

The boring sponge *Cliona vastifica* in a subarctic population of *Chlamys islandica* – An example of balanced commensalism?

Dagmar Barthel

Abteilung Meeresbotanik, Institut für Meereskunde, Kiel, Germany

Jan Sundet

Norwegian Institute for Fisheries and Aquaculture, Breivika, Tromsø, Norway

Klaus-Günther Barthel

The Norwegian College of Fishery Science, University of Tromsø, Norway (Currently: Commission of the European Communities, DG XII/D3 - Mast Programme, Brussels, Belgium)

ABSTRACT: The investigation was performed on a stable population of the edible Iceland Scallop *Chlamys islandica* (Müller) in the subarctic Balsfjord, Tromsø, Northern Norway. 470 *Chlamys* specimens were collected and dry weight of the soft parts and of the shell, height of the shell, age of the animal and number of holes bored into each valve were determined. The population was found to be heavily infested by the boring sponge *Cliona vastifica* Hancock, which is here close to its northern distribution limit. Nearly 90 % of all scallops had borings in their shells. Only specimens with an age of 3 years and less and a shell height of 35 mm or less were not infested. 100 % of scallops aged 16 years or more harbour *C. vastifica* in their shells. The average degree of infestation as judged by number of borings in the shell increases with age. However, statistical analysis of the relation of number of borings to both scallop body mass and shell weight at certain shell sizes indicates that *C. vastifica* does not impair the development of its substrate clams. The reason for this is the high growth rate of *Chlamys islandica* in a fully suitable habitat and the comparatively low growth rate of *Cliona vastifica* living close to the limit of its geographical distribution; this long-term coexistence may represent a subtle balance between the commensalistic boring sponge and substrate bivalve hardly possible in warmer areas.

1 INTRODUCTION

In tropical and subtropical areas, many species of boring sponges are well known to be major agents in bioerosion of both biogenic and non-biogenic (e.g. Neumann, 1966; Pang, 1973; Thomas, 1979) calcareous substrates. In living coral reefs, activities of boring sponges can be strong enough to balance or even supersede rates of calcification (e.g. Hein & Risk, 1975), and can lead to the production of large amounts of fine grained calcareous sediments (Fütterer, 1974; Rützler, 1975; Moore et al., 1976; Moore & Shedd, 1977). In both tropical and temperate waters boring sponges contribute to the breakdown of accumulations of subfossil shell material (Akpan & Farrow, 1985; Young & Nelson, 1985) and heavily infest living shellfish populations (Hopkins, 1956a,b; Warburton, 1958a,b; Evans, 1969; Comely, 1978; Krakatitsa & Kaminskaya, 1979; Thomas, 1979). The latter case can have severe economic consequences for oyster farmers; oyster shells with many borings in them are so soft that they break when they are opened for consumption, and besides, even a mild infestation with boring sponges will lead to an unappetizing odor when the sponges in the shells die upon removal of oysters from the water (e.g. Warburton, 1958a). Also pearl oysters can suffer when infested with boring sponges; the animals are weakened, the pearl formation process can be inhibited and mass mortality can ensue (Korringa, 1952;

Algarswami & Chellam, 1976; Thomas, 1979). When the infestation in oysters reaches the attachment area of the adductor muscle, the ability to close the valves is impaired or even destroyed. In an *Ostrea edulis* population in the Black Sea infested with *Cliona vastifica*, Krakatitsa & Kaminskaya (1979) observed polychaetes, sponges and amphipods to settle in the mantle cavity of oysters that could not close their valves properly anymore. Disturbance by these organisms and easy accessibility to predators resulted in mass mortality in these oyster beds.

Even though represented by relatively few species only, boring sponges do occur in northern temperate waters (e.g. Hartman, 1958), in dead shell accumulations as well as in living shellfish populations. During investigations on various aspects of the biology and physiology of a population of the edible Iceland Scallop *Chlamys islandica* (Müller) in the Balsfjord, Northern Norway (e.g. Vahl, 1981a,b, 1982; Sundet & Lee, 1984) this population was found to be infested with boring sponges. *C. islandica* occurs in a number of Norwegian fjords north of the Arctic Circle. These fjords have one or more sills at the entrance, ensuring low bottom temperatures (Wiborg, 1963; Wiborg & Böhle, 1968). Balsfjord also conforms to this pattern, with a bottom temperature of 2°C (March) to 8°C (August) at the site of the *Chlamys*-population (Vahl, 1978).

The questions arose which species of boring sponges

infested *C. islandica*, how strong the infestation was and whether it would influence the physical condition of the scallops.

