

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

# Oceanography

#### CITATION

Govenar, B. 2012. Energy transfer through food webs at hydrothermal vents: Linking the lithosphere to the biosphere. *Oceanography* 25(1):246–255, <http://dx.doi.org/10.5670/oceanog.2012.23>.

#### DOI

<http://dx.doi.org/10.5670/oceanog.2012.23>

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# Energy Transfer Through Food Webs at Hydrothermal Vents

Linking the Lithosphere to the Biosphere

BY BREEA GOVENAR

Vent community associated with the mussel *Bathymodiolus thermophilus* and the tubeworm *Riftia pachyptila* at the East Pacific Rise. Photo courtesy of C.R. Fisher (Pennsylvania State University), © Woods Hole Oceanographic Institution



**ABSTRACT.** Tectonic and volcanic processes that drive hydrothermal fluid flow and influence its chemistry also regulate the transfer of energy to hydrothermal vent ecosystems. Chemoautotrophic bacteria use the chemical energy generated by mixing the reduced chemicals in hydrothermal fluids with deep-ocean ambient seawater to fix inorganic carbon and produce biomass. These and other microbes, or their products, are then consumed by other organisms, which are subsequently consumed by other organisms. The connections between nutritional sources and consumers form a complex food web that links the lithosphere to the biosphere at hydrothermal vents. This article traces the path of energy transfer from geochemical to biological processes in hydrothermal vent food webs and explores the implications of changes in hydrothermal fluid flux on food web structure. One of the goals of studying food webs at hydrothermal vents is to develop better predictions of community resilience to disturbance and the relationships between community structure and ecosystem function, including productivity and nutrient cycling. In addition, improved understanding of energy transfer through hydrothermal vent food webs is critical for constructing models of chemical fluxes from chemosynthetic-based ecosystems to the open ocean.

## INTRODUCTION

Food webs represent the flow of energy in ecosystems through a network of nutritional relationships. Due to the relative inefficiency of energy transfer from food source to consumer, food webs are generally thought to be limited to three to four trophic levels (Pimm, 2002, but see Banasek-Richter et al., 2009, for exceptions). Unlike food chains, which depict a single food source for each organism, food webs often include multiple food sources for each consumer that are interconnected by many different trophic links. Based on the strength of species interactions, small food webs can be structured by either top-down factors that result from consumer pressure, by bottom-up factors related to resource availability, or a combination of both (Menge and Sutherland, 1987). Important ecological processes in food webs that contribute to the maintenance of species diversity and overall community stability include: trophic cascades, in which predators suppress the abundance

of prey and increase the abundance of the next lower trophic level; intraguild predation, in which predators consume one another; and apparent competition, in which predation on one species gives a competitive advantage to other species. Indirect effects and nontrophic interactions, such as habitat provision by foundation species or facilitation by conspecifics, can further influence food web dynamics (the interactions among trophic levels that affect energy transfer through the ecosystem) and community structure. The network of interactions in food webs ultimately affects the transfer of energy from resource to consumer and can determine the productivity and rates of nutrient cycling in an ecosystem.

Historically, the open-ocean food web was viewed as a linear chain from phytoplankton to zooplankton, to larger zooplankton, and eventually to fish and mammals. Over the past 30 years, however, there have been significant advances in the recognition of a microbial loop, in which viruses, bacteria,

archaea, and protists alter the transfer of energy through biogeochemical processes, as well as food web dynamics (Pomeroy et al., 2007). It is now recognized that rather than greater trophic connectance (the proportion of trophic links to the total of all possible species interactions), weak trophic links among many interacting species may determine community stability or resilience to disturbance in large food webs (Banasek-Richter et al., 2009).

