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A review of predators and predation at deep-sea hydrothermal vents

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Abstract: The very few predators at deep-sea hydrothermal vents have been hypothesized to allow extremely vulnerable, relic taxa to survive in these habitats. If vents are viewed as ephemeral habitats in which disturbance is so frequent that few endemic predators can survive, their scarcity, rather than being an anomaly, is seen as a logical consequence of habitat transience. Toxins, however, may minimize exploitation of the habitat by most opportunistic predators.

Rates of lethal predation remain undetermined, but vent limpets and vestimentiferans, including those from areas with high sulphide levels, show frequent evidence of non-lethal predation.

Characterizing vent habitats as unchanged over geological time and as home to "relic" taxa of ancient groups ignores historic anoxic episodes and the increasing fossil history of vent assemblages. Although trophic relations of vent predators remain poorly known, deep-sea predators are more diverse both taxonomically and in their foraging habits than had been expected; the reportedly vulnerable vent fauna may show unsuspected defenses.

Variation in Carbon and Nitrogen isotopes among chemosynthetic taxa and bacteria complicates isotope analyses which are most powerful when supplemented by direct observations and specimen-based documentation of prey. Technological advances offer new promise for these analyses.

Résumé : *Prédateurs et prédation au niveau des sources hydrothermales profondes.* Le faible nombre de prédateurs présents, associés aux sources hydrothermales profondes, laisse sous-entendre que des proies très vulnérables et des taxons reliques puissent y survivre. Ces sources sont des habitats éphémères au niveau desquels les perturbations sont si fréquentes que seuls quelques prédateurs peuvent survivre, conséquence logique d'habitats transitoires. La présence d'éléments toxiques tels que H_2S peut aussi minimiser l'exploitation de la biomasse hydrothermale par des prédateurs opportunistes.

Les "Patelles" et les Vestimentifères, y compris ceux qui vivent dans des zones à très forte concentration en hydrogène sulfuré, montrent de fréquentes traces de prédation non mortelles.

Les sources hydrothermales profondes sont généralement considérées comme des habitats conservés à l'échelle des temps géologiques, ignorant ainsi l'histoire des épisodes anoxiques des océans et celle des fossiles de ces zones. Bien que les relations trophiques entre prédateurs et consommateurs primaires des sources hydrothermales soient presque inconnues, la diversité taxonomique et nutritionnelle de ces prédateurs est plus élevée qu'escomptée et la faune hydrothermale, reconnue vulnérable, peut en fait présenter des défenses insoupçonnées. Les variations des isotopes stables du carbone et de l'azote chez les organismes chimiosynthétiques rendent les analyses isotopiques compliquées. Des observations supplémentaires de prédation in situ sont nécessaires.

Keywords : Hydrothermal vents, predation, deep-sea, Predators, selection, habitat disturbance.

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Introduction

At deep-sea hydrothermal vents, chemoautotrophic bacteria oxidize reduced chemicals released from beneath the Earth's surface to sustain extraordinarily productive biological systems on the otherwise resource-poor seafloor. The few predators from the surrounding areas that are reported to exploit the seemingly readily available vent-produced biomass appear counterintuitive, as do the few predators that are endemic or specialized for the vent habitats. This paper examines these views of predation at deep-sea hydrothermal vents in light of recent observations and discoveries and from the view point of evolutionary ecology. The goal is to establish similarities between deep-sea vents and more familiar and accessible habitats, to facilitate study and increase our understanding of the former.

Our biological knowledge of deep-sea vent systems relies exclusively on the limited number of submersible-based observations and collections that have been made since the discovery of these systems in 1977. Producer animals, such as tube worms and bivalves that host endosymbiotic chemosynthetic bacteria, are among the most intensively studied vent fauna (Childress & Fisher, 1992). Taxa such as gastropods and annelids that graze on bacterial mats or filter-feed are also familiar components of the biological system at most vents. Although comparatively rare in collections, both opportunistic predators and those that appear to be vent-specialized are known from direct observations and baited camera records at hydrothermal vents on Back-Arc basins in the West Pacific (WP), and on ridges in the Northeast Pacific (NEP), East Pacific Rise (EPR) and Mid-Atlantic Ridge (MAR).

Predators documented at vents in each of four regions that have received biological study are here reported as the number of species by family (Table 1). Reference to the recent compendium of hydrothermal vent fauna (Tunnicliffe et al., 1998), also available on the World Wide Web through the InterRidge site (the location of which changes periodically), will allow the 133 species of vent predators listed to be readily discerned. Molluscan, annelid and arthropod species make up 92% of the total vent fauna (Tunnicliffe et al., 1998). This phylum-level representation largely extends to vent predators, which include gastropods and octopuses, polychaetes, and pycnogonids and crabs, however, 24.1% of vent predators are fishes.

The composition of the predatory guild differs among the four vent regions considered (Table 1), possibly in association with differences in the dominant taxa of each region. At MAR vents, fishes constitute a significantly higher proportion of predators than at any other vent system. The abundant shrimps at MAR vents (Gebruk et al., 1997) that fall prey to several species of fishes (Geistdoerfoer, 1991; 1994; Saldanha, 1994) may be essentially unavailable to benthic predators (Table 1). Crab species are exceptionally, but not significantly, more diverse at WP Back-Arc vents where gastropods, barnacles and mussels compose most of the vent fauna (Desbruyères et al., 1994). Among predatory polychaetes, recent taxonomic research has discovered twelve new species from MAR vents (D. Desbruyères, S. Hourdez, pers. comm.). Polychaete diversity shows a subtle peak at EPR and NEP vents where dominant tube worms provide a three-dimensional structure to the biotic assemblage, although again the taxonomic composition of predators at these vents is not significantly biased.

