Cah. Biol. Mar. (2013) 54 : 491-497

Biodiversity of echinoderms on underwater lava flows with different ages, from the Piton de La Fournaise (Reunion Island, Indian Ocean)

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Abstract: Echinoderms from Reunion Island have been studied mostly from west coast reefs. A recent faunal inventory (BIOLAVE) was conducted on the underwater lava flows of *Piton de La Fournaise* and constitutes the first submarine survey on the south-east side of the island. The aim of the present study was to evaluate the species richness in the different echinoderm classes and assess their potential as indicator of the colonisation of lava with different ages. During 8 days, 9 sites with different habitats defined by depth and substrate homogeneity were explored using a stratified sampling. Description of echinoderms and comparison of the taxonomic composition between sites of different ages and depths were presented. 45 species of the 5 classes were identified, belonging to 23 families and 32 genera. Ophiuroid was the most diverse class (22 species), followed by echinoids (13 species), asteroids and holothuroids (6 species each), and crinoids (2 species). Species number increased with lava flow's age, except for echinoids, which showed a higher species number on recent sites, but ophiuroids only showed a significantly higher species number on the oldest sites. On the contrary, species number tended to decrease with depth, but echinoids only showed a significantly higher species number on shallow water. Some asteroid, echinoid and holothuroid species, such as *Aquilonastra richmondi*, *Asthenosoma varium*, *Echinothrix* spp., *Echinometra mathaei* and *Euapta godeffroyi*, were observed on the most recent sites only, while some ophiuroid species were observed in deeper sites only. These characteristic species could be seen as bioindicators of disturbed environment or have a distribution restricted to deeper areas.

Résumé : *Biodiversité des Echinodermes sur les laves sous-marines d'âges différents du Piton de La Fournaise (Ile de la Réunion, Océan Indien).* Les Echinodermes de La Réunion ont été principalement étudiés sur les récifs de la côte ouest. Un inventaire récent de la biodiversité (BIOLAVE) a été mené sur les laves sous-marines du Piton de La Fournaise et constitue les premiers résultats collectés dans le sud-est de l'île. L'objectif de la présente étude était d'évaluer la richesse spécifique des différentes classes d'Echinodermes et leur potentiel comme indicateurs de la colonisation sur des coulées d'âges différents. Pendant 8 jours, 9 sites ont été explorés, dans des habitats de différentes profondeurs et homogénéité de substrat, avec un échantillonnage stratifié. Des bases de données photographique et globale ont été établies. La liste d'espèces d'échinodermes et la comparaison des compositions taxonomiques entre sites de profondeur et d'âge différents, ont été présentées. Au total 45 espèces ont été recensées et identifiées, appartenant à 5 classes, incluant 23 familles et 32 genres. La classe des ophiurides est la plus diversifiée avec 22 espèces, suivie par les échinides avec 13 espèces, les astérides et les holothurides avec 6 espèces chacune (1 espèce de Chiridotidae a été observée pour la première fois à La Réunion) et les crinoïdes avec 2 espèces. Le nombre d'espèces recensées augmente avec l'âge des coulées, sauf pour les échinides qui présentent un nombre d'espèces légèrement plus élevé sur les sites récents, mais les ophiurides montrent un nombre moyen d'espèce significativement plus élevé sur les sites les plus anciens. Au contraire, le nombre d'espèces tend à décroitre en profondeur, mais seulement les échinides montrent un nombre moyen d'espèces significativement plus élevé dans les eaux peu profondes. Toutefois, certaines espèces comme *Aquilonastra richmondi*, *Asthenosoma varium*, *Echinothrix* spp., *Echinometra mathaei* et *Euapta godeffroyi* n'ont été recensées que sur les sites les plus récents. De la même manière, d'autres espèces comme *Ophiactis quadrispina* et *Ophiothrix sp.* n'ont été recensées qu'en profondeur. Ces espèces caractéristiques pourraient être considérées comme des bioindicateurs d'environnements perturbés ou de distribution restreinte aux eaux plus profondes.

