effects, that bring into play ecological processes responding to specific changes in components of the ichtyofauna, whatever their cause, have been much less documented. Dulvy et al. (2004) have shown that the removal of fish, even under low fishing pressure, was followed by a compensatory increase of the densities of small-size individuals of the targeted species; this was a direct response of these fish populations to the chronic removal of large and medium-size individuals. Surprisingly, in the study of Jennings and Polunin (1997) which concerned non-targeted species, the removal of predators did not produce any clear increase in the abundance of their prey. This demonstrates the complexity of the interrelationships among reef fish species. To improve our use and management of these ecosystems, we studied a single fish family, which includes both targeted and non-targeted species, in order to reach a better understanding of how some specific compartments of the fish community may evolve following an external and chronic stress.

Species of the Scarid family (parrotfish) occupy a privileged position among the species targeted by fishers in coral reef fisheries (Dalzell 1996). While all Scarids are herbivorous (algae grazers), with an exception for the bumphead parrotfish *Bolbometopon muricatum* which significantly feeds on live coral (Belwood et al. 2003), they display a variety of life history traits. In particular, the average and maximum size of some of these species makes them to be highly targeted by fishers; other Scarid species are of little interest for local fisheries because of the limited biomass they represent. The observed heterogeneity in life history traits amongst closely related and abundant species such as the Scarids made them potentially interesting to focus on for the present study. The interest of that choice was recently confirmed by a study of reef fish communities in 36 fishing grounds: Campbell and Pardede (2006) showed that the abundance of Scarids was the feature that most differentiated the fish communities among the examined reefs.

In this paper, we hypothesized that the removal of Scarids by fishing had an obvious direct effect on the abundances of the targeted species, and also an indirect effect on the relative abundances of other Scarid species, including the ones not targeted by fishers. That indirect effect is linked to an ecological process called shifting dominance. Shifting dominance is a process by which a trophic network reacts to an external perturbation by transferring the dominance in abundance from one group of species to another. The concept was first used in vegetation systems (e.g. Clark et al. 2001; Levin et al. 2006) but it has also been applied to faunal assemblages (Bradford et al. 1998; Bernot et al. 2004). Fish communities were surveyed in fishing areas representing different levels of fishing pressure in the Kingdom of Tonga. To test our hypothesis, we first estimated the gradient of fishing pressure, which was acting as an external stress on the community, using two different and independent methods. We then described the ecological structuring processes induced by fishing pressure that formed the "shifting dominance" response of the Scarids. We will show the relevance of our findings for monitoring multi-species reef fisheries, in which Scarids are always present.

2 Materials and methods

2.1 Study areas

Field work was conducted in five fishing areas of the Kingdom of Tonga (South Pacific). Data on fish communities and fishing pressure were collected in November 2001 at two sites on the archipelago of Ha'apai (Koulo: 174°21'E, 19°46'S and Lofanga: 174°33'E, 19°49'S), in March 2002 at one site on Vava'u (Ovaka: 174°06'E, 18°44'S) and in August 2002 at two sites on the main island, Tongatapu (Manuka: 175°06'E, 21°08'S and Ha'atafu: 175°20'E, 21°03'S) (Fig. 1). These sites were selected to encompass a gradient of fishing pressures. Fishing pressure at this stage was preliminarily assessed from information obtained from the Tonga Ministry of Fisheries and local fishers.

