

ORIGINAL ARTICLE

Bivalve populations inhabiting hydrothermal vents on submarine volcanoes: using size frequency distributions to infer potential regulatory factors

Anna Metaxas

Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada, B3H4R2

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Correspondence

Anna Metaxas, Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada B3H4R2.
E-mail: metaxas@dal.ca

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Abstract

In this study, I used length frequency distributions of bivalve populations at hydrothermal vents on submarine volcanoes at the South Tonga Arc and the Valu Fa Ridge to infer processes that may be responsible for the observed population structures. On Volcano 19, the lucinid *Bathyaustriella thionipta* co-occurred with the sea star *Rumbleaster eructans* at two sedimented sites. At one site, live clams were significantly smaller (in shell length, SL) than dead ones (showing signs of predation by sea stars), whereas at the other site, both, live and dead clams had similarly small SL, suggesting a size refuge from predation. At Volcano 1, mussel beds of *Bathymodiolus* sp. were present in two areas: one with vigorous hydrothermal discharge ('Bubbles'), and another with some discharge but also in the photic zone ('Barracuda'). Mussels were smaller in SL at 'Bubbles' than at 'Barracuda', a consequence of either a younger population or a nutritionally less favourable environment at 'Bubbles'. At 'Barracuda', mussels utilized both chemo- and photosynthetically derived carbon, possibly allowing them to reach larger sizes. At Hine Hina on Valu Fa Ridge, a population of mussels was composed mainly of large individuals (>55 mm SL), estimated to be on average 7–13 years old. The combination of old mussels, absence of recruits, and presence of abundant empty mussel shells and of dead chimneys suggests that this is a waning hydrothermal system. My results indicate that the population structure of bivalves at hydrothermal vents can provide information on the processes that regulate these populations, which in turn can be used to generate testable hypotheses for the same location, should return visits occur, or for other locations with similarly structured populations.

Introduction

The processes that regulate populations at deep-sea hydrothermal vents are less well understood than regulatory processes in marine populations that occupy shallow water ecosystems. Their relatively recent discovery, remoteness (in terms of depth and distance from shore) and their discontinuous distribution along a narrow region of sea-floor spreading and subduction zones have all contributed to the utilization of a few focal locations for comprehensive studies of vent ecosystems in the

Atlantic and Pacific Oceans. Much research has focussed on the unique trophic relations that are based on chemo-synthesis (e.g. Childress & Fisher 1995; Dubilier *et al.* 2008); fewer studies have examined the role of other processes in the regulation of these populations, such as dispersal, recruitment, competition and predation (e.g. Micheli *et al.* 2002; Mullineaux *et al.* 2003; Metaxas 2004; Kelly *et al.* 2007; Adams & Mullineaux 2008). Although we have a reasonable understanding of vent ecosystems at a few locations on the East Pacific Rise, Juan de Fuca Ridge and Mid Atlantic Ridge, most of the world's vents

remain to be discovered and explored (Beaulieu *et al.* 2013). During exploration, multiple locations are visited during any one expedition, repeat visits often being unfeasible, resulting in a snapshot of the biological communities there. It is, therefore, important that the information obtained during these exploratory expeditions is maximized to attempt a mechanistic understanding of the regulatory processes at play.

Although estimates of abundance are imperative in describing the biological assemblages at any one location, size frequency distributions can be useful for generating hypotheses about the processes that regulate populations. Most commonly at hydrothermal vents, size distributions (particularly of bivalves and polychaetes) have been used to infer patterns in settlement and recruitment (e.g. Zal *et al.* 1995; Van Dover *et al.* 1996; Comtet & Desbruyères 1998; Van Dover 2002). Specifically, the shapes and the modality of size distributions have been used to infer whether recruitment is variable in space and time, continuous (unimodal) or discontinuous (polymodal), and recent or not (left skewed *versus* no skew). In some instances, effects of processes such as reproductive mode, individual growth and competition for access to resources (*i.e.* hydrothermal fluid) have been implicated in the generation of the observed patterns in size frequency (e.g. Comtet & Desbruyères 1998; Van Dover 2002).