Keywords: Echinoderm ● Diversity ● Volcano ● La Reunion ● Species colonization

Introduction

Marine ecosystems in active volcanic areas are regularly subject to natural hazards such as being covered by incandescent lava flows, acoustic phenomena caused by microseisms, temporary changes in physicochemical conditions of water bodies and exceptional elevations of temperature (Okubo & Clague, 2009). This geologic context is ideal for the study of ecological successions, at the origin of complex ecosystems like coral reefs. The study of these successions is essential to understand the mechanisms of colonization and establishment of pioneer organisms, characterized by low competitiveness and high demographic dynamics. The colonization of underwater lava flows from active volcanoes, in contrast to the terrestrial area, has not been intensely studied in the tropics but several references relate to the cold Alaska and Iceland regions (Gullisken et al., 1980; Gunnarsson & Hauksson, 2009; Jewett et al., 2010). The main studies on tropical sites refer to coral colonization and the other benthic fauna components are rarely cited (Townsley et al., 1962; Grigg & Maragos, 1974; Tomascik et al., 1996; Martínez García et al., 2009).

The *Piton de la Fournaise* (Reunion Island) is one of the most active effusive volcanoes in the world with 27 eruptions between 1998 and 2007 and a mean frequency, over a century, of an eruptive phase every 9 months (Michon & Saint-Ange, 2008; Tanguy et al., 2011). Its lavas commonly reach the ocean (Coppola et al., 2005; Michon & Saint-Ange, 2008). It provides a natural laboratory to study the colonization of a blank substrate. The eruption from 2007 relocated a big burned area in the sea and killed all the sea life around a few kilometres of the coastline. This phenomenon allowed the discovery of new species of fish (Durville et al., 2009; Quero et al., 2009a & b) and demonstrated that the biodiversity in this area was higher than expected.

Therefore, a project called BIOLAVE was launched in 2010 in order to study species and habitat diversity on the coastal marine area of the volcano, including the first taxonomic inventory for the southeast side of the Island.

Echinoderms from Reunion Island have been mostly studied from coral reefs of the west coast during the last 30 years, and a total of 133 species are presently recorded from Reunion Island (Conand, 2003; Conand et al., 2013). BIOLAVE included the first diversity study of the five extant classes of echinoderms (asteroids, crinoids, echinoids, holothuroids and ophiuroids) along the southeast coast of the island and permitted to assess their potential as indicators of the colonization of lava with different ages and depths.

Material and Methods

Sampling area

Located at 21.0°N-55.4°E, 800 km from the eastern coast of Madagascar, La Reunion is an island of the Mascarene archipelago, together with Mauritius and Rodrigues. Mauritius is dated at 8 My and Reunion at 2 My (Tessier et al., 2008). These recent oceanic islands, of volcanic origin, have undergone various changes during successive eruptive phases (Chevallier et al., 1982). Reunion is composed of two volcanoes: the *Piton des Neiges* and the *Piton de la Fournaise*. The *Piton des Neiges* went extinct about 70 000 years ago while the *Piton de la Fournaise* is still active (Chevallier et al., 1982). The island coastline is characterized by a very narrow insular shelf, steep slopes and the presence on its western coast of a 25 km long fringing coral reef, which represents about 12% of the total coastline of the island. The south-east of Reunion, strongly marked by the volcanic activity of *Piton de la Fournaise*, presents little urbanization, compared with the high density of population on the other littoral areas. The majority of the most recent lava flows spreads towards the ocean inside a caldera and forms the area known as the "Volcanic Enclosure" (VE). This coast, exposed to trade winds, is further characterized by regular swell, which can reach very high intensities particularly during the austral winter (Tessier et al., 2008).