2.2 Data collection

2.2.1 Fish data

To assess the fish stocks, we used underwater visual censuses along 50-m transects with open distances on both sides of the transect where all fish over 10 cm in length were identified and counted, as described in Clua et al. (2006a). Compared to strip-transects with predetermined width, this method allows the inclusion in the survey of any fish present within the limit of visibility, in particular the mobile and shy species which are usually of fishing interest. Interviews of fishers allowed the determination of the fishing areas within the fishing grounds. Soft lagoon bottoms and mangrove areas with poor visibility were eliminated from the study area, which focused on reefs (from fringing to barrier reefs, including intermediate structures but excluding the outer slope). The reefs were divided into three strata: flat, slope, and reef bottom. Sampling units (transects) were randomly positioned within each stratum and their number per stratum was proportional to the stratum surface area. Since we were implementing open-distance transects, they were also chosen to have a minimum distance from one another in order to avoid double counting the same fish. During the study, a total of 198 transects were surveyed, ranging from 25 in Lofanga, the smallest number, to 50 in Koulo, the largest number. The mean number was 40 at the other sites. 25 randomly selected transects per site have been used in the present study to achieve a balanced design.
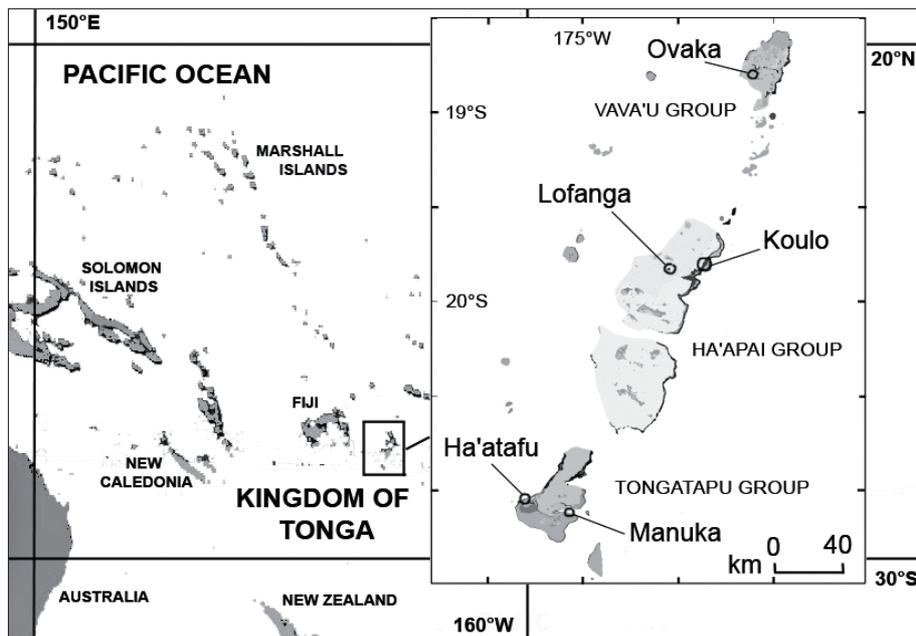
Fig. 1. Map of the Kingdom of Tonga showing the study sites.

2.2.2 Environmental data

A total of 23 environmental variables were recorded: 21 variables from underwater data and 2 from maps. When the two divers had completed the fish census along a transect, habitat variables were recorded along the same transect following the Medium Scale Approach described by Clua et al. (2006a). This method is based on the description of 10 quadrats of 5×5 m on either sides of the 50-m transect used for the fish census. This description includes a semi-quantitative assessment of the coverage of the substratum based on 16 potential components divided in 9 "abiotic" elements (mud, sand and gravel, small boulders, big boulders, rock and eroded dead coral, slab, dead coral debris, branching dead coral, and massive dead coral) and 7 "live coral shapes" (encrusting, massive, digitate, foliose, table, small branches, and large branches). An optimized computer-based calculation allows afterwards to efficiently transform the semi-quantitative data to quantitative form and obtain 16 coverage-related variables. In addition to these variables, depth was assessed as the mean of the 20 depths measured in the centres of the quadrats (variable #17). The coefficient of variation of the 20 depths was calculated and used as a topographic index (McCormick 1994), which provided variable #18. We also calculated the difference between the mean depths on either sides of the transect and used it as an index of slope (variable #19). Habitat heterogeneity was calculated using the Shannon diversity index based on the 16 components of the habitat following the formula of Zand (1976) (variable #20). Fish shelter availability (Friedlander and Parrish 1998) was also assessed per quadrat on a 4-value scale (from 1 for no shelter availability to 4 for high amount of shelter). The 20 values of the variables were then averaged per transect to form the last aggregated variable (#21). In addition to these 21 variables based on underwater information, the oceanic and the terrigenous influences were estimated, providing the last 2 variables. Oceanic influence was assessed along a 3-value scale (1 to 3) describing the exposure of the transect to the open ocean (from 1 for enclosed bays to 3 for barrier reefs; class 2 was used for intermediate reefs). To estimate terrigenous influence, the GPS coordinates of the transects were used to calculate the "distance to the coast" as the distance between the transect and the nearest point of any land whose surface exceeded 5 km^2.

2.3 Data analysis

2.3.1 Assessment of fishing pressure and effects on targeted fish

A study on fishing practices and household fish consumption was conducted for each fishing ground in parallel with the underwater censuses. This study used a qualitative approach which confirmed that there was no critical difference among the five fishing grounds in terms of gear types (hooked lines, spearfishing, and nets) and main target species (Clua 2007). This approach did not, however, allow an accurate assessment of the fishing pressure. We therefore used two different and independent approaches to rank the villages along a semi-quantitative scale of fishing pressure.

Because subsistence fishing plays a critical role in the Kingdom of Tonga (Kronen 2003), we first used demography as a surrogate for fishing pressure. The study sites located in the Ha'apai and Vava'u archipelagos were lightly populated and each fishing ground under study clearly belonged to a single village, with marginal external impacts. For these villages, the ranking was established by dividing the fishing surface area (reef plus lagoon) by the number of inhabitants. During the preliminary assessment of fishing pressure, it also appeared that the two sites located on the main and most highly populated island, Tongatapu, did not belong to a single village, but were used by the whole Tongatapu community (over 60 000

Table 1. Description of six basic reef fish groups based on the following life history traits (LHT): average maximum size, reproduction patterns, behaviour, growth rate, natural mortality rate, and life span. After Kulbicki (1992). GTI = gonado-trophic index.