The Rarity of Vent Predators

Cohen & Haedrich's (1983) comparison of fishes on and off Galapagos Rift vents offers the most thorough documentation of predator diversity and density at a vent site. Submersible observations and baited camera deployments documented only 14 fish species in the immediate area of the vents; with only about one third the effort, 17 species were observed several hundred meters away from the vents. Despite the abundance and the apparent availability of prey at vents, both the diversity and density of large predators decrease near vents (Cohen & Haedrich, 1983). Cohen & Haedrich's (1983) conclusions, that 1) vent biomass does not increase the representation of animals in higher trophic guilds; 2) the biological impact of vent production is very local; and 3) fish predation in vent habitats is relatively unimportant, form the basis of the view that vents function as biological islands rather than having trophic links to the surrounding deep-sea ecosystem.

Various hypotheses have been erected to explain the rarity of predators at deep-sea hydrothermal vents. Elevated temperatures and toxic vent fluids have been argued to create a stressful habitat that reduces predation (McLean, 1981; Cohen & Haedrich, 1983; Turner, 1985). Stressful habitats, however, have been defined by an evolutionary ecologist as those in which the physical rigors of the habitat limit production, such as cold in high latitudes or aridity in deserts (Grime, 1977). Residents of stressful habitats survive by either undergoing periodic dormancy or by very slow growth and delayed reproduction. Predation in stressful habitats may be comparatively reduced at any one time, but residents have extensive anti-predator defenses, possibly to ensure their survival over their long life spans in these stable habitats (Sih, 1987). Vent habitats impose physiological demands on their inhabitants, but vents are not stressful in the above sense. Vents are physically unstable habitats in which residents show very rapid growth (e.g., Fustec et al., 1987, Lutz et al., 1994) that appears to be unimpeded by the rigors of the habitat.

Table 1. The number of predators at hydrothermal vent systems are enumerated as the number of species in each family of predators, with the total number of predators known from each of the four ridge systems. Sources are primarily Tunnicliffe et al. (1998), Desbruyères & Segonzac (1997) and original species descriptions. A list of the vent fauna is presented on the InterRidge web page, posted in 2000 to http://triton.ori.u-tokyo.ac.jp/~intridge

Tableau 1. Le nombre d'espèces prédatrices présentes sur les sources hydrothermales est donné pour chaque famille ainsi que le nombre total de prédateurs connus dans les quatre provinces biogéographiques. Les références sont : Tunnicliffe et al. (1998), Desbruyères & Segonzac (1997) et les descriptions originales des espèces. Une liste de la faune des sources hydrothermales est accessible sur le site internet de InterRidge : http: //triton.ori.u-tokyo.ac.jp/~intridge

West Pacific (WP) $\Sigma = 37$

Annelida: Polychaeta (n = 14)
Dorvilleidae 1
Eunicidae 2
Hesionidae 1
Polynoidae 10
Mollusca: Gastropoda (n = 7)
Buccinidae 2
Elachisinidae 1
Turridae 4
Arthropoda: Pycnogonida (n = 1)
Ammotheidae 1
Crustacea (n = 13)
Bythograeidae 2
Galatheidae 5
Chirostylidae 4
Lithodidae 2
Echinodermata: Asteroidea (n = 1)
Goniasteridae 1
Chordata: Fishes **(n = 1)**
Synaphobranchidae 1

Northeast Pacific (NEP) $\Sigma = 27$

Annelida: Polychaeta (n = 16)
Dorvilleidae 2
Hesionidae 4
Nereidae 1
Phyllodocidae 1
Polynoidae 8
Mollusca: Gastropoda (n = 2)
Buccinidae 1
Turridae 1
Cephalopoda (n = 2)
Octopodidae 2
Arthropoda: Pycnogonida (n = 2)
Ammotheidae 2
Crustacea (n = 3)
Galatheidae 1
Lithodidae 1
Majiidae 1
Chordata: Fishes **(n = 2)**
Macrouridae 1
Zoarcidae 1

East Pacific Rise (EPR) $\Sigma = 36$

Annelida: Polychaeta (n = 21)
Archinomidae 1
Dorvilleidae 1
Eunicidae 1
Hesionidae 2
Nereidae 1
Phyllodocidae 2
Polynoidae 12
Mollusca: Gastropoda (n = 1)
Turridae 1
Cephalopoda (n = 2)
Octopodidae 2
Arthropoda: Pycnogonida (n = 1)
Ammotheidae 1
Crustacea (n = 6)
Bythograeidae 4
Galatheidae 2
Chordata: Fishes **(n = 5)**
Bythitidae 1
Cyclopteridae 1
Macrouridae 1
Zoarcidae 2

