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INFLUENCES OF GEOTHERMAL SULFUR BACTERIA ON A TROPICAL COASTAL FOOD WEB

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Running Head: Geothermal sulfur bacteria in a coastal food web

Abstract

The activity of the geothermal plant at Bouillante in Guadeloupe (French West Indies) releases thioautotrophic bacteria into the coastal environment. Fish counts reveal that fish abundance increases with higher availability of this bacterial resource. In order to evaluate the trophic role of those bacteria, isotopic compositions (C, N, and S) of potential consumers were evaluated on transects of increasing distance from the source of bacteria. The three mobile fish species examined *Abudefduf saxatilis*, *Acanthurus bahianus* and *Stegastes partitus* ingested and assimilated chemosynthetic bacteria. Similarly, the isotopic composition of the mobile sea urchin *Diadema antillarum* was different close to the discharge channel suggesting a diet mainly composed of sulfur bacteria. On the contrary, endofauna sampled from the nematode community did not show a diet influenced by chemosynthetic bacteria. A broad variety of epifaunal organisms with passive and active suspension-feeding activities were also investigated: sponges (*Aplysina fistularis* and *Iotrochota birotulata*), barnacles (*Balanus* sp.), bivalve molluscs (*Spondylus tenuis*) and cnidarians (*Pseudopterogorgia* sp.) but no strong evidence for sulfur bacteria contributions were determined in any of these organisms' diet. The same can be said for the omnivorous predator annelid (*Hermodice carunculata*). In this coastal oligotrophic environment, only certain opportunistic species seem to benefit from the emergence of a new food item such as chemosynthetic bacteria.

Introduction

Shallow water hydrothermal vents are generally located above subducting slabs, especially along volcanic arcs, and are commonly detected by the presence of streams of gas bubbles (Gamo & Glasby 2003). They are found in many regions of the world, from tropical to polar environments (Tarasov et al. 2005), and present a general functioning similar to deep-sea vents. Heat-driven chemical reactions with rocks generate emissions of hot fluid with abundant sulfur compounds suitable for chemosynthetic bacteria (Van Dover 2000). Shallow vents present a low faunal biomass with few, if any, obligate species (Tarasov et al. 2005). They differ from deep-sea vents which are characterized by a high biomass of associated fauna with low species diversity, principally consisting of species obligate to such sites (Tunnicliffe 1991, Van Dover 2000). This transition between shallow and deep vents coincides approximately with the change from euphotic zone to aphotic zone (Tarasov et al. 2005). In the euphotic environment of shallow vents, food webs appear to be principally based on pelagic and benthic photosynthetic primary production, whereas chemosynthetic components often play a secondary trophic role (Tarasov et al. 2005, Sweetman et al. 2013). According to studies, chemosynthetic bacteria appear as an alternative resource ingested when other food items are not available. However, they can also play a trophic role for species from vents were food resources are not limited (Stein 1984, Trager & De Niro 1990, Comeault et al. 2010, Zapata-Hernández et al. 2014a). Results from cold seep environments are also variable as important trophic roles for chemosynthetic bacteria are observed from intertidal to subtidal seeps of brine (Powell et al. 1986), petroleum (Spies & DesMarais 1983, Montagna & Spies 1985) and methane (Jensen et al. 1992, Judd et al. 2002, Sellanes et al. 2011).

The aim of the present study is to evaluate the trophic role of large sulfur bacteria released by a geothermal plant in the tropical environment of Guadeloupe Island (French West Indies). Geothermal hot water is artificially pumped from deep reservoirs in order to produce electricity and then cooled with seawater before being released in the sea. Environmental conditions in the discharge channel support development of sulfur-oxidising bacteria. Water discharges are linked with plant functioning and are regularly stopped for maintenance work. This irregular but predictable flux of geothermal chemosynthetic bacteria gives a unique opportunity to determine its influence on the diet of coastal fauna. In order to evaluate the effects of this bacterial biomass, abundance of their potential consumers was measured along a transect of increasing distance from the mouth of the discharge river. Then, C, N, S isotopic compositions of these potential consumers were analysed to assess the extent of bacterial assimilation.

Material and method

Study area

The Bouillante geothermal field is located on the west coast of Basse-Terre Island, the western island of Guadeloupe belonging to the volcanically active islands of Lesser Antilles (Fig. 1). The town has been named "Bouillante", which means "boiling" in French, as this area is characterized by hydrothermal manifestations such as hot springs, mud pools, steaming grounds and fumaroles. The deep geothermal fluid (total dissolved solids around 20 g L^{-1}, pH = 5.3) is the result of a mixture comprising 58% seawater and 42% meteoric water reacting with volcanic rocks (Brombach et al. 2000, Sanjuan et al. 2001). The water flowing through the geothermal aquifer has a homogeneous composition at the spatial scale of the Bouillante region and the reservoir represents a total volume larger than 30 million m^3 with a temperature of 250-260°C (Mas et al. 2006). In 1986, a geothermal plant without reinjection started producing electricity by exploiting water coming from a 340 m deep well (Jaud & Lamethe 1985). Additional deeper wells (1000-1200 m) are now used to reach a power output of 16 MWe (Mas et al. 2006). All the residual water is mixed with pumped seawater in order to drop the temperature to 45 °C before it is all returned to the sea through a discharge channel (Fig. 1). The salinity of released water is approximately 33 and the pH is 7.3. Compared to normal seawater, the water released by the plant is enriched in trace metal ions (Sanjuan et al. 2001, Lachassagne et al. 2009) and characterized by a high concentration of dissolved H_2S reaching 35-45 mg L^{-1} in the steam condensate (Mas et al. 2006). In the discharge channel, environmental conditions are favourable for the development of benthic sulfur-oxidizing bacteria of the genus *Thiomicrospora* sp., covering the surface of the benthic cyanobacteria *Pectonema* sp. (O. Gros pers. obs.) (Fig. 2). Because of the strong channel outflow (2.5 m^3 s^{-1}), these white bacteria are continuously ripped off and spread into the bay. Under regular weather conditions, coastal currents in the bay are oriented to the north (ANTEA 2005). Previous experiments releasing dye into the channel revealed a progressive dilution of water from the outlet to a distance of approximately 300 m (PARETO-IMPACTMER 2009). This channel is the only source of sulfur bacteria in the surficial environment of the bay.

Sampling

Sulfur bacteria were sampled in the discharge channel during four consecutive periods throughout the month of January, 2014. Spatial and temporal approaches were simultaneously used to determine the influence of released bacteria. Potential consumers were sampled at five different sampling stations along a transect: at the discharge channel outlet (hereafter called 0 m station) and 80, 160, 280 and 400 m away from the outlet (Fig. 1). Moreover sampling was performed both during the regular functioning of the geothermal plant (4th and 6th February, 2014) and after two weeks of pause due to maintenance works (26th and 27th March, 2014). Each sampling session was conducted within less than three days. After 24 hours of inactivity of the geothermal plant, sulfur bacteria completely disappeared from the channel.

Abundance

Diver-operated video was used to evaluate fish abundances. At each station, two open width line transects of 20 m long were demarked by ropes at the surface of the rocky substrate (≈ 3 m depth). The same operator filmed all videos with a small action camera (GoPro) while swimming at regular speed (0.8 m s^{-1}) along the transect lines (5 cm above the bottom) and keeping the camera steady and perpendicular to the bottom. Each transect was repeated five times with at least four minutes between each shooting. A single viewer analysed all videos. Fish were counted and identified to species or genus levels, and abundances were estimated using freeze-frame when the number of specimens in movement was too great to count accurately otherwise. Due to the frequent large schools of *Haemulon* spp. repeatedly crossing transects and inducing large variability in fish counts, this species was consequently removed from the analysis of the total fish community.

Isotopic composition

Potential consumers of bacteria were randomly collected within a 20 m^2 area around each sampling station (*n*=3 for each species of consumers sampled at each station). One centimetre of surficial sediment was collected from each station and each nematode sample (*n*=3) was composed of 700 specimens haphazardly removed from each sample after extraction using Ludox HS40 (de Jonge & Bouwman 1977). According to their availability, three types of potential bacteria consumers were collected at each sampling station: grazers (echinoderm: *Diadema antillarum*), suspension-feeders (sponges: *Iotrochota birotulata*, *Aplysina fistularis*; crustacea: *Balanus* sp.; mollusc: *Spondylus tenuis*; cnidaria: *Pseudopterogorgia* sp.) and predators (annelid: *Hermodice carunculata*). Fishes with a grazing behaviour were collected in stations 0 and 400 m and three adult specimens of *Abudefduf saxatilis*, *Acanthurus bahianus* and *Stegastes partitus* were speared. Sub-samples of coarse sponges and gorgonian were acid-treated (1 M HCl) for $\delta^{13}C$ measurement whereas, untreated sub-samples were used for $\delta^{15}N$. Calcium carbonate ($CaCO_3$) is the principal source of inorganic carbon in coral reefs (Gattuso et al. 1999) and is significantly more enriched in ^{13}C than organic carbon (Kennedy et al. 2005). When manual extraction is not possible, acidification is thus required to remove those calcareous components whose isotopic composition is not related to animal diet (Kolasinki et al. 2008). A dissecting microscope was used to isolate muscles of crustacean, mollusc, echinoderm, annelid and fish as well as the stomach contents of fishes. Samples were frozen, freeze-dried and ground into a homogeneous powder by using a ball mill. C, N, S elemental and isotopic compositions were then measured with an isotope ratio mass spectrometer (IsoPrime100, Isoprime, UK) coupled in continuous flow to an elemental analyser (vario MICRO cube, Elementar, Germany). Isotope ratios were conventionally expressed as δ values in ‰ (Coplen 2011) relative to C, N and S international standards, i.e. Vienna PeeDee Belemnite (VPDB) for carbon, atmospheric air for nitrogen and Canyon Diablo triolite (VCDT) for sulphur. International Atomic Energy Agency (IAEA, Vienna, Austria) certified reference materials calibrated against the international isotopic references IAEA-C6 ($\delta^{13}C$ = -10.8 ± 0.5 ‰), IAEA-N2, ($\delta^{15}N$ = 20.3 ± 0.2 ‰) and IAEA-S1 ($\delta^{34}S$ = -0.3 ‰) were used as primary analytical standards, and sulphanilic acid ($\delta^{13}C$= -25.9 ± 0.3; $\delta^{15}N$ = -0.12 ± 0.4; $\delta^{34}S$= 5.9 ± 0.6) as a secondary analytical standard. Isotopic ratios of samples were normalized using primary analytical standards. Standard deviations on multi-batch replicate measurements of secondary analytical (sulphanilic acid) and lab standards (fish tissues) analyzed interspersed among the samples (2 lab standards for 15 samples) were 0.1 ‰ for $\delta^{13}C$, 0.3 ‰ for $\delta^{15}N$ and 0.5 ‰ for $\delta^{34}S$.

Data analyses

One-way analysis of variance (ANOVA) was used to analyse the differences in fish abundances along the transects and the Tukey test was used for *post-hoc* comparisons. The relationship between variations in abundance and geothermal plant activity was tested using bilateral-independent-samples t-tests. All those data were previously tested for normality by

Shapiro-Wilk test. The nonparametric Kruskal-Wallis test was used to test differences in isotopic composition (C, N and S) of consumers. All statistical analyses were performed using R. Values are presented as means ± standard deviations (s.d.) excepted when specified.

Bayesian isotopic mixing models were used to determine contributions of bacteria to diets of *D. antillarum*, *A. bahianus*, *A. saxatilis* and *S. partitus*. SIAR (Version 4.2) (Parnell et al. 2010) incorporates the variability of consumers and trophic enrichment factors (TEFs) (i.e., the net isotopic composition change in a consumer and its ingested food sources) to produce the percent contribution of each source to a consumer's diet. TEFs are key factors when it comes to evaluate contributions of food sources to animal diets. TEFs used were 1.1 ± 0.5‰ for δ^{13}C, 2.2 ± 0.5 for δ^{15}N and 2.0 ± 0.7‰ for δ^{34}S (McCutchan et al. 2003). These TEFs are typically used in isotope study and are appropriate when consumers are not starved (Vander Zanden et al. 2015, Lefebvre & Dubois 2017). Variations of 20% in these TEFs do not change the conclusion of the present study as they induce only small variations of 1.5 ± 0.9% in model results.

A two-step procedure was performed to run the SIAR modelling at station 0 m. First, TEFs (McCutchan et al. 2003) were subtracted from isotopic compositions of consumers caught at station 400m in order to determine the isotopic compositions of bulk diets of each consumer in an environment without bacteria; 400 m from the discharge outlet being beyond the 300 m extent of dilution in water established in earlier dye-releasing experiments (PARETO-IMPACTMER 2009). Then, average values and standard deviations of those results are used as "food sources" in models using isotopic compositions of consumers from station 0 m in contact with bacteria. For each consumer, three isotopes ratios (C, N, S) and two potential food sources are considered: *i*) bacteria and *ii*) average isotopic composition of consumers' bulk food sources at station 400 m. It should be noted that this evaluation of the contribution of bacteria to diets is based on the assumption that bacteria is the only food item in which contribution is changing in fauna diets between 0 and 400 m stations. A second assumption is that consumers are not moving along transect. As consumers such as fishes are mobile, 400 m fishes can ingest bacteria. As a result, SIAR model tends to underestimate the contribution of bacteria for mobile consumers.

The model was run with 10^6 iterations and burn-in size was set as 10^5. Model solutions are presented using credibility intervals of probability density function distributions (Parnell et al. 2010).

Results

Abundance

During geothermal plant production activity, the total number of fish at the discharge channel outlet was significantly higher than in other stations (ANOVA; $p < 0.001$) and significantly higher than when the plant was stopped (bilateral t-test; $p < 0.001$) (Fig. 3). Fish abundances at other stations were not affected by the geothermal plant activity (bilateral t-test; non-significant). When bacteria were being released, *A. bahianus* and *A. saxatilis* at station 0 m both presented higher abundances than in other stations (ANOVA; $p < 0.001$) and higher abundances than in station 0 m when the plant was stopped (bilateral t-test; $p < 0.001$). Variations were different for *Stegastes* spp. as abundances were higher in station 0 m (ANOVA; $p < 0.001$) but were not affected by the functioning of the plant (bilateral t-test; non-significant).

Isotopic composition

Bacteria released by the geothermal plant of Bouillante were regularly collected during the month preceding the sampling of their potential consumers and presented a δ^{13}C of -18.2 ± 2.9 ‰, a δ^{15}N of -2.4 ± 2.3 ‰ and a δ^{34}S of 10.9 ± 3.1 ‰. Among potential consumers of station 400 m, the lowest δ^{15}N was presented by the two sponge species *A. fistularis* (δ^{15}N = 2.75 ± 0.42 ‰) and *I. birotulata* (δ^{15}N = 3.80 ± 0.22 ‰) and the cnidaria

Pseudopterogorgia sp (δ^{15}N = 3.46 ± 0.10 ‰) (Fig. 4). Potential consumers with highest δ^{15}N were the fish *S. partitus* (δ^{15}N = 8.69 ± 0.21 ‰), the urchin *D. antillarum* (δ^{15}N = 5.99 ± 0.42 ‰) and the annelid *H. carunculata* (δ^{15}N = 5.65 ± 2.49 ‰) and those organisms also present the highest δ^{13}C (-15.24 ± 2.49, -13.26 ± 0.42 and -13.63 ± 1.50 ‰ respectively).

Proximity to bacteria release did not affect δ^{13}C and δ^{15}N (Kruskall-Wallis tests, $p > 0.05$) for 7 of the 11 studied organisms: nematode, suspension-feeders (*I. birotulata*, *A. fistularis*, *Balanus* sp., *S. tenuis* and *Pseudopterogorgia* sp.) and predator (*H. carunculata*) (Fig. 5). However, the urchin *D. antillarum* presented δ^{13}C, δ^{15}N and δ^{34}S significantly affected at station 0 m (Kruskall-Wallis tests, $p < 0.01$, $p < 0.01$ and $p < 0.05$ respectively) (Fig. 6). Between stations 0 and 400 m, the fish *A. bahianus* presented significant differences in δ^{13}C and δ^{34}S of muscle (Kruskall-Wallis tests, $p < 0.05$) and in δ^{13}C of gut content (Kruskall-Wallis tests, $p < 0.05$). *A. saxatilis* and *S. partitus* both presented significant differences in δ^{15}N of muscles (Kruskall-Wallis tests, $p < 0.05$) and in δ^{15}N of gut contents (Kruskall-Wallis test, $p < 0.05$).

After a two week pause in activity at the plant for maintenance work, C and N isotopic compositions of all studied species of fish followed the same trend: an enrichment in ^{13}C and in ^{15}N. Statistically, changes in isotopic composition of muscle tissues were only significant for δ^{13}C of *A. bahianus* and *A. saxatilis* (Table 1).

SIAR was run only for the organisms showing statistically different isotopic composition between station 0 and 400 m. SIAR outputs suggested that among the four studied organisms, all assimilated bacteria but in different proportions. Mean bacterial contributions (with lower and higher 95% credibility interval) to the diets of *D. antillarum*, *A. bahianus*, *A. saxatilis* and *S. partitus* were respectively 66% (44-92), 47% (7-86), 27% (6-50) and 37% (15-58) (Fig. 7).

Discussion

The most striking results of our study are that fishes seem to assimilate significant amount of bacteria at geothermal outlets and show dramatically increased abundance when sulfur bacteria are released. The three studied fish species present omnivorous feeding habits. *A. bahianus* has a broad diet ingesting filamentous algae, macroalgae and detritus (Ferreira & Goncalves 2006, Burkepile & Hay 2008). *A. saxatilis* presents an opportunistic feeding behaviour with the ability to shift between food items according to season and environmental disturbances (Ferreira et al. 2004, Di Iulio Ilarri et al. 2008). Damselfish also present a high level of trophic plasticity, varying their diet composition according to their environment (Ceccarelli 2007, Frédérich et al. 2009, Feitosa et al. 2012). This study's results show that sulfur bacteria from the Bouillante geothermal plant are ingested by all these fish species and to our knowledge, such feeding behaviour has not been previously described. When this food resource is available, Acanthuridae such as *A. bahianus* and *A. saxatilis* are more abundant even while *S. partitus* abundance does not vary. It has been shown that abundances of species similar to Bouillante fish species (*A. saxatilis*) or genus (*Stegastes fuscus* and *Acanthurus chirurgicus*) are negatively affected by increased temperature (Teixeira et al. 2009, 2012). Consequently their occurrences around the Bouillante discharge channel are likely associated with their feeding behaviour. Abundances of Sergeant majors in Brazilian reefs similarly increased along with the availability of supplementary food (Di Iulio Ilarri et al. 2008). Damselfish are usually territorial species (Robertson 1996), additional food released by geothermal plant would consequently not increase size of territories and would not change damselfish abundances. After two weeks of absence of bacterial resource, *A. bahianus* and *A. saxatilis* presented a modified δ^{13}C, highlighting the role of bacteria in their diet. Isotopic turnover dynamics can vary according to species, tissue and the age of the taxon analysed (Bosley et al. 2002). Changes observed in the present study are consequently particularly rapid for adult fishes (Gajdzik et al. 2015). Our results show that the overall abundance of fish increased when sulfur bacterial food resource is available. This result is supported by several other studies, as in a shallow vent in Azores where fish, including species of the sergeant-major genus *Abudefduf*, were found stationing themselves near the base of the plume, allowing them to benefit from food particle flows (Cardigos et al. 2005). Increased fish concentrations were also observed around a Californian oil seep (Spies & Davis 1979) and a brine seep in the Gulf of Mexico (Bright et al. 1980). The irregular but predictable bacterial abundances in Bouillante allow us to determine that the fish aggregations are likely linked to the availability of sulfur bacteria as food.

Another organism was significantly affected by the presence of bacteria, namely, the sea urchin *D. antillarum*. This is a very common south Atlantic species which can occur in very high densities (Sammarco 1982). This species graze upon algae growing on rocks and is currently considered as a generalist herbivore ingesting micro- and macro-algae (Hawkins 1981). However *D. antillarum* can also be omnivorous (Karlson 1983, Rodríguez-Barreras et al. 2015) with the ability to selectively ingest food (Tuya et al. 2001). In Bouillante, *D. antillarum* is an opportunistic species with a diet composed mainly of sulfur bacteria when this resource is available. This data strengthens what is known about sea urchin trophic adaptation and also reveals that sulfur bacteria are a good food source for this species. In shallow hydrothermal vents, mats of sulfur oxidizing bacteria can be actively grazed by epistrate feeders such as abalone (Stein 1984), limpet (Trager & De Niro 1990, Comeault et al. 2010) and nassariid (Southward et al. 1997). Similar ingestions of chemosynthetic bacterial filaments have been reported in a shallow cold seep for gastropods and the echinoid *Pseudoechinus* sp. (Zapata-Hernández et al. 2014b). At the hydrothermal vents of Kraternaya Bight, the sea urchin *Strongylocentrotus droebachiensis* is a dominant species in term of biomass and abundance (Tarasov 2006) and fatty acid reveals a considerable ingestion of sulfur bacteria by this urchin (Kharlamenko et al. 1995). As for fishes, this species was very abundant at our study sites and, therefore, its grazing activity may imply significant transfer of chemosynthetic production to a higher trophic level.

Nevertheless, most of the species sampled in this study did not used bacteria as a significant food source. The isotopic composition of the nematode community revealed a limited trophic role for bacteria coming from the geothermal source. Nematodes usually dominate meiofaunal communities in sediments around shallow hydrothermal vents, as in Italy (Colangelo et al. 2001), Greece (Thiermann et al. 1997), New Zealand (Kamenev et al. 1993), Papua New Guinea (Tarasov et al. 1999) and Indonesia (Zepilli & Danovaro 2009). Dominance of nematodes over copepods is though to be due to their higher tolerance to chemical compounds released by vents (Jensen 1986). Depending on site conditions, abundances of nematodes around shallow vents can be reduced due to stressful chemical conditions (Thiermann et al. 1997, Tarasov et al. 1999, Colangelo et al. 2001) or increased when environmental conditions are less unfavourable (Kamenev et al. 1993, Tarasov 2006). Those increased abundances would be due to higher availability of food resources such as sulfur bacteria (Tarasov 2006). Despite environmental conditions suitable for meiofauna at the Bouillante discharge channel outlet, the diet composition of nematodes remains unchanged whether the chemosynthetic bacterial food is available or not.

The suspension-feeding mode dominates the studied epifauna. In order to extract a sufficient amount of food from a dilute environment, suspension-feeders present different mechanisms to screen, collect and transport particles (Riigsård & Larsen 2010). Our sampling represented these different feeding modes. However, our results did not show any significant contribution of bacterial material to suspensivores, whatever their feeding modes. For instance, sponge filtering activity is based on pumping ambient water through aquiferous canals to choanocyte chambers where particles are retained (Riigsård & Larsen 2010). This filtering system is specialized in retaining small prey, and bacteria are considered one of the primary sources of energy in sponge diets (Pile et al. 1996, Kowalke 2000). Symbiotic bacteria can also contribute to the nutrition of sponges and can represent 40% of their volume (Hentschel et al. 2006). *A. fistularis* is a bacteriosponge with nutrient resource dominated by DOM matter (Reiswig 1981). In the present study, this species is not affected by released water, suggesting that the geothermal plant is a limited influence on the total amount of DOM. *I. birotulata* is similarly uninfluenced even if this species is not considered as a bacteriosponge and should rely mostly on particulate organic carbon. Limited ingestion of sulfur bacteria by sponge species in comparison with other suspension-feeders has previously been observed in a shallow Mediterranean cave containing hot sulfur springs (Southward et al. 1996). It was also shown that the growth of sponges in Matupi Harbour is stimulated by hydrothermal fluid, meaning silicon concentration is increased aiding production of their skeleton, rather than by higher food resource availability with sulfur bacteria (Tarasov et al. 1999).

Barnacles rely principally on large prey such as zooplankton (Kuznetosa 1978, Richoux et al. 2014) or large macroalgae fragments (Dubois & Colombo 2014) whereas the contribution of smaller prey like bacteria would be insignificant (Silina & Zhukova 2016). Filaments of sulfur bacteria displaced from the discharge channel at Bouillante are large and visible with naked eye but are not assimilated by the barnacle *Balanus* sp. Using a fatty-acid profile approach, similar results were obtained with barnacles from a shallow hydrothermal vent in the Kurile Islands (Kharlamenko et al. 1995).

Bivalve species usually retain the majority of particles larger than 4 µm (Riisgård et al. 2000). Qualitative factors of particles can influence their capture even if qualitative selection is assumed to be principally post-capture through a pre-ingestive selection using labial palps (Beninger et al. 1995, Riisgård et al. 2000). In the shallow vent of Kraternaya Bight, a bivalve species obtained most of its nutrition from endosymbiotic sulfur-oxidising bacteria whereas the bacterial input from food is limited for two other non symbiotic species (Kharlamenko et al. 1995). In California, the non symbiotic bivalve *Mytilus edulis* ingested only a small amount of sulfur-oxidising bacteria detached from mat of an intertidal vent (Trager & De Niro 1990). Similarly, in the present study, sulfur-bacteria did not affect the diet composition of the non-symbiotic bivalve *S. tenuis*.

The gorgonian *Pseudopterogorgia* sp. is the only passive suspension-feeder examined in this study. Gorgonians can consume particulate organic matter ranging in size from nanometres to millimetres with a preference for nanoeukaryotic organisms such as ciliates and dinoflagellates (Ribes et al. 1998, 1999, Rossi et al. 2004). The present study suggests a limited trophic role for sulfur bacteria in gorgonians, but to our knowledge, such a role has never been documented. Similarly, the passive filter-feeder coral *Porites californica* was not affected by sulfur bacteria from a shallow vent in the Gulf of California (Forrest 2004).

Another trophic guild seemed unaffected by bacterial filament presence. The polychaete *Hermodice carunculata* is an important omnivorous scavenger in coral reef ecosystems (Jumars et al. 2015), feeding on various organisms including sea anemone, gorgonians, coral, benthic jellyfish (Barroso et al. 2015), starfish (Wolf et al. 2014) and dead fishes (Stoner & Layman 2015). This opportunistic feeding behavior leads to highly variable isotopic composition in Bouillante fireworms, potentially preventing detection of any diet modification associated with sulfur bacteria. Nevertheless, shallow vent activity can be suitable for omnivorous scavengers such as gastropods (Southward et al. 1997) or crabs (Jeng et al. 2005, Wang et al. 2014) feeding on organisms killed by the chemical or thermal conditions of a vent plume. However, this trophic link seems to be limited in Bouillante where environmental conditions are less extreme and therefore less profitable for scavengers.

Unlike in deep-sea environments, communities associated with shallow vents are not composed of vent-obligate species adapted to a chemosynthetic metabolism (Melwani & Kim 2008). Shallow vent communities are often dominated by opportunistic species relatively scarce in the surrounding habitat (Southward et al. 1996, Karlen et al. 2010, Chan et al. 2016). Among some of the opportunistic species are polychaetes, gastropods and oligochaetes (Dando et al. 1995, Thiermann et al. 1997, Levin et al. 2003). In Bouillante, species benefiting from sulfur bacterial release are also opportunists regarding their feeding behaviour. All these species are mobile grazers or active pelagic feeders, whereas the suspension-feeders and predators were unaffected. Such restriction according to feeding mode was also observed in an intertidal hydrothermal vent, with ingestion of sulfur bacteria limited to grazers while suspension-feeders were similarly unaffected (Trager & De Niro 1990).

In oligotrophic deep-sea environments most of the vent fauna rely on carbon fixed by chemosynthesis for nutrition (Van Dover 2000). At upper bathyal depths, inputs from photosynthetic organisms increase and dependence on chemosynthetic carbon would proportionally decrease (Levin & Michener 2002, Levin 2005, Levin & Mendoza 2007). In shallow vents the major food source is usually photosynthetic rather that chemosynthetic (Kharlamenko et al. 1995, Tarasov et al. 2005, Chan et al. 2016). However, despite this lower relative abundance of sulfur bacteria, they can still be used as food source in some shallow vent locations (Thiermann et al. 1997, Bosley et al. 2002, Forrest 2004, Comeault et al. 2010). The present study suggests that the emergence of chemosynthetic bacteria can influence food webs in coastal environments. The irregular flux of geothermal chemosynthetic bacteria reveals a trophic role restricted to mobile and opportunist species.

Figure and table

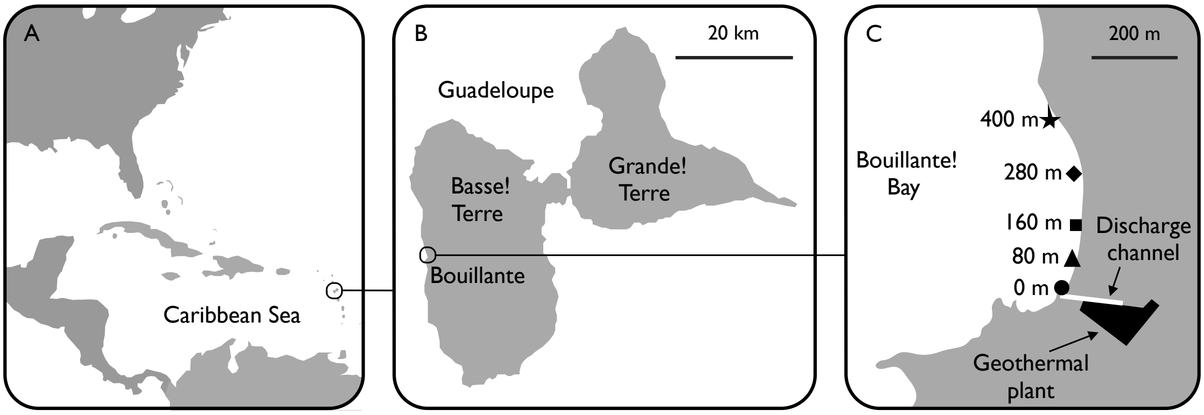

Figure 1. A: Location of Guadeloupe archipelago in the Caribbean Sea, B: Location of Bouillante in Guadeloupe, C: Location of geothermal plant, discharge channel and five sampling stations in Bouillante Bay

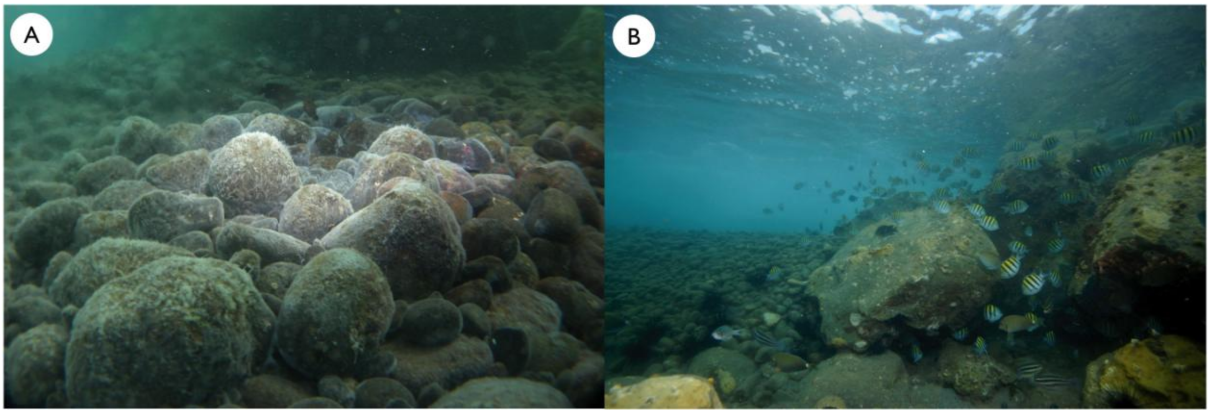

Figure 2. A: Thick biofilm of sulfur bacteria covering the bottom of the discharge channel, B: Discharge channel outlet (in the left background of the picture) and aggregation of associated fishes (principally *A. saxatilis* and *A. bahianus*)

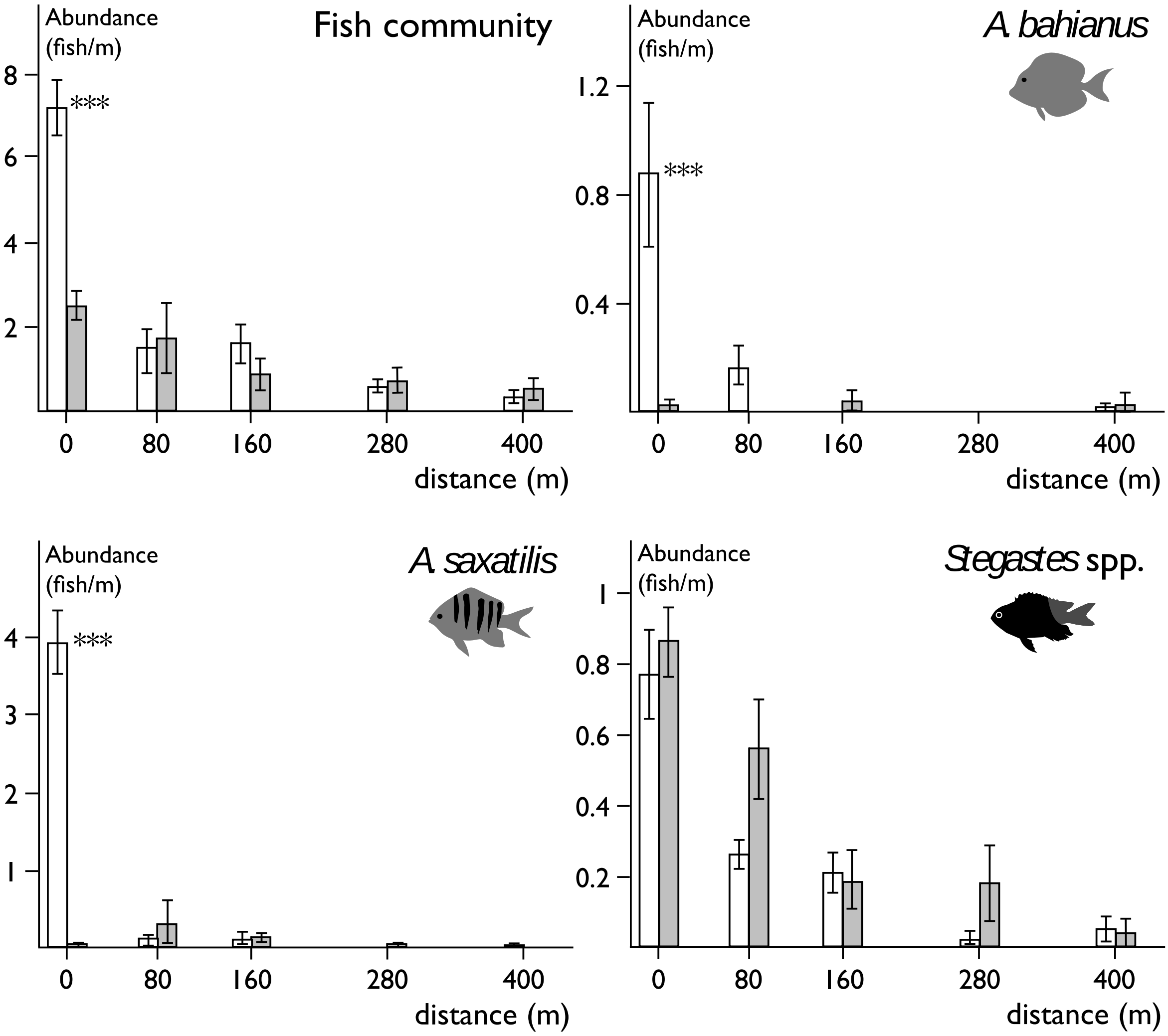

Figure 3. Abundance of fish community, *A. bahianus*, *A. saxatilis* and *Stegastes* spp. observed per meter of transect, per station, along the transect during regular (white) and stopped (grey) activity of the geothermal plant (n = 10). ***: Significant differences related to plant activity (bilateral t-test, p < 0.001)

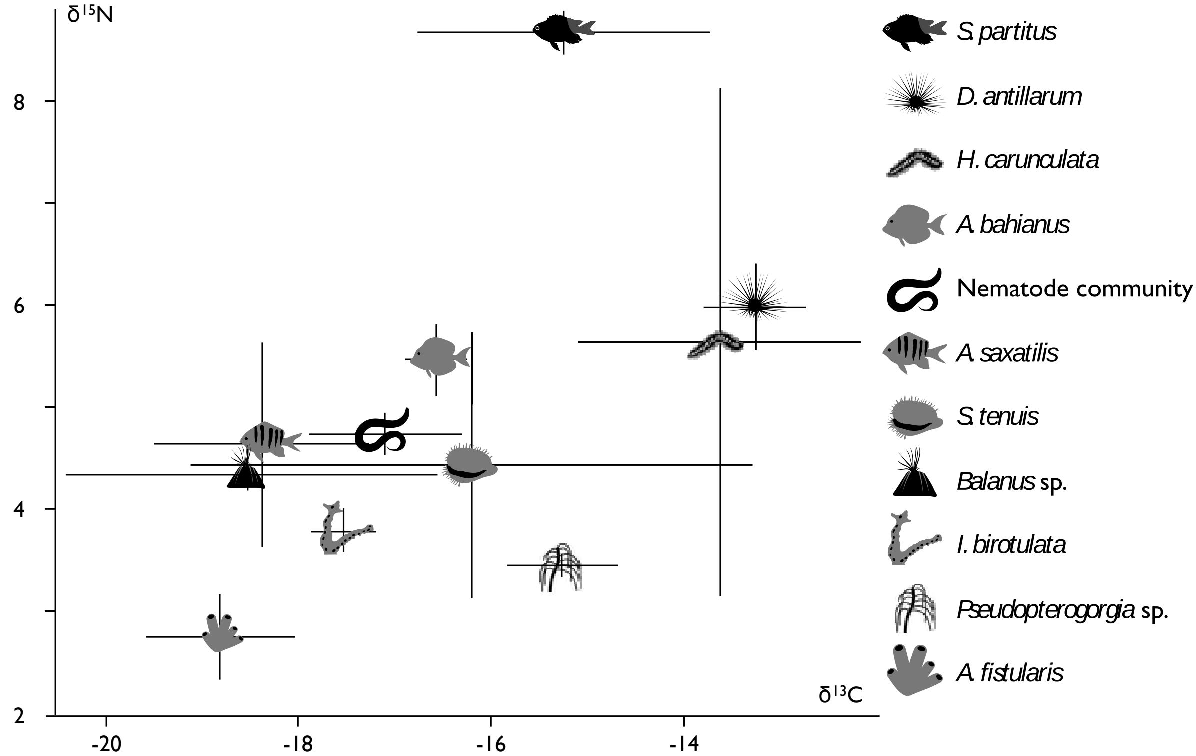

Figure 4. Isotopic composition (δ^{13}C and δ^{15}N) of organisms at station 400 m (± SD; n = 3).

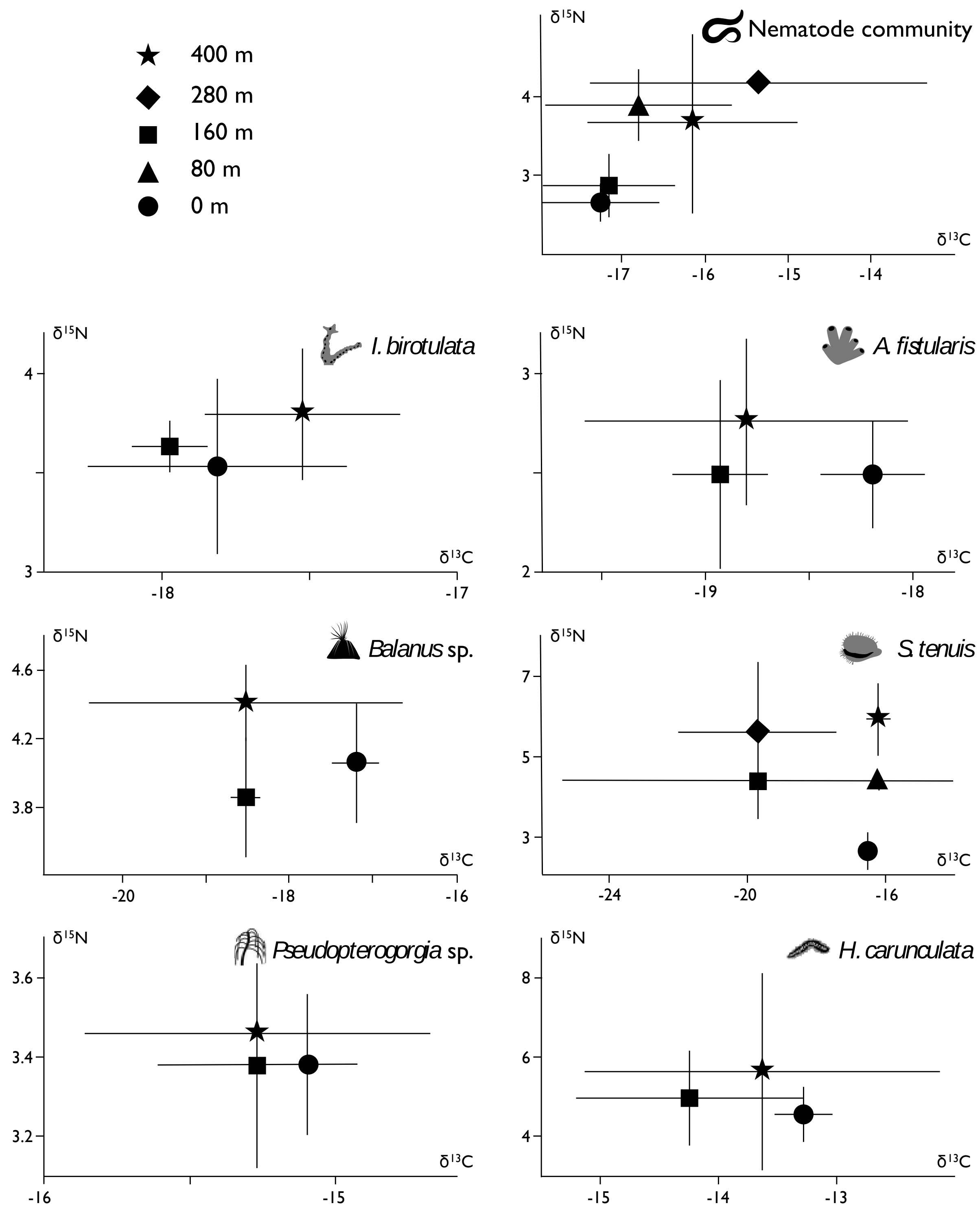

Figure 5. Isotopic compositions (δ^{13}C and δ^{15}N) of nematode community, *I. birotulata*, *A. fistularis*, *Balanus* sp., *S. tenuis*, *Pseudopterogorgia* sp. and *H. caruncluata* along transect stations (± SD; n = 3). Isotopic compositions are not significantly different according to station (Kruskall-Wallis tests, $p > 0.05$)

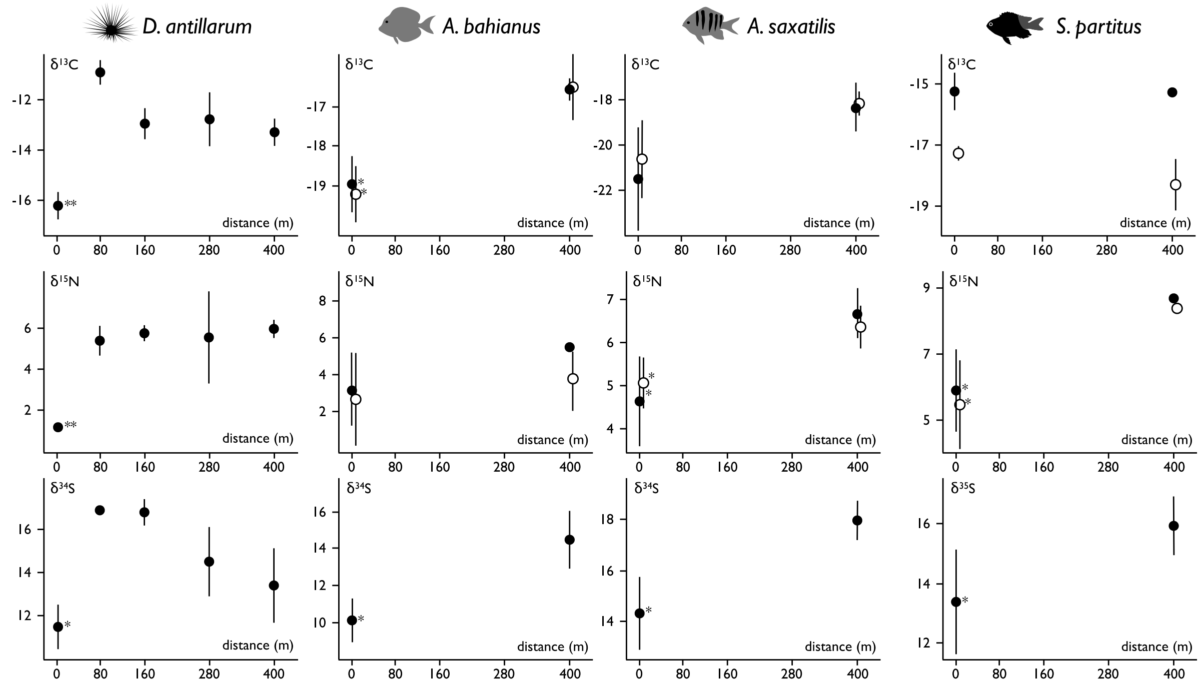

Figure 6. Isotopic compositions (δ^{13}C, δ^{15}N and δ^{34}S) of *D. antillarum*, *A. bahianus*, *A. saxatilis* and *S. partitus* of muscle (black dot) and stomach content (white dot) along transect stations (± SD; *n* = 3). *: Significant differences between station 0 and others (Kruskall-Wallis tests, ** p < 0.01, * p < 0.05)

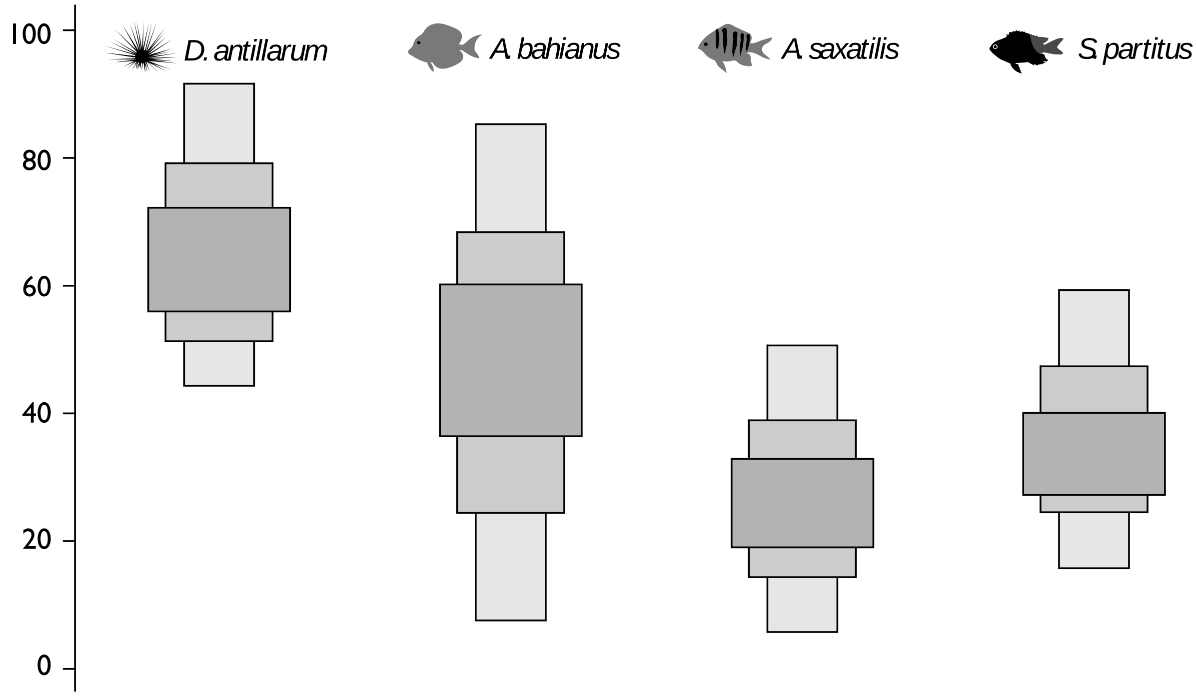

Figure 7. Contribution (%) of bacteria to the diet of *D. antillarum*, *A. bahianus*, *A. saxatilis* and *S. partitus* at station 0 m. Results were issued with the SIAR (Stable Isotope Analysis in R) mixing model with three isotopes (C, N and S) and two food sources (bacteria and average diet of each consumer evaluated at station 400 m). 95, 75 and 25 % credibility intervals of probability distributions are reported.

		Regular bacterial release	After two weeks of absence of bacterial release
A. bahianus	$\delta^{13}C$	-18.94 ± 0.74	-16.60 ± 0.95*
	$\delta^{15}N$	3.21 ± 1.99	4.89 ± 0.10
A. saxatilis	$\delta^{13}C$	-21.49 ± 2.31	-16.95 ± 0.61*
	$\delta^{15}N$	4.64 ± 1.02	5.70 ± 0.31
S. partitus	$\delta^{13}C$	-15.24 ± 0.62	-14.19 ± 0.79
	$\delta^{15}N$	5.88 ± 1.00	6.58 ± 0.60

Table 1. Isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$) of muscles of three fish species (*A. bahianus*, *A. saxatilis* and *S. partitus*, n = 3). during regular functioning of the geothermal plant and after two weeks' pause in functioning (*Kruskall-Wallis test, $p < 0.05$)

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