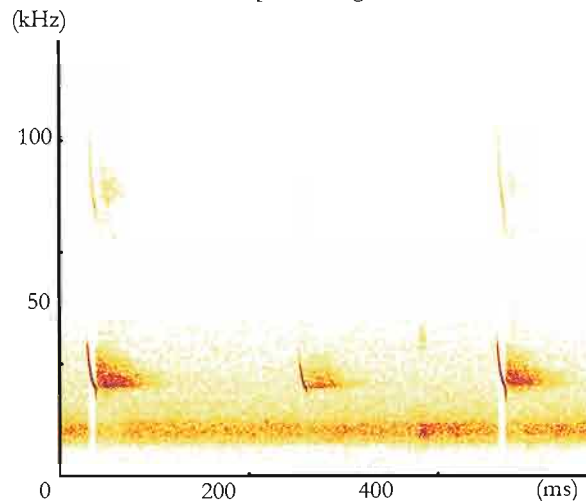
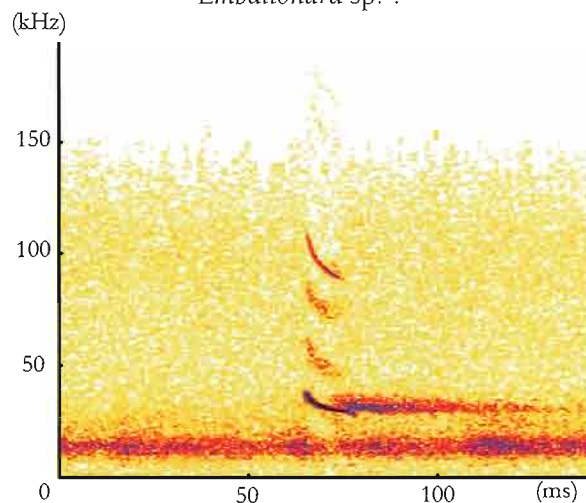


Fijian mastiff bat
Chaerephon bregullae



Only a few sequences have been recorded from caught animals. The call is a quasi-constant frequency, much deeper and more spaced than that of any other bat from Santo as size would suggest.
ME : 14-17 kHz.

Emballonura sp. ?



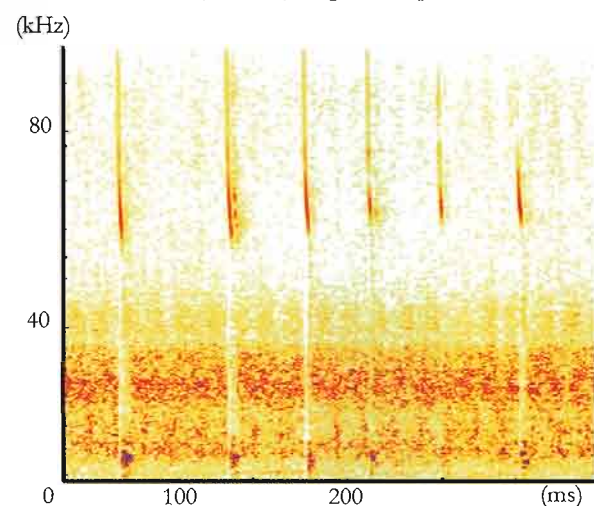
Some unidentified calls have been recorded in the wild. Their characteristics cope with what is known

about the genus *Emballonura*: Emballonurid bats use the second harmonic as main call, the first harmonic being masked. The ME could correspond to the Polynesian sheath-tailed bat, but it is a modulated to quasi-constant frequency, low and spaced.

ME: 28 kHz
CD: 12 (8-15) kHz
BW: 14 (9-21) kHz
TBC: 270 ms

*** Frequency-modulated calls

Myotis/Nyctophilus sp.



Abrupt frequency modulated calls, with a somewhat "explosive" beginning and a high terminal frequency, were recorded in forest habitat. This type of call is characteristic of *Myotis* species. They were tentatively attributed to the Large footed mouse-eared bat *Myotis adversus*.

Type 1: TF: 38 kHz (37,9-38,9)
CD: 4,5 ms (3-6)
BW: 13 kHz (12-14)
TBC: 136 ms (117-179)

Type 2: Similar to type 1,
but TF higher, up to 42 kHz (N = 15).

FISH AND SHRIMPS OF SANTO KARSTIC SYSTEMS

Marc Pouilly & Philippe Keith

The eastern part of Espiritu Santo Island is constituted by a coral karst, which nowadays presents an important subterranean system with freshwater habitats such as sinks, lakes and rivers. These specific habitats increase the local diversity of ecological conditions and may be colonized by species with ecological and behaviour predispositions to living in lightless environment. Espiritu Santo is around 22 millions of years old, making it one of the oldest islands of the Vanuatu Archipelago, old

enough to have led to local speciation (appearance of new species through a specialisation from an ancestor) adapted to subterranean conditions.