Mid-Atlantic Ridge (MAR) $\Sigma = 44$

Annelida: Polychaeta (n = 12)
Archinomidae 1
Dorvilleidae 1
Glyceridae 1
Hesionidae 2
Phyllodocidae 1
Polynoidae 6
Mollusca: Gastropoda (n = 1)
Turridae 1
Arthropoda: Pycnogonida (n = 2)
Ammotheidae 2
Crustacea (n = 5)
Bythograeidae 1
Galatheidae 1
Geryonidae 1
Homolidae 1
Portunidae 1
Chordata: Fishes **(n = 24)**
Scyliorhinidae 1
Squalidae 4
Chimaeridae 2
Synaphobranchidae 3
Notacanthidae 1
Bythitidae 1
Gadidae 1
Macrouridae 2
Moridae 2
Berycidae 1
Oreosomatidae 1
Apodonidae 1
Scorpaenidae 1
Chaunacidae 2
Zoarcidae 1

The rarity of vent-specialized predators has also been attributed to the transience of vent habitats (Hessler et al., 1985; Turner, 1985; Tunnicliffe & Juniper, 1990; Carney, 1994; Lutz et al., 1994). Lava flows and tectonic forces can close vent fluid conduits instantaneously; metallic sulphides deposited in fluid conduits reduce the flow of vent fluid to zero over years or decades (Tunnicliffe, 1991). When fluid flow ceases, the vent-dependent biological assemblage collapses and, perhaps after scavenging on vent biota, vent-specialist predators must locate a suitable new vent habitat. The temporal instability of vents, their seemingly chaotic distribution along the ridge axis and the very small proportion of the ocean floor that they occupy make this difficult.

If vents are transient habitats, they should follow the predictions made based on observations and study of similar habitats. Transient habitats that are subject to frequent disturbance are predicted to have reduced levels of predation because predators may only slowly recolonize a habitat after disturbances or, if disturbances are very frequent, predators may be unable to persist (Sih, 1987). Although residents of such ephemeral habitats risk being preyed upon by opportunistic predators that randomly encounter the habitat, the primary source of mortality is predicted to be habitat disturbance. Residents therefore invest heavily in rapid growth and development and comparatively little in anti-predator defenses. These biological features characterize vent residents, as physical transience characterizes the vent habitat itself. When vent habitats are viewed as ephemeral habitats, the diversity and abundance of endemic predators rather than being anomalously low, is consistent with predictions for transient habitats (Sih, 1987). The comparatively few opportunistic predators seen at vents, however, suggest that additional factors contribute to their rarity.

Sulphides and Predator Deterrence

The chemical toxicity of vent fluids may prevent opportunistic predators from entering the vent habitat (McLean, 1981; Cohen & Haedrich, 1983; Turner, 1985). Animals on vent fields may suffer due to limited oxygen availability. Hydrothermal vent temperatures, well- known for their high maxima, are less well known for their extreme spatial and temporal variation which have been suggested to impact residents more than do the maxima (Johnson et al., 1988). Locally abundant radiation and chemical toxins such as methane, hydrocarbons (Simoneit, 1985) and ammonia (Tivey et al. 1998) increase the physiological rigors that must be overcome to survive on-vent. The metal-rich fluids released at vents appear to result in elevated concentrations of heavy metal in the tissues of vent residents (Roesijadi & Crecelius, 1984; González et al., 1998). These chemical toxins have been suggested to increase mutation rates in vent organisms (Jollivet, 1996).

Chief among vent toxins, however, is hydrogen sulphide which is readily absorbed across epidermal and respiratory surfaces. Sulphide interferes with cytochrome *c* oxidase, an enzyme critical to the electron transport phase of aerobic metabolism (Childress & Fisher, 1992). Elevated sulphide concentrations also amplify the effects of low oxygen availability and impair anaerobic metabolism in various invertebrate groups (Vistisen & Vismann, 1997 and references therein).

Members of diverse taxonomic groups have evolved the ability to oxidize or detoxify sulphide through various physiological means and thus can tolerate exposure to the chemical (Childress & Fisher, 1992). The hypothesis that large, active predators with complex nervous systems are very sensitive to sulphide (Cohen et al., 1990) may partially explain why few opportunistic predators are seen at vents. Carney (1994), however, argues that the rarity of large predators at deep-sea hydrothermal vents is due to their rarity in the deep sea. If a group of predators, such as the drill snails that are major molluscan predators, does not occur in the deep sea, none of its member taxa will occur at deep-sea hydrothermal vents.

If large deep-sea predators are few and sulphide tolerance evolves rarely, large deep-sea predators tolerant of sulphide exposure will be very rare indeed. Groups such as turrid gastropods, ammotheid pycnogonids, galatheid crabs and zoarcid fishes are unusual in being represented at most vent systems around the world (Table 1) and at other sulphide-rich habitats such as cold seeps and whale falls (Sibuet & Olu, 1998). Resolution of phylogenetic relationships within these groups would determine whether the species that enter sulphide-rich habitats form monophyletic clades that have uniquely evolved sulphide tolerance. If so, the distributions of related species might help reconstruct relationships among the fauna of these high sulphide habitats. If not, that is, if sulphide tolerance has evolved repeatedly in each group, the distribution of sulphide-tolerant species would offer minimal insight into the history of faunal exchanges among sulphide-rich areas.

The substrate characteristic of most vents may also affect what opportunistic predators are present. The sediment-free surface of the near zero-age basalt at most mid-ocean ridges contrasts sharply with the hemipelagic sediment that covers the surrounding sea floor and may further reduce the pool of predatory taxa that approach most vent habitats. The increased abundance of taxa such as spider crabs, *Macroregonia macrochira* Sakai, 1978 near NEP hydrothermal vents may relate to the species' apparent avoidance of soft substrate (Tunnicliffe & Jensen, 1987). Substrate preferences may also contribute to age- or stage-specific appearances of other taxa near vents. Octopuses of the genus *Graneledon*e are typically found on soft substrates, although late in the life cycle, females move to hard substrate on which to attach and brood their eggs (Voight & Grehan, 2000). The chemical cues that scavenging fishes rely upon to locate food may be more readily detected at topographic highs that characterize ridges.

Although substrate may influence some species, the contrast between the many individual opportunistic predators that appear to scavenge among tube worms at vents where fluid flow has declined or ceased (R. W. Embley, pers. comm.; pers. obs.) and the few that are seen peripheral to active vents supports the hypothesis that sulphide-rich fluids deter opportunistic predators (McLean, 1981; Cohen & Haedrich, 1983; Turner, 1985).

If vent-endemic predators are few and opportunistic predators avoid sulphide-rich fluids, animals that occur in sulphide-rich vent fluids are predicted to be comparatively safe from predation. Specimens of tube worms of *Ridgeia piscesae* Jones, 1985 at NEP vents may be used to test this prediction. The morphology of the tubes of *R. piscesae* appears to vary with sulphide availability (Southward et al., 1995), as it does in tube worms of *Riftia* and *Tevnia* (D. Jollivet, pers. comm.). Worms that occur in warmer water with higher sulphide concentrations tend to have flexible, transparent or translucent-whitish tubes and few (1-2) terminal saucers; worms in cooler water, likely with low sulphide concentrations, have brittle, brown or transparent tubes that are capped with more (up to 11) saucers (Tunnicliffe et al., 1990; Southward et al., 1995). The saucers top the obturaculum which must be extended from the tube to allow the branchial filaments to exchange gases. If sulphide-rich fluids deter predation, flexible tube worms will show less evidence of predation than do brittle tube worms.

Tunnicliffe et al. (1990) report the incidence of predator-linked damage on the obturaculum, branchial filaments and vestimentum of flexible and brittle specimens of *Ridgeia,* which were then considered to represent distinct species, from two vent fields on Juan de Fuca Ridge. Of 74 flexible (high sulphide) tube worms collected from Axial Volcano, 73 showed predator-linked damage; only three of 30 brittle (low sulphide) tube worms from Endeavour Segment showed comparable damage (Tunnicliffe et al., 1990). This significant difference (G-test; $G = 90.85$; $df = 3$; $p<0.005$) refutes the prediction that animals living in higher sulphide concentrations face reduced predation. The three types of damage flexible tube worms show may relate to the actions of three different types of predators. Time lapse cameras document vent-endemic polynoid polychaetes and two opportunistic predators, macrourid fishes and a majid crab, among tube worm clusters (Tunnicliffe et al., 1990). Additional studies that contrast the damage shown by tube worms collected from habitats with different sulphide concentrations may provide additional insight into whether and how predation rates are affected by sulphide concentrations.

Relic Taxa At Hydrothermal Vents

Fossil evidence of members of barnacle and gastropod taxa indicate that they were widely distributed in shallow water habitats during the Paleozoic and Mesozoic. They are now known only from deep-sea hydrothermal vents. These relic taxa are suggested to be restricted to vents because global extinction events have not affected vent habitats and, in contrast to other marine habitats, predation intensity at vents has not escalated over time (Newman, 1979; 1985; McLean, 1981; 1985; Turner, 1985; Newman & Hessler, 1989; Newman & Yamaguchi, 1995).

An alternate to this hypothesis is based on geological evidence that the world's deep oceans have experienced repeated episodes of anoxia that resulted in the extinction of deep-sea fauna (Jacobs & Lindberg, 1998 and references therein; Harries & Little, 1999; Racki, 1999). Ancestors of modern vent taxa may have survived these anoxic events at the boundary layer between the anoxic bottom water and the oxygenated surface waters. The marginally oxygenated boundary layer may have been the deepest viable habitat for animals. To survive here, animals had to have evolved physiological tolerance of low oxygen, and perhaps high sulphide conditions. As anoxia lessened, these animals may have moved deeper, potentially following the boundary layer, as they may have had irreversible adaptation to low oxygen conditions. Some taxa may have colonized and diversified at low-oxygen hydrothermal vents that were comparable in oxygen concentration to the boundary layer. The geological data that document the history of deep-sea anoxia indicate that to have survived these extinctions at other than the shallowest depths, where oxygen was continuously available due to exchange with the atmosphere, taxa must have adapted to low-oxygen conditions.