LHT Group	Size	Reproduction patterns	Behaviour	Growth rate	Mortality rate	Life span
1 1	Small to medium <30 cm	Very early sexual maturity. High GTI and high reproduction capacity.	Often in schools. S Simple sexual behaviour.	Very fast	High	0.5 to 3 years
2	Small to medium <30 cm	Early sexual maturity (1-3 years). High GTI	Often in schools. Sometimes territorial species. Sexual behaviour sometimes complex	Initially very fast	Medium	3 to 7 years
3	Medium to large >30 cm	Early sexual maturity 2-3 years). High GTI	Often in schools. Rarely territorial species. Simple sexual behaviour	Initially very fast, may last	Medium	3 to 7 years
4	Small to medium < 30 cm	Late sexual maturity (>50% of maximum size at the first mating). Medium GTI	Often in schools. Sometimes territorial species. Sexual behaviour sometimes complex.	Initially very fast. Slow after first mating	Low	7 to 12 years
5	Medium to large >30 cm generally >50 cm	Late sexual maturity (>60% of maximum size at the first mating). Low GTI	Rarely in schools. Sometimes territorial species	Initially very fast. Slow after first mating	Low	7 to 12 years
6	Large to very large > 50cm Generally >1 m	Very late sexual maturity (>60% of maximum size at the first mating). Low GTI. Often ovoviviparous species.	Rarely in school, excepting for mating	Slow to very slow, mainly after first mating	Very low	>12 years

people) and were subjected to a significantly higher fishing pressure than the other 3 sites. We therefore considered this archipelago separately, but applied the same calculation as described above to discriminate these two sites from each other.

Ranking of sites according to their fishing pressure was independently calculated by analysing the total fish abundance data (all species, not only the Scarids). This method was developed to corroborate the ranking obtained from the method described in the previous paragraph. The response of fish stocks to fishing pressure depends, among other factors, on life histories traits (LHT, Jennings et al. 1998). Russ and Alcala (1998) concluded that an assessment of fishing pressure based on the effects on specific groups of LHT was a good way to determine trends regarding the level of exploitation of fisheries. Using characteristics such as the average maximum size, reproduction pattern, behaviour, growth rate, natural mortality rate, and life span, Kulbicki (1992) defined six reef fish groups based on LHT (Table 1). We used Kulbicki's classification to aggregate the total fish abundances by LHT types. The sums were subjected to a Hellinger transformation, which is described in the next section. The table was then subjected to a principal component analysis (PCA).

Fish caught by Tongan fishers are home-consumed for one third, and bargained or sold in local markets for the other two thirds. Scarid species are, before Serranids and Acanthurids, the main targeted coral reef fishes in the three archipelagos of the Kingdom of Tonga, with no differential preference for any given species between archipelagos (Clua 2007). This allowed us to consider the ranking of villages, which was established by two independent approaches using all species, to be applicable to Scarids.

In order to better detect the effect of fishing on Scarid size spectra, the fish were grouped into 5 size classes, from small (1) to large (5). This was done separately for each species by calculating 5 equal intervals, from 10 cm to the theoretical maximum size of the given species. The number of individuals belonging to size class 1 was summed over all species, and similarly for classes 2, 3, 4, and 5, to create a table with 5 rows (study sites) and 5 columns (size classes). The relative abundances of the fish in the 5 size classes was then calculated for each site.

2.3.2　Isolation of effects of fishing pressure from environmental structuring processes

The fish assemblages found on different transects may vary for at least three different reasons: (1) differences in fishing pressure (our hypothesis), (2) differences in environmental

Table 2. Ranking of the villages according to the gradient of fishing pressure.

Archipelago	Village	Population of village	Reef surface (km^2)	Size of community using fish divided by reef surface	Ranking within group	Global ranking
Fishing grounds belonging to village						
Vava'u	Ovaka	103[1]	10.94	9.4	1-1	1
Ha'apai	Lofanga	295[1]	29.87	9.9	1-2	2
Ha'apai	Koulo	216[2]	8.52	25.4	1-3	3
Fishing grounds used by whole island (about 60 000 people)						
Tongatapu	Ha'atafu	197[2]	9.79	60 000/9.79 = 6129	2-1[3]	4
Tongatapu	Manuka	287[2]	8.54	60 000/8.54 = 7026	2-2[3]	5

(1) Source: Tonga population census, 2002.

(2) Source: Mecki Kronen (pers. comm.); the 2002 Tonga population census only provided the population per island; no population data were specifically available for Koulo, Ha'atafu and Manuka.