Sampling method

The fieldwork took place over an 8-day period in late November 2011 (austral summer). The estimation of species richness in presence/absence was conducted by underwater techniques, mainly using a collection of samples and photographic devices. 36 stations at depths ranging from 0 to 30 m were sampled within 9 radials perpendicular to the shore (Fig. 1). Each radial contained 3 to 5 sampling stations located within 3 intervals of depth: (1)]0-10 m]; (2)]10-20 m]; (3)]20-30 m]. Moreover, the radials were located along the shore in two sectors: (1) inside the VE (R5, R6, R7, R8, R9) and (2) outside the VE (R1, R2, R3, R4), on different aged flows. The second sector included the lava flows older than 30 years (eruption from 1977, prehistoric flows), while the first sector concerned the flows younger than 10 years (eruptions from 2004, 2005, 2007). Sampling methods were subject to standard time and surface defined by dive protocols (30-60 min, 200-400 m^2 per station). All sampling took place between 09:00 and 16:00 hours. The samples collected have been identified by relevant experts in the laboratory. A photograph catalogue and a global database were completed.

Data analysis

Firstly, a species checklist and the number of species in each class were compiled. Secondly, a study of the frequency of species occurrence was established to define the most commonly occurring echinoderm species (occurrence superior than 15%). Thirdly, the influence of two factors (depth and age of lava flows) on species richness was analyzed comparing different groups of stations. As the normality (Shapiro test) and homoscedasticity of the data (Bartlett test) were tested and not verified, non-parametric tests were used to compare samples. The Mann-Whitney test was implemented to compare mean

