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# Marine Ecology: Special Issue

*Edited by Tom Webb and Alison Holt*

## Marine Ecology: Exploring the Marine Environment

### Islands in the Deep Sea

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Islands have long held a fascination for naturalists, from Darwin's observations in the Galapagos to MacArthur and Wilson's models of island biogeography. One might therefore think that islands have been thoroughly picked over by ecologists and the days of tripping over new species on previously-unexplored archipelagos are long gone. But for those of us working in the deep ocean, that golden age of discovery is still a reality.

Thirty years ago marine biologists were astounded by pictures from a newly discovered phenomenon on the ocean floor: deep-sea hydrothermal vents. These undersea volcanic springs, first found 2500 metres deep in the Pacific, were home to abundant populations of new animal species. Such islands of life in the otherwise sparsely populated abyss are supported by local chemosynthetic primary production, where microbes use sulphide and methane gushing from the seafloor as an energy source to fix inorganic carbon.

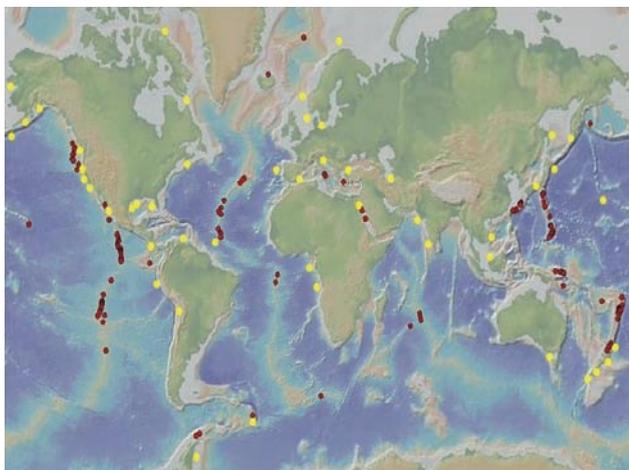
After the discovery of hydrothermal vents came that of cold seeps, another category of chemosynthetic island on the ocean floor driven by a variety of other geological processes. And we now know that whale carcasses also support islands of chemosynthetic life during the degradative succession of their skeletons. So deep-sea chemosynthetic islands are far more widespread than originally realised, in settings such as volcanic vents, brine pools, mud volcanoes, whale falls, gas hydrate beds and asphalt seeps.

Physiologists have rushed to understand the adaptations to these environments, from the symbiotic relationships between some animal species and chemosynthetic microbes, to the solutions evolved by many species to the problems of high sulphide conditions. But the development of our ecological understanding has arguably been much slower, while we gradually obtain prerequisite data on species distributions.

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More than 600 new animal species have been described so far from vents and seeps, which is an average of one new species every three weeks. And those are just the large, obvious megafaunal species such as the metre-long red-plumed vestimentiferan tubeworms that have become the poster child of hydrothermal vents. Our investigation of the smaller meiofauna – animals typically smaller than 1 mm, such as nematodes – has only just begun. When you encounter an animal at a depth of more than 3000 metres, there is a 50% chance that it will be a new species.

What is now beginning to emerge, however, is an appreciation of biogeographic patterns in chemosynthetic environments, thanks to efforts such as the International Census of Marine Life's ChEss (Chemosynthetic Ecosystems) programme. We are at last piecing together a global jigsaw puzzle of species distributions in these islands on the ocean floor. Eastern Pacific vents, for example, are dominated by vestimentiferan tubeworms and chemosynthetic mussels. But while mussels are also known at Mid-Atlantic vents, no tubeworms have been found there so far. Instead, some deep Mid-Atlantic vents are dominated by dense aggregations of shrimp that are highly adapted to the vent environment. Similar shrimp are present at vents in the Indian Ocean, first visited in the early 2000s. But many gaps remain, as only a tiny fraction of the ocean floor has been explored. The challenge now is to understand the processes that shape the emerging global patterns of biogeography at vents and seeps – and solving that puzzle should advance our understanding of patterns of marine life in general.



