

Total for climatic regions ...: 1 (1.4%)

The Holocene Skagen: 71 (28.7%)

From the Skagen boring, 71 Holocene species have been recorded.

The Boreo-Lusitanian group dominates with 54 species (76.1%) of the Holocene mollusc species from the Skagen Well.

One purely Lusitanian species, *Vitreolina collensi*, has been found, while all the other species occur in the Boreal and to some extent the Arctic. In this way the Skagen Well material resembles that of other regions like the Vendsyssel, Limfjord and North Sea during the Holocene.

The Skagen Well material has all been recorded to certain stratigraphical levels, as seen in Appendix 6, so the climatic indications through time appear, but the number of molluscan species is very low. In the Pre-

boreal/Boreal, only three species have been recorded. This has been explained as a result of a deeper water where the echinoids dominate.

Higher up in the sequence, the number of molluscs increases – 23 species in the Subboreal and 68 species in the Subatlantic.

Through the chronostratigraphical levels, the climatic regions of the Boreo-Lusitanian from the dominating one, and the purely Lusitanian *Vitreolina collensi* as mentioned above occurs in the Subboreal and Subatlantic. However, as already stated, the development of the facies in the Skagen Well during the Holocene does change the environment from the deeper-water facies with few molluscs through the bottom community with *Turritella communis* into the prolific shallow-water community. In this way the youngest part covering the Subboreal–Subatlantic is also by far the part with the highest species diversity.

The environmental changes within the seven regions through the Late Quaternary evaluated by the molluscan communities met with in the seven stages

The seven chronological stages which have been described according to their climatic affinities are seen in Fig. 102 and Fig. 103 covering the Eemian, the Early/Middle Weichselian, the Late Weichselian, the Preboreal/Boreal, the Atlantic, the Subboreal, and the Subatlantic.

In this way the climatic cycle during the Late Quaternary is demonstrated on the basis of marine mollusc species which indicate that the Eemian has by far the highest amount of the more temperate species, while the Holocene reached its maximum during the Atlantic, although only slightly more than the other stages within the Holocene, as already commented upon in the previous chapter.

It is generally accepted that the Eemian summer temperatures were higher – about 2°C above the present. With glaciers smaller than the present day, this means that the sea level was 4–6 m higher than today (Andersen & Borns 1994, pp. 44–49). And as pointed out by Donner (1995, p. 39): “the submergence was clearly greater after the Saalian glaciation than after the Weichselian and possibly after the older glaciations”.

Donner sees this in northern Europe as “a result of a comparatively great downwarping of the earth’s crust during the extensive Saalian glaciation”. The rebound since the last glaciation has come to an end within the Danish area (Petersen 1985c, 1991b). This means that the Eemian deposits, when found in Denmark in non-glacio-dislocated state, can be regarded as being in the original position related to sea level, although there might be some movements in relation to neo-tectonic activities, as mentioned earlier. In the light of the observations mentioned above, the seven regions will be discussed according to the environmental characteristics such as the climatic affinities for the molluscs recorded in Appendix 6 for each region, as appearing in Fig. 103. However, for the Holocene still as many as 130 species including the recent ones (95) not found as subfossil have not been dated to give their first appearance, see Fig. 102: Unknown arrival in Holocene. At the end of each of the seven stages the molluscan communities *sensu* C.G.J. Petersen will be presented in Tables 3–9.

Eemian stage 130 000 – 115 000 B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

Already Forchhammer (1842, p. 64) designated *Cyprina (Arctica) islandica* to be the characteristic bivalve of the Bælt Sea Eemian, as known to the present-day geologists. Furthermore, Forchhammer points out that the characteristic bivalve, *Cyprina islandica*, occurs every where in large quantities, but always in crust specimens. However, all the shell fragments occurring together show that the specimen has been broken after deposition in the clay, most probably by the cataclysms which have given the beds their tilt.

Johnstrup (1882a, p. 55) points to the indications of the molluscs as being a deposition of a shallow-water sea and also mentioned the *Mytilus* beds.

Johnstrup points out (1882a, p. 56) that the dislocated floes – as already noticed by Forchhammer – have the original succession within each floe, saying that the *Cyprina* clay and the *Mytilus* beds have not been disconnected during the dislocations.

Later investigations by Nordmann (Harder 1900; Nordmann 1908, 1913) demonstrated that the *Venus aurea* as observed by Johnstrup (1882a, p. 66) could be regarded in parts as the no longer living *Tapes aureus* Gm. var. *eemiensis* Nordmann or *Tapes senescens* Doederlein; in this book *Paphia aurea senescens*. The *Tapes* species do represent shallow-water environments (see the chapter on the molluscan species), and therefore the whole of the Bælt Sea region can be characterised by the three bivalves mentioned above, from the eulittoral to the infralittoral shallow-water zones: *Mytilus*, *Tapes* and *Cyprina*. Among the three species mentioned, the *Tapes* species (*Paphia aurea senescens*) also remains as the only subfossil bivalve from Denmark which can be regarded as an index fossil from the marine Eemian. The stratigraphical position of the marine Eemian is according to Jessen & Milthers (1928, p. 179) contemporaneous with the mixed oak forest zone and the *Carpinus* zone in the interglacial bogs; furthermore, Jessen & Milthers conclude (1928, p. 341) that the climate of Jylland and NW Germany in that part of the interglacial period which answers to zone f [culmination of the curves for mixed oak forest] was no less Atlantic in character than

Climatic affinity	Time: The seven Stages Frequency: Number of Molluscs Column per cent, %								Total number of species		
	Pleistocene			Holocene							
	Eemian	Early/Middle Weichselian	Late Weichselian	Unknown arrival in Holocene	Preboreal/Boreal	Atlantic	Subboreal	Subatlantic			
Arctic	-	1 (3%)	2 (5%)	35 subfossil species	95 recent species	-	-	-	-	3	
Arctic, Subarctic	-	6 (17%)	5 (12%)			-	-	-	-	-	11
Arctic, Subarctic, Boreal	10 (7%)	19 (53%)	14 (34%)			1 (4%)	1 (1%)	2 (3%)	1 (1%)	48	
Arctic, Subarctic, Boreal, Lusitanian	11 (8%)	7 (19%)	11 (27%)			2 (7%)	6 (6%)	5 (6%)	6 (8%)	48	
Subarctic, Boreal	3 (2%)	2 (6%)	4 (10%)			-	2 (2%)	3 (4%)	2 (3%)	16	
Subarctic, Boreal, Lusitanian	15 (11%)	1 (3%)	5 (12%)			3 (11%)	14 (15%)	7 (9%)	8 (11%)	53	
Boreal	1 (1%)	-	-			-	-	1 (1%)	1 (1%)	3	
Boreal, Lusitanian	90 (64%)	-	-			21 (78%)	70 (75%)	56 (73%)	53 (74%)	290	
Lusitanian	10 (7%)	-	-			-	-	3 (4%)	1 (1%)	14	
Total number of species Column per cent, %	140 (100%)	36 (100%)	41 (100%)				27 (100%)	93 (100%)	77 (100%)	72 (100%)	486

Fig. 102. The seven stages from the Eemian through the Weichselian – comprising the Early/Middle Weichselian and Late Weichselian – to the end of the Holocene. Preboreal–Boreal, Atlantic, Subboreal, and Subatlantic are here shown according to their climatic affinities based on the molluscan record.

Epoch	Age	Region	Climatic Affinity								Total of species: in number Row per cent, % Column per cent, %	
			A: Arctic, S: Subarctic, B: Boreal, L: Lusitanian									
			Arctic	A, S	A, S, B	A, S, B, L	S, B	S, B, L	Boreal	B, L		Lusitanian
Pleistocene	Eemian	1. Bælt Sea	-	-	-	1 (2%)	2 (3%)	6 (10%)	-	43 (73%)	7 (12%)	59 (100%)
		2. Baltic Sea	-	-	1 (5%)	1 (2%)	1 (5%)	4 (5%)	-	12 (21%)	-	19 (100%)
		3. Kattegat	-	-	-	1 (3%)	-	3 (9%)	-	23 (72%)	5 (16%)	32 (100%)
		5. North Sea	-	-	1 (2%)	5 (8%)	1 (5%)	10 (12%)	-	66 (73%)	8 (9%)	91 (100%)
		6. Vendsyssel	-	-	9 (16%)	7 (11%)	1 (2%)	6 (5%)	1 (2%)	31 (56%)	-	55 (100%)
		7. Skagen	-	-	1 (7%)	4 (29%)	-	2 (6%)	-	6 (43%)	1 (7%)	14 (100%)
		3. Kattegat	1 (14%)	1 (14%)	2 (8%)	3 (4%)	-	-	-	-	-	-
	6. Vendsyssel	1 (3%)	6 (17%)	19 (53%)	7 (19%)	2 (6%)	1 (3%)	-	-	-	-	36 (100%)
	7. Skagen	1 (25%)	-	3 (75%)	-	-	-	-	-	-	-	4 (100%)
	Late Weichselian	6. Vendsyssel	2 (6%)	4 (11%)	13 (33%)	8 (23%)	3 (9%)	5 (14%)	-	-	-	35 (100%)
	7. Skagen	1 (11%)	1 (8%)	3 (5%)	3 (5%)	1 (5%)	-	-	-	-	-	9 (100%)
	Holocene	Preboreal/ Boreal	5. North Sea	-	-	1 (4%)	2 (8%)	-	3 (12%)	-	20 (77%)	-
7. Skagen			-	-	-	-	-	1 (33%)	-	2 (67%)	-	3 (100%)
Atlantic		1. Bælt Sea	-	-	-	2 (6%)	1 (3%)	5 (16%)	-	23 (74%)	-	31 (100%)
		2. Baltic Sea	-	-	-	-	-	2 (13%)	-	13 (87%)	-	15 (100%)
		3. Kattegat	-	-	-	-	-	5 (22%)	-	18 (78%)	-	23 (100%)
		4. Limfjorden	-	-	1 (1%)	6 (8%)	2 (3%)	13 (17%)	-	55 (71%)	-	77 (100%)
		5. North Sea	-	-	-	2 (7%)	-	2 (7%)	-	23 (85%)	-	27 (100%)
		6. Vendsyssel	-	-	-	-	1 (50%)	-	-	1 (50%)	-	2 (100%)
		7. Skagen	-	-	-	-	-	-	-	8 (100%)	-	8 (100%)
Subboreal		3. Kattegat	-	-	-	-	-	1 (50%)	-	1 (50%)	-	2 (100%)
		4. Limfjorden	-	-	2 (6%)	2 (3%)	-	2 (6%)	-	28 (78%)	2 (6%)	36 (100%)
		5. North Sea	-	-	-	3 (16%)	2 (11%)	1 (5%)	1 (5%)	12 (63%)	-	19 (100%)
		6. Vendsyssel	-	-	-	-	-	1 (33%)	-	2 (67%)	-	3 (100%)
		7. Skagen	-	-	-	1 (4%)	1 (4%)	2 (9%)	-	18 (78%)	1 (4%)	23 (100%)
		4. Limfjorden	-	-	-	-	-	-	-	1 (100%)	-	1 (100%)
		5. North Sea	-	-	-	1 (13%)	-	2 (25%)	-	5 (63%)	-	8 (100%)
Subatlantic		7. Skagen	-	-	1 (1%)	5 (7%)	2 (3%)	7 (10%)	1 (1%)	51 (75%)	1 (1%)	68 (100%)
		4. Limfjorden	-	-	-	-	-	-	-	1 (100%)	-	1 (100%)
	5. North Sea	-	-	-	1 (2%)	-	2 (2%)	-	5 (63%)	-	8 (100%)	
Total of species in number Row per cent, % Column per cent, %			6 (100%)	12 (100%)	57 (100%)	64 (100%)	20 (100%)	84 (100%)	3 (100%)	462 (100%)	25 (100%)	733

Fig. 103. Climatic characterisation (affinity) of mollusc assemblages for each region over the seven stages (ages) since the Eemian.

the climate of the Litorina period in postglacial time.

Also S.T. Andersen (1965, pp. 499–500) points to the Eemian as having an oceanic and warm climate. In his diagram from Hollerup, zone 5 represents the climax forest.

Jessen & Milthers (1928, p. 179) bring forth the view of Nordmann saying that the Lusitanian mollusc fauna was moving into the Baltic basin by way of the sounds that cut diagonally through the southern portion of the Cimbrian peninsula. However, this idea is, as discussed earlier, not accepted by the present author, where a connection to the west is advocated to be over the Kattegat–Vendsyssel–Skagen regions.

An eastern open connection to the White Sea over Finland and Russia will be discussed in connection with the Baltic region.

The Baltic, region 2

Appendix 6 and Fig. 103

In the Baltic Sea part of Denmark the number of recorded marine molluscs from the Eemian has fallen to 19 species compared to the Bælt Sea region, and no purely Lusitanian species occur. However, as pointed out earlier, this change in the climatic situation regarding the Baltic fauna can be seen as a consequence of the fact that here only the deeper-water assemblage characterised by *Turritella communis* occurs, although one of the species known from the characteristic part of the Bælt Sea fauna is recorded, i.e. *Arctica islandica*. However, the *Tapes* species are not met with in this region.

The deeper-water environment is therefore well characterised by the *Turritella* community.

Although the decline in number of species very much resembles the present-day situation between the Bælt Sea and the Baltic as mentioned earlier, five species in the Eemian fauna, including *Turritella communis*, show a salinity above the present conditions in the Baltic.

From the study of diatoms at Ollala in eastern Fennoscandia, Forsström *et al.* (1988, p. 322) write: “This mixture of warm and cold indicators probably means that the Eemian sea in the Baltic Basin had a connection both to the North Sea in the west and to the Arctic Ocean via the White Sea Basin in the northeast”.

Only a few works from eastern Fennoscandia have been based on molluscan studies. However, among the papers by Zans (1936), Sokolova *et al.* (1972), and Gross (1967), Gross mentions the following molluscs:

Portlandia arctica, *Clinocardium ciliatum*, *Heteranomia squamula*, *Macoma calcarea*, *Littorina littorea*, and *Cerastoderma edule*. Here the three last mentioned species occur in the Eemian from the Danish Baltic and *Clinocardium ciliatum* from the Vendsyssel region, although here in the upper *Turritella terebra* zone correlated to the Early Weichselian, as discussed later.

Portlandia arctica has not been recorded from the Danish Eemian, although it occurs in the beds below the Eemian in the Anholt boring (the Kattegat region), where Seidenkrantz (1993, p. 284) also has demonstrated foraminiferal zones A–D with Arctic species.

Gross (1967, p. 118) regards the Arctic and Arctic–Boreal molluscs in the Eemian clay as: “Relikte aus der *Portlandia*-Transgression des Dnepr II-Spätglazials, die nach dem Pollen-Profil und -Diagramm der Eem-Transgression voranging”.

The older correlation of the so-called Weissmeer transgression by Zans (1936, table 1) contains further details on the molluscs upon which the correlation has been based, and it also includes the Danish area, mentioning ‘Dänische Inseln’ after Ødum (1933) and ‘Skaerumhede’ after Jessen *et al.* (1910). However, the occurrence of the High-Arctic *Portlandia arctica* should be placed in the Late Saalian, as seen in the Kattegat region mentioned above, while the Arctic–Boreal species *Clinocardium ciliatum* could be taken as a relict in the Skærumhede sequence from the Late Saalian environment within the Danish area or introduced by the cooling in the Early Weichselian.

The faunal development has been worked out in more detail between the eastern Fennoscandia and the Danish area (Funder *et al.* 2002). The connection to the Arctic over the White Sea during the Eemian seems to be well established, but only for a shorter time, 1000–2000 years of the more than 10 000 years that the Eemian Sea existed in the Baltic region (Funder 2000, p. 68).

The Kattegat, region 3

Appendix 6 and Fig. 103

From the Kattegat region, 32 species have been recorded, with a high amount of Boreo-Lusitanian species (72%). Five species are Lusitanian, among which are found the characteristic Eemian species of the shallow-water environment, including the *Tapes* species. However, also the deeper-water environment is represented by the *Turritella* community in this region.

On Anholt, the *Turritella* community occurs at a depth of around 70 m b.s.l., and the *Tapes* fauna in the Isefjord area at Ejby at a depth of around 10 m a.s.l. The latter is considered to be *in situ* (Madsen 1968). It is tempting to regard the two localities as being at about their original elevation in relation to an Eemian sea level some what higher than the recent one, since the glacio-isostatic rebound had expired (Petersen 1991b).

On the basis of the scattered Eemian localities of which some are floes in the Weichselian glacial deposits, the maximum extent of the Eemian sea cannot be given. However, both the shallow-water environment characterised by the *Tapes* species and the deeper water by the *Turritella* species have been demonstrated. In this way both of the characteristic marine environments from the Bælt Sea and the Baltic respectively are represented in the Kattegat region.

The North Sea, region 5

Appendix 6 and Fig. 103

The largest amount of mollusc species within the Eemian have been recorded from the North Sea region, or to be more precise from the coastal region of the North Sea. In the Danish part of the North Sea, many studies on microfossils from the oil and gas fields have demonstrated Eemian deposits in the central North Sea, but their macrofossils have not been studied (Knudsen 1985a, 1986). However, the large amount (91) of molluscs from the coastal region fall into different facies, as seen in the previous regions when a much lower number was looked at.

Gripp (1964) uses the 'Senescens Sand' and 'Turritella Ton' to give his idea of the marine order of the strata. However, in this context, working with regions and not with localities, it should be emphasised that the development of different facies most probably happened in parallel. Gripp (1964, p 223) expresses this himself in saying: "Tapes-Sand und Turritellen-Ton sind die beiden Facies, die während des Anstiegs des Meeresspiegels entstanden".

As seen from the species found in the Danish North Sea coastal region, we do find the *Turritella* species and *Tapes* species, but also the occurrences of *Donax vittatus* should be mentioned as a facies indicator, characterising the high-energy coastal environment from this area facing the Eemian North Sea.

From recent studies on Foraminifera in northern

Germany at the Kiel Canal, Knudsen (1986) shows that the marine transgression took place in the warm part of the Eemian, and Hinsch (1985) in his mollusc study from the same area revealed three mollusc communities characterising the shallow-water environment, with such genera as *Mytilus-Cerastoderma*, *Acanthocardia-Venerupis* and *Bittium-Varicorbula*. However, the old material from many localities in the Danish North Sea region cannot be worked out to such detail, although all the marine mollusc species mentioned by Hinsch (1985) have been recorded from the Danish Eemian North Sea region.

When the molluscan fauna in the Danish Eemian North Sea region is compared with the Eemian on the west coast of Norway as described by Mangerud *et al.* (1981), 20 molluscan species out of the 35 species recorded from the Fjøsangerian are known from the North Sea region and 7 species from other Eemian regions in Denmark. Here *Macoma calcarea* and *Nuculana pernula* belonging to the Arctic-Boreal group occur in the Vendsyssel and Skagen regions, and in the Baltic region *Macoma calcarea* representing deeper water during the Eemian, while *Chlamys islandicus*, which does not occur in the Danish Eemian deposits, is found in the Weichselian recorded from the Vendsyssel region. This means that the Fjøsangerian can be regarded as slightly cooler than the Danish North Sea Eemian deposits.

Another marine Eemian deposit in Norway described by Andersen *et al.* (1983) at Bø on Karmøy (SW Norway) revealed 25 molluscan species from the Avaldsnes Interglacial described in detail by Sejrup (1987). Here as many as 20 species are in common with those in the Danish North Sea region, and one, *Hinia incrassata*, has been recorded from the Eemian in the Vendsyssel region.

Four species have not been found in the Danish Eemian. These are the Arctic-Lusitanian and Arctic-Boreal species *Puncturella noachina* and *Boreotrophon clatbratus* respectively, the latter occurring in the Late Weichselian deposits in the Vendsyssel region. This is much in line with the observations from the Fjøsangerian deposits. The four non-occurrences in the Danish Eemian among the Boreo-Lusitanian species *Pecten maximum* and *Lucinoma borealis*, the latter being common at both Norwegian localities, are difficult to explain. Among the 8 purely Lusitanian species recorded from the North Sea region, only *Plagiocardium papillosum* occurs in the Norwegian Eemian at Fjøsanger, which again points to a slightly cooler position for the Norwegian localities.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The Eemian mollusc fauna from Vendsyssel comprises 55 species with no purely Lusitanian climatic affinity, while quite a few (nine species ~ 16%) are found in the Arctic and the Boreal zones. The stratigraphical position has been well elucidated through foraminiferal investigations (Knudsen & Lykke-Andersen 1982; Knudsen 1984, 1985b, 1992; Lykke-Andersen 1987).

The study by Lykke-Andersen (1987, fig. 5) also involves the molluscs, and references are made to the zones established on the basis of macrofossils. According to the foraminiferal studies, the transition to the Early Weichselian takes place around 120 m b.s.l. in the Skærumhede I sequence (Jessen *et al.* 1910), which is about 140 m b.s. This means that the upper part of the *Turritella terebra* zone falls within the Early Weichselian.

The two Arctic to High Boreal species *Serripes groenlandicus* and *Clinocardium ciliatum* at depths of 132 m and 127 m b.s. respectively are discussed by Nordmann (Jessen *et al.* 1910, pp. 124–128), and the climatic indications from *Turritella communis* mean that the assemblage existed at the transition between the High and Middle Boreal.

In the paper by Knudsen (1992), it is said that an abrupt faunal change at the Eemian–Weichselian boundary reflects a drop in water depth of at least 50 m and a subsequent drop in temperature of several degrees.

The drop in temperature might well be reflected in the mollusc fauna by the occurrences of the two bivalves mentioned above, and for the drop in sea level it is tempting to recall the observed occurrence of the eulittoral *Mytilus edulis* at a depth of 135 m b.s.l. in the Skærumhede I boring and up to the *Abram nitida* zone, which forms the transition to the Arctic *Turritella erosa* community as mentioned earlier. Therefore, within the Vendsyssel area the Eemian (isotopic stage 5e) is represented by a *Turritella* community that continues into the beds representing the isotopic stages 5d–a (Knudsen 1992, fig. 4). The Hordalandian stage in western Norway contains *Serripes groenlandicus* and *Clinocardium ciliatum* species and is referred to the Early Weichselian (Mangerud *et al.* 1981). Arctic conditions first occurred in the macrofossil zones *Turritella erosa*, *Balanus crenatus* and *Macoma calcarea* (Bahnsen *et al.* 1974), which cover the *Portlandia arctica* zone *sensu* Nordmann (Jessen *et al.* 1910, fig. 8).

The Skagen region, region 7

Appendix 6 and Fig. 103

The 14 Eemian molluscs found in the Skagen boring are the lowest number recorded within the Eemian sites. However, the finds are a clear omen of the deeper-water environment not encountered earlier in Denmark on the basis of molluscs. The recorded molluscs point to an environment like the deeper part of the Skagerrak today, with a community such as the *Amphilepis norvegica*/*Pecten vitreus*, where the latter (*Delectopecten vitreus*) occurs in the Skagen Well, as mentioned earlier.

The boundary to the overlying Arctic deposits characterised by the occurrences of *Portlandia arctica* is sharp and coincides with a sedimentological change to a diamicton with dropstones in the Arctic part, as found in the Skærumhede sequence within the *Turritella erosa* zone (Bahnsen *et al.* 1974). Therefore, in the Skagen Well no transition zone from substage 5e to 5d–a can be demonstrated in the molluscan faunas.

The recorded Eemian communities and/or characteristic molluscan species for six regions with Eemian marine deposits are given in Table 3.

Table 3. Eemian communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea		<i>Mytilus edulis</i>	littoral shallow deeper
		<i>Tapes</i> spp.	
		<i>Arctica islandica</i>	
2. Baltic			littoral shallow deeper
	<i>Turritella</i>	<i>T. communis</i>	
3. Kattegat		<i>Mytilus edulis</i>	littoral shallow deeper
		<i>Tapes</i> spp.	
	<i>Turritella</i>	<i>T. communis</i>	
5. North Sea		<i>Donax vittatus</i>	littoral shallow deeper
	<i>Turritella</i>	<i>T. communis</i>	
6. Vendsyssel	<i>Turritella</i>	<i>T. communis</i>	littoral shallow ~ 100 m
7. Skagen		<i>Amphilepis/Pecten</i> <i>Delectopecten vitreus</i>	littoral shallow > 100 m

Early/Middle Weichselian stage 115 000 – 25 000 B.P.

The Kattegat, region 3

Appendix 6 and Fig. 103

Although the number of mollusc species recorded from the Kattegat region during the Early/Middle Weichselian is low – seven species – the climatic indications for the Arctic environment are clear, considering that all species can be found in the High Arctic, and that one species, *Portlandia arctica*, is High Arctic *par excellence*, and *Macoma calcarea* indicates shallow water.

The stratigraphical position of the Arctic *Macoma* community found in the Kattegat region – Holmstrup on Sjælland – has been determined by foraminiferal correlation and aminostratigraphical investigations, as mentioned earlier (Petersen & Buch 1974; Miller & Mangerud 1985). Recently, the foraminiferal studies of the Quaternary sequence in the Anholt boring have demonstrated a Middle Weichselian deposit at a depth of about 50 m b.s.l. (Seidenkrantz 1993). Considering the information given by Knudsen (1992) on a drop of sea level of around 50 m during the transition from the Eemian to the Weichselian, the Middle Weichselian beds in the cored section on Anholt may represent rather shallow-water deposits. This is in accordance with the occurrence of the Arctic *Macoma* community.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

Foraminiferal studies by Lykke-Andersen (1987) indicate that the Early Weichselian beds are represented by the upper *Turritella terebra* zone, and that the deeper-water temperate *Turritella* community continued into the first part of the Weichselian with the following *Abra nitida* zone as a transition to the Arctic deeper-water *Turritella* community (*Turritella erosa*).

Together with the Arctic and Arctic-subarctic species (seven in number, forming nearly 20% of the mollusc species), the sedimentological data show the occurrences of ice-rafted material recorded both from the Skærumhede I and the Skærumhede II borings (Jessen *et al.* 1910, p. 76; Bahnson *et al.* 1974, figs 3, 4, 7) reflecting Arctic conditions.

It has been argued by Nordmann (Jessen *et al.* 1910) that species within the genera *Mytilus*, *Cyprina*,

Zirpbaea, *Nassa*, and *Bittium* must be regarded as allochthonous and older elements. However, they could also be regarded as stray finds from contemporary shallow-water to littoral deposits occurring within times of higher temperatures in the near-shore areas, similar to the near-shore fauna of Middle Weichselian age – the Bø Interstadial (40–64 ka) with *Gibbula cineraria* and *Mytilus edulis*, the latter occurring frequently (Sejrup 1987).

During the younger part of the marine Middle Weichselian – around 32 000 B.P. – when the shallow-water Arctic *Macoma* community was established, no *Mytilus edulis* or *Bittium reticulatum* have been recorded.

The development of the bottom communities within the Older Weichselian sequence is therefore given by the transition from the *Turritella* communities in deeper water to the Arctic *Macoma* community in shallow water.

The Skagen region, region 7

Appendix 6 and Fig. 103

Very few molluscs have been found in the Skagen boring of Older Weichselian age. The four species are all Arctic, and the occurrence of *Portlandia arctica* shows that High Arctic conditions have prevailed and ice-rafted material occurs. There is no indication of near-shore fauna as recorded from the Vendsyssel region. From this, it might be concluded that the deposition of these beds took place in the first part of the Middle Weichselian, contemporaneous with the deposition of the *Turritella erosa* beds of the Skærumhede sequence, but at a water depth of more than 100 m, as demonstrated earlier.

From the few finds, it is not safe to point to a certain community on the basis of molluscs. However, the community in deeper Arctic waters is described by other animals than molluscs, i.e. the Ascidia–Spongia epifauna, and at depths exceeding 200 m by *Gorgonocephalus* species. From the estimate on water depth taken in comparison with the early part of the Arctic sequence in the Vendsyssel region, the palaeodepth must have been well above 100 m.

The recorded Early/Middle Weichselian communities and/or characteristic molluscan species are given in Table 4.

Table 4. Early/Middle Weichselian communities and/or characteristic molluscan species

Region	Community	Species	Depth
3. Kattegat	Arctic <i>Macoma</i>	<i>M. calcarea</i>	littoral shallow deeper
6. Vendsyssel	Arctic <i>Macoma</i> Arctic <i>Turritella</i> <i>Turritella</i>	<i>M. calcarea</i> <i>T. erosa</i> <i>T. communis</i>	littoral shallow ~ 90 m ~ 90 m
7. Skagen	Ascidia-Spongia		littoral shallow 100–200 m

Late Weichselian stage 25 000 – 10 000 B.P.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The 35 mollusc species found in the Vendsyssel region are in number very close to the number of species encountered in the Vendsyssel region during the Early/Middle Weichselian (36 species). However, as seen in Fig. 103, the percent of molluscs with a wide range and only connected to the Subarctic and southwards is higher in the Late Weichselian (46%) compared to the Early/Middle Weichselian (28%). This can be explained by the way the development in the two seas before and after the Main Glaciation, the Older and Younger *Yoldia* Sea respectively took place.

The deposits from the Older *Yoldia* Sea reflect the transition from deeper Arctic to shallow-water Arctic communities, the *Turritella* and *Macoma* communities respectively. The Late Weichselian beds within the shallow-water environment show a development from the Arctic *Macoma* community to the Boreo-Arctic *Mytilus-Zirphaea* community after 13 000 B.P., with a deeper-water community characterised by the *Portlandia arctica* species, as outlined by Petersen (1984), which could be part of the deeper *Macoma* community – the so-called *Ophiocten* zone.

These observations form the background for the earlier given explanation of the occurrences of Boreal shallow-water species such as *Mytilus edulis* in the deeper-water Arctic community in the Older Weichselian deposits from the Vendsyssel region.

The occurrences of the *Mytilus edulis* species in the Late Weichselian deposits in large quantities are described by Jessen (1899). The dates of the earliest occurrences of *Zirphaea* and *Mytilus* go back to 12 770 and 12 520 B.P. ¹⁴C years respectively.

All the 30 ¹⁴C dates forming the base for the evaluation of the Late Weichselian sea levels and occurrences of fauna communities as figured in Petersen (1984, fig. 1) have been listed by Petersen & Rasmussen (1995a, table 1). It appears that the dates older than 13 000 B.P. ¹⁴C years all come from *Hiatella arctica* and *Macoma calcarea* (only one date) going as far back as 14 650 ± 190 B.P. ¹⁴C age. Considering the mollusc species inhabiting the waters “of the Swedish west coast shortly after deglaciation” (Fredén 1986, p. 55), one finds also *Chlamys islandica* and *Mytilus edulis* shortly after 13 000. The latter within the time span of its first dated occurrence in the Younger *Yoldia* Sea deposits in Denmark.

As to the deeper-water deposits also around 13 000, one can take the sample from the Dybvad clay pit (Fig. 1) dated to 13 010 ± 190 B.P. ¹⁴C which contained the following molluscs: *Hiatella arctica*, *Mya truncata*, *Macoma torelli*, *Portlandia arctica*, *Buccinum groenlandicum* and *Cylichna occulta* (Petersen 1984). It is seen that still after the immigration of Boreo-Arctic fauna to the shallow-water environment, showing an amelioration in climate, the Arctic community persisted in the deeper water as shown by the dating from the Bindslev clay pit giving 12 650 ± 180 ¹⁴C age B.P., with species such as *Macoma calcarea* and *Portlandia arctica*.

The same situation can be estimated from the investigation of the Pleistocene/Holocene Boundary in south-western Sweden (the Moltemyr core) where “zone Z comprising the samples from 560 cm to 650 cm, is characterised by *Portlandia arctica* and *Nucula tenuis* (*Nuculoma tenuis*, here taken as a species with a wide climatic range), and by the absence of many of the species of the overlaying zone (such as *Mytilus edulis*) ... The water depth during deposition of zone Z was greater than during any of the other zones (above) probably more than 20 m” (Feyling-Hanssen 1982, p. 128).

Regarding the climatic indication of *Portlandia arctica*, Feyling-Hanssen (1982, p. 131) quotes Andersen (1975, p. 54) saying: “Evidently, *Portlandia arctica* lived near the ice fronts [in southern Norway] also during older, glacial phases, but it seems to have disappeared from our coasts shortly after the Ra event, probably due to a warming of the sea”.

According to Sørensen (1979), the disappearance of *Portlandia arctica* from the Oslo Fjord area occurred somewhat before 10 000 B.P.

The Younger Dryas marine deposits have not been demonstrated in the Vendsyssel region but are recorded from the Skagen region, which will be discussed next.

The Skagen region, region 7

Appendix 6 and Fig. 103

The nine species recorded from the Skagen Well indicate an Arctic deeper-water community very much like the *Arca-Astarte crenata* community (Ockelmann 1958). There are no finds of species which could be referred to the more shallow-water environment as seen in the case of the Vendsyssel region to the south both during the Early/Middle Weichselian and the Late Weichselian.

Through most of the history of the cored section of Pleistocene age, the Skagen Well has revealed mollusc assemblages from a deeper-water environment. Also the transition to the Holocene takes place in deeper water.

The purely Arctic species *Portlandia arctica* together with *Bathyarca glacialis* is found right up to the strata dated to around 10 000 B.P. forming the Pleistocene–Holocene boundary in the Skagen Well. However, in the description of the shell fauna of the marine clays in the Oslo Fjord region, Brøgger (1900, p. 685) states: “*Portlandia arctica* is never found in the *Arca* Clay”. Later datings of the ‘Middle *Arca* Clay’ and the ‘Younger *Arca* Clay’ given by B.G. Andersen (1965, p. 118) yielded early Preboreal ages. In the Younger *Arca* Clay from Norway, species such as *Mytilus edulis*, *Zirfaea crispata*, and *Macoma balthica* (B.G. Andersen 1965, table 2) are also found, which characterise the shallow-

water deposits in Vendsyssel after 13 000 B.P. ¹⁴C age. The recorded recent occurrence of *Bathyarca glacialis* from southern Iceland implicates extension into the High-Boreal region, although the main extension is in the Arctic. The Norwegian records of *Bathyarca glacialis* come from a more shallow-water environment, as seen from the occurrences of the three shallow-water species mentioned above.

The recorded Late Weichselian communities and/or characteristic molluscan species are given in Table 5.

The Preboreal–Boreal stage 10 000 – 8000 ¹⁴C years B.P.

The North Sea, region 5

Appendix 6 and Fig. 103

Mollusc faunas from the Late Weichselian have here been recorded only from the Vendsyssel and Skagen regions. As seen in Fig. 103, the early part of the Holocene, the Preboreal and Boreal, have a record of 26 species, with as many as 77% (20 species) Boreo-Lusitanian. This is in contrast to the records from the Late Weichselian, when the Arctic–Boreal elements dominated, with 54% in the Vendsyssel region and 55% in the Skagen Well, the latter with only a few species and representing a deeper-water environment. The Preboreal–Boreal North Sea faunas contain eulittoral as well as shallow-water species.

Mytilus edulis, *Littorina littorea* and *Cerastoderma edule* characterise the littoral zone and *Macoma balthica* the shallow-water zone. Using the characteristic species from the C.G.J. Petersen community concept, the oldest recorded faunal communities from the North Sea might be the *Mytilus* epifauna community with *Littorina littorea*, and the *Macoma* infauna community with *Cerastoderma edule*. Also the *Abra* community on mixed bottoms with *Phaxas pellucidus*, *Corbula gibba* and *Mya truncata* might be reflected in the recorded species.

Table 5. Late Weichselian communities and/or characteristic molluscan species

Region	Community	Species	Depth
6. Vendsyssel	<i>Mytilus/Zirphaea</i>	<i>Z. crispata</i>	littoral
	Arctic <i>Macoma</i>	<i>M. calcarea</i>	shallow
	Ophiocten zone	<i>Portlandia arctica</i>	deeper
7. Skagen			littoral
	<i>Arca-Astarte</i>	<i>Bathyarca glacialis</i>	shallow deeper

The Skagen region, region 7

Appendix 6 and Fig. 103

As discussed earlier, the environment of the earliest Holocene, the Preboreal and Boreal, can be referred to the *Maldane-Ophiura sarsi* community. This deep-

Table 6. Preboreal–Boreal communities and/or characteristic molluscan species

Region	Community	Species	Depth
5. North Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
7. Skagen			littoral
	Maldana/Ophiura		shallow > 150 m

water community observed in the Skagen region compared to the shallow-water communities recorded from the North Sea coastal region once more demonstrates the unique position of the deeper-water communities observed in the Skagen Well material compared to the other regions in Denmark through the Late Quaternary.

The recorded Preboreal–Boreal communities and/or characteristic molluscan species are given in Table 6.

The Atlantic stage 8000–5000 ¹⁴C years B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

Out of the 47 species known from the Bælt Sea region, 31 have been recorded from the Atlantic (Fig. 103).

The littoral zone with *Mytilus edulis*, *Littorina littorea*, *Littorina saxatilis*, *Cerastoderma edule*, and *Macoma balthica* from the shallow-water zone, is recorded; furthermore, the *Abra alba* community together with *Corbula gibba*.

These faunal elements reveal the *Mytilus* epifauna community with *Ostrea edulis*, which no longer occurs in this area. In the infralittoral zone is the *Macoma* infauna community where such species as *Paphia aurea*, *Tapes decussatus*, and *Venerupis pullastra* have been found, and finally the *Abra* community with *Corbula gibba*.

Also the epifauna on the vegetation is reflected in *Rissoa albella*, *R. membranacea*, and *R. inconspicua* and other gastropods. Also the bivalve *Parvicardium exiguum* is associated with the vegetation.

The communities mentioned are still to be found in the Bælt Sea region, whereas *Paphia*, *Tapes*, *Venerupis* and *Ostrea* are no longer found in this region.

The Baltic, region 2

Appendix 6 and Fig. 103

Fifteen mollusc species out of the 19 recorded from the Baltic region during the Holocene can be referred to the Atlantic (Fig. 103).

The occurrences of *Mytilus edulis* and *Littorina littorea* are referred to the *Mytilus* epifauna community in the littoral zone, while species, as *Macoma balthica*, *Cerastoderma edule*, and *Scrobicularia plana* represent the *Macoma* infauna community in shallow water.

The occurrences of both *Littorina littorea* and *Scrobicularia plana* are characteristic for the Atlantic in the Baltic and are now absent. Spärck (1950) points to the wider extent of *Scrobicularia plana* in the Stone Age as a consequence of warmer water in those days; however, in the present work the higher salinity is preferred as an explanation, as mentioned earlier. This is supported by the occurrences of gastropods like *Bittium reticulatum*, *Rissoa albella*, and *Aporrhais pes-pelicani*, species recorded from other regions today with higher salinity.

It should be noticed that *Scrobicularia plana* and *Littorina* species have been demonstrated as far north in the Baltic as Estonia (Kessel & Raukas 1979, fig. 9), although only with a low percentage but persisting into the Subboreal. The unexpected find of *Ostrea edulis* from Estonia has later been re-evaluated as transported there by some seamen and thrown then overboard (in a letter from Prof. A. Raukas, May 1995).

According to Nordmann (1903b, 1906), Madsen (1944), and Spärck (1942, fig. 21), the southernmost finds of subfossil oysters are the Bælt Sea and Øresund off Landskrona.

The Kattegat, region 3

Appendix 6 and Fig. 103

From the Kattegat region, only half of the recorded species have been dated so as to give a first appearance date. This amounts to 23 species from the Atlantic (Fig. 103).

All of the dated species come from geologically mapped areas and not from the Kattegat proper. Therefore the observed species all come from shallow-water environments, excluding the deeper-water environment recorded from foraminifera (Christiansen *et al.* 1993; Seidenkrantz & Knudsen 1993).

From the listed species dated to the Atlantic the *Mytilus* epifauna community with *Littorina littorea* and the *Macoma* infauna community with *Cerastoderma edule* and *Tapes decussatus* can be pointed out. Furthermore, the *Abra* community with *Corbula gibba*, which is common in present-day inner Danish waters (Thorson 1950), is present.

The Limfjord, region 4

Appendix 6 and Fig. 103

This region has the highest number of recorded mollusc species from the Holocene, viz. 147 species, and 77 have been dated to the Atlantic (Fig. 103).

Petersen (1918, pp. 22–36) described the communities in the Limfjord region covering the *Macoma balthica*, the *Venus* and the *Abra* communities. Also an area with *Mya truncata* is mentioned, forming a transition zone between the *Macoma* and the *Abra* communities. In patches the epifauna elements such as *Mytilus edulis* and *Modiola modiolus* are found.

From the *Zostera* vegetation, the *Rissoa* and *Bittium* species are mentioned.

All of the characterising species from these communities have been recorded from the Atlantic. *Paphia aurea*, *Tapes decussatus*, *Venerupis rhomboides* and *Venerupis pullastra* were represented during the Atlantic, where as only *Venerupis pullastra* is present in the Limfjord today. *Ostrea edulis* was well established during the Atlantic, as seen from the species composition of the 'køkkenmødding' (kitchen midden) (Petersen 1986a, figs 3, 4). The above-mentioned species and *Cerastoderma edule* occurred in the infralittoral zone in large quantities most probably in the tidal zone which was the best collecting grounds for the Stone Age people. In a multi-lobed body of water such as the Limfjord, many habitats have existed during the Atlantic. However, also the development through time has been considered, as seen in the case of the marine stages in Tatum Sø – once the southernmost part of Skive Fjord (Rasmussen & Petersen 1980).

In the northern part of the former Limfjord during the Atlantic, the deeper-water fauna with *Abra alba* and *Corbula gibba* can be demonstrated at the Vust locality (Petersen 1981, p. 502). The recorded Atlantic communities have very much in common with the recent communities.

The North Sea, region 5

Appendix 6 and Fig. 103

Twenty-seven species immigrated during the Atlantic in the North Sea coastal region (Fig. 103), and *Chamelea striatula* and *Spisula subtruncata* characterise the *Venus* community and are very common in the recent North Sea region.

Also *Paphia aurea* and *Tapes decussatus* make their appearance in the North Sea region during the Atlantic.

According to Hessland (1943), *Tapes decussatus* should immigrate to the west coast of Sweden already in the Boreal, while *Paphia aurea*, *Venerupis rhomboides* and *Venerupis pullastra* followed in the Atlantic. This is a close parallel to the recorded immigration to the Limfjord region, although here following the transgression and not superjacent to older marine deposits as in the North Sea.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The dates from the Vendsyssel region during the Holocene are made on only a few species. However, the faunal assemblages *sensu* Nordmann (Jessen 1905) can be commented upon in the light of immigration dates observed in the neighbouring Limfjord region.

Nordmann (Jessen 1905, p. 145) operates with five assemblages (from a to e) with the following headings:

- a) Beach deposits
- b) Oyster banks
- c) Deposits in coves and sounds
- d) Deposits in fjords and sounds with muddy bottoms and no current
- e) Lagoonal deposits

- a) Beach deposits

The first type – the beach deposits – cannot be considered in any relation to the community concept *sensu* C.G.J. Petersen, since the dominating part of the shell material has been redeposited. However, as a geological unit, it points to a former sea level stand, albeit difficult to date, because of the allochthonous character of these deposits.

Among the 90 species listed from this region (south-

ern part of Vendsyssel), Nordmann (Jessen 1905, table a) points to *Spisula subtruncata* and *Fabulina fabula* as being conspicuous, but other species may dominate at some localities, as seen from the table. Both species pointed out by Nordmann are recorded from the Limfjord during the Atlantic.

b) Oyster banks

As pointed out by Petersen (1918, p. 52), the so-called oyster banks in the recent Limfjord have 1 or 2 specimens per m². However, the places recorded by Nordmann are located on former narrow channels where the oysters occurred in large quantities together with *Chlamys varia*, *Hiatella arctica*, *Retusa truncatula*, *Mysella bidentata*, *Parvicardium exiguum*, *Paphia aurea*, *Venerupis pullastra*, *Bittium reticulatum*, *Rissoa inconspicua*, *Rissoa parva*, *Buccinum undatum*, *Nucula nitidosa*, *Tripbora adversa*, *Cerastoderma edule*, and *Hydrobia ulvae*, all of which are recorded from the Limfjord during the Atlantic. Only two species mentioned by Nordmann (Jessen 1905, p. 147) as being characteristic from some of the oyster banks, *Caecum glabrum* and *Acmaea virginea*, have their earliest record from the Limfjord in the Subboreal. Therefore the oyster banks *sensu* Nordmann seem to be well established in the Vendsyssel region already during the Atlantic, considering the dates obtained from the Limfjord region.

The oyster banks from the Atlantic appear to be characteristic features with their high diversity of species and huge quantities of *Ostrea edulis* not met with in present-day Danish waters. This could be seen as a parallel to the fluctuation in the population of oysters observed during the last hundred years in Danish waters, but should rather be connected with changes in the tidal currents which changed to a minimum during the following stage – the Subboreal (Petersen 1993), and put an end to the large oyster banks.

c) Deposits in coves and sounds

From these deposits Nordmann points to species such as *Spisula subtruncata*, *Modiolus modiolus*, *Thracia phaseolina*, and *Corbula gibba* as being characteristic of coves and sounds. They have all been recorded from the Limfjord during the Atlantic, and they represent species known from the deeper-water deposits both as epifaunal elements (*Modiolus modiolus*) and infaunal elements as found in the C.G.J. Petersen communities, the *Modiola* and *Abra* communities respectively.

This is further demonstrated by the following spe-

cies mentioned by Nordmann (Jessen 1905, p. 148): *Cerastoderma edule*, *Parvicardium scabrum*, *Nucula nitidosa*, *Hiatella arctica*, *Chamelea striatula*, *Timoclea ovata*, *Venerupis pullastra*, *Fabulina fabula*, *Tellimya ferruginosa*, *Lunatia alderi*, and *Retusa truncatulus*. Also these species have been dated back to the Atlantic in the Limfjord region. *Ostrea edulis* occurs, but as stray finds among the infauna elements dominating in the above-mentioned assemblage that includes *Abra alba*, which occurs in most of the samples, although not frequently (Jessen 1905, table c).

d) Deposits in fjords and sounds with muddy bottoms and no current

From such deposits Nordmann mentioned the finds of *Zostera*, which was a well established vegetational element in the recent Limfjord, according to Petersen & Jensen (1911, map 1).

The dominating species in this assemblage, which resembles the present-day fauna in such environments, are *Hydrobia ulvae*, *Littorina littorea*, *Littorina obtusata*, *Rissoa membranacea*, *Cerastoderma edule*, *Mytilus edulis*, *Scrobicularia plana*, *Paphia aurea*, *Bittium reticulatum*, *Hinia reticulata*, *Onoba semicostata*, *Parvicardium exiguum*, *Macoma balthica*, and *Ostrea edulis*, the last two species only with a few specimens. All the above-mentioned species occurred in the Limfjord region during the Atlantic.

The *Littorina*, *Rissoa*, and *Parvicardium* species might often be found on the *Zostera* vegetation.

Among the dominating species also mentioned by Nordmann, some have not been dated back to the Atlantic (in the Limfjord region) but occur in the Subboreal, viz. *Littorina tenebrosa*, *Akera bullata*, and *Retusa obtusa*. However, already the species recorded from the Atlantic point to the so-called *Echinocyamus* community (Spärck & Lieberkind 1921), although the echinoids have not been recorded by Nordmann (Jessen 1905).

e) Lagoonal deposits

These deposits represent two assemblages, according to Nordmann (Jessen 1905, p. 150), viz. an older more open-water environment with species such as *Macra stultorum*, *Tellimya ferruginosa*, *Chamelea striatula*, *Fabulina fabula*, *Ensis ensis*, *Lunatia catena*, *Lunatia alderi*, and *Aporrhais pespelicani*, which are mixed with faunal elements from the lagoon itself, such as *Hydrobia ulvae*, *Scrobicularia plana*, and *Mytilus edulis*. In connection with a *Zostera* vegetation, *Rissoa membranacea* and *Lacuna vincta* may occur in huge quantities.

Such a deposit cannot be compared to any of the Petersen communities, although they play an important role in the geological setting, as was the case also with the beach deposits.

In the northern and eastern part of Vendsyssel, further comments will be added to the shallow-water and beach deposits with the finds of the *Dosinia* and *Mya arenaria* species. They have been dated to the Subboreal and Subatlantic respectively and are therefore commented upon later.

The Skagen region, region 7

Appendix 6 and Fig. 103

Nearly all of the eight recovered species from the Atlantic (Fig. 103) show a deep-water fauna, which on the basis of the dominating role of the echinoids is tentatively referred to the *Amphiura* community known from the present-day Skagerrak.

The final large eustatic rise took place during the Late Boreal – Early Atlantic, and the difference in

isostatic rebound from 8000 B.P. between the Skagen and Limfjord regions is around 31 m, with the highest amount in the north (Skagen). It appears that the water depth in the Skagen region must have been up to 100 m during the Atlantic (Petersen 1981, 1991b). Therefore, the occurrence of a single *Spisula subtruncata* shell must be taken as far outside its habitat, considering that the modern depth range of this species is 0–36 m (Petersen 1986c, table 2).

The recorded Atlantic communities and/or characteristic molluscan species are given in Table 7.

The Subboreal stage 5000–2500 ¹⁴C years B.P.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

There are no dated mollusc finds from the Subboreal in the Bælt Sea region. As stated for the Atlantic in this region, the bottom communities known from the present day were already established, but they included some species such as *Tapes* and *Ostrea* which are no longer extant in this area. However, as *Paphia aurea* and *Ostrea edulis* still occurred in the Iron Age sites – from the Subatlantic – it is most probable that these species persisted there, while *Tapes decussatus* and *Venerupis pullastra* expired during the Subboreal in the Bælt Sea region (Petersen 1985c, fig. 5).

The Baltic, region 2

Appendix 6 and Fig. 103

There is no dated record of molluscs from the Subboreal in the Danish part of the Baltic. Therefore the change in the Atlantic *Littorina* fauna, into the *Lymnaea* Sea fauna, which occurred during the Subboreal around 4000 B.P. (Fredén 1980, p. 70), must be taken from observations outside Denmark. The mollusc fauna from Estonia shows that *Littorina littorea*, *Rissoa membranacea*, and *Scrobicularia plana* persisted there until about the end of the Subboreal (Kessel & Raukas 1979, fig. 9). The implications of this should be that these species must have been present in the Danish area throughout the Subboreal.

In the central part of the Baltic, around Gotland, *Lymnaea peregra* f. *baltica* re-immigrates after the

Table 7. Atlantic communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis/Ostrea edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica/Tapes</i> spp.	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis/Littorina littorea</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica/Tapes</i> spp.	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis/Tapes</i> spp.	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra/Venus</i>	<i>A. alba</i>	deeper
5. North Sea			littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow deeper
6. Vendsyssel	<i>Modiola</i>	<i>M. modiolus</i>	littoral
	<i>Abra</i>	<i>A. alba</i>	shallow deeper
7. Skagen			littoral
	<i>Amphiura</i>	<i>Parvicardium minimum</i>	shallow ~ 100 m

maximum of the *Littorina* transgression (Munthe 1940, p. 124). This gastropod was also present in the early, more brackish part of the *Littorina* Sea deposits in Fakse Bugt.

In Estonia (Kessel & Raukas 1979, fig. 9), the reappearance of *Lymnaea* took place around 4000 B.P., implying that the salt-demanding species (*Littorina*, *Rissoa*, and *Scrobicularia*) occurred together with the brackish *Lymnaea* species throughout the later part of the Subboreal!

The Kattegat, region 3

Appendix 6 and Fig. 103

The mollusc faunas recorded from the Kattegat region represent only part of the total faunal complex within this large region, and have been dated only on Djursland. However, this demonstrates the expiring tidal amplitude in the early part of the Subboreal.

The only dated immigrants to the fauna from the central part of Djursland during the Subboreal are *Onoba semicostata* and *Littorina tenebrosa*. Both extended into the Baltic today and tolerate brackish water. In this way they are typical for the environmental changes recorded in the marine faunas from Djursland.

The fauna during the Atlantic was characterised by *Ostrea edulis*, *Tapes decussatus*, *Macoma balthica*, and *Corbula gibba*. *Bittium reticulatum* was present in large quantities, but disappeared in the Subboreal. Also the decline in numbers of *Hydrobia ulvae* and its replacement in equal numbers by *Hydrobia ventrosa* speak in favour of a more brackish-water influence. The implications of the study of mollusc species on a quantitative basis in connection with ¹⁴C dates and pollen analyses confirm that the fauna during the *Tapes* Sea period was more prolific than nowadays. However, it also demonstrates as a new point of view that this applies only for the Atlantic. In Petersen (1993, p. 368) it is argued that the change in sedimentation rate from the Atlantic to the Subboreal, which has been calculated for the Korup Sø area on Djursland, points to a lowering of the tidal range in Danish waters since the Atlantic. This is explained in that way that sedimentation will stay low as far as the tidal current reaches and allows halophilous species to live far up in the fjords according to the observations on the faunal record. Furthermore, an older record from the mapping of the area of flaser bedding seen as a tidal bedding supports such an explanation.

It was tempting to see the change from the *Littorina* Sea to the *Lymnaea* Sea in the Baltic on the background of such a lowering of the tidal impact in the inner Danish waters. However, as shown in the preceding section on the Baltic, the change occurred around 4000 B.P.

Recalling the statement by C.G.J. Petersen that the deposition of the *Tapes* layers has happened in a period when the Danish waters from a hydrographical point of view have been more like the North Sea or the open sea than now, it is clear that a tidal impact could make the difference and explain the large oyster banks far into the Roskilde Fjord in north-eastern Sjælland and other former fjord regions facing the Kattegat region.

The well-dated Ertebølle coastal sites ('køkkenmøddinger' – kitchen middens) from all over Denmark also present a large amount of *Ostrea edulis* from the Atlantic and demonstrate that the molluscan diet later in the Subboreal was based on the *Cardium* species (Andersen 1991, 1995). This situation has lasted into the Iron Age, as seen in the shell middens from the Bælt Sea area (Petersen 1985c, fig. 5).

However, this change mostly affected the fjord complex. Consequently the Kattegat region still has the communities listed for the Atlantic.

The Limfjord, region 4

Appendix 6 and Fig. 103

The 36 species which immigrated into the Limfjord during the Subboreal (Appendix 6) can be considered according to their way of life, presented from the list below.

Age: Subboreal

Climatic regions: asb.

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Margarites helicinus (Phipps 1774)

Subclass Opisthobranchia

Order Anaspidea

Retusa obtusa (Montagu 1803)

Total for climatic regions asb. : 2 (5.6%)

Climatic regions: asbl

Class Gastropoda

Subclass Prosobranchia
 Order Archaeogastropoda
Acmaea tessulata (Müller 1776)
 Order Neotaenioglossa
Lacuna pallidula (da Costa 1778)
 Total for climatic regions asbl: 2 (5.6%)

Climatic regions: .sbl
 Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
Acmaea virginea (Müller 1776)
 Class Bivalvia
 Subclass Pteriomorpha
 Order Pterioidea
Delectopecten vitreus (Gmelin 1791)
 Total for climatic regions .sbl: 2 (5.6%)

Climatic regions: ..bl
 Class Gastropoda
 Subclass Prosobranchia
 Order Archaeogastropoda
Helcion pellucidum (Linnaeus 1758)
Gibbula tumida (Montagu 1803)
Skenea basistriata (Jeffreys 1877)
 Order Neotaenioglossa
Littorina tenebrosa (Montagu 1803)
Lacuna parva (Montagu 1803)
Cingula semistriata (Montagu 1808)
Rissoa violacea Desmarest 1814
Caecum glabrum (Montagu 1803)
Aporrhais pespelicani (Linnaeus 1758)
 Order Heterogastropoda
Epitonium turtonis (Turton 1819)
Vitreolina philippii (Rayneval & Ponzi 1854)
 Order Neogastropoda
Hinia incrassata (Ström 1768)
Raphitoma purpurea (Montagu 1803)
Raphitoma linearis (Montagu 1803)
 Subclass Heterobranchia
 Order Heterostropha
Chrysallida decussata (Montagu 1803)
Chrysallida indistincta (Montagu 1808)
Ebala nitidissima (Montagu 1803)
Eulimella laevis (Brown 1827)
Ondina divisa (J. Adams 1797)
Ondina diaphana (Jeffreys 1848)
 Subclass Opisthobranchia
 Order Anaspidea
Akera bullata Müller 1776
 Class Bivalvia

Subclass Palaeotaxodonta
 Order Nuculoida
Nucula nucleus (Linnaeus 1767)
 Subclass Pteriomorpha
 Order Pterioidea
Palliolum striatum (Müller 1776)
Palliolum tigrinum (Müller 1776)
 Subclass Heterodonta
 Order Veneroida
Mactra stultorum (Linnaeus 1758)
Lutraria lutraria (Linnaeus 1758)
Ensis ensis (Linnaeus 1758)
 Order Myoida
Pholas dactylus Linnaeus 1758
 Total for climatic regions ..bl: 28 (77.8%)

Climatic regions: ...l
 Class Gastropoda
 Subclass Prosobranchia
 Order Neotaenioglossa
Alvania lactea (Michaud 1830)
Onoba proxima (Forbes & Hanley 1850)
 Total for climatic regions ...l: 2 (5.6%)

Total for age Subboreal: 36 (14.6%)

The Archaeogastropoda are all (six) epifauna on seaweeds or on hard substrates.

The Neotaenioglossa have seven epifaunal elements mostly on seaweeds and two infauna species, of which *Aporrhais pespelicani* is a shallow infauna animal.

The Heterogastropoda with *Epitonium turtonis* and *Vitreolina philippii* are associated with other animals, the former feeding on anemone or preying on other species and the latter being an intermittent parasite of echinoderms (Fretter & Graham 1982, p. 387).

The Heterostropha with six species are predators or external parasites.

The Anaspida with two species, *Akera bullata* and *Retusa obtusa*, are epifauna and infauna species respectively, the former on *Zostera* in shallow water and the latter in mud or fine sand connected with the *Macomma* community.

The only Nuculoida found, *Nucula nucleus*, belongs to the shallow infauna.

The Pterioidea with three species are referred to the epifauna, since the *Delectopecten vitreus* is found attached with its byssus on hard substrates.

The Veneroida have three species which are all referred to the infauna. *Lutraria lutraria* and *Ensis ensis* are deep-borrowing.

The Myoida with *Pholas dactylus* bores in different substrates.

When taking the above-mentioned groups of species associated with other animals, carnivores, predators, and boring species as a whole, we have three categories: the epifauna with 47.2%, the infauna with 19.4%, and other elements with 33.4% of the species immigrated during the Subboreal. When the same procedure is followed for the 77 species which have been dated to the Atlantic in the Limfjord region, we find that the percentages for the epifauna, the infauna and other elements are 31%, 46.8% and 22% respectively, which shows that the epifauna element becomes the dominating one in the Subboreal among the newcomers. This might tentatively be connected with a denser vegetation in the Subboreal of sea-weed.

The North Sea, region 5

Appendix 6 and Fig. 103

Nineteen species make their first appearance in the Danish North Sea during the Subboreal.

When considering their way of living and their grouping into epifauna, infauna and other elements, it appears that the groups are of equal size, i.e. five, six and eight species respectively. However, the number is too low to be used for any comparison with other regions. In the North Sea region the dates of first appearance go back to the Preboreal–Boreal stage, showing that the initial stages were dominated by the infauna species; the Preboreal–Boreal: seven epifauna, 16 infauna, and four other elements; the Atlantic: six epifauna, 17 infauna, and four other elements.

The development of the bottom communities in the North Sea region seems in this way to corroborate the changes observed in the Limfjord region from the Atlantic to the Subboreal.

These changes are in facies rather than climatic. A slightly more temperate fauna was met with during the Atlantic, as mentioned earlier, and it has consequently no bearing on the observed changes. But the expiring tidal influence in the Danish waters taking place in the early Subboreal might have been of some importance for the environmental changes reflected through the bottom communities.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The Vendsyssel region does not give much information on the immigration of species during the Holocene. However, the *Dosinia* beds were described from this area and have been dated quite recently in the type area around Strandby north of Frederikshavn (Nordmann 1904; Petersen 1991b). The oldest date for the *Dosinia exoleta*, which is the characteristic species for the *Dosinia* beds, is 4240 ± 85 B.P. in ^{14}C years (K-5318). This earliest dated occurrence of *Dosinia exoleta* corresponds to a hydrographical change in the Kattegat region described by Nordberg & Bergsten (1988) and Nordberg (1989). The demonstrated lowering of the tidal influence in the inner Danish waters took place also in the early part of the Subboreal.

Petersen (1976) pointed out that seven mollusc species hitherto known only from the *Dosinia* beds also occur in the raised marine deposits from the western part of the Limfjord, i.e. *Lucinoma borealis*, *Hinia incrassata*, *Venerupis rhomboides*, *Abra prismatica*, *Lutraria lutraria*, *Pholas dactylus*, and *Helcion pellucidum*.

Furthermore, not only ten species from the *Dosinia* beds are also in the deposits from the Limfjord but five of them occurred already during the Atlantic: *Gari fervensis*, *Turritella communis*, *Lucinoma borealis*, *Abra prismatica*, and *Venerupis rhomboides*. These species, representing an infauna assemblage very much like the *Dosinia* species, were also characteristic of the early Holocene dominating infauna mollusc assemblage.

Mörner (1969, pp. 384–386, and table 1) points out that some species in the *Dosinia* fauna occur in older layers along the Swedish west coast, referring to the works by Hessland (1943) and Antevs (1917). However, this is not the case with the characterising *Dosinia* species, in as much as *Dosinia exoleta* has not been demonstrated in the studies by Hessland and Antevs and *Dosinia lincta* occurs only in the younger deposits referred to the Subboreal.

Among the 15 species listed, eight have been recorded from the Limfjord, out of which *Epitonium turtonis*, *Oenopota turricola*, *Acteon tornatilis*, and *Cylichna cylindracea* have their first appearance in the Atlantic, and *Lutraria lutraria*, *Pholas dactylus*, and *Alvania lactea* appeared in the Subboreal, whereas the occurrence of *Modiolus adriaticus* in the Limfjord has not been dated. In this way, we are left with only six species which have not been found in other re-

gions outside Vendsyssel older than the Subboreal: *Pecten maximus*, *Dosinia exoleta*, *Dosinia lincta*, *Gari depressa*, *Alvania cimicoides*, and *Trivia monacha*.

Only the characterising species *Dosinia exoleta* has been dated as mentioned above, and recently *Donax vittatus* from Vr. Holmen in the northern part of Vendsyssel, west of Strandby, with the oldest date of this bivalve hitherto obtained in the Danish deposits, 4240 ± 75 ^{14}C age B.P. (AAR-1481).

This date shows that *Donax* characterising the high-energy shore deposits occurred in Danish waters since the Subboreal.

The further revision of the *Dosinia* fauna shows that only very few species are limited to the Vendsyssel region both in time and space. Therefore, it cannot be sustained for the Danish material as mentioned by Mörner (1969, p. 384) that: "The *Dosinia* layers contains a great number of new boreo-lusitanic immigrants" of the molluscs entirely belonging to the *Dosinia* layers according to Nordmann (1904), only three species, out of the 26 species mentioned, do not occur in Danish waters today, according to Jensen & Knudsen (1995), viz. *Trivia monacha*, *Gari depressa*, and *Alvania cimicoides*.

Only *Trivia monacha* seems to be purely Lusitanian, since a recent distribution to the North Sea is questioned by Fretter & Graham (1981, p. 329), and there is no record from Scandinavia. The other two species have a Boreo-Lusitanian distribution.

The Skagen region, region 7

Appendix 6 and Fig. 103

The 23 species, out of which only *Vitreolina collensi* is purely Lusitanian, can be evaluated according to their way of life.

Vitreolina collensi belongs together with *Aclis minor* and *Melanella alba* to the Eulimacea, which are probably associated with echinoderms (Fretter & Graham 1982, p. 397). The Eulimacea, together with the Epitoniacea, usually prey on anthozoans. The Heterostropha, including the Family Pyramidellidae which lives ectoparasitically on other marine organisms (Jensen & Knudsen 1995), are here represented by *Eulimella scillae*. Finally within the Veneroidae, *Mysella bidentata* and *Tellimya ferruginosa* are commensals on echinoids, but can also be found free-living.

For the rest of the 23 species found during the Subboreal in the Skagen Well, it applies that 16 species

Table 8. Subboreal communities and/or characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> / <i>Ostrea/Paphia</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Venus/Abra</i>	<i>A. alba</i>	deeper
5. North Sea			littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow deeper
6. Vendsyssel	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Dosinia</i>	<i>D. exoleta</i>	shallow deeper
7. Skagen			littoral
	<i>Venus/Turritella</i>	<i>T. communis</i>	shallow deeper

belong to the infauna, including *Onoba vitrea* which tends "to live in muddy places, often so muddy that one wonders how the animals keep the mantle cavity clear" (Fretter & Graham 1978b, p. 170).

It appears from the above-mentioned dates based on type of bottom-dwelling animals that the fauna belongs to the deep-level sea bottoms which goes well together with the *Turritella-Venus* communities.

The recorded Subboreal communities and/or characteristic molluscan species are given in Table 8.

The Subatlantic stage 2500– ^{14}C years B.P.

The configuration of land and sea in the Danish realm was very close to that of today. The isostatic movements during this time span have been so small that they did not affect the general outline (Petersen 1991b). However, the coastal development, in the formation of simplified coastline and spits especially in the west towards the North Sea and in the north facing the Skagerrak and the Kattegat respectively, still affected the contour of the land.

For the main part of the Danish waters, the recent marine bottom communities were established, some of them already since the Atlantic, although the few characterising *Tapes* and *Ostrea* species are no longer extant in great numbers or have totally vanished from the Danish seas. Therefore, the actual map of the Petersen (1914, 1918) bottom communities as seen today will be commented upon in relation to the few, but important changes observed during the Subatlantic, region by region.

The Bælt Sea, region 1

Appendix 6 and Fig. 103

The bottom communities mapped from the Bælt Sea region comprise the *Macoma balthica* community in the shallow-water area and the *Abra alba* community in deeper water (Petersen 1918), the latter community with *Tridonta borealis* and *Macoma calcarea*. The former has been recorded from the subfossil finds but not dated, while the latter has a dated occurrence back in the Atlantic and is considered part of the *Abra alba* community as a deep infauna element.

Considering the present distribution of the *Astarte* species, it is most probable that *Tridonta borealis* invaded the Bælt Sea and the Baltic already in the early Holocene along with the transgression in the Early Atlantic.

The gregarious occurrences of *Ostrea edulis* recorded from the Atlantic in the Bælt Sea region vanished in the Iron Age (Petersen 1985c). This species is no longer found in the Bælt Sea region, nor is *Paphia aurea*, which also occurred at the Iron Age sites too (Petersen 1985c, fig. 5). The steady occurrence of *Ostrea edulis* since the Atlantic, although in reduced numbers, might have led to an experiment in cultivating oysters south of Lolland in the Fehmern Bælt (Winther 1876, p. 114), although an unsuccessful one.

The distribution of oysters within the Danish waters seems to have changed very much right up to the present day, with many records from the 19th century of oyster banks from places where no records are found today (Krøyer 1837; Seaman & Ruth 1997).

The Baltic, region 2

Appendix 6 and Fig. 103

The *Macoma balthica* community covers the whole area of the Baltic, implying that in this area the otherwise shallow-water bivalve extends into greater depths – more than 50 m (Petersen 1918).

Also in this area, *Tridonta borealis* and *Tridonta elliptica* have been found in great quantities east of Bornholm but not dated. However, according to Johansen (1916, fig. 5), *Tridonta borealis* and *Tridonta elliptica* are recorded only from areas with a salinity of more than 10‰, but Zenkevitch (1963, p. 338, fig. 167) points to many finds further to the north in the Baltic, where the salinity is lower.

As stated earlier, the change from the *Littorina* Sea stage to the *Lymnaea* Sea stage took place during the Subboreal. The present situation with a *Mya* Sea stage – a term established by Munthe (1894) – took place at a very late date. Munthe (1894, p. 14) said: “Since *Mya arenaria* is an easily identified and characteristic species in the present Baltic it seems suitable to call the present time the ‘*Mya-time*’ or ‘*Mya arenaria-time*’ in opposition to ‘*Littorina-time*’ etc.”

The Kattegat, region 3

Appendix 6 and Fig. 103

Among the subfossil species both, dated and undated, no records of *Chlamys striatula* and *Turritella communis* are found. These characterising species for the *Venus* and deeper *Venus* communities respectively have a wide extension on the map by Petersen (1918) in the Kattegat region. Also the deeper-water epifaunal elements – characterised by *Modiolus modiolus* – are missing in our subfossil record. Only the *Macoma balthica* and *Abra alba* communities are recognised in the subfossil material. However, the development in the Skagen Well sequence to the north in the Kattegat region of mollusc species reveals the *Venus-Turritella* communities and can be taken as part of the development in the central Kattegat region not sampled at the time of this study on molluscs.

In the present day northern Kattegat, stray specimens of *Ostrea edulis* have been recorded (Jensen & Knudsen 1995, p. 40). Otherwise among the more spectacular *Tapes* Sea species, *Tapes decussatus*, dated from the Atlantic, and *Paphia aurea*, not dated but occur-

ring in the subfossil fauna, have disappeared from the Danish waters.

The Limfjord, region 4

Appendix 6 and Fig. 103

This region has been studied in more detail, regarding the recent fauna, than the other regions, and references can be made also to Jensen (1919).

The *Abra* community is here divided into three associations, i.e. *Nucula-Corbula*, *Abra-Solen*, and *Abra-Solen-Mya* associations. In more shallow water the *Abra* community is replaced by the *Macoma balthica* community. All of these communities are recorded by their mollusc species in the subfossil fauna, here including the *Mya arenaria* in the subfossil assemblage. However, the only dated subfossil immigrating species from the Subatlantic is *Donax vittatus*, which appeared around 2000 years B.P. in the northernmost part of the Limfjord region in the beach ridges, around 1000 years before the closing of the western and northern entrance to the Limfjord.

The closing of the entrances from the North Sea and Skagerrak changed the Limfjord region into a freshwater basin between A.D. 1200 and 1825, however, with periods of saltwater influence (Kristensen *et al.* 1995).

A comparison between the subfossil fauna before the freshwater stage and the recent one after the North Sea broke through in the western part of the Limfjord in 1825 shows that the subfossil fauna had only a slightly higher affinity to more temperate water than the recent one. Also in this place the *Tapes*, *Venerupis* and *Paphia* species make the difference, in the way that only *Venerupis pullastra* finds its way back to the region after 1825.

Paphia aurea, however, has a dated occurrence from the same deposits as *Donax vittatus* to 1910 ± 100 ¹⁴C years B.P. (Petersen 1976). It is seen that *Paphia aurea* in this region, as in the Bælt Sea, has a record up into the Iron Age before it became extinct in the Danish waters.

Ostrea edulis repopulated the Limfjord region after 1825 and reached a wide extension in this region already in the second half of the 19th century (Collin 1871). However, the population has suffered from strong fluctuations not only in the Limfjord but also in other Danish waters, as shown on the map by Krøyer (1837).

Spärck in several papers on the biology of oysters (*Ostrea edulis*), published in Reports of the Danish Biological Station, also discussed the fluctuations in the NW European population of oysters (Spärck 1950, pp. 43–45). Spärck reached the conclusion that the summer temperature of the water was crucial, both being too low and too high, which affected the oyster in its reproduction and in food supply respectively. Furthermore, severe winters might affect the population, although less than the summer temperatures. However, these changes did not mean a total disappearance of the oyster, but only a reduction to such a level that the industrial exploitation had to stop.

When taking into account the many studies on the population of oysters, one could use the results in a general conclusion on the variations found in the whole population of molluscan species, especially for the group having their northern limit within the Boreal region: even small variations in the climate may influence the size of the population.

Also the environmental changes as shown within the Danish area during the Holocene, such as the lowering of the tidal amplitude in the early part of the Subboreal, had a severe influence on the populations in the inner Danish waters. Here again, oysters can be taken as an example by the termination of the huge oyster banks known from the Atlantic. Spärck (1950, p. 44) draws attention to the oyster banks in Holland and the British Isles, where the density of the population is far greater because of the tidal movements. However, not only the hydrographical changes through time, in the tide, but also the coastal evolution, such as the formation of simplified coastline and spits, play an important role in the distribution and new finds of molluscan species.

The North Sea, region 5

Appendix 6 and Fig. 103

Only eight species have been recorded as immigrants during the Subatlantic. However, two of them, *Donax vittatus* and *Dosinia lincta*, deserve special attention.

Only *Parvicardium ovale* and *Dosinia lincta* have their first dated appearance. The other species, except *Donax vittatus* with occurrence in the Subboreal, have been recorded from the Atlantic at various places listed in Appendix 6.

In referring to the C.G.J. Petersen bottom community map covering also the North Sea, the *Macoma*

balthica and the *Venus* communities are found in the Danish North Sea coastal region, the former in bays and off the southern part of the west coast (Petersen 1914), the latter around the westernmost part of the Limfjord and the Jydske Rev WNW of the Bovbjerg coastal cliff (Petersen 1994a).

A landscape like the Limfjord of today was found 75 km towards WNW in the area of the Jydske Rev. Following the transgression in the early part of the Holocene, the glacial landscape in an area of the present Jydske Rev was eroded and the high-energy coast approached the appearance of the present one. In the northern part forming an erosion coast and in the southern part at Blåvands Huk an aggradation coast, both characterised by the presence of *Donax vittatus*.

In the southern part the aggradation started around 800 BC some 2000 m east of the present coastline (Petersen 1994a, p. 24) as seen from the dating of *Donax vittatus* to 2620 ± 75 B.P. ^{14}C years (AAR-1480) off the inland cliff at Grærup (Fig. 1).

At Bovbjerg, the strata with *Donax vittatus* in the Agger spit are dated to 410 ± 65 B.P. (Petersen 1985a). The formation of the spits closing the former bays on the Jylland west coast is a consequence of the formation of a simplified coast. Further to the north, *Donax vittatus* from Kovad Bro in the northernmost part of the Limfjord, 6 km inland, gave a date of 1910 ± 100 B.P. (Petersen 1976), showing that the beach progressed 6 km during approximately 2000 years (Petersen & Andreasen 1989, fig. 1).

It is tempting to introduce the idea that the enormous change in the land–sea configuration in the eastern part of the North Sea affected the tidal currents in the inner Danish waters. This could possibly have occurred when most of the Jydske Rev Formation was eroded to such a level that the tidal current from the south was no longer braked and consequently the present-day interference with the tidal current came into existence. It is the interference between the two tidal currents in the Skagerrak today that makes the tidal amplitude small in the inner Danish waters (Nielsen 1939; Kuenen 1950).

Dosinia linctia has been dated (870 ± 110 B.P. ^{14}C years) in the Jydske Revsand Formation in the vibrocore 562001 around 75 km off the coast of Jylland at a depth of 32 m (Petersen 1994a, p. 18, fig. 3).

The assemblage from these strata comprises *Spisula subtruncata*, *Phaxas pellucidus*, *Fabulina fabula*, *Chamelea striatula*, *Dosinia exoleta*, *Corbula gibba*, *Cochlodesma praetenua* and *Thracia phaseolina*, most of them characterising the Jydske Revsand Formation.

The Vendsyssel region, region 6

Appendix 6 and Fig. 103

The coastal development in the eastern part of the region facing the Kattegat takes place in the form of migrating bars (Schou 1949, fig. 17b), the so-called Rimmer and Doppe system *sensu* Jessen (1905).

The *Venus* and the *Macoma balthica* communities are found in the coastal zone, the former dominating in the northern part, whereas the latter forms a small area between shore and the *Venus* community to the south towards the entrance to the Limfjord at Hals (Petersen 1918).

In the north at Strandby, *locus typicus* of the *Dosinia* beds, the layers with *Dosinia exoleta* are superposed by a layer characterised by *Spisula subtruncata*. These beds with *Spisula* in great quantities were dated to 2640 ± 75 (Petersen 1991b), the end of the Subboreal, and at a level of 4.2 m a.s.l. This corresponds to a stage in the development of the Skagen spit up to 4 km south of Højen, where the beach ridges have an elevation of 5 m a.s.l.

In the southern part of the Vendsyssel region around Hals another of the faunal elements of the *Dosinia* beds – *Lutraria lutraria* – has for long been regarded as extinct (Petersen 1992). However, “from 1990 onwards live specimens have been collected regularly near Frederikshavn and on the Skagerrak-coast” (Jensen & Knudsen 1995, p. 43).

Also many shells of *Lutraria lutraria* were found along the shore south of Jerup halfway between Frederikshavn and Aalbæk.

The immigration of *Mya arenaria* cannot be taken as an indication of changes in climate, as this species mainly belongs to the Boreal region and has been transferred by man from North America. What made the find so important has a more historical than geological bearing, namely that the dates obtained from the sampling at Jerup demonstrated that the American soft-shell clam (*Mya arenaria*) predated Columbus' voyage in 1492, having an age of A.D. 1245–1295 at ± 1 s.d. This led to the conclusion that the Vikings were better candidates than Columbus to be the first to find North America (Petersen *et al.* 1992b).

The significance of changes in facies is clearly demonstrated in the next and final section describing the Subatlantic faunal development in the Skagen region.

The Skagen region, region 7

Appendix 6 and Fig. 103

The Subatlantic molluscan fauna from the Skagen Well comprises 68 species with 75% belonging to the Boreo-Lusitanian region and only one Lusitanian species, *Vitreolina collensi*. However, the more interesting fact from the younger part of the Skagen sequence is the total lack of *Macoma balthica*. In this way it presents the finest resemblance with the recent bottom community map (Petersen 1918), and shows that the *Macoma balthica* community disappears in the northern part of the east coast of Jylland. This means that during the last stage of the spit formation at the site of the present Skagen animals, from the *Venus* community dominated along shore. This is also documented by the high amount of infauna elements, with 35 out of the 68 species recorded.

Furthermore, some of the 11 epifauna gregarious species usually connected with the vegetation can be excluded, since they occur only as stray finds, viz. *Lacuna pallidula*, *Rissoa violacea*, and *Bittium reticulatum*, as discussed earlier.

The rest of the molluscs (22 species) are carnivores, predators, external parasites, and commensals.

Turning these figures into percentages, the epifauna species amount to 16.2% and the infauna to 51.5%.

Comparing this with the Limfjord region where an equal number of species have been found during the Atlantic and the Subboreal, it appears that the number of infauna species from the Atlantic to the Subboreal falls from 46.8% to 19.4% and the epifauna elements rise from 31.2% to 47.2% in the Limfjord.

Counting the Limfjord region as an inner Danish water today, it is worth noticing that during the Atlantic the situation was much more like the 'open' waters as seen in the Skagen figures.

Table 9. Subatlantic communities according to the bottom community maps* with characteristic molluscan species

Region	Community	Species	Depth
1. Bælt Sea	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> ± <i>Ostrea/Paphia</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
2. Baltic	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> + <i>Mya arenaria</i>	shallow
	<i>Macoma</i>	<i>M. balthica</i>	deeper
3. Kattegat	<i>Mytilus</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Abra/Venus</i>	<i>A. alba</i>	deeper
4. Limfjord	<i>Mytilus/Modiola</i>	<i>M. edulis</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i> ± <i>Paphia aurea</i>	shallow
	<i>Abra</i>	<i>A. alba</i>	deeper
5. North Sea	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Macoma</i>	<i>M. balthica</i>	shallow
	<i>Venus</i>	<i>Chamelea striatula</i>	deeper
6. Vendsyssel	<i>Macoma</i>	<i>M. balthica</i>	littoral
	<i>Venus</i>	<i>Chamelea striatula</i>	shallow
			deeper
7. Skagen	<i>Donax</i>	<i>D. vittatus</i>	littoral
	<i>Spisula</i>	<i>S. subtruncata</i>	shallow
	<i>Venus</i>	<i>Chamelea striatula</i>	deeper

*Petersen (1914, 1918).

Considering that the tidal amplitude really was lowered in the early part of the Subboreal, this would to some extent explain the observed changes in the Limfjord from the Atlantic to the Subboreal.

The recorded Subatlantic communities according to the maps by Petersen (1914, 1918) with characteristic molluscan species are shown in Table 9.