To argue that predation pressure has not increased over geological time at vents, as it has in other marine habitats, requires that one overlook the phylogenetic relationships of several vent-restricted predators. Vent fishes (Cohen et al., 1990) and bythograeid crabs (Williams, pers. comm. cited by Guinot, 1989) are considered to be members of derived rather than basal clades, although their status is yet to be tested with phylogenetic analysis. If vent-specialized predators are members of relatively derived clades, one would expect that they would exert predation pressure comparable to that of non-vent members of the clade. In addition, the presence of opportunistic predators at vents, especially at MAR and NEP, indicates that at least locally, predation at vents is comparable to that in other deep-sea habitats. If vents are ephemeral habitats in which the strongest selective pressures stem from habitat transience rather than from predation, the presence of relic taxa at vents suggests that these taxa have successfully specialized to exploit vent habitats and the suite of selective pressures they present which differ dramatically from the stability of most deep-sea habitats.

The Prey of Vent Predators

The prey taken by most, if not all, vent predators remains very poorly known. Even gut content analysis, seemingly among the most reliable means to identify what an animal has eaten, may provide erroneous data. The radula of a gastropod, *Neomphalus fretterae* McLean, 1981 found in the gut of a turrid gastropod led Warén & Bouchet (1989) to conclude that these were prey and predator. Fisher et al. (1994), however, rejected this conclusion based on isotope studies and observations. They suggested that the turrid had preyed on the neomphalid after the animals were collected because at EPR vents, turrids occur in different microhabitats than do neomphalids. One safe conclusion seems to be that vent predators are able to take diverse prey.

Even among large predators, the prey taken is known only for a very few taxa, and is usually based on a very limited number of individuals. An octopus of *Graneledone boreopacifica* Nesis, 1982 was found to prey on snails and polychaetes (Voight, in press), as were zoarcid fishes of *Thermarces cerberus* Rosenblatt & Cohen, 1986 (Rosenblatt & Cohen, 1986) and majid crabs of *Macroregonia macrochira,* the latter also take tube worms (Tunnicliffe & Jensen, 1987). Polychaetes also fall prey to bythograeid crabs of *Cyanagraea praedator* de Saint-Laurent, 1984 (Desbruyères et al., 1985; Warén & Bouchet, 1989; Geistdoefer & Seuront, 1995). Predatory polychaetes, including species of hesionid, phyllodocid and eunicid polychaetes, likely take small invertebrates (Fauchald & Jumars, 1979; Desbruyères & Segonzac 1997). Fishes take shrimps and mussels at MAR vents (Geistdoerfer, 1991; 1994; Saldanha, 1994; Marques & Porteiro, 1998). Crabs of *Segonzacia mesatlantica* Williams, 1980 also take shrimps and small invertebrates; those of *Chaceon affinis* Milne Edwards & Bouvier, 1984 take mussels (A. Colaço, unpubl. ms.).

Possibly the most complete study of a vent predator is the analysis of the stomach contents of 17 crabs of *Bythograea thermydron* Williams, 1980 from 13° N, reported by Jollivet (1993). The prey taken appeared to vary with habitat. Limpets and *Paralvinella* spp. were most common in stomachs of crabs from diffuse vents. Amphipods and *Alvinella* spp. were the most abundant prey types in the stomachs of crabs collected from a black smoker and individuals of *Alvinella* spp. were most abundant in those of crabs taken near a white smoker (Jollivet, 1993). Vestimentiferans, leptostracan crustaceans, copepods, other gastropods, polynoid polychaetes, other decapods, including members of *Bythograea* itself, and bacterial mats each contributed modest amounts to the crabs' stomach contents. These data suggest the crabs do not specialize on prey but forage on small animals as available among vent sites (Jollivet, 1993).

The Perceived Vulnerability of Vent Taxa

Hydrothermal vent taxa have been said to be so vulnerable to predation that they survive only because the vent habitat shields them from predation pressure that has increased over geological time (Newman, 1979; Cohen & Haedrich, 1983; McLean, 1981; 1985; Turner, 1985; Newman & Yamaguchi, 1995). In addition to the toxic vent emissions, depth and distance have been cited as isolating the mid-ocean ridge vent fauna from predators that tolerate chemically similar cold seep environments on the continental shelf (Carney, 1994). Because we know little of how deep-sea predators detect and secure potential prey, and of whether deep-sea taxa use physical, behavioral or chemical defenses, it is difficult to assess their vulnerability to predation.

Gastropods

The shell is first and best defense against predators for most mollusks. The exceptionally thin shells of vent limpets which in the vent environment can dissolve from live molluscs (Tunnicliffe & Fontaine, 1987; Warén & Bouchet, 1993) appear to leave the animals highly vulnerable to predators. Although an exceptionally thick periostracum may mediate shell dissolution in some taxa (Warén & Bouchet, 1993), whether a thicker shell would offer significant benefit has been questioned. Thicker shells would not protect vent gastropods from predators such as deep-sea fishes that commonly swallow snails whole (Warén & Bouchet, 1989), but they may help defend against shell-crushing predators. Shell fragments have been found in the gut of spider crabs of *Macroregonia macrochira* (Tunnicliffe & Jensen, 1987) and of the octopus, *Graneledone boreopacifica* (Voight, in press) collected from NEP vents. Shell fragments, as well as whole animals, have also been removed from the gut of bythograeid crabs (Jollivet, 1993). Although such predators may increase selection for thicker gastropod shells, secreting additional calcium carbonate at these depths may impose such a high physiological cost that secretion of only a thin shell maximizes gastropod fitness. In addition, if vent habitats are typical of transient habitats, an individual's risk of mortality due to habitat disturbance would be much greater than that due to predation. Individuals would then be under greater selection for fast growth and early reproduction than for increased anti-predator defenses.

The incidence of repair scars on gastropod shells has been used to estimate the frequency of attempted predation and predator effectiveness (e.g. Vermeij et al., 1981), with the assumptions that the shell is damaged in failed predation attempts and that at least some snails survive predatory encounters to repair their shells. If many gastropods in a population show shell repair, the shells have been concluded to resist predation. If few members of a population show repaired shell damage, they are concluded to either be wholly resistant to predation or to be so susceptible that few individuals survive encounters with predators.

In their taxonomic treatment of vent gastropods, Waren & Bouchet (1989) note that few of the vent gastropods examined showed shell repair scars. Voight & Sigwart (unpubl.), however, report that limpets of *Lepetodrilus fucensis* McLean, 1988 collected from a NEP vent with abundant potential predators, such as zoarcid fish and galatheid crabs, are significantly more likely to have repair scars on their shells than are conspecifics collected from vents with few potential predators. Vent limpets apparently survive shell damage inflicted during predatory encounters and the frequency of shell repair may accurately reflect their incidence of predatory encounter rates.

The apparent inability of vent limpets to clamp tightly onto substrates has also been suggested to increase their vulnerability (Turner, 1985). Although the shells of vent limpets are recognized as fragile, a limpet with its foot exposed is considered to be more vulnerable to potential predators than is one covered by a fragile shell with its foot attached to a substrate. As support for this hypothesis, Turner (1985) cited videotapes showing that vent limpets move with their shells raised "well above" the substrate and that, in contrast to limpets collected on sunken wood, most vent limpets recovered on-board ship have dropped from the substrate on which they were collected. In reference to the latter observation, two alternates have to be considered. First, a gastropod may avoid predation by dropping from its substrate. The potential predator would then be forced to choose between relocating an individual gastropod that has functionally disappeared and seeking other prey that may be more sedentary, and therefore predictable. The curved shells of vent limpets, as in *L. fucensis,* would help the limpet right itself after displacement. Second, collection and retrieval expose limpets on both wood and vent substrates to changes in hydrostatic pressure. Vent limpets, however, are exposed to additional physiological stresses associated with changes in oxygen concentrations and temperatures. Anatomical comparisons of the foot of vent limpets and shallow-water limpets do not indicate that the taxa differ in their ability to adhere to substrate (R. Guralnick, pers. comm.).

Bivalves

Because vesicomyid clams can access sulphide-rich fluid in the sediment with their extensible foot (Childress & Fisher, 1992), they need not be immersed in sulphide-rich water as do tube worms. Vent mussels of *Bathymodiolus* can tolerate extended periods without access to water-borne sulphide by filter-feeding (Childress & Fisher, 1992). Although vent bivalves are not necessarily bathed in sulphide-rich fluids, the thick shells of living vesicomyid specimens collected from NEP vents can be reduced through apparent dissolution to thin veneers (Juniper et al., 1992; pers. obs.) as they are at North Pacific cold seeps (Barry & Kochevar, 1999). Despite the apparent vulnerability of vent clams, predation on clams appears to be minor.

Photographs of Galapagos Rift clam beds documented few "obviously dead" clam shells other than those that could be attributed to fluid flow reductions; predation was concluded to be a trivial source of clam mortality (Hessler et al., 1985). Vesicomyids reportedly do not retract their mantle or siphons when crabs or shrimps touch their mantles (Berg & Turner, 1980), suggesting that these clams have no need to withdraw from potential predators. Although crabs of *Bythograea,* snails of *Phymorhynchus* and various fishes readily feed on clams and mussels after they are damaged by submersibles (Suess et al., 1985; Fisher et al., 1994), intact bivalves are not reported to be exploited. Guinot & Segonzac's (1997) report that brachyuran crabs of *Bythograea* on the southern EPR were eating a "still living" mussel of *Bathymodiolus* referred to an individual that had been damaged prior to the crab attack (D. Jollivet, pers. comm.). Octopuses, reported to frequent chemosynthetic clam beds at Galapagos Rift vents (Corliss & Ballard, 1977; Berg & Turner, 1980), NEP vents (Juniper et al., 1992) and off-vent warm springs (Mottl et al., 1998), may be among the few deep-sea predators able to prey on large clams; they are not yet documented to do so. The apparent invincibility of adult clams to most deep-sea predators cannot be argued to be vent-related, unless the vent-derived sulphur that accrues in the blood and on their gills (Vetter, 1985) deters predators. Observations that predators feed on clams damaged by submersibles, however, makes this seem unlikely.

In contrast to the seemingly predator-free vesicomyids, an extraordinarily high proportion of vent mussels (76% of 139 specimens) from Galapagos Rift carry scars inferred to relate to predatory crab attacks (Rhoads et al., 1982). Mussels under 2 cm in length were thought to suffer the greatest mortality; those between 2 and 7 cm long were scarred, but had survived apparent predatory attacks (Rhoads et al., 1982). This very high incidence of shell damage requires closer examination. Van Dover et al. (1988) noted that shallow-water mussel shells exposed to heavy metals show shell damage (Sunila & Lindström, 1985) that appears to be very similar to that Rhoads et al. (1982) illustrate in vent mussels. The high concentrations of metals in vent emissions suggest that vent mussel shells may be damaged by factors other than predation.

The locally heavy recruitment of mussels at some vents, particularly on the MAR (Van Dover et al., 1996; Comtet & Desbruyères, 1998), may provide a feast for predators able to crush post larvae or very young and delicate mussels. If recruitment is periodic and different-sized mussels are spatially segregated, as collections from Lucky Strike on MAR in 1993 (Van Dover et al., 1996) and in 1994 (Comtet & Desbruyères, 1998) indicate, one would expect that collections of larger mussels would show cohorts as clearly as do collections of small mussels. Among larger mussels, however, cohorts can be recognized, but not readily. Predators could help blur the cohorts' resolution by feeding heavily on very small (< 5 mm) mussels, or within-cohort growth variation could equalize the size distribution. Because of the very small sizes involved, predation is not likely to be directly observed.

Barnacles

Vent barnacles are argued to represent some of the most ancient groups extant at hydrothermal vents (Newman, 1985; 1989; Newman & Yamaguchi, 1995). Although on average, pedunculate barnacles are more common in the deep sea than are sessile barnacles, at vents the reverse is true. The under-representation of pedunculate barnacles at vents has been suggested to relate to their vulnerability to crabs, which are comparatively common at vents (Newman & Yamaguchi, 1995). The report of a brachyuran crab of *Bythograea* feeding on a pedunculate barnacle of *Neolepas* at Southern EPR vents (Guinot & Segonzac, 1997) supports the hypothesis.

Although predation pressure is cited as a possible factor contributing to the sudden development shift from pedunculate to sessile in members of *Neoverruca brachylepadoformis* Newman, 1989 at about 2 mm in length (Newman, 1989), predation may not be the sole contributor to the distributional pattern. The availability of unsedimented near zero-age basalt near spreading centers may affect their abundance as do the dispersal abilities of the taxa.

Tube Worms

Tube worms appear to be vulnerable to predators due to their apparent lack of sensory organs, their large biomass, sessile habit and feeding mode in which the obturaculum with its feathery branchial filaments is extended into the water column. The worms, however, have muscles and a giant axon (Jones & Gardiner, 1989) and can draw the obturaculum very rapidly into the tube. In addition, saucers on the obturaculum tip of NEP tube worms of *Ridgeia* can form an "operculum", effectively closing the tube, perhaps to defend the worm against predation (Tunnicliffe et al., 1990). Among these worms, the number of saucers varies with the environment (Jones, 1985; Southward et al., 1995). Brittle tube worms from more stable areas with lower sulphide concentrations have more saucers than do flexible tube worms from areas with higher sulphides that may offer high growth potentials, but that carry an increased risk of mortality due to habitat instability. The increased number of saucers on tube worms from more stable habitats may offer the animals a better defense against predators (Tunnicliffe et al., 1990) or, as Southward et al. (1995) suggested, indicate the tube worms' age or past level of predation.

Isotope Analyses and Inferred Trophic Interactions

Because predation is rarely observed, indirect methods that can help reveal trophic interactions are being sought. Chief among these for hydrothermal vent systems is the analysis of $\delta^{13}C$ and $\delta^{15}N$ values (Van Dover & Fry, 1994; Fisher et al., 1994; Fisher, 1995). Because chemosynthesis produces $\delta^{13}C$ and $\delta^{15}N$ signals that are distinct from those produced by photosynthesis, isotope analysis helped confirm the role of chemosynthesis in energy production at vents and seeps (e. g., Rau, 1981; Rau et al., 1990). If isotope differences were perpetuated in a systematic way through the vent ecosystem, they could help reveal trophic relationships. Although isotopes can distinguish among different diets that are each based entirely on one source with a distinct isotope signal, such as marine or terrestrial or freshwater (DeNiro & Epstein, 1978; Schoeninger & DeNiro, 1984), diets that combine sources with different isotope signatures can be very difficult to interpret (Schoeninger & DeNiro, 1984; Day, 1996). This is the situation at hydrothermal vents where the $\delta^{13}C$ signatures of vent clams (-38 to -31.4‰) and vent tube worms (-24.4 to -8.8‰) partially overlap and even bracket the signatures of non-vent deep-sea fauna (-25 to -17‰) (Childress & Fisher, 1992; Fisher, 1995).

To compensate, $\delta^{13}C$ analyses are increasingly being augmented by $\delta^{15}N$ analyses (Van Dover & Fry, 1989; 1994; Fisher et al., 1994). $\delta^{15}N$ values of animals in marine systems range from near 0 to +15 ‰, with animals from greater depths tending toward higher values due to the high degree of recycling of organic nitrogen (Owens, 1987). Non-vent deep-sea animals have $\delta^{15}N$ values of from 11 to 18‰ (Fisher et al., 1994; Van Dover & Fry, 1989; 1994); those at vents tend to have $\delta^{15}N$ values below 11‰ (Fisher, 1995). Carbon isotope values tend to match the food source within 1‰, but $\delta^{15}N$ values tend to increase by 3.4‰ with each subsequent trophic level (DeNiro & Epstein, 1981; Rau, 1981; Minagawa & Wada, 1984; Schoeninger & DeNiro, 1984; Sealy et al., 1987). Therefore if the isotope signature of all dietary sources were known, analyses that combine $\delta^{15}N$ and $\delta^{13}C$ values would help identify subsequent trophic levels in the vent food web.

$\delta^{13}C$ and $\delta^{15}N$ analyses have been applied to EPR vent crabs of *Bythograea thermydron*. Known only from vents, members of this species have $\delta^{13}C$ values identical to those of non-vent animals that use carbon that was initially fixed in surface waters (Childress & Fisher, 1992). Combining their mean "normal" $\delta^{13}C$ (-17.0‰; n = 10) with their relatively heavy $\delta^{15}N$ (8.8‰; n = 7) values indicates that these crabs are top predators at vents, a view that in situ observations and morphology support (Fisher et al., 1994). The importance of such observations and anatomical knowledge for understanding isotope values becomes clear when one compares the isotope signature of *B. thermydron* to that of the vent limpet, *Neomphalus fretterae*. The isotope signatures of these nearly sessile, filter-feeding (McLean, 1981) limpets ($\delta^{13}C$ = -18.2‰; $\delta^{15}N$ = 8.6 ‰; n = 6), despite their similarity to those of *B. thermydron*, are argued to reveal that the limpets feed on an unknown particulate source with a characteristic isotope signal (Fisher et al., 1994).

The hypothesized existence of unknown food resources with characteristic isotope signatures appears to be a liability for our greater understanding of hydrothermal vent food webs. Based on isotope studies, Van Dover & Fry (1994) argued that most consumers at vents feed on free-living bacteria rather than on large invertebrates with endosymbiotic bacteria. The wide range of isotope values (-41.6 to -16.8‰ $\delta^{13}C$; -9.6 to 1.6‰ $\delta^{15}N$) of three bacterial mats from Gorda Ridge and the isotope signatures of the consumers lead them to hypothesize the existence and trophic significance of other, isotopically distinct bacteria at vents. Conclusions that most consumers feed on unknown bacteria that may be fueled by any of a diversity of metabolic pathways (Van Dover & Fry, 1994), or that filter feed on unknown particulate matter with a distinct isotope value (Fisher at al., 1994), illustrate the difficulties that remain to be overcome in using isotope analyses to understand food webs at hydrothermal vents. Isotope analyses can be used to support hypothesized dietary sources, when the source and its isotopic signature are well documented.

Further complicating the problem are differences among and within ridge systems (Van Dover & Fry, 1994; Southward et al., 1994) which complicate making extrapolations among vent sites. In addition, isotopes may differ among microhabitats within a vent field, as seen in the -8.7 to +6.8‰ range in $\delta^{15}N$ values among vent mussels of *Bathymodiolus thermophilus* Kenk & Wilson, 1985 (Fisher et al., 1988; 1994). Although isotope comparisons can help confirm the existence of a close trophic relationship between members of two taxa, e. g. the mussel *Bathymodiolus thermophilus* and its commensal *Branchipolynoe symmytilida* Pettibone, 1984 (Fisher et al. 1994), because as noted above, many vent predators forage on diverse vent residents, with the taxonomic composition of their prey varying with microhabitat (Jollivet, 1993), isotope studies may be less helpful in resolving these trophic relationships. $\delta^{15}N$ values, which exhibit considerable variation within a species, genus and among animals that function at the same trophic level (DeNiro & Epstein, 1981; Schoeninger & DeNiro, 1984), may show more variation at vents due to the release of elevated inorganic nitrogen substrates and bacterial fixation of organic nitrogen (Van Dover & Fry, 1994).

The promise of breakthroughs exists. A comprehensive isotope study of the biota at MAR vents illustrates the potential of the technique (A. Colaço, unpub. ms.). In addition, the use of lipids and $\delta^{13}C$ data in MAR shrimps has contributed not only to our understanding of the trophic relations of each species, but also to the mechanisms allowing their co-existence (Pond et al., 1997). Technological improvements illustrated in this work may offer new insights into trophic interactions at vents.

Conclusions

Predators and predation are normal components of every known biological system at deep-sea hydrothermal vents. The magnitude of predation pressure, however, may be small compared to selective forces that result from physical disturbances in these dynamic habitats. The frequent habitat disturbances, the rapid growth documented among vent residents and the few vent-specialized predators known are all consistent with considering deep-sea hydrothermal vents to be transient habitats, as defined by Sih (1987). In this view, rather than being anomalous, the few predators endemic to vent habitats are logical consequences of the selective regime that these dynamic habitats impose on their residents. Hydrothermal vent habitats may be comparable to sandbars in flood-prone riparian habitats which can be inundated and even removed by physical forces.

The few seemingly normal deep-sea predators that appear in vent habitats as opportunists may be attributed to the small pool of potential predators in the deep sea and to the comparative rarity of sulphide tolerance among members of that pool. At this point, we know little of how opportunistic predators forage on chemosynthetic-produced biomass at vents. This knowledge might allow us a better understanding of not only predation at vents, but how predators locate and identify potential prey.

Further research concerning predation in the deep sea as a whole and at vent trophic systems specifically is needed. Analysis of gut contents can establish prey taken, but without supplementary data can produce misleading data, as may analyses of stable isotopes. The best course of research may be to combine methods; different approaches that produce congruent results would likely be the most reliable.

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