Crustacean decapods (crabs and shrimps) are regularly found in subterranean freshwater or brackish habitats. Due to their ecological predispositions, they can survive in such habitat with or without genetic adaptation. More than 90 subterranean fish species are now described from

around the world. Directly related to the recent increase in karst system exploration, this number has risen continuously from 1970. The majority of known species comes from the Asian (especially China) and South American continents. However, some species have been described from different regions of the Indo-pacific: Madagascar (three species), Australia (two species), Papouasia, Malaysia, Sulawesi and Galapagos (one species in each area). Two of the principal fish families that colonized freshwater habitats of Vanuatu Islands show species adapted to subterranean conditions elsewhere: Gobiidae (*Glossogobius ankaranensis* from Madagascar) and Eleotridae (*Typhleotris pauliani*, *T. madagascariensis*, *Oxyeleotris caeca*). Many species of the family Anguillidae (eels), which is also common in the Vanuatu Islands, are able to survive in subterranean habitats without any adaptation. It is therefore possible that local species of Espiritu Santo Island may have colonized subterranean rivers, sinks or lakes and developed adaptations to maintain such populations. However, two important factors may limit this colonization and, moreover, prevent adaptation of the species to subterranean conditions. Firstly, the local species have a predominantly herbivorous diet. In order to survive in subterranean habitats, such species would have to shift their diet toward resources that are not light-dependant, such as detritus or small prey. Second, most of these species present a priori a diadromous migration cycle (they spend part of their biological cycle in freshwater habitats and the rest in marine habitats). For example, eels are generally catadromous. They carry out their reproduction in the ocean, the larvae migrate to rivers and, once adult, the eels return to the ocean for reproduction. On the contrary, Gobiidae and Eleotridae are generally amphidromous. In this case, the species spawn in freshwater and the free embryos drift downstream to the sea, where they undergo a planktonic phase before returning to the rivers to grow and reproduce. A complete shift to subterranean life would require a total change of the reproduction strategy and biological cycle of these species, with a shift from a migration to a sedentary cycle, because subterranean life requires profound morphological and physiological adaptations (regression of ocular system, pigmentation loss, etc.) that are incompatible with an oceanic existence.

Study sites, material and method

There are only a few records of freshwater fish and decapods crustaceans (crab and shrimp) available for Vanuatu Island. Sampling carried out since 2000 by the National Museum of Natural History, Paris (MNHN) and the Santo 2006 expedition are under evaluation and should rapidly improve this situation. Currently, 29 species are known from Vanuatu and 26 from Santo.

For fish, Keith and collaborators have inventoried 67 species on the archipelago, the majority of which are amphidromous. Most of these species are restricted to the lower parts of the river (altitude below 50 m) and in the estuarine area.

Espiritu Santo Island is the largest of the 80 islands of the Vanuatu republic archipelago. The western part of the island is volcanic and the eastern part is covered by calcareous coral that culminate at an altitude of c. 600 m. In this landscape rivers are short and steep. Only the bigger ones (Sarakata, Jourdain) present a lower part with a small alluvial floodplain.

During the Santo 2006 expedition we sampled different karst freshwater aquatic habitats (rivers, sinks and blue holes) to identify crab, shrimp and fish species that colonize these habitats, and to look for evidence of subterranean adaptations. We carried out a comparative sampling of the aquatic fauna (fish and decapods) of superficial (EXT) and subterranean (INT) freshwater aquatic habitats belonging to four systems:

- Fapon system (Butmas region): river upstream of Fapon Cave (EXT) and in the Fapon doline (INT);
- Amarur system (Nambel region): Amarur River in the cave (INT), at the resurgence (EXT) and downstream near Nambel village (EXT);
- Patunar system (Funafus region): river in Kafae Cave (INT), upstream (EXT) and downstream (INT) of the Patunar doline, resurgence (EXT) and downstream reaches at altitudes of 90 m and 15 m;
- Fioha system (Funafus region): Fioha River in the cave (INT) and at the resurgence (EXT).