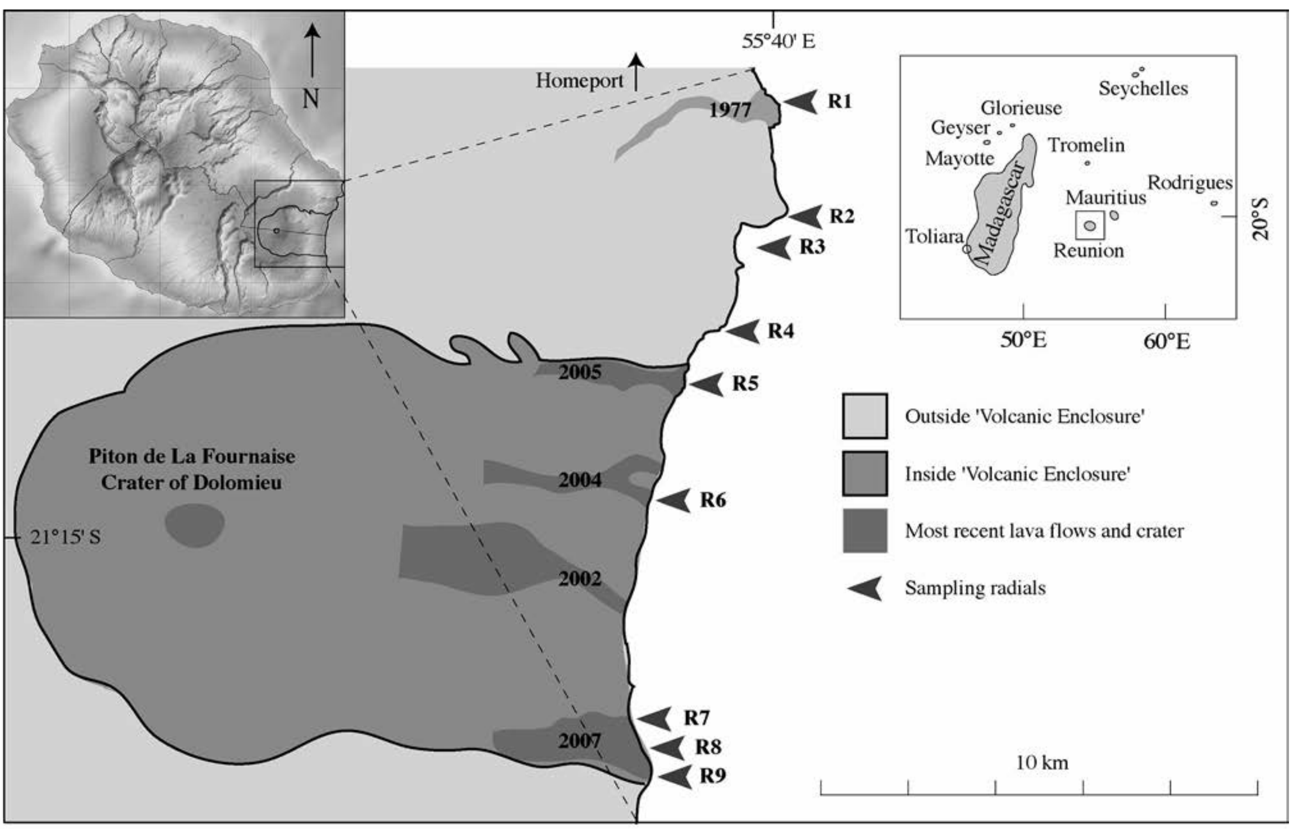

Figure 1. Study area map and sampling sites at lava flows of Piton de la Fournaise at Reunion Island.

number of species grouped together in two sectors of different ages (inside and outside the VE). The Kruskall-Wallis test, followed by the Dunn post hoc test, was implemented to compare mean number of species grouped together in three depth intervals (0-10 m, 10-20 m, 20-30 m). Statistical significance threshold was set at $P \leq 0.05$. All statistical analyses were performed with R (R development Core Team, 2008).

Results

Species and representative estimation of each class

A total of 50 echinoderm species was collected. These samples belonged to the 5 extant classes, 23 families and 32 genera (Table 1). Ophiuroid was the most diverse class with 22 species, 44% of the total number of species (18 identified and 4 species yet unidentified), followed by echinoids with 13 species (26% of the total), asteroids and holothuroids both with 6 species (12% of the total, respectively), and crinoids with 2 species or 6% of the total (Table 1). One Chiridotid species, *Chiridota stuhlmanni,* identified during this survey, represents the first record for Reunion Island.

Twelve species (Table 2) were very commonly recorded (occurrence >15%) in this study. Among these, the first 8 species were echinoids (5 species) and asteroids (3 species); the last four were ophiuroids (3 species) and crinoid (1 species).

Influence of depth and age of lava flows on species richness

Depth. The depth-stratified sampling permitted to precisely isolate the vertical distribution of species in the different classes and families. Thus, several species, such as the 2 small asteroids *Aquilonastra conandae* and *A. richmondi*, the crinoid *Stephanometra indica*, the echinoids *Echinometra mathaei, Colobocentrotus (Podophora) atratus* and *Asthenosoma varium* and the holothuroids *Euapta godeffroyi* and a not identified species, were only found in the shallow water (0-10 m). Moreover, the ophiuroids *Ophiopeza fallax fallax*, *Ophiarachnella cf. septemspinosa*, *Macrophiothrix* spp., *Ophiocoma dentata, O. doederleini, O. erinaceus, O. pica* and *O. pusilla* as all the holothuroids species were only found at depths of less than 20 m.

Conversely, some rare species, such as the ophiuroids *Ophiactis quadrispina* and *Ophiothrix sp.*, were only found in deep water (20-30 m).

Regarding statistical comparisons between depth-intervals (Table 3), only the echinoids mean numbers of species showed significant differences (Kruskal-Wallis test, $P = 0.015$). The Dunn post hoc test revealed decreasing values towards the deep water, with maximum mean species richness measured in shallow water (0-10 m). No between-interval differences were found for the other classes or for the overall community.