Bivalves are one of the most abundant, both numerically and in terms of biomass, taxa at hydrothermal vents on mid-ocean ridges, island arcs and back arcs in the Atlantic, Pacific and Indian Oceans (Van Dover 2000; Desbruyères *et al.* 2001; Hashimoto *et al.* 2001; Podowski *et al.* 2009). They can form extensive beds that rival those in shallow-water environments and support similar diversities of associated fauna (e.g. Van Dover & Trask 2000; Van Dover 2002; Tunnicliffe *et al.* 2009). Their distribution within vent fields has been shown to be strongly correlated with temperature and chemical composition of the hydrothermal fluid and the distance from the point of discharge (Fisher *et al.* 1988; Shank *et al.* 1998; Desbruyères *et al.* 2000; Henry *et al.* 2008). Competitive interactions with conspecifics, as well as other species, have been associated with the regulation of bivalve populations (Mullineaux *et al.* 2003). The combination of suspension feeding and utilization of symbiotically produced carbon in bathymodiolin mussels places them in a unique position in the food webs of some of the vents that they inhabit. Therefore, understanding the mechanisms that regulate populations of bivalves can provide insights into the function of the entire vent ecosystem.

In this study, I sampled populations of lucinid and bathymodiolin bivalves at hydrothermal vents on three submarine volcanoes along the South Tonga Arc and southern Lau Basin. These volcanoes were sampled as

part of an exploratory expedition in the arc in 2007, and multiple repeat visits were not possible. I used the length frequency distributions of different sampled populations to infer processes that may have given rise to the observed population structures.

Material and Methods

Study sites

The Kermadec-Tonga Arc is a 2500-km-long chain of submarine volcanoes located off the northern coast of New Zealand and extending to the southern coast of Fiji (Fig. 1). In the north, the Tonga Arc extends from 16°S to 27°S, and, in the south, the Kermadec Arc extends from 27°S and 38°S. Volcano 19 and Volcano 1 were sampled along the South Tonga Arc.

Volcano 19 is a large volcano (14 × 12 km) located at the southernmost part of the Tonga Arc, which rises from 1400 to ~385 m depth (Schwarz-Schampera *et al.* 2007). The summit includes an old collapsed caldera, an infilling cone and a younger caldera on the western side. In 2007, there were two areas of hydrothermal vent fields on Volcano 19. One was an area of low-temperature venting located on the southern wall of the western caldera, and the other included high-temperature vents (~250–270 °C) and was located near the summit of the central cone. These sites were sampled in detail in 2005 and descriptions can be found in Stoffers *et al.* (2006). In 2007, bivalves were sampled at two sites on the central cone (Marker 40 and Fish Spa), separated by tens of metres from one another. At Volcano 19, the site at Marker 40 was sedimented and hydrothermal flow was mostly diffusive, except for a small anhydrite chimney (~1 m high), the bottom of which was covered with fluffy microbial mat. The temperature ~10 cm into the sediment was 6–11 °C, and the temperature of the fluid being discharged from the chimney was 40 °C. Shells of live and dead clams were visible at the sediment surface. At Fish Spa, the sediment included more gravel than at Marker 40.

Near Marker 40, several sea stars (*Rumbleaster eructans*) were foraging on clams (*Bathyaustriella thionipta*). Similarly, Stoffers *et al.* (2006) reported sea stars foraging amongst the shells in 2005. Abundance of the clams and sea stars, estimated from frame grabs taken from video, was $405 \pm 143 \text{ m}^{-2}$ ($n = 5$) for *B. thionipta* and $14 \pm 8 \text{ m}^{-2}$ ($n = 4$) for *R. eructans* (Metaxas 2011). At Fish Spa, the flatfish *Symphurus macullopis* and *Symphurus* sp. A were present (Tunnicliffe *et al.* 2010; Munroe *et al.* 2011).

