

Colonization strategies of three dominant families of reduced systems

-Vestimentiferan tubeworms, Vesicomyid clams, Mytilid mussels-

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Summary

Reduced systems, as hydrothermal vents and cold seeps in the deep ocean, are communities depending on reduced inorganic material as an energy source instead of solar energy. The rich benthic community of hydrothermal vents and cold seeps is depending on the inorganic rich fluid that comes out of the ocean crust as result of geographical processes and on the chemosynthetic bacteria. The chemosynthetic bacteria are the primary producers of the system that are able to convert the reduced substrates into organic substrates. Most of the benthic species living close to the opening of the reduced system are endemic species, living in a symbiotic association with the chemosynthetic bacteria. To be able to sustain in vent and seep systems, as these systems are short living and ever-changing systems, the organisms should have high dispersal abilities and able to colonize newborn systems. Is it possible to distinct different colonization strategies for the macroorganisms in these systems?

Organisms can adapt to environmental variability by developing different life-history strategies. Two opposite strategies, the r- and K-strategy are discussed. R-selected organisms usually have rapid development, early reproduction, high reproductive output, relatively short lives and relatively short lives. K-selected organisms have the opposite characteristics. K-selected strategists occur in more stable environments, with maintenance and competitive abilities as the optimal strategy for the organisms.

The short living vent and seep systems as short living and ever-changing systems selects for r-selected organisms, however, within the benthic communities some species are relatively more K-selected than others that are more r-selected. Comparing the life-history of three dominant families, the vestimentiferan tubeworms seem to be early colonizers, while the vesicomylid clams and the mytilid mussels seem to be later successional species. The worms seem to change the system in such a way to facilitate the colonization by the other organisms, although it could also be only the change in fluid emissions.

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1. Introduction

All life on earth needs an energy source to be able to sustain. For a long time the sun was thought to be the only energy source for all life on earth (Chevaldonne 1997). Green plants and microorganisms that are able to photosynthesize can only use the solar energy directly. In the process of photosynthesis the primary producers use the solar energy to convert inorganic substrates, carbohydrogen and water into essential organic substrates. Therefore the activity of the primary producers is necessary for the animal community, as animals are not able to perform photosynthesis themselves. As the sun was thought to be the only energy source, life could not occur in the absence of the sun. As light is not able to penetrate deeper than 300 meter into the ocean, scientists believed that no life could occur deeper than 550 meter in the ocean (Chevaldonne 1997). The deep ocean was thought to be a desert deprived of local primary producers (Hessler and Kaharl 1995). The organic matter that settled from the sea surface was considered to be the energy source. Although quite weak and therefore the ocean was one of the poorest ecosystems in terms of biomass (Jannasch 1995).

The discovery of an abundant animal community around hot springs called hydrothermal vents at a depth of 2500 meter on the crest of the Galapagos Rift in 1977 (Corliss *et al.* 1979) has proven that a high productive community could occur in the deep sea. This highly productive community was completely relying on an energy source other than solar energy. Fluids emitted from beneath the ocean crust turned out to have a high amount of reduced inorganic material, which could be used, by chemosynthetic bacteria (Hessler and Kaharl 1995). These chemosynthetic bacteria are the primary producers of the food chain of the hydrothermal vent (Cavanaugh 1985; Corliss *et al.* 1979). The bacteria are able to oxidize reduced inorganic material, mainly sulfide, from the fluid emissions and convert the inorganic substrate into organic material. The organic material is used as an energy source by the heterotrophic macrofauna (Jannasch and Wirsén 1985). Therefore the animal community is totally relying on the fluid emission and the chemosynthetic activity of the bacteria.

Since the discovery of the animal community around the hydrothermal vent on the Galapagos Rift other reduced systems surrounded by rich biological communities were found, as cold seeps (Jollivet *et al.* 1990) and the rotting carcass of a dead whale (Bennett *et al.* 1994). The primary production of these two communities is also based on the chemosynthetic activity of bacteria (Craddock *et al.* 1995). The animals of these three types of reduced systems are mostly sessile organisms (as adults) and endemic to the system; the organisms are not able to live outside the reduced systems. As great distances can separate these reduced systems, the reduced systems are like islands on the ocean floor (Vrijenhoek 1997). With the fact that these reduced systems are relatively short living systems with a rather fluctuating energy source (Hessler and Kaharl 1995) the systems have proven to be rather extreme. The sessile inhabitants of the systems have to be highly adapted to the system in order to continue to exist as a species. As the adult organisms are not able to move themselves, the offspring of these organisms have to

have high dispersal abilities. The offspring also must be able to survive for a long time in an unsuitable environment, by either be tolerant to the environment or to carry the resources themselves. These benthic communities are also selected on their colonizing (Craddock *et al.* 1995; Karl *et al.* 1996; Lutz 1988).

In all community systems species have their own constraints and adaptations to the environment. Some of them are able to colonize a newborn environment, while others are better competitors and are able to remain in the system. Is it possible that the species have different types of colonization strategies in these short living and ever-changing reduced systems where selection on colonization abilities is high?

In this paper I would like to discuss the differences in colonization strategies of three dominant species of hydrothermal vents and cold seeps.

In the first chapter I will explain the systems, hydrothermal vents and cold seeps in more detail and compare them with each other, not geologically, but mainly ecologically. The three dominant endemic species I shall introduce in chapter two, and give the characteristics of the life history and morphology of these species. Chapter three will be a chapter about two types of colonization strategies. The information in these chapters will be used in the discussion, followed by conclusions.

2. Reduced systems

2.1. Hydrothermal vent

Hydrothermal vents are spread along the mid-ocean ridges and back-arc basins in the Atlantic, Eastern and Western Pacific oceans, on locations with active plate tectonics and volcano activity (Craddock *et al.* 1995)(see figure 2.1.). At one location more than one vent can occur. Mostly the vent system is a multiple hydrothermal field with two types of vents; warm-water vents (0-80 °C) and high-temperature vents (80–350 °C) (Karl *et al.* 1996; Vrijenhoek 1997). Hundreds to thousands of kilometers can separate these fields and therefore these systems are like islands in cold, nutrient poor ocean water (Vrijenhoek 1997). The hydrothermal vent consists of a circulation of seawater that penetrates into the young ocean crust. Inside the earth there are underlying magma chambers. Inside these magma chambers high temperatures appears and in the surrounded rocks a high amount of inorganic material is located. The inward streaming seawater is chemically altered by the interaction with the temperature and the inorganic compounds, before it is spread out through another crack in the ocean crust. The escaping fluid consists of mainly sulfide and a few other reducing substrates (Butterfield *et al.* 1990; Hessler and Kaharl 1995). The system is depending on the geological processes, which will last for relatively short periods; times of decades (Grassle 1986; Tunnicliffe and Juniper 1990)). In time the volcanic action of the hydrothermal vent diminishes and with it the concentration of H₂S (Shank *et al.* 1998). The communities of the system will slowly die.

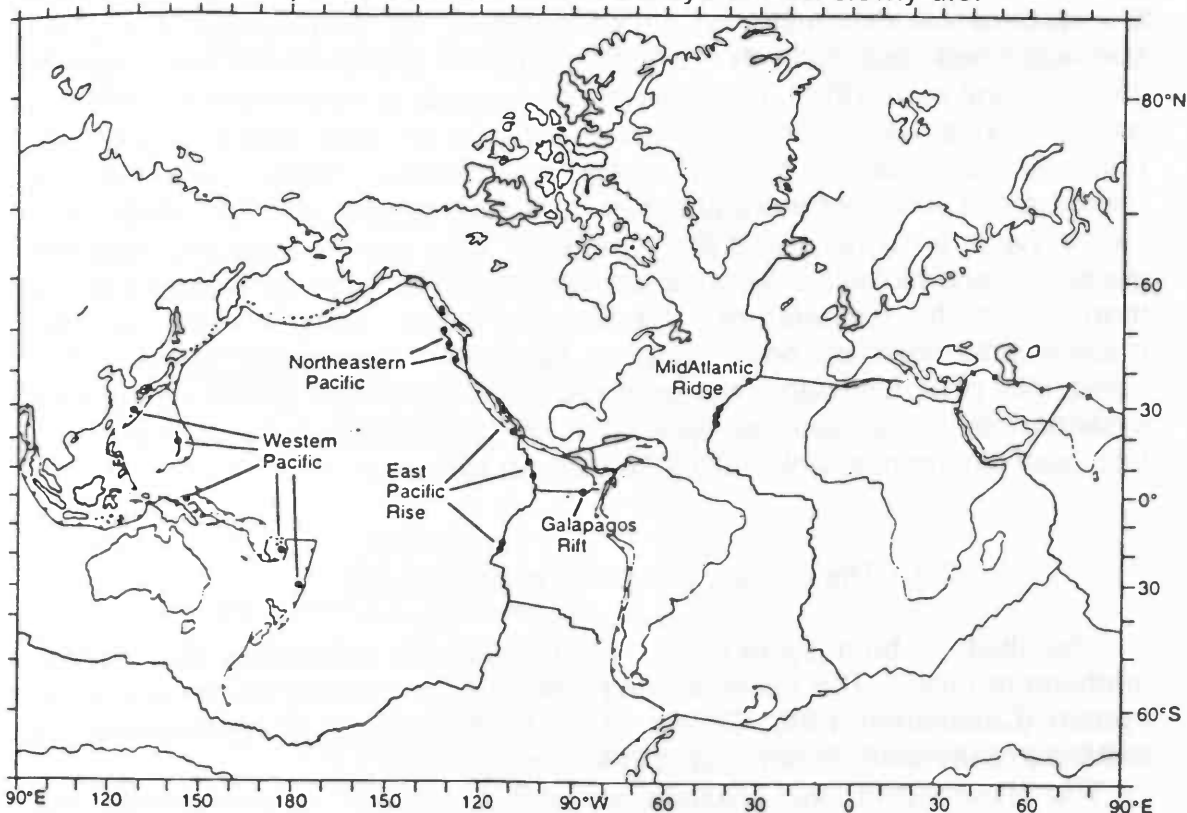


Figure 2.1.: The map shows mid-ocean ridge. The dots indicate hydrothermal vents that have been studied by biologists (Hessler and Kaharl 1995).

2.2. Cold seep

Cold seeps occur at locations with different geological context along passive and active margins in the Atlantic, Eastern and Western Pacific oceans and the Mediterranean Sea along continental margins, in a depth range from 400 to 6000 meters (Olu *et al.* 1996). There are several forms of seafloor seepage (Corselli and Basso 1996; Olu *et al.* 1996). Seeps are related to geological processes like tectonically induced high-fluid pressures, petroleum or natural gas escapes, artesian flow or catastrophic erosion and slides (Corselli and Basso 1996; Olu *et al.* 1996). The principle of the system looks like that of the vent, however it is cold water that is chemically altered that seeps through the bottom mud (Jollivet *et al.* 1990; Sibuet and Olu 1998). In this system the fluid is mainly rich of methane both of thermogenic and biogenic origin (Sibuet and Olu 1998). Methane is therefore used as a substrate by the chemosynthetic bacteria. But also sulfide is used as a substrate as in hydrothermal vents. Also this system is short living and ever-changing, like the vent system.

2.3. The community of the reduced systems

Although the geological and physiological processes of these reduced systems and the origin of the reduced substrates are different (Sibuet and Olu 1998), the adaptations of the animal community of these systems are alike (Kenicutt *et al.* 1985; Olu *et al.* 1996; Sibuet *et al.* 1988). Both communities of the systems are depending on the continuity of the fluid emissions and the chemosynthetic activity of the primary producers (Desbruyères and Segonzc 1997; Jollivet *et al.* 1990). Chemosynthetic bacteria of hydrothermal vents use mainly sulfide as a substrate, while bacteria of cold seeps mainly use methane, but also sulfide (Corselli and Basso 1996). Although the hydrothermal vents got more attention from science than the cold seeps, cold seeps have a higher biological diversity. Also the interactions between geological and biological systems are considered to be more complex at low than at high temperature (Sibuet and Olu 1998). Most of the macroinvertebrates of both systems seems to be closely related. The community of both systems has quite the same basis. The community of both systems can be divided into several zones discriminated by chemical and biological differences, which are alike for both systems.

2.3.1 The primary producers of the system

The fluid of both systems is rich in reduced substrates like sulfide, methane or others. The bacteria living there are the primary producers of the system (Cavanaugh 1985; Corliss *et al.* 1979). Without these bacteria the metazoan community is not able to live (see figure 2.3.1.).

The chemoautotrophic bacteria are able to convert carbon dioxide and water into essential organic sugars, according to the process of chemosynthesis. In this process the reduced substrates are used as an

electron donor. In an aerobic situation oxygen is the electron acceptor (Fisher 1995) (see figure 2.3.2).

Bacterial Sulfide Oxidation, Aerobic Chemosynthesis

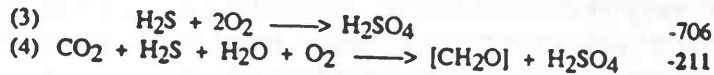


Figure 2.3.1: chemosynthetic reaction with sulfide (Jannasch 1995)

These bacteria are either free-living bacteria or symbionts with metazoans. As free-living bacteria they can live in large microbial mats on the sediment or in the ambient water. In symbiosis with macroinvertebrates the bacteria live inside the gastrointestinal tracts and the gill tissues, but they can also live extracellular on the gill filaments (Jannasch 1995). This relationship is called mutualism as both organisms benefit: the host provides the symbionts with the essential inorganic nutrients, while the symbionts give organic sugars to the host in return (Hessler and Kaharl 1995). Not all bacteria found near vents and seeps are chemosynthetic bacteria, also heterotrophic bacteria are able to live in this system. They use the organic byproducts of the system as food source (Hessler and Kaharl 1995).

These bacteria have a great ability to disperse in large numbers along the reduced systems at the ocean floor, due to their ability to sustain in metabolic dormancy in the absence of their specific substrate (Jannasch 1995). Therefore they are quite ubiquity. When substrates become available they are able to become active without almost any delay. Therefore an immediate arrival of microorganisms and their growth in response to emission of hydrogen sulfide at newly forming vent sites can be expected (Jannasch 1995).

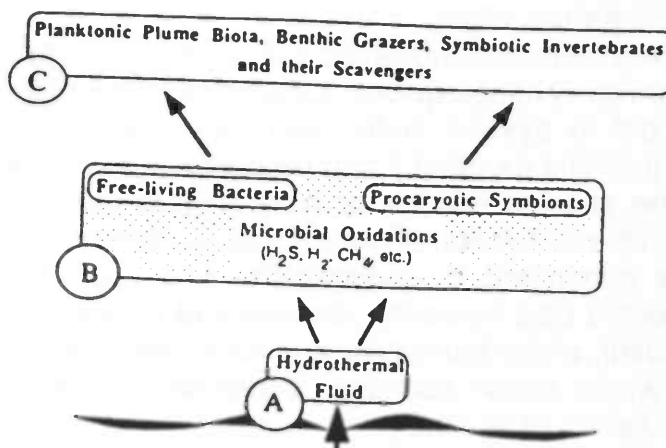


Figure 2.3.2.: The relation between the energy source, the primary producers and the metazoan community (Jannasch 1995).

2.3.2. The metazoan community

An extreme environment is characterized by stress of many kinds from chemical and physical to biological, which often results in a significant decrease in biodiversity (Vanreusel *et al.* 1997). The reduced systems are an example of extreme environments that have a relatively low biodiversity. The community of a reduced system consists of well-adapted, endemic species. Very high biomass and high densities characterize this system (Corselli and Basso 1996). The animals have a high metabolic rate that makes rapid growth possible (Desbruyères *et al.* 1994). As the fluid of reduced material of the energy source is constant, they are able to grow and probably reproduce continuously.

The area around the opening of a vent or seep system can be divided into several zones: the opening, the near-field and the periphery (Hessler and Kaharl 1995).

Around the opening the concentration of the substrates is highest. Most of the species living near this opening are endemic and are new to science. They are living in symbiosis with the chemosynthetic bacteria (Grassle 1986). They have to have evolved mechanisms to tolerate the toxic level of the reduced substrates. They can not simply shield themselves from the environment, because their internal symbionts need to be provided with the substrates (Fisher 1995). These organisms are not able to live outside this system. Therefore they can only be found at other reduced systems as for instance a whale carcass, which is temporarily also a source of reduced substrates (Bennett *et al.* 1994).

In the cold seep in the Gulf of Mexico this zone is subdivided in smaller areas. With separate zones for mussels, two vesicomyid clams and the tubeworms (Callender *et al.* 1990). These organisms are the largest and dominant species for both systems (Olu *et al.* 1996). Other commonly smaller creatures are living among these dominant, large animals (Desbruyères and Segonzac 1997; Hessler and Kaharl 1995).

This system has a marked boundary, however, it is not static (Hessler and Kaharl 1995). The circulation can change quickly. One moment the plume of a vestimentiferan can be held in system water with high concentration of reduced substrates, while the next moment it can be exposed to oxygen rich ambient water. Most of the species acquire both substrates and are thus depending on fluctuations in the circulation (Tunnicliffe *et al.* 1985).

The near-field zone is dominated by suspension- and deposit-feeding organisms. Suspension-feeders filter bacteria, plankton and organic particles out of the plume of the effluent, while deposit-feeders suck their food from the bottom. Among these animals occur sponges, bryozoans and barnacles (Hessler and Kaharl 1995; Jollivet *et al.* 1990).

Also non-vent species are attracted by the rich nutrition of the system, living in the next zone, the periphery as closely as possible to the source without being poisoned by the fluid (Somero *et al.* 1989).

Mostly the food chain of these systems is short (Grassle 1986; Tunnicliffe 1991). Most of the heterotrophic organisms are primary consumers feeding on the primary producers. Among the heterotrophic organisms are hosts of the

symbionts, grazers and suspension feeders. (Craddock *et al.* 1995; Hessler and Kaharl 1995) In long food chains the herbivores are preyed upon by primary carnivores, which on their turn are eaten by secondary carnivores etc. In such a food chain there are many carnivores of different trophic levels (secondary, tertiary, etc). However only a few secondary consumers (primary carnivores) seem to live in reduced systems. Among the few secondary consumers are scavengers and carnivores (Hessler and Kaharl 1995; Olu *et al.* 1996). They do not seem to live around the opening of the as they are rarely spotted there; they seem to live in the near-field or periphery.

3. Three dominant families of reduced systems

The metazoan communities of hydrothermal vents and cold seeps living at the opening of the system consist of a few dominant species (Grassle 1986; Tunnicliffe 1991). It is remarkable that although only a few species are found in both systems, the families of several phyla are quite the same. As though only some families within a phylum have been able to evolve mechanisms to sustain in these extreme habitats (Tunnicliffe 1991). Vestimentiferan tubeworms, Vesicomysids clams and Mytilids are three of the dominant families found in both systems (Hessler and Kaharl 1995; Olu *et al.* 1996; Shank *et al.* 1998). All of them are endemic families living in symbiosis with chemosynthetic bacteria. They are either partly or completely depending on the activity of the bacteria. Research has revealed that all sulfur-oxidizing endosymbionts of the metazoans of both systems are coming from the same type of bacteria. They are all members of the γ subdivision of Proteobacteria (Distel *et al.* 1988; 1994; 1995). DNA sequences of bacterial symbionts from bivalves species *Calyptogena magnifica* (a vesicomysid clam) and *Bathymodiolus thermophilus* (a mytilid mussel) and a vestimentiferan tubeworm *Riftia pachyptila* are used to investigate whether the symbionts of the species are different from each other. And whether the symbiosis between the bacteria and its host is species-specific. The results suggest that the symbionts may be host-specific at phylum level (Distel *et al.* 1988). In addition, these phylogenetic differences between the symbionts of these three species give an indication that the symbiosis originated separately in the vent bivalves and vestimentiferans (Distel *et al.* 1988).

The juveniles of the host species can obtain their symbionts in two different ways. They can get them from their parents through the zygote, termed vertical transmission, or they have to find free-living bacteria, horizontal transmission (Cary *et al.* 1993).

As most of the organisms of vent and seep systems are sessile, the recruitment of them has to have the ability to disperse along great distances. Planktonic larvae that can spend a long time in the water column are thought to disperse along greater distances, therefore planktonic larvae would be advantageous over brooded larvae for the species of reduced systems (Hessler and Kaharl 1995). The swimming capacity of planktonic larvae is minimal relative to flow velocity near the reduced systems; thus flow may strongly influence larval distribution patterns (Lutz 1988).

3.1. Vestimentiferan Tubeworms

Vestimentiferan tubeworms are characteristic inhabitants of hydrothermal vent habitats in the Eastern Pacific, and they commonly occur at cold-water sulfide-hydrocarbon seeps (Young *et al.* 1996). Although the taxonomic status of vestimentiferans has been debated since their discovery, morphologic analysis suggests they constitute a discrete evolutionary group (the Obturata) within the phylum Pogonophora. Different morphological forms of tubeworms are found at distinct location and represent separate species. However research of allozyme surveys in either the genus of *Ridgeia* or *Riftia*, two

vestimentiferan species, did not detect evidence for multiple species or geographical isolation. Current evidence indicates that *Riftia* and *Ridgeia* represent monotypic genera, whose species (*Riftia pachyptila* and *Ridgeia piscesae*) display exceptional morphological variability and adaptive plasticity. These tubeworms seem to be very important species in the system. They are often found as one of the first species at a reduced system, but seem to loose the competition with both mytilids and vesicomysids (Hessler and Kaharl 1995; Johnson *et al.* 1986; Shank *et al.* 1998). A lot of other smaller species are also found associated with these animals (Desbruyères and Segonzac 1997). They can use the tube or the plume of the tubeworm as location of attachment. Some animals like the mollusk *Cyathernia naticoides* are living inside the tube of the vestimentiferan, cleaning up the walls. Samples of the animal communities of several research projects often reveal these organisms in washings of the tubeworms animals (Desbruyères and Segonzac 1997).

3.1.1. Morphological characteristics.

The vestimentiferans are thought to be one of the most specialized hosts of the species in symbiosis with chemosynthetic bacteria (Felbeck and Childress 1988). They have no mouth, gut and anus, and are therefore completely depending on their symbionts (Feldman *et al.* 1997; Young *et al.* 1996). The body of the tubeworm can be divided into 4 regions: obturaculum, vestimentum, trunk and opisthosome (see figure 3.1.1.).

At the anterior end of the worm the obturacular region is located with a primitive nerve system; the obturaculum and an efficient gas exchange organ; the branchial plume (Jones 1981). The plume is exposed to the environment outside the tube, but is immediately withdrawn with disturbance. The borrow of the tubeworm is made of chitin proteoglycan/ protein complex (Gaill *et al.* 1988; 1991). The tube is variable in its rigidity and thickness, both between as within species. The glands that secrete the new material of the tube as the worm grows are located at the region directly below the plume, the vestimentum. In this part of the body also other organs, like the heart and gonopores (reproductive openings) are located (Fisher 1995). Besides its function as providing new tube material, it has a function to anchor the anterior part of the worm in its tube. The function as anchor explains why this region is muscular (Gardiner and Jones 1993).

The trunk determines the majority of the length of the worm. Between a pair of coelomic cavities gonads and a tissue termed the trophosome are located. Edwards and Nelson (1991) found that the trophosome of the tubeworm species *R. pachyptila* comprises about 75 % of the body length. The trophosome is mainly built up of bacteriocytes; hosts cells that contain the symbiotic bacteria, associated cells around the bacteriocytes and blood vessels (Fisher 1995). As the symbionts are living inside the host and have no contact with the external environment, the worm uses its circulatory system to provide the bacteria with the required chemosynthetic substrates (Cavanaugh 1985). The vestimentiferans have in their blood special hemoglobin molecules that can bind and transport both sulfide and oxygen. Both substrates are bound with high affinity and without being affected by the binding of the other substrate (Childress *et al.* 1984). The capacity of the transport of both

substrates is high, due to the abundance of haemoglobins. All bacteriocytes will be well supplied with substrates, as they are all located nearby a blood vessel.

The posterior end of the worm consists of a short segmented region; the opisthosome (Gardiner and Jones 1993). It serves as an anchor at the base of the worm. Recent findings concerning cold seep vestimentiferan of the Louisiana Slope in the Gulf of Mexico revealed that they do not seem to obtain their sulfide from the ambient water as sulfide is rarely detectable around the plume of the individuals (Scott and Fisher 1995; Simpkins 1994). It has been proposed that these tubeworms acquire the sulfide from the sediment. They take up the sulfide by diffusion across the thin walled posterior end of the tube and the body wall. This way of uptake will be less efficient than the uptake of sulfide across the highly vascularized plume (Fisher 1995). It might be a possible explanation for the very slow growth (less than 0.5 cm/ yr.) of these seep species in contrast to the vent species that are known as the fastest growers of all deep-sea invertebrates (Lutz *et al.* 1994; Vrijenhoek 1997). Tunnicliffe and Jupiter 1990 recorded growth rates of 50 cm/ yr. of the vent species *Ridgea pascesae*. These worms are known for their large body length. Species with lengths of 1.5 meter are recorded with a tube of about 3 meters (Fisher 1995).

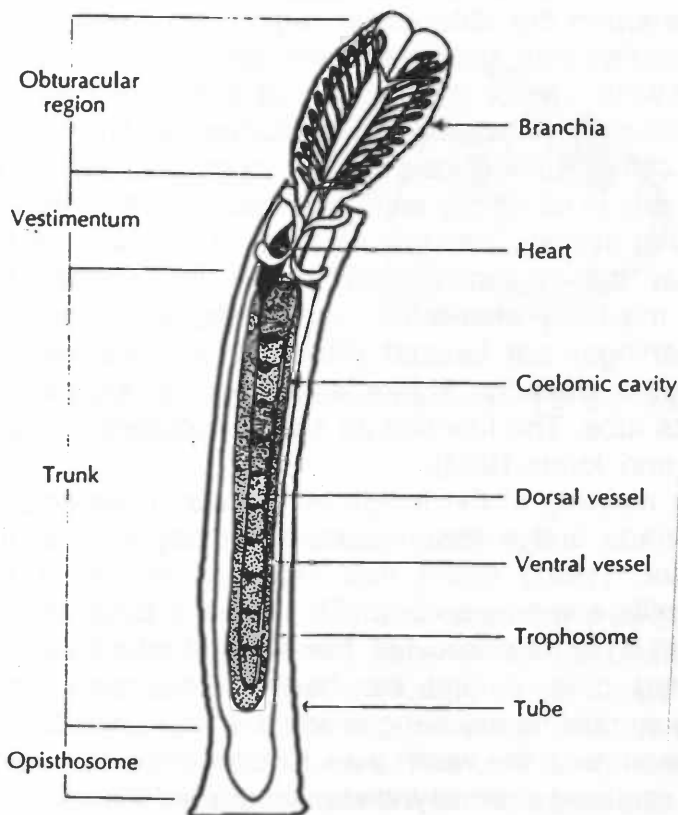


Figure 3.1.1.: Morphological characteristics of the vestimentiferan tubeworm. (Desbruyères and Segonzac 1997).

3.1.2. Colonization abilities

As the adults are sessile, the dispersal of vestimentiferan has to occur through the juveniles (Fisher 1995). They seem to have the potential for long distance dispersal, as they are able to survive for several weeks as free-swimming pelagic larvae (Young *et al.* 1996). In their early life they appear to live without symbionts, as no bacteria can be found in this stage. Nucleic acid hybridization studies (using symbiont DNA) of vestimentiferan ovarian tissues and eggs, provided no evidence for vertical transmission of bacteria from the adults to their offspring (Cary *et al.* 1993). Also microscopic examination of the planktonic larvae of the vestimentiferans failed to reveal an association with symbionts (Young *et al.* 1996). The discovery of a temporary gut in the larvae of the tubeworms (Jones and Gardiner 1988) also suggests that they are able to survive without symbionts. This free-living stage may have a function in selecting the right symbiont species at a suitable location, as the presence of a gut suggests that they can feed themselves and therefore possibly survive for a longer period without establishing a symbiotic association with bacteria. Jones and Gardiner (1989) hypothesize that this family acquires endosymbionts from free-living bacteria (horizontal transmission). Recent examination of free-living bacteria from rock and chimney structures at vents of Eastern Pacific Ridges using DNA probes directed at vestimentiferan endosymbionts sequence found evidence for these bacteria in new basaltic areas where no adult tubeworms had settled (Gary, unpublished in Feldman *et al.* 1997).

Feldman *et al.* (1997) found evidence that suggests that vestimentiferan harbor a single species of endosymbionts, one for the vent and one for the seep vestimentiferans.

3.2. Vesicomyids clams

The vesicomyids are deep-sea family of bivalves, characterized by their large individuals. Two genera are found till this moment; Calyptogena and Vesicomya. The species of these genera can be extremely diverse. At one location several species of Calyptogena and Vesicomya can be present (Brooks *et al.* 1987; Nelson and Fisher 1995). All species belonging to these two genera are found living in symbiosis with chemosynthetic bacteria. They live semi-epibiotic; buried with their anterior part about one half to three quarters of the length in vertical or oblique position on bare basalt, in cracks or in mud (Desbruyères and Segonzac 1997).

3.2.1. Morphological characteristics

These clams have a characteristic morphology (see figure 3.2.1.). Their gut is vestigial; only a short simple gut is left. Also their ability to filter feed is reduced by the reduction of the feeding groove on the ventral margin of the gills. These characteristics suggest that these clams still have the ability (though limited) to obtain nutrients by filter feeding in contrast to the

gills. These characteristics suggest that these clams still have the ability (though limited) to obtain nutrients by filter feeding in contrast to the tubeworms (Bos and Turner 1980). As the vestimentiferans, these clams have a variety of adaptations to the sulfide supply to their symbionts. Their blood has the ability to bind both sulfide and oxygen simultaneously with high affinity and capacity Childress *et al.* 1993). Functionally the clam's blood is analogous to that of the vestimentiferan tubeworm, but biochemically it is rather distinct. The blood has hemoglobin in erythrocytes to bind oxygen with moderate affinity and an extracellular binding component to bind the sulfide from the environment. The two substrates are not from the same source according to the model of Arp *et al.* (1984). The oxygen with the Dissolved Inorganic Carbohydrate (DIC) is obtained from the ambient water with the siphons, while the sulfide is mainly originating from the cracks of the sediment below the shells. With their highly vascularized foot that can be extended deep into the sulfide rich water the sulfide source is reached. The sulfide can be accumulated into the blood of the foot and transported to the symbionts that live in the large fleshy gills of the clam. As they need to get their sulfide from below their shells, these clams live semi-epibiotic, buried about one half to three quarters of the length in vertical or oblique position on bare basalt or in cracks (Desbruyères and Segonzac 1997). Individuals of these clams are found to reach large dimensions with shell lengths from 6.8 till 26.3 cm (Desbruyères and Segonzac 1997).

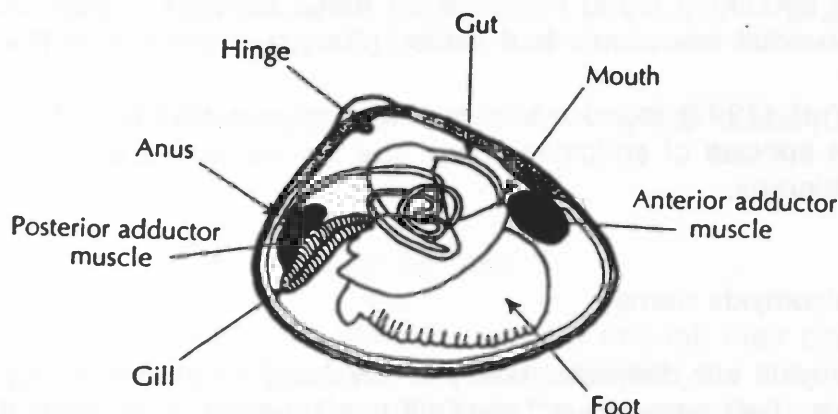


Figure 3.2.1.: Morphological characteristics of the vesicomyid clam (Desbruyères and Segonzac 1997).

3.2.2. Colonization abilities

These clams are sessile and therefore their dispersal is depending on their larvae. These clams have large yolky eggs, which are believed to produce non-feeding larvae. This is thought to be a less capable manner to disperse (Vrijenhoek 1997). However, research has revealed that they are able to disperse over long distances. The cold surrounding water might possibly slow down or hold the development of the eggs, with the result that the eggs will survive for a longer period. A longer survival will increase the dispersal ability (Vrijenhoek 1997).

Distel *et al.* 1988, 1994) has investigated the symbiont-host specificity of these clams and they appear to live in symbiosis with species-specific

same location as their parents and therefore can settle at the same location as their parents.

3.3. Mytilids mussels

The mytilids mussels are deep-sea mussels of either genus *Bathymodiolus* or closely related genera (Fisher 1995). Life habit of the adult is epibiotic on bare basalt and other hard substrates (e.g. tubes of vestimentiferans). The mytilid mussels appear to be good competitors for both space and food supply in regard with vestimentiferans. They seem to win the contest for food by removal of the sulfide from the effluent before it reaches the plume of the tubeworm (Johnson 1986). By using the tube and plume of the worm as location of attachment, the mussels are able to push away the tubeworms from their location (Hessler *et al.* 1988). Therefore the mussels gradually replace the vestimentiferans (Vrijenhoek 1997; Johnson *et al.* 1986; Shank *et al.* 1998).

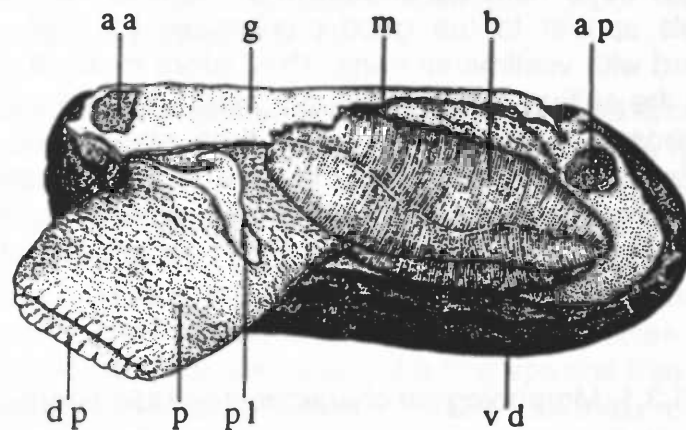
3.3.1. Morphological characteristics (see figure 3.3.1.)

These mollusks seem to be very interesting organisms due to their nutritional plasticity: some of the species harbor only chemoautotrophic symbionts, some only methanotrophic symbionts, and some even more than one type of symbiont (Fisher *et al.* 1993). The wide range of areas they are found also indicates the plasticity of the mytilid mussels. These mytilids are one of the most widely distributed species of all symbiont-containing species over the world. And around the vent and seep system the mytilids are also found to tolerate a wide range different chemical exposure of the system water. Their ability to tolerate this wide range in conditions might be due to the fact that they are not fully dependent on their symbionts as they have retained the ability to filter feed. It is suggested that these mussels are able to sustain themselves even as the source of the vent or seep shuts down (Fisher 1995). However, these mussels are not able to live outside the system and individuals found living at the boundary of the systems were all in bad condition (Smith 1984).

Unlike vesicomyid clams and vestimentiferan tubeworms, these mussels have not evolved specialized molecules for the uptake and transport of sulfide (or methane) and oxygen. They do have abundant symbiotic bacteria in the cells on the surface of the gill filaments (Fiala-Médioni *et al.* 1986). These filaments are quite abundant in the mussels' gills. It is found that, unlike the symbionts of vestimentiferan and vesicomyids, the symbionts of the mytilids are stimulated by thiosulfate instead of sulfide. Childress and Fisher 1992 and Nelson and Fisher 1995 suggested that these organisms are able to oxidize the sulfide themselves into thiosulphate. The latter substrate will be transported to the bacteria and used by them. There is, however, not enough known about the biology of the mytilids to fully understand it.

Mytilids found at hydrothermal vents on the East Pacific Rise have a growth rate of about 2.26 – 11.1 cm/ yr. They seem to reach shell lengths with

Mytilids found at hydrothermal vents on the East Pacific Rise have a growth rate of about 2.26 – 11.1 cm/ yr. They seem to reach shell lengths with a maximum length of 12 cm. The growth rate of these mussels is higher than found before at vent endemic mussels (Shank *et al.* 1998).



Acharax alinae, paratype II, schematic drawing of external morphology of the animal (left valve removed). aa: anterior adductor. ap: situation of the posterior adductor (destroyed in the studied specimen). b: gills. g: situation of the gonads. m: mantle (partly remodeled). p: foot. dp: pedal disk. pl: labial palps. vd: right valve with periostracum folded towards the interior.

Figure 3.3.1.: Morphological characteristics of the mytilids mussel (Desbruyères and Segonzac 1997).

3.3.2. Colonization abilities

Like the tubeworms the mytilids disperse through their planktonic larvae (Craddock *et al.* 1995). Even as with vesicomysids the symbionts are transmitted vertically from the parents to the offspring (Cary *et al.* 1993).

4. Colonization

4.1. r- and K-strategy

Most species have evolved strategies to be highly adapted to patterns of environmental variabilities. The difference in variability of the environment selects for different strategies. A constant environment generally favors individuals with better competitive abilities, while more unstable environments favor individuals with high fecundity and rapid development. The unpredicted nature of an unstable environment selects organisms with early reproduction, as the life span has high changes to be short (Battaglia and Beardmore 1978).

Two strategies, opposites of each other, are developed (MacArthur and Wilson 1967). The 'K-selection' and 'r-selection' represent a trade-off in reproduction potentials (the K refers to the carrying capacity and r to the maximal intrinsic rate of the natural increase). The terms r and K are also used in the logistic equation and therefore unfortunately chosen according to Pianka (1970). Pianka (1970) believe other characteristics to be also associated with the two strategies. The K- and -r selection represent two extremes, however, an organism is neither completely K-selected nor completely r-selected. It is a compromise between the two strategies (Pianka 1970).

The selection of r-strategists evolved in those ideal environments with no density effects and no competition. Under this ideal situation the optimal strategy is to put all energy into reproduction, with the smallest energy amount as possible into each individual offspring. With the optimal strategy the individuals produce as many progeny as possible. As the chance to die early in live is high for r-strategists, the individuals gain little from being robust and long-lived. Therefore r-strategists are short living individuals, that mostly remain small (Pianka 1970). K-strategists are selected in an environment saturated with organisms. In such an environment the optimal strategy is to have high competitive abilities and thus to put all energy in maintenance and slow development. The offspring that are produced by K-strategists are few in numbers, but extremely fit to survive. In an environment saturated with organisms it is important that the offspring replace the elder individuals (Pianka 1970). Therefore K-selected individuals have to be robust and long lived as adults (Battaglia and Beardmore 1978).

4.2. Succession models

According to Connell and Slatyer (1977) 'succession refers to the changes observed in an ecological community following a perturbation that opens up a relatively large space. The open space will be colonized by a sequence of species that are able to settle in that type of habitat. During the succession of such an open space the influence of certain characteristics of the habitat will change. For instance in the begin of the succession the open space will be highly exposed to fluctuations in the abiotic characteristics, as temperature and flow (of air or water), while in the presence of early colonizing species these abiotic factors have less influence upon the habitat. The habitat will

become a more stable environment. Because of the stability of the environment the habitat become more suitable for the settlement of other species that do not tolerate high environmental fluctuations. Many researchers have been interested in the changes in species composition in an ecological community during succession. Many succession models have been made. Connell and Slatyer (1977) have given an overview of three models dealing with the succession possibilities of a new born site: the facilitation, the tolerance and the inhibition models. The models are based upon the assumption that no further significant changes occur in the abiotic environment (Connell and Slatyer 1977).

A difference between the facilitation model on one hand and the tolerance and inhibition model on the other hand is the difference in the type of species that will first colonize a new created open site after natural or human perturbation (Connell and Slatyer 1977). The facilitation model assumes that only certain early successional species are able to colonize the open space, while the other two models assume that any arriving species may be able to colonize the location. However as early successional species have evolved colonizing characteristics, they are usually the first species that will appear at an open site. Therefore the type of species that first colonize a certain habitat is hard to use in distinguishing the type of succession model. Early succession species, r-selected organisms, have evolved the ability to produce a large number of progeny that have good dispersal abilities, to germinate and to become established in unoccupied places, and to grow quickly to maturity. However they are not well adapted to germinating, growing and surviving in occupied sites due to less competitive abilities with other organisms. Therefore their offspring seldom survive in the presence of their parents or other adults. As in all models mostly early succession species will be the first to colonize the open site, the three models all agree that early occupants modify the environment in such a way that the habitat is unsuitable for further recruitment of early succession species.

The three models differ mainly in the mechanisms that determine how new species appear later in the sequence (Connell and Slatyer 1977). In the facilitation model the early succession species may alter the condition or the availability of resources in a habitat in such a way that the entry of later-succession species is facilitate. The later species invade the habitat and grow to maturity. The presence of the early-succession species is necessary for the later-succession species, as they are not able to settle themselves at a newborn site as the first species.

In the tolerance model early succession species modify the environment, but the modifications do not influence (neither increase nor reduce) the rate of settlement of later-succession species. The sequence of the species colonizing a newborn site is just determined by the life-history characteristics of the species. In contrast to the early species the later will have less dispersal abilities and their juveniles will grow more slowly to maturity. This model is a combination of both the facilitation and the inhibition model. Although the model is theoretically right, in nature this model is not (commonly) found.

In the inhibition model the early succession species will secure the space and the resources of a newborn site. Therefore the invasion of later succession species is inhibited and the growth of those organisms already

present suppressed. New species can only settle as they bring their own resources or if resources become free to use when (an individual of) early succession species has died.

The models also differ in the cause of death of the early succession species (Connell and Slatyer 1977). In the first two models (facilitation and tolerance) the early succession species are eliminated from the community in competition with the later succession species. In the inhibition model the early species are killed by local disturbances caused by physical extremes or natural enemies as herbivore and parasites.

Discussion

Hydrothermal vents and cold seeps are known as short living and ever-changing systems that can last for several decades depending on the geological activity of the systems. According to the 'r- and K-strategy theory' of MacArthur and Wilson (1967) unstable environments favor r-selected organisms. Following the succession of the vent and seep systems vestimentiferan tubeworms are commonly found as one of the first species at a newborn site (Hessler and Kaharl 1995), while later in the succession these worms are eliminated and vesicomyid clams and mytilid mussels take the dominant place in the animal community (Johnson *et al.* 1986; Shank *et al.* 1998). Thus within this systems that favor r-selected organisms not all species have evolved the same life history characteristics. The worms seem to be more r-selected, while the clams and mussels seem to have evolved relatively more K-selected characteristics.

A newborn vent or seep system can be seen as an environment with no density effects and no competition (Pianka 1970). The optimal strategy then is to have high reproductive output. As the chances of a short live are high for these early colonists, they do have a high metabolic rate and mostly remain small individuals (Pianka 1970). Not enough is known of the age of maturity and about the amount of progeny produced by the species inhabiting vents and seeps. Thus nothing can be said about the reproduction strategy of the three families with regard to the two types of strategies. However, the tubeworms produce small planktonic progeny (Young *et al.* 1996), while the vesicomyid clams produce large yolky eggs (Vrijenhoek 1997). Large yolky eggs are thought to be costly in production. Thus the clams seem to put relatively more energy in one progeny than the tubeworms. But also the mussels have small progeny (Craddock *et al.* 1995), thus this characteristic is not totally balanced. The worms have evolved the highest growth rates of all vent species (Lutz *et al.* 1994) and thus also in comparison to the two bivalves. Thus tubeworms have possibly put their energy in low reproduction costs per progeny and in high growth rates. These tubeworms are therefore thought to have a short life span and early age of maturity. However these latter two characteristics have to be investigated in the future.

K-selected individuals have put their energy in maintenance and slow development, as high competitive abilities are the optimal strategy in an environment with many other organisms (Pianka 1970). Both the mussels and the vesicomyids seem to have put more energy in competitive abilities, as they are better competitors than the vestimentiferan (Hessler and Kaharl 1995; Johnson *et al.* 1986; Shank *et al.* 1998). The vestimentiferan seem to lose all competition for space and resources with the two bivalves. The vestimentiferan are replaced. The clams and mussels are more slow growers than the tubeworms (Lutz *et al.* 1994), possibly putting the energy in maintenance. A few but extremely fit progeny are produced, as replacement is an important factor for the species to be able to sustain their position in the community. The juveniles produced are found at the same location as their adults and possibly replacing the elder individuals. Juveniles of the vestimentiferan however, do not seem to replace their adults. The tubeworms even seem to have evolved a mechanism to let their juveniles disperse to new

location as Gary (unpublished in Feldman *et al.* 1997) has found evidence that the symbionts of the vestimentiferan are found at reduced systems where no adult tubeworms are found. As the juveniles have to get their symbionts by horizontal transmission (Gary *et al.* 1993; Jones and Gardiner 1989) instead of vertical transmission, they have to find locations with chemosynthetic bacteria and no adult vestimentiferan. Locations with symbionts, but no adult vestimentiferan are possibly newborn locations. Horizontal transmission of the symbionts could be an adaptation of the parents to enhance the chance their juveniles will colonize a new location and not stay at the location of their parents, as the tubeworms will lose the competition in a system saturated with organisms.

Although the species are not typical r- and k-selected organisms, the characteristics of the three families seem to fit for more r-selected organisms, the tubeworms and relatively more K-selected organisms, the two bivalves families within the community of vent and seep systems. However one characteristic is remarkably different. R-species are commonly known as small individuals, because they put their energy in high reproductive output rather than growth and maintenance (Battaglia and Beardmare 1978; Pianka 1970). Therefore it is expected that vestimentiferan tubeworms are small individuals, but remarkably these organisms are characterized by large body length (Fisher 1995). They can even reach the length of approximately 1 meter. The majority of these organisms body length consist of the trunk (Edwards and Nelson 1991). In this part the trophosome is located, the organ where the symbionts are active (Fisher 1995). This large surface area of the trophosome may serve to support the high growth rates of these tubeworms and is therefore an indication of the importance of the bacteria. Shank *et al.* 1998 have also made this suggestion. They have done research at the colonization of a new hydrothermal vent at the East Pacific Rise. The fluid emission of this new spot had unusual high H_2S levels. They found tubeworms as one of the first organisms at the spot. The worms found at that location had remarkably high growth rates; largest ever found. They suggested that this might be possible due to the bacterial activity.

Also the bivalves vesicomyids and mytilids have relatively large individuals with the organ where the bacteria are located quite enhanced in comparison with non-symbiotic bivalves (Olu *et al.* 1996). Probably the activity of these bacteria is that important that this area is that enlarged. Possibly due to the high productivity of the bacteria the individuals can reach high body lengths. As the tubeworms are completely depending on their symbionts it is imaginable that they have more bacteria inside than the bivalves and therefore are able to reach larger body lengths.

Another feature that is remarkable and quite interesting to solve, is the fact that the tubeworms as r-species have evolved the mechanism of horizontal transmission to obtain their symbionts, while both the bivalves, relatively more K-selected species have evolved the other mechanism, the vertical transmission to obtain their symbionts. I think there might be a relationship between the evolved mechanism of obtaining symbionts by transmission and the evolved colonization strategy. The mechanism of horizontal transmission by vestimentiferans can be seen as a mechanism to let the juveniles disperse to and colonize a new location where no adult vestimentiferan are found yet. If

the progeny of the vestimentiferan obtain their symbionts by vertical transmission it could be that the juveniles will try to settle at an environment already saturated with organisms with the security the progeny probably do not survive as they are not good competitors. For the clams and mussels on the other hand replacement of the adults and thus the remaining of the position in the community is important. By transmitting the chemosynthetic bacteria vertically the progeny do not have to find their own symbiont. Now the progeny only have to compete for space to be able to settle at a suitable environment instead of compete for symbionts and space. Whether there is a relationship between the evolved mechanism of obtaining symbionts by transmission and the evolved colonization strategy would be an interesting feature to investigate.

Succession model

All the three succession models agree that early occupants of a new open site modify the environment in such a way that the habitat becomes unsuitable for further recruitment of early succession species (Connell and Slatyer 1977). The early succession species of the vent and seep system, the vestimentiferan indeed seem to have evolved a mechanism to make the environment less attractive for their own juveniles. As the juveniles do not get their symbionts from their parents (vertical transmission) (Gary *et al.* 1993; Jones and Gardiner 1988), but by horizontal transmission the juveniles need to find their symbionts. (Gary, unpublished in Feldman *et al.* 1997) has found evidence that the symbionts of the vestimentiferans are free-living bacteria at locations where no adult tubeworms are found.

The three models differ mainly in the mechanisms that determine how new species appear later in the sequence and in the causes of death for the early succession species (Connell and Slatyer 1977). In the facilitation and tolerance model the early succession species are eliminated from the community in competition with the later succession species. In the inhibition model early species are killed by local disturbance caused by physical extremes or natural enemies (Connell and Slatyer 1977). In vent and seep systems the early species can sometimes be killed by natural disturbance, when the effluent of the system suddenly diminish or after fluctuations in other geological activities as volcanic activities. But when the succession is not disturbed the vestimentiferan are eliminated in competition with the vesicomyid clams and mytilid mussel (Hessler and Kaharl 1995; Johnson *et al.* 1986; Shank *et al.* 1998). The inhibition model is not valid then, but one of the other two models is. The inhibition model is also not valid as in the model early succession species secure the resources and space and thus inhibit the invasion of new species and suppressed the growth of other species present (Connell and Slatyer 1977). In vent and seep systems vestimentiferan tubeworms are found to lose the competition with the mussels and clams and thus do not suppress any species.

The other two models are left as possibility. The two models do not differ in the cause of death of the early succession species, but do differ in the way new species enter the community (Connell and Slatyer 1977). In the facilitation model the early succession species facilitate the entry of later

succession species. Without the presence of the early ones the later species are not able to colonize the system. While in the tolerance model the early succession species do not seem to facilitate or suppress the later species (Connell and Slatyer 1977).

Around the vestimentiferans a lot of associated organisms are found that either use the tube or the plume of the tubeworms to attach to (Desbruyères and Segonzac 1997). The mussels use both tube and plume as place of attachment (Hessler *et al.* 1988). This could mean that without the presence of the tubeworms the associated organisms are not able to settle and therefore could be concluded that the tubeworms facilitate the settlement of later species. Thus the facilitation model is possibly valid and not the tolerance model.

Further research?

More knowledge about the colonization of reduced systems by the three families, but also other organisms of the reduced systems could be arrived from observations of the succession of newborn sites and new area's created by recent eruptions at existing sites. However it will be a process of chance to detect such a site in time to follow the total succession, therefore it would be preferably to find a mechanism to be able to manipulate the situation more and thus to have control over the situation as much as possible. In plant ecology new open sites are followed for a long period of time after human interference. These new open sites are created by the researches themselves in order to manipulate the situation. They take away the living organisms and follow the recolonization of the new created site. Scientists that investigate the colonization of reduced systems could also use this technique beside observing the colonization process at new sites to have more control over the situation instead of being depending on the chance a new site is created. However, according to my opinion this unique system can hardly be changed in such a way just to serve science. Therefore also another option can be used.

In some research projects the colonization of new sites in both terrestrial and marine ecosystems is investigated by the introduction of a plate of some material as a new site. Mullineaux *et al.* (1998) have used this technique in a hydrothermal vent system. They have introduced basalt plates to create a new open site and followed the colonization of the plates. With this technique of research the similarity of the microorganisms of the existing system and the introduced plate can be tested with 16S rRNA/ DNA sequence. The advantage of this technique is that the experiments can be done with control situations and can be easily repeated, which will provide stronger (statistical) proof. Also the natural situation will not be damaged that much as it would be with the first suggested option. However a problem might be that the introduced plates do not have the same components as the natural system and therefore the colonization of the plates might not be representative for the natural situation. Tubeworms for instance have to be able to bury and make their tube in the plate. Thus this technique have to be used with caution.

Conclusions

- Within the short living and ever-changing vent and seep systems that favor r-selected organisms in the community, vestimentiferan tubeworms seem to be more r-species than the vesicomyid clams and the mytilid mussels that seem to be relatively more K-selected within the r-selected community.
- The succession of reduced systems seems to follow the facilitation model, as the early succession species, the vestimentiferan are eliminated from the system in competition with later succession species, the vesicomyids and mytilids and the presence of the early succession species seem to facilitate settlement of later succession species.

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