The discovery of high-biomass benthic communities at deep-sea hydrothermal vents along the Galápagos Rift in 1977 was completely unexpected, given what was known about food webs and energy transfer at the time. At first, scientists hypothesized that the warm water released from the vents was causing a circulation cell to deliver higher concentrations of photosynthetically derived carbon to the benthic communities (Lonsdale, 1977). A combination of histological, enzymatic, and stable isotope analyses revealed that one of the most unusual organisms, *Riftia pachyptila*, harbored sulfur-oxidizing chemoautotrophic bacteria as internal symbionts, which provided the bulk of the animal's nutrition (see Childress and Fisher, 1992, for review). Later, stable isotopes showed that heterotrophic fauna generally do not consume these visually dominant foundation species (Fisher et al., 1994), which can comprise more than 90% of the community biomass (Govenar et al., 2005). Instead, the majority of vent-endemic fauna appear to feed on free-living microbes

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or other animals with microbial diets (e.g., Phleger et al., 2005a,b). To date, surprisingly little is known about which microbes are consumed at the base of the food web, the interactions within and among trophic levels, how food web structure contributes to the resilience of vent communities, or how food web dynamics affects ecosystem function at hydrothermal vents.

As other hydrothermal vents are found along the global mid-ocean ridge system and analogous deep-sea habitats are discovered at active and inactive volcanic seamounts, hydrocarbon seeps, and whale falls, examples of ecosystems based on chemosynthetic primary production continue to grow. In addition, chemoautotrophic bacteria have been shown to have rates of primary production that rival rates of photosynthesis in some marine habitats, including the Cariaco Basin (Taylor et al., 2001), the Black Sea (Yilmaz et al., 2006), and the Baltic Sea (Jost et al., 2008). Active areas of research at hydrothermal vents are focused on the phylogenetic and physiological diversity of chemoautotrophic bacteria and archaea (e.g., Takai et al., 2006), the relative importance of different carbon-fixation pathways in primary production (e.g., Hugler and Sievert, 2011), and the variation in diets among consumers. Furthermore, there has been increasing interest in the resilience of chemosynthesis-based ecosystems to disruption by seabed mining (e.g., Van Dover, 2011), as well as the role of hydrothermal vents and other chemosynthesis-based ecosystems in chemical fluxes to the open ocean (e.g., Tunnicliffe et al., 2003; Bennett et al., 2011).

The literature that characterizes trophic relationships in hydrothermal vent communities has rapidly expanded

in the past two decades, but this article specifically focuses on describing the transfer of energy from the lithosphere to the biosphere and developing a generalized food web model that integrates patterns from vent communities across the global mid-ocean ridge system. For this purpose, details about the food web structure are not exhaustive and examples are more heavily weighed to hydrothermal vents at the East Pacific Rise, the Juan de Fuca Ridge, and, to a lesser extent, the Mid-Atlantic Ridge, where there has been the greatest effort to identify trophic relationships. Far more information is available in extensive reviews than could be presented here, regarding the formation of hydrothermal fluids (e.g., Kelley et al., 2002), the phylogenetic and metabolic diversity of microbes (Takai et al., 2006), carbon fixation pathways (Hugler and Sievert, 2011), and symbioses (Dubilier et al., 2008). This article aims to employ the transfer of energy in food webs as a framework for understanding the resilience of communities to disturbance and the relationship between community structure and ecosystem function at hydrothermal vents.

## ENERGY TRANSFER

The flow of energy in hydrothermal vent ecosystems begins with large-scale volcanic and tectonic processes that form hydrothermal fluids 2–8 km subseafloor (Kelley et al., 2002, for review). First, seawater is entrained into the deformed crust of oceanic spreading centers and then reacts with the surrounding hot rocks to become chemically altered. The temperature and chemical composition of the surrounding rocks determine the chemical composition of the fluids, as well as how much water has

previously passed through the same network of cracks (Kelley et al., 2002). In volcanically active mid-ocean ridges, hydrothermal fluids can also boil and separate into brine and vapor phases that further influence the spatial and temporal variation in the fluid composition. These high-temperature fluids are then released from weak or thin sections of the seafloor. Upon contact with the cold ambient seawater, dissolved metals precipitate and form metal-sulfide deposits or chimney-like structures that continue to focus the flow and modify the composition of the hydrothermal fluids. Some fluids are also carried upward into plumes that release mineral particulates back to the seafloor or transport these particulates across long distances. In addition, subsurface dilution results in low-temperature hydrothermal fluids that escape from cracks in the basalt seafloor or sulfide chimneys to form diffuse-flow vents (see Bemis et al., 2012, in this issue). Low-temperature (< 100°C) diffuse flow can be coupled with the plumbing of neighboring high-temperature chimneys, but additional water-rock reactions and microbial activity can also significantly alter the composition of the diluted hydrothermal fluids (Von Damm and Lilley, 2004).