Volcano 1 is also a large volcano with a basal diameter of 28 km, ~360 km north of Volcano 19, and rising from 1800 m to a summit at 65 m depth (see also Stoffers

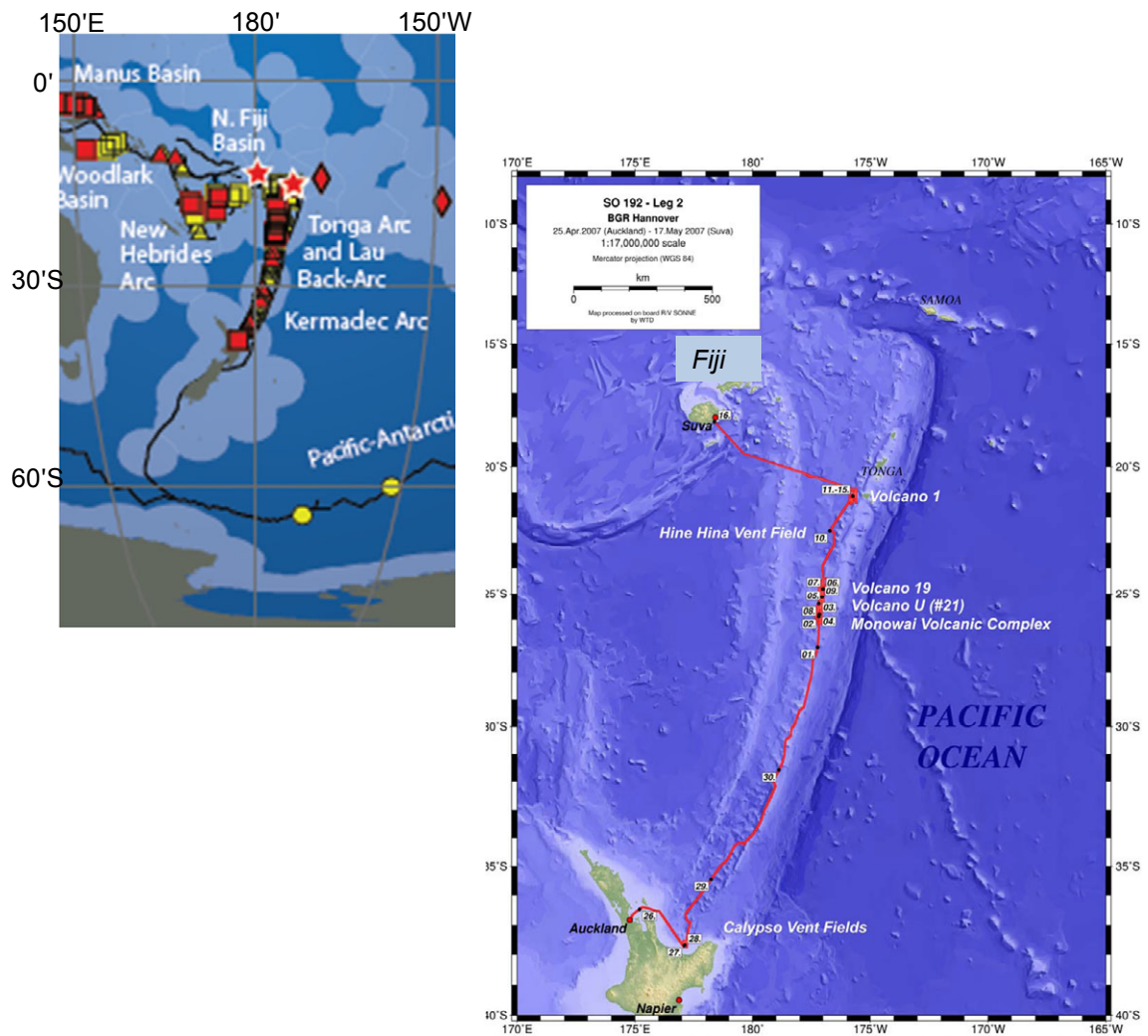


Fig. 1. Location of underwater volcanoes on the Kermadec–South Tonga Arc in the southwestern Pacific, sampled along the cruise track SO 192 – Leg 2.

et al. 2006). The floor of its collapsed central caldera is at 400–500 m depth. Low-temperature hydrothermal activity is located on the slopes of western and southwestern post-caldera scoria cones, at ~100–200 m depth (sites: ‘Super Cool’, ‘Barracuda’ and ‘Bubbles’; Schwarz-Schampera *et al.* 2007). ‘Sulfur field’ was located at the top of the scoria cone but south of these three sites in the chain of craters.