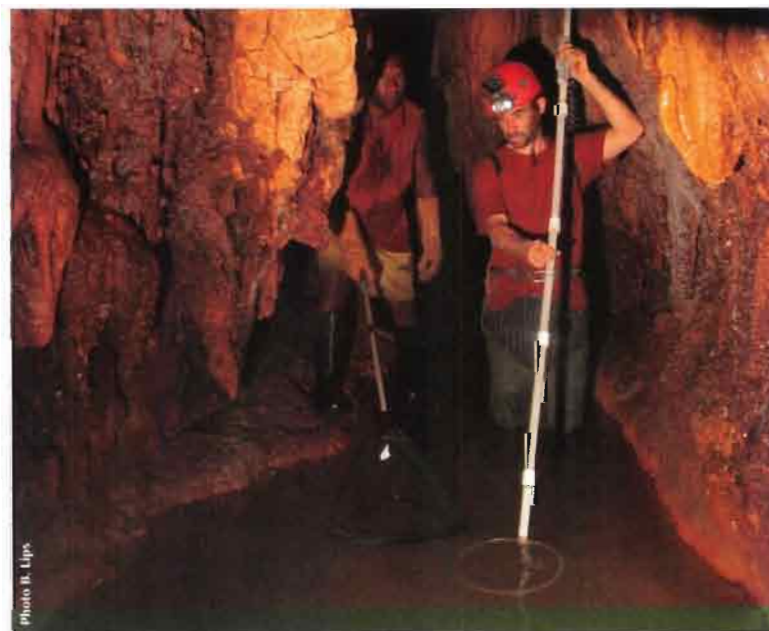


Figure 398: Electrofishing in the subterranean river of the Amarur Cave in Santo, during the Santo 2006 expedition.

Most of the sampling sites were situated at altitude above 50 m and correspond to small streams, less than 10 m wide and 1 m deep, with gravel or rock substrate. All present an alkaline pH (8.0 to 8.2) in the upper reaches and neutral pH (7.0 to 7.4) in the lower reaches. Conductivity increased with the downstream gradient from (130 $\mu\text{S}\cdot\text{cm}^{-1}$) to salted water. Most of the sampling sites had a conductivity between 200 and 350 $\mu\text{S}\cdot\text{cm}^{-1}$. Other occasional observations were made in sink parts of the same systems by divers of the Santo 2006 karst team and in four blue holes (Sarabo, CIRAD, Nanda and Porpor spring) situated near the ocean.

Due to these characteristics and difficulties of access, electrofishing is likely to be an efficient sampling method (Fig. 398). It was the most used and was sometimes, when possible, complemented by dipnets and traps.

Table 36: List of freshwater fish, shrimp and crab genera captured in karst systems of Santo during the Santo 2006 expedition.

Family	Genus	Species	> 50m	Subterranean
Fish				
Ambassidae	<i>Ambassis</i>	1	0	0
Anguillidae	<i>Anguilla</i>	2	1	1
Eleotridae	<i>Butis</i>	1	0	0
	<i>Eleotris</i>	1	0	0
	<i>Hypseleotris</i>	2	0	0
	<i>Ophieleotris</i>	2	0	0
Gobiidae	<i>Awaous</i>	1	0	0
	<i>Lentipes</i>	1	1	0
	<i>Psammogobius</i>	1	0	0
	<i>Redigobius</i>	2	0	0
	<i>Schismatogobius</i>	1	0	0
	<i>Sicyopterus</i>	2	1	0
	<i>Sicyopus</i>	1	1	0
	<i>Smilosicyopus</i>	1	1	
	<i>Stenogobius</i>	1	0	0
	<i>Stiphodon</i>	3	2	0
Kraemeriidae	<i>Gobitrichinotus</i>	1	0	0
Kuhliidae	<i>Kuhlia</i>	3	0	0
Ophichthidae	<i>Lamnostoma</i>	2	0	0
Syngnathidae	<i>Microphis</i>	3	0	0
Shrimp				
Palaemonidae	<i>Macrobrachium</i>	8	7	3
Atyidae	<i>Caridina</i>	3	3	2
	<i>Atyoida</i>	1	1	1
Crab				
Grapsidae	<i>Utica</i>	1	1	1

Results

The karstic rivers of Espiritu Santo Island are colonized by 20 fish species, belonging to 10 different families (Table 36). The most diverse family (that showing the highest number of species) is Gobiidae (Fig. 399), represented by nine genera and 14 species. Eleotridae is the second most diverse family, with four genera and six species. The family Poecilidae is only represented by *Gambusia affinis*, which is a non-native species introduced for mosquito control.

Most of the native species colonize only the lower parts of the rivers (< 50 m), or only the estuary and river mouth: Ambassidae, Kraemeriidae, Kuhliidae, Ophichthidae and Syngnathidae. Only three families (Anguillidae, Eleotridae and Gobiidae) colonize the rivers at higher altitude and include species typical of these rivers. Species richness decrease drastically with altitude, falling from 30 species in river reaches below 50 m in altitude to eight species in upper reaches.

