Symbiosis, 4 (1987) 37–50
Balaban Publishers, Philadelphia/Rehovot

Review article

A Review of the Relationships Between Bivalve Molluscs and Bacteria in the Marine Environment

DANIEL PRIEUR

Laboratoire de Zoologie
Université de Bretagne Occidentale, 29287 Brest Cedex, France
Tel. 98 03 16 94

Received February 13, 1987; Accepted April 25, 1987

Abstract

The bivalve Molluscs are very common and numerous in the marine environment. Because of the commercial interest of several species (oysters, mussels, clams, scallops), bacteria were first investigated in regard to their effect on food quality. Some bivalve molluscs are known to accumulate fecal bacteria becoming possible sources of human diseases. Recent studies have shown that the accumulation of bacteria is a digestive process which allows the hind gut to contain up to 10^9 bacteria per gram. Depending on the environmental conditions, the composition of the gut microflora may fluctuate, but seems to be mainly composed of bacteria which are active in organic matter degradation. The bivalves are also sensitive to marine pathogenic bacteria and this is particularly evident for the larval forms reared in hatcheries. Vibrios are involved in many larval diseases and recently, the inhibition of mussel filtration by several strains of *Vibrio* was demonstrated. Although they can concentrate bacteria in their gut, bivalves can also feed on bacteria, and lyzozymes have been purified from several species of mytilids. Symbiotic relationships have also been demonstrated for some bivalves. Cellulolytic nitrogen fixing bacteria have been isolated from the gills of wood boring molluscs. Moreover, the discovery of the fauna associated with the deep sea hydrothermal vents, revealed the occurrence of autotrophic sulfur oxidizing bacteria in the gills of two hydrothermal bivalves. Very similar associations were also demonstrated recently in bivalve living in coastal anoxic or oxygenated sediments. External relationships also occur, and the role of the LST strain in the metamorphosis of *Crassostrea gigas* and other species have been demonstrated. For all these

reasons, bivalves are fascinating examples of the possible interactions between bacteria and marine invertebrates.

Keywords: marine bivalves, enteric bacteria, marine bacteria, pathology, trophic interaction, symbiosis, metamorphosis, gut microflora

Abbreviations: LST = code name for a new bacterium, meaning Lewes Spat Tank; (Lewes is the name of a town in Delaware (USA) where a hatchery is located); CFU = Colony Forming Unit

Because some species are appreciated as seafood in many countries, the first bacteriological studies of marine bivalves dealt with their bacteriological quality as human food. The papers on this subject are particularly numerous, the oldest being one century old. Thus, in 1899, Herdmann and Boyce (fide Vasconcelos and Lee, 1972) already considered that oysters could be a possible source for human typhoid diseases, and depuration processes involving filtered seawater were proposed since 1912 (Fabre-Domergue). Enteric and terrestrial bacteria can be concentrated by the bivalves (Kueh and Chan, 1984), and for instance, the survival time of *Vibrio cholerae* inside oysters is around 15 days at 15°C to 30 days at 22°C (Brisou, 1968). Pathogens from the marine environment also, like *Vibrio parahaemolyticus*, can be concentrated, inducing enteric diseases as it has been reported in Japan (Sakasaki, 1969). These diseases are possible, even if the concentration of usual non pathogenic bacteria becomes too high (Buttiaux, 1962, fide Plusquellec, 1984).

Such observations were reported very often; however, only a few studies were carried out in order to understand the process of bacterial accumulation. The main papers were published by Cabelli and Heffernan (1970), and dealt with the accumulation of *E. coli* and other coliforms, by the hard clam, *Mercenaria mercenaria*. These authors noted that the density of bacteria in the bivalve's tissues depended on the bacterial density in seawater. The digestive gland and the siphons were the most contaminated parts of the animals. The level of bacterial accumulation also depends on the filtration activity of the molluscs, which is to a great extent controlled by seawater parameters (temperature, salinity...). Thus, in the case of *Mercenaria*, bacterial density in the clam's meat remains low, even in polluted waters, when the temperature is below 10°C.

The accumulation factors were estimated for several species of bivalves and bacteria. According to Cabelli and Heffernan (1970), with concentrations of 10 to 10^5 *E. coli* per 100 ml of water, the accumulation factor in the hard clam fluctuates between 6.5 and 8.5. In the case of the mussel, *Mytilus*

edulis, Delattre and Delesmont (1981) obtained similar accumulation factors for *E. coli*, but higher values (150), for fecal streptococci. Several hypotheses were proposed to explain these results. Streptococci are usually linked in chains, so, when the mussel's meat is ground before analysis, the chains could be disrupted, increasing the number of colony forming units. But, despite these differences, several authors including Plusquellec (1984), have suggested the use of common bivalves such as mussels to monitor the pollution level of coastal waters, and to eliminate the direct sampling of waters which are often subjected to tide, currents or winds.

Compared to the numerous papers about sanitary microbiology of bivalves, the publications dealing with the natural microflora of these invertebrates are very few. The oldest observations revealed the occurrence of spirochaetes (genus *Cristispira*), living in the crystalline style or in the stomach of bivalves. The type species, *Cristispira pectinis*, was isolated from a mediterranean pectinid, *Pecten jacobeus*, but several observations in bivalves from the Canadian Pacific coast were also reported (Bernard, 1970). However, these bacteria have never been cultivated and isolated in pure culture, so their metabolism and possible role in the mollusc's physiology is not yet understood.

The other publications on this topic concern the heterotrophic bacteria associated with the bivalve's tissues. The first results obtained in this field are rather difficult to summarize, because of the diversity of the methods used. Colwell and Liston (1960), studied the microflora of *Crassostrea gigas* and found the genera *Pseudomonas* and *Vibrio* to be the most abundant components. However, the two genera were not well separated at this time. Lovelace et al. (1968) analysed the microflora of *Crassostrea virginica* from two stations of the Chesapeake Bay. They found different bacteria in the gill filaments and the mantle cavity, according to the sampling station, the genus *Vibrio* being the most abundant in many cases. Murchelano and Brown (1968) studied the microflora of the same species and noted the preponderance of the genus *Pseudomonas*. Brisou (1962), identified 44 strains from *Mytilus galloprovincialis* as *Vibrio*. But he did not give the proportion of the genus among the isolates, and did not indicate the organs (mantle, gills, whole meat) he analysed. Chakroun (1964) studied the bacteria associated with different parts of the mussel, *Mytilus galloprovincialis*. She found the highest densities in the digestive tract, with high proportions of *Achromobacter* and *Vibrio*. More recently, Martin (1976) compared the microflora of mussels and seawater. He also found a large proportion of *Vibrio* within the bivalves, especially in the digestive tract.

Prieur (1981b) studied the bacteria associated with the adults and larvae of *Crassostrea gigas*, *Venerupis semidecussata* and *Mytilus edulis*. The analyses were done on the whole meat and the ambient seawater. Several experiments were undertaken in order to explain the occurrence of this microflora within the larvae and adults of *Mytilus edulis*. The animals were fed with different types of bacteria, and examined under transmission and scanning electron microscopy. These experiments showed that the mussels could ingest various bacteria, and digest them by an extracellular process in the stomach within 3 or 4 hr. However, some bacteria escaped to lysis by stomach enzymes, and were found, untouched, in the hind gut, where they could remain up to 2 or 3 days before expulsion into the mantle cavity. The above results allowed the proposal of the following hypothesis (Prieur, 1981a). The bacterial cells that enter the digestive tract of the molluscs are submitted to an extracellular digestion in the stomach, or an intracellular digestion in the digestive gland. Some bacteria are not digested because of a poor sensitivity to the mollusc's enzymes (Birkbeck and McHenery, 1982), and then are still viable when they enter the hind gut. Moreover, when the digestive gland is full of food particles, the ingested material goes directly into the hind gut, and so escapes the digestion process. The transit of the gut material (waster and viable cells) takes a long time, up to 3 days (Cabelli and Heffernan, 1970), which allows some bacteria particularly adapted to the gut environment, to survive or to grow. The anaerobic conditions and the low pH of the hind gut (Mathers, 1974) could be particularly favourable for Vibrio-like bacteria. Such an hypothesis could also be proposed to explain the concentration of enteric bacteria in the bivalves, because of some features (facultative anaerobiosis) they have in common with Vibrios.

Very recently, Minet et al. (1987), analysed different organs of the mussel *Mytilus edulis*, including mantle, gills, water of the mantle cavity, digestive mass, and isolated hind gut. They demonstrated that the hind gut is really the place where the bacteria, from marine or continental origins, are accumulated in the bivalves. When the total viable microflora, estimated by the plate count method on Zobell agar was around 10^2 CFU ml^{-1} in seawater, bacterial concentrations in intervalvar water, whole meat and hind gut, were respectively 10^3 to 10^6, and 10^7 to 10^9 CFU g^{-1} humid weight. These results confirmed the role of the intestinal transit in the accumulation of bacteria, and could provide a new method of bivalve analysis in order to improve the detection of human pathogenic bacteria in the marine environment. For instance, during a recent survey (Minet et al., 1987), coliforms were counted

in a range of 0.1 to 10^2 CFU ml^{-1} in seawater, while these bacteria were counted in a range of 60 to 10^5 CFU g^{-1} in the hind gut of mussels living in the same stations. In these cases, the accumulation factor from the seawater to the hind gut fluctuated between 30 and 1000.

However, in this last study, the high proportion of vibrio-like bacteria previously found in the bivalves, has not been noted in all the samples. The results of Barbosa (1987) revealed that the active parameter on the selection of bacteria during the accumulation process is more the ability to degrade organic matter than the facultative anaerobic metabolism. By now, the role of the gut microflora has not been clearly established. However, because of their high density and metabolic activity, the hind gut bacteria could complete the digestive process and provide some dissolved compounds to the bivalves.

The demonstration of the occurrence of living and active bacteria in the gut of the bivalves could raise the question of the existence of trophic relationships. In the case of adults, Zobell and Landon (1937) showed that the growth of *Mytilus californianus* was possible on a bacterial diet. Newell (1965), estimated that the bacteria, and especially bacteria attached to detritus are a component of the bivalve diet. Birkbeck and McHenery (1982) demonstrated the occurrence in the digestive gland of *Mytilus edulis*, of lyzozymes capable to lyse the cell walls of bacteria. These enzymes were identified as N-acetyl-muramyl-hydrolase. Seiderer et al. (1984) demonstrated the occurrence in the crystalline style of the mussel *Choromytilus meridionalis* of lyzozyme-like enzymes, capable of lysing free living bacteria from the water column adjacent to kelp beds. Estimates of the biomass of these bacteria through an upwelling-downwelling cycle suggested that free-living bacteria could meet the estimated nitrogen requirements of the mussels. Moreover, some adaptive changes in the enzyme activity of the style could be possibly induced by the qualitative differences in particulate matter available in the water column.

Only little information is available concerning the larvae. The experiments using larvae and bacteria are critical: the bacterial proliferations are always possible and the addition of bacteria in a larval culture can enhance this danger. So, such results as those of Davis (1953), Masson (1975), are not encouraging. However, Carriker (1956) reared *Mercenaria* larvae with cereals extracts and estimated that the good growth results were due to the presence of a consumable bacterial population in the culture. Hidu and Tubiash (1963) observed a good larval growth, and estimated that it was

due to the presence of an abundant antibiotic resistant population. Martin and Mengus (1977) showed that the addition of bacteria to algal food could improve the larval growth. The ingestion of radio-labelled bacterial cells by larvae was demonstrated by Mengus (1978), and the lysis of bacteria by the mussel larvae was established by Prieur (1981b) using transmission electron microscopy.

The bivalve molluscs are sometimes victims of pathogenic bacteria and several diseases of adults and hatchery reared larvae have been reported. It is rather difficult to appreciate the good or bad health of adult bivalves. Generally, moribund individuals, gaping at the surface of the sediment are sampled as sick animals (Corwell and Sparks, 1967). These workers isolated from moribund and dead oysters (*Crassostrea gigas*) bacterial strains identified as *Pseudomonas enalia*. This bacterium was able, in some laboratory conditions to induce the death of injected animals. Kaneko et al. (1975), isolated an enterobacterium and an unidentified *Vibrio*, as potential pathogens for *Mya arenaria*. These authors pointed out the difficulties encountered when doing experiments with animals which are not in a good physiological state. Thus, Lipowsky and Chew (1972), noted the death of oysters kept in the laboratory to be matured out of season. The mortalities appeared with an increase of temperature, and if a bacterial proliferation of Vibrios occurs, it was considered as a secondary invasion. Tubiash et al. (1973), studied some specimens of *Crassostrea virginica* with cardiac oedema, and isolated several strains of *Vibrio anguillarum*. However, the infection assays with these strains were unsuccessful. Grischkowsky and Liston (1974), after some experiments with *Crassostrea gigas*, estimated that *Vibrio anguillarum* and *Vibrio alginolyticus*, are only facultative pathogens, because they are sometimes observed in healthy oysters. This conclusion was also assumed by Tubiash (1974), who concluded that *Vibrio alginolyticus* has only a limited role in the pathology of adults of *Crassostrea gigas*, but is a real pathogen for the larvae which are very sensitive to this bacterium.

The bacterial pathology of bivalve larvae was discovered and studied in experimental and commercial hatcheries. From moribund larvae of *Mercenaria mercenaria*, Guillard (1959) isolated two pathogenic strains of *Vibrio* and *Pseudomonas*. From larvae of the same species, Tubiash et al. (1965), isolated pathogenic strains identified as *Vibrio* and *Aeromonas*. The disease induced by these bacteria, called "Bacillary necrosis", can destroy completely a culture of larvae within 24 hr. More recently, Disalvo et al. (1978) isolated *Vibrio alginolyticus* from moribund and dead larvae of *Ostrea edulis*

and *Crassostrea gigas*, in a California hatchery. The pathogenic strain produced a water soluble, thermostable exotoxin, which inhibited the swimming of larvae, and contributed to the mortality. This result can be compared to those of McHenery and Birkbeck (1986), who demonstrated that *Vibrio alginolyticus* could produce a toxin which inhibited the filtration activity of adult mussels. Brown and Losee (1978) studied a vibriosis of *Crassostrea virginica*. They established that the pathogenic bacterium, at low concentrations, could invade the larvae and then induce the mortality by producing a toxin. At high concentrations of bacteria, the invasion of the larvae was not necessary, and the toxin also produced teratogenic effects. Brown (1974) identified a strain of *Pseudomonas*, producing a pink pigment which discolors the walls of the rearing tanks. This pathogenic bacterium also produced a toxin, probably linked to the pigment.

At the time of metamorphosis, some bacteria can play an important and favourable role for the pediveliger larvae. It is well known that all the surfaces immersed in seawater are rapidly covered by a bacterial film which precedes the fixation of algae, protozoa and invertebrate larvae. In a hatchery of the United States (east coast), Weiner and Colwell (1982) isolated a new unidentified bacterial strain, named LST. This strain appeared to be able to promote the fixation of the pediveliger larvae of *Crassostrea virginica*. This bacterium produces a black, melanic pigment, a precursor of which is L-dopa (di-hydroxy-phenyl-alanine). This compound could act as a nervous transmitter, and stress the larvae, inducing the fixation. A mutant of this strain (LST-D) was tested with pediveligers of *Ostrea edulis* and *Crassostrea gigas* (Tritar and Prieur, unpublished data). In several cases, collectors prefouled with LST-D, were colonized by higher percentages of larvae. One interesting question is the habitat of such bacteria. Preliminary results of Tritar and Prieur (unpublished data) suggested that these bacteria could be present in the larvae before the metamorphosis.

The previous examples of relationships between bivalves and bacteria concerned species of commercial interest, which have been more studied. However, other kinds of interactions between bacteria and non commercial molluscs, sometimes more fascinating, have been reported during the last 15 years. Their common point is that they take place in the gill filaments, some of them being intracellular.

The wood boring molluscs were mainly studied from a microbiological point of view, in order to demonstrate the occurrence of an associated cellulolytic microflora. The occurrence of such bacteria in the gut was reported

in some cases, but may be considered as a particular gut microflora, depending on the particular habitat of this bivalve. However, Popham and Dickson (1973) examined under transmission electron microscopy a particular structure of the gills of some Teredinids (so-called gland of Deshayes), and found that this organ was composed of Gram negative procaryotic cells. Dean (1978) suggested that because of their food, especially composed of wood and carbohydrates, the woodboring bivalves are nitrogen deficient, and could perhaps balance their nitrogen requirements by a nitrogen fixation, performed by the bacteria of the gland of Deshayes. Trytek and Allen (1980), demonstrated that some essential aminoacids were produced by the gill bacteria. The hypothesis of Dean was verified by Waterbury et al. (1983), who found that these bacteria were both cellulolytic and nitrogen fixing.

The interest of marine biologists in the interactions between bacteria and invertebrates increased considerably with the discovery of the deep sea hydrothermal vents and associated fauna. Among the new species that have been described are two bivalves: *Calyptogena magnifica* and *Bathymodiolus thermophilus*. *C. magnifica*, sampled from several sites on the East Pacific Rise, is a large white shelled species. Its digestive tract is almost straight, and was found empty in the sampled animals. But the gill filaments, observed under TEM, revealed important concentrations of bacterial cells, within the gill cells. Several figures of bacterial division were observed, so indicating the viability of the bacteria which are likely sulfur oxidizing (Fiala-Médioni, 1984). *Bathymodiolus thermophilus* is a smaller species, sampled from all the hydrothermal vents prospected on the East Pacific Rise. Jannasch and Wirsen, (1981) described various morphological types of bacteria attached to the periostracum of the shell. The digestive tract is rather straight, but appeared to be functional and filled of various materials, debris of diatoms, benthic foraminifera, and numerous bacteria (Le Pennec and Prieur, 1984). The gill filaments revealed also associated bacteria, clustered in pockets inside the gill cells. Some bacterial cells seemed to be lysed, and the hypothesis of an uptake of bacteria by the epithelial cells of the gill filaments have been proposed (Le Pennec and Hily, 1984).

These results incited the biologists to examine other species of bivalves living in coastal reduced sediments. The observations were very profitable and new examples of gill associated sulfur oxidizing bacteria were reported in *Lucina florida* (Fisher and Hand, 1984), and *Myrtea spinifera* (Dando et al., 1985) both the species belonging to the family of Lucinaceae. More recently, Bouvy et al. (1986) described two bacterial types associated to the gills of a

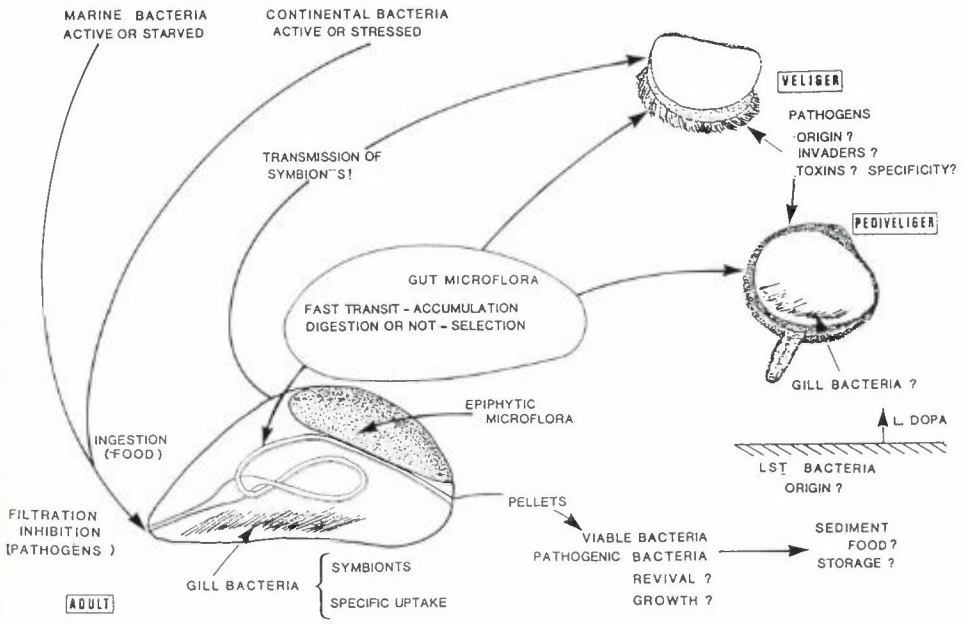

Figure 1. Tentative scheme of interactions between bacteria and bivalve molluscs in the marine environment

littoral bivalve, *Spisula subtruncata*, living this time in oxygenated habitat. These bacteria could be also sulfur oxidising, but this point needs further investigation. But in any case, the bacteria have not been isolated in pure cultures.

The interactions between bacteria and bivalves in the marine environment are summarized in Fig. 1. At this time, some questions seem particularly interesting.

Among the bacteria which are ingested by the bivalves, some cells are probably starved (marine bacteria) or stressed (terrestrial bacteria). If these bacteria escape the digestion process and are accumulated in the hind gut, do they recover their viability and ability to grow in culture, during the intestinal transit?

Concerning the bacteria which seem to be uptaken by the epithelial gill cells, two questions may be raised. Is there any specificity in the uptake? At which stage do the young bivalves start to feed with this process?

In the case of the symbiotic gill bacteria, one of the questions is the stage and the process of infestation, or the possible transmission from the adult to

the larvae.

These points, and some others, have to be solved in the future. As of now, marine bivalves represent a set of fascinating examples of interactions between bacteria and invertebrates in the marine environment and may induce marine biologists to increase investigations in this field.

REFERENCES

Barbosa, T.C. 1987. Le processus d'accumulation des bactéries chez les mollusques bivalves. Etude expérimentale chez *Mytilus edulis*. *Thèse Doct. Océanogr. Biol. Brest*. 134 pp.

Bernard, F. 1970. Occurence of the spirochaete genus *Cristispira* in western Canadian marine bivalves. *Veliger*. **13:** 33–57.

Birkbeck, T.H. and McHenery, J.G. 1982. Degradation of bacteria by *Mytilus edulis*. *Mar. Biol.* **72:** 7–15.

Bouvy, M., Cahet, G., de Billy, F., Soyer, J., Soyer-Gobillard, M-O., and Thiriot-Quievreux, C. 1986. Sur le présence de bactéries dans la branchie d'un Mollusque bivalve littoral *Spisula subtruncata* (Da Costa) (Mactridae). *C.R. Acad. Sci. Paris* **303:** 257–262.

Brisou, J., Tysset, C., Mailloux, M. and Espinasse, S. 1962. Recherches sur les vibrions marins. A propos de 44 souches isolées de moules (*Mytilus galloprovincialis*) du littoral algérois. *Bull. Soc. Path. Exot.* **55:** 260–275.

Brisou, J. 1968. La pollution microbienne virale et parasitaire des eaux littorales et ses conséquences sur la santé publique. *Bull. Hlth. Org.* **38:** 79–118.

Brown, C. 1974. A pigment producing *Pseudomonas* which discolors culture containers of embryos of a bivalve mollusk. *Cheasapeake Sci.* **15:** 17–21.

Brown, C. and Losee, E. 1978. Observations on natural and induced epizootics of vibriosis in *Crassostrea virginica*. *J. Invertebr. Pathol.* **31:** 41–47.

Cabelli, V.J. and Heffernan, W.P. 1970. Elimination of bacteria by the soft shell clam, *Mercenaria mercenaria*. *J. Fish. Res. Bd. Canada* **27:** 1579–1587.

Carriker, M.R. 1956. Biology and propagation of young hard clams, *Mercenaria mercenaria*. *J. Elisha Mitchell Sci. Soc.* **72:** 57–60.

Chakroun, F. 1964. Contribution à l'étude des microflores bactériennes de la moule *Mytilus galloprovincialis* Lamarck. *Thèse de 3ème cycle Océanogr. Biol. Paris.* 110 pp.

Colwell, R. R. and Liston, J. 1960. Microbiology of shellfish. Bacteriological study of the natural flora of pacific oysters (*Crassostrea gigas*). *Appl. Microbiol.* **8:** 104–109.

Colwell, R.R. and Sparks, A.K. 1967. Properties of *Pseudomonas enalia*, a marine bacterium pathogenic for the invertebrate *Crassostrea gigas* (Thunberg). *Appl. Microbiol.* **15:** 980–986.

Dando, P.R., Southward, A.J., Terwilliger, N.B., and Terwilliger, R.C. 1985. Sulphur oxidising bacteria and haemoglobin in gills of the bivalve mollusc *Myrtea spinifera. Mar. Ecol. (Prog. Ser.)* **23:** 85–98.

Davis, H.C. 1953. On food and feeding of larvae of the American oyster, *Crassostrea virginica. Biol. Bull. Woods Hole* **104:** 334–350.

Dean, R.C. 1978. Mechanisms of wood digestion in the shipworm *Bankia gouldi* Batsch: enzyme degradation of celluloses, hemicelluloses and wood cell walls. *Biol. Bull.* **155:** 247–316.

Delattre, J-M. and Delesmont, R. 1981. L'analyse des coquillages peut elle servir au contrôle microbiologique du littoral. *Rev. Int. Oceanog. Med.* **63:** 11–16.

Disalvo, L.H., Blecka, J., and Zebal, R. 1978. *Vibrio anguillarum* and larval mortality in a California coastal shellfish hatchery. *Appl. Environ. Microbiol.* **35:** 219–221.

Fabre-Domergue, M. 1912. Bacterial purification of oysters standing in filtered artificial seawater. *C.R. Acad. Sci.* **154:** 393–395.

Fiala-Médioni, A. 1984. Mise en évidence par la microscopie électronique à transmission de l'abondance de bactéries symbiotiques dans la branchie de Mollusques bivalves de sources hydrothermales profondes. *C.R. Acad. Sci. Paris.* **298:** 487–492.

Fisher, M.R. and Hand, S.C. 1984. Chemoautotrophic symbionts in the bivalve *Lucina florida* from seagrass beds. *Biol. Bull. Woods Hole* **167:** 445–459.

Grischkowsky, R.S. and Liston, J. 1974. Bacterial pathogenicity in laboratory induced mortality of the Pacific oyster (*Crassostrea gigas*, Thunberg). *Proc. Natl. Shellfish Ass.* **64:** 82–91.

Guillard, R.L. 1959. Further evidence of the destruction of bivalve larvae by bacteria. *Biol. Bull. Woods Hole* **55:** 260–282.

Hidu, H. and Tubiash, H.S. 1963. A bacterial basis for the growth of antibiotic treated bivalve larvae. *Proc. Natl. Shellfish Ass.* **54:** 25–39.

Jannasch, H.W. and Wirsen, C.O. 1981. Morphological survey of microbial mats near deep sea thermal vents. *Appl. Environ. Microbiol.* **41:** 528–538.

Kaneko, T., Colwell, R.R., and Hamons, F. 1975. Bacterial studies of Wicomico river soft-shell clam (*Mya arenaria*) mortalities. *Chesapeake Sci.* **16:** 3–13.

Kueh, C.S.W. and Chan, K. 1984. Bacteria in bivalve shellfish with special reference to the oyster. *J. Appl. Bact.* **59:** 41–47.

Le Pennec, M. and Hily, A. 1984. Anatomie, structure et ultrastructure de la brnachie d'un Mytilidae des sites hydrothermaux du Pacifique oriental. *Oceanologica Acta* **7:** 517–523.

Le Pennec, M. and Prieur, D. 1984. Observations sur la nutrition d'un Mytilidae d'un site hydrothermal actif de la dorsale du Pacifique oriental. *C.R. Acad. Sci. Paris* **298:** 493–497.

Lipowsky, V.P. and Chew, K.K. 1972. Mortality of pacific oysters (*Crassostrea gigas*): the influence of temperature and enriched seawater on oyster survival. *Proc. Natl. Shellfish Ass.* **62:** 72–82.

Lovelace, T.E. Tubiash, H. and Colwell, R.R. 1968. Quantitative and qualitative commensal bacterial flora of *Crassostrea virginica* in Chesapeake Bay. *Proc. Natl. Shellfish Ass.* **62:** 72–82.

McHenery, J.G. and Birkbeck, T.H. 1986. Inhibition of filtration in *Mytilus edulis* L. by marine vibrios. *J. Fish Dis.* **9:** 257–261.

Martin, Y. 1976. Importance des bactéries chez les mollusques bivalves. *Haliotis.* **7:** 97–103.

Martin, Y.P. and Mengus, B.M. 1977. Utilisation de souches bactériennes sélectionnées dans l'alimentation des larves de *Mytilus galloprovincialis* Lmk (Mollusque bivalve) en élevages expérimentaux. *Aquaculture* **10:** 253–262.

Masson, M. 1975. Etude expérimentale de la croissance et de la nutrition de la larve de *Mytilus galloprovincialis* (Lmk) (Mollusque pélécypode). *Thèse 3ème cycle Univ. Caen.* 91 pp.

Mathers, N.F. 1974. Digestion and pH variation in two species of oysters. *Proc. Malac. Soc. Lond.* **41:** 37–40.

Mengus, B. 1978. Rôle des bactéries dans l'alimentation de larves de mollusques bivalves marins, en élevages expérimentaux. *Thèse 3ème cycle Océanogr. Biol. Univ. Aix-Marseille II.*

Minet, J., Barbosa, T., Prieur, D., and Cormier, M. 1987. Mise en évidence du processus de concentration des bactéries par la moule *Mytilus edulis* (L.). *C.R. Acad. Sci. Paris. sous presse.*

Murchelano, R.A. and Brown, C. 1968. Bacteriological study of the natural flora of the eastern oyster, *Crassostrea virginica. J. Invertebr. Pathol.* **11:** 520–521.

Newell, R.C. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae*, and the bivalve *Macoma baltica. Proc. Zool.Soc. Lond.* **143:** 25–45.

Plusquellec, A. 1984. Contribution à l'étude de la pollution bactérienne des eaux littorales. Cas particulier de la Baie de Concarneau- La Forêt. *Thèse Doct. 3ème cycle. Brest.*

Popham, J.D. an Dickson, M.R. 1973. Bacterial associations in the Teredo *Bankia australis* (Lamellibranchia: Mollusca). *Mar. Biol.* **19:** 338–340.

Prieur, D. 1981a. Experimental studies of trophic relationships between marine bacteria and bivalve molluscs. *Kiel Meerersf.* **5:** 376–383.

Prieur, D. 1981b. Les relations entre les mollusques bivalves et les bactéries hétérotrophes en milieu marin. Etude analytique et expèrimentale. *Thèse Doc. es Sc. nat. Brest.* 266 pp.

Sakasaki, R. 1969. Halophilic vibrio infections in "Food borne infections and intoxications". Academic Press, New York, pp. 115–118.

Seiderer, L.J., Davis, C.L., Robb, F.T., and Newell, R.C. 1984. Utilisation of bacteria as nitrogen resource by kelp-bed mussel *Choromytilus meridionalis. Mar. Ecol. (Prog. ser.)* **15:** 109–116.

Trytek, R.E. and Allen, W.V. 1980. Synthesis of essential aminoacids by bacterial symbionts in the gills of the shipworm *Bankia setacea* (Tryan). *Comp. Biochem. Physiol.* **67:** 419–427.

Tubiash, H.S. 1974. Single and continuous exposure of the adult American oyster *Crassostrea virginica* to marine vibrios. *Can. J. Microbiol.* **20:** 513–517.

Tubiash, H.S., Chanley, P.E., and Leifson, E. 1965. Bacillary necrosis, a disease of larval and juvenile bivalve mollusks. *J. Bacteriol.* **103:** 272–273.

Tubiash, H.S., Otto, S.V., and Hugh, R. 1973. Cardiac oedema associated with *Vibrio alginolyticus* in the American oyster. *Proc. Natl. Shellfish Ass.* **63:** 39–42.

Vasconcelos, G.J. and Lee, J.S. 1972. Microbial flora of Pacific oysters (*Crassostrea gigas*) subjected to ultra-violet-irradiated seawater. *Appl. Microbiol.* **23:** 11–16.

Waterbury, J.B., Turner, R.D., and Calloway, C.B. 1983. A cellulolytic nitrogen-fixing bacterium form the gland of Deshayes in shipworms (bivalvia: Teredinidae). *Science* **221:** 1401–1403.

Weiner, R.M. and Colwell, R.R. 1982. Induction of settlement and metamorphosis in *Crassostrea virginica* by a melanin-synthesizing bacterium. *Tech. Rep. Maryland Sea Grant Prog.* **UM. SG. TS.82.05.** 43 pp.

Zobell, C.E. and Landon, N.A. 1937. Bacterial nutrition of the California mussel. *Proc. Soc. Exp. Biol. N.Y.* **36:** 607–609.