The three sampled locations on Volcano 1 represented very different habitats for the mussel *Bathymodiolus* sp. At ‘Bubbles’, there was an extensive mussel bed spanning ~1 km² with a sharp transition to fine sediment. Mean per cent cover of mussels ranged from 52.4% (SD: 34.3%; *n* = 8; dive R1050) to 87.3% (SD: 7.9%; *n* = 3; dive R1051), depending on the location within the bed (Metaxas 2011). Ambient water temperature was 18 °C, whereas the temperature in the mussel bed ranged from



Fig. 2. The mussel bed at ‘Barracuda’ on Volcano 1 was in the photic zone at ~100 m depth.

30 to 70 °C, and vigorous gas discharge along with thick clouds of white particles were evident (Schwarz-Schampera *et al.* 2007). Non-vent fish (e.g. grouper, butterfly-fish) were seen occasionally swimming above the mussel bed and local aggregations of 2–3 individuals·m⁻² of the sea star *R. eructans* were present in three different locations within the bed. The flatfish *Symphurus* sp. A was abundant throughout the mussel bed (Tunnicliffe *et al.* 2010). Although these fish may be consuming molluscs, only polychaetes and small crustaceans were present in the guts of dissected specimens (Tunnicliffe *et al.* 2010). A smaller mussel bed (~0.5 km²) was present in 'Barracuda', at ~100 m depth within the photic zone (Fig. 2). Schools of butterfly fish swam within the mussel bed and sharks and barracudas were swimming tens of metres above the bed. Ambient temperature was 19 °C and it was 19–30 °C in the sediment below the mussel bed. Locally, the sediment was covered with a thick, white microbial mat and the water above it was milky. Mean mussel cover was 18.7% (SD: 5.5%; n = 4; dive R1053; Metaxas 2011). The only evidence of predation was an eel attempting to feed on a mussel. The limpet *Shinkailepas* sp. was abundant at both 'Bubbles' and 'Barracuda', both on the substratum, as well as on mussel shells (Metaxas 2011). 'Sulfur field' covered a small area (<10 m²) at 196 m depth with visible venting but no gas discharge, and scattered blocks of sulphur crust. Ambient temperature was 16 °C and temperature of the fluid measured in cracks was 26–35 °C.

Hine Hina Segment is located on the Valu Fa Ridge in southern Lau Basin, ~25 km west of the Tonga Arc. It is ~1 km long and 350 m wide, and its shallowest depth is ~1800 m (Schwarz-Schampera *et al.* 2007). Hydrothermal activity during this study was mainly diffusive and of low temperature, resulting in iron- and manganese-hydroxide crusts; inactive chimneys were present along a fault scarp. In 1989, Hine Hina was dominated by bathymodiolins, with tubeworms (*Alaysia spiralis* and *Lammelibrachia columna*), shrimp (*Alvinocaris* sp. and *Lebeus* sp.) galatheids (*Munida* and *Munidopsis*) and deep-sea eels (*Thermobiotus mytiligeiton*) also being present (Desbruyères *et al.* 1994).

Biological sampling and statistical analyses

Bivalves were collected from each site either using a scooping net (~1 mm mesh) held by one of the manipulator arms of the ROV ROPOS (Table 1). In a single case, a sample was collected by a TV-guided, hydraulically operated grab sampler, towed at about 1 knot while suspended 1–6 m above the seafloor, and capable of retrieving about 0.7 m³ of largely undisturbed sediment. The scooping net allows precise location of the collection by the ROV. The precision of the sampling location of the TV-guided grab is generally lower than that, but based on the video could be identified relative to the imagery collected by the ROV during sampling. However, the minimum size of individual animals collected by the TV-grab is probably larger than what can be collected by a scooping net.