Ages of lava flows. As for the effect of depth, the age-stratified sampling allowed to precisely isolate the age distribution of species in the different classes and families. Thus, several species, such as the asteroids *Aquilonastra conandae* and *Dactylosaster cylindricus*, the crinoid *Stephanometra indica*, the echinoids *Colobocentrotus (Podophora) atratus* and *Diadema setosum* and the ophiuroids *Ophiocoma erinaceus complex, O. pica, Ophiolepis cincta garretti, Ophiomyxa sp., Macrophiothrix longipeda* and *Ophiura kinbergi*, were only found on the old lava flows (35 years or more – outside the VE).

In contrast, some other species, such as the asteroid *Aquilonastra richmondi*, the echinoids *Asthenosoma varium*, *Echinothrix* spp., and *Echinometra mathaei* and the holothuroids *Euapta godefroyi* and the not identified chiridotid species, were only found on the most recent lava flow (eruption from 2007). They could so be considered as pioneer species, with a particular affinity for disturbed environments.

About comparisons between sectors (Table 4), only the ophiuroids mean numbers of species showed significant differences (Mann-Whitney test, $P = 0.022$) for which the maximum mean was measured outside the VE, on the old lava flows (35 years or more). No between-sector differences were found for the other classes or for the overall community.

Discussion

This study has allowed the collection of 50 echinoderm species (5 remainded not identified) on the Southeast coast of La Reunion, the observation of several potentially new ophiuroid species and a new occurrence of a holothuroid (Chiridotidae) for Reunion Island. This diversity corresponds to 38% of the Echinoderms already known for La Reunion. The species richness found during this rather short expedition is nevertheless important compared to the 133 species inventoried on the western coast of the island during the last 30 years (Conand, 2003; Conand et al., 2013). Some difficulty arose from the cryptic behaviour of crinoids and some ophiuroids, which could not be collected. Furthermore, habitats on the recent lava flows are less complex than on the older ones, and the important coral cover on the old lava flows (Faure, pers. comm.) increases the possibilities of finding more species with cryptic behaviour. Moreover, some of these species are active during the night (Conand et al., 2010) and the sampling was done only during the day, which may have biased our

Table 1. List of Echinoderm species collected during surveys at lava flows on the Piton de la Fournaise at Reunion Island (BIOLAVE) and representative estimation for each class. (ni: not identified).

Class	Family	Genus species	Auteur/Date	Representative estimation (%)
Asteroidea	**Asteridae**	*Aquilonastra conandae*	O'Loughlin & Rowe,2006	**12%**
		Aquilonastra richmondi	O'Loughlin & Rowe,2006	
	Ophiasteridae	*Dactylosaster cylindricus*	Lamark, 1816	
		Ferdina flavescens	Gray, 1840	
	Goniasteridae	*Fromia milleporella*	Lamark, 1816	
		Fromia monilis	Perrier, 1869	
Crinoidea	**Mariametridae**	*Stephanometra indica*	(Smith, 1876)	**6%**
	Tropiometridae	*Tropiometra cf. carinata*	(Lamarck, 1816)	
Echinoidea	**Cidaridae**	*Eucidaris metularia*	Lamark, 1816	**26%**
	Colobocentridae	*Colobocentrotus (Podophora) atratus*	(Linnaeus, 1758)	
	Diadematidae	*Diadema savigny*	Audouin, 1829	
		Diadema setosum	Leske, 1778	
		Diadema sp		
		Diadematid sp		
		Echinothrix calamaris	Pallas, 1774	
		Echinohtrix diadema	Linnaeus, 1758	
		Echinotrix sp		
	Echinometridae	*Echinometra mathaei*	Blainville, 1825	
		Echinostrephus molaris	Blainville, 1825	
	Echinothuriidae	*Asthenosoma varium*	Grube, 1868	
	Stomopneustidae	*Stomopneustes variolaris*	Lamark, 1816	
Holothuroidea	**Chiridotidae**	*Chiridota stuhlmanni*	Lampert, 1896	**12%**
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	Holothuriidae	*Holothuria nobilis*	Selenka, 1867	
		Actinopyga mauritiana	Quoy & Gaimardd, 1834	
	Stichopodidae	*Thelenota ananas*	Jaeger, 1833	
	Synaptidae	*Euapta godeffroyi*	(Semper, 1868)	
Ophiuroidea	**Ophiactidae**	*Ophiactis quadrispina*	Clark, 1915	**44%**
	Ophiocomidae	*Ophiocoma dentata*	Müller & Trosche,l 1842	
		Ophiocoma doederleini	de Loriol, 1899	
		Ophiocoma erinaceus	Müller & Troschel, 1842	
		Ophiocoma erinaceus complex	Müller & Troschel, 1842	
		Ophiocoma sp.		
		Ophiocoma pica	Müller & Troschel, 1842	
		Ophiocoma pusilla	Brock, 1888	
	Ophiodermatidae	*Ophiopeza fallax fallax*	Peters, 1851	
		Ophiarachnella cf. septemspinosa	Müller & Troschel, 1842	
	Ophiolepididae	*Ophiolepis cincta garretti*	Lyman, 1865	
	Ophiomyxidae	*Ophiomyxa sp*		
	Ophionereididae	*Ophionereis porrecta*	Lyman, 1860	
	Ophiotrichidae	*Ophiothrix sp*		
		Macrophiothrix longipeda	Lamark, 1816	
		Macrophiothrix sp		
		Macrophiothrix sp2		
	Ophiuridae	*Ophiura kinbergi*	Ljungman, 1866	
	ni	*ni sp*		
		ni sp1		
		ni sp2		
		ni sp3		