Chemoautotrophic bacteria and archaea use chemical energy, derived from mixing of reduced chemicals in hydrothermal fluids with oxygenated seawater, to convert inorganic carbon into simple sugars. This process, called chemosynthesis, is analogous to photosynthesis. Chemosynthetic primary producers can use a variety of electron donors (e.g., H<sub>2</sub>S, H<sub>2</sub>, metals) and electron acceptors (e.g., O<sub>2</sub>, NO<sub>3</sub><sup>-</sup>) as energy sources and up to six different pathways for carbon fixation (see Hugler and

Sievert, 2011, for review). In another form of chemosynthetic primary production called methanotrophy, methane can be oxidized as an energy source and used as a carbon source.

Other chemical reactions and biological processes additionally contribute to the base of the food web. Chemosynthetic organics (dissolved organic carbon, DOC, and particulate organic matter, POM) can be formed through chemosynthetic primary production, by the degradation of biomass of either chemosynthetic or photosynthetic origin, or by abiotic chemical processes (McCollom and Seewald, 2007; Shock and Canovas, 2010). Heterotrophic bacteria and archaea that use DOC can further add to the free-living microbial biomass. POM derived from the subsurface or above the seafloor can also be a food source for protists (Sauvadet et al., 2010) and some small benthic invertebrates (Limén et al., 2007), as well as zooplankton ~ 20 m above the seafloor (Skebo et al., 2006). The result of these diverse chemical reactions and biological processes at hydrothermal vents is a productive ecosystem that provides abundant food sources to support high biomass in the deep sea and rapid turnover in carbon and other nutrient cycles.

Although estimates of chemosynthetic primary production are as high as  $10^{13}$  g biomass per year (McCollom and Shock, 1997), the biomass transferred into hydrothermal vent food webs is far less. In part, the decrease is likely due to the low efficiency in energy transfer between trophic levels, as observed in other food webs (Pimm, 2002). In addition, consumers occupy a smaller range of habitats than primary producers, which would effectively reduce the amount of

energy available to be transferred from the chemosynthetic primary producers to consumers. Although chemosynthetic primary producers are found in the subsurface biosphere, on and near the seafloor, in the vent effluent, and in the hydrothermal plume, metazoan consumers are more or less confined to the seafloor and overlying water column

that mixes with the rising hydrothermal fluids and to temperatures less than 100°C (Figure 1).

## FOOD WEB STRUCTURE

Hydrothermal vent food webs are generally organized into five groups: (1) chemosynthetic primary producers and other microbes at the base of

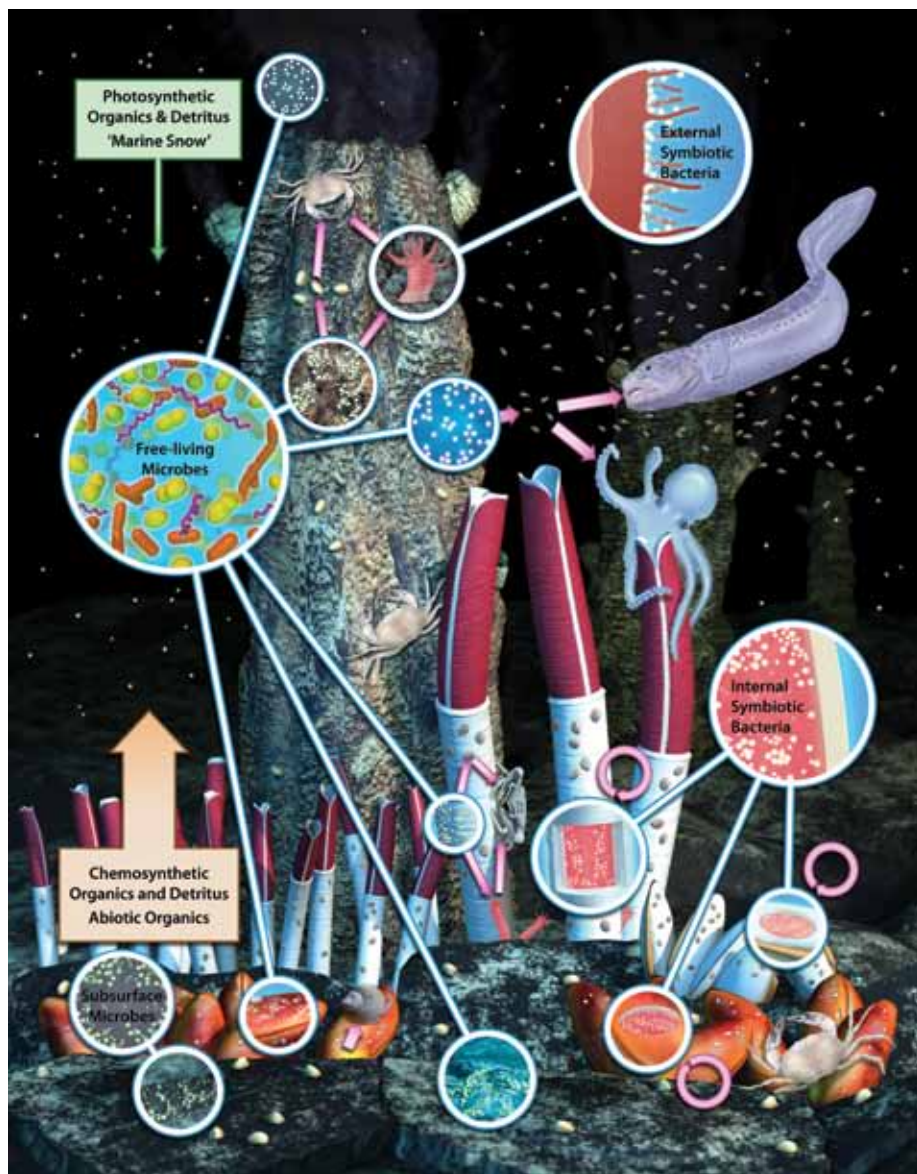


Figure 1. Chemosynthetic primary producers are found in the subsurface biosphere as free-living microbes on the surfaces of rocks and animals, as internal and external symbionts of invertebrates, and in the vent effluent (highlighted in white circles). Trophic relationships are indicated with pink arrows from food source to consumer. Additional energy and biomass enter vent food webs through photosynthetic organics and detritus, chemosynthetic organics and detritus, and abiotic organics. Illustration: Thomas Moore

the food web, (2) symbiont hosts that include both invertebrates with internal symbionts and invertebrates with external symbionts, (3) primary consumers, (4) secondary consumers as either predators or scavengers, and (5) parasites (Figure 2). This simplification of vent food webs builds upon and expands earlier models proposed by Tunnicliffe (1991) and Bergquist et al. (2007). The additions and modifications are primarily to emphasize the transfer of energy and the interactions among groups, as opposed to distinctions based on feeding mode or diet. Specifically, primary consumers are used here instead of suspension-feeders and grazers (Tunnicliffe, 1991) or

bacterivores (Bergquist et al., 2007) to include all consumers of chemosynthetic primary producers, other free-living microbes, POM, or DOC derived from chemosynthetic primary production or chemical processes. Clearly, both chemosynthetic primary producers and primary consumers in vent food webs are complex groups that require much further investigation to be fully understood, much like in the microbial loop that has been elucidated for upper ocean food webs (Pomeroy et al., 2007).