Decapods are represented by two shrimp families, Palaemonidae (genus *Macrobrachium*) and Atyidae, and one crab family, Grapsidae. *Macrobrachium* shrimps are widely distributed in the Pacific region and eight species are present on Santo Island. As for fish, species richness decreased with altitude and there are only two or three species that colonize the rivers above an altitude of 50 m.

Globally, at higher altitudes (> 50 m) rivers present a high abundance of shrimps and only a few fishes (< 10 individuals/100 m²). This tendency is reversed in rivers at low altitudes and in habitats near the estuaries (blue holes and river mouths).

No fish or decapods species captured or observed showed clear evidence of strong adaptation to subterranean conditions (depigmentation, ocular system regression). Shrimps, especially of the family Atyidae, sometimes showed pigmentation differences between individuals captured in superficial and in subterranean rivers. However these differences fade with the conservation of the specimens, so that it is likely that they correspond more to a response to light stimulus than to a genetic difference. Only few individuals of Atyidae captured



Figure 399: *Sicyopterus lagocephalus*. (Gobiidae). A common fish species in Santo freshwater rivers (male is coloured and female drab).

presented a strong depigmentation accompanied by a slight microphtalmly (reduction of the size of external ocular system) (Fig. 400).

All the aquatic subterranean habitats (sinks, rivers and small lakes) are colonized by decapods (crabs and shrimps). The same species colonize both superficial and subterranean rivers (five of the eight *Macrobrachium* species are present in both conditions). Habitats with low velocities (small lakes, sinks) appeared to be more favourable for Paleomonidae shrimps, although lotic habitats are more suitable for Atyidae shrimps. Some family density variations exist between the different systems. For example, the Amarus system has a high density of Paleomonidae, whereas the Fioha system has high density of Atyidae. These variations remain unexplained and require a more detail study to understand the environmental factors that determine the quality of an habitat for each type of organisms.

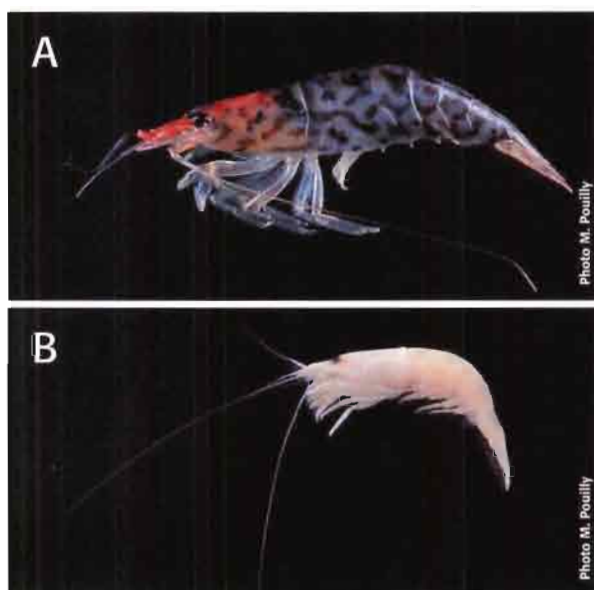


Figure 400: Specimens of *Atyoida pilipes* (decapods shrimps). The first (A) was captured in a superficial river reach and the second (B) from a subterranean reach. The pigmentation difference is obvious, but in almost all the case it did not appear to correspond to an adaptation to subterranean life.



Figure 401: Eels (here *A. marmorata*) are the only fish that colonize the subterranean rivers of Santo. Due to their nocturnal behaviour and carnivorous diet, they can colonize indifferently both superficial and subterranean rivers without any kind of adaptation. However, their biological cycle requires a migration to the ocean for reproduction, thus limiting the probability of an adaptation to a strictly subterranean way of live. The eel is one of the few freshwater fish appreciated by local people.

Fish are absent in the subterranean habitats, with exception of eels (*Anguilla marmorata* and *A. obscura*) (Fig. 401) that were observed in almost all the explored sinks and in many sampled rivers at different altitudes.

The presence of eels can be explained by their carnivorous diet and nocturnal activity. This is in contrast to most of the other species of other groups, which are limited in their colonization of subterranean habitats by their herbivorous diets, as well as by local physical conditions, such as the openness and connectivity of the subterranean systems (river or sink vs groundwater), altitude, high inclinations and waterfalls that characterize the upper river reaches. However, even if these fish species have not colonized the subterranean habitats, it should be noted that most of them use it at least to pass through and attain the river upper reaches. Indeed, because most of these species are amphidromous, they sometimes need to pass through long subterranean sections (e.g. the Patunar system, which is more than 1 km long) to get to the upper reaches.

Pouilly Marc, Keith P.

Fish and shrimps of Santo karstic systems.

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