At Volcano 19, I collected clams with the scooping net (and five sea stars for identification) near Marker 40 (z = 560 m) on the Central Cone Complex (dive R1047) and at Fish Spa (dive R1048). At Volcano 1, I collected mussels using the scooping net from three locations: 'Bubbles' (dive R1050), and 'Barracuda' and 'Sulfur field' (dive R1053). An additional sample of mussels was collected from 'Sulfur field' with the TV-grab (TVG65). At Hine Hina, mussels were collected with the scooping net at 'Mussel Ridge'. For all bivalves, maximum shell length was measured with callipers along the longest axis of the shell, as in Comtet & Desbruyères (1998) and Tunnicliffe *et al.* (2009) (accuracy: ±0.01 mm).

Size frequency distributions and mean size of bivalves were compared between live and dead specimens (Volcano 19) or between pairs of sites (Volcano 1) using Kolmogorov–Smirnov and Student's *t*-tests, respectively.

Results

The samples from both sites on Volcano 19 contained live clams and empty shells (cluckers), which were intact but gaping with no remaining tissue, most likely reflecting predation by sea stars (Barbeau *et al.* 1994). At Marker 40, the size distributions of live and dead clams were significantly

Table 1. Characteristics of and sampling effort at each sampling site.

vent	site	depth (m)	temperature (°C)	bivalve species	sample size
Volcano 19	Marker 40	560	6–11	<i>Bathyaustriella thionipta</i>	103
	Fish Spa	560	6–11	<i>Bathyaustriella thionipta</i>	69
Volcano 1	Bubbles	198	30–70	<i>Bathymodiolus</i> sp.	141
	Barracuda	100	19–30	<i>Bathymodiolus</i> sp.	31
	Sulfur field	196	26–35	<i>Bathymodiolus</i> sp.	ROPOS: 6 TV grab: 10
Hine Hina	Mussel Ridge	1825	4	<i>Bathymodiolus brevior</i>	29

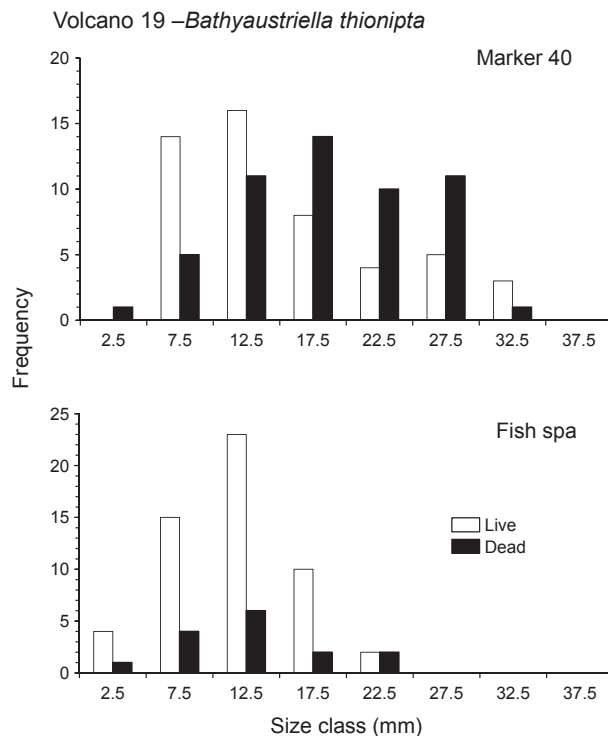


Fig. 3. Length frequency distributions of live and dead *Bathyaustriella thionipta* clams, sampled at two locations on Volcano 19 with the ROV ROPOS.