The metabolic and phylogenetic diversity of chemosynthetic primary producers enables them to live in a variety of habitats, including on and near the basalt seafloor, within and on

the surface of metal-sulfide deposits or chimneys, on the surfaces of organisms, in the vent effluent, and in the hydrothermal plume (Figures 1 and 2). Some chemosynthetic primary producers are also found in interstitial spaces beneath the seafloor in a heterogeneous “subsurface” habitat, and some are found as internal and external symbionts of invertebrates (Figures 1 and 2). In contrast, the metazoan consumers that compose the more conspicuous component of the vent food web are more or less confined to the seafloor, chimneys, and vent effluent (Figure 1). Within this smaller range of habitats, many studies have identified two or more isotopically distinct microbial food sources for consumers (e.g., Van Dover and Fry, 1989), but surprisingly little is known about which chemosynthetic primary producers are consumed. In a survey of lipid profiles from different consumers at the East Pacific Rise, archaea do not appear to be an important food source (Phleger et al., 2005a,b). Additional studies are needed to identify the diets of consumers in environments where archaea are more prevalent, such as high-temperature chimneys and vents with high methane concentrations, where there could be a higher incidence of methanogens (Takai et al., 2006). Heterotrophic bacteria, abiotic organics, and photosynthetic detritus can also be important sources of organic carbon in areas of lower hydrothermal fluid flux (Tunnicliffe et al., 2003; Levesque et al., 2005; Limén et al., 2008).

Sessile invertebrates with internal symbionts (Figure 2), particularly siboglinid tubeworms and bathymodiolin mussels, tend to grow to large sizes and/or high densities, and the architecture of their physical structure can facilitate

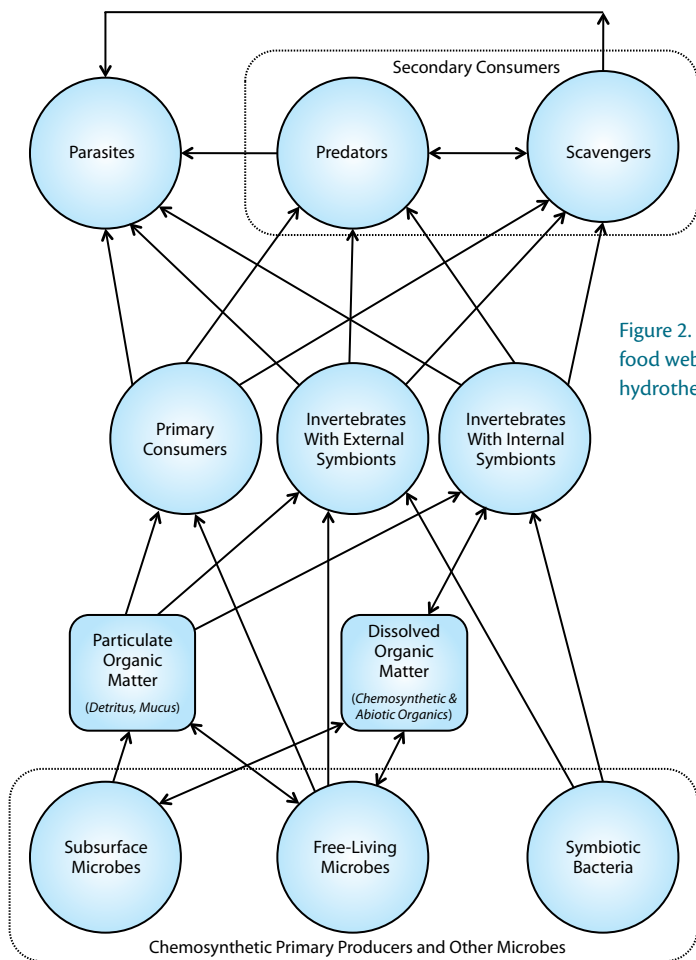


Figure 2. A generalized food web model for hydrothermal vents.



