Reconstruction of the marine paleoenvironment and paleoecology of the middle Holocene in the Oslo fjord area

Mees Floris Auener

Master Thesis
Sedimentology, paleontology and stratigraphy
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The Faculty of Mathematics and Natural Sciences

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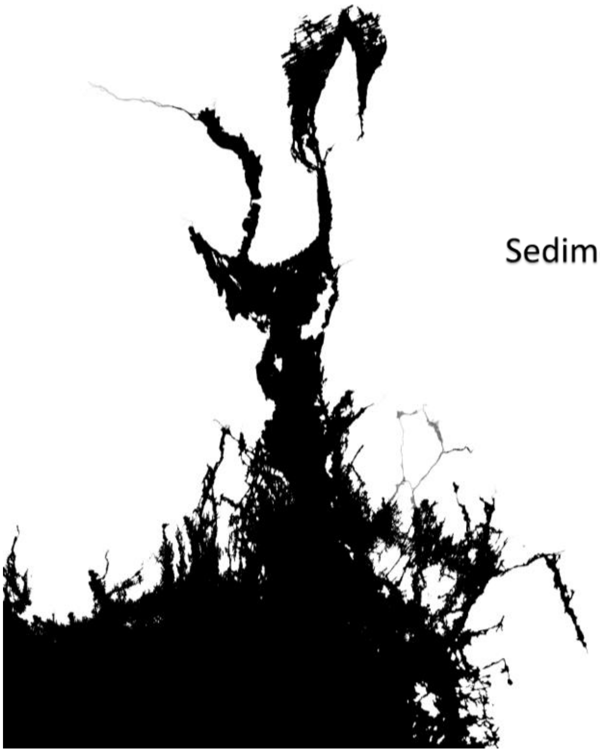

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Abstract

A warm phase has previously been observed in the early to middle Holocene geological record of the Northern hemisphere. Holocene invertebrate faunas in the Oslo fjord, Norway, are here studied in order to investigate their response to a changing climate. Studying ecological changes during this Holocene Thermal Maximum can help predicting the impact of present and future anthropogenic warming. Previous research around the Oslo fjord stated molluscs indicate a warm signal during deposition of the Tapes banks in the middle Holocene. Five beds are radiocarbon dated, placing the Upper Tapes banks between 7,800 and 5,000 cal yr BP. The faunal composition of the Upper Tapes banks has been studied, and compared with other Holocene deposits. Some interesting changes in faunal composition are observed, but no clear sign of a thermal maximum is found. Most species occurring in the Atlantic stage still live in the area nowadays, although a few of them decreased in abundance.

Acknowledgments

First I would like to thank my main supervisor Øyvind Hammer, for always being available for questions, taking me on fieldwork, review my writings and showing so much interest in my project. I would also like to thank co-supervisor Mona Henriksen for helping with writing the thesis and Hans Arne Nakrem for the technical help and showing me the field localities. Very important were Slemmestad Geologisenter, which provided a large collection of shells, and Ole Bundgaard, who found them in 2002. In addition, I want to thank Elizabeth Alve for her help with identifying foraminifera, and Kjell Bjørklund for explaining me more about taxonomy. Last but not least, my fellow students at Økern, Synnøve and Audun in particular, who took care of the good atmosphere, were always willing to help, and motivated me to arrive before lunch and work until it was time to play Dinosaurdalen.

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1 Introduction

A changing climate will affect ecosystems, and is expected to cause a decrease in biodiversity. Even if global warming is limited to 2 °C, in accordance with the Paris Agreement, this will have a significant impact on many ecosystems (Nunez et al., 2019). By investigating analogue conditions in the geological record, it can be estimated what impact such changes can have on the present ecosystem. Sediments with invertebrate faunas recording the Holocene Thermal Maximum (HTM) present an analogue case to the present and future anthropogenic warming in the Oslo fjord, Norway. A rapid warming, up to 2 °C Celsius above current temperatures, has been observed in the early to middle Holocene geological record of this area (Seppä et al., 2009). More knowledge about the interactions between climate and ecosystems of this period contributes to a better predictability of current and future developments. With a warming of 2 °C, Southward et al. (1995) expect a large variety of marine species to migrate 300-600 km northward. According to similar previous studies from the British coast the biodiversity of the area will not change, but the species composition will be affected by a warming of 2 °C (Warwick & Turk, 2002). Results of a study in the western North Atlantic show no patterns of expanding suitable environments northwards (Saupe et al., 2014). These different outcomes show that it is unclear what effect future climate change will have on the distribution of species. Using ecological developments from the past to estimate future developments is part of conservation paleobiology. Data acquired from the paleontological record can be used for conservation policies (Dietl & Flessa, 2011).

1.1 Aim of research

Holocene faunal and sea level stages of the Oslo fjord area were studied extensively by Brøgger et al. (1900), reporting that the faunal composition was indicating a warmer climate during the mid-Holocene. Several later studies confirmed the hypothesis of a Holocene Thermal Maximum (Brown et al., 2012; Davis et al., 2003; Kaufman et al., 2020; Marcott et al., 2013). Paleontological studies reported a response of mollusc fauna to this warming period in the Arctic (Funder & Weidick, 1991; Mangerud & Svendsen, 2018). In this thesis I have investigated whether the marine invertebrate fauna of the Oslo fjord responded to a warmer climate during the HTM. With new contemporary knowledge and techniques, gained through the 20th and 21st century, this study will supplement Brøgger's work in order to get a better insight into the interactions between climate and the marine ecosystem.

1.2 Objectives

In this thesis, the marine invertebrate fauna of the Holocene in the Oslo fjord is studied, with focus on the warmer period in Europe during the middle Holocene. Mainly shallow intertidal to subtidal faunas are included in this study, corresponding to the "bank" stages of Brøgger et al. (1900) in contrast with the deeper-water "clay" stages. Sandy marine deposits around the Oslo fjord, characterized by the occurrence of oyster banks, will be sampled and studied in detail. By supplementing earlier faunal indices, we gain more knowledge about the ecological response to climatic changes. Where Brøgger et al. (1900) made qualitative faunal lists of the different banks, this study will also take into account quantitative data and possible changes within one section. Using radiocarbon dating, the age of several samples can be determined. This allows the data obtained from this study and the results from Brøgger et al. (1900) to be linked and compared to other studies.

The hypothesis is that the oyster beds of this study have a middle Holocene origin and together with accessory shell assemblages they reflect a warmer period as documented in previous studies (Brown et al., 2012; Davis et al., 2003; Kaufman et al., 2020; Marcott et al., 2013).

1.3 The Oslo fjord

The Oslo fjord is located in south-east Norway, and is debouching into the Skagerrak (Fig. 1.1). Because of its high latitude (59 ˚), the area was strongly influenced by glaciers during the ice ages of the Pleistocene. The fjord contains several thresholds, of which the shallowest is found at Drøbak. This separates the inner from the outer Oslo fjord and has a depth of 20 m. The inner fjord has a maximum depth of 160 m. Fresh water brought in to the fjord by rivers, floats on top of the heavier salt water as a lid. Under the current conditions, this lid is approximately 20 m thick, which means that the lid is prohibiting bottom waters to circulate (Qvale et al., 1984). As the glaciers retreated, uplift of Scandinavia started as a result of isostatic rebound. This caused a forced regression along the Norwegian coast, resulting in on-land outcrops with shallow-water faunas from the Holocene at several places around the Oslo fjord. Faunas representing the HTM are found at several places, among which Slemmestad, Søndre Sandøy (Hvaler) and Malmøya (Fig. 1.1).

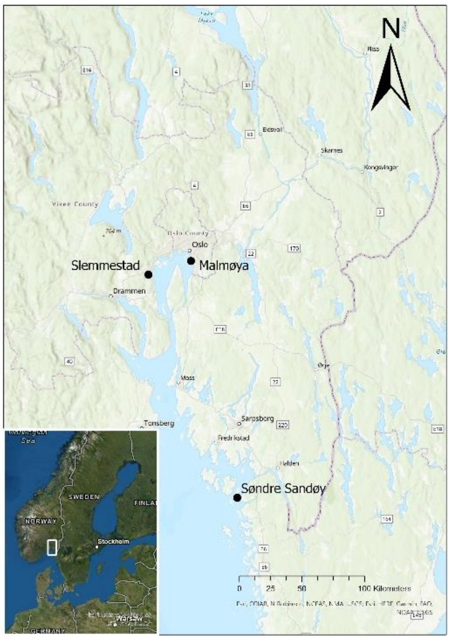

Figure 1.1 Map of the Oslo area with the localities of this study

1.4 Holocene climate in Norway

The Holocene is the current interglacial period following the Weichselian glaciation and began 11,700 years ago. Many studies have been done on the Holocene climate in Fennoscandia. Research on peat-stratigraphy by Blytt and Sernander led to use of the Blytt-Sernander scheme (Sernander, 1908), representing a timescale with climatological stages. In chronological order these are the Preboreal, Boreal, Atlantic, Subboreal and Subatlantic stages. After this scheme was adopted by many scientists in and outside Europe, most evidence shows that the scheme's assumptions regarding climatological stages are not precise. Therefore, currently the diagram is predominantly used as a chronostratigraphic scheme (Birks & Seppä, 2010b) .

During the early Holocene, Northern Europe experienced temperatures similar to present day. A cool period is observed from around 8,200 cal yr BP, often referred to as the 8.2 ka event (Alley et al., 1997). From 8,100 yr BP temperatures rose until they reached their maximum around 7,000-6,000 yr BP, however this timing may differ with location. Estimates reach a maximum of 0.8 up to 2.5 °C above Holocene average. The timing of the HTM is not clear, as many different estimates have been made. In general, pollen-based studies dated the HTM between 8,000 yr and 4,800 yr BP (Antonsson & Seppa, 2007; Davis et al., 2003; Velle et al., 2005). Differences might be explained by local variation, but it could also be dependent on the use of different proxies since some ecosystems react quicker to climate change than others. As an example, migration of deciduous trees is delayed compared to pollen and aquatic proxies (Paus & Haugland, 2017). Seppä et al. (2009) reconstructed annual mean temperatures (T_{ann}) and summer mean temperatures (T_{jul}) based on 36 studies in Scandinavia and Fennoscandia (Fig. 1.2).

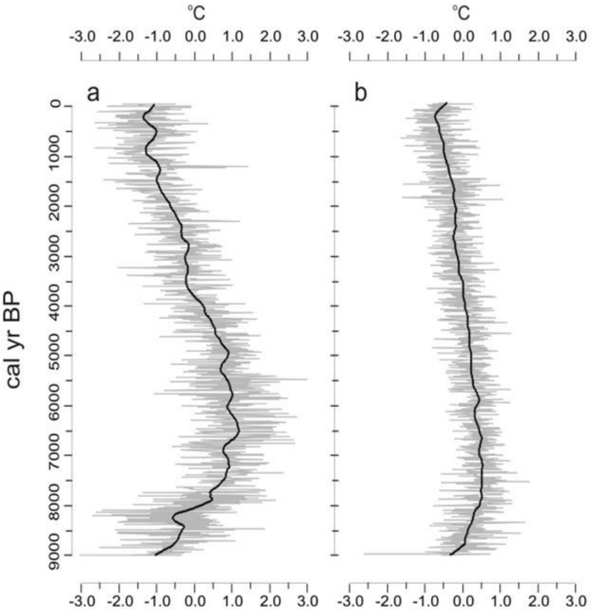

Figure 1.2 Pollen-based temperature curves for annual mean temperatures T_{ann} (a) and summer mean temperatures T_{jul} (b) (Seppä et al. 2009). The temperature is given as deviation from the mean Holocene temperature.