different from one another (Kolmogorov–Smirnov $Z = 2.77$, $P < 0.001$), and mean SL of live clams (15.57 mm; SD: 7.23 mm; $n = 50$) was significantly less than that of dead ones (23.37 mm; SD: 6.74 mm; $n = 53$) ($t_{101} = -5.63$; $P < 0.001$) (Fig. 3). In contrast, at Fish Spa the size distributions of live and dead clams were not significantly different from one another (Kolmogorov–Smirnov $Z = 0.596$, $P > 0.05$), and mean SL of live clams (11.85 mm; SD: 4.22 mm; $n = 54$) was similar to that of dead ones (12.87 mm; SD: 4.88 mm; $n = 15$) ($t_{67} = -0.787$; $P > 0.05$). At Marker 40, 50% of the shells belonged to dead clams, whereas at Fish Spa only 22% did.

The length frequency distributions of *Bathymodiulus* sp. varied widely amongst the three sampled locations on Volcano 1 ('Bubbles' versus 'Barracuda': Kolmogorov–Smirnov $Z_{172} = 4.52$, $P < 0.001$; 'Bubbles' versus 'Sulfur field': Kolmogorov–Smirnov $Z_{157} = 3.24$, $P < 0.001$; 'Barracuda' versus 'Sulfur field': Kolmogorov–Smirnov $Z_{47} = 2.23$, $P < 0.001$; Fig. 4). Mean SL was smaller at 'Bubbles' than 'Barracuda' ($t_{170} = -14.2$; $P < 0.001$) and 'Sulfur field' (pooled ROPOS and TV-grab samples; $t_{15,9} = -8.19$; $P < 0.001$). Mean SL was also smaller at 'Barracuda' than 'Sulfur field' ($t_{18,9} = -2.49$; $P = 0.022$).

At Hine Hina, 'Mussel Ridge' was the area with the highest observed biomass, and included galatheid crabs,

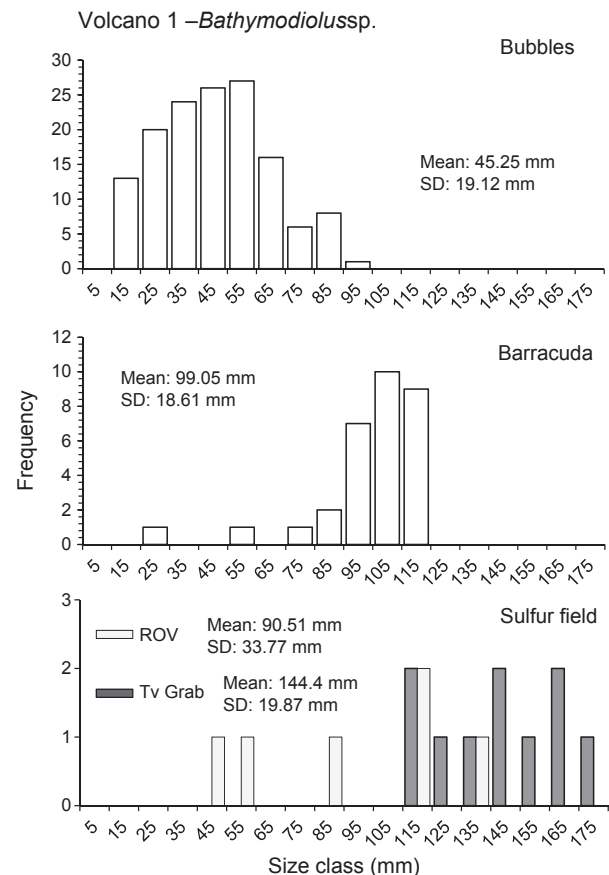


Fig. 4. Length frequency distributions of the mussel *Bathymodiulus* sp. sampled at three locations on Volcano 1. Samples at all locations were collected by the ROV ROPOS, but an additional sample was collected by TV grab at 'Sulfur field'. n was 141 at 'Bubbles', 31 at 'Barracuda', and 11 and 7 at 'Sulfur field' sampled by ROPOS and TV grab, respectively.

shrimp, tubeworms, stalked barnacles, and limpets mainly on the mussel shells, whereas no vent fauna was evident in the remainder of the vent field. 'Mussel Ridge' appeared to harbour a dying vent community, as patches of empty mussel shells were found throughout the area at a depth of ~1825 m. Ambient temperature was 2 °C and a temperature anomaly of 4 °C was measured in the sediment only at the location where *Bathymodiulus brevior* was collected. All collected mussels (except one) were >55 mm SL and the largest was 145 mm SL (Fig. 5).