Table 2. Occurrence of the 12 most common species at lava flows of Piton de la Fournaise at Reunion Island.

Class	Species	rank	occurence (%)
Echinoidea	*Echinothrix calamaris*	1	61.5
Asteroidea	*Fromia milleporella*	2	50.0
Echinoidea	*Echinostrephus molaris*	3	46.2
Asteroidea	*Ferdina flavescens*	4	34.6
Echinoidea	*Stomopneustes variolaris*	5	34.6
Echinoidea	*Diadema savignyi*	6	26.9
Echinoidea	*Eucidaris metularia*	7	23.1
Asteroidea	*Fromia monilis*	8	19.2
Ophiuroidea	*Ophiocoma nov sp*	9	19.2
Ophiuroidea	*Ophiopeza fallax fallax*	10	19.2
Crinoidea	*Tropiometra cf carinata*	11	15.4
Ophiuroidea	*Ophiocoma erinaceus complex*	12	15.4

results. Additional night sampling could increase the species richness or change the occurrence observed here.

The habitats of the south-east coast of Reunion Island are mostly hard substrata, with very little sediment; this could explain the paucity of aspidochirotid holothurians that are deposit-feeders. Depth is known as a structuring factor for these communities (Pinault et al., 2013a & b). In terms of the mean number of species, differences between depth-intervals were found only for the echinoids, but some species of the other classes were also found preferentially in one or the other depth zone. The ophiuroids *Ophiactis quadrispina* and *Ophiothrix sp*., may thus represent two indicators of deep water as they were only found deeper than 20 m

Differences between ages of the lava flows were found only for the ophiuroids, but some species of the other classes were also found preferentially in one age zone. The asteroid *Aquilonastra richmondi*, the echinoids *Asthenosoma varium, Echinothrix spp., Echinometra mathaei*, the holothuroids *Euapta godefroyi* and the juvenile chiridotid species and the crinoids, may thus represent indicators of colonization as they were only found on the recent lava flows. Nevertheless, further studies are needed to evaluate the potential of these species as pioneer species, with a particular affinity for disturbed environments.

Globally, the colonization of a new lava flow by echinoderms is fast, as shown also for the corals (Faure, pers. comm) and fishes (Pinault et al., 2013a & b). The comparison with other localities, such as the Hawaii archipelago the most studied repository of a tropical high volcanic activity island (Hunter & Evans, 1995), shows that the first stages of marine colonization are faster than the terrestrial ones and that the recruitment by larval stages is an important factor (Townsley et al., 1962). The exposure to swell is known to act on the time needed for colonization (Grigg et al., 1974). The rapidity of colonization by corals and their growth after an eruption have been shown to be dependent on substrate and exposure characteristics (Tomascik et al., 1996; Faure, pers. comm.), but no studies have already been done on the role of echinoderms in the colonization of a virgin substrate in the tropics. In the cold waters, Gulliksen et al. (1980) found that the fauna, including echinoderms, on the new and old grounds, in the shallow waters (down to 10 m) were more similar than deeper, where the suspension feeders were dominant.

The BIOLAVE results, still in progress from the surveys of the other flora and fauna components, will allow a better understanding of the colonization processes. This is of paramount importance because these lava flows represent the first stage of the coral reef ecosystems. It appears rather rapid in our case, and the species could come from recruitment from adjacent coral reefs. Nevertheless, further investigations on these sites and abundance estimates of the main populations are still necessary to complete this work and improve our knowledge of the relations between the dominant species and the lava flow ages. These results will also be useful to better understand the resilience or recolonization processes of ecosystems impacted by natural (hurricanes), or human induced (*Acanthaster* outbreaks, new constructions, artificial reefs) activities.

Acknowledgements

We would like to thank the BIOLAVE program and H. Magalon, A. Dayde and F. Trentin for their help during the

Table 3. Mean number of species presented by class of Echinoderms and compared between depth intervals. Significant differences are indicated in bold (Kruskal-Wallis test, $P < 0.05$). Dunn post hoc test specifies intervals that have higher mean number of species.

Classes	0-10 m	11-20 m	21-30 m	Total	*P-value*	Post hoc test
Asteroidea	0.7 ± 0.8	1.1 ± 0.8	1.3 ± 1.0	1.0 ± 0.9	*0.252*	
Crinoidea	0.7 ± 0.7	0.3 ± 0.7	0.4 ± 0.7	0.5 ± 0.7	*0.255*	
Echinoidea	3.3 ± 1.5	1.9 ± 1.3	1.4 ± 1.4	2.2 ± 1.6	***0.015***	0-10 > 11-20 > 21-30
Holothuroidea	0.2 ± 0.6	0.3 ± 0.7	0.0 ± 0.0	0.2 ± 0.5	*0.181*	
Ophiuroidea	1.2 ± 1.1	2.0 ± 2.0	1.5 ± 2.2	1.5 ± 1.8	*0.481*	
Total	5.9 ± 3.2	5.7 ± 2.6	4.5 ± 4.0	5.4 ± 3.2	*0.255*	

Table 4. Mean number of species presented by class of Echinoderms and compared between ages of lava flows. Significant differences are indicated in bold (Mann-Whitney test, $P < 0.05$).

Classes	> 30 yrs	< 10 yrs	Total	*P-value*
Asteroidea	1.2 ± 1.0	0.8 ± 0.8	1.0 ± 0.9	*0.288*
Crinoidea	0.5 ± 0.8	0.4 ± 0.5	0.5 ± 0.7	*0.685*
Echinoidea	2.0 ± 1.2	2.4 ± 1.9	2.2 ± 1.6	*0.748*
Holothuroidea	0.2 ± 0.6	0.1 ± 0.5	0.2 ± 0.5	*0.310*
Ophiuroidea	2.3 ± 2.2	0.8 ± 1.0	1.5 ± 1.8	***0.022***
Total	6.2 ± 3.3	4.6 ± 3.1	5.4 ± 3.2	*0.156*

sampling for observations and photographies. Thanks to S. Coppard, H. Lessios and C. De Ridder for their help for the identification of the Echinoids, C. Mah and M. O'Loughlin for the Asteroids, and M. Eléaume for the Crinoids. BIOLAVE program was funded by the French ministries through the "Délégation Régionale de la Recherche et de la Technologie", and co-financed by the European Union. The comments of two anonymous referees helped to improve the manuscript.

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