Global distribution of hydrothermal vent (in red) and cold seep (in yellow) sites discovered so far. The gaps represent where no one has looked yet! Image courtesy of Census of Marine Life ChEss programme, [www.noc.soton.ac.uk/chess/](http://www.noc.soton.ac.uk/chess/)

### Patchiness in vent ecosystems

Individual vent and seep sites are small features on the ocean floor, each typically the size of a couple of football pitches. And they can be tens to hundreds of kilometres apart. Within each island, the environment is very patchy. At hydrothermal vents, temperature can vary by tens of degrees C over tens of centimetres – and temperature is a good proxy for the mixing between acidic, anoxic and sulphide-rich vent fluids and surrounding seawater. Although cold seeps by definition lack such temperature gradients, they exhibit similar sharp gradients in features such as sulphide and oxygen concentrations.

This patchiness and these gradients have consequences for the distribution of animals at individual vent and seep sites. Population distributions at vents and seeps often follow zonation patterns on similar scales to those of rocky shores. The patchiness can also affect processes such as reproduction, with zonation of brooding crustaceans around sites and patchiness in the reproductive development of some less motile species.

As well as being very patchy environments, they are also highly dynamic. Motile vent shrimp seem to vary their distribution on a tidal timescale in response to tidal fluctuations in the flow from vents, even at a depth of 3600 metres. And some polychaete species at vents appear to have reproductive cycles on lunar timescales – a frequency unprecedented elsewhere in the deep sea – again possibly linked to tidal cues.

Several other vent and seep species exhibit seasonal reproduction, despite plenty of food all year round from chemosynthetic primary production. These seasonal-reproducing species produce planktotrophic larvae, which feed on phytodetrital material as they develop away from vents and seeps. Reproduction in these species appears to be timed so that larval release coincides with the end of spring blooms of phytoplankton in sunlit waters far above – a hitherto overlooked link between the ecology of chemosynthetic and photosynthetic ecosystems.

With their sharp physical gradients and dynamics, chemosynthetic environments have been described as deep-sea analogues of the intertidal zone. The development of ecological understanding of these environments is following similar lines to those followed in the history of intertidal ecology. Vent and seep ecology is progressing from considering the role of solely physical factors in determining zonation patterns, for example, to also recognising the

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importance of biological interactions. Devising and executing field experiments on the ocean floor to demonstrate interactions such as competition, however, requires considerable practical and logistic ingenuity. But despite their remoteness, these islands may offer a similar sandbox to the intertidal for testing and developing ecological ideas.



A 'black smoker' vent chimney in action, at the TAG hydrothermal vent site on the Mid-Atlantic Ridge at 26 degrees N and a depth of 3600 m

### Vent and seep biogeography

On a larger scale, deep-sea chemosynthetic environments are not only insular, but also ephemeral. Vent sites become clogged by mineral deposits, buried by lava flows, or have their underlying plumbing in the oceanic crust cut off by earthquakes. Along the sections of the mid-ocean ridge that are most volcanically active, a vent site may only last a few decades, while in less active regions one may last centuries. Cold seeps, meanwhile, sow the seeds of their own demise. The flux of sulphide at cold seeps is usually produced by the reduction of seawater sulphate by microbes in seafloor sediments, coupled to the oxidation of methane. Another by-product of this process is biogenic carbonate rock – and over a few centuries enough of this rock forms in the sediments that it caps further seepage of methane and sulphide to the surface at that site.

When venting or seeping stops, most of the animal populations at that island are doomed. Few adult forms can migrate to another vent or seep site. Many vent and seep species, such as the vestimentiferan tubeworms, are sessile as adults. Even for those species that are motile as adults, it can be hundreds of kilometres to the next chemosynthetic island, across an impenetrable desert in terms of productivity. Yet clearly the species that populate these islands have some means of

overcoming this apparent problem. Understanding dispersal in these environments – and its consequences for gene flow, population differentiation, speciation and biogeography – is currently a key question in vent and seep ecology.

For many animals, the answer lies in their larval forms, which often seem adapted for island-hopping. Vestimentiferan tubeworms, for example, produce lecithotrophic larvae that cannot feed but are provisioned with energy reserves. The larvae eke out their reserves as they are carried by ocean currents, because their metabolism ticks over very slowly in the cold deep waters away from vents. But even so, a vent tubeworm larva can only survive for around forty days in the wilderness before its reserves are spent. Fortunately that lifespan is sufficient to ensure that some are carried from vent to vent in their eastern Pacific, where vents are quite close together as a result of more intense volcanic activity at the mid-ocean ridge in the region.

In contrast, the vent shrimp found on the Mid-Atlantic Ridge and in the Indian Ocean produce planktotrophic larvae that can feed while away from the vents. Consequently these larvae may be more capable of dispersal across the larger distances that separate vents in those oceans. Chemosynthetic islands therefore offer an ideal system in which to study the roles of life history strategy and larval ecology in shaping patterns of population differentiation and biogeography in the marine environment.



Typical vent fauna: aggregations of the vent shrimp *Rimicaris exoculata* and the vent crab *Segonzacia mesatlantica*. From the TAG hydrothermal vent site on the Mid-Atlantic Ridge at 26 degrees N and a depth of 3600 m.

### The future of vent and seep research

As I write this my colleagues and I are aboard a ship in the Southern Ocean, on an expedition looking for vents and seeps around Antarctica. This region is one of the missing pieces of the global jigsaw puzzle. Will life at chemosynthetic

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environments around the Drake Passage, between the Antarctic Peninsula and South America, be similar to that of the Pacific, or the Atlantic, or completely different to both? We have an onboard sweepstake about the animals we may find. A safe bet is that there may be mussels – the most geographically widespread taxon found so far at vents and seeps. Their wide distribution may in part be attributed to their planktotrophic larvae.

Shrimp may be another good bet for the same reason, though cold water temperatures can have a narcotising effect on decapod crustaceans, which has excluded them from Antarctic waters further south. I am hedging my bets on tubeworms, however, because of their lecithotrophic larvae. Based on our geological knowledge, the likely spacing of vents in this area may be around the threshold for tubeworm larvae to be able to hop from island to island with their limited food reserves. But the deep sea always contains surprises. Technology and weather permitting, within the next four weeks we should get our first glimpse of life at vents down here.

Another missing piece of the global jigsaw puzzle may lie at the bottom of a rift in the seafloor of the Caribbean. This rift, known as the Cayman Trough, contains the world's deepest undersea volcanic ridge, 6000 metres beneath the waves. This ridge has been volcanically active for at least 50 million years. Before the Isthmus of Panama closed between 10 and 3 Mya, vent species could have dispersed from the eastern Pacific to the Trough. Today, however, a deep ocean current links the Trough with the Mid-Atlantic.

So if geological history is a key feature determining biogeographic patterns at deep-sea vents, then we expect to find species in the Cayman Trough with affinities to those at the Pacific vents. If modern-day hydrography is a key factor, however, then we may find Atlantic-type vent fauna. The Trough could also be so isolated that it hosts its own unique fauna to some degree, which would tell us something about the scale and type of isolation required to produce distinct biogeographic provinces in the marine environment.

Any vents on the very deepest reaches of the ridge in the Cayman Trough could also be unlike any we have seen before, theoretically erupting water as hot as 550 deg C with a unique chemistry as a consequence of the higher pressure at greater depth. The microbial processes and physiological adaptations in such an environment are a tantalising prospect. Right now we are waiting to hear when the ship that we need will be scheduled for our first expedition to the area.

Although our expeditions will collect samples for molecular phylogenetics and population genetic studies, our first-order measure of gene flow between different sites is the presence / absence of species – much the same as that used by nineteenth century naturalists. And we share the same excitement that they experienced when visiting previously unexplored islands. Just as they rushed to peer through telescopes from the ship's rail or upper yards for the first sight of the inhabitants of new shorelines, so we cram around video monitors as our underwater vehicles arrive at newfound vent and seep sites.

In the three decades of exploration at vents and seeps, our view of these islands has changed from considering them a mere footnote in marine ecology to recognising them as widespread features of our planet's largest landscape, the deep ocean. As we start using them as "natural laboratories" to examine interactions between biogeography, evolution, genetics and ecology in determining patterns of marine life, I hope that they will eventually warrant more than just a passing mention in ecology textbooks of the future.

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