Discussion

Based on the length frequency distributions of different bivalve populations at hydrothermal vents on the South Tonga Arc and the Valu Fa Ridge, I can infer some of the processes that may regulate these populations, such as predation, access to multiple sources of food, and low

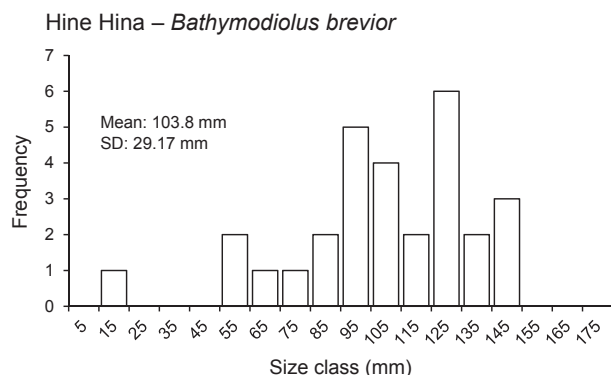


Fig. 5. Length frequency distributions of the mussel *Bathymodiolus brevior* sampled on Hine Hina with the ROV ROPOS. $n = 29$.

recruitment or fast growth. The relative importance of each of these processes varied amongst populations (e.g. predation at Volcano 19, food availability and recruitment at Volcano 1, and an ageing population in a waning vent system at Hine Hina). However, the identification of the potentially most relevant process at each vent field can allow the generation of testable hypotheses either for the same locations, should the opportunity for a return visit arise, or for other locations where similar patterns may be documented. It should be noted that the role of stochastic processes in generating the observed patterns cannot be accounted for in these 'snapshot' views of these populations. The relative importance of stochasticity can only be evaluated using long-term studies that allow the manifestation of temporal variability in population structure.

Size-selective predation by the sea star *Rumbleaster eructans* most probably affected the population of *Bathyaustriella thionipta* at Volcano 19. At Marker 40, mortality was high and the live clams much smaller than the cluckers, whereas at Fish Spa, mortality was lower and both live clams and cluckers were smaller than the live clams at Marker 40, indicating a size refuge of small clams from predation. The sea stars were of a size (mean radius: 18.7 mm, SD: 5.63, $n = 18$) capable of consuming large clams, making the smaller individuals less preferred. Size-selective feeding on bivalves is common in asteroids, and typically correlated with predator size (McClintock & Robnett 1986; Dolmer 1998; Sommer *et al.* 1999; Wong & Barbeau 2005). Size-selective predation has been shown to regulate size frequency distribution and abundance of bivalves, such as mussels and clams, in shallow water in temperate regions (Penney & Griffiths 1984; Ross *et al.* 2002; Gaymer *et al.* 2004). Based on their significant role in regulating the structure of marine communities through the consumption of mussels in shallow water, sea stars have been considered 'keystone predators' (Paine 1966).

At Volcano 1, the variation in SL of *Bathymodiolus* sp. is probably the result of a combination of food availability, predation and recruitment. The lack of large individuals at 'Bubbles' could be the result of predation by the sea stars, as was the case for clams at Volcano 19. However, sea stars were only present at three locations during the survey of the mussel bed and not in particularly high densities, making this explanation unlikely. The preponderance of smaller size classes at 'Bubbles' compared with the other two sites, as well as the larger number of individuals collected for the same sampling effort, indicate recent and probably continuous recruitment at this site. By contrast, the lack of small individuals at the other two sites suggests low (and perhaps no) recent recruitment at 'Barracuda' or 'Sulfur field'. Alternatively, the differences in mean SL between 'Bubbles' and the other two sites may be indicative of conditions more favourable to growth that allowed a larger size to be achieved at 'Barracuda' or 'Sulfur field'. Smith *et al.* (2000) suggested that spatial differences in the abundance, maximum size and condition of the seep mussel *Bathymodiolus childressi* in the Gulf of Mexico were related to the chemical composition of the fluids in which the animals were bathed. In my study, the same site did not exhibit both the highest abundance and maximum size of mussels. Tissue from mussels from 'Barracuda' was more enriched (by $\sim 2\text{‰}$) in ^{13}C and had different fatty acid compositions compared with tissue from mussels at 'Bubbles', both indicative of greater utilization of photosynthetically derived carbon (Comeault *et al.* 2010). This extra source of carbon may allow mussels at 'Barracuda' to reach a greater SL than mussels at 'Bubbles'. Similarly, although abundance was very low, probably because of the small spatial extent of 'Sulfur field', the fluid composition there may have allowed mussels to grow large. Alternatively, 'Bubbles' may have been formed relatively recently and the populations there may be younger (and thus contain smaller individuals) than at the other two sites.

At Hine Hina, the size frequency distribution of *Bathymodiolus brevior* was indicative of a population with almost no recruitment and mostly old individuals. A few recent studies have estimated daily growth rate of bathymodiolins at hydrothermal vents, either from patterns of growth lines on the shell (*B. brevior* and *Bathymodiolus thermophilus* – Schöne & Gierb 2005; Tunnicliffe *et al.* 2009) or by labelling live mussels *in situ* (*B. thermophilus* – Nedoncelle *et al.* 2013). In these studies, Growth rates generally varied with shell size, decelerating with age and eventually reaching an asymptote, and were strongly affected by fluid flux. The estimated average growth rate of *B. brevior* was $\sim 21 \mu\text{m}\cdot\text{day}^{-1}$ (60–140 cm SL) for individuals from

Monowai on the Kermadec Arc (Tunnicliffe *et al.* 2009), and $\sim 40 \mu\text{m}\cdot\text{day}^{-1}$ for those (44–106 mm SL) from the North Fiji Basin (Schöne & Gierb 2005). Based on these growth rates, the age of a mussel of the mean SL at Hine Hina is estimated as 7–13 years old, whereas the single small and the largest individuals collected are estimated as 1–2 and 10–19 years old, respectively. These age patterns, in combination with the low temperature of the hydrothermal fluids and the multiple dead chimneys, indicate a waning vent system. In fact, in 1989, temperature within the mussel bed at Hine Hina was higher than in 2007, and ranged from 2.4 to 18.8 °C (Chevaldonné *et al.* 1991). The mussel populations in this vent field were covered with a thick microbial mat in 1989 (Desbruyères *et al.* 1994) that was not visible in 2007. If this is indeed a slowing vent system, the more conservative estimates of growth are likely to be more accurate. It should be noted that recruitment may be underestimated because of our sampling method; however, most individuals collected at ‘Bubbles’ on Volcano 1, using the same technique as at Hine Hina, were <45 mm SL. Metaxas (2011) suggested that although local recruitment may be high through larval retention given a sufficiently large adult population, colonization of new locations within or amongst seamounts (even at distances of tens to hundreds of kilometres) is probably low because of hydrodynamics and larval behaviour. This may also explain the low recruitment rate inferred for Hine Hina.

Conclusions

Length frequency distributions of bivalves inhabiting hydrothermal vents, in combination with measures of abundance, can provide useful information on the processes that regulate these populations, particularly in locations that are only surveyed on a few occasions or opportunistically during exploration. In my study, such processes included: predation, the impact of which is not well studied in vent ecosystems; concurrent access to photosynthetic and chemosynthetic sources of carbon; limited recruitment; and a waning hydrothermal system. Such information can be used to formulate hypotheses for the same or similar systems, and increase our understanding of the importance of different ecological processes in regulating these assemblages.

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