2 MATERIAL AND METHODS

In summer 1984, samples were taken from a population of *Chlamys islandica* at 32 m depth at Nordberg in the subarctic Balsfjord, Northern Norway (69°35'N 18°54'E) (Fig. 1), where dense populations of *C. islandica* occur on soft bottoms. The population was sampled by towing a triangle dredge (5 min at a speed of 0.5 - 1 knot) and 470 live, intact scallops were collected at random from the catch. In the laboratory, the following data were recorded for each scallop: height of shell, age (by counting seasonal shell growth rings), where possible sex, dry weight of soft parts (dried at 60°C for 48 h), and number of surface papillar borings and dry weight (dried at 60°C for 24 h) of each valve (including the boring sponge dry mass in infested scallops). Dried valves were freed of any epifauna prior to weight determination and holes were recorded using penetrating light. The number of borings (sum of the two shells) was taken as a parameter for the degree of infestation, and classes of animals with 0-5 holes (negligible infestation), 6-50 holes (light infestation), 51-200 holes (medium infestation) and more than 200 holes (severe infestation) were erected. In 83 specimens, only one of the shells was analysed for borings, as part of the sample disappeared during the drying procedure. For another 29 specimens data on shell

weight or age respectively were not complete so that a total of 358 full data sets were available for statistical analysis. A total of 12 shells randomly chosen from the same site in 1989 were subjected to X-raying.

In order to test whether infestation of *Chlamys islandica* with boring sponges would lead to an impairment or enhancement of growth of soft tissue, shell or both, a number of different relations were tested by means of regression analysis. The relations tested were: 1) Shell weight vs. hole number at constant shell height; 2) shell weight vs. shell height in different infestation classes, both in order to analyze whether shells get on average lighter with increasing infestation as a result of sponge excavating or whether they would get on average heavier because of repairs made by the scallop; 3) shell height vs. age separated into different infestation classes, in order to analyse whether animals with comparable age but different degree of infestation would have different size; 4) dry weight soft tissue vs. shell height separated into different infestation classes, in order to test whether amount of soft tissue of *C. islandica* in a given size class would decrease with increasing degree of infestation, thus indicating tissue growth inhibition.

3 RESULTS

Analysis of shell height and of the scallop sample showed it to consist of animals with shell heights between 19 and 93 mm of ages between 2 and 21 years. Boring holes were visible on the outer surface of many individuals, as well as repairs of bored areas on the inner side of the valves. Spicule analysis of the boring sponges in 12 scallops taken from the same location in spring and summer 1989 showed that the borings were due to the action of the sponge *Cliona vastifica* Hancock, 1849. The numbers of borings in the scallop shells ranged from 0 to 601, and the holes were usually distributed unevenly over the two valves (Fig. 2). X-ray inspection of shells of individuals collected in 1989 showed infested valves to be inhabited by one sponge individual only (Fig. 3), as can be seen by the continuous network of excavations. In some cases, there remain only thin bridges of shell substance in between the cavities. However, the inner shell substance is never completely removed. Usually, diameter of cavities and density of cavity distribution decrease from the hinge area towards the front margin (compare Fig. 3).

The degree of infestation with boring sponge is high in *Chlamys islandica* from Balsfjord: Out of the 470 individuals where records on hole numbers exist, 330 animals where both valves were analyzed and 60 animals where only one valve was analyzed, i.e. a total of 390 animals or 83 %, were definitely infested. Only 57 specimens were found to be without any holes; this means that 12 % of the population are definitely not infested. The remaining 23 animals (5 %) where one shell only was analyzed did not show holes. Of these

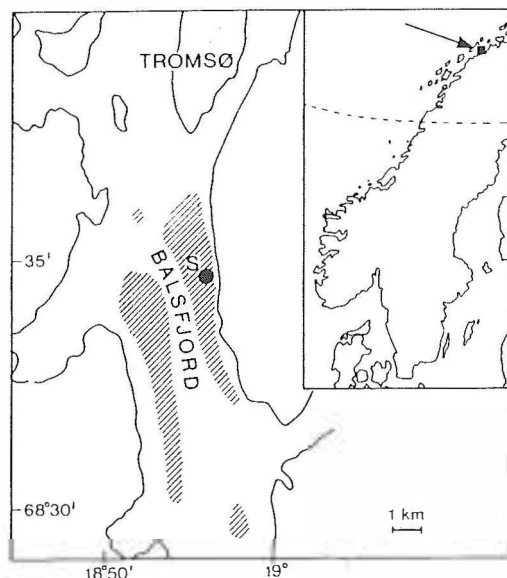


Figure 1. Study area, hatched areas indicate extension of *Chlamys islandica* beds, S is the sample location. From Vahl (1981a).