(3) The two Tongatapu sites, Ha'atafu and Manuka, are ranked after Koulo because their reefs are exploited by the entire population of the island (>60 000 people).

conditions, and (3) random variation; the latter includes the high variance which characterizes underwater visual surveys, because they cover very small surface areas and the surveyed species are mobile. We used the following approach to determine if there was a significant effect of fishing pressure, above and beyond that of the environmental variables: (1) the community composition data were subjected to a Hellinger transformation, which makes them amenable to linear modelling such as principal component analysis (PCA) and canonical redundancy analysis (RDA). The Hellinger transformation (Legendre and Gallagher 2001) consists of two steps: first, the counts are divided by the row (transect) total to turn them into relative abundance; then these proportions are square-rooted to reduce the importance of the most abundant species. (2) The environmental variables to which the species are responding were identified by forward selection in RDA. (3) The relationship between the community composition data and the fishing pressure ranking of the villages was assessed for significance by a permutation test in RDA, in the presence of the significant environmental variables, which were used as co-variables. If the relationship between community composition data and the fishing pressure gradient remains significant, this approach insures that this is not due to a linear confounding effect of environmental variation (Legendre and Legendre 1998, Sects. 10.3.5 and 11.3.1).

2.3.3 Scarid species associations

The differential effect of fishing pressure was displayed in two different ways to illustrate the phenomenon of shifting dominance. (1) We used the results of the partial RDA to divide the 20 Scarid species in two groups: 9 that were abundant when fishing pressure was higher than average, and 11 that were abundant when fishing pressure was lower than average. Then we added the relative abundances of the fish in the two groups, per fishing site, and displayed these abundances on a graph with the sites ordered from low to high fishing pressure. (2) For the second approach, we first identified the species that were significantly associated, following the procedure described by Legendre (2005). The steps were the following: (a) subject the species to some form of preliminary clustering or partitioning; we used K-means partitioning applied to the standardized Hellinger-transformed species data. The same two groups of Scarids as in the first approach emerged: a group of 9 species less sensitive than average to fishing pressure, and a group of 11 species that were more sensitive than average. (b) The members of each group were separately subjected to a concordance analysis, with *a posteriori* testing of the contribution of each species to the overall concordance. Only the species that significantly contributed to the within-group concordance were recognized as belonging to a fish association. As in the first approach, we added up the relative abundances of the species of the two associations, per fishing site, and displayed these abundances on a graph with the sites ordered from low to high fishing pressure.

3 Results

3.1 Assessment of fishing pressure and effects on Scarid species

Following the reef surface versus population approach, we obtained the following ranking of the study sites in terms of fishing pressure: Ovaka (1, lowest pressure), Lofanga (2), and Koulo (3). In the separate assessment of the two sites on Tongatapu, Ha'atafu received ranking (4) for fishing pressure and Manuka received ranking (5, highest pressure) (Table 2).

In the analysis of the life history trait (LHT) data, among the six LHT groups of Kulbicki (1992), species representing groups 2 to 6 were present in our survey. PCA of the LHT data produced an ordination along principal component 1 (PCA axis 1 in Fig. 2) which confirmed the ordination of the sites in terms of fishing pressure (Table 1), and in particular the fact that the Ha'atafu site in the island of Tongatapu was subjected to a higher fishing pressure than the Koulo site. That conclusion is based upon the fact that the Ovaka and Lofanga sites had more fish than Koulo that belonged to LHT groups 5 and 6, which correspond to low fishing pressure, whereas the Ha'atafu and Manaku sites had more fish than Koulo that belonged to LHT groups 2 and 3, which correspond to higher fishing pressure. This exercise resulted in the following ranking of the sites: (1) Ovaka had the lowest fishing pressure, followed by (2) Lofanga, (3) Koulo, (4) Ha'atafu and (5) Manuka.
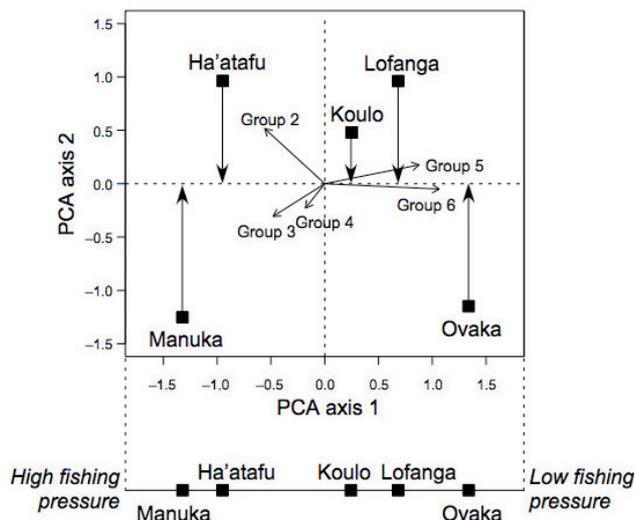
Fig. 2. Biplot of the principal component ordination of the 125 transects showing the site centroids as well as the relative abundances of life history traits (LHT) fish groups (Group 2 to Group 6, described in Table 2) calculated for the 81 species. The centroids of all transects of each site are represented by squares and labelled by the site names. The information of interest is the ranking of the sites along principal component 1 (horizontal axis underneath the biplot), which represents the gradient of fishing pressure.

The two methods of estimation of fishing pressure produced the same ranking of the sites. This ranking was therefore used in the remainder of the study.

In our underwater surveys, 81 reef fish species were observed; 33 of these species (close to 40%) were herbivorous. Amongst the 28 species of the Scaridae family potentially present in Tonga (Randal et al. 2005), 20 parrotfish species were identified and counted during the survey of the 125 transects used in the present study. They belonged to the genera *Cetoscarus* (1 species), *Chlorurus* (3 species), *Hipposcarus* (1 species), and *Scarus* (15 species). Their densities and biomasses varied from 2.824 and 1.426 fish m^{-2} respectively for the most common species, *Chlorurus sordidus* and *Scarus psittacus*, to 0.018 and 0.027 fish m^{-2} respectively for the rarest species, *S. rubroviolaceus* and *S. forsteni* (Table 3). The fish classified by size classes showed a clear decrease of large animals (class 5) along the fishing pressure gradient (Fig. 3). This is especially obvious when comparing the two ends of the gradient: large fish (class 5) were over three times denser in Ovaka and Lofanga (low fishing pressure) than in Ha'atafu and Manuka (high fishing pressure). The opposite effect is visible for the small fish (class 1).

3.2 Isolation of fishing pressure effect from environmental structuring processes

Forward selection identified the following four environmental variables as significantly related to the community composition data at the 5% significance level: depth (in m), proportion of soft substrate (0 to 1), oceanic influence (3 classes), and distance to the nearest coast (in km). The
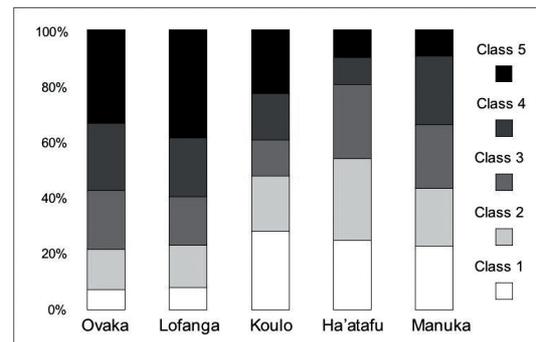
Fig. 3. Relative densities of Scarids per size class and per site. The classes were calculated separately for each species by creating 5 equal intervals, from 10 cm to the theoretical maximum size of the given species. Five size classes are represented, from small (class 1) on the bottom to large (class 5) on the top. The sites are ordered from low (left) to high fishing pressure (right).

partial relationship between the community composition data and the fishing pressure gradient, assessed in the presence of these four environmental variables, was very highly significant ($p = 0.001$ after 999 random permutations in RDA). The use of the statistically significant environmental variables as covariables in our analysis allowed us to efficiently isolate the effect of fishing pressure on the structure of the fish community, separately from that of the environmental factors. As a secondary output of our analysis, we were also able to group the Scarid species according to their responses to fishing pressure.

3.3 Scarid species associations

The above-mentioned analysis allowed the splitting of the 20 Scarid species in two groups: 9 species with a lower-than-average sensitivity to fishing pressure, which were more abundant at the most highly impacted sites (*Hipposcarus longiceps*, *Scarus schlegeli*, *Scarus ghobban*, *Scarus psittacus*, *Chlorurus sordidus*, *Scarus dimidiatus*, *Scarus rivulatus*, *Scarus rubraviolaceus* and *Scarus oviceps*), and 11 species with a higher-than-average sensitivity to fishing pressure, which were more abundant at the least impacted sites (*Chlorurus bleekeri*, *Chlorurus microrhinos*, *Scarus longipinnis*, *Scarus frenatus*, *Scarus niger*, *Scarus chameleon*, *Scarus spinus*, *Cetoscarus ocellatus*, *Scarus globiceps*, *Scarus forsteni* and *Scarus altipinnis*). The relative cumulated abundances of the two groups, plotted as a function of the sites ranked from low to high fishing pressure, show a clear shift from one group to the other as fishing pressure increases (Fig. 4a).

After computing a Holm correction for multiple testing (20 simultaneous tests in the present study), the species in each group that significantly contributed to their group concordance (significance level of 0.05) were identified and recognized as belonging to a fish association; their Holm-corrected *P*-values were actually all smaller than 0.005. Association 1 contained 5 species that had lower-than-average sensitivity to fishing pressure and were more abundant at the most highly impacted sites: *Hipposcarus longiceps*, *Scarus schlegeli*, *Scarus*

Table 3. Density and biomass of Scarid species per sites from the lowest (Ovaka village in the Haapai archipelago) to the highest fishing pressure (Manuka village in the Tongatapu archipelago). Association 1 (Assoc.1): species least sensitive to fishing pressure; association 2 (Assoc.2): species most sensitive to fishing pressure. First row for each species: relative biomass (g m^{-2}); second row: relative density (no. fish m^{-2}). LHT: life history trait.

	Ovaka	Lofanga	Koulo	Ha'atafu	Manuka	Mean density (fish m^{-2})	Theoretical max. size (cm)	LHT group
Cetoscarus ocellatus	77.8	25.7	8.6	0.2	14.4	0.056	70	5
	0.152	0.028	0.043	0.007	0.049			
Chlorurus bleekeri (Assoc.2)	106.8	0.2	0.8	0.0	11.5	0.067	49	5
	0.256	0.008	0.026	0.000	0.046			
Chlorurus microrhinos	261.4	79.6	198.9	12.3	19.6	0.228	70	6
(Assoc.2)	0.637	0.121	0.301	0.025	0.056			
Chlorurus sordidus (Assoc.1)	231.2	210.1	373.3	310.5	495.7	2.824	33	3
	1.500	1.336	4.108	2.870	4.305			
Hipposcarus longiceps (Assoc.1)	41.3	21.3	8.3	4.2	1.9	0.023	55	6
	0.059	0.007	0.021	0.020	0.007			
Scarus altipinnis	191.1	78.5	202.1	51.2	8.0	0.211	60	5
	0.264	0.156	0.387	0.104	0.144			
Scarus chameleon	93.8	47.5	78.5	9.2	34.0	0.285	30	3
	0.571	0.182	0.379	0.076	0.219			
Scarus dimidiatus	20.9	1.5	54.4	9.3	30.7	0.078	35	3
	0.061	0.001	0.160	0.043	0.127			
Scarus forsteni	13.0	15.3	10.3	1.0	2.6	0.027	40	5
	0.049	0.048	0.033	0.003	0.004			
Scarus frenatus (Assoc.2)	67.0	38.5	76.7	26.3	44.2	0.163	47	5
	0.229	0.070	0.265	0.128	0.125			
Scarus ghobban (Assoc.1)	18.8	9.7	96.0	19.6	59.2	0.153	70	5
	0.047	0.034	0.247	0.163	0.273			
Scarus globiceps	33.0	29.4	55.2	15.9	32.4	0.202	28	3
	0.151	0.137	0.468	0.068	0.184			
Scarus longipinnis (Assoc.2)	35.1	0.3	3.0	2.2	12.3	0.062	28	3
	0.205	0.001	0.017	0.008	0.081			
Scarus niger (Assoc.2)	92.1	108.8	63.8	46.7	27.1	0.220	40	5
	0.265	0.296	0.265	0.155	0.119			
Scarus oviceps	24.3	6.2	60.8	15.4	29.8	0.128	33	3
	0.099	0.019	0.322	0.088	0.114			
Scarus psittacus (Assoc.1)	83.8	63.3	119.6	103.9	375.6	1.426	27	3
	0.485	0.548	0.779	1.362	3.955			
Scarus rivulatus	22.1	7.1	31.5	183.4	144.9	0.610	45	3
	0.158	0.048	0.359	1.121	1.362			
Scarus rubraviolaceus	37.2	5.7	1.0	0.3	13.2	0.018	70	5
	0.020	0.006	0.004	0.001	0.057			
Scarus schlegeli (Assoc.1)	224.8	135.2	260.5	118.1	255.5	1.108	35	3
	1.021	0.513	1.142	0.795	2.069			
Scarus spinus	28.9	12.4	60.4	18.1	20.4	0.102	30	3
	0.083	0.038	0.234	0.077	0.077			

ghobban, *Scarus psittacus*, and *Chlorurus sordidus*. The 5 species of association 2 had higher-than-average sensitivity to fishing pressure and were more abundant at the least impacted sites: *Chlorurus bleekeri*, *Scarus longipinnis*, *Chlorurus microrhinos*, *Scarus frenatus* and *Scarus niger*. As for all Scarid species (Fig. 4a), the relative cumulated abundances of the two groups, plotted as a function of the sites, show an even clearer shift from the high-sensitive to the low-sensitive species as fishing pressure increases (Fig. 4b).

4 Discussion

In a situation where the environmental factors had comparable effects and could not be considered as predominant, Dulvy et al. (2004) showed that a reef fish community structure can be modified by fishing methods representing even low pressure. Our work was conducted in fishing grounds located quite close to one another (they were only distant from each other by 22 to 288 km) that were thus quite comparable in their
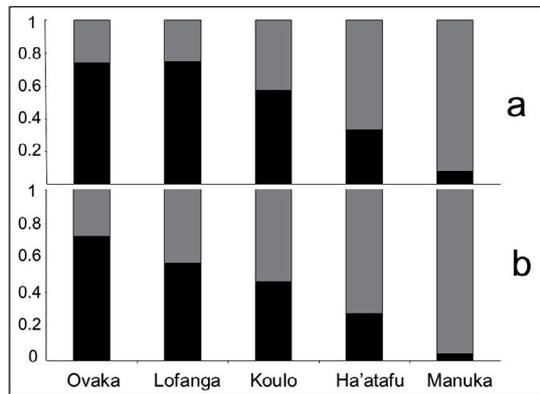
Fig. 4. Total cumulated densities, per site, of (a) all 20 Scarid species and (b) the 10 Scarids that are significant members of the two species associations, representing different groups of sensitivity to fishing pressure. In each case: relative abundance of the species most sensitive (black) and least sensitive (grey) to fishing pressure. The sites are ordered from low (left) to high fishing pressure (right).

fauna. Over the Great Barrier Reef, which is one of the largest marine reserves in the world, Gust et al. (2001) showed that, in the absence of fishing, environmental variables at different scales were able to explain large differences in abundance and biomass of parrotfish species. Thanks to a balanced sampling design and collection of appropriate data on fish habitat, we were able, in our analysis, to control for the most influential environmental factors and statistically isolate the effect of fishing pressure. Therefore, the differential distribution of Scarid species that we observed among the sites is likely to be essentially due to interspecific competition interacting with the gradient of fishing pressure. Understanding the mechanism of shifting dominance in Scarids requires an in-depth analysis of the effects of fishing pressure on these fish.

Our results clearly show a reduction of the size of the species targeted by fishers which, as expected, follows the gradient of fishing pressure. The reduction of the size of individuals in a fish population submitted to fishing extraction can be attributed first to the selective removal of large animals (Roberts 1995; Russ and Alcala 1998). That phenomenon can be enhanced by more complex mechanisms such as genetic loss, as well as more intrinsically biological factors. Bergh and Gets (1989) showed that populations that were initially genetically homogeneous for traits such as those that govern body size lost genetic diversity as genotypes producing large body size were selectively removed by intense fishing. The smaller individuals are the ones left to breed: this influences the size of the following generations. This effect has been shown for Scarids (among other families) on the Jamaican coast subjected to a gradient of fishing pressure (Klomp et al. 2003). One would expect the Tongan Scarid species to follow the same evolution, especially in locations with high fishing pressure such as the Tongatapu archipelago.

Since parrotfish are protogynous hermaphrodites, large specimens constitute the male terminal phase. Chronic removal of these highly targeted animals will dramatically decrease sperm availability which can act as a limiting factor during mating, since fecundity in fish is a direct function of

size (Sadovy 1996). Such a phenomenon of disproportionate targeting of males, resulting in a decrease in the density and proportion of terminal-phase individuals, was documented in the Mediterranean for the rainbow wrasse *Coris julis* (Harmelin-Vivien et al. 1995). According to the size-advantage model for explaining sex change (Ghiselin 1969; Warner 1988), the largest females in the community (assuming they have reached a genetically determined size threshold) are likely to change sex to fill the lack of terminal-phase males. If large fish are not removed too quickly, this process should allow the replenishment of males. However, Shapiro (1988) gave evidence for an additional constraint, which consists for a female in being first inhibited from changing sex by the presence of a male individual, before being disinhibited by the absence of any male individual (this same male or another one). This second constraint suggests that in the case of a sustained overfishing situation, the lack of terminal-phase males will amplify the condition, contributing to the vulnerability of a given species regarding direct competitors, which parrotfish species can be to one another.

Our results suggest that such mechanisms of genetic loss and gain of vulnerability, due to the chronic removal of large Scarids, may affect only certain species in the family and contribute to a shift in dominance, unbalancing the pattern of competition among species found at unstressed sites. Therefore, in the presence of a recruitment overfishing (Murawsky 2000), the shift in dominance may be a stage which prefigures the local extinction of certain species among certain families, as was witnessed by Watson and Munro (2004) in the Caribbean.

In addition to the direct removal of large animals by fishers and the decline in the average size of some species due to genetic loss and the hermaphrodism constraints mentioned above, our results suggest that shifts in dominance within a family may play a critical role by promoting, in an overfishing situation, non-targeted species with specific life history traits, including small maximum size, which can replace large-bodied species. Our results show that small and medium-size species with LHT promoting high resilience capacity (early sexual maturity, high gonado-trophic index, fast growth), such as the very common parrotfish *Scarus psittacus* (maximum size 27 cm, LHT group 3), the daisy parrotfish *Chlorurus sordidus* (maximum size 35 cm, LHT group 3) or the yellowband parrotfish *Scarus schegeli* (maximum size 40 cm, LHT group 3), tend to replace large species such as the steephead parrotfish C. *microrhinos* (maximum size 70 cm, LHT group 6), the bridled parrotfish *Scarus frenatus* (maximum size 47 cm, LHT group 5) or the dusky parrotfish *Scarus niger* (maximum size 40 cm, LHT group 5), which are specifically targeted by fishers because of their large size (Table 3) and show LHT traits with low resilience capacity (late sexual maturity, low gonado-trophic index, slow growth; groups 5 and 6).

As the strong and chronic removal of large animals encompasses large non-Scarid predators feeding on small fish (Russ and Alcala 1989), one could argue that the release of pressure on prey species could explain the trends that we are describing; however, that effect has never clearly been shown (Jennings and Polunin 1997) mainly because it cannot be distinguished from the effect of interspecific competition. Whatever its importance amongst the Scarid species, which

constitute common targets for reef predators (Hiatt and Strasburg 1960), this process would enhance the trend which is clearly detectable in our study if we look at the species with the highest densities, both vulnerable and non-vulnerable regarding removal due to fishing.

Following our hypothesis, the Pacific longnose parrotfish *H. longiceps* (maximum size 55 cm, LHT group 6) and the blue-barred parrotfish *S. ghobban* (maximum size 70 cm, LHT group 5) should not belong to the non-vulnerable group: low resilience is rather a condition which leads to high sensitivity to fishing pressure. Division of the species in two groups was the result of an analysis conducted on relative species densities. Even though their relative densities did significantly respond to the RDA statistical test regarding the gradient of fishing pressure, they were actually in very low densities: respectively 0.023 fish m^{-2} and 0.153 fish m^{-2} (mean densities) (Table 3). The same remark should be made about the highfin parrotfish *S. longipinnis* (maximum size 28 cm, LHT group 3) which is found in the vulnerable group despite its high resilience, but with a very low mean density of 0.062 fish m^{-2}. Our hypothesis should not be applied to rare species, even only because underwater survey data for these species are less reliable.

Beside these exceptions, our results are consistent with a previous demonstration that fishing has greater effects on species with low resilience (Jennings et al. 1999). Not a single specimen of the bumphead parrotfish *B. muricatum* was observed in our survey although that species is known to be present in Tonga (Randall et al. 2005); this confirms the very poor resilience of that species to even low fishing pressure. This finding suggests that the Tongan Islands have already reached a warning stage: the removal of key species such as this giant parrotfish, responsible for massive bioerosion, may have a critical impact on the normal functioning of these reef ecosystems, lowering their long-term resilience to physical stresses (Bellwood et al. 2003). One might think that the process of shifting dominance described in this study should not have a dramatic ecological impact since it (only) results in a decrease in the average size of herbivorous fish. However, these fish play a critical role in terms of limiting algal shifts that can strongly affect reef resilience (Hughes et al. 2007). Recent studies have shown that different Scarid species differ in their herbivory activity (Fox and Belwood 2007) and that each reef shelf system is shaped by fundamentally different processes involving different parrotfish species (Hoey and Belwood 2007). Future studies should carefully assess the effects of shifting dominance amongst Scarid species in order to better understand their specific feeding-linked roles in maintaining reef systems.

Shifts in size induced by fishing pressure are certainly inconvenient for fishers who will only have small fish to catch. Quantification of the shift in dominance may, however, constitute an asset for assessing the stage of maturity of reef fisheries. Innovative state indicators are becoming increasingly necessary to implement an Ecosystem-Based Approach to Fisheries (EBFM) (Jennings 2005; Scandol et al. 2005). In reef ecosystems, fish communities are commonly assessed through techniques such as underwater visual census. This technique is critically penalized by the necessary presence of one or two divers who induce an escape behaviour in some fish, in particular the ones usually targeted by spearfishers who are quite numerous in reef fisheries. This factor strongly affects the accuracy and reliability of surveys, with the consequence that the assessment of the density of targeted species does not constitute a good variable for assessing fishing pressure, as stressed by Russ and Alcala (1998). Because the shift in dominance is correlated to the increase in fishing pressure, it represents an interesting way to investigate how the assessment of the density of the more numerous and less shy species, which do not constitute fishing priority targets, would provide more reliable results. In the present study for example, considering that all 5 fishing grounds under study were originally comparable, the observed differences in Scarid community structure would indicate that Ha'atafu and Manuka are overfished, which is the case.

Recognizing a dominance shift may be a critical step towards the identification of indicator species, which could be useful in the indicator-based management systems promoted by several authors (Boyd and Charles 2006; Clua et al. 2006b), after being validated as reliable indicators of the stage of maturity of a reef fishery or the impact of a fishery on the ecosystem. It may also be an asset for setting up more specific and accurate size-spectra indicators that were shown to be relevant for coral reef ecosystems at the fish assemblage level (Graham et al. 2005). Finally, our argument supports the suggestion that local monitoring of fishing effort contributes to the goal of global conservation of reefs, as larger-scale disturbances linked to climate change are impractical to manage directly (Hughes et al. 2007).

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