species coexistence for microbial and macrofaunal communities by providing area for colonization, increasing access to food sources, adding to habitat heterogeneity, and potentially altering the chemistry of the habitat (Bruno and Bertness, 2001; Govenar and Fisher, 2007; Govenar, 2010). While these foundation species contribute as much as 90% of the community biomass (Govenar et al., 2005; Bergquist et al., 2007), stable isotope analyses suggest that few if any animals derive their nutrition from tubeworms or mussels (Fisher et al., 1994; Bergquist et al., 2007; DeBusserolles et al., 2009). Animals that have been observed to pick at tubeworms and mussels seem to be either foraging without lethal predation or scavenging on dead or dying individuals (Figure 3). In either case, neither tubeworms nor mussels appear to be the sole food source for any of the free-living metazoan consumers in vent communities. Smaller foundation species with internal (and external) symbionts, such as the blue folliculinid ciliate at the Juan de Fuca Ridge, can also increase habitat heterogeneity. Like tubeworms and mussels, the blue ciliates may be consumed opportunistically, but are not the sole food source for any of the vent consumers in the epifaunal community (Bergquist et al., 2007; Kouris et al., 2010). Instead, habitat provision by foundation species appears to influence food web dynamics through indirect, bottom-up forces that lead to an increase in food sources for consumers (Govenar and Fisher, 2007).

It is not entirely clear how invertebrates with external symbionts (Figure 2) contribute to food webs at hydrothermal vents. Although these species, including alvinellid polychaetes, rimicarid shrimp, and some lepetodrilid gastropods,



Figure 3. A crab, *Bythograea thermydron*, feeding on a mussel, *Bathymodiolus thermophilus*, at the East Pacific Rise. Photo courtesy of R. Lutz (Rutgers University), Stephen Low Productions, and the Woods Hole Oceanographic Institution

maintain the ability to feed and could potentially consume a variety of food sources, evidence suggests that the external symbionts form the basis of their nutrition (Polz et al., 1998; Phleger et al., 2005a,b; Bates, 2007). Whether invertebrates with external symbionts function as other symbiont-containing fauna or as primary consumers requires further study.

Primary consumers at hydrothermal vents (Figure 2) include microscopic protists, meiofauna (32–1 mm), and macrofauna (> 1 mm). With the exception of the internal and external bacteria associated with the blue folliculinid ciliate (Kouris et al., 2007, 2010), little is known about the trophic ecology of protists at hydrothermal vents (Sauvadet et al., 2010). There has been, however, increasing interest in the diversity and ecology of meiofauna (e.g., Gollner et al., 2010; Vanreusel et al., 2010). With a combination of stable isotope analyses, lipid profiles, and scanning electron microscopy, Limén et al. (2007) found that the nematode *Leptolaimus* and the

copepods *Stygiopontius quadrispinosus* and *Benthoxinus spiculifer* feed on different bacterial diets, whereas another copepod *Aphotopontius forcipatus* feeds primarily on particulate organic matter (Limén et al., 2007, 2008). Macrofauna, including polychaetes, crustaceans, and gastropods, have also been observed scraping bacteria off rocks or other organisms, and the data suggest that morphologically similar species can likewise partition their food sources among different groups of bacteria and POM sources (DeBevoise et al., 1990; Levesque et al., 2003; Phleger et al., 2005a,b; De Busserolles et al., 2009).

Secondary consumers consist of both predators and scavengers (Figure 2) that include meiofaunal and macrofaunal invertebrates, as well as both megafaunal invertebrates and vertebrates. Examples of meiofaunal secondary consumers are the nematode *Paracanthochus* sp., which has a wide mouth with a large tooth and could function as either a predator or scavenger, and the ostracod *Euphilomedes climax* that seems to prey