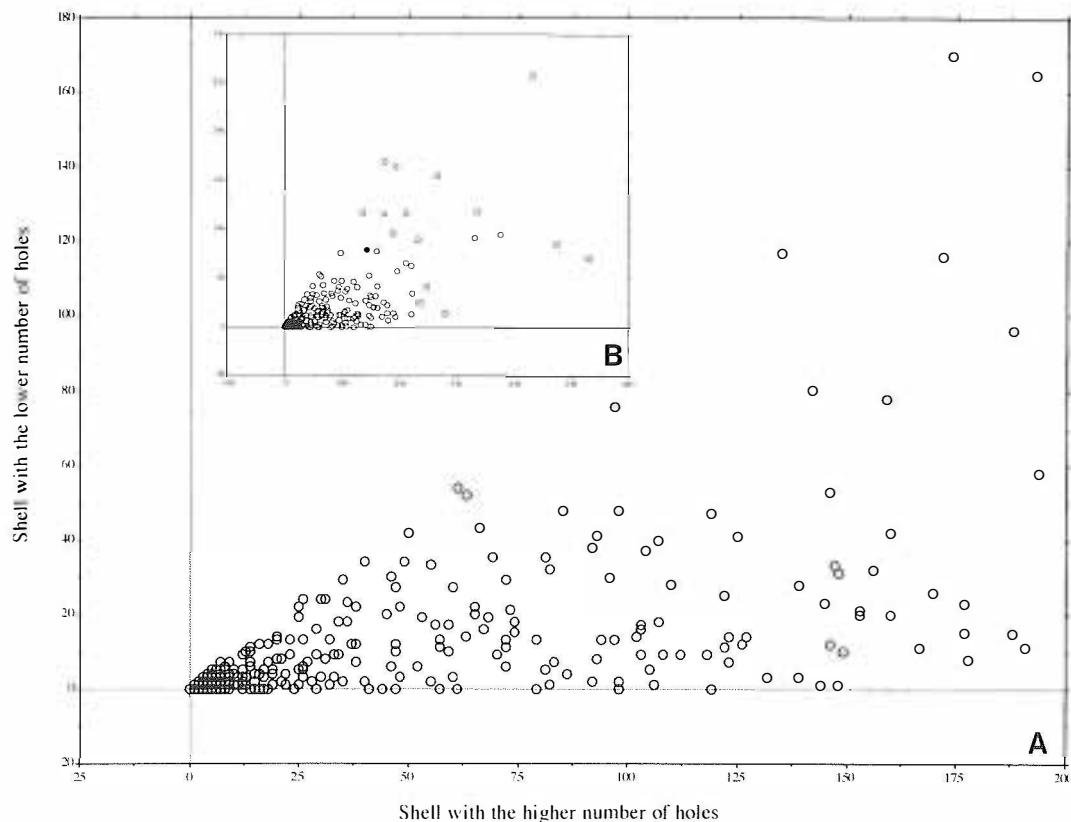


Figure 2. *Cliona vastifica* borings in the two valves of *Chlamys islandica*, consisting of 358 complete data sets. The data are organised to show the value for the valve with more holes on the x-axis, the lower number of holes on the y-axis. Degree of infestation is unequally distributed over the two valves; A. shows data for individuals with up to 200 borings per shell, B. shows the whole data matrix.

we cannot know how many had holes in the other shell, but the proportion of infested scallops in the sample lies somewhere between 83 % (minimum, if the second valve of all 23 specimens were not bored either) and 88 % (maximum if the second valve of all 23 specimens were bored) of the whole sample.

The analysis of boring sponge infestation with regard to shell size (Fig. 4) shows that in animals of up to 65 mm shell height, 90 % of the scallops have only negligible infestation; in animals larger than that, there is a drastic increase in the proportion of infested animals as well as in the average degree of infestation. The boring sponges virtually take over in the older, slow growing individuals.

The degree of infestation, both as to number of scallops bearing *C. vastifica*, as well as to average number of holes is higher in older animals (Fig. 5). Only scallops of an age of 3 years or less are virtually free from boring sponges, up to an age of about 8 years the largest part (85 %) of the scallop population is only infested to a negligible degree (0 to 5 holes). 48 % of the animals in age class 9 were found to have a light

infestation (6 to 50 holes). In animals older than 9 years, there is a marked decrease in the proportion of negligibly and lightly infested animals, and about 45 % of animals have a medium infestation. Above the age of 15, only one single 20 year old scallop has a negligible infestation, while the proportion of medium and severe infections is by far the largest in the older animals. The number of severely infested animals is usually much lower than that of lightly and medium infested scallops, except for the very largest size class of 86-93 mm shell height. The proportion of severely infested animals does not increase to the same degree, as with the other infestation classes.

