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Article *in* Hydrobiologia · August 2003

DOI: 10.1023/B:HYDR.0000008495.24479.4f

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Hydrobiologia **503:** 131–141, 2003.
M.B. Jones, A. Ingólfsson, E. Ólafsson, G.V. Helgason, K. Gunnarsson & J. Svavarsson (eds), Migrations and Dispersal of Marine Organisms.

Settlement of bivalve spat on artificial collectors in Eyjafjordur, North Iceland

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Key words: artificial collectors, bivalve settlement, byssal drifting, Iceland, secondary settlement, spat

Abstract

The seasonal pattern of bivalve spat settlement in Eyjafjordur, North Iceland, was investigated using artificial collectors of monofilament netting over 14 months (March 1998–January 2000) at 5, 10 and 15 m depth. SCUBA divers replaced the collectors at 4-weekly intervals. Twelve bivalve species settled on the collectors but only *Mytilus edulis* and *Hiatella arctica* were present throughout the year; they were the most abundant bivalve taxa. Of the remaining species, only *Chlamys islandica*, *Heteranomia* spp., *Arctica islandica*, *Serripes groenlandicus* and *Mya* spp. were sufficiently abundant to enable statistical analysis. All settled in late summer and autumn. Peak settlement of *M. edulis*, in September, consisted mainly of primary settlers (0.25–0.5 mm) although secondary settlers (>0.5 mm) were present in all samples. *Mytilus edulis* settled mostly at 5 m depth, especially larger individuals, possibly reflecting stronger currents at shallower depth and the proximity of mussel beds in the intertidal zone. Primary (<1 mm) and secondary *H. arctica* settlers (>1 mm) were present in most months, with the former being most numerous in September, 1999; settlement was equally abundant at 5 and 10 m depth. Primary settlement of *C. islandica* and *S. groenlandicus* occurred in autumn (mainly in September), and secondary settlers were very scarce and only seen in winter. *Arctica islandica, Heteranomia* spp. and *Mya* spp. settled mainly in September 1999 at 10 m depth, except for *A. islandica*, which was more numerous in August.

Introduction

Many biotic and abiotic factors affect larval abundance in the water column and influence the temporal variability of settlement. Amongst the most important are the reproductive cycles of adults, patterns of winds (Hawkins & Hartnoll, 1982), hydrography of the area (Gaines & Bertness, 1992) and changes in rates of larval mortality due to predation (Thorson, 1950; Day & McEdward, 1984) or to a prolonged planktonic stage (Day & McEdward, 1984). Alterations in abundance and spatial distribution of a population during early stages of benthic life can also arise from secondary settlement (Armonies, 1994). Following settlement, postlarvae of many bivalve species can secrete a byssal thread, resuspend in the water column and drift away to resettle somewhere else (Sigurdsson et al., 1976; Lane et al., 1985; Armonies, 1994). The process can occur several times, as long as postlarvae do not grow above a threshold size and become too heavy. Byssus drifting has been observed for several species of cockels and clams (Mountaudouin, 1997), mytilids (Sigurdsson et al., 1976), tellinids (Sörlin, 1988; Armonies & Hellwig-Armonies, 1992; Cummings et al., 1996; Baker & Mann, 1997) and scallops (Beaumont & Barnes, 1992). Each species has its own maximum size at which this kind of dispersal can be used (Beaumont & Barnes, 1992).

Artificial collectors of monofilament netting have been used successfully to collect many different species of drifting bivalve spat for use in aquaculture (Paul et al., 1981), estimation of recruitment in wild bivalve stock fisheries (Sause et al., 1987; King et al., 1990), monitoring settlement, early growth and mortality of bivalves (Knuckey, 1995; Chauvaud et al., 1996), and establishing patterns of distribution of benthic epifauna (Ardisson & Bourget, 1992). Sampling of bivalve spat on artificial collectors was

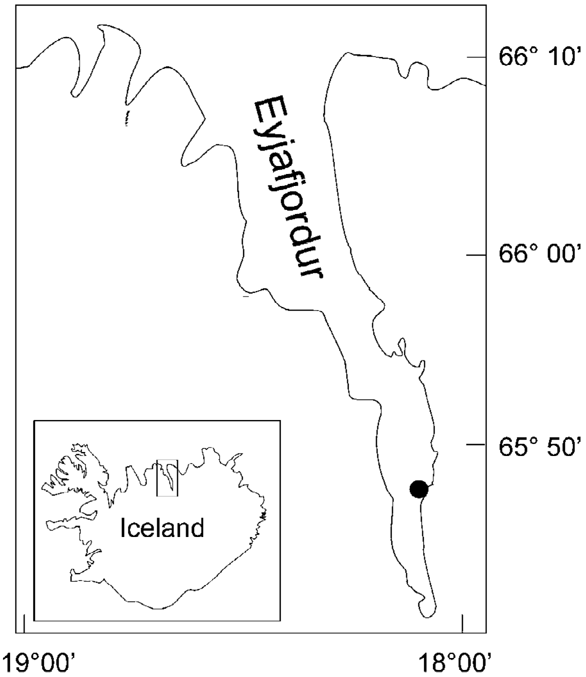

Figure 1. Map of Eyjafjordur, showing its location in Iceland. The sampling site is marked with a dot.

also used previously in Icelandic waters to determine the time of maximum settlement and optimal depth of settlement in two commercially important species, *Chlamys islandica* (Müller, 1776) and *Mytilus edulis* (L., 1750) (Thorarinsdottir, 1991, 1996).

In this paper, we present results from a study focusing on settlement patterns of bivalve larvae in shallow waters in relation to season and water depth. Some species recorded during our study are very rare or absent in the scientific literature for Iceland.

Materials and methods

Study area and experimental setup

The study was carried out in Eyjafjordur, North Iceland (Fig. 1). The fjord deepens from the head to the entrance, reaching a maximum depth of 200 m (Jonsson, 1996). Tides are semi diurnal, the amplitude of mean spring tide is 1.3 m and tidal currents flow at a few cm s^{-1} (Jonsson & Gudmundsson, 1994). Information on salinity, available for 1992 and 1993 (Jonsson, 1996), indicated a range from 30.0 to 34.3, with the greatest variability at 5 m depth (30.0–34.3). At 10 m depth, salinity ranged from 32.0 to 34.5 and at 15 m it was similar throughout the year (34.0–34.5). Highest salinity measurements were taken from January to April at 15 m depth, and the lowest from June and July at 5 m depth (Jonsson, 1996). Temperature was not recorded at the sampling site; however, data from a nearby location (65° 49.4′ N, 18° 08.0′ W) were available (MRI, unpubl. res.) (Fig. 2).

Spat collectors, deployed at the head of the fjord (65° 50.0′ N, 18° 10.0′ W) at 5, 10 and 15 m depth on a flat bottom composed of sand of medium grain size, consisted of plastic scourers made of a tubular monofilament net rolled over onto itself. The net had a mesh size of 5 mm and a volume of roughly 250 cc. Each scourer was attached to a stainless steel rod, and three of these were fixed onto a concrete block measuring 30×30×6 cm. Two blocks were attached together by a rope and weighted with stones to maintain stability on the bottom. At each depth (5, 10 and 15 m), a pair of blocks (with six spat collectors in total) was submerged and a buoy marked their location.

Sampling

SCUBA divers replaced the spat collectors at 4-weekly intervals from March 1998 to January 2000. The collectors were kept in separate plastic bags before taking them to the surface to minimize loss of animals. Once on deck, each collector was kept in a jar and filled with 10% formalin. No samples were collected from September to November, 1998 and from February to July, 1999. In the laboratory, spat collectors were washed thoroughly on a 63 μm sieve to collect the animals. The entire sample was analyzed, except for the months of heavy settlement, in which the sample was split. Bivalves were identified to species, counted and their shell length measured by means of a micrometer.

Data analysis

Tests of significance on the abundance of the most common species were carried out using two-way ANOVA (α=0.05), with depth and month as fixed factors after log $(x+1)$ transformation of the data (Zar, 1996). Lack of replication at depth, due to the occasional absence of bivalves, excluded the use of a two-way ANOVA to examine interaction effects. Consequently, the log $(x + 1)$ transformed shell length of spat (Zar, 1996) at month and depth was compared using two separate one-way ANOVAs.

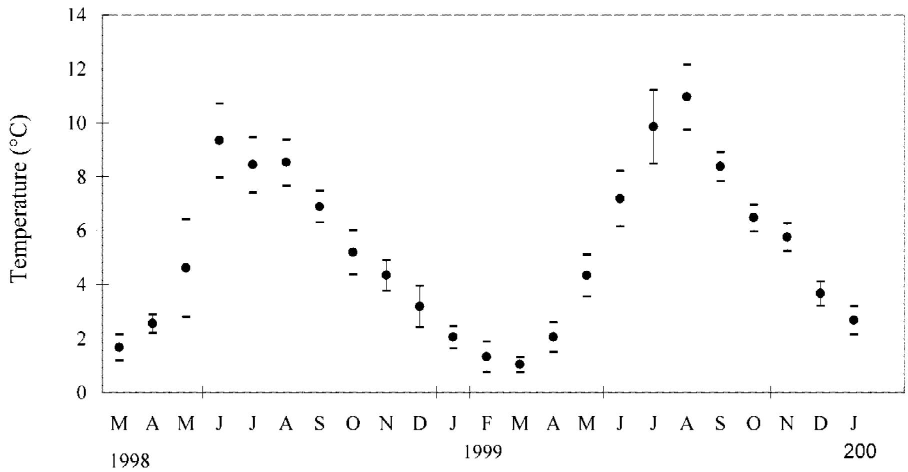

Figure 2. Mean temperature ± SD at month from March 1998 to January 2000. Note that no sampling was conducted in the time periods September–November 1998 and February–July 1999.

Table 1. Total number of individuals of the most common taxa collected each month and at each depth. Myt=Mytilidae, Hiat=*Hiatella arctica*, Cisl=*Chlamys islandica*, Heter=*Heteranomia* spp., Aisl=*Arctica islandica*, Sgro=*Serripes groenlandicus*, Mya=*Mya* spp

Month	Myt	Hiat	Cisl	Heter	Aisl	Sgro	Mya
March 98	23	1	0	0	0	0	0
April 98	31	0	0	0	0	0	0
May 98	142	1	0	0	0	0	0
Jun 98	264	0	0	0	0	3	0
Jul 98	248	34	0	0	0	1	0
Aug 98	423	853	0	0	1	0	0
Sep–Nov 98	*	*	*	*	*	*	*
Dec 98	107	60	0	0	0	0	0
Jan 99	219	83	0	0	0	0	0
Feb–Jul 99	*	*	*	*	*	*	*
Aug 99	1631	1027	13	0	129	26	30
Sep 99	165 398	43 084	1989	276	26	65	31
Oct 99	14 398	4201	594	38	29	4	0
Nov 99	686	251	29	3	1	1	6
Dec 99	208	56	1	0	0	1	0
Jan 00	577	78	1	0	0	0	0
Depth							
5 m	175 767	21 454	117	34	31	52	
10 m	6302	26 568	1537	280	149	56	30
15 m	2286	1707	973	1	6	40	35
All groups	184 355	49 729	2627	317	185	101	67

* No data were collected in these months.

Table 2. Results of the two-way ANOVA test (α=0.05) for number of individuals of the most abundant bivalve species recorded in the spat collectors in relation to months (m) and depth (d), and the interactions between both variables (m×d)

Taxa	Variable	Df	*F*	*P*-level
Mytilus edulis	m	13	77.89	0
	d	2	375.90	0
	m×d	26	7.17	<0.001
H. arctica	m	11	136.75	0
	d	2	156.29	0
	m×d	22	12.22	<0.001
C. islandica	m	5	185.55	0
	d	2	54.11	<0.001
	m×d	10	56.09	0
Heteranomia spp.	m	2	23.36	<0.001
	d	2	37.21	<0.001
	m×d	4	28.51	<0.001
A. islandica	m	4	13.51	<0.001
	d	2	8.00	<0.001
	m×d	8	5.31	<0.001
S. groenlandicus	m	6	18.17	<0.001
	d	2	11.61	<0.001
	m×d	12	5.97	<0.001
Mya spp.	m	2	1.65	0.202
	d	2	7.19	0.001
	m×d	4	1.40	0.246

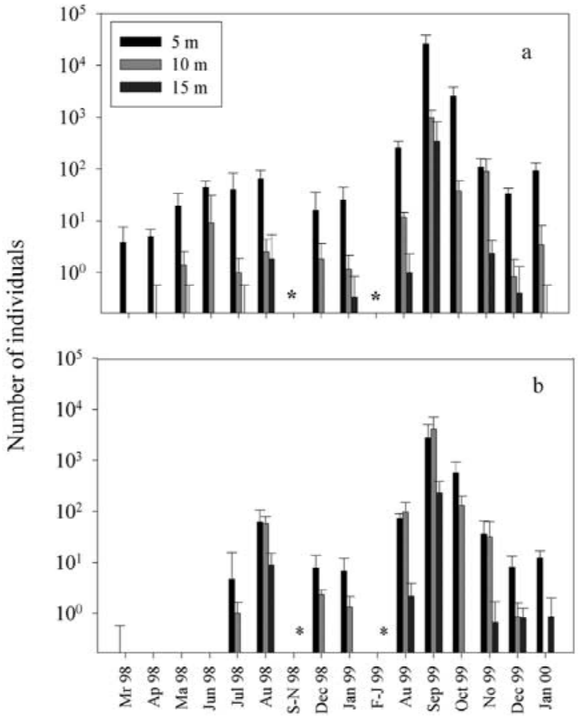

Figure 3. Logarithm of the average number (bars) of (a) *Mytilus edulis*, (b) *Hiatella arctica*, found each month and at each depth in the spat collectors. The whiskers indicate the standard deviation. The asterisks (*) indicate that no sampling was conducted in those months. S–N stands for the time period September–November 1998 and F–J for February–July 1999.

Results

Twelve bivalve taxa settled on the collectors during the sampling period, but five, *Thyasira* spp., *Thracia myopsis* (Möller), *Turtonia* spp., *Modiolaria discors* (L.) and *Astarte borealis* (Schumacher, 1817), were collected in too low number to carry out any analysis. The remaining species, *Mytilus edulis*, *Hiatella arctica* (L., 1767), *Chlamys islandica*, *Heteranomia* spp., *Arctica islandica* (L., 1767), *Serripes groenlandicus* (Bruguière, 1798) and *Mya* spp., showed marked seasonal changes in abundance and length, settling predominately from August to October (Table 1). Two-way ANOVA identified significant month and depth effects on abundance for each species except *S. groenlandicus* and *Mya* spp. (Table 2). Furthermore, significant month×depth interaction was also found for each species except *S. groenlandicus* and *Mya* spp., indicating that differences between depths and sampling months were not consistent. Similarly, significant month and depth effects were found for most species based upon shell length (one-way ANOVA). Findings indicate that even though there were marked seasonal differences, they were not concomitant at each depth.

Mytilus edulis (blue mussel) was the only species present in each sampling month and was the most abundant, constituting 78% of the total number of bivalves collected. From March to August 1998, there was a steady increase in *M. edulis* numbers. Most settled in September and October 1999, with over 165 000 and 14 000 mussels, respectively. A sharp decline followed from November onwards (Table 1). The majority of blue mussels (95%) settled at 5 m depth, with only 3.7 and 1.3% settling at 10 and 15 m, respectively (Fig. 3). The monthly mean shell length of mussels from April to August 1998 ranged from 1.10

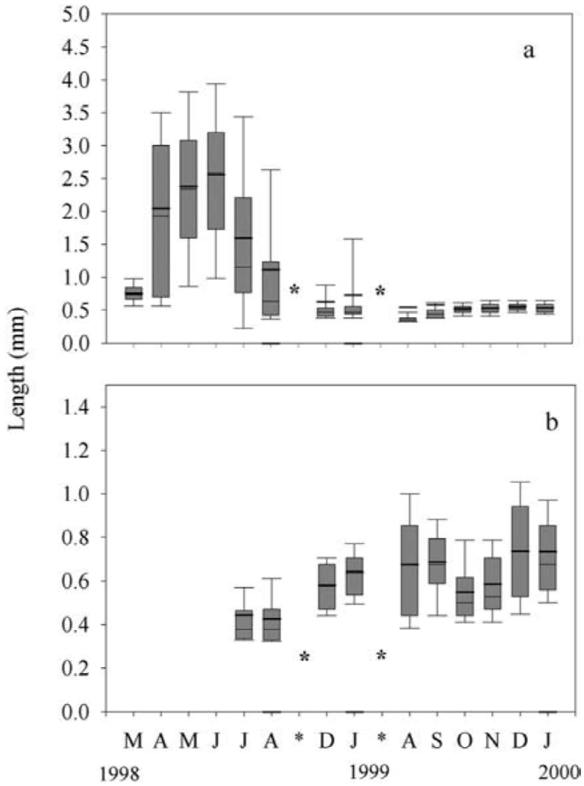

Figure 4. Mean length (bold line) and median length (regular line) at month of (a) *Mytilus edulis*, (b) *Hiatella arctica* recorded in the collectors. The 10th and 90th and 25 and 75 percentiles are represented by whiskers and boxes, respectively. The asterisks (*) indicate that no sampling was conducted in those months. The first asterisk in the tick labels stands for the time period September–November 1998 and the second for February–July 1999. Note the different scales in the *y*-axis of each graph.

Table 3. Results of the two one-way ANOVA (α=0.05) to test effect of the variables month and depth on length of the most common bivalve species

Taxa	Month			Depth		
	Df	*F*	*P*-level	Df	*F*	*P*-level
Mytilidae	13	303.64	<0.001	2	197.04	<0.001
H. arctica	9	206.95	<0.001	2	75.11	<0.001
C. islandica	2	14.00	<0.001	2	17.32	<0.001
Heteranomia spp.	2	0.63	0.533	1	5.63	0.019
A. islandica	2	23.27	<0.001	2	62.86	<0.001
S. groenlandicus	3	5.75	0.001	2	0.03	0.970
Mya spp.	2	11.51	0	2	3.89	0.027

to 2.60 mm. In contrast, the mean shell length was at minimum (0.50 mm) after the main settlement in September 1999, when most shells measured between 0.30 and 0.50 mm in length (Fig. 4a). The size range was from 0.25 to <5.00 mm in most sampling months, except for March 1998 and from October 1999 onwards, when individuals larger than 1.50 mm were rare or absent. Differences in the shell length of mussels between both months and depths was highly significant (Table 3). Mussels found at 5 m had an average length of 1.00 mm, whereas those collected at 10 and 15 m were 0.49 and 0.45 mm, respectively (Fig. 5a). These data indicate that most secondary settlers were collected at 5 m depth.

Spat of *H. arctica* settled in all but 2 months and amounted to 21% of the total number of bivalves collected. With the exception of August 1998, *H. arctica* settled scarcely from March 1998 to January 1999; predominant settlement being between August and October 1999 (Table 1). The 43 000 individuals that settled in September alone represented 87% of all the *Hiatella* collected during this study. The pattern of settlement at depth showed great variability between months; high numbers were generally at 5 m depth but, during August and September 1999, it was most abundant at 10 m depth (Fig. 3). Shell length of *H. arctica* ranged from 0.25 to 3.7 mm and rarely exceeded 2.00 mm; in August 1999 and January 2000; few individuals over 3.30 mm in shell length were found. The mean shell length of *H. arctica* varied significantly (Table 2) throughout the sampling period (0.43–0.74 mm), indicating that secondary settlers were scarce (Fig. 4b). The same conclusion was reached when comparing the mean shell length (0.57–0.66 mm) at all three depth levels (Table 3, Fig. 5b).

Chlamys islandica, *Heteranomia* spp., *A. islandica* and *S. groenlandicus* settled mainly between August and November 1999. All but *S. groenlandicus* were most abundant at 10 m depth, whereas *S. groenlandicus* was equally abundant at 10 and 15 m (Table 1). Two-way ANOVA showed significant month and depth effects in abundance for all species (Table 2). Despite the narrow range of shell length recorded for these species (Figs 5 and 6), variability in shell length at month and depth was also found to be significant for all but *Heteranomia* spp., for which no month effects were detected and *S. groenlandicus*, for which no depth effects were found (Table 3).

Mya spp. was most abundant in August and September 1999 (Table 1), but was scarce at 5 m depth and settled in similar numbers at 10 and 15 m

(Table 1). This difference between depths was significant (Table 2). Variability in shell length was small (Figs 5 and 6) but, nevertheless, differed significantly between months and depths (Table 3).

No correlation was found between monthly average water temperature and settlers abundance for any species ($R^2 = 0.137$).

Discussion

Of the seven bivalves, only *M. edulis* and *H. arctica* settled throughout the year, accounting for 98% of all bivalves collected. The remaining bivalve species were collected mostly in late summer or early autumn. The number of settlers of each species varied in the different months and depths. Unfortunately, lack of data from September and October 1998 increased greatly the variability between years, and precluded direct comparison of the settlement patterns between the two years. Nevertheless, all bivalve species showed significantly greater settlement from August to November 1999 than at other times, which might reflect the cycle of gonad development and spawning for these species. Secondary settlers of most species were present on the collectors during the study period. Although especially obvious for blue mussels and *H. arctica*, all species showed a decrease in main shell length during their main settlement.

Settlement patterns in time

The blue mussel, *M. edulis*, outnumbered all other taxa throughout the year, although both abundance and mean shell length varied greatly over the study period. Secondary settlement of *M. edulis* has been widely reported and it has been suggested that mussels over 1.0 mm in shell length are almost definitely secondary settlers (King et al., 1989; Snodden & Roberts, 1997). Unlike other studies of settlement of blue mussels on artificial collectors (King et al., 1990; Hunt & Scheibling, 1996), mussels with shell length over 5 mm settled during the period May–October 1998, although in very low number. It may be that the filamentous substrata, generally used in artificial collectors, may be more suitable for smaller, early postlarvae than for larger later stages. Blue mussels are thought to use byssus drifting as a means of transport to resettle until they are at least 2.5 mm (Sigurdsson, 1976; Seed & Suchanek, 1992), but mussels over 5 mm shell length may disperse by crawling, which could explain their presence on the collectors in this study, as they were deployed on the sea bottom. It is also possible that mussels grew in the collectors; Warren (1936), recorded 2–4 mm growth of *M. edulis* during 1 month in artificial collectors. Alternatively, larger-sized mussels may have been detached from their original substratum by currents or storms, and induced to secondary settlement (Cáceres-Martínez et al., 1994).

This study detected only one spawning period for blue mussels. The main spawning season in southwest Iceland has been observed to be from the middle of June to end of July, with primary settlement taking place from the middle of August to late September (Thorarinsdottir, 1996). However, settlement is delayed further north, and in western Iceland, the main spawning of *M. edulis* has been recorded in August (Thorarinsdottir & Gunnarsson, in press). Unlike other *M. edulis* populations (Ackefors & Haamer, 1987; King et al., 1989; Tammi et al., 1996), in Icelandic waters, blue mussels spawn only once a year, probably due to environmental restrictions. Short spawning periods have been described in other northern populations of *M. edulis* (Kautsky, 1982).

Settlement of *H. arctica* is poorly known from other areas. Spawning time and duration of the pelagic phase are unknown, but secondary settlement has been described (Sigurdsson et al., 1976) and a peak of settlement during July has been reported in France (Chauvaud et al., 1996). In our study, *H. arctica* was most abundant between August and October, but this could be related to the differences in sea temperature, which is known to be a trigger for spawning in bivalves (Bayne & Newell, 1983).

Harvey et al. (1995) obtained similar results for the Iceland scallop *C. islandica* as here when sampling in the Gulf of St. Lawrence. Data are in agreement with a previous study in which spawning was reported at the beginning of July in western Iceland, with settlement taking place in middle September at 0.3 mm in shell size (Thorarinsdottir, 1991). Byssus drifting and secondary settlement has been observed in other scallop species, such as *Pecten maximus* and *Aequipecten opercularis* (Beaumont & Barnes, 1992), and it is known that *C. islandica* spat can resettle when dislodged from the substrata (Harvey et al., 1993).

A previous study of *Heteranomia* spp., confirmed that settlement takes place in September in waters off Denmark (Jørgersen, 1936). Byssus drifting and secondary settlement have also been reported for *H. squamula* (Sigurdsson et al., 1976).

Absence of the ocean quahog, *A. islandica*, from the collectors during this study cannot be attributed directly to spawning time, as this species seems to spawn all year, with the main spawning from June to August (Mann, 1982; Thorarinsdottir, 2000). Spawning of *A. islandica* in northwestern Iceland is prolonged during the whole year, with the main spawning season in July (Thorarinsdottir, 2000). Larvae of *A. islandica* have been found in the plankton all months of the year in Denmark but settlement has only been observed from January to September, with a maximum in April (Muus, 1973). The shell length of ocean quahogs at metamorphosis is 0.23–0.3 mm, but smallest individuals collected in Denmark were 0.3–0.6 mm, a similar size to those measured during the present study. The mean shell growth during the first 6 months after settlement was less than 1 mm (Muus, 1973).

No investigations of settlement or growth of *Mya* spp. and *Serripes* spp. have been carried out in Icelandic waters, and published data on these genera are scarce in general. However, Muus (1973) recorded settlement of *Mya truncata* in Danish waters from January to July, with highest settlement in February. Shell length at metamorphosis was between 0.20 and 0.36 mm, and spat were first observed at 0.3–0.5 mm shell size. The mean monthly shell growth during the first 6 months after settlement was less than 0.1 mm (Muus, 1973), which may support the possibility of having secondary settlers of *Mya* spp. among the specimens collected in Eyjafjordur. Sigurdsson et al. (1976) reported byssal drifting and secondary settlement of *M. truncata*. Our data do not agree entirely with previous studies. *Mya arenaria* is known to spawn once a year off the east coast of North America and twice in Norway, where the main settlement has been recorded in September (Winther & Gray, 1985). Spawning behaviour of this species may also vary between years, switching from a large single spawning event to continuous small spawning events throughout the season (MacLean et al., 1999).

Nothing has been reported previously on spawning time or settlement for *S. groenlandicus*. In general, settlement may also have been conditioned by the material used in the artificial collectors, as it is known that bivalve spat shows preferences for certain types of substrata (Harvey et al., 1993, 1995; Cáceres-Martínez et al., 1994; Harvey & Bourget, 1995; Hunt & Scheibling, 1996).

Settlement patterns at depth

Most bivalve species settled in highest number at 10 m depth. Exceptions included *M. edulis* that was more abundant at 5 m, and *Mya* spp. that settled in very similar numbers at 10 and 15 m. However, 83.2% of the spat was collected at 5 m, but this was due to the high number of blue mussels. Excluding them from the analysis, 41% of all bivalves were collected at 5 m and 54% collected at 10 m. The significant month × depth interaction found for most species indicates that the proportion of settlers at the three different depths in each month varied throughout the period of study.

The relationship between depth and settlement has been investigated previously (Brand et al., 1980; Sause et al., 1987), using spat collectors attached to ropes anchored to the bottom and buoyed a few meters below the sea surface. In these studies, higher settlement was found in collectors in the middle of the water column. The authors suggested that settlement in near surface waters could be affected by fouling by algae or by the effects of wave action and turbulence; in collectors closest to the sea bed, silting could have inhibited settlement or caused high mortality among the settlers. However, settlement of many bivalve species on collectors appears to be greatest at a narrow depth near the sea bed, reflecting the behavior of the larvae at the time of settlement (Ventilla, 1977; Brand et al., 1980; Fraser & Mason, 1987). In the present study, all collectors were placed at the same distance from the sea bottom in contrast with the studies mentioned above. Changes in depth are accompanied by variations in several factors including temperature and food availability and quality. It might be that the bivalve distribution on the collectors at the three depths reflected better environmental conditions at 5 and 10 m than at 15 m (Mann, 1985). The significantly higher settlement of *M. edulis* at 5 m may be related directly to the fact that the spat comes from the intertidal zone and it is, therefore, more abundant in shallow waters.

Temperature and settlement

The average monthly temperature during 1998–1999 and 1987–1996 was similar with the exception of June 1998 and August and September 1999, which were considerably warmer (between 2 and 5 °C) compared to the same period in 1998 (Jonsson, 1999). August and September 1999 were the months of highest settlement; however, it is difficult to assess the influence of temperature alone on settlement processes. Some stud-

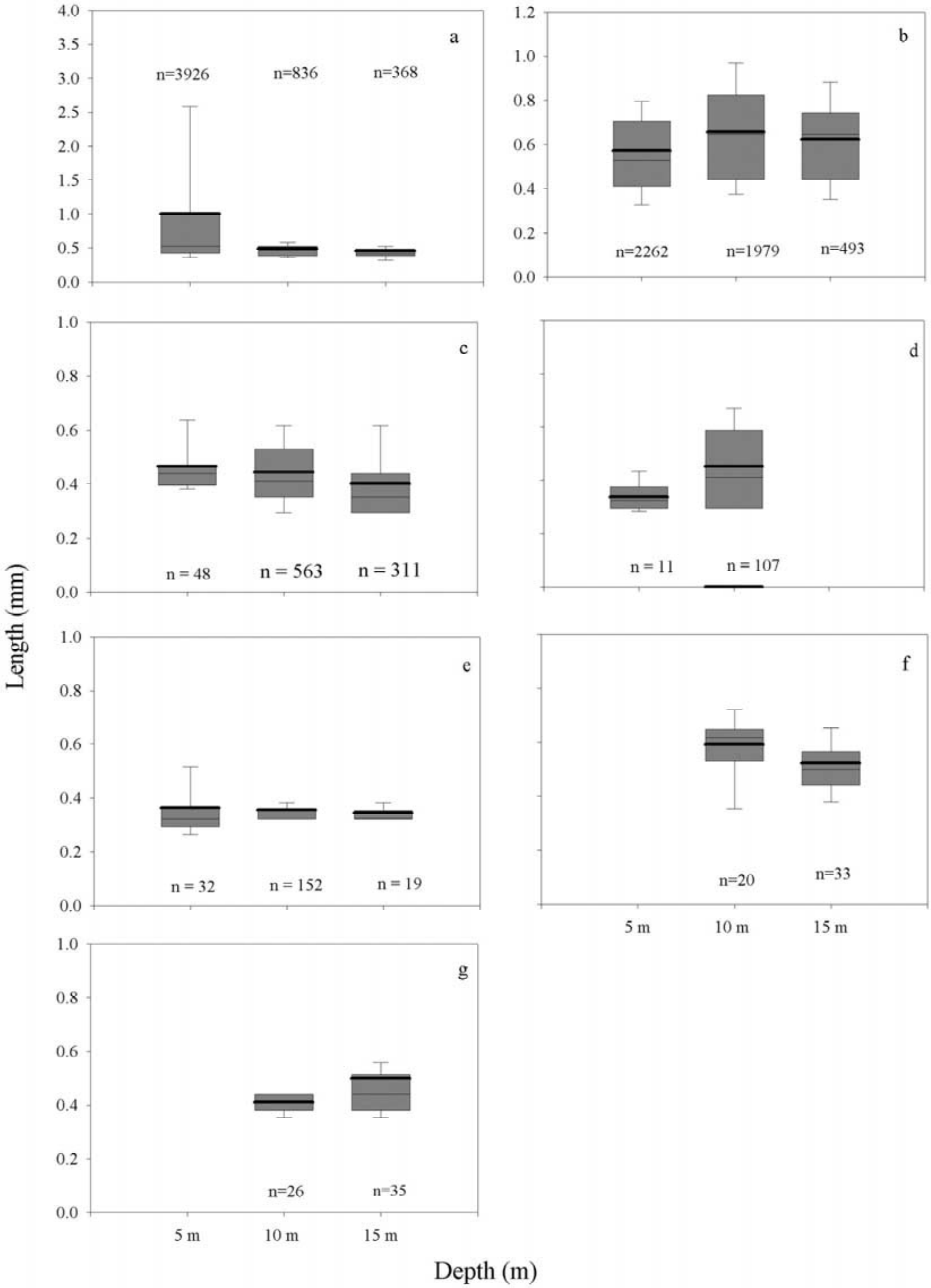

Figure 5. Mean length (bold line) and median length (regular line) at depth of (a) *Mytilus edulis*, (b) *Hiatella arctica*, (c) *Chlamys islandica*, (d) *Heteranomia* spp., (e) *Arctica islandica*, (f) *Serripes groenlandicus*, (g) *Mya* spp., recorded in the collectors. The 10th and 90th and 25 and 75 percentiles are represented by whiskers and boxes, respectively. The number of individuals measured (*n*) is given. Note the different scales in the *y*-axis for *M. edulis* and *H. arctica*.

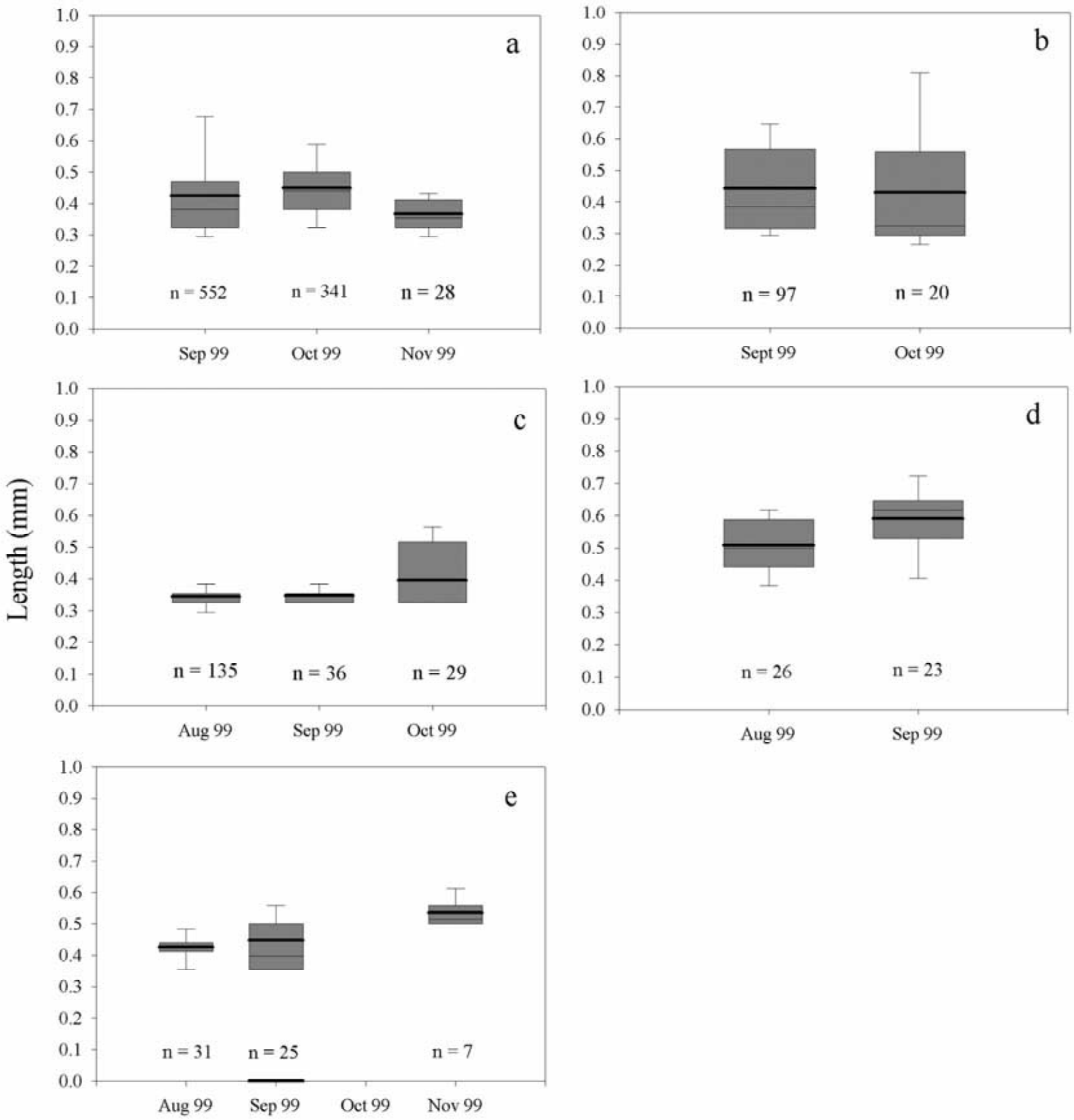

Figure 6. Mean length (bold line) and median length (regular line) at month of (a) *Chlamys islandica*, (b) *Heteranomia* spp., (c) *Arctica islandica*, (d) *Serripes groenlandicus*, (e) *Mya* spp. recorded in the collectors. The 10th and 90th and 25 and 75 percentiles are represented by whiskers and boxes, respectively. The number of individuals measured (*n*) is given. Note the different scales in the *x*-axis of each graph.

ies have demonstrated a positive correlation between water temperature and density of settlers (Robinson et al., 1991, 1999), whereas others have not found any correlation (Harvey et al., 1995). Nevertheless, it is widely regarded that settlement patterns are influenced predominately by the combined effects of temperature and food availability (Seed & Suchanek, 1992).

Acknowledgements

This study was funded by the Marine Research Institute of Reykjavik, Iceland. For that we thank the former director of the MRI, Prof. Jakob Jakobsson. Dr Lorna Taylor and Dr Karl Gunnarsson are thanked for comments on earlier versions of the manuscript, and Dr Roger Mann and an anonymous referee for their suggestions to improve this paper. Lina Gunnarsdottir, librarian at the MRI, is thanked for her valuable assistance in searching the literature, and Erlendur Bogason for the collection of samples.

References

Ackefors, H. & J. Haamer, 1987. A new Swedish technique for culturing blue mussel. ICES C.M.1987/K: 36.

Ardisson, P. L. & E. Bourget, 1992. Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna. Mar. Ecol. Prog. Ser. 83: 15–34.

Armonies, W., 1994. Drifting meio- and marobenthic invertebrates on tidal flats in Königshafen: a review. Helgoländerwiss Meeresunters. 48: 299–320.

Armonies, W. & M. Hellwig-Armonies, 1992. Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. Neth. J. Sea Res. 29: 371–378.

Bayne, B. L. & R. C. Newell, 1983. Physiological energetics of marine molluscs. In Saleuddin, A. S. M. & K. M. Wilbur (eds), The Mollusca 4. Academic Press, London: 407–515.

Baker, P. & R. Mann, 1997. The postlarval phase of bivalve molluscs: a review of functional ecology and new records of postlarval drifting of Chesapeake Bay bivalves. Bull. mar. Sci. 61: 409–430.

Beaumont, A. R. & D. A. Barnes, 1992. Aspects of veliger larval growth and byssus drifting of the spat of *Pecten maximus* and *Aequipecten* (*Chlamys*) *opercularis*. ICES J. mar. Sci. 49: 417–423.

Brand, A. R., J. D. Paul & J. N. Hoogesteger, 1980. Spat settlement of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. J. mar. biol. Ass. U.K. 60: 379–390.

Cáceres-Martínez, J., J. A. F. Robledo & A. Figueras, 1994. Settlement and post-larvae behaviour of *Mytilus galloprovincialis*: field and laboratory experiments. Mar. Ecol. Prog. Ser. 112: 107–117.

Chauvaud, L., G. Thouzeau & J. Grall, 1996. Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: settlement patterns in relation to spatio-temporal variability of environmental factors. Aquacult. Int. 4: 263–288.

Cummings, V. J., R. D. Pridmore & S. F. Thrush, 1996. Effect of the spionid polychaete *Boccardia syrtis* on the distribution and survival of juvenile *Macomona liliana* (Bivalvia: Tellinacea). Mar. Biol. 126: 91–98.

Day, R. & L. McEdward, 1984. Aspects of the physiology and ecology of pelagic larvae of marine benthic invertebrates. In Steidinger, K. A. & L. M. Walker (eds), Marine Plankton Life Cycle Strategies. CRC Press, Boca Ratón (FL): 93–120.

Fraser, D. I. & J. Mason, 1987. Pectinid spat studies in selected areas off the west coast of Scotland, 1982–1986. ICES C.M.1987/K: 4.

Gaines, S. D. & M. D. Bertness, 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360: 579–580.

Harvey, M. & E. Bourget, 1995. Experimental evidence of passive accumulation of marine bivalve larvae on filamentous epibenthic structures. Limnol. Oceanogr. 40: 94–104.

Harvey, M., E. Bourget & G. Miron, 1993. Settlement of Iceland scallop *Chlamys islandica* spat in response to hydroids and filamentous red algae: field observations and laboratory experiments. Mar. Ecol. Prog. Ser. 99: 283–292.

Harvey, M., E. Bourget, C. Legault & R. G. Ingram, 1995. Short term variations in settlement and early spat mortality of Iceland scallop, *Chlamys islandica* (O. F. Müller). J. exp. mar. Biol. Ecol. 194: 167–187.

Hawkins, S. J. & R. G. Hartnoll, 1982. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). J. exp. mar. Biol. Ecol. 62: 271–283.

Hunt, H. L. & R. E. Scheibling, 1996. Physical and biological factors influencing mussel (*Mytilus edulis*) settlement on a wave-exposed rocky shore. Mar. Ecol. Prog. Ser. 142: 135–145.

Jonsson, S. & K. Gudmundsson, 1994. An interdisciplinary study of Eyjafjordur, North Iceland. ICES C.M.1994/C: 6.

Jonsson, S., 1996. Ecology of Eyjafjordur Project: Physical parameters measured in Eyjafjordur in the period April 1992–August 1993. Hafrannsoknastofnun, Fjolrit 48 160 pp.

Jonsson, S., 1999. Temperature time series from Icelandic coastal stations. Rit Fiskid. 16: 59–68.

Jørgensen, C. B., 1946. Lamellibranchia. Meddl. Komm. Dan. Fisk. Havundersøg., Ser. Plankton 4: 277–311.

Kautsky, N., 1982. Growth and size structure in a Baltic *Mytilus edulis* population. Mar. Biol. 68: 117–133.

King, P. A., D. McGrath & E. M. Gosling, 1989. Reproduction and settlement of *Mytilus edulis* on an exposed rocky shore in Galway Bay, West Coast of Ireland. J. mar. biol. Ass. U.K. 69: 355–365.

King, P. A., D. McGrath & W. Britton, 1990. The use of artificial substrates in monitoring mussel (*Mytilus edulis* L.) settlement on an exposed rocky shore in the west of Ireland. J. mar. biol. Ass. U.K. 70: 371–380.

Knuckey, I. A., 1995. Settlement of *Pinctada maxima* (Jameson) and other bivalves on artificial collectors in the Timor Sea, Northern Australia. J. Shellfish Res. 14: 411–416.

Lane, D. J. W., A. R. Beaumont & J. R. Hunter, 1985. Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. Mar. Biol. 84: 301–308.

MacLean, L. A., N. G. MacNair, T. J. Davidson & G. G. Johnson, 1999. Two-year comparison of spawning patterns in soft shell clams (*Mya arenaria*). J. Shellfish Res. 18: 310.

Mann, R., 1982. The seasonal cycle of gonadal development in *Arctica islandica* from the southern New England shelf. Fish. Bull. 80: 315–326.

Mann, R., 1985. Seasonal changes in the depth-distribution of bivalve larvae on the southern New England shelf. J. Shellfish Res. 5: 57–64.

Montaudouin, X., 1997. Potential of bivalve's second settlement differs with species: a comparison between cockle (*Cerastoderma edule*) and clam (*Ruditapes philippinarum*) juvenile resuspension. Mar. Biol. 128: 639–648.

Muus, K., 1973. Settling, growth and mortality of young bivalves in the Øresund. Ophelia 12: 79–116.

Paul, J. D., A. R. Brand & J. N. Hoogester, 1981. Experimental cultivation of the scallops *Chlamys operculary*s (L.) and *Pecten maximus* (L.) using naturally produced spat. Aquaculture 24: 31–44.

Robinson, M. C. S., J. D. Martin, R. A. Chandler & G. J. Parsons, 1991. Spatial patterns of spat settlement in the sea scallop, *Placopecten magellanicus*, compared to hydrographic conditions in Passamaquoddy Bay, New Brunswick, Canada. J. Shellfish Res. 10: 274.

Robinson, M. C. S., J. D. Martin, R. A. Chandler & G. J. Parsons, 1999. An examination of the lingake between the early life history processes of the sea scallop and local hydrographic characteristics. J. Shellfish Res. 10: 272–273.

Sause, B. L., D. Gwyther & D. Burgess, 1987. Larval settlement, juvenile growth and the potential of use of spatfall indices to predict recruitment of the scallop *Pecten alba* Tate in Port Phillip Bay, Victoria, Australia. Fish. Res. 6: 81–92.

Seed, R. & T. H. Suchanek, 1992. Population and community ecology of *Mytilus*. In Gosling, E. G. (ed.), The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Dev. Aquacult. Fish. Sci. 25: 87–170.

Sigurdsson, J. B., C. W. Titman & P. A. Davies, 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. Nature 262: 386–387.

Snodden, L. M. & D. Roberts, 1997. Reproductive patterns and tidal effects on spat settlement of *Mytilus edulis* populations in Dundrum Bay, Northern Ireland. J. mar. biol. Ass. U.K. 77: 229–243.

Sörlin, T., 1988. Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). Oecologia 77: 273–277.

Tammi, K. A., W. H. Turner, M. Brumsted & M. A. Rice, 1996. Veliger vodoo and other witchcraft in the Wesport River: Bay scallop, *Argopecten irradians*, veliger abundance and the variability of spatfall recruitment to artificial spat collectors in the Wesport Estuary, Massachussetts. J. Shellfish Res. 15: 461–462.

Thorarinsdottir, G. G., 1991. The Iceland scallop, *Chlamys islandica* (O. F. Müller) in Breidafjordur, west Iceland. I. Spat collection and growth during the first year. Aquaculture 97: 13–23.

Thorarinsdottir, G. G., 1996. Gonad development, larval settlement and growth of *Mytilus edulis* L. in a suspended population in Hvalfjordur, south-west Iceland. Aquaculture Res. 27: 57–65.

Thorarinsdottir, G. G., 2000. Annual gametogenetic cycle in ocean quahog, *Arctica islandica* (Linnaeus, 1767), from north-western Iceland. J. mar. biol. Ass. U.K. 80: 661–666.

Thorson, G., 1950. Reproduction and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1–45.

Ventilla, R. F., 1977. A scallop spat collector trial off the Northern Ardnamurchan Coast. White Fish Authority, Field Report 485. 16 pp.

Warren, A. E., 1936. An ecological study of the sea mussel (*Mytilus edulis*). J. Biol. Bd. Can. 2: 89–94.

Winther, U. & J. S. Gray, 1985. The biology of *Mya arenaria* (Bivalvia) in the eutrophic inner Oslofjord. Sarsia 70: 1–9.

Zar, J. H., 1996. Biostatistical Analysis. Prentice Hall International Editions, New Jersey. 662 pp.