on copepods or other small invertebrates (Limén et al., 2007). Under different environmental conditions, some of the same macrofaunal species that consume free-living bacteria may function as secondary consumers, such as the crab *Bythograea thermydron* (DeBevoise et al., 1990), paralvinellid polychaetes (Limén et al., 2008), and gastropods (recent work of the author). Based primarily on their morphology and gut contents, other polychaetes are considered predators, including *Archinome rosacea* (Ward et al., 2003) and nearly all polynoid polychaetes. Buccinid snails and decapod crustaceans are also predators, feeding primarily on polychaetes, gastropods, and other primary consumers (Voight and Sigwart, 2007; De Busserolles et al., 2009). Megafaunal predators ( $\gg 1$  mm), such as the octopus *Vulcanoctopus hydrothermalis* (Voight, 2005) and the fishes *Thermarces cerebus* and *Pachycara gymminium* (Micheli et al., 2002; Sancho et al., 2005; Voight and Sigwart, 2007), have similar diets to the macrofaunal consumers, feeding primarily on gastropods and amphipod crustaceans.

An important but often overlooked component of food webs is the role of parasites. Hydrothermal vents harbor a wide diversity of parasites, ranging from bacteria and protists to nematodes, acanthocephalans, copepods, and polychaetes (de Buron and Morand, 2002; Terlizzi et al., 2004; Britayev et al., 2007; Van Dover et al., 2007; Tunnicliffe et al., 2008), and probably many more await discovery. Of the parasitized species, the most common are molluscs, including gastropods and bivalves (Terlizzi et al., 2004; Britayev et al., 2007; Van Dover et al., 2007; Tunnicliffe et al., 2008), but parasites have also been observed in siboglinid tubeworms and crustaceans

(de Buron and Morand, 2002, and references therein). Parasites can have a range of effects on food webs, either by creating short trophic links between two species, as observed for bathymodiolin mussels and their “commensal” or kleptoparasitic polynoid polychaete (Britayev et al., 2007), or by potentially causing trophic cascades that affect multiple trophic levels through the reduction of consumers or apparent competition that gives an advantage to the unparasitized species. Although the role of parasitism in hydrothermal vent food webs is not well understood and warrants further study, the high densities in vent communities would seem to be conducive to rapid transmission of parasites that could lead to extensive mortality and affect food web dynamics.

#### IMPLICATIONS FOR FOOD WEB DYNAMICS

In order to understand how food web structure affects community resilience and ecosystem processes at hydrothermal vents, it is critical to determine how environmental changes affect food web dynamics. Changes in hydrothermal fluid flow or chemistry can alter the availability of resources for chemosynthetic primary producers, causing bottom-up effects on community structure, and abiotic factors associated with hydrothermal fluid flux determine the distribution of consumers and consequently result in top-down control. While additional work is needed to identify the extent of trophic relationships, the degree of connectance, and the strength of species interactions in hydrothermal vent food webs, researchers have gained insight into food web dynamics by examining changes in microbial and metazoan community composition and variation

in trophic relationships in response to changes in environmental conditions.

Seafloor eruptions such as those observed at the East Pacific Rise and the Juan de Fuca Ridge provide drastic examples of how changes in the flow of hydrothermal fluids can influence the availability of resources and cause bottom-up changes in the food web. At stasis, sulfur-oxidizing and other types of microbes seem to grow in subsurface habitats and accumulate elemental sulfur (Taylor and Wirsén, 1997; Huber et al., 2003; Crowell et al., 2008). Immediately following an eruption, the microbial biomass and sulfur floc is expelled in a “bloom” of productivity (Haymon et al., 1993; Tunnicliffe et al., 1997). In response, there is an increase in consumers around the vent openings, presumably to take advantage of the increase in food availability (Tunnicliffe et al., 1997; Shank et al., 1998). As hydrothermal fluid flux decreases, ecological succession continues with the colonization of foundation species that have internal symbionts; they eventually dominate the biomass, concentrate food sources, and provide additional area for colonization (Tunnicliffe et al., 1997; Shank et al., 1998; Govenar and Fisher, 2007; Marcus et al., 2009). Thus, the changes in hydrothermal fluid flux following seafloor eruptions affect both direct and indirect bottom-up processes that ultimately facilitate the reassembly of vent communities.

Changes in fluid chemistry can also lead to the decline of foundation species but result in shifts in the composition of chemosynthetic primary producers that maintain the food web structure. At the East Pacific Rise, the fluid chemistry at a diffuse flow site changed from high sulfide/low iron concentrations to



low sulfide/high iron concentrations (Govenar et al., 2004, 2005), and the population of *Riftia pachyptila* tube-worms at the site reflected the environmental changes. Most of the remaining tubeworm aggregations were small and recumbent, and the plumes of the individuals were pallid (Govenar et al., 2005). However, the density and biomass of the epifaunal community were not significantly different from another site that had high sulfide/low iron concentrations (Govenar et al., 2005). This observation suggests that the sulfide concentrations may not have been sufficient for the internal symbionts of the tubeworms or free-living sulfur-oxidizing chemoautotrophic bacteria, but the consumers were able to persist within the physical architecture of the tubeworm tubes with available resources, provided by chemosynthetic primary producers using sources of chemical energy other than sulfide oxidation, heterotrophic bacteria, or POM. Thus, the metabolic diversity of chemosynthetic primary producers may contribute to the resilience of the macrofaunal community through weak trophic links with the versatile consumers.

Abiotic factors associated with vent fluid composition can also affect the distribution of consumers and consequently impact food web dynamics. At the East Pacific Rise, the effect of predation is greater in areas of increased hydrothermal fluid flux, which can lead to a greater rate of grazing by gastropods and other invertebrates, subsequently removing invertebrate recruits and reducing microbial biomass (Micheli et al., 2002). At the Juan de Fuca Ridge, paralvinellid polychaetes shift from competing for shared resources in areas of high hydrothermal fluid flux to resource partitioning in areas of

lower fluid flux (Levesque et al., 2003). Moreover, they switch from feeding primarily on bacteria to diets based more on POM (Levesque et al., 2003), suggesting that grazing on chemosynthetic primary producers in areas of high fluid flux could limit local productivity and shift consumers to lower-productivity habitats for lower-quality food sources (Levesque et al., 2005). Therefore, in areas of high hydrothermal fluid flux, there may be additional influences from top-down processes on community structure (Micheli et al., 2002; Mullineaux et al., 2003).


## CONCLUSIONS

A key aim of the Ridge 2000 Program was to identify linkages from mantle to microbe. Food webs form a direct connection from the lithosphere to the biosphere through chemoautotrophy, or more generally chemosynthetic primary production, in which chemical energy is used to generate biomass. Changes in the flow or chemistry of hydrothermal fluids can influence the availability of resources at the base of the food web, as well as the distribution of consumers. Consequently, both bottom-up and top-down factors, as well as indirect nontrophic species interactions, can affect food web dynamics or the transfer of energy within the ecosystem at hydrothermal vents.

The response of food web dynamics to environmental changes could have important implications for conservation and environmental protection efforts at hydrothermal vents and other chemosynthesis-based ecosystems. Several researchers have compared food webs at active and extinct hydrothermal vents to find that there are differences in the composition of consumers, but the resident fauna continue to depend

on energy derived from chemosynthetic primary production after venting has ceased (Erickson et al., 2009; Levin et al., 2009). The extent to which these patterns demonstrate resilience of the community remains to be seen and requires continued sampling over time and at a range of spatial scales. It is also critically important to continue to identify the linkages in food webs from the sources of energy in the lithosphere, to the phylogenetic and metabolic diversity of chemosynthetic primary producers, and to the web of trophic and nontrophic interactions among the consumers. Furthermore, quantifying the impacts of environmental changes on the transfer of energy through food webs is necessary to determine the flux of carbon and other nutrients from chemosynthesis-based ecosystems to the open ocean.

## ACKNOWLEDGEMENTS

This manuscript was greatly improved by the suggestions of two anonymous reviewers and the guest editors of this issue of *Oceanography*. Ideas developed in this manuscript were generated through work supported by a Deep Ocean Exploration Institute Postdoctoral Fellowship at the Woods Hole Oceanographic Institution, NSF award (OCE-0937395) to T.M. Shank and B. Govenar, and in part by the NSF EPSCoR cooperative agreement (EPS-1004057) and the state of Rhode Island. 

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