As regards the statistical tests of a relationship between condition parameters and degree of infestation, in no case could there be shown any significant relation to the number of holes, i.e. the degree of infestation. The only relation showing at least slight trends is that of shell weight to hole number at constant shell height (Fig. 6): Shells of the same size get increasingly heavier with increasing number of holes. However, the relation is not statistically significant.

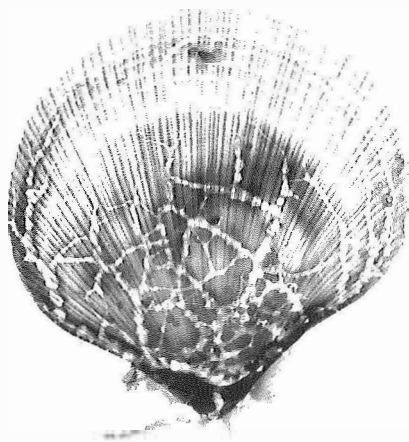


Figure 3. X-radiograph of a *Chlamys islandica* valve showing the string of pearl-like cavities typical for the action of *Cliona vastifica*. The infestation starts at the umbral region and is effected by a single sponge specimen, as can be seen by size and density of cavities decreasing towards the shell margin. Natural size.

4 DISCUSSION

Vahl (1978) gives 20-21 years as maximum age of the animals found by him and 23 years as the absolute maximum age of scallops found in this population. Thus, the sample of *Chlamys islandica* taken for this study covers the usual age spectrum of this scallop population. The age/frequency structure of the population at this site can vary very much between years (Vahl, 1982), so we cannot state whether all age classes present were sampled representatively. However, the sample used by us contains a higher number of older, larger specimens than encountered by Vahl (1982) in the years 1971 to 1979.

The only boring sponge species encountered in the scallop population in 1989 is *Cliona vastifica*. This species is cosmopolitan (compare Volz, 1939; Hopkins, 1956 a,b; Tendal, 1973), found to excavate a variety of substrates including limestone (Adriatic: Volz, 1939), coralline algae, corals, and shells of many gastropods and bivalves (Indian Seas: Thomas, 1979). In the North Atlantic it is wide-spread with the northern distribution limit at Vardø, Northern Norway (Bromley & Hanken, 1981). Thus Balsfjord lies close to the distribution limit of *C. vastifica*. Even though no sponge spicule preparations were made of the sponges in the shells of the 1984 sample, we can be fairly certain that no other boring sponge species is involved: The cavities in the shells of this sample conform to the string-of-pearl like pattern typical for *C. vastifica*. Furthermore, no other