1.5 Holocene sea level in Norway

After the last ice age, the Norwegian coast experienced regression as a result of isostatic rebound caused by melting glaciers. Isostatic rebound has the strongest impact in north-east Sweden, which was the centre of the former Weichselian ice sheet. The amplitude of isostatic rebound decreases with distance from this centre. Therefore, Oslo and south-east Norway has experienced a higher rate of regression compared to Norway's west-coast. For sea level to surpass this rebound a strong global eustatic sea level rise is needed, something which is confirmed on the west coast during the early-mid Holocene Tapes transgression. In south-east Norway, the eustatic sea rise was able to slow down regression, but a strong transgression as found in the west is not indicated (Fjeldskaar & Bondevik, 2020).

Specifically for the Oslo region, studies in the early 20th century reported marine sand deposits at high elevations (Brøgger et al., 1900; Øyen, 1903). The highest marine limit, found in Skådalen, Oslo, is 221 m.a.s.l. and has an age of 10,260 ± 70 ^{14}C yr BP (Johansen, 2020). Based on shell banks around the fjord, depositional depths and therewith paleo sea level was interpreted. Later it turned out that assumed life conditions of many molluscs were not properly investigated, and therefore water depth could not be reconstructed accurately. Moreover, not many shells indicate in situ deposition, which means they could have come from deeper or (usually) shallower waters (Hafsten, 1958; Peacock, 1989). To reconstruct a proper sea level curve, the study of shell banks should be combined with other indicators, for example by dating the age of isolation of lakes surrounding the fjord. For the inner Oslo fjord a sea level curve has been made for Ski , about 20 km south of Oslo (Bargel & Sørensen, 2005) (Fig. 1.3). A sea level curve for Halden, located east of the mouth of the Oslo fjord, was made by Danielsen (1970)(Fig. 1.3). This curve was revised by Sørensen (1999) by adding supplementing data obtained from ^{14}C dating of marine material to the original curve which was based on pollen analysis. According to this curve the fastest land rise was at 10,000-12,000 years ago with a rate around 50 mm/yr. After this time the land rise has slowed down until 5 mm/yr nowadays.

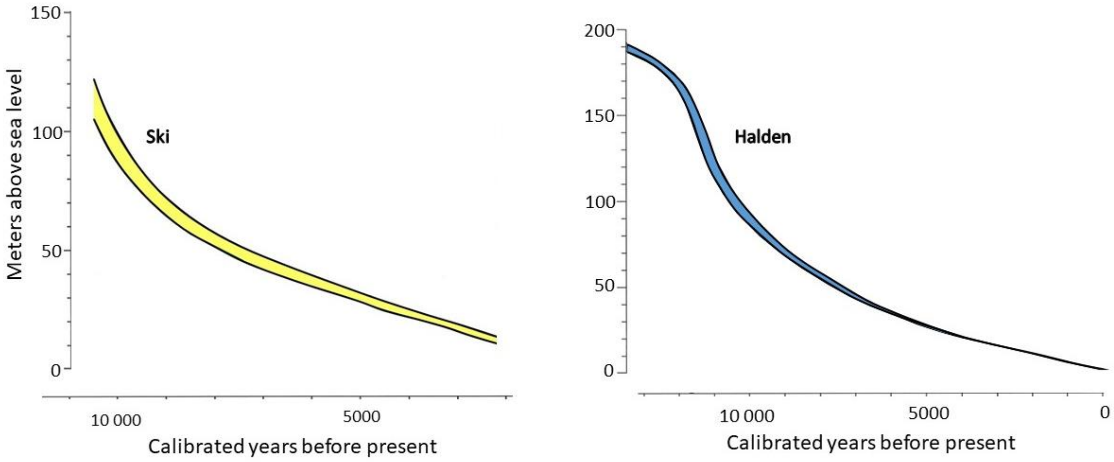

Figure 1.3 Sea level curves Ski and Halden, edited from Bargel & Sørensen (2005) *and Sørensen (1999).*

1.6 Holocene fauna of the Oslo fjord

After the Weichselian ice age, the fauna in the Oslo region changed gradually during the transition from glacial to interglacial. Below the marine limit in Oslo (221 m), many shallow-water shell banks are found around the Oslo fjord. Due to the land rise, generally, the lower the deposits are found, the younger they are. Brøgger et al. (1900) did not have access to methods for dating the shell banks. Because of the regional difference in land rise, simply linking of deposits with the same elevation was not an option. Therefore they related the different deposits with each other by calculating the percentage of land rise, using interpreted depositional depths. They divided the post-glacial deposits into several stages. The Lower Mya banks were deposited during the transition from the glacial to interglacial period. The four banks deposited after the Weichselian from old to young are: Upper Oyster banks, Upper Tapes banks, Lower Tapes banks and the Modern Littoral shell banks. Those sandy deposits were temporally linked to their deeper clay equivalents. These are respectively: Upper oyster clay, Isocardia clay, Scrobicularia clay and Mya arenaria-clay.

However, when giving percentages of land rise, many deposits were assumed to be beach deposits. Later it turned out these deposits might have been part of more distal facies (Hafsten, 1958; Peacock, 1989), making these percentages unreliable. In case the sediments were deposited at a greater depth than assumed, the land rise could also have been at an earlier stage (i.e. lower percentage).

Molluscs in the European seas are often divided into biogeographic groups. The Arctic group is the northernmost community, the Boreal group is the cold temperate group, and the Lusitanian group is the most southern group. The latter however, is not often used in modern literature and the category is debatable (Brøgger et al., 1900). Figure 1.4 shows the categories used in this study, a zonation defined by Feyling-Hanssen (1955).

Species names used in old literature are often deprecated, and therefore renewed according the current names as used on the World register Marine Species (WoRMS, 2022).

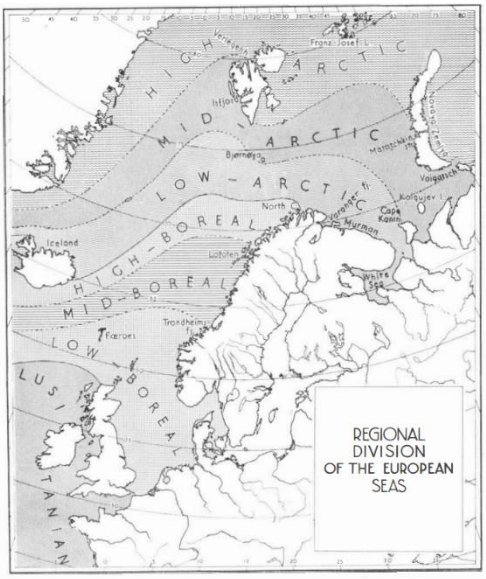

Figure 1.4 Zoogeographical zonation of the northwest coast of Europe (Feyling-Hanssen, 1955)

1.6.1 Upper Oyster banks

Ten localities found between Nesodden and Kragerø were included in the Upper Oyster banks. Their elevation is between 33 and 56 m.a.s.l. At five of those localities *Ostrea edulis* was found. Species occurring in most of these deposits are *Mytilus edulis, Acanthocardia tuberculata, Timoclea ovata, Mya truncata, Hiatella arctica, Tectura virginea, Littorina littorea, Buccinum undatum* and *Tritia reticulata* (Brøgger et al., 1900).

1.6.2 Upper Tapes banks

Around Oslo, the Upper Tapes deposits are found at an elevation around 30-40 m. In total, 47 species are found in the Upper Tapes banks around Oslo. The most common species found in the Upper Tapes banks are *Ostrea edulis, Mytilus edulis, Timoclea ovata, Tritia reticulata, Bittium reticulatum,* and species within the genera *Astarte, Cardium/Cerastoderma* and *Littorina.* Some Arctic species that were present in the Mya banks disappeared from the record and some new species appeared. These new species are *Terebratulina retusa, Antalis entalis, Polititapes aureus, Ruditapes decussatus* and *Polititapes virgineus* (Brøgger et al., 1900).

Along the outer Oslo fjord, more Upper Tapes bank localities are found. Here they have an elevation between 10 and 30 m.a.s.l. They are quite numerous, and not all of them have been studied yet. According to Brøgger et al. (1900), some of them are significantly richer in species compared to the inner Oslo fjord. This difference in species richness could be caused by the threshold at Drøbak, which started to restrict circulation in the inner Oslo fjord as sea level dropped. At a shellbank at Kirkøy, Hvaler, Brøgger found 80 mollusc species. Striking is the brachiopod *Gwynnia capsula*, which is recently only found along the British and Irish coasts and in the south east of Europe (WoRMS, 2020). All the other species are still found along the southern coast of Norway.

1.6.3 Lower Tapes banks

The elevation of the Lower Tapes banks is below 13 m. In these banks both some Arctic and some Lusitanian species have disappeared from the record, but also some new Lusitanian species occurred and get more widely distributed. The Lower Tapes banks in the inner Oslo fjord contain 124 species, and have a higher species richness than the Upper Tapes banks. New species occurring in multiple Lower Tapes banks are *Eulimella nitidissima* and *Eulimella vitrosa* and *Solecurtus antiquatus* (Brøgger et al., 1900).

2 Methods

2.1 Field work

Field work was done at three locations around the Oslo fjord.

On Malmøya one locality has been investigated. Due to lush vegetation and soil formation logging was not possible, but many shells could still be found. Shells were taken to the lab for further investigation. One should keep in mind that here the sediments have not been systematically searched through, but the shells were picked from the ground. Therefore there is a strong bias towards bigger specimens, because of their visibility. In Slemmestad two localities are found, but only one is thoroughly investigated. In this case, most samples were already present at the Natural History Museum (NHM) or provided by Slemmestad Geologisenter. Beside samples that were already sorted, also bags with unsorted sediments were available and used to determine the abundance per species. Hvaler has the most completely preserved sediments, and therefore provides most of the data. In July 2021 fieldwork was done at Søndre Sandøy. In a sand pit the sequence of sediments was nicely exposed, in such a way that it was suitable for logging. From every distinct layer a sediment sample of circa 200 grams was taken, and brought to NHM for further analyses. On three other localities marine faunas were found. Those places and their elevation are noted down, but those locations did not provide enough information for extensive analyses.

2.2 Grain size analyses

To analyse the variations in grainsize, the samples from Hvaler were sieved. The process divided the grains in size of larger than respectively 5.6 mm, 4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63 µm and smaller than 63 µm, and every fraction was weighed. Afterwards the sediments were put into bottles, divided into three fractions: <125 µm, 125 µm – 1 mm, >1 mm. This was done to separate the 125 µm - 1 mm category since this is the category in which foraminifera are expected to be found. The abundance per grain size was calculated in percentages and analysed using GRADISTAT (Blott & Pye 2001). This Excel plug-in can be used to get an overview of several statistics like mean and median grain size, sorting and sediment description. A factor that should be taken into account is that at some levels, the sediments contain lots of shell fragments. In these samples the size of shell grains disturbs the record of the siliciclastic particles.

2.3 Ecological analysis

The specimens of marine invertebrates were mostly looked at under the microscope and identified mainly based on descriptions and drawings from literature and biological data bases from the internet (Hayward & Ryland, 2017; Brøgger et al., 1900; WoRMS, 2022). As often as possible the identification was done at species level, but for some specimens only the genus could be established due to damages on the shell or because species are very alike. An overview with all species is found in the appendix under “Taxonomy”. In the appendix one can also find photographs of all species, including their identification numbers at NHM (PMO

(Paleontological Museum Oslo) number), location and synonyms as used by Brøgger et al. (1900).

For Hvaler 1, occurrences of species are quantified. Diversity can be expressed by the Shannon-Wiener information function (eq. 1). In this function both the number of species and the number of individuals within each species are included. The higher the value, the more equally abundant the different species are. When the value is high it represents a high biodiversity and when the value is low it represents a low biodiversity. In Eq. 1, *S* is the number of species and p_i the proportion of species *i* (Legendre & Legendre, 2012)

$$H_S = -\sum_{i=1}^{S} p_i log p_i \qquad \text{(Eq. 1)}$$

To measure biodiversity, a random sample of ± 20 grams was taken from the bigger sample bags. The exact weight was written down and specimens were counted and identified. Many shells were undamaged or only small pieces were missing. In some cases, particularly with *Mytilus edulis* and *Ostrea edulis*, only small pieces are found. Therefore it is very hard to count those species, because one should avoid counting one organism more than once. To avoid this, only umbos were counted, unless there was only one fragment found of a species. In this case it is still possible to count the organism twice, since bivalves have two valves, but this is a deviation that cannot be avoided. Gastropods are generally less fragile, and more rarely found in pieces. In this case, only the apertures are counted.

To get a more complete picture, semiquantitative estimates were done for all samples. Using semiquantitative estimates, bigger samples can be covered and more rare species are included. For each sampled level at Hvaler 1, it is defined whether a species is absent, observed once, rare or common. These definitions got the numbers 0, 1, 2 and 3 respectively. These numbers are used for ordination, using correspondence analysis (Legendre& Legendre), with help of the software Past (Hammer, 2001). This method is chosen because it shows samples and species in one graph, which is a good way to show similarity and differences between the samples together with the species that are responsible for these differences. Correspondence analysis also has been done based on previous literature. In this case, presence-absence data were used. The data were taken from Brøgger et al. (1900) and digitalized. In an Excel sheet the absence (0) and presence (1) is given for every species in every sample.

To divide the biogeographic distributions of species into categories, the northern limit of species is defined by Lusitanian, Boreal and Arctic whereas the two latter are divided by Low, Mid, and High Boreal/Arctic. This is done by looking at data provided by the websites WoRMs, OBIS and Artsdatabanken. Outliers are ignored to achieve a more representative picture of species ranges.

2.4 Radiocarbon dating

To get a better understanding of the timing of the Holocene Thermal Maximum, several shells were radiocarbon dated. Three samples were taken from the excavation outcrop at Hvaler. These samples from Hvaler are a *Modiolus* shell (sample HV-1B, weight 820 mg) and two oysters (sample HV-60, 960 mg and sample HV-80, 420 mg). From Malmøya one oyster (sample MALM, 320 mg) was dated. All shells were sampled near the outer edge (i.e. the youngest part of the shell). Radiocarbon dating was performed with the AMS method at the National Laboratory for Age Determination at the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway.

Given the ^{14}C age, the ages are calibrated using the marine reservoir calibration curve by Heaton et al. (2020) and the radiocarbon calibration module in the software Past (Hammer, 2001). To take the local reservoir age into account an ΔR value of 20±30 years is added (Mangerud et al., 2006). The ages are given in years before present (BP), where 1950 is taken as starting point.

2.5 XRF analysis

To investigate the composition of the sediments taken from Hvaler, semi-quantitative chemical analysis was carried out, with a Niton XL3t GOLDD handheld XRF instrument in the "Testall Geo" mode and 120 s integration time. The most useful element from this analysis was Ca, reflecting the amount of bioclastic calcium carbonate.

3 Results

3.1 Hvaler

On Søndre Sandøy, four localities with marine deposits were found (Fig. 3.1). Hvaler 1 and 2 are found in an excavation along Buvikveien (59.02025ºN 11.09141ºE), and are described in detail. At Hvaler 3, north east of Buvikveien 189 (59.01916ºN 11.10091ºE) some oysters were found under tree roots at an elevation about 15 m.a.s.l. Hvaler 4 is found at the same elevation close to house nr. 97 (59.01743ºN 11.07448ºE).

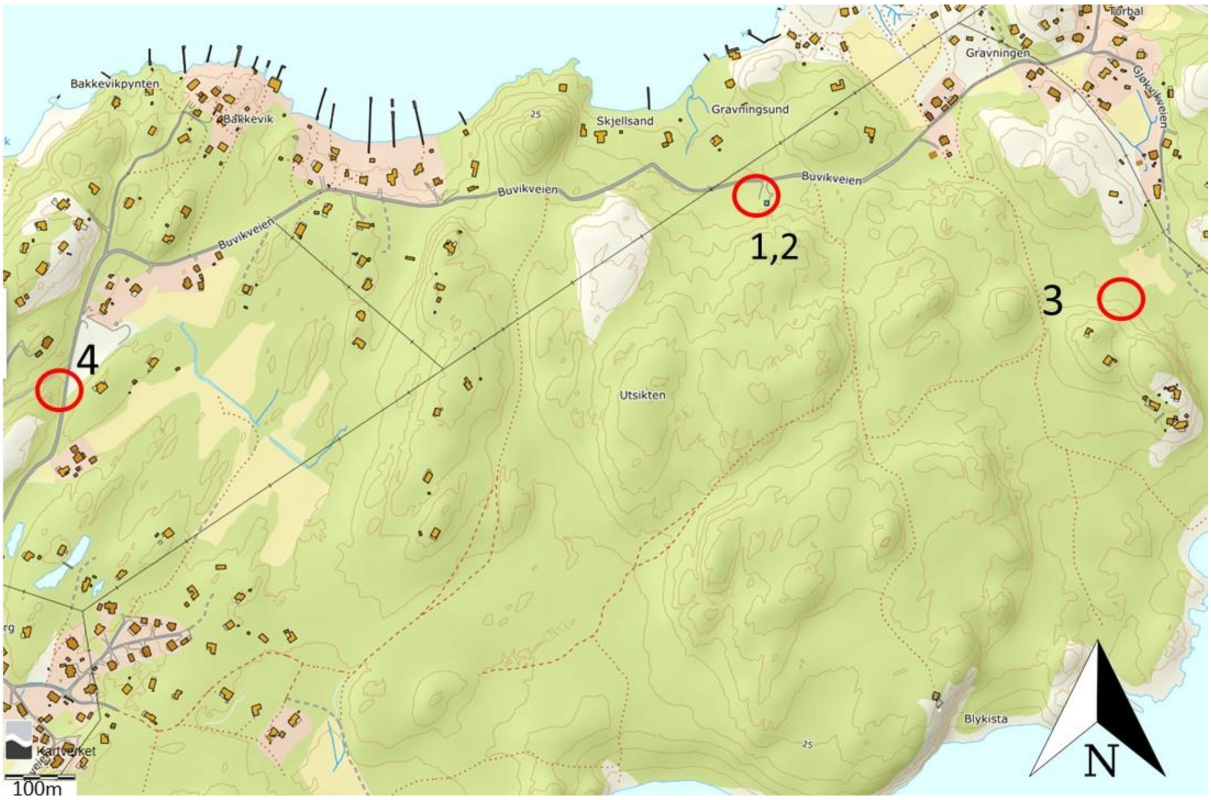

Figure 3.1 Four localities on Søndre Sandøy, containing Holocene marine deposits

3.1.1 Hvaler 1

A small excavation close to Buvikveien 161 exposes 1.5 m of marine deposits directly under the current soil. This outcrop is located 11-12 m.a.s.l. The section is divided in five clearly visible units, which are slightly dipping towards the north. Hvaler 1 is logged in detail focussing on grain sizes and shell fragments (Fig. 3.2).

The lower 20 cm (Unit A) contain poorly sorted sand. The grain sizes are distributed bimodally with medium sand and fine gravel as dominant grain sizes. Few clasts are found, varying between 0.5 and 2 cm. The grains have black, white and orange colours. The deposit does not contain mud. There are barely any molluscs apart from some pieces of small gastropods in the Rissoidae family. A couple of very weathered foraminifera were present as well.

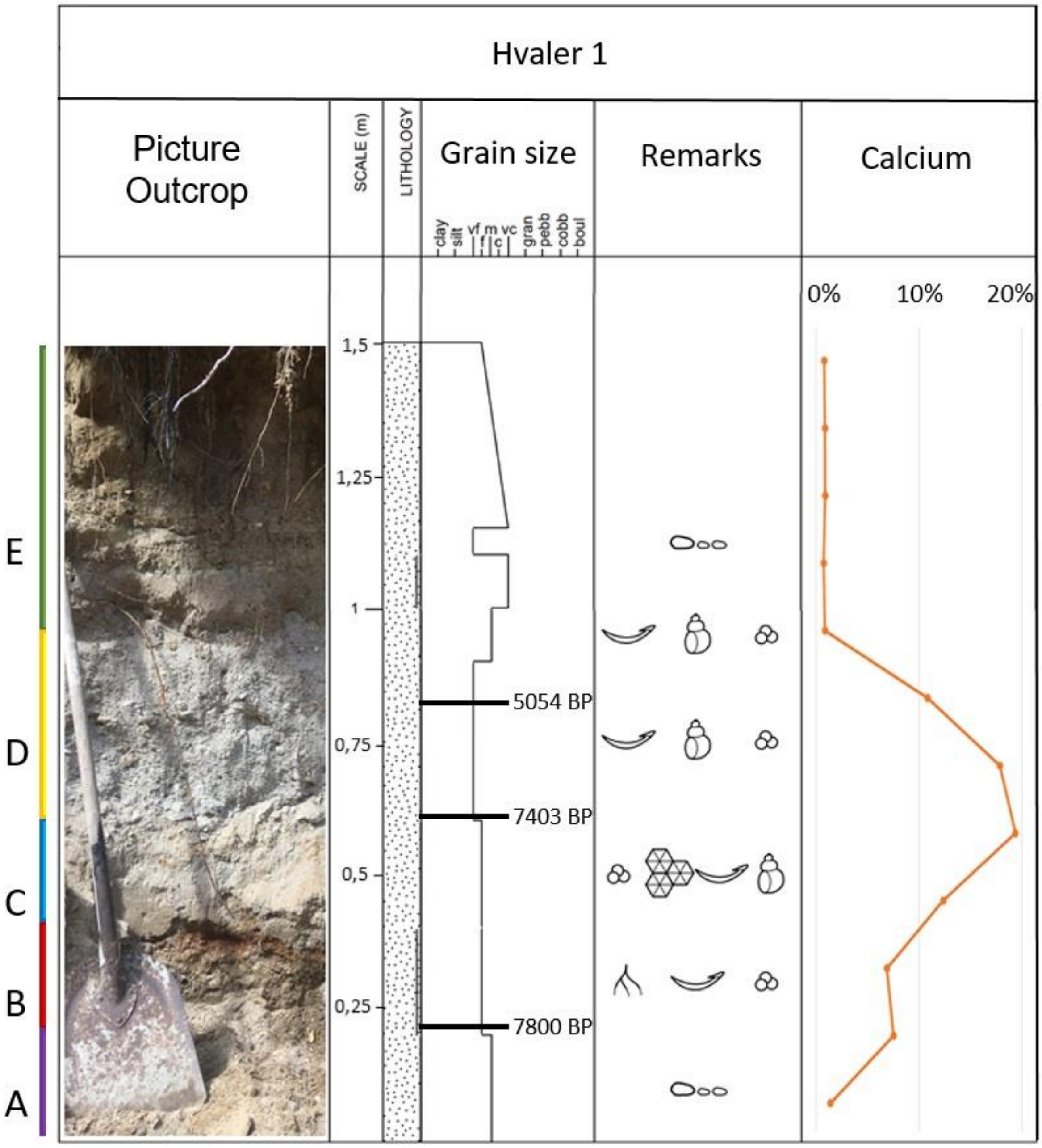

Figure 3.2 Stratigraphic log Hvaler 1 summarizing grain size, radiocarbon dates, remarks and calcium content

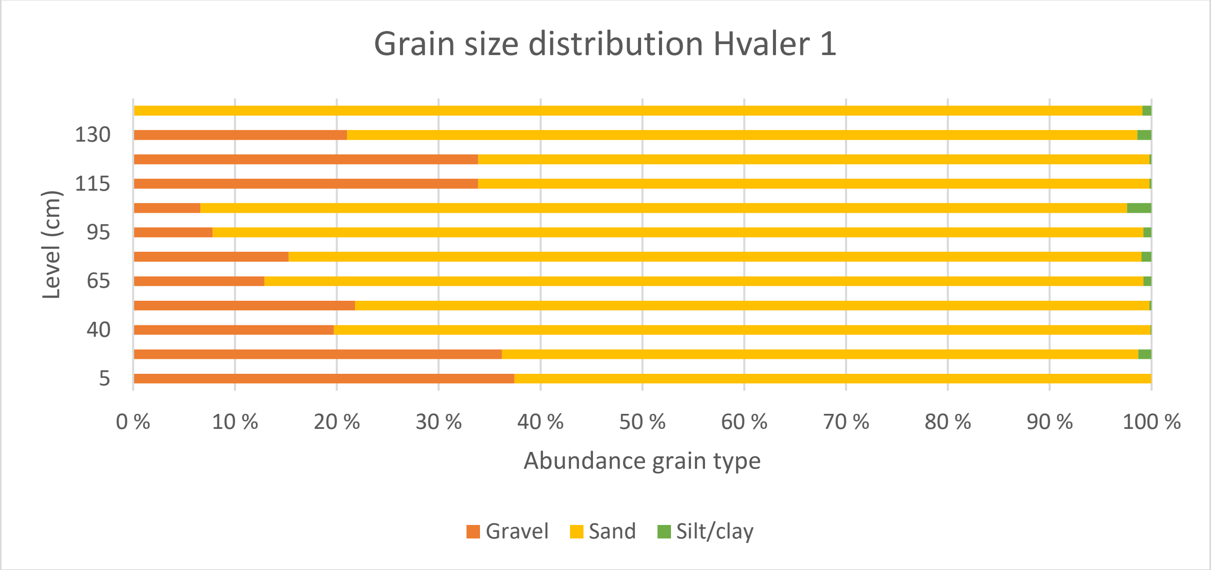

Figure 3.3 Gravel-sand-clay ratio Hvaler 1

Between 20 and 40 centimetres (Unit B) the average grain size is coarse sand, but it is poorly sorted and bimodally distributed with mostly medium sand, coarse sand and fine gravel. The layer is strongly oxidised, giving the sediments a red colour. Many roots, which might be modern, are found. A clay lens with a width around 10 cm and thickness around 2 cm is observed. While sieving the sediments, more clay lumps became visible. At 20 cm the deposit contains many shell fragments, and one complete *Modiolus modiolus*. A CT-scan of the *Modiolus modiolus* found at 20 cm shows many small boreholes (Fig. 3.4)

The rest of the shell fragments vary between very fine up to 3 cm. Dominating are *Rissoa parva* and *Alvania* sp. Other common species are *R. parva (var. interrupta)*[1], *Euspira montagui* and *Tectura virginea*. Rare species at this level are *Astarte montagui, Emarginula fissura, Steromphala umbilicalis, Hiatella arctica, Lacuna parva, Leufrouia leufroyi, Onoba semicostata, Retusa truncatula* and *Parvicardium* sp. Noticeable is that many *Parvicardium* bivalves are found with articulated valves.

Figure 3.4 CT-scan of Modiolus modiolus (PMO 236.648) found on Søndre Sandøy

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[1] See appendix for an extensive discussion about the identification of *Rissoa parva* and *Rissoa parva (var. interrupta)*

Between 40 and 60 cm (Unit C) the amount of shell fragments increases. Due to the high amount of shell fragments the grain size distribution is partly defined by shell fragments instead of siliciclastic material. Most sand is categorized as fine to medium, and the bigger fractions are predominantly shell fragments. *Rissoa parva*, *R. parva (var. interrupta),* and *Tectura virginea* are common species. Around the level of 50 cm *T. virginea* is bigger (± 1.0 cm) then in the rest of the section (± 0.5cm). A remarkable finding is *Tetrarca tetragona*, (± 0.3 cm), only observed once. Besides molluscs, common findings are polychaete worms, coral fragments (PMO 236.620) and sea urchin spines. Both gastropods and bivalves have boreholes, but in contrast with *M. modiolus*, in other samples there is only one borehole per mollusc.

Between 60 and 100 cm (Unit D) the sediments are full of shell fragments, and the bed has sharp boundaries with the beds below and above (Fig. 3.5). At 60 cm there is a continuous oyster bed with a thickness around 3 cm. From there upwards there is a deposit containing many shell fragments, some whole specimens and some pebbles (1-3 cm). The average and most abundant grain size is medium sand. Many gastropods and bivalves are smaller than in lower levels and very fragile. Common species are *Rissoa parva, R. parva (var. interrupta)* and *Bittium reticulatum*. The latter is not only smaller than below but also lighter in color. Species within the *Parvicardium* genus are not bigger than 0.5 cm, some of them are found with articulated valves. *Hiatella arctica* appears regularly and has a size between 0.5 and 1 cm. Many foraminifera are found. This layer continues up to 80 cm where a second oyster layer appears. This one has the same thickness as the lower one and is also overlaid by deposits with the same characteristics as below the oyster bed. This is continuing up to 100 cm. Besides the oyster beds at 60 and 80 cm, the oyster is also the most common of the larger molluscs in the intermediate layer, followed by *Mytilus edulis* and *Lucinoma borealis*. Noteworthy is that the *Ostrea edulis* are most often undamaged in the oyster beds but only found as fragments in the layers above. *Mytilus edulis* are mostly found as fragments, but the *Lucinoma borealis* are often found as undamaged specimens with articulated valves. The majority of the *Timoclea ovata* found in this layer have boreholes in their shell.

Figure 3.5 Shell rich deposit in unit D, containing two oyster beds.

From 100 cm up to the top of the section (Unit E) all shells disappear from the record. Between 100 and 105 cm mostly fine to medium sand is deposited, together with some bigger clasts with a size up to 2 cm. The mud content throughout the section has been very low (<1%), but slightly increasing upwards in the section until reaching its maximum in this layer (2.4%). Between 100 and 120 cm the sand is poorly sorted and containing very fine sand up to fine gravel. The following 5 cm, in contrast, consist of 75% very fine and fine sand and is better sorted than underlying sediments. Whether this thin layer is continuous is unclear. From 125 cm upwards the sand is poorly sorted and coarser grained again, but fining upwards to 150 cm, where all the grains are classified as sand, without any gravel or bigger clasts. Above 150 cm the section ends into soil of modern vegetation.

The gravel-sand ratio shows two fining upwards trends, the lower one from the bottom up to 105 cm and the second from 115 to the top. The calcium content is very low in the lower 5 cm, from there on it is increasing until it reaches its highest value at 65 cm. From there it decreases to almost 0 at 105 cm and upwards (Fig. 3.4). This is in accordance with the field observations regarding shell abundance. Most samples contain many foraminifera. Common are *Cibicides lobulatus* and *Eplhidium* sp. Other less common foraminifera found are *Ammonia beccari*, *Quinqueloculina* sp. and *Bucella* sp.

Radiocarbon dating

The *Modiolus modiolus* taken from layer B has a modal age of 7,800 cal yr BP, with a 95% confidence interval from 7,688 to 7,934 cal yr BP. An oyster taken from the lower oyster layer has an age of 7,403 (7,251-7,523) cal yr BP and one taken from the upper oyster layer is dated at 5,054 (4,885-5,261) cal yr BP. This places the section in the Atlantic stage of the Holocene.

Table 3.1 Radiocarbon dates of three mollusc shells on Søndre Sandøy

Sample	^{14}C age	Cal age, mode	Cal age BP, lower and higher boundary (95%)
Hvaler 20 cm (*M. modiolus*)	7,540 ± 20	7,800	7,652-7,933
Hvaler 60 cm (*O. edulis*)	7,100 ± 15	7,403	7,251-7,523
Hvaler 80 cm (*O. edulis*)	4,980 ± 15	5,054	4,885-5,261

Ecology

Per sample level, the specimens larger than 2 mm are counted. The sample taken from 65 cm contains the most individual specimens. The development of the amount of taxa is parallel to the amount of individuals. At most levels, *Bittium reticulatum* is the dominant species, except for 20 cm, where *Tectura virginea* is dominant. The Shannon Wiener value is rather stable throughout the section (Table 3.2). A complete overview of mollusc abundance is given in table 3.3 (page 20 +21).

Table 3.2 Biodiversity values of different levels in Hvaler 1, based on amount of specimens (bigger than 2mm) per 20 grams sediment.

	20 cm	**40 cm**	**55 cm**	**65 cm**	**85 cm**	**95 cm**
Taxa	9	6	8	11	10	10
Individuals	19	10	25	42	34	35
Dominance	0.20	0.11	0.12	0.15	0.16	0.16
Shannon	1.99	1.95	2.05	2.14	2.10	2.03

Using correspondence analysis, the sample level and the species are plotted in an ordination diagram (Fig. 3.6). The numbers correspond to the level of the sample. These are all shell containing samples taken from Hvaler 1. The first axis is explaining 47% of the variance, the second axis 24%

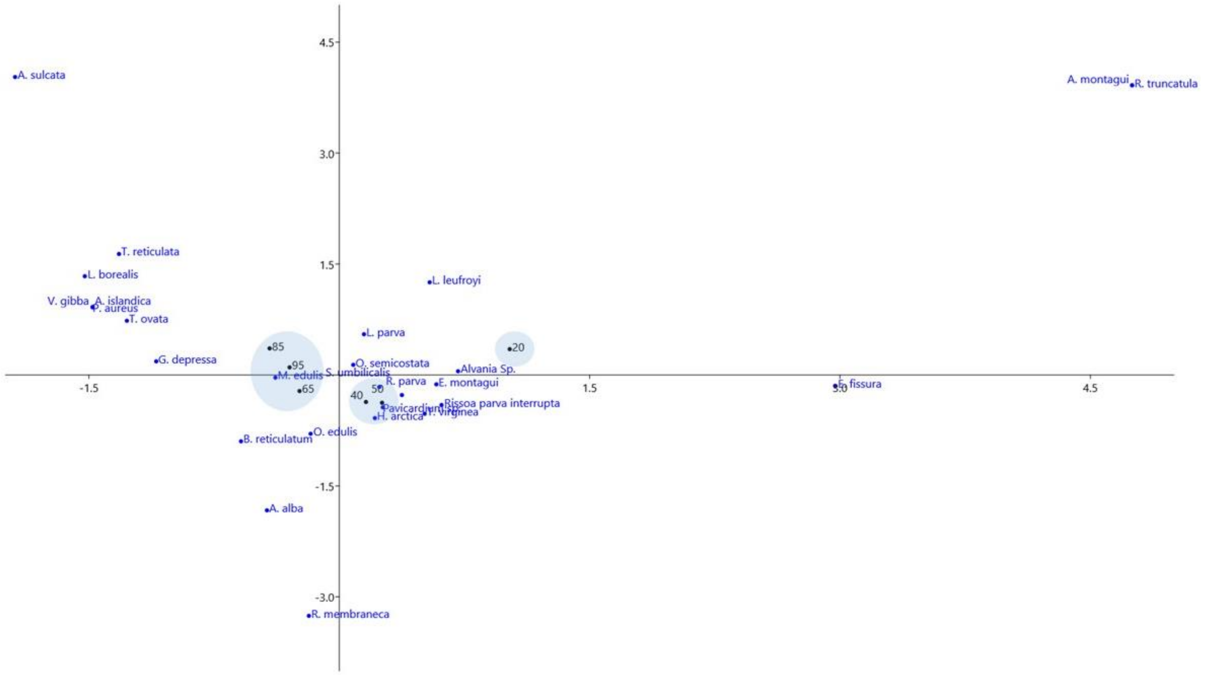

Figure 3.6 Correspondence analysis of molluscs occurring at the different levels in Hvaler 1. In the diagram the species are shown as well as the different samples, named after their level in the section. The three groups of localities are shown in blue circles.

The ordination diagram shows roughly that the closer the level of samples, the more alike they are (e.g. the lower sample is more similar to the samples taken from the middle part of the section than to the upper part of the section). The samples are divided into three groups: Sample 20 is on the right side (group I), 40 and 50 (group II) are very close to each other in the middle, and 65, 85 and 95 (group III) are found on the left side. This indicates a strong stratigraphic trend in species composition.

Group I is the most distinct one compared to the others. That is not only because it contains species that disappear above this level, but also because it lacks species that appear above this level and keep occurring throughout the section.

Species that appear in group I and not in the others are *R. truncatula, M. modiolus* and *A. montagui*. Also *Alvania* sp. has a far higher abundance in this level than in the rest of the section. In addition, the sample is characterized by the absence/low abundance of *B. reticulatum, O. edulis and M. edulis*. The community of group II is more similar to group III than to group I, but shows some differences with both other groups. One of them is the high abundance of *T. virginea, H. arctica* and *Parvicardium* sp*.* There are no occurrences of species that are absent in the other levels. The occurrences of species are either continuing from lower levels, or with first appearances that continue occurring in higher levels. The species distinguishing group III from the rest are *A. islandica, P. aureus, T. ovata, T. reticulata* and *L. borealis*. Some species are occurring throughout the whole section. These ones are *R. parva, R. parva (var. interrupta), O. semicostata, Pavicardium* sp*., S. umbilicalis, H. arctica, T. virginea* and *O. edulis.*

3.1.2 Hvaler 2

The excavation was broad enough to see the layers continuing in cross section. At Hvaler 2, taken approximately 20 m south west of Hvaler 1, the same layers appear, just a bit higher due to the dip (Fig. 3.7). In contrast with the description above, here the lower part does not contain any shells or clasts and unit D has changed laterally into a layer without shells, but with many pebbles and cobbles.

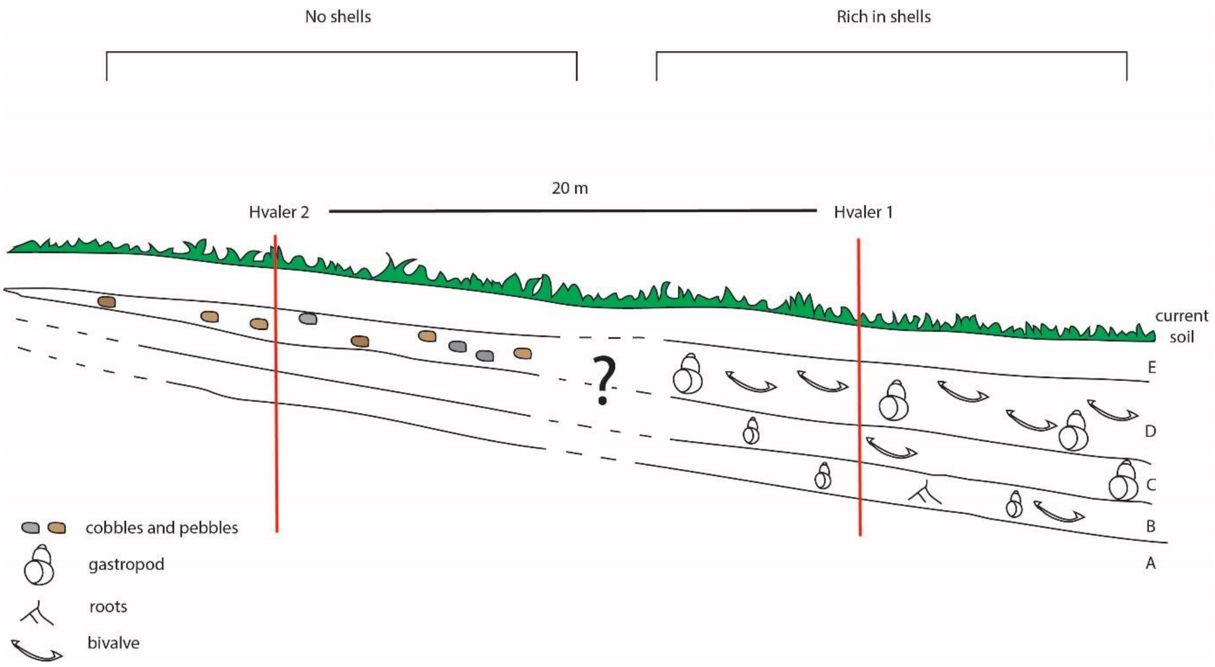

Figure 3.7 Sketch of outcrop and relationship between Hvaler 1 and 2.

From 0 cm up to 70 cm the deposits at Hvaler 2 consist of homogeneous fine sand. It is mostly transparent quartz grains, and about 5% orange (assumed to be feldspar) grains and black lithic fragments. The sand between 70 cm and 150 cm has a medium grain size but contains many pebbles and cobbles. The biggest ones have a diameter of 10 cm, but most have a size around 4 cm. The amount of pebbles and cobbles decreases in the upper part of this layer.

At 150 cm there is an abrupt change to very coarse, well sorted sand. There are few pebbles at this level, varying in size between 0.5 and 5 cm. The upper 20 cm between 180 and 200 cm consist of medium sand without pebbles.

3.1.3 Hvaler 3 and 4

Figure 3.8 Hvaler 4, Søndre Sandøy

Hvaler 3 and 4 are the ones with the highest elevation. Both localities have an elevation of 15 m.a.s.l. Because of the overgrown situation at Hvaler 3, only some oysters could be found. This does not provide enough data to say anything about the depositional environment, other than that it once was marine. At Hvaler 4 several oysters were exposed to the surface. Marine deposits were found underneath the upper weathered material and soil (Fig. 3.8). The sediment is poorly sorted and every grainsize between fine sand and fine gravel is abundant. Besides *Ostrea edulis, Arctica islandica* was represented with large specimens up to 9 cm. Most common smaller species are *Bittium reticulatum, Rissoa parva* and species of the *Parvicardium* genus. Rarer are *Onoba semicostata, Euspira montagui, Steromphala umbilicalis, Tectura virginea,* and *Alvania* sp. Other species found are *Mimachlamys varia*, one *Rissoa membranacea* and one *Emarginula fissura*. The mollusc specimens are slightly more deteriorated than the ones at Hvaler 1, but most are still recognizable. Except for one *Parvicardium* sp. all bivalves had disarticulated valves. Fragments of more fragile gastropods and bivalves are found, but these specimens could not be identified. Foraminifera are found but are not very common.

Table 3.3 List of species and their occurrence in the described outcrops. C / thick line = common, R / thin line = Rare and O / dot = observed once. LB= Low Boreal, MB= Mid Boreal, HB= High Boreal, LA = Low Arctic, MA = Middle Arctic, HA= High Arctic.

Locality	**Hvaler 1**						**Hvaler 4**	**Malmøya**	**Heimansåsen, Slemmestad**	**Northern Limit**[2]
Level[3]	**20**	**40**	**50**	**65**	**80**	**95**	**15 m.a.s.l**	**35 m.a.s.l.**	**33 m.a.s.l.**	
Abra alba			─	─		─			C	LB
Alvania sp.	━	─	─	─	─	─	R	R	R	HB
Aporrhais pespelecani					●			O		LB
Tetrarca tetragona			●							LB
Arctica islandica				─	─	─	R			HA
Astarte elliptica								C	R	MA
Astarte montagui	─									MA
Astarte sulcata					─				R	HB
Balanus **sp.**			─		─				R	HA
Bittium reticulatum		─	━	━	━	━	C	C	C	LB
Boreotrophon truncatus									R	LB-HA
Emarginula fissura	─		─				O		R	LB
Euspira montagui	━	─	─	━	─	─	R			LB
Gari depressa			●	─	─	─			R	LB
Glossus humanus									R	MB
Hiatella arctica	─	─	━	━	─	━			C	HA
Lacuna parva	─		─	─	─	━				LB
Laevicardium crassum							O			MB
Leufroyia leufroyi	─	─			─	─			R	HB
Littorina littorea								C	C	LB
Littorina saxatalis			●							HA
Lucinoma borealis				─	━	━			R	LB
Mangelia costata									R	LB

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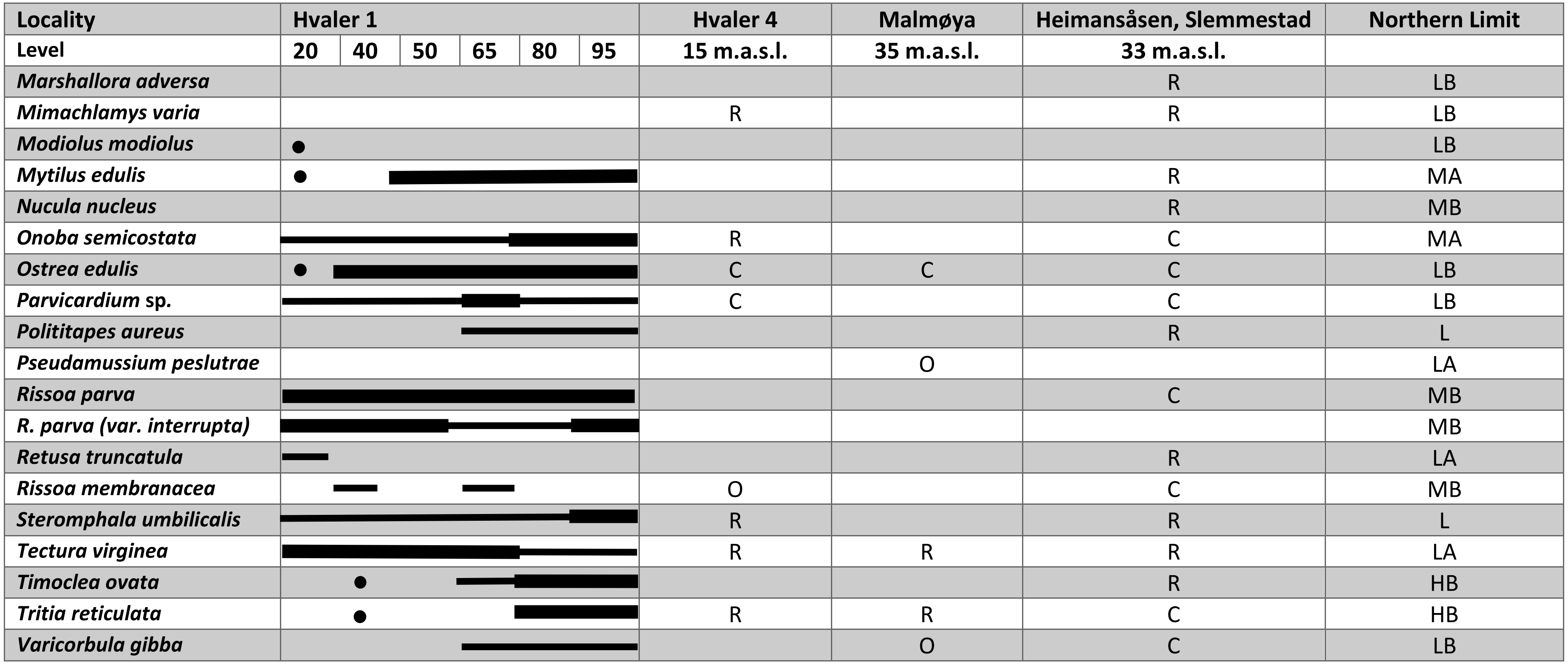
[2] In this column the northern limit of occurrence is given. All species do live as far south as the Lusitanian zone, with exception of the Arctic gastropod *Boreotrophon truncatus*, which southern limit is in the Low Boreal zone.

[3] The level for Hvaler 1 is given in cm above the bottom of the stratigraphic log, which is located 11 meters above sea level.



Locality	Hvaler 1						Hvaler 4	Malmøya	Heimansåsen, Slemmestad	Northern Limit
Level	20	40	50	65	80	95	15 m.a.s.l.	35 m.a.s.l.	33 m.a.s.l.	
Marshallora adversa									R	LB
Mimachlamys varia							R		R	LB
Modiolus modiolus	●									LB
Mytilus edulis	●	▬	▬	▬	▬	▬			R	MA
Nucula nucleus									R	MB
Onoba semicostata	—	—	—	—	▬	▬	R		C	MA
Ostrea edulis	●	▬	▬	▬	▬	▬	C	C	C	LB
Parvicardium sp.	—	—	—	▬	—	—	C		C	LB
Polititapes aureus				—	—	—			R	L
Pseudamussium peslutrae								O		LA
Rissoa parva	▬	▬	▬	▬	▬	▬			C	MB
R. parva (var. interrupta)	▬	▬	▬	—	—	▬				MB
Retusa truncatula	▬								R	LA
Rissoa membranacea		▬		▬			O		C	MB
Steromphala umbilicalis	—	—	—	—	—	▬	R		R	L
Tectura virginea	▬	▬	▬	▬	—	—	R	R	R	LA
Timoclea ovata		●		—	▬	▬			R	HB
Tritia reticulata		●			▬	▬	R	R	C	HB
Varicorbula gibba				—	—	—		O	C	LB

3.2 Malmøya

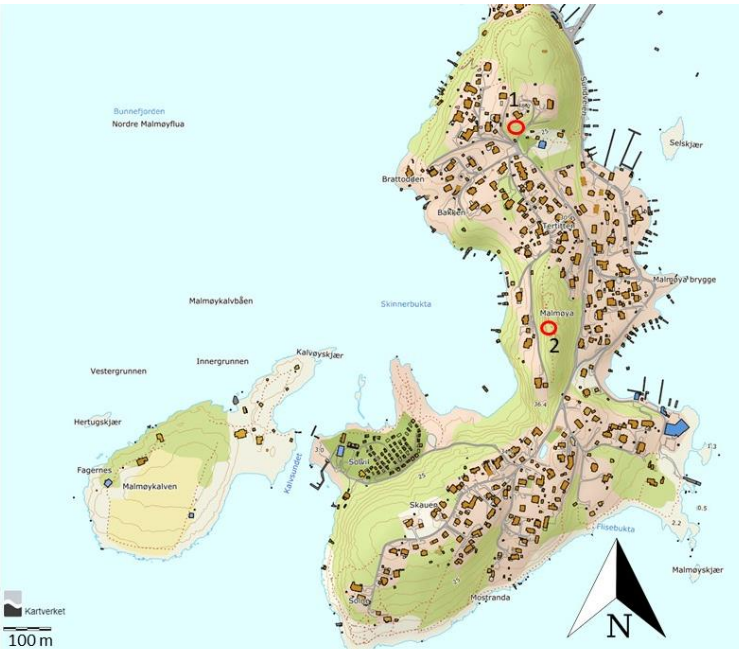


Figure 3.9 The two localities on Malmøya, containing Holocene marine deposits

Locality 1 on Malmøya is found directly south of Høyboveien 16 (59.87137^{o}N 10.75622^{o}E) (Fig.3.9). Only two shells are found close to the top of the slope (40 m), most shells are found further down (30-35 m). Whether these shells are in situ or have fallen down from the hill was not clear, because due to weathering no sedimentary structures can be found. However, the visible shells are mostly found within the same level, and sand taken from this level contains many tiny marine molluscs and some foraminifera. This indicates that this is the place where the shells were originally deposited. The grainsizes vary from very fine sand to gravel. Large *Ostrea edulis*, up to 9 cm, are characterizing the deposit. Also many *Littorina* gastropods are present. Several of them are full of boreholes. Some complete *Alvania* sp. specimens are found, but they were mostly found as shell fragments. Other common species are *Tritia reticulata* and *Astarte sulcata*. Some fragments of other bivalve are found but due to damages it was not even possible to determine the genus. A complete overview of specimens is shown in table 3.3. The age of an oyster in this deposit is 5,162 cal yr BP (Table 3.4).

At locality 2 (59.86778^{o}N 10.75761^{o}E), four specimens of *Mytilus edulis* and one *Mya arenaria* are found, but whether these are leftovers from marine deposits or thrown there by humans recently is uncertain. The elevation of this locality is ± 54 m.a.s.l.

Table 3.4 Radiocarbon dates of mollusc shell on Malmøya

Sample	**^{14}C age**	**Cal age, mode**	**Cal age BP, lower and higher boundary (95%)**
Malmøya (*O. edulis*)	5,050 ± 15	5,162	4,971-5,324

3.3 Slemmestad

In Slemmestad, oyster rich deposits are found at two localities close to the former cement factory at the harbour. Locality 1 is found in a road cut along Heimansåsen (59.78107^{0}N 10.48972^{0}E). In 2002 a road was being built, and surrounded by bedrock, loose sediments showed up at the surface. Shells were gathered and sand samples were taken. An oyster from locality 1 has been dated 5,545 ± 50 uncalibrated ^{14}C yr BP (1950) (Hammer & Nakrem, unpublished) (Table 3.5). Locality 2 is at a slope along Dølstuløkka (59.78425^{0} N 10.48939^{0} E) (Fig. 3.10). It is a deteriorated outcrop in which oysters have been found on the overgrown soil. The elevation of both localities is 33 m.a.s.l., and they could therefore possibly be of similar age.

Table 3.5 Radiocarbon dates of mollusc shell in Slemmestad

Sample	**^{14}C age**	**Cal age, mode**	**Cal age BP, lower and higher boundary (95%)**
Heimansåsen (*O. edulis*)	5,545 ± 50	5,707	5,535-5,892

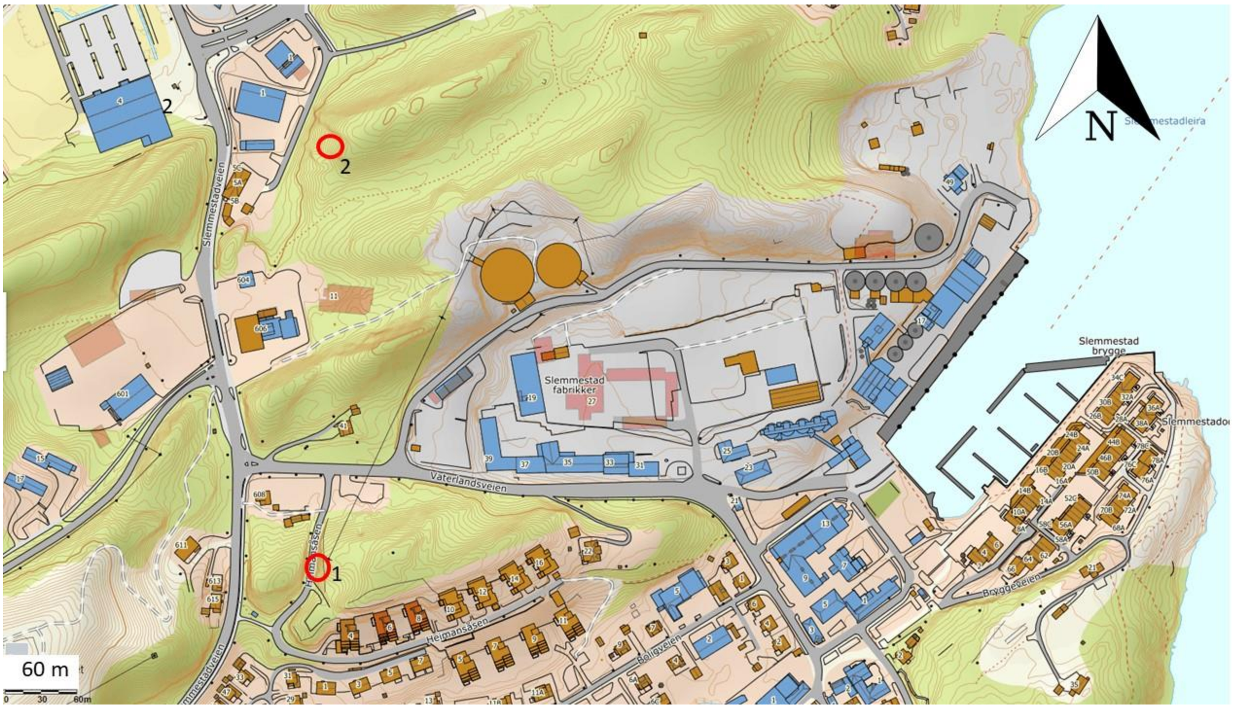


Figure 3.10 The two localities in Slemmestad, containing Holocene marine deposits

The deposit contains large amounts of *Ostrea edulis*, with shells up to 20 cm, and *Mytilus edulis* with very rigid shells with a length up to 8 cm. Just like on Malmøya, *Littorina littorea* is common. Most of them have a size around 1 cm, some bigger ones are up to 3 cm. Other common gastropods are *Bittium reticulatum, Tritia reticulata, Retusa truncatula, Alvania* sp., *Onoba semicostata* and *Rissoa parva*. A large diversity of bivalves is found, often without damages and regularly with articulated valves. A common species is *Hiatella arctica*, here considerably bigger (2-3 cm) compared to Hvaler (0.5-1 cm). Common species which are also found in Hvaler are *Tectura virginea, Mimachlamys varia, Timoclea ovata* and *Emarginula fissura*. Several fragments Lepidopleurida are found, but they are not recognizable to genus or species level. In Slemmestad not only the spines of echinoderms were found, but also a couple of bodies of *Echinocyamus pusillus*.

Figure 3.11 Outcrop at Heimsåsen, Slemmestad 2002. The lighter sediments in the middle of the picture consist of unconsolidated material and are surrounded by the darker bed rock (Photo: H.A. Nakrem)

3.4 Earlier described localities

Brøgger et al. (1900) described many Holocene marine deposits around the Oslo fjord. The ones that have been investigated thoroughly are included in this study. 231 species were observed, spread over 24 localities. The localities were previously divided into Upper Oyster, Upper Tapes and Lower Tapes banks. Possibly wrong assumptions about depositional depth make it unsure whether these categories are appropriate. The categories are based on the current elevations of the deposits. To investigate whether the faunal composition reflects this division, a correspondence analysis of the localities and deposits is done. The plot show a correspondence analysis of the localities (Fig. 3.12), where the symbols reflect whether they belong to the Upper Oyster, Upper Tapes or Lower Tapes banks. The first axis explains 13% of the variation and the second axis 9%. To keep it readable, the 231 species are not shown in the diagram. In order to analyse relationships between faunal composition, location and bank stage a map of the localities is made (Fig. 3.13).

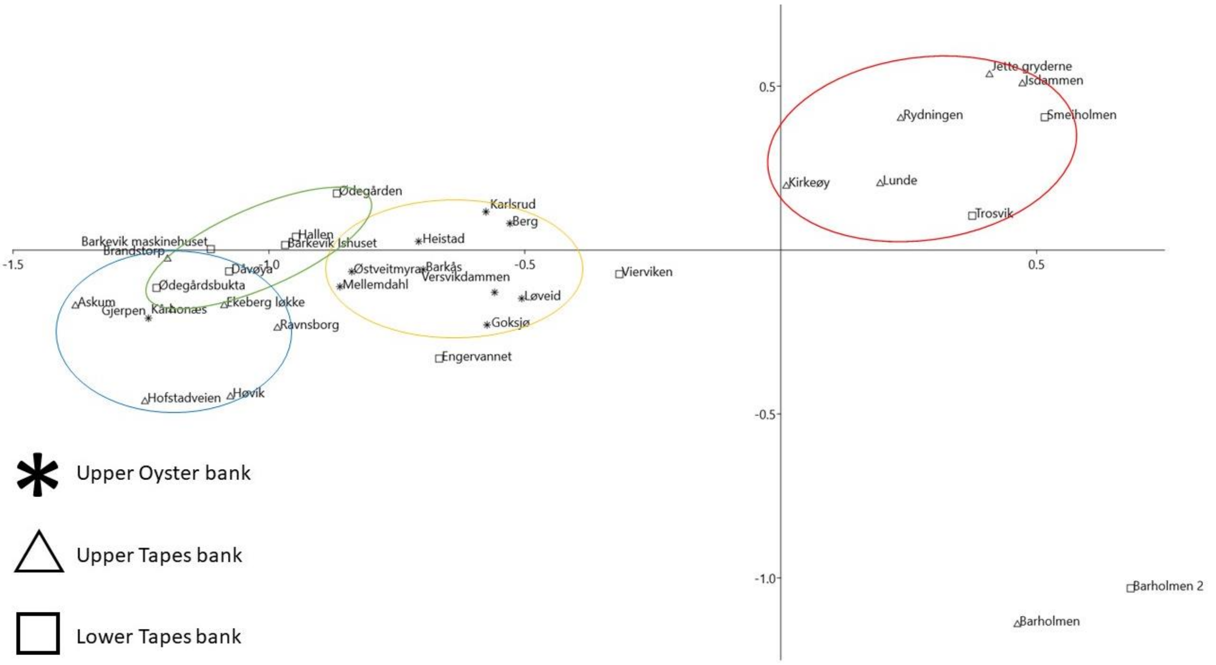


Figure 3.12 Present-absent correspondence analysis of localities described by Brøgger et al. (1900), with circles emphasizing different clusters.

The localities categorized as the Upper Oyster banks do cluster together, meaning they show a similar faunal composition. Gjerpen is an exception and shows fauna more similar to the Tapes banks. It is located near Drammen at 56.5 m.a.s.l. and has the highest elevation of the Upper Oyster banks. Most Upper Oyster banks are located along the outer fjord. One Upper Oyster bank (Mellemdahl) is located in the inner Oslofjord (Fig.3.13). This one is clustering together with all other Upper Oyster banks in the outer fjord.

The Upper Tapes banks, are also located in both the inner and outer fjord. The blue cluster contains Upper Tapes banks in and around Oslo, but also around Fredrikstad and across the Swedish border in Askum. However, not all Upper Tapes banks cluster together, they are divided into two clusters. The second cluster, the red one in the upper right corner, contains four localities on the west side of the outer fjord and one locality at Kirkøy, Hvaler. Two localities (Smeiholmen and Trosvik) within this cluster belong to the Lower Tapes banks. Their location is close to the other banks in the cluster.

Almost all Lower Tapes banks do cluster together with each other, between and partly overlapping with The Upper Oyster and Upper Tapes banks. Engervannet and Vierviken do plot further to the right. The two localities at Bergholmen, near Kragerø, show a faunal composition very different from the other localities, but relatively similar to each other.

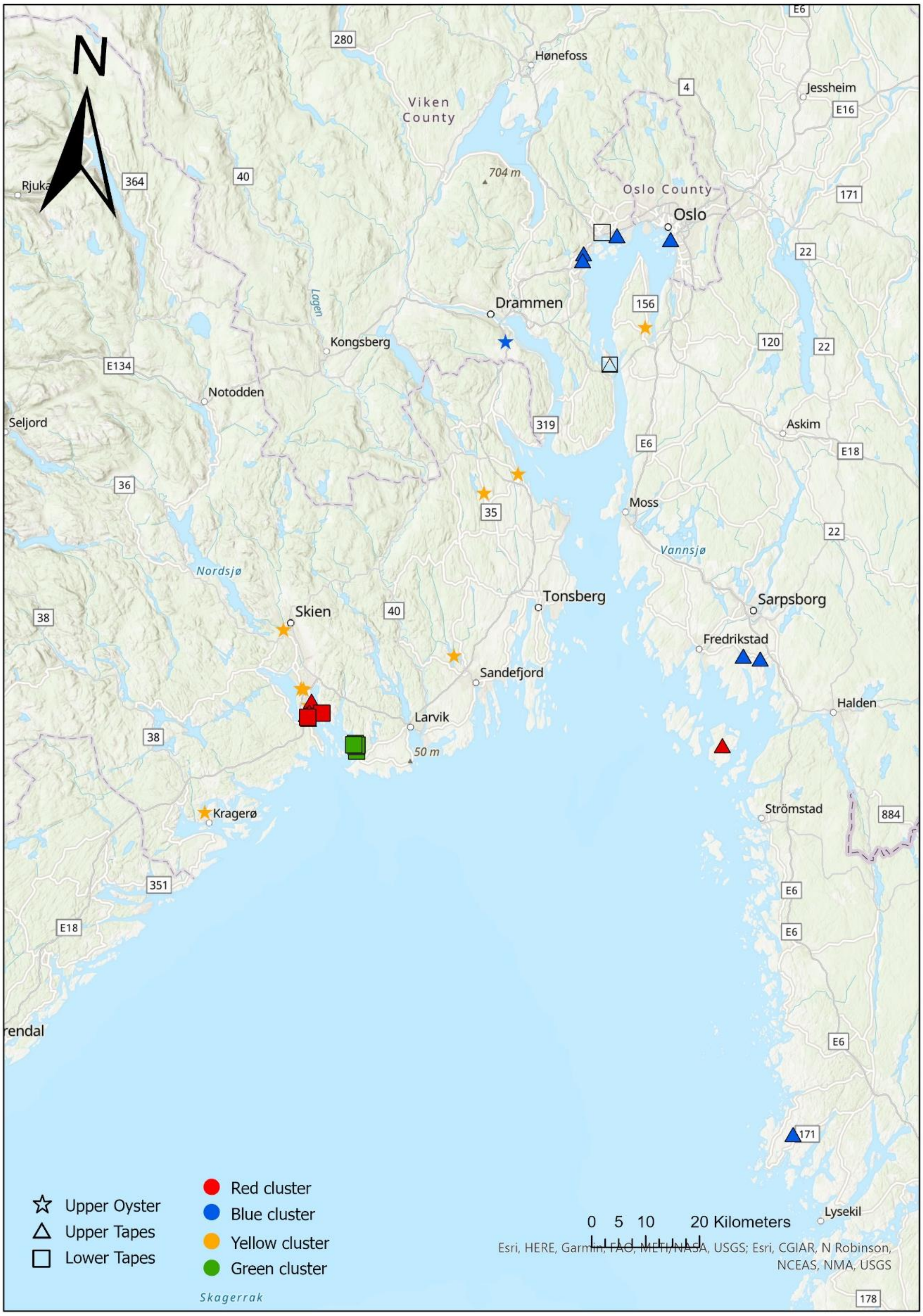


Figure 3.13 Overview of localities described by Brøgger et al. (1900). The type of symbol represents the classification according to Brøgger, and the colour of the symbol is corresponding to the colour of the cluster in the correspondence analysis shown in Fig. 3.12. The coordinates per locality and their elevation is given in the appendix.

When including the new localities of this study in the correspondence analysis (Fig. 3.14), it is striking that Hvaler and Slemmestad do plot far away from the rest. Malmøya does plot together with other Upper Tapes banks, while Hvaler and Slemmestad have lower scores on the second axis. Just like the previous correspondence analysis, only a low percentage of the variation is explained by the first two axes. The first axis explains 12% of the variation and the second axis 8%.

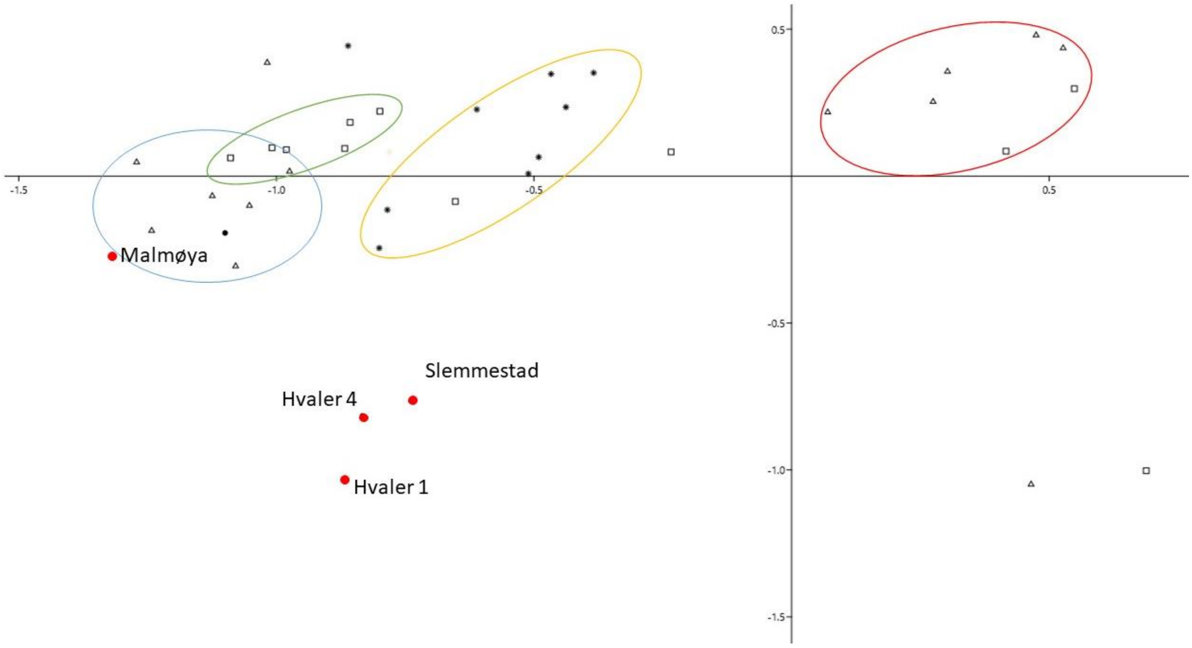


Figure 2.14 Correspondence analysis of previously described localities supplemented with the newly studied localities.

3.5 Present day fauna

The Atlantic assemblage, as found in this study, is compared to the modern assemblage. Figure 3.15 is visualizing the abundance of species found in Hvaler 1, based on the countings off all levels taken together. The pie chart of current mollusc assemblage (Fig. 3.16) is based from the coast of the counties Aust-Agder and Vest-Agder, located across the fjord slightly south of Hvaler (Molltax, 2022).

Nowadays, *Varicorbula gibba* is the most common species of the area. It is observed only a few times in the Atlantic deposits in Hvaler, but is common in Slemmestad. 25% of the modern fauna is also found in the Atlantic section in Hvaler, referred to as Atlantic species, and this is the part focused on in Figure. 3.16. Currently abundant Atlantic species are *Aporrhais pespelecani, Mytilus edulis, Timoclea ovata, Bittium reticulatum* and *Parvicardium sp*[4].

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[4] Different Parvicardium species from the modern data set are put together in order to compare it with the Atlantic assemblage, were they are not identified to species level either.

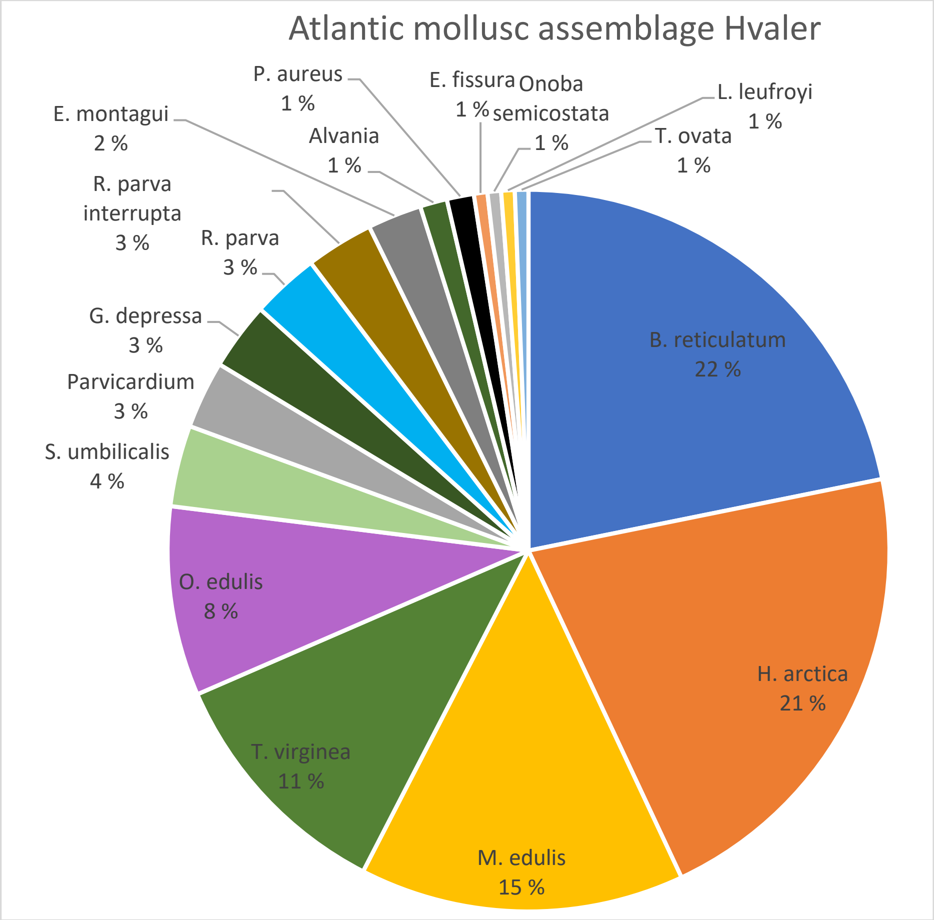

Figure 3.15 (left) Atlantic mollusc faunal composition of Hvaler 1.

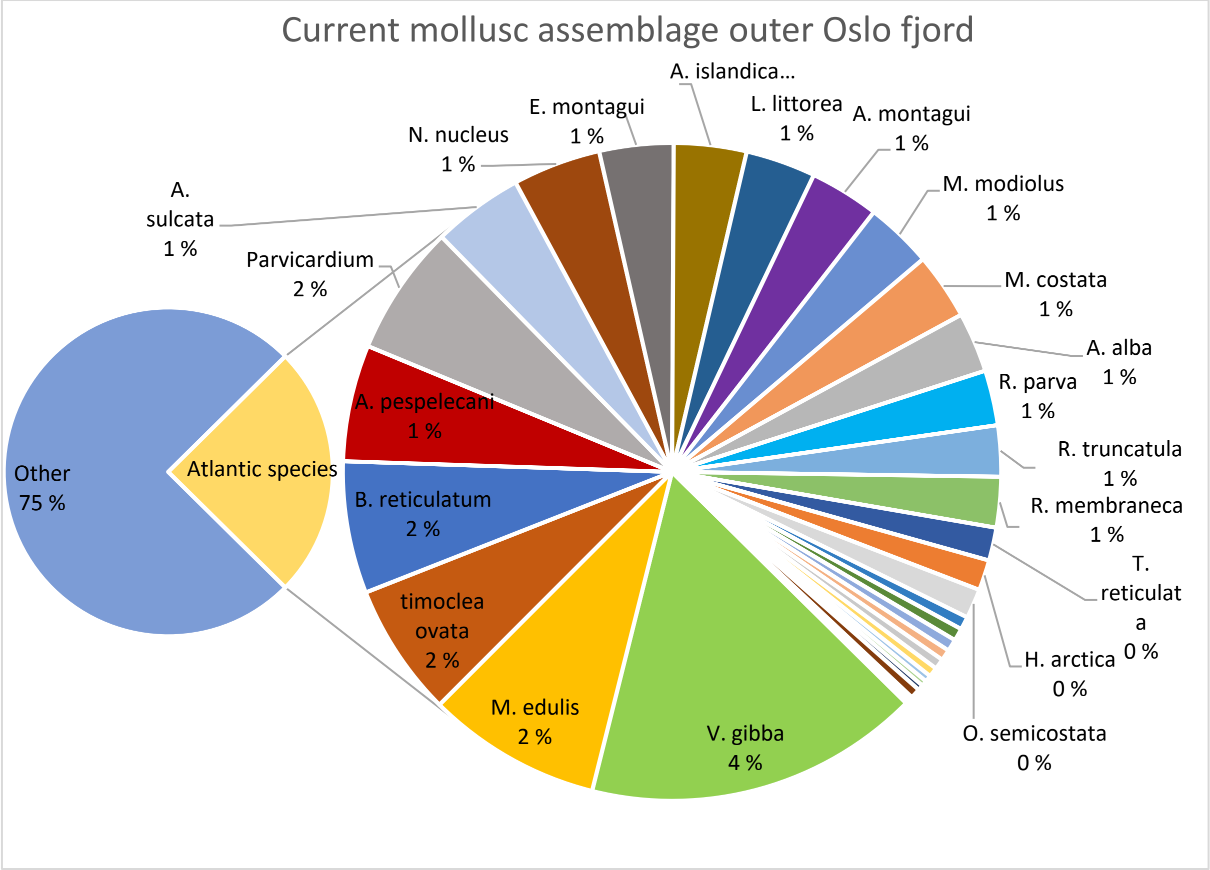

Figure 3.16 (below) Mollusc faunal composition of the Skagerrak. 25% of the species found in modern assemblages are also found in the Atlantic sediments from Hvaler. The figure zoomed in on the species that both have in common. The names of the rarest species are not shown.

Species that occurred in more than 20 middle Holocene localities are *Aporrhais pespelecani*, *Bittium reticulatum, Hiatella arctica, Littorina littorea, Lucinoma borealis, Mya truncata, Mytilus edulis, Ostrea edulis, Steromphala cineraria, Tectura virginea, Timoclea ovata* and *Varicorbula gibba* (Brøgger et al., 1900). Although there has not been done more quantitative research per locality, those species are expected to be common throughout the region. *V. gibba, A. pespelecani, B. reticulatum, L. littorea,* and *M. edulis and T. ovata* are still more than 1% of the mollusc assemblage. *H. arctica, L. borealis, M. truncata, O. edulis* and *T. virginea* are species that appear to be common during the Atlantic but are nowadays less than 1% of the mollusc assemblage.

4 Discussion

4.1 Lusitanian, Boreal and Arctic zones

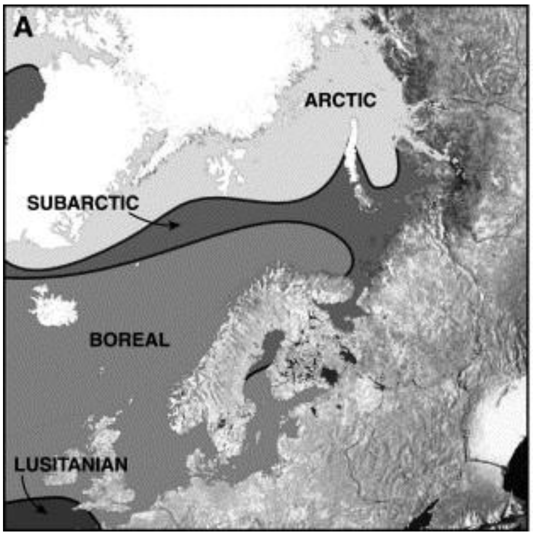

Figure 4.1 Lusitanian, Boreal, Subarctic and Arctic zones according to Funder et al. (2002)

Several attempts have been made to create climatological and zoogeographical zones of the European seas. Brøgger et al. (1900) put the Arctic-Boreal boundary at the polar circle, and the Boreal-Lusitanian boundary at 48°. However, by only taking latitude into account the effect of the Gulf Stream is neglected. A more detailed visual overview of the different zones was given some decades later by Feyling-Hanssen (1955) (Fig. 1.4), who based the zones on indicator mollusc species and their northern limits. This is more accurate than simply taking latitudes, since temperature is not solely defined by latitude. Several other studies followed this classification (Funder & Weidick, 1991; Petersen et al., 2005). More recently, an overview of the zones has been given by Funder et al. (2002) (Fig. 4.1). This one is based on oceanography, and has some slight differences compared to Feyling-Hanssen (1955). According to this modern classification, the Lusitanian zone is warmer than 9°C in the winter and higher than 16°C in the summer. For the Boreal zone, summer sea surface temperatures are above 8°C, and the waters are ice free throughout the year. North of the Boreal-Arctic border sea ice occurs regularly. The Boreal zone goes from southernmost England up to the northern most part of Norway. Therewith, the differences between low and high Boreal species go unnoticed. In addition, there is a sizable group of molluscs (e.g. *Steromphala umbilicalis, Barleeia unifasciata, Polititapes aureus*) that barely occur north east of the English Channel, but do live further north on the west coast of England. To distinguish those species from the other low Boreal species, the Lusitanian zone should go further north on the British west coast. To not lose those differences in biogeography, at least for molluscs, the Feyling-Hanssen division is preferable over the one made by Funder et al. (2002). Therefore this one is used for this study.

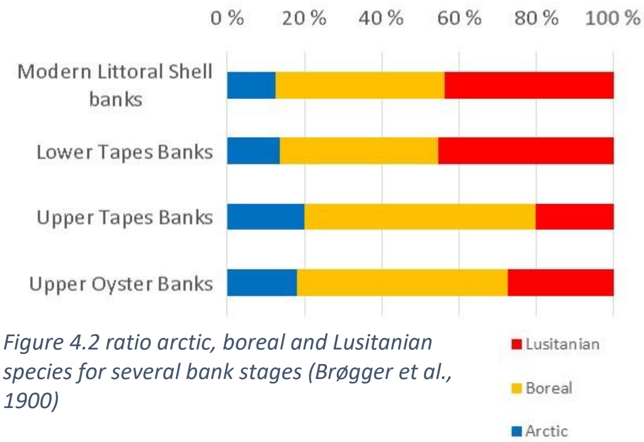

Figure 4.2 ratio arctic, boreal and Lusitanian species for several bank stages (Brøgger et al., 1900)

Almost all species found in this study have their southern limit down to at least the Lusitanian zone. Warmth does not seem to be a stress factor for the species in this region. The limit is defined by the cold towards the north.

Brøgger et al. (1900) used an increase in Lusitanian species to argue that the mollusc assemblage in the Tapes banks showed a warm signal in the sedimentary record. According to their data the Lower Tapes banks are containing most Lusitanian species (Fig. 4.2). Several comments can be made about his methods and a possible link of their finding and the HTM.

Using modern data (WoRMS, Artsdatabanken, OBIS), investigation of the way Brøgger et al. (1900) assigned categories, shows the following; Generally, Brøgger's "Lusitanian species" live in the Lusitanian and Low Boreal zone nowadays. Examples of these species are *Rissoa parva, Varicorbula gibba, Mimachlamys varia* and *Bittium reticulatum*. However, some species categorized as Lusitanian, for example *Similipecten similis, Nucula nucleus,* are nowadays observed all the way to northern Norway. The distribution of Brøgger's "Boreal species" is most often from Lusitanian to Mid Boreal/High Boreal, but also some species just reach the Low Boreal region, equal to Brøgger's "Lusitanian species". Arctic species are occurring from the Lusitanian zone up to at least the Low Arctic regions, so this is a properly assigned category. The other two are imprecise and should be re-evaluated. This has been done for the species occurring in this study (Table 3.3). The subgroups given by Feyling-Hanssen (1955), using low, mid and high, are used for separating species that only live in the south of Norway (Low Boreal) and species that penetrated northwards to northern Norway (High Boreal).

According to Brøgger et al. (1900) the share of Lusitanian species in the Upper Oyