Marine fish communities in shallow volcanic habitats

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This survey of the marine ichthyofauna of the Piton de La Fournaise volcano at Reunion Island is the first explanatory study of fish community structures in this area. It describes and analyses the main qualitative descriptors of the fish communities (*i.e*. species richness, diet, life history and geographical distribution) and their spatio-temporal organization. This investigation in 2011 examined lava flows of different ages, including the most recent flows that entered the ocean between 1977 and 2007. In all, 263 species belonging to 45 families were observed. Overall, the fish community was notable for an absence of top predators and a predominance of opportunistic small-bodied species, with dietary flexibility and high reproductive rates, characteristic of the early stages of ecological succession. Between-site analysis indicated that the fish assemblages differed essentially according to the intensity of the last volcanic disturbances. Fish communities in the most disturbed sites showed the highest numbers of Serranidae and the highest proportions of omnivores and small-bodied opportunistic carnivores, including a high proportion of endemic south-western Indian Ocean species. The spatial pattern of this last category of species could be the result of convergent biological traits, and their adaptation to unstable environments at the expense of their competitiveness in more biodiverse, mature communities. Conversely, fish communities in the less disturbed sites showed the highest number of Holocentridae and the highest proportion of browsers of sessile invertebrates. This last characteristic could be a consequence of higher ecological maturity, illustrated by a more specialized trophic network, for assemblages in areas with less intense disturbances. Otherwise, high structural complexity, either in unconsolidated lava boulders, rocks and rubble or high coral-covered sites, could favour the increase of the total number of species independent of disturbance intensity. Regarding the broader effects, this study helps better understand how ecosystems can resist or recover from acute disturbances and the process of ecological succession that leads to the establishment of fish communities in newly submerged habitats.

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INTRODUCTION

Marine ecosystems in active volcanic areas are regularly exposed to natural hazards such as incandescent lava flows, landslides caused by micro-seismic events, changes in physicochemical conditions or water warming (Okubo & Clague, 2009). Both the frequency and the intensity of these disturbances can influence the structure of communities, including species richness (Connell, 1978), life-history strategies (Odum, 1969; Leps *et al*., 1982) or trophic structure (Odum, 1969; Sandin & Sala, 2012). These acute natural disturbance events result in shallow-water biocoenoses that maintain a relatively simple ecological structure (Grigg & Maragos, 1974). This geological context is ideal for studying the developmental stage of ecological successions that eventually lead to complex ecosystems such as coral reefs. The study of these successions is essential in helping to understand the mechanisms of colonization and establishment used by pioneer organisms, particularly in the conservation and management of marine protected areas that rely on artificial reefs or other tools for ecological restoration. Reunion Island is one of the few places in the world where volcanic activity is very frequent, with 27 eruptions occurring between 1998 and 2007 and a mean frequency of an eruptive phase every 9 months in the past century (Tanguy *et al*., 2011). It is also one of the few places where lava flows into the ocean on a frequent basis (Coppola *et al*., 2005; Michon & Saint-Ange, 2008). Community development on lava flows is a subject of considerable interest in the study of the natural history of Reunion Island and the Mascarene Archipelago. Although terrestrial succession on lava has been well studied in Reunion Island (Strasberg, 1995), the development of fish assemblages has never been monitored on the submerged flows. In April 2007, lava from a continuing eruption of the Piton de la Fournaise volcano entered the ocean at Saint Philippe (south-east coast). The underwater portion of the flow created an area of new substratum several hundred metres in width. This event presented a rare opportunity to study two different, but related aspects of coastal fish ecology. The primary aim of the study was to establish a baseline inventory of the overall fish species of the Piton de la Fournaise lava flows by describing a fish community in an area including recent basaltic substratum (4 years). The second aim was to compare fish assemblages sampled from different lava flows, in relation to successional theory.

MATERIALS AND METHODS

STUDY SITE

Located at 21·0° N; 55·4° E, 800 km from the eastern coast of Madagascar, Reunion is an island of the Mascarene Archipelago, which also includes Mauritius and Rodrigues (Fig. 1). Mauritius is dated at 8 million years, Reunion 3 million years and Rodrigues 1·5 million years (Fricke, 1999). These three geologically young oceanic islands are entirely of volcanic origin and have undergone various changes during successive eruptive phases. Reunion is composed of two volcanoes: the Piton des Neiges and the Piton de la Fournaise. The former has been extinct for *c*. 70 000 years, while the latter is still active with effusive activity (Chevallier & Vatin-Perignon, 1982).

The island's coastline is characterized by a very narrow insular shelf and steep slopes. The west coast has discontinuous stretches of fringing reef for 25 km and is highly urbanized (Tessier *et al*., 2005). In contrast, the south-east region, marked by the volcanic activity of the Piton de la Fournaise, is sparsely inhabited. The majority of the most recent lava flows entered the ocean inside a caldera, forming the area known as the volcanic enclosure (VE)

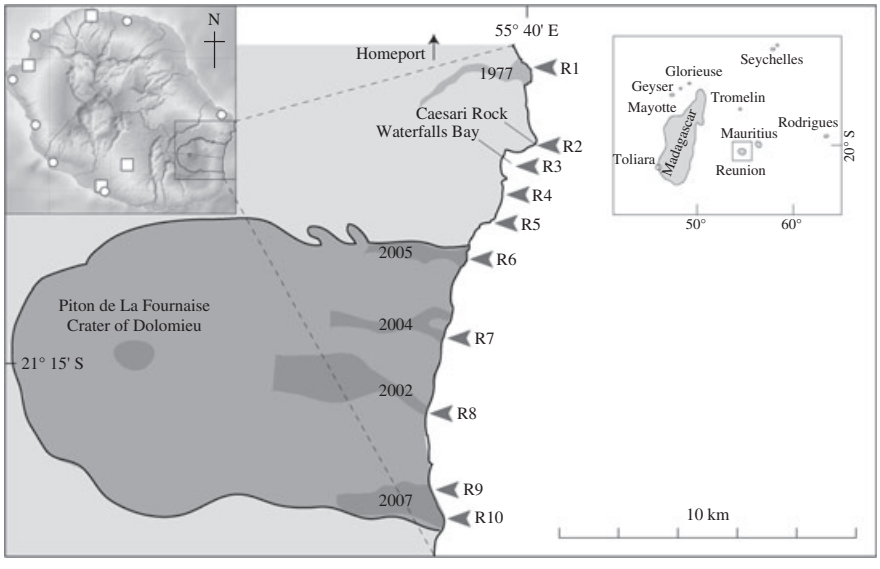


FIG. 1. Location of the 10 sampling transects (R1–R10) along the slopes of the Piton de la Fournaise, Reunion Island, south-western Indian Ocean. □, outside volcanic enclosure; ▩, inside volcanic enclosure; ■, most recent lava flows and crater; ◄, sampling transects; □, major population centres (>60 000 inhabitants); ○, ports.

(Fig. 1). This coast is exposed to trade winds and is further characterized by regular swell, which can sometimes be very strong, particularly during the austral winter (Letourneur, 1998), and by widespread runoff and percolation generated by very heavy rainfall, exceeding 6 m year^{-1} (Barcelo *et al*., 1997).

The shoreline of the VE, which forms the southern area of the study site, consists of sea cliffs 3–8 m high that continue vertically underwater to depths of between 3 and 5 m. The deeper areas of the flows consist largely of unconsolidated lava boulder, loose rocks and rubble, with the bottom sloping into deep water at an angle of *c*. 30°. The area immediately to the north of the VE, which forms the central area of the study site, is on a prehistoric flow of undetermined age. First evidence of an eruption of the Piton de la Fournaise dates from 1640, but many flows occurred well before that date (McDougall, 1971). The northern area of the study site consists of a flow that occurred in 1977, which entered the sea outside the VE, creating a shoreline *c*. 750 m wide with sea cliffs 3–5 m high and small black-sand beaches on either side. The substratum immediately offshore from the prehistoric and the 1977 flows consists of large (1–3 m diameter) angular boulders and slopes steeply to a depth of 8 m. Between 8 and 20 m, the bottom slopes downwards more gradually and beyond the 20 m contour the bottom once again drops away at a steep angle. The substratum between 8 and 20 m consists of wave-smoothed compact lava with high algal cover. *Pocillopora verrucosa*, *Pocillopora eydouxi*, *Pocillopora damicornis* and *Pocillopora meandrina* were the most abundant corals, but cover was sparse and tended to grow towards the north. Well-developed coral communities were found between 10 and 25 m north of the study site, on the 1977 flow and the Caesari Rock and Waterfalls Bay areas (Fig. 1). Although the health status of the coral communities was good in the two northernmost areas, they were partially dead or necrotic in Waterfalls Bay.

SAMPLING METHOD

The fieldwork took place over an eight-day period in late November 2011 (austral summer). Thirty-eight stations at depths ranging from 5 to 30 m were sampled within 10 transects pendicular to the shore (Fig. 1). Each transect contained four sampling stations (20-30,

15-20, 10-15 and 5-10 m) except for R2 and R10, which contained three stations (20-30, 15-20 and 10-15 m) because of the difficult weather conditions faced on the last sampling day. Moreover, high surge conditions and limited visibility due to a mist of fine air bubbles made it impossible to survey the shallow sub-tidal communities. The transects were located along the shore in two sectors: (1) inside and (2) outside the VE, on the different aged flows. All sampling took place between 0900 and 1600 hours.

Qualitative sampling of fish species richness, based on presence or absence, was conducted with underwater visual census (UVC) techniques, mainly using slate with video recording devices (Labrosse *et al*., 2002). The deepest end of each transect (30 m) was located by dropping a weighted float overboard after recording the station position with a Garmin eTrex GPS receiver (www.garmin.com). Two trained divers then moved randomly over an estimated area of 300 m^2 for 15 min, between 20 and 30 m depth, carefully recording each observed species (station 1). Once this time elapsed, the two divers moved towards the shore and repeated the protocol between 20 and 15 m (station 2), then 15 and 10 m (station 3) and finally 10 and 5 m depth (station 4). UVCs are non-destructive, fishery-independent methods and therefore far superior to destructive collection techniques, especially in sensitive areas. UVCs require little post-processing, whereas collections take many hours to complete. This method is, however, known for its tendency to underestimate the small-bodied, nocturnal and cryptic components of the fish fauna (Harmelin-Vivien *et al*., 1985; Fowler, 1987; Willis, 2001). In order to minimize this source of bias, a stratified sampling method was implemented. This method consisted of dividing the population into more homogeneous sub-groups (Labrosse *et al*., 2002). In this study, two strata were introduced, based mainly on the behaviour of the sampled fish species: (1) demersal and semi-pelagic species (*e.g*. Labridae, Pomacentridae and Carangidae) and (2) mimetic, cryptic and buried species (*e.g*. Gobiidae, Scorpaenidae and Muraenidae). Each stratum was sampled in exactly the same way by the ichthyologists. Any species that could not be identified during the survey were determined retrospectively from references (Lieske & Myers, 1994; Taquet & Diringer, 2007).

ANALYSED VARIABLES

With reference to the extensive literature (Hiatt & Strasburg, 1960; Hobson, 1974; Myers, 1999; Froese & Pauly, 2012), a study was carried out on diet and eight categories were considered: (1) herbivores (grazing on microalgae or macrophytes), (2) omnivores (feeding opportunistically on available food, including organic debris), (3) browsers of sessile invertebrates (feeding especially on coral polyps, but also on other fixed organisms), (4) diurnal and (5) nocturnal carnivores (consuming benthic invertebrates), (6) piscivores (preying on other fishes), (7) diurnal and (8) nocturnal planktivores (capturing plankton, mainly animal). Each reference describes the specific trophic assignments of the fish species. Only the main trophic assignment of each species was included in the analyses (Appendix). When several references showed conflicting results for a given species, the most commonly attributed trophic assignment was selected.

Using published literature, the life history of each recorded species was defined, based on biological and behavioural characteristics, such as asymptotic length, length at first maturity, sexual and social behaviour and fertility (Lieske & Myers, 1994; Colin, 1996; Taquet & Diringer, 2007; Froese & Pauly, 2012). The species were then assigned to three classes (Mellin *et al*., 2006): (1) class 1 is composed of small-bodied species (asymptotic length <30 cm) with early breeding and high reproductive effort; often occuring in schools, have simple sexual behaviour, rapid growth and a high mortality rate. (2) Class 2 is also composed of small-bodied species but are characterized by a later age of first reproduction (1–3 years). Their sexual behaviour can be complex and their growth rate, which is initially rapid, slows after the first reproduction. (3) Class 3 consists of medium to large species (>30 cm) with first reproduction at 2–3 years of age; they are often territorial; their growth can be rapid initially and then slows after the first reproduction; their mortality rate is low to medium (Appendix).

The species distribution patterns were grouped into four categories: (1) circumtropical, (2) Indo-Pacific, (3) Indo-West Pacific and (4) south-western Indian Ocean, which included strictly endemic species of the Mascarene Islands (Fig. 2). This biogeographic information was

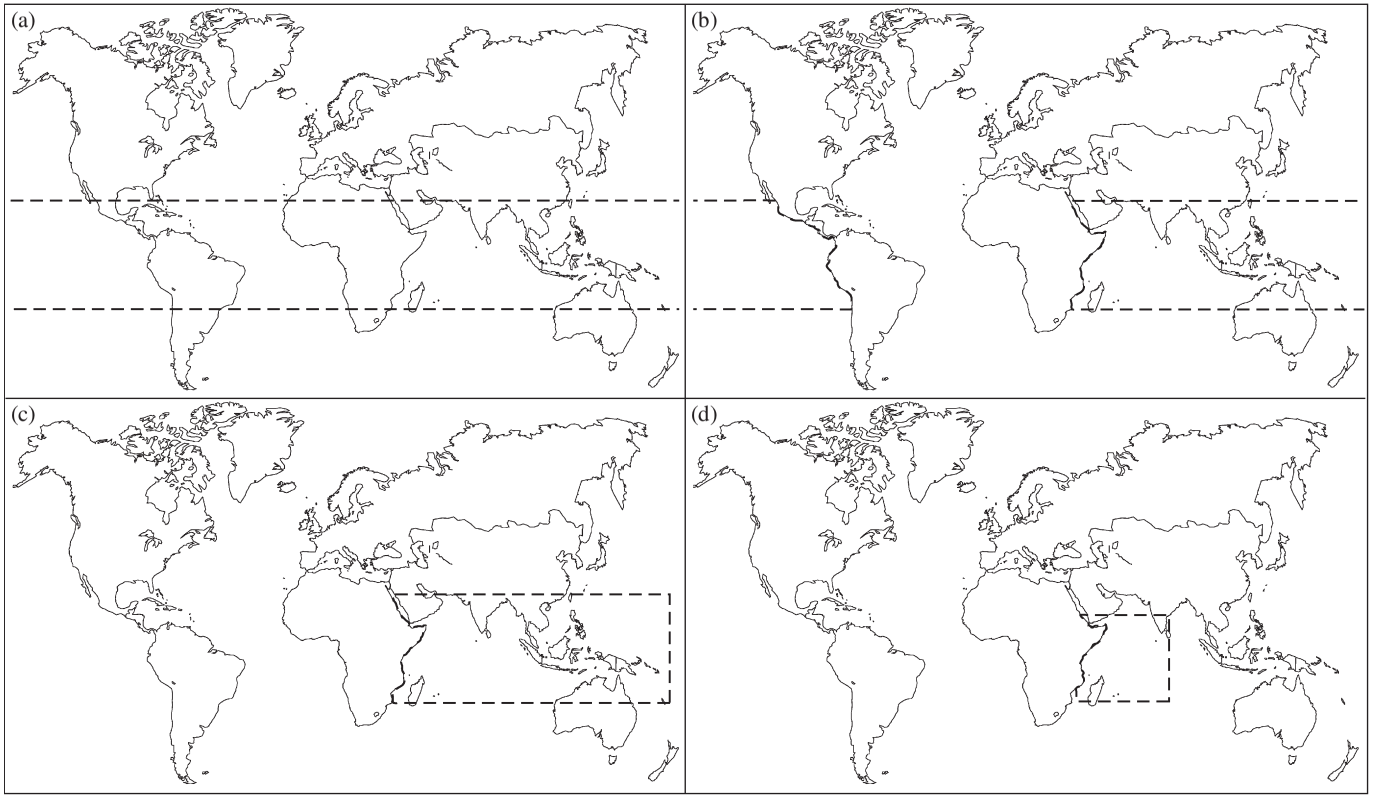


FIG. 2. Species distribution patterns of (a) circumtropical, (b) Indo-Pacific Ocean, (c) Indo-West Pacific Ocean and (d) south-western Indian Ocean.

provided by the online information system AquaMaps (Kaschner *et al*., 2010). This tool uses a niche modelling approach (Hutchinson, 1957) to generate predicted distributions for marine species based on available distribution data or described ecological tolerances. In essence, provided that a minimum acceptable level of information is available, the tool will generate a modelled predicted distribution for any species, as calculated by the probability of occurrence in the entire ocean. Predicted distributions based on ecological tolerances often present ranges that exceed the actual known distributions of species, because the geographic distributions of suitable ecological variables usually extend over a much greater area than the known ranges of species (Rees, 2008). This theoretical approach was essential in order to assess the distribution of rare species and especially species that were never before recorded from Reunion Island. This method ignores the evolutionary constraints of historical biogeography, however, providing potential ranges that would be possible if dispersal was unlimited instead of actual ranges, limited by evolutionary origins and real dispersal capabilities. It is therefore possible that some model-based distribution patterns are slightly wider than the real ones.

DATA ANALYSIS

Pair-wise similarities between transects were measured and integrated into a similarity matrix. The Jaccard similarity index (Downton & Brennan, 1980) was used in this study because of the asymmetric and binary nature of the data. It is calculated by dividing the number of species found in both the samples by the number found in only one sample or the other. It is defined as the size of the intersection divided by the size of the union of the sample sets (A and B): $J(A, B) = \frac{|A \cap B|}{|A \cup B|}$.

The cluster analysis consisted of performing hierarchical cluster analysis using a set of similarities for the 10 transects, employing Ward's minimum variance method (Ward, 1963), aimed at finding compact, spherical clusters, as the clustering method.

The normality of the statistical distribution of the numbers or percentages of species was controlled by a Shapiro–Wilk test (Shapiro & Wilk, 1965). Bartlett's test for homogeneity of variances (Snedecor & Cochran, 1989) was used to verify whether k samples (*i.e*. measured in different groups of stations) had equal variances. When necessary, the one-parameter Box–Cox transformation (Box & Cox, 1964) was implemented on variables in order to reduce anomalies such as non-additivity, non-normality and heteroscedasticity (Sakia, 1992). A comparison of the k samples was then made using a parametric one-way ANOVA (Cockerham, 1969, 1973). Student–Newman–Keuls multiple comparisons (Zar, 1984) were used for pair-wise comparisons. The number of species is a discrete quantitative variable with a limited range of possible values. The ANOVA statistical procedure is based on the assumption of a Gaussian distribution of the outcome at each level of the explanatory variable (Cockerham, 1973). In this case, it is judged to be a reasonable approximation to treat the number of species as a continuous variable. Although there is no hard-and-fast rule, 11 different values might be considered borderline, whereas, for example, five different values would be hard to justify as possibly consistent with a Gaussian distribution (Seltman, 2012). In this study, the number of species per station presented 23 different values, so the approximation of normal distribution is tolerated.

Statistical significance testing was set at 0·05. All statistical analyses were performed with R (R Development Core Team; www.r-project.org) using package ade-4 (Chessel *et al*., 2004).

RESULTS

SPECIES RICHNESS

The total number of species (N_{TS}) was 263 and the total number of families (N_{TF}) was 45 (Appendix). The mean ± S.D. number of species per station (N_{MS}) was 53·9 ± 11·8 (Table I). Only two species were cartilaginous fishes (Chondrichthyes). The other 261 species were bony fishes (Osteichthyes). It was noted that 109 species (41% N_{TS}) belong to four main families: Labridae (42 species), Pomacentridae (26

TABLE I. Mean ± S.D. numbers of species per station (N_{MS}) and total numbers of species (N_{TS}) presented by sampling transect (see Fig. 1)

Sector	Age of the lava flow	Transect	Number of stations	N_{MS}	N_{TS}
Outside the volcanic enclosure	1977 (34 years)	R1	4	55·3 ± 4·9	101
	Prehistoric	R2	3	73·0 ± 24·0	106
	Prehistoric	R3	4	55·5 ± 4·8	124
	Prehistoric	R4	4	48·8 ± 5·3	133
	Prehistoric	R5	4	47·7 ± 7·3	107
Inside the volcanic enclosure	2005 (6 years)	R6	4	58·7 ± 10·4	108
	2004 (7 years)	R7	4	51·5 ± 7·1	104
	2007 (4 years)	R8	4	52·4 ± 5·4	126
	2007 (4 years)	R9	4	55·0 ± 9·6	98
	2007 (4 years)	R10	3	62·5 ± 2·1	92
		Total	38	53·9 ± 11·8	263

species), Acanthuridae (23 species) and Chaetodontidae (18 species). Moreover, nine species (3% of the N_{TS}) were not recorded in the latest checklist for Reunion Island (Fricke *et al*., 2009) (Table II). They were included in this study as range extension species (Appendix). They comprised a majority of small-bodied and mimetic species, except for two large species belonging to the *Scarus* and *Scorpaenopsis* genera.

Twelve species (5% of the N_{TS}) were observed with a frequency of occurrence exceeding 80%: brown surgeonfish *Acanthurus nigrofuscus* (Forsskål 1775), darkfin hind *Cephalopholis urodeta* (Forster 1801), stout chromis *Chromis chrysura* (Bliss 1883), chocolatedip chromis *Chromis dimidiata* (Klunzinger 1871), blacktail chromis *Chromis nigrura* Smith 1960, adorned wrasse *Halichoeres cosmetus* Randall & Smith 1982, bluestreak cleaner wrasse *Labroides dimidiatus* (Valenciennes 1839), elegant unicornfish *Naso elegans* (Rüppell 1829), bluespine unicornfish *Naso unicornis* (Forsskål 1775), boomerang triggerfish *Sufflamen bursa* (Bloch & Schneider 1801), red-cheek wrasse *Thalassoma genivittatum* (Valenciennes 1839) and moorish idol *Zanclus cornutus* (L. 1758). Conversely, 87 species (33% of the N_{TS}) were observed with a frequency of occurrence <5%. Most of these rare species were cryptic [*e.g.* combtooth blennie *Aspidontus tractus* Fowler 1903 and spotted croucher *Caracanthus madagascariensis* (Guichenot 1869)], semi-pelagic [*e.g.* bluefin trevally *Caranx melampygus* Cuvier 1833 and dogtooth tuna *Gymnosarda unicolor* (Rüppell 1836)], usually found in deeper [*e.g.* Indian butterflyfish *Chaetodon mitratus* Günther 1860 and thornback cowfish *Lactoria fornasini* (Bianconi 1846)] or restricted to some very specific habitats [*e.g.* high-hat triplefin *Enneapterygius tutuilae* Jordan & Seale 1906, whip coral goby *Bryaninops yongei* (Davis & Cohen 1969) and Michel's ghost goby *Pleurosicya micheli* Fourmanoir 1971].

Cluster analysis was performed to examine the overall similarity of assemblages between sampling transects (Fig. 3). There was a clear separation between the most recent sites (R6–R10) and both the prehistoric sites (R2–R5) and the 34 year site (R1). There was, however, no clear separation between the prehistoric sites and 34 year site. Three different groups of sites were identified (Fig. 3). The first group (group I) consisted of the most recent sites, which had also felt the most intensive

TABLE II. Species of teleosts identified during the survey and not recorded in the most recent checklist of the fish species of Reunion Island (Fricke *et al*., 2009)

Family	Genus and species	Habitat description	Transect
Apogonidae	*Apogon fukuii*	In small groups at the entrance of crevices beyond 25 m	7, 8
Gobiidae	*Bryaninops yongei*	In contact with antipatharians, sometimes in pairs, beyond 25 m	4, 5
Gobiidae	*Lotilia graciliosa*	At the entrance of small crevices, in high sedimentation environment	4
Ostraciidae	*Lactoria fornasini*	Single specimen near the bottom, beyond 25 m	4
Pomacentridae	*Abudefduf notatus*	In small schools, near the edge between boulders and rocky drop-offs	8
Pomacentridae	*Chromis lepidolepis*	In schools, in sympatry with other *Chromis* species (*Chromis nigrura*; *Pomachromis richardsoni*)	4, 5, 6, 7
Scaridae	*Scarus tricolor*	Single specimen observed near the edge of the volcano area	1
Scorpaenidae	*Scorpaenopsis oxycephala*	Large specimens (40 cm) observed resting on rocky bottom beyond 25 m	1, 2
Tripterygiidae	*Enneapterygius pusillus*	Alone or in pairs, resting on encrusting corals (*e.g*. *Acanthastrea* sp. and *Favia* sp.)	2, 3, 4, 5, 6, 7, 8, 10

effects from the volcanic activity inside the VE in recent years. It was the only group where similarity indices were closely linked to the age of the sites (R7, R8: 2002–2004; R6: 2005; R9, R10: 2007). The second group (group II), composed of prehistoric sites adjacent to the VE, was considered as a transitional group with a former substratum, but also subjected to a relatively high influence from volcanic activity perpetuated by water warming. The third group (group III), composed of the 34 year site and prehistoric sites located further from the VE, was considered as the group that had been less intensively affected by volcanic activity in recent decades and whose assemblages had been stable for at least 34 years. Thus, the groups can be sorted by the strength of the influence of the very last eruption, which is highly linked to the distance to the most recent flow.

The above analysis is limited to the similarities of the entire assemblages at each of the sites. To determine which groups contributed to the differences, the family and species distributions had to be examined individually. Thus, the N_{MS} of the eight richest families were compared across the groups (Table III). Differences among groups were found for two families: Serranidae and Holocentridae. No between-group differences were found for Labridae, Pomacentridae, Acanthuridae, Chaetodontidae,

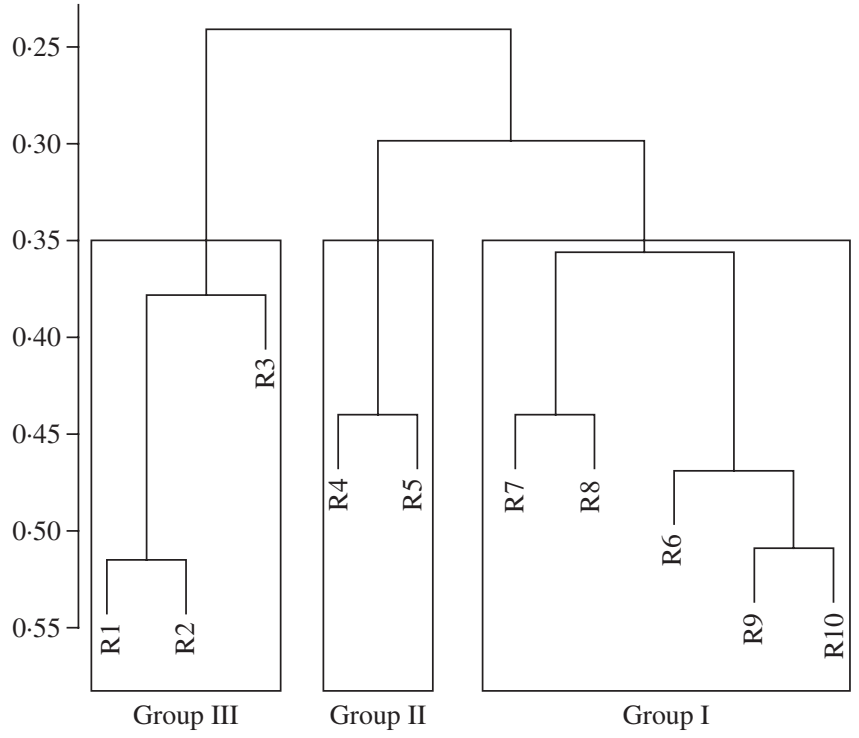


FIG. 3. Dendrogram depicting results of cluster analysis of species counts. The vertical axis indicates Jaccard similarity index. Group numbers are shown along bottom (group I: R6–R10, group II: R4–R5, group III: R1–R3; see Fig. 1).

Balistidae, Blenniidae, Muraenidae and Mullidae. The N_{MS} of Serranidae (groupers and anthias) measured in group I showed significantly higher value than that measured in group III (all tests were ANOVA, $F_{2,35} = 6{\cdot}28$, $P < 0{\cdot}001$); group II presented an intermediate value. Moreover, the N_{MS} of Holocentridae (soldierfishes and squirrelfishes) was higher in group III than in either group I or II ($F_{2,35} = 6{\cdot}59$, $P < 0{\cdot}001$). The entire N_{MS} (of all families combined) also showed significant differences between groups ($F_{2,35} = 6{\cdot}09$, $P < 0{\cdot}05$). It was lower in group II than in either group I or III. The entire N_{MS}, however, showed no significant differences between ages of sites (4, 6, 7 and 34 years, and prehistoric: $F_{4,35} = 0{\cdot}70$, $P > 0{\cdot}05$).

TROPHIC STRUCTURE

The most common guild was carnivores, with 178 species (68% of the N_{TS}), feeding on zooplankton, fishes or invertebrates. Among them, small diurnal carnivores were the most highly represented with 61 species (23% of the N_{TS}, *e.g.* Labridae), followed by piscivores composed of 32 species (12%, *e.g.* Muraenidae, Serranidae, Scorpaenidae and Synodontidae). Nocturnal carnivores (10%, *e.g.* Serranidae and Lethrinidae), diurnal planktivores (9%, *e.g.* Pomacentridae), browsers of sessile invertebrates (7%, *e.g.* Chaetodontidae) and nocturnal planktivores (7%, *e.g.* Apogonidae and Holocentridae) were the least represented carnivorous

TABLE III. Mean ± S.D. number of species per station (N_{MS}) of the eight richest families compared among groups of sites. Student–Newman–Keuls-type multiple comparisons test specifies the groups that have higher N_{MS}. Means on the same row with the same lower-case superscript letter are significantly different from each other at the P-value indicated

Family	N_{MS}			$F_{2,35}$	P
	Group I	Group II	Group III		
Labridae	9·9 ± 2·5	7·5 ± 2·2	10·0 ± 4·8	2·69	
Pomacentridae	6·8 ± 2·8	8·3 ± 2·8	7·8 ± 1·6	1·30	
Acanthuridae	6·8 ± 2·8	7·8 ± 2·3	8·4 ± 2·1	2·05	
Chaetodontidae	4·9 ± 1·7	4·5 ± 1·9	5·8 ± 2·9	0·81	
Serranidae	4·4 ± 1·5[a]	3·4 ± 1·1	2·6 ± 1·2[a]	6·28	**<0·001**
Balistidae	1·9 ± 1·1	1·6 ± 0·7	2·0 ± 0·9	0·50	
Blenniidae	1·8 ± 1·3	1·3 ± 0·9	1·7 ± 0·7	0·92	
Holocentridae	1·1 ± 1·4[a]	0·3 ± 0·5[b]	2·2 ± 1·5[ab]	6·59	**<0·001**
Muraenidae	0·7 ± 0·8	0·3 ± 0·7	0·1 ± 0·3	2·78	
Mullidae	2·5 ± 1·2	1·8 ± 1·1	2·4 ± 1·4	1·23	
All families combined	54·9 ± 7·6[a]	48·3 ± 6·1[ab]	59·3 ± 12·1[b]	6·09	**<0·05**

categories. Among the other diets, omnivores were composed of 47 species (18%, *e.g.* Pomacentridae), while herbivores were represented by 38 species (14%, *e.g.* Acanthuridae and Scaridae).

The mean percentages of species per station ($\%N_{MS}$) of the eight dietary categories were compared between the groups of sites previously identified by the cluster analysis [Table IV(a)]. The $\%N_{MS}$ of browsers of sessile invertebrates measured in group III showed significantly higher value than that measured in group I ($F_{2,35} = 6{\cdot}36$, $P < 0{\cdot}001$); group II presented intermediate values. In the same way, the $\%N_{MS}$ of omnivores measured in groups I and II were significantly higher than that measured in group III ($F_{2,35} = 7{\cdot}04$, $P < 0{\cdot}001$). Finally, the $\%N_{MS}$ of piscivores measured in group I showed a significantly higher value than that measured in group II ($F_{2,35} = 5{\cdot}21$, $P < 0{\cdot}05$); group III presented an intermediate value. No between-group differences were found for the $\%N_{MS}$ of diurnal and nocturnal carnivores, herbivores and diurnal and nocturnal planktivores.

GEOGRAPHICAL DISTRIBUTION AND LIFE HISTORY

The main elements of the fish fauna of the Piton de la Fournaise consisted of widespread tropical Indo-Pacific species (177 species, 69% of the N_{TS}). Only five species (2%) were circumtropical, 43 species (17%) were Indo-West Pacific and 31 (12%) were endemic to the south-western Indian Ocean and the Mascarene Islands. The $\%N_{MS}$ of the south-western Indian Ocean measured in group III showed significantly lower values than those measured in group I or II ($F_{2,35} = 10{\cdot}02$, $P < 0{\cdot}001$) [Table IV(b)]. No differences were found between the groups for the $\%N_{MS}$ of circumtropical, Indo-Pacific and Indo-West Pacific.

The analysis of species life history showed a dominance of classes 1 (*e.g.* Pomacentridae and Chaetodontidae) and 2 (*e.g.* Labridae and Acanthuridae), which accounted for 55 and 26% of the N_{TS}, respectively. Class 3 was composed of 51

TABLE IV. Mean ± S.D. percentages of species per station ($\%N_{MS}$), presented by (a) diet, (b) geographical distribution and (c) life history, compared among groups of sites. Student–Newman–Keuls-type multiple comparisons test specifies the groups that have higher $\%N_{MS}$. Means on the same row with the same lower-case superscript letter are significantly different from each other at the P-value indicated

Variables	$\%N_{MS}$ Group I	$\%N_{MS}$ Group II	$\%N_{MS}$ Group III	$F_{2,35}$	P
(a) Diet					
Browsers	$8{\cdot}1 \pm 3{\cdot}1^{a}$	$10{\cdot}9 \pm 3{\cdot}2$	$13{\cdot}5 \pm 5{\cdot}0^{a}$	6·36	**<0·001**
Diurnal carnivores	$25{\cdot}4 \pm 3{\cdot}1$	$22{\cdot}3 \pm 4{\cdot}6$	$23{\cdot}5 \pm 6{\cdot}5$	1·71	
Nocturnal carnivores	$6{\cdot}8 \pm 2{\cdot}1$	$6{\cdot}3 \pm 4{\cdot}4$	$8{\cdot}0 \pm 3{\cdot}7$	0·89	
Herbivores	$14{\cdot}8 \pm 4{\cdot}5$	$17{\cdot}9 \pm 4{\cdot}0$	$17{\cdot}5 \pm 3{\cdot}5$	2·61	
Omnivores	$19{\cdot}2 \pm 3{\cdot}2^{a}$	$21{\cdot}4 \pm 5{\cdot}1^{b}$	$15{\cdot}7 \pm 3{\cdot}3^{ab}$	7·04	**<0·001**
Piscivores	$8{\cdot}6 \pm 3{\cdot}5^{a}$	$5{\cdot}0 \pm 2{\cdot}1^{a}$	$7{\cdot}0 \pm 3{\cdot}1$	5·21	**<0·05**
Diurnal planktivores	$13{\cdot}1 \pm 3{\cdot}1$	$13{\cdot}8 \pm 4{\cdot}5$	$9{\cdot}9 \pm 4{\cdot}1$	2·79	
Nocturnal planktivores	$4{\cdot}1 \pm 2{\cdot}8$	$2{\cdot}4 \pm 2{\cdot}1$	$4{\cdot}8 \pm 2{\cdot}9$	2·33	
(b) Distribution					
Circumtropical	$2{\cdot}1 \pm 1{\cdot}3$	$2{\cdot}1 \pm 1{\cdot}6$	$1{\cdot}8 \pm 1{\cdot}7$	0·13	
Indo-Pacific Ocean	$70{\cdot}8 \pm 4{\cdot}6$	$71{\cdot}4 \pm 4{\cdot}8$	$75{\cdot}4 \pm 6{\cdot}6$	2·10	
Indo-west Pacific Ocean	$12{\cdot}2 \pm 2{\cdot}6$	$13{\cdot}2 \pm 3{\cdot}6$	$13{\cdot}7 \pm 4{\cdot}2$	0·72	
South-western Indian Ocean	$14{\cdot}9 \pm 3{\cdot}3^{a}$	$13{\cdot}3 \pm 2{\cdot}9^{b}$	$9{\cdot}2 \pm 2{\cdot}8^{ab}$	10·02	**<0·001**
(c) Life history					
Class 1	$56{\cdot}9 \pm 6{\cdot}8$	$60{\cdot}8 \pm 3{\cdot}6$	$56{\cdot}5 \pm 3{\cdot}5$	2·44	
Class 2	$30{\cdot}1 \pm 4{\cdot}7$	$28{\cdot}7 \pm 3{\cdot}4$	$32{\cdot}2 \pm 5{\cdot}5$	1·85	
Class 3	$13{\cdot}0 \pm 4{\cdot}1$	$10{\cdot}5 \pm 3{\cdot}7$	$11{\cdot}3 \pm 3{\cdot}0$	1·62	

species (*e.g.* Muraenidae and *Naso* genus Acanthuridae), representing 19% of the N_{TS}. Life-history classes showed highly homogeneous $\%N_{MS}$, with no significant differences between groups [Table IV(c)].

DISCUSSION

SPECIES RICHNESS

The 263 species recorded in this study represented 27% of the 965 marine fishes listed for the Reunion Island territory (Fricke *et al*., 2009) and 23% of the 1123 species indexed in the fish checklist for the Mascarene Islands [Reunion, Mauritius and Rodrigues; (Fricke, 1999)].

The Hawaiian Archipelago is the most studied area of tropical oceanic islands with high volcanic activity, but only few studies have dealt with the most recent lava flows of the main active volcanoes, Mauna Loa and Kilauea (Gosline *et al*., 1954; Grigg & Maragos, 1974; Godwin & Kosaki, 1989). Godwin & Kosaki (1989) observed fish community development in an essentially similar situation at Kapa'ahu, on the eastern coast of the Kilauea volcano, for 3 months after a flow. Their study had an essentially quantitative approach (fish densities); however, there are few points

of comparison with the present work, which was exclusively conducted using the qualitative presence or absence method.

Despite the limited duration of the study (8 days) and the use of the UVC method, which typically underestimates the total community (Harmelin-Vivien *et al*., 1985; Fowler, 1987; Willis, 2001), the N_{TS} of the Piton de la Fournaise was elevated for a non-reef area (*i.e*. outside the fringing reefs), especially one situated on an active volcano. Some families such as the Syngnathidae, Pinguipedidae, Scombridae and Haemulidae were, however, only represented by a single species. It is probable that other species of these common families in the Indian Ocean islands (Fricke, 1999; Fricke *et al*., 2009) were present in this area, but the survey design (*e.g*. UVC methods) was not set-up to identify these mimetic, cryptic or elusive species. Likewise, no species of large-bodied pelagic and semi-pelagic families such as Carcharhinidae, Sphyrnidae, Sphyraenidae and Belonidae were observed during the sampling period; yet, these species are occasionally observed by divers in this type of habitat, with an extremely narrow insular shelf (Hampton, 1992; Lawson *et al*., 2000). Although there is plenty of evidence to suggest that for large-bodied species their habitat ranges span many kilometres (Meyer *et al*., 2007; Heupel *et al*., 2010; Williams *et al*., 2010) and there are probably days when the conditions are favourable to moderate levels of fisheries exploitation that can have an effect, especially on large-bodied species, which tend to be slow-growing and long-lived (Russ & Alcala, 1989; Jennings & Polunin, 1996), it is quite unlikely that this scarcity is the unique consequence of overfishing, given that two environmental variables, swell and a narrow insular shelf, significantly reduce the potential for the exploitation of coastal fisheries in the south region of Reunion Island (Leblond *et al*., 2010). Moreover, the sampling sites were located >10 km from the nearest fishing port (Fig. 1), *i.e*. quite a long distance for the 5–7 m traditional boats that constitute 67% of the Reunionese fleet (Leblond *et al*., 2010). Thus, it is more likely that the sample size or the area covered may have been too small to assess large-bodied rare species. Also, the sampling season may partly explain the scarcity of these pelagic species. Indeed, some species, including Carangidae and Scombridae, tend to move away from the coast in November for breeding out at sea (Soria *et al*., 2009).

The entire N_{MS} showed the highest values in groups I and III. Odum (1969) suggested that as ecosystems develop they gain complexity and become more resistant and resilient, gaining system-wide buffers to extrinsic and intrinsic perturbations. He indicated that the variety of species tends to increase during the early stages of community development. Rate-of-change curves are usually convex, however, with changes occurring most rapidly at the beginning (Odum, 1969; Connell, 1978). Moreover, after these early stages of ecological succession, the relationship between variety of species and ecosystem development becomes more controversial (Odum, 1969). This relation was not observed in this study, as group I, the most recent group, also presented one of the highest N_{MS}. It is likely that the most recent group, which is composed of 4–7 year flows, was old enough to minimize the effect of the age of sites on N_{MS} (asymptotic tendency of the convex rate-of-change curves). While an increase in the variety of species, together with reduced dominance by any one species or small group of species, can be accepted as a general probability during succession (Connell, 1978), there are other community changes that may work against these trends. A decrease in the interval between disturbances and an

increase in the intensity of these disturbances are trends that may reduce the number of species that can live in a given area (Connell, 1978; Grigg, 1983). The decreasing intensities of the volcanic disturbances, from the most recent flows (group I) to the north of the study site (group III), with the same interval between disturbances, however, do not appear to be linked to an increase in N_{MS}. Finally, intrinsic and extrinsic habitat characteristics such as slope (Bell & Galzin, 1984), structural complexity (Chabanet *et al*., 1997) and exposure to swell or currents (Lara & Gonzalez, 1998; Floeter *et al*., 2007) can also have an effect on species richness. The habitat characteristic of high structural complexity observed in both groups I and III, due to unconsolidated lava boulders, rocks and rubble (group I; Godwin & Kosaki, 1989) and high coral richness and cover (group III; Chabanet *et al*., 1997) respectively, could be implicated in the high N_{MS} observed for these two groups. By comparison, group II was characterized by wave-smoothed compact lava with low coral cover, considered to be a habitat with low structural complexity (Chabanet *et al*., 1997; Letourneur, 1998).

The higher N_{MS} of Holocentridae observed in group III could be due to the high coral cover observed on the well-developed coral communities in the north of the study site. Indeed, 60% of the Holocentridae species sampled during the survey were considered as species that occur exclusively in coral-reef habitat (Fricke *et al*., 2009). By comparison, only 22% of the Chaetodontidae and 12% of the Serranidae sampled during this survey possessed this status (Fricke *et al*., 2009). The higher N_{MS} of Serranidae observed in group I could be due to the higher densities of juvenile fishes on the most recent flows. Despite the lack of quantitative data collected during the study, this distributional trend was described by Godwin & Kosaki (1989), who noted that juvenile densities were highest on the youngest flows. The Serranidae species sampled during the survey comprised 71% of small-bodied demersal species with a relatively opportunistic diet, in which fishes (mainly juveniles) can be an important part of their food [*C. urodeta*, strawberry hind *Cephalopholis spiloparaea* (Valenciennes 1828) and starspotted grouper *Epinephelus hexagonatus* (Forster 1801)] (Myers, 1999; Froese & Pauly, 2012).

TROPHIC STRUCTURE

Despite the location of the study site on a rocky coast, the results obtained for the trophic structures during the survey were comparable to the values for the western Indian Ocean coral reefs (Table V). The regional differences observed in trophic structures appear to indicate that they are more dependent on local conditions than on regional features (Chabanet *et al*., 2002). Thus, the trophic structure of the fish communities in the volcanic area was very similar to those observed in Rodrigues (Heemstra *et al*., 2004) and the Geyser and Zélée banks (Chabanet *et al*., 2002). Conversely, it was very different from those measured on Reunion Island's coral reefs, which have relatively low percentages of carnivore species compared with herbivores. The presence of a large number of carnivore species, generally varying between 60 and 80% of the N_{TS}, is a characteristic of fish communities in coral-reef environments (Harmelin-Vivien, 1989). Thus, the trophic structure of the rocky-coast ichthyofauna sampled during this study was common to coral-reef communities. On the contrary, Reunion Island's coral reefs showed a percentage of carnivore species (Chabanet *et al*., 2002) below these reference values. The small surface area of coral

TABLE V. Trophic structure of the fish communities, expressed as percentages of the total number of species on different western Indian Ocean coral-reef areas

Region	Island and banks	Reference	Carn	Omn	Herb
Mozambique Channel	Toliara (Madagascar)	Harmelin-Vivien (1981)	74	13·5	12·5
	Glorieuses Islands	Durville *et al*. (2003)	73	12	15
	Geyser and Zélée banks	Chabanet *et al*. (2002)	69	16	15
	Mayotte	Chabanet (2002)	69	12·5	18·5
Western Indian Ocean and Mascarene Islands	Seychelles	Daw *et al*. (2011)	60	14	26
	Tromelin	Unpubl. data	62	22	16
	Mauritius	Roberts *et al*. (2001)	60	24	16
	Rodrigues	Heemstra *et al*. (2004)	68	18	14
	Reunion (coral reef)	Chabanet *et al*. (2002)	51	24	25
	Reunion (volcano)	This study	69	17	14

Carn, carnivore; Omn, omnivore; Herb, herbivore.

reefs in Reunion Island and their level of perturbation due to high anthropogenic stresses must be taken into account, however, when interpreting these findings (Tessier *et al*., 2008).

The trophic structure of the entire fish community in the study site was characterized by the absence of top predators and the persistence of opportunistic species, mainly composed of small-bodied lower-level carnivores (diurnal consumers of benthic invertebrates and zooplanktivores). This trophic feature is characteristic of a disturbed environment (Odum, 1969; Sandin & Sala, 2012). Indeed, disturbed areas are often characterized by a reduction in the length of food chains that promotes the establishment of opportunistic species (Caswell & Cohen, 1991). It is assumed that the sample size or the area covered may have been too small to assess large-bodied rare species and that even moderate levels of fisheries exploitation can have an effect especially on large-bodied species (Russ & Alcala, 1989; Jennings & Polunin, 1996). Ecological characteristics, such as high inter and intraspecific competition and temporal resource availability, however, could also favour intraguild predation between higher-level carnivores and could contribute to their scarcity (Polis *et al*., 1989; Holt & Polis, 1997; Arim & Marquet, 2004).

The higher $\%N_{MS}$ of browsers of sessile invertebrates measured in group III is probably due to the high coral cover observed in the well-developed coral communities in the north of the study site. Chabanet & Faure (1994) and Chabanet *et al*. (1997) relate the effect of high coral cover on the occurrence and richness of browsers of sessile invertebrates, as coral polyps represent a significant part of their diet (Hiatt & Strasburg, 1960; Hobson, 1974; Myers, 1999). The higher $\%N_{MS}$ of omnivores in groups I and II could be a trophic response to the infrequent, but acute, volcanic disturbances affecting these two groups. High diet flexibility can occur in response to temporal resource availability, density-dependent behavioural shifts and facultative responses to novel food or its disappearance following a disturbance to the habitat (Sandin & Sala, 2012). The higher $\%N_{MS}$ of piscivores observed in group I, such as that of Serranidae, could be a consequence of higher densities of juvenile fishes on the most recent flows (Godwin & Kosaki, 1989).

GEOGRAPHICAL DISTRIBUTION AND LIFE HISTORY

The 965 marine fish species in the inventory of Fricke *et al*. (2009) in Reunion Island were mainly composed of widespread tropical Indo-Pacific species (631 species, 65% of the total indexed species). Only 126 species (13%) were circumtropical, 128 species (14%) were Indo-West Pacific and 81 (8%) were endemic to the south-western Indian Ocean and the Mascarene Islands. Compared to these global results, censuses of this study were mainly characterized by a relatively high richness in the south-western Indian Ocean endemics (12%) and a lack of circumtropical species (2%). The rarity of this last category, largely composed of pelagic and semi-pelagic species, is consistent with previous observations on species richness that mentioned a virtual absence of pelagic species in faunal inventories of the Piton de la Fournaise. These results were also consistent with the observations of Pinault *et al*. (in press) who observed that fish communities in the south-east of Reunion Island harboured the island's lowest percentage of circumtropical species and the highest proportion of south-western Indian Ocean endemics. The 31 endemic species recorded during this survey had very convergent characteristics. Almost all were small-bodied (25 species, 81%, had an asymptotic length of <30 cm), were encountered in shallower waters (25 species, 81%, had a maximum depth of <40 m), with high reproductive rate (23 species, 74%, had a minimum population doubling time of <15 months), non-selective diet (10 species, 32%, were omnivores) and small habitat range (22 species, 71%, were sedentary) (Froese & Pauly, 2012).

The higher $\%N_{\mathrm{MS}}$ of the south-western Indian Ocean observed in groups I and II could be the result of these convergent biological traits, which are characteristic of species commonly found in the early stages of ecological succession (Sandin & Sala, 2012), as the two groups were the most intensively affected by volcanic disturbances. Thus, the adaptability of the south-western Indian Ocean species and their strategy of colonization could compensate for their low competitiveness (Odum, 1969; Ramade, 2003).

There were very few regional data references on species life history. Pinault *et al*. (in press), however, showed that the southern fish communities of Reunion Island are composed almost entirely of species of classes 1 and 2 (91%). In addition, although fewer species of class 3 are present in the south, their number increases to 30% of recorded species on the north coast of the island. The results of this study, with 81% of species from classes 1 and 2 and only 19% from class 3, were consistent with this spatial pattern. Odum (1969) showed that in the developmental stage of succession, organisms tend to be small and have simple life histories and rapid rates of reproduction. As the ecosystem develops, however, the selective advantage shifts to larger organisms, which have greater storage capacities and more complex life histories and are therefore better adapted to exploiting seasonal or periodic releases of nutrients or other resources (MacArthur & Wilson, 1967; Odum, 1969). Levins (1969) and Galarza *et al*. (2009) have also shown that genetic viscosity caused by the fragmentation of a homogeneous population into several subpopulations, for various reasons, including habitat and behavioural changes, could favour intraspecific competition, especially for access to food, and could affect reproductive rates among sub-populations, thus favouring opportunistic species with high fertility. Lava flows are probably the most acute and the most influential causes of disturbance and fragmentation of habitats on the south-east coast of Reunion Island. The stringency of the

environmental variables (swell and rain) and the extreme narrowness of the insular shelf could, however, likewise favour the sustainability of the developmental stage of ecological succession.

In conclusion, this first survey of the fish communities in the Piton de la Fournaise lava flows revealed ecological features of great interest, both in terms of total species richness and of percentage of the south-western Indian Ocean endemics. Moreover, the overall sampled fish community showed very unusual life-history strategies and trophic structure, with a large majority of small-bodied lower-level carnivores having dietary flexibility and high fertility. These tendencies, which increased significantly from the north to the south of the study site, appear to be a consequence of, or an adaptation to, acute and intensive disturbances caused by volcanic activity. The fact that these biological traits were found throughout the study site could imply, however, that stringent environmental conditions (*e.g.* the high hydrodynamic energy, widespread runoff and percolation and the narrowness of the insular shelf) and the seasonal fluctuation of food resources, including pelagic nutrients, are also responsible for this situation. Regarding the broader influences, this study increases the understanding of other types of acute disturbances (*e.g.* increased storm activity as a result of climate change and increased acute anthropogenic pressures due to dangerous maritime practices) and helps to better understand how ecosystems can resist or recover from these perturbations. This study also helps to better understand the process of ecological succession that leads to the establishment of fish communities on newly submerged habitats, such as artificial reefs. It would be interesting to continue the investigation in a different season (*e.g.* austral winter) and at depths beyond 30 m, as many other authors have recognized that depth is the variable with the most significant effect on the structure of fish communities (Booth & Wellington, 1995; Friedlander & Parrish, 1998), both in their composition (species richness) and trophic and demographic structures. Most species sampled during this investigation were restricted to shallow water and it is likely that many were not observed as they live in deeper areas. Quantitative data, with a focus on recruitment periods on new lava flows, especially for the south-west Indian Ocean endemic species, might help to test some of the hypotheses made in this study. This quantitative approach to the community would also provide a basis for comparison with the results obtained by Godwin & Kosaki (1989) on recent lava flows of the Kilauea in Hawaii.

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References

Arim, M. & Marquet, P. A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* **7,** 557–564.

Barcelo, A., Robert, R. & Coudray, J. (1997). A major rainfall event: the 27 February–5 march 1993 rains on the southeastern slope of Piton de la Fournaise massif (Reunion Island, southwest Indian Ocean). *American Meteorological Society* **125,** 3341–3346.

Bell, J. D. & Galzin, R. (1984). Influence of live coral cover on coral reef fish communities. *Marine Ecology Progress Series* **15,** 265–274.
Booth, D. J. & Wellington, G. (1995). Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology* **23,** 274–279.
Box, G. E. P. & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical Society B* **26,** 211–252.
Caswell, H. & Cohen, J. E. (1991). Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In *Ecological Heterogeneity* (Kolasa, J. & Pickett, S. T., eds), pp. 97–122. New York, NY: Springer-Verlag.
Chabanet, P. (2002). Coral reef fish communities of Mayotte (western Indian Ocean) two years after the impact of the 1998 bleaching event. *Marine and Freshwater Research* **53,** 107–113.
Chabanet, P. & Faure, G. (1994). Interrelations entre peuplements benthiques et ichtyologiques en milieu corallien (Interrelationships between benthic and ichthyologic communities in coral environment). *Comptes Rendus de l'Académie des Sciences de Paris* **317,** 1151–1157.
Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G. & Galzin, R. (1997). Relationships between coral reef substrata and fish. *Coral Reefs* **16,** 93–102.
Chabanet, P., Tessier, E., Durville, P., Mulochau, T. & René, F. (2002). Fish communities of Geyser and Zélée coral banks (western Indian Ocean). *Cybium* **26,** 11–27.
Chessel, D., Dufour, A. B. & Thioulouse, J. (2004). The ade4 package-I- one-table methods. *R News* **4,** 5–10.
Chevallier, L. & Vatin-Perignon, N. (1982). Volcano-structural evolution of Piton des Neiges, Reunion Island, Indian Ocean. *Bulletin of Volcanology* **45,** 285–298.
Cockerham, C. C. (1969). Analysis of gene frequencies. *Evolution* **23,** 72–84.
Cockerham, C. C. (1973). Analysis of gene frequencies. *Genetics* **74,** 679–700.
Colin, P. L. (1996). Longevity of some coral reef fish spawning aggregations. *Copeia* **1996,** 189–192.
Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199,** 1302–1310.
Coppola, D., Staudacher, T. & Cigolini, C. (2005). The May–July 2003 eruption at Piton de la Fournaise (La Reunion): volume, effusion rates, and emplacement mechanisms inferred from thermal imaging and global positioning system (GPS) survey. In *Kinematics and Dynamics of Lava Flows, Special Paper 396* (Manga, M. & Ventura, G., eds), pp. 103–124. Boulder, CO: The Geological Society of America.
Daw, T. M., Robinson, J. & Graham, N. A. J. (2011). Perceptions of trends in Seychelles artisanal trap fisheries: comparing catch monitoring, underwater visual census and fishers' knowledge. *Environmental Conservation* **38,** 75–88.
Downton, M. & Brennan, T. (1980). Comparing classifications: an evaluation of several coefficients of partition agreement. In *Proceedings of the Meeting of the Classification Society*, pp. 418–425. Boulder, CO: Classification Society.
Durville, P., Chabanet, P. & Quod, J. P. (2003). Visual census of the reef fishes in the natural reserve of the Glorieuses Islands (western Indian Ocean). *Western Indian Ocean Journal of Marine Science* **2,** 95–104.
Floeter, S. R., Krohling, W., Gasparini, J. L., Ferreira, R. L. C. & Zalmon, I. R. (2007). Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environmental Biology of Fishes* **78,** 147–160.
Fowler, A. M. (1987). The development of sampling strategies for population studies of coastal reef fishes. A case study. *Coral Reefs* **6,** 49–58.
Fricke, R. (1999). *Fishes of the Mascarene Islands (Réunion, Mauritius, Rodriguez)*. Königstein: Koeltz Scientific Books.
Fricke, R., Mulochau, T., Durville, P., Chabanet, P., Tessier, E. & Letourneur, Y. (2009). Annotated checklist of the fish species (Pisces) of La Réunion, including a Red List of threatened and declining species. *Stuttgarter Beiträge zur Naturkunde A* **2,** 1–168.
Friedlander, A. M. & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* **224,** 1–30.

Galarza, J. A., Boulay, R., Cerdá, X., Doums, C., Federici, P., Magalon, H., Monnin, T. & Rico, C. (2009). Development of single sequence repeat markers for the ant *Aphaenogaster senilis* and cross-species amplification in *A. iberica*, *A. gibbosa*, *A. subterranea* and *Messor maroccanus*. *Conservation Genetics* **10,** 519–521.

Godwin, J. R. & Kosaki, R. K. (1989). Reef fish assemblages on submerged lava flows of three different ages. *Pacific Science* **43,** 289–301.

Gosline, W. A., Brock, V. E., Moore, H. L. & Yamaguchi, Y. (1954). Fishes killed by the 1950 eruption of Mauna Loa I. The origin and nature of the collections. *Pacific Science* **8,** 23–27.

Grigg, R. W. (1983). Community structure, succession and development of coral reefs in Hawaii. *Marine Ecology Progress Series* **11,** 1–14.

Grigg, R. W. & Maragos, J. E. (1974). Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* **55,** 387–395.

Hampton, I. (1992). The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. *South African Journal of Marine Science* **12,** 1031–1050.

Harmelin-Vivien, M. L. (1981). Trophic relationships of reef fishes in Tulear (Madagascar). *Oceanologica Acta* **4,** 365–374.

Harmelin-Vivien, M. L. (1989). Reef fish community structure: an Indo-Pacific comparison. In *Vertebrates in Complex Systems* (Harmelin-Vivien, M. & Bourlière, F., eds), pp. 21–60. Berlin: Springer-Verlag.

Harmelin-Vivien, M. L., Harmelin, J., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J. & Lasserre, G. (1985). Visual assessment of fish populations and communities: methods and problems. *Revue d'Ecologie La Terre et la Vie* **40,** 467–539.

Heemstra, E., Heemstra, P., Smale, M., Hooper, T. & Pelicier, D. (2004). Preliminary checklist of coastal fishes from the Mauritian island of Rodrigues. *Journal of Natural History* **38,** 3315–3344.

Heupel, M. R., Simpfendorfer, C. A. & Fitzpatrick, R. (2010). Large-scale movement and reef fidelity of grey reef sharks. *PLoS One* **5,** e9650.

Hiatt, R. W. & Strasburg, D. W. (1960). Ecological relationship of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* **30,** 65–127.

Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin* **72,** 915–1031.

Holt, R. D. & Polis, G. A. (1997). A theoretical framework for intraguild predation. *American Naturalist* **149,** 747–764.

Hutchinson, G. E. (1957). Concluding remarks, Cold Spring Harbor symposium. *Quantitative Biology* **22,** 415–427.

Jennings, S. & Polunin, N. V. C. (1996). Impacts of fishing on tropical reef ecosystems. *Ambio* **25,** 44–49.

Labrosse, P., Kulbicki, M. & Ferraris, J. (2002). *Underwater Visual Fish Census Surveys - Proper Use and Implementation*. Noume: Secretariat of the Pacific Community.

Lara, E. N. & Gonzalez, E. A. (1998). The relationship between reef fish community structure and environmental variables in the southern Mexican Caribbean. *Journal of Fish Biology* **53,** 209–221.

Lawson, G. L., Barange, M. & Fréon, P. (2000). Species identification of pelagic fish schools on the South African continental shelf using acoustic descriptors and ancillary information. *ICES Journal of Marine Science* **58,** 275–287.

Leps, J., Osbornova-Kosinova, J. & Rejmanek, M. (1982). Community stability, complexity and species life history strategies. *Vegetatio* **50,** 53–63.

Letourneur, Y. (1998). Composition, structures and trophic networks of the fish communities of the windward coast of Réunion Island. *Cybium* **22,** 267–283.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15,** 237–240.

Lieske, E. & Myers, R. F. (1994). *Collins Pocket Guide to Coral Reef Fishes, Indo-Pacific and Caribbean*. New York, NY: HarperCollins.

MacArthur, R. H. & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

McDougall, I. (1971). The geochronology and evolution of the young volcanic island of Reunion, Indian Ocean. *Geochimica et Cosmochimica Acta* **35,** 261–270.

Mellin, C., Ferraris, J., Galzin, R., Kulbicki, M. & Ponton, D. (2006). Diversity of coral reef fish assemblages: modelling of the species richness spectra from multi-scale environmental variables in the Tuamotu Archipelago (French Polynesia). *Ecological Modelling* **198,** 409–425.

Meyer, C. G., Holland, K. N. & Papastamatiou, Y. P. (2007). Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of marine protected areas. *Marine Ecology Progress Series* **333,** 13–25.

Michon, L. & Saint-Ange, F. (2008). Morphology of Piton de la Fournaise basaltic shield volcano (La Reunion Island): characterization and implication in the volcano evolution. *Journal of Geophysical Research Solid Earth* **113,** 19.

Myers, R. F. (1999). *Micronesian Reef Fishes: A Comprehensive Guide to the Coral Reef Fishes of Micronesia*, 3rd edn. Barrigada: Coral Graphics.

Odum, E. P. (1969). The strategy of ecosystem development. *Science* **164,** 262–270.

Okubo, P. & Clague, D. A. (2009). Earthquakes. In *Encyclopedia of Islands* (Gillespie, R. G. & Clague, D. A., eds), pp. 240–244. Berkeley, CA: University of California Press.

Pinault, M., Chabanet, P., Loiseau, N., Durville, P., Galzin, R. & Quod, J. P. (in press). Influence des facteurs environnementaux sur la structure des peuplements ichtyologiques côtiers de l'île de La Réunion (Sud-Ouest de l'Océan Indien). [Influence of environmental factors on the structure coastal fish communities of Reunion Island (south-western Indian Ocean)]. *Cybium* (in press).

Polis, G. A., Myers, C. A. & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20,** 297–330.

Ramade, F. (2003). *Éléments d'écologie : écologie fondamentale [Elements of Ecology: Fundamental Ecology]*, 3rd edn. Paris: Dunod.

Rees, T. (2008). Using AquaMaps for biodiversity assessment, including a prototype MPA (marine protected area) network design tool. In *Proceedings of the 2008 Annual Conference of the Taxonomic Databases Working Group* (Weitzman, A. & Belbin, L., eds), pp. 73–74. Fremantle: Biodiversity Information Standards (TDWG) and the Missouri Botanical Garden.

Roberts, C. M., Hawkins, J. P., McAllister, D. E. & Schueler, F. W. (2001). Global distribution and conservation of coral reef fish biodiversity. In *Coral Reef Fish Status Report* (Roberts, C. M., Hawkins, J. P. & McAllister, D. E., eds), pp. 182–194. Washington, DC: IUCN Species Survival Commission.

Russ, G. R. & Alcala, A. C. (1989). Effects of intense fishing pressure on an assemblage of coral-reef fishes. *Marine Ecology Progress Series* **56,** 13–27.

Sakia, R. M. (1992). The Box–Cox transformation technique: a review. *Statistician* **41,** 169–178.

Sandin, S. A. & Sala, E. (2012). Using successional theory to measure marine ecosystem health. *Evolutionary Ecology Research* **26,** 435–448.

Seltman, H. J. (2012). *Experimental Design and Analysis*. Pittsburgh, PA: Carnegie Mellon University.

Soria, M., Dagorne, L., Potin, G. & Fréon, P. (2009). First field-based experiment supporting the meeting point hypothesis for schooling in pelagic fish. *Animal Behaviour* **78,** 1441–1446.

Shapiro, S. S. & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika* **52,** 591–611.

Snedecor, G. W. & Cochran, W. G. (1989). *Statistical Methods*, 8th edn. Ames, IO: Iowa State University Press.

Strasberg, D. (1995). Processus d'invasion par les plantes introduites à La Réunion et dynamique de la végétation sur les coulées volcaniques [Process of invasion by introduced plants in Reunion Island and vegetation dynamics on volcanic flows]. *Ecologie* **26,** 169–180.

Taquet, M. & Diringer, A. (2007). *Poissons de l'Océan Indien et de la Mer Rouge*. Versailles: Quae.
Tanguy, J. C., Bachèlery, P. & Le Goff, M. (2011). Archeomagnetism of Piton de la Fournaise: bearing on volcanic activity at La Réunion Island and geomagnetic secular variation in southern Indian Ocean. *Earth and Planetary Science Letters* **303,** 361–368.
Tessier, E., Chabanet, P., Pothin, K., Soria, M. & Lasserre, G. (2005). Visual censuses of tropical fish aggregations on artificial reefs: slate versus video recording techniques. *Journal of Experimental Marine Biology and Ecology* **315,** 17–30.
Tessier, E., Bigot, L., Cadet, C., Cauvin, B., Chabanet, P., Conand, C., Nicet, J. B. & Quod, J. P. (2008). Coral reefs of Réunion Island in 2007: status report and monitoring network. *Revue d'Ecologie la Terre et la Vie* **63,** 85–102.
Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58,** 236–244.
Williams, A. J., Little, L. R., Punt, A. E., Mapstone, B. D., Davies, C. R. & Heupel, M. R. (2010). Exploring movement patterns of an exploited coral reef fish when tagging data are limited. *Marine Ecology Progress Series* **405,** 87–99.
Willis, T. J. (2001). Visual census methods underestimate density and diversity of cryptic reef fishes. *Journal of Fish Biology* **59,** 1408–1411.
Zar, J. H. (1984). *Biostatistical Analysis*, 2nd edn. Englewood Cliffs, NJ: Prentice-Hall.

Electronic References

Froese, R. & Pauly, D. (2012). FishBase. Available at www.fishbase.org (last accessed 13 June 2012).
Kaschner, K., Rius-Barile, J., Kesner-Reyes, K., Garilao, C., Kullander, S. O., Rees, T. & Froese R. (2010). *AquaMaps*: *Predicted Range Maps for Aquatic Species*. *Version 08/2010*. Available at www.aquamaps.org (last accessed 13 June 2012).
Leblond, E., Demaneche, S., Blond, S. L., Merrien, C., Berthou, P., Daures, F., Pitel-Roudaut, M., Ru, L. L., Lajeunesse, M., Laurence, A. & Evano, H. (2010). Fisheries Information System (FIS) – Fishing Vessels Activity in 2008 at the Maritime District of Saint-Denis of La Réunion. Brest: IFREMER. Available at http://wwz.ifremer.fr/lareunion/Les-projets/SIH/ (last accessed 13 June 2012).

APPENDIX

APPENDIX I. List of the species observed during this work (families are in capital letters)

	Occur.	Diet	Life H.	Geogr.
Acanthuridae				
Acanthurus dussumieri Valenciennes 1835	0·50	H	3	IP
Acanthurus guttatus Forster 1801	0·08	H	1	IP
Acanthurus leucosternon Bennett 1833	0·18	H	2	IW
Acanthurus mata (Cuvier 1829)	0·39	O	3	IP
Acanthurus nigricauda Duncker & Mohr 1929	0·29	H	1	IP
Acanthurus nigrofuscus (Forsskål 1775)	0·97	H	2	IP
Acanthurus tennentii Günther 1861	0·34	H	1	IW
Acanthurus thompsoni (Fowler 1923)	0·18	Pd	1	IP
Acanthurus triostegus (L. 1758)	0·03	H	2	IP

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Acanthurus xanthopterus Valenciennes 1835	0·05	H	3	IP
Ctenochaetus striatus (Quoy & Gaimard 1825)	0·71	H	1	IP
Ctenochaetus truncatus Randall & Clements 2001	0·08	H	1	IW
Naso brachycentron (Valenciennes 1835)	0·08	H	3	IP
Naso brevirostris (Cuvier 1829)	0·24	Pd	3	IP
Naso elegans (Rüppell 1829)	0·84	H	2	IW
Naso hexacanthus (Bleeker 1855)	0·53	Pd	3	IP
Naso thynnoides (Cuvier 1829)	0·03	O	2	IW
Naso tuberosus Lacépède 1801	0·05	H	3	IW
Naso unicornis (Forsskål 1775)	0·82	H	3	IP
Paracanthurus hepatus (L. 1766)	0·03	Pd	1	IP
Zebrasoma desjardinii (Bennett 1836)	0·55	H	2	IW
Zebrasoma gemmatum (Valenciennes 1835)	0·42	H	1	SW
Zebrasoma scopas (Cuvier 1829)	0·05	H	2	IP
Antennariidae				
Histrio histrio (L. 1758)	0·03	P	1	CT
Apogonidae				
**Apogon fukuii* Hayashi 1990	0·05	Pn	1	IW
Apogon holotaenia Regan 1905	0·13	Pn	1	IW
Cheilodipterus lineatus Lacépède 1801	0·13	P	1	IP
Ostorhinchus angustatus (Smith & Radcliffe 1911)	0·05	Pn	1	IP
Ostorhinchus apogonoides (Bleeker 1856)	0·03	Pn	1	IP
Ostorhinchus taeniophorus (Regan 1908)	0·13	Pn	1	IP
Pristiapogon kallopterus (Bleeker 1856)	0·13	Pn	1	IP
Aulostomidae				
Aulostomus chinensis (L. 1766)	0·39	P	3	IP
Balistidae				
Balistapus undulatus (Park 1797)	0·05	Cd	2	IP
Balistoides conspicillum (Bloch & Schneider 1801)	0·29	Cd	3	IP
Balistoides viridescens (Bloch & Schneider 1801)	0·03	Cd	3	IP
Melichthys niger (Bloch 1786)	0·13	O	3	CT
Odonus niger (Rüppell 1836)	0·05	Pd	3	IP
Pseudobalistes fuscus (Bloch & Schneider 1801)	0·03	Cd	3	IP
Rhinecanthus rectangulus (Bloch & Schneider 1801)	0·08	O	2	IP
Sufflamen bursa (Bloch & Schneider 1801)	0·95	Cd	1	IP
Sufflamen chrysopterum (Bloch & Schneider 1801)	0·03	Cd	2	IP
Sufflamen fraenatum (Latreille 1804)	0·08	Cd	2	IP
Xanthichthys auromarginatus (Bennett 1832)	0·11	Pd	2	IP
Blenniidae				
Aspidontus dussumieri (Valenciennes 1836)	0·03	O	1	IP
Aspidontus tractus Fowler 1903	0·05	Pd	1	IW
Cirripectes castaneus (Valenciennes 1836)	0·08	H	1	IP
Cirripectes randalli Williams 1988	0·03	H	1	SW
Cirripectes sp.	0·11			
Ecsenius lineatus Klausewitz 1962	0·58	H	1	IW
Ecsenius midas Starck 1969	0·08	O	1	IP
Exallias brevis (Kner 1868)	0·05	Bi	1	IP

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Plagiotremus rhinorhynchos (Bleeker 1852)	0·11	Cd	1	IP
Plagiotremus tapeinosoma (Bleeker 1857)	0·47	Cd	1	IP
Bothidae				
Bothus mancus (Broussonet 1782)	0·03	P	3	IP
Caesionidae				
Caesio teres Seale 1906	0·37	Pd	1	IP
Pterocaesio marri Schultz 1953	0·08	Pd	1	IP
Pterocaesio tile (Cuvier 1830)	0·24	Pd	1	IP
Callionymidae				
Callionymus sp.	0·03			
Caracanthidae				
Caracanthus madagascariensis (Guichenot 1869)	0·05	Cn	1	IW
Carangidae				
Caranx melampygus Cuvier 1833	0·03	P	3	IP
Decapterus macarellus (Cuvier 1833)	0·11	Pn	1	CT
Elagatis bipinnulata (Quoy & Gaimard 1825)	0·03	Pn	3	CT
Chaetodontidae				
Chaetodon auriga Forsskål 1775	0·37	Bi	1	IP
Chaetodon blackburnii Desjardins 1836	0·16	O	1	SW
Chaetodon dolosus Ahl 1923	0·13	O	1	SW
Chaetodon guttatissimus Bennett 1833	0·37	Bi	1	IW
Chaetodon interruptus Ahl 1923	0·13	Bi	1	IW
Chaetodon kleinii Bloch 1790	0·74	O	1	IP
Chaetodon lunula (Lacépède 1802)	0·16	Bi	1	IP
Chaetodon madagaskariensis Ahl 1923	0·55	Bi	1	IW
Chaetodon meyeri Bloch & Schneider 1801	0·34	Bi	1	IP
Chaetodon mitratus Günther 1860	0·05	Bi	1	SW
Chaetodon trifasciatus Park 1797	0·11	Bi	1	IP
Chaetodon vagabundus L. 1758	0·18	O	1	IP
Chaetodon xanthocephalus Bennett 1833	0·03	Bi	1	IW
Forcipiger flavissimus Jordan & McGregor 1898	0·55	O	1	IP
Forcipiger longirostris (Broussonet 1782)	0·03	O	1	IP
Hemitaurichthys zoster (Bennett 1831)	0·39	O	1	IW
Heniochus acuminatus (L. 1758)	0·47	O	1	IP
Heniochus monoceros Cuvier 1831	0·21	Bi	1	IP
Cirrhitidae				
Cirrhitichthys guichenoti (Sauvage 1880)	0·47	Cn	1	SW
Cirrhitops mascarenensis Randall & Schultz 2008	0·63	Cn	1	SW
Cirrhitus pinnulatus (Forster 1801)	0·08	Cn	1	IP
Paracirrhites arcatus (Cuvier 1829)	0·53	Cn	1	IP
Paracirrhites forsteri (Schneider 1801)	0·21	Cn	1	IP
Fistulariidae				
Fistularia commersonii Rüppell 1838	0·03	P	3	IP
Gobiidae				
**Bryaninops yongei* (Davis & Cohen 1969)	0·05	O	1	IP
Gnatholepis cauerensis (Bleeker 1853)	0·18	O	1	IP

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Gnatholepis sp.	0·08			
**Lotilia graciliosa* Klausewitz 1960	0·03	Cd	1	IW
Pleurosicya micheli Fourmanoir 1971	0·03	O	1	IP
Valenciennea helsdingenii (Bleeker 1858)	0·03	Cd	2	IP
Valenciennea strigata (Broussonet 1782)	0·26	Cd	1	IP
Haemulidae				
Plectorhinchus picus (Cuvier 1828)	0·13	Cn	3	IP
Holocentridae				
Myripristis berndti Jordan & Evermann 1903	0·45	Pn	1	IP
Myripristis chryseres Jordan & Evermann 1903	0·08	Pn	1	IP
Myripristis murdjan (Forsskål 1775)	0·05	Pn	1	IP
Myripristis vittata Valenciennes 1831	0·16	Pn	1	IP
Neoniphon aurolineatus (Liénard 1839)	0·03	Cn	1	IP
Neoniphon sammara (Forsskål 1775)	0·03	Cn	1	IP
Sargocentron caudimaculatum (Rüppell 1838)	0·05	Cn	1	IP
Sargocentron diadema (Lacépède 1802)	0·21	Cn	1	IP
Sargocentron ittodai (Jordan & Fowler 1902)	0·03	Cn	1	IP
Sargocentron punctatissimum (Cuvier 1829)	0·03	Cn	1	IP
Kuliidae				
Kuhlia mugil (Forster 1801)	0·03	Pn	3	IP
Kyphosidae				
Kyphosus cinerascens (Forsskål 1775)	0·13	H	3	IP
Labridae				
Anampses caeruleopunctatus Rüppell 1829	0·08	Cd	2	IP
Anampses lineatus Randall 1972	0·11	Cd	1	IP
Anampses meleagrides Valenciennes 1840	0·08	Cd	2	IP
Anampses twistii Bleeker 1856	0·03	Cd	2	IP
Bodianus anthioides (Bennett 1832)	0·11	Cd	2	IP
Bodianus axillaris (Bennett 1832)	0·21	Cd	2	IP
Bodianus bilunulatus (Lacépède 1801)	0·29	Cd	3	IP
Bodianus diana (Lacépède 1801)	0·08	Cd	2	IP
Bodianus macrourus (Lacépède 1801)	0·68	Cd	2	SW
Cheilio inermis (Forsskål 1775)	0·03	Cd	3	IP
Choerodon robustus (Günther 1862)	0·03	Cd	2	IP
Coris aygula Lacépède 1801	0·16	Cd	3	IP
Coris caudimacula (Quoy & Gaimard 1834)	0·47	Cd	2	IW
Coris cuvieri (Bennett 1831)	0·16	Cd	2	IW
Epibulus insidiator (Pallas 1770)	0·05	Cd	3	IP
Gomphosus caeruleus Lacépède 1801	0·63	Cd	2	IW
Halichoeres cosmetus Randall & Smith 1982	0·82	Cd	1	SW
Halichoeres hortulanus (Lacépède 1801)	0·16	Cd	1	IP
Halichoeres lamarii (Valenciennes 1839)	0·24	Cd	1	IW
Halichoeres lapillus Smith 1947	0·32	Cd	1	SW
Halichoeres nebulosus (Valenciennes 1839)	0·05	Cd	1	IP
Hemigymnus fasciatus (Bloch 1792)	0·11	Cd	3	IP
Hologymnosus annulatus (Lacépède 1801)	0·11	Cd	2	IP
Hologymnosus doliatus (Lacépède 1801)	0·18	Cd	3	IP

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Iniistius pavo (Valenciennes 1840)	0·08	Cd	2	IP
Iniistius sp.	0·03			
Labroides bicolor Fowler & Bean 1928	0·32	Cd	1	IP
Labroides dimidiatus (Valenciennes 1839)	0·82	Cd	2	IP
Macropharyngodon bipartitus Smith 1957	0·16	Cd	1	SW
Macropharyngodon sp.	0·03			
Novaculichthys taeniourus (Lacépède 1801)	0·03	Cd	2	IP
Pseudocheilinus dispilus Randall 1999	0·55	Cd	1	SW
Pseudocoris yamashiroi (Schmidt 1931)	0·26	Pd	1	IP
Pseudodax moluccanus (Valenciennes 1840)	0·08	Cd	2	IP
Stethojulis albovittata (Bonnaterre 1788)	0·24	Cd	1	IW
Stethojulis strigiventer (Bennett 1833)	0·05	Cd	1	IP
Thalassoma amblycephalum (Bleeker 1856)	0·11	Pd	2	IP
Thalassoma genivittatum (Valenciennes 1839)	0·92	Cd	2	SW
Thalassoma hebraicum (Lacépède 1801)	0·03	Cd	2	SW
Thalassoma purpureum (Forsskål 1775)	0·11	Cd	2	IP
Thalassoma trilobatum (Lacépède 1801)	0·13	Cd	2	IP
Xyrichtys pentadactylus (L. 1758)	0·05	Cd	2	IP
Lethrinidae				
Gnathodentex aureolineatus (Lacépède 1802)	0·13	Cn	2	IP
Gymnocranius grandoculis (Valenciennes 1830)	0·05	Cn	3	IP
Monotaxis grandoculis (Forsskål 1775)	0·21	Cn	3	IP
Lutjanidae				
Aphareus furca (Lacépède 1801)	0·16	P	2	IP
Lutjanus kasmira (Forsskål 1775)	0·11	Cn	2	IP
Microdesmidae				
Nemateleotris magnifica Fowler 1938	0·53	Pd	1	IP
Ptereleotris evides (Jordan & Hubbs 1925)	0·03	Pd	1	IP
Ptereleotris heteroptera (Bleeker 1855)	0·21	Pd	1	IP
Monacanthidae				
Cantherhines dumerilii (Hollard 1854)	0·21	Bi	2	IP
Cantherhines pardalis (Rüppell 1837)	0·71	Bi	2	CT
Pervagor janthinosoma (Bleeker 1854)	0·26	Bi	1	IP
Mullidae				
Mulloidichthys auriflamma (Forsskål 1775)	0·16	Cn	2	IW
Mulloidichthys pfluegeri (Steindachner 1900)	0·03	Cd	2	IP
Parupeneus ciliatus (Lacépède 1802)	0·05	Cd	2	IP
Parupeneus cyclostomus (Lacépède 1801)	0·32	P	3	IP
Parupeneus heptacanthus (Lacépède 1802)	0·05	Cd	1	IP
Parupeneus macronemus (Lacépède 1801)	0·79	Cd	2	IP
Parupeneus pleurostigma (Bennett 1831)	0·16	Cd	1	IP
Parupeneus trifasciatus (Lacépède 1801)	0·74	Cd	2	IP
Muraenidae				
Enchelycore pardalis (Temminck & Schlegel 1846)	0·03	P	3	IP
Gymnothorax eurostus (Abbott 1860)	0·03	P	3	IP
Gymnothorax flavimarginatus (Rüppell 1830)	0·08	P	3	IP
Gymnothorax griseus (Lacépède 1803)	0·08	P	3	SW

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Gymnothorax javanicus (Bleeker 1859)	0·03	P	3	IP
Gymnothorax meleagris (Shaw & Nodder 1795)	0·13	P	3	IP
Gymnothorax rueppelliae (McClelland 1844)	0·03	P	3	IP
Gymnothorax undulatus (Lacépède 1803)	0·03	P	3	IP
Rhinomuraena quaesita Garman 1888	0·03	P	3	IP
Myliobatidae				
Aetobatus ocellatus (Kuhl 1823)	0·03	Cn	3	IP
Ostraciidae				
**Lactoria fornasini* (Bianconi 1846)	0·03	Cd	2	IP
Ostracion cubicus L. 1758	0·03	H	2	IP
Ostracion meleagris Shaw 1796	0·16	Bi	2	IP
Ostracion trachys Randall 1975	0·03	Bi	1	SW
Pempheridae				
Pempheris nesogallica Cuvier 1831	0·13	Pn	1	SW
Pempheris schwenkii Bleeker 1855	0·05	Pn	1	IP
Pinguipedidae				
Parapercis maculata (Bloch & Schneider 1801)	0·03	Cd	1	SW
Pomacanthidae				
Apolemichthys trimaculatus (Cuvier 1831)	0·08	Bi	2	IW
Centropyge acanthops (Norman 1922)	0·16	O	1	SW
Centropyge bispinosa (Günther 1860)	0·29	H	1	IP
Centropyge multispinis (Playfair 1867)	0·13	H	1	IW
Genicanthus caudovittatus (Günther 1860)	0·03	O	1	IW
Pomacanthus imperator (Bloch 1787)	0·63	Bi	2	IP
Pomacentridae				
Abudefduf margariteus (Cuvier 1830)	0·32	O	2	SW
**Abudefduf notatus* (Day 1870)	0·03	O	2	IP
Abudefduf sordidus (Forsskål 1775)	0·03	O	2	IP
Abudefduf sparoides (Quoy & Gaimard 1825)	0·13	O	1	SW
Abudefduf vaigiensis (Quoy & Gaimard 1825)	0·05	O	1	IP
Amphiprion chrysogaster Cuvier 1830	0·21	O	1	SW
Chromis chrysura (Bliss 1883)	0·87	Pd	1	IP
Chromis dimidiata (Klunzinger 1871)	0·87	O	1	IW
**Chromis lepidolepis* Bleeker 1877	0·16	Pd	1	IP
Chromis leucura Gilbert 1905	0·11	O	1	IP
Chromis nigrura Smith 1960	0·92	Pd	1	IW
Chromis opercularis (Günther 1867)	0·29	O	1	IW
Chromis sp.	0·11			
Chromis ternatensis (Bleeker 1856)	0·58	Pd	1	IP
Chromis weberi Fowler & Bean 1928	0·16	O	1	IP
Chrysiptera glauca (Cuvier 1830)	0·21	H	1	IP
Dascyllus trimaculatus (Rüppell 1829)	0·34	O	1	IP
Plectroglyphidodon dickii (Liénard 1839)	0·24	O	1	IP
Plectroglyphidodon imparipennis (Vaillant & Sauvage 1875)	0·18	H	1	IP
Plectroglyphidodon johnstonianus Fowler & Ball 1924	0·21	O	1	IP
Plectroglyphidodon lacrymatus (Quoy & Gaimard 1825)	0·11	H	1	IP
Plectroglyphidodon randalli Allen 1991	0·26	H	1	SW

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Pomacentrus caeruleus Quoy & Gaimard 1825	0·42	O	1	IW
Pomachromis richardsoni (Snyder 1909)	0·05	O	1	IP
Stegastes luteobrunneus (Smith 1960)	0·29	O	1	IW
Stegastes pelicieri Allen & Emery 1985	0·45	O	1	SW
Priacanthidae				
Priacanthus hamrur (Forsskål 1775)	0·08	Pn	1	IP
Scaridae				
Calotomus carolinus (Valenciennes 1840)	0·13	H	1	IP
Chlorurus enneacanthus (Lacépède 1802)	0·08	H	2	IW
Chlorurus sordidus (Forsskål 1775)	0·08	H	2	IP
Scarus caudofasciatus (Günther 1862)	0·08	H	3	SW
Scarus sp.	0·03			
**Scarus tricolor* Bleeker 1847	0·03	H	2	IP
Scombridae				
Gymnosarda unicolor (Rüppell 1836)	0·03	P	3	IP
Scorpaenidae				
Dendrochirus biocellatus (Fowler 1938)	0·03	Cn	2	IP
Pterois antennata (Bloch 1787)	0·32	P	2	IP
Pterois miles (Bennett 1828)	0·11	P	3	IW
Scorpaenopsis diabolus (Cuvier 1829)	0·03	P	3	IP
**Scorpaenopsis oxycephala* (Bleeker 1849)	0·05	P	3	IW
Sebastapistes tinkhami (Fowler 1946)	0·08	Cn	1	IP
Serranidae				
Cephalopholis leopardus (Lacépède 1801)	0·03	Cn	1	IP
Cephalopholis spiloparaea (Valenciennes 1828)	0·11	P	2	IP
Cephalopholis urodeta (Forster 1801)	0·89	P	2	IP
Epinephelus hexagonatus (Forster 1801)	0·34	P	1	IP
Epinephelus macrospilos (Bleeker 1855)	0·05	Cn	3	IP
Epinephelus oceanicus (Lacépède 1802)	0·24	Cn	3	IW
Epinephelus rivulatus (Valenciennes 1830)	0·03	P	1	IW
Grammistes sexlineatus (Thunberg 1792)	0·21	Cn	2	IP
Pogonoperca ocellata Günther 1859	0·03	P	2	IW
Pseudanthias cooperi (Regan 1902)	0·32	Pd	1	IW
Pseudanthias evansi (Smith 1954)	0·61	Pd	1	IW
Pseudanthias pulcherrimus (Heemstra & Randall 1986)	0·08	Pd	1	SW
Pseudanthias squamipinnis (Peters 1855)	0·63	O	1	IP
Variola louti (Forsskål 1775)	0·11	P	3	IP
Siganidae				
Siganus argenteus (Quoy & Gaimard 1825)	0·18	H	1	IP
Siganus luridus (Rüppell 1829)	0·26	H	2	SW
Siganus sutor (Valenciennes 1835)	0·03	H	1	SW
Syngnathidae				
Doryrhamphus bicarinatus (Dawson 1981)	0·08	O	1	SW
Synodontidae				
Saurida gracilis (Quoy & Gaimard 1824)	0·03	P	1	IP
Synodus dermatogenys Fowler 1912	0·13	P	1	IP

APPENDIX I. Continued

	Occur.	Diet	Life H.	Geogr.
Synodus variegatus (Lacépède 1803)	0·05	P	1	IP
Tetraodontidae				
Arothron hispidus (L. 1758)	0·05	O	3	IP
Arothron meleagris (Anonymus 1798)	0·29	O	3	IP
Arothron nigropunctatus (Bloch & Schneider 1801)	0·34	O	2	IP
Canthigaster amboinensis (Bleeker 1865)	0·11	O	1	IP
Canthigaster natalensis (Günther 1870)	0·08	O	1	SW
Canthigaster smithae Allen & Randall 1977	0·34	O	1	SW
Canthigaster valentini (Bleeker 1853)	0·13	O	1	IP
Torpedinidae				
Torpedo fuscomaculata Peters 1855	0·03	P	3	IW
Trichonotidae				
Trichonotus setiger Bloch & Schneider 1801	0·05	Pd	1	IW
Tripterygiidae				
**Enneapterygius pusillus* Rüppell 1835	0·29	Pn	1	IW
Enneapterygius tutuilae Jordan & Seale 1906	0·03	Pn	1	IP
Zanclidae				
Zanclus cornutus (L. 1758)	0·95	Bi	2	IP

*range extension species for Reunion Island; Occur., occurrence (number of observations per total number of stations); Diet, diet category (H, herbivore; O, omnivore; Cd, diurnal carnivore; Cn, nocturnal carnivore; Pd, diurnal planktivore; Pn, nocturnal planktivore; Bi, browser of sessile invertebrates; P, piscivore); Life H., life history (1, small-body, rapid growth, very high gonado-somatic index; 2, small-body, growth initially rapid, slows after first reproduction, high gonado-somatic index; 3, medium to large-body, growth initially rapid, slows after first reproduction, medium to low gonado-somatic index); Geogr., geographical distribution (CT, circumtropical; IP, Indo-Pacific Ocean; IW, Indo-West Pacific Ocean; SW, south-western Indian Ocean and Mascarene Islands).