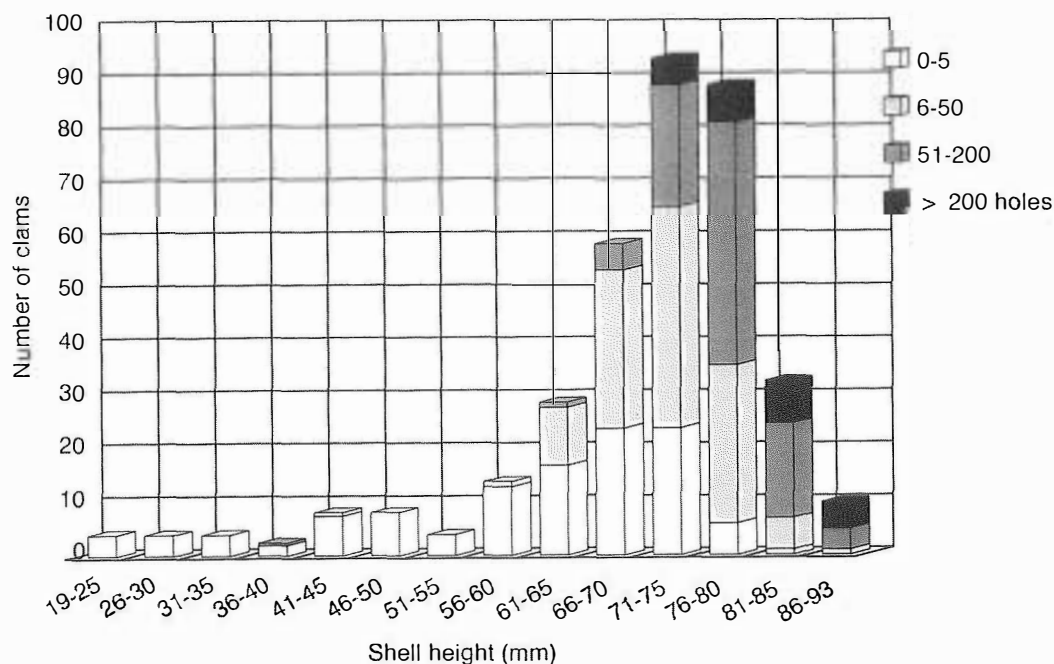


Figure 4. Size-specific degree of infestation of *Chlamys islandica* with *Cliona vastifica*. Numbers of holes summed up over both valves, n = 358.

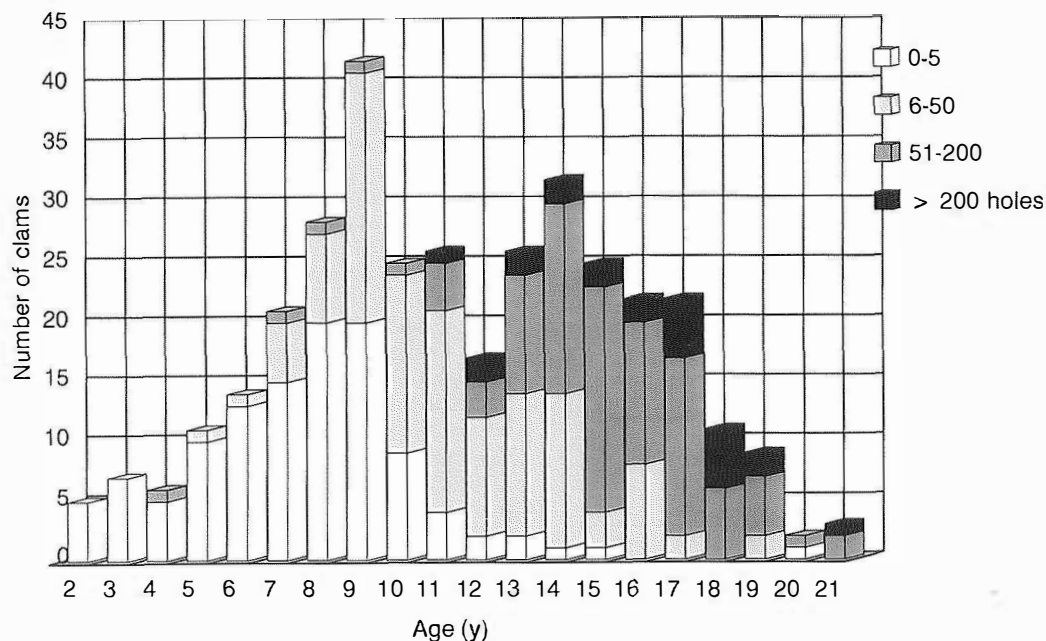


Figure 5. Age-specific degree of infestation of *Chlamys islandica* with *Cliona vastifica*. Numbers of holes summed up over both valves, n = 358.

boring sponge species has been found to occur in the area (e.g. own unpublished observations).

The unequal distribution of the number of holes in the two valves of the scallop is obvious. It is the result of the infestation starting on one valve and spreading to the other. As no distinction between right and left valves was made at the time of hole counting, we cannot ascertain whether the infestation in *Chlamys islandica* always starts at the same spot; but autoradiographs of excavated *Chlamys* shells show the infestation with the sponge usually to begin at the hinge region, from where it extends over the rest of the valve. This agrees with the results of Evans (1969), who found New Foundland *Pecten magellanicus* to be infested from the umbo region or, occasionally, from the margin of the lower valve. He attributes this find to a preferential settlement of *C. vastifica* larvae on the lower valve because of negative phototaxis (Evans, 1969). However, he has not actually observed this larval behaviour. Hartman (1958) observed certain undifferentiated papillae of *C. vastifica* to produce linear bulbous expansions, which after some time come loose from the mother sponge; these bulbs might grow large enough to touch the next shell and make contact there. These reports together with the finds from our own X-radiographs lead us to the assumption that infestation in the Balsfjord *Chlamys islandica* usually starts at the lower umbonal region and spreads from there. Also in other species of bivalves it was found that infestation

usually starts on the same side of the animal: Edible oysters of the genera *Ostrea* and *Crassostrea* are usually infested at the attached valve first, with the sponge spreading onto the free valve (Hopkins, 1956b; Warburton, 1958a; Krakatitsa & Kaminskaya, 1979; Thomas, 1979). Also in these cases, a spreading from a neighboring infested individual is proposed.

All shells X-rayed by us had only one sponge individual boring in them, as could be seen by the continuous network borings. At present, it is not possible to say whether this is the result of an avoidance behaviour by a *C. vastifica* larva to settle on a shell already bored by an individual of the same species or whether statistically each scallop is found by one boring sponge larva only. Avoidance behaviour of adult specimens of *Cliona celata* has been observed by Bromley & Tendal (1973), who found phototropism of two specimens of *C. celata* boring in the same valve of *Arctica islandica*. In the zone where the two specimens came close to each other, both made only thin canals, which were not developed into the normal wide excavations. This suggests a contact avoidance reaction (Bromley & Tendal, 1973).

Judging from the sample analyzed, the overall degree of infestation of *C. islandica* with *C. vastifica* (between 83 and 88 % of the population) is high compared with what was found in most other bivalve populations (Table 1). And even if we consider just the part of the population within the age range found by Vahl (1982)

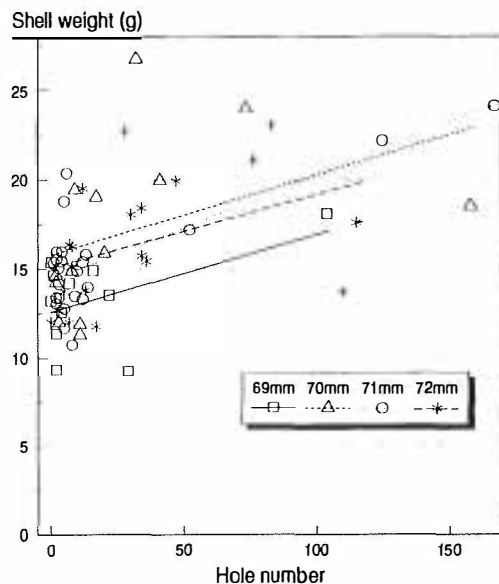


Figure 6. Example of relation of shell weight to number of borings in different size classes of *C. islandica*. Shell weight increases slightly with increasing degree of infestation, but the relation is not statistically significant.

between 1971 and 1979, i.e. up to 14 years of age, the degree of infestation would still be between 80 and 85 % and thus very high as compared to other situations. Obviously, the subarctic population of *Chlamys islandica* is able to survive a much higher degree of boring sponge infestation than the tropical and temperate populations of other bivalves. In fact, the distribution of the infestation over size and age classes of *Chlamys* and the absence of significant changes in the relation of e.g. tissue weight to shell size or age in heavily infested specimens as compared to only lightly infested specimens indicates that the bivalves are not damaged by the

action of the boring sponges to more than a negligible degree during most of their life span. The characteristics of the infestation with scallops of up to 3 years not visibly bored, young animals generally with little damage and old animals with high infestation rates conform with observations on other bivalve species (e.g. Korringa, 1951). Warburton (1958 a) suggests that initially, small sponges have an absolute low size increase, while the young bivalve grows very quickly; later, the sponges increase in size more rapidly, because their size specific growth rate remains constant, while the growth rate of the ageing host bivalve decreases. In the case of the *Cliona/Chlamys* combination in Balsfjord, we may observe a very subtle balance between two commensals, the boring sponge and its host: While the arctic species *Chlamys islandica* lives in what can be considered an optimal habitat, does the temperate water species *Cliona vastifica* live close to the northern limit of its geographic distribution with temperatures much below the optimum for quick growth. Thus, the medium and severe infections found predominantly in scallops older than 9 years and larger than 65 mm shell height probably are the result of a comparatively low overall growth rate of the boring sponge. The fact that the proportion of severely infested animals is low in the very large scallops, may also be an indication of scallop death as an eventual result of stress by repair activity in a less active life stage or fragmentation of the shell, so the heavily infested animals are constantly removed from the population; it might also indicate slowing down of sponge growth when the point of substrate exhaustion is approaching, i.e. "substrate management" on the side of the boring sponge.

In his study on the energy budget of *Chlamys islandica* Vahl (1981a) found that the net growth efficiency decreases rapidly in animals older than 7 years and Sundet (unpubl. data) observed the reproductive output of scallops with shell sizes of more than 70 mm height to drop sharply. This implies that the heavy infestation by boring sponges would in any case

Table 1. Infestation of bivalve populations with boring sponges of the genus *Cliona*.

Location	boring sponge spec.	Bored bivalve spec.	% individuals bored	Reference
Indian waters	<i>Cliona celata</i> Grant	Pearl oyster (<i>Pinctada fucata</i>)	20.7	Algarswami & Chellam (1976)
Indian waters	<i>Cliona vastifica</i> <i>C. celata</i>	Pearl oyster (<i>Pinctada fucata</i>)	8.5	Thomas (1979)
Scotland	<i>C. celata</i>	Horse mussel (<i>Modiolus modiolus</i>)	36 23 - 47.6	Comely (1978)
Black Sea	<i>C. vastifica</i>	Edible oyster (<i>Ostrea edulis</i>)		Krakatitsa & Kaminskaya (1979)
North Atlantic (South Carolina)	<i>C. celata</i> , <i>C. lobata</i> , <i>C. vastif.</i> , <i>C. truiti</i>	Oysters (no species name given)	15 - 100, depending on station	Hopkins (1956)

hit specimens past their maximum contribution to overall production. The only indication of an influence of *C. vastifica* on *Chlamys islandica* is the slightly higher relative weight in heavily bored shells as compared to little bored shells, but this correlation was not found to be significant. The shell weight increase may be due to repairs of holes going through to the mantle cavity, or to presence of sponge spicules in the shells. In oysters, the energy expenditure for shell repairs is thought to be one of the factors leading to a bad physiological condition (for a discussion see e.g. Thomas, 1979). However, in contrast to scallops, oysters have to lay down considerable layers of conchiolin in their shells (e.g. Herdman & Hornell, 1904). Korringa (1952) gives a proportion of 4 % conchiolin in the prismatic layers of *Ostrea edulis* and confirms Topsent's (1900) observation that oysters repair breakthroughs of boring sponges by secreting patches of conchioline (Korringa, 1951). The energy expenditure on laying down sheer calcareous substance is certainly lower and this may be an additional reason for the tolerance of *C. islandica* against *Cliona vastifica*. This way, there is no danger of *Cliona* overexploiting its own substrate in an environment which otherwise hardly offers other suitable substrate. Even the shells of dead *Chlamys* have to be considered inferior as substrate, because they will easily be covered with sediment.

ACKNOWLEDGEMENTS

Part of the study was performed while D.B. and K.-G.B. held fellowships awarded by the Norges Almenvitenskapelige Forskningsråd (NAVF) and the Norges Teknisk Naturvitenskapelige Forskningsråd (NTNF) respectively. The authors thank Prof. Dr. C.C.E. Hopkins from the Norwegian College of Fishery Science, University of Tromsø, for his continuing support. The members of the Marinbiologisk Stasjon and the crew of its ships gave valuable assistance during the sampling procedure. We are grateful to Dr. Ole Tendal, Zoological Museum of the University of Copenhagen for helping with sponge identification and for critically reading this manuscript. Mr. Tammes Menne, Zoological Museum University of Copenhagen, kindly supplied the X-ray photographs.

REFERENCES

- Akpan, E.B. & G.E. Farrow 1985. Shell bioerosion in high-latitude low-energy environments: Firths of Clyde and Lome, Scotland. *Mar. Geol.* 67: 139-150.
- Algarwami, K. & A. Chellam 1976. On fouling and boring organisms and mortality of pearl oysters in the farm at Veppalodai, Gulf of Mannar. *Indian J. Fish.* 23 (1-2): 10-22.
- Bromley, R.G. & N.-M. Hanken 1981. Shallow marine bioerosion at Vardø, arctic Norway. *Bull. geol. Soc. Denmark* 29: 103-109.
- Bromley, R.G. & O.S. Tendal 1973. Example of substrate competition and phototropism between two clonid sponges. *J. Zool. London* 169: 151-155.
- Comely, C.A. 1978. *Modiolus modiolus* (L.) from the Scottish West Coast. I. Biology. *Ophelia* 17(2): 167-193.
- Evans, J.W. 1969. Borers in the shell of the Sea Scallop, *Placopecten magellanicus*. *Am. Zool.* 9: 775-782.
- Fütterer, D.K. 1974. Significance of the boring sponge *Cliona* for the origin of fine grained material of carbonate sediments. *J. sediment. Petrol.* 44(1): 79-84.
- Hartman, W.D. 1958. Natural history of the marine sponges of southern New England. *Bull. Peabody Mus. nat. Hist.* 12: 1-155.
- Hein, F.J. & M.J. Risk 1975. Bioerosion of coral heads: Inner patch reefs, Florida Reef tract. *Bull. mar. Sci.* 25(1): 133-138.
- Herdman, W.A. & J. Hornell 1904. Anatomy of the pearl oyster. (*Margaritifera vulgaris*, Schum.). In: W.A. Herdman (ed.), *Report to the Government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar, Part II*: 37-76 London: The Royal Society.
- Hopkins, S.H. 1956a. The boring sponges which attack South Carolina Oysters, with notes on some associated organisms. *Contr. Bear Bluff Lab.* 23: 1-30.
- Hopkins, S.H. 1956b. Notes on the boring sponges in gulf coast estuaries and their relation to salinity. *Bull. mar. Sci.* 6(1): 44-58.
- Korringa, P. 1951. The shell of *Ostrea edulis* as a habitat. *Arch. Néerland. Zool.* 10: 32-152.
- Korringa, P. 1952. Recent advances in oyster biology. *Quart. Rev. Biol.* 27: 266-308.
- Krakatitsa, T.F. & L.D. Kaminskaya 1979. Boring activity of sponges - pests of Black Sea oyster beds. *Biologia Morya* 6: 15-20 (translated by the Plenum Publishing Corporation 1980).
- Laubenfels, M.W. de 1947. Ecology of the sponges of a brackish water environment at Beaufort, N.C. *Ecol. Monogr.* 17: 31-46.
- Moore, C.H. & W.W. Shedd 1977. Effective rates of sponge bioerosion as a function of carbonate production. In: D.L. Taylor (ed.), *Proc. 3d. Int. Coral Reef Symp. 2, Geology*: 449-505. Miami: Rosenstiel School.
- Moore, C.H., E.A. Graham & L.S. Land 1976. Sediment transport and dispersal across the deep fore-reef and island slope (-55 m to -305 m), Discovery Bay, Jamaica. *J. sediment. Petrol.* 46: 174-187.
- Neumann, A.C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Clionalampa*. *Limnol. Oceanogr.* 11(1): 92-108.
- Pang, R.K. 1973. The systematics of some Jamaican excavating sponges (Porifera). *Postilla Peabody Museum* 161: 1-75.
- Rützler, K. 1975. The role of burrowing sponges in bioerosion. *Oecologia (Berlin)* 19: 203-216.
- Sundet, J.H. & J.B. Lee (1984). Seasonal variations in gamete development in the Iceland Scallop, *Chlamys islandica*. *J. mar. biol. Ass. U.K.* 64: 411-416.
- Tendal, O.S. 1973. De danske farvandes boresvampe. *Flora og Fauna* 79: 105-108.
- Thomas, P.A. 1979. Boring sponges destructive to economically important molluscan beds and coral reefs in Indian seas. *Indian J. Fish.* 26 (1-2): 165-200.

- Vahl, O. 1981a. Energy transformations by the Iceland Scallop, *Chlamys islandica* (O.F. Müller), from 70°N. I. The age-specific energy budget and net growth efficiency. *J. exp. mar. Biol. Ecol.* 53: 281-296.
- Vahl, O. 1981b. Energy transformations by the Iceland Scallop, *Chlamys islandica* (O.F. Müller), from 70°N. II. The population energy budget. *J. exp. mar. Biol. Ecol.* 53: 297-303.
- Vahl, O. 1982. Long-term variations in recruitment of the Iceland Scallop, *Chlamys islandica* from Northern Norway. *Neth. J. Sea Res.* 16: 80-87.
- Volz, P. 1939. Die Bohrschwämme (Clioniden) der Adria. *Thalassia* 3(2): 1-64.
- Young, H.R. & C.S. Nelson 1985. Biodegradation of temperate-water skeletal carbonates by boring sponges on the Scott Shelf, British Columbia, Canada. *Mar. Geol.* 65: 33-45.
- Warburton, F.E. 1958a. The effects of boring sponges on oysters. *Fish. Res. Board Canada, Atl. Prog. Rept.* 68: 3-8.
- Warburton, F.E. 1958b. Control of the boring sponge on oyster beds. *Fish. Res. Board Canada, Atl. Prog. Rept.* 68: 7-11.
- Wiborg, K.F. 1963. Some observations on the Iceland Scallop *Chlamys islandica* (Müller) in Norwegian waters. *Fisk. Dir. Skr., Ser. Havunders.* 13: 38-53.
- Wiborg, K.F. & B. Bøhle 1968. Forekomster av matnyttige skjell (muslinger) i norske kystfarvann. *Fiskets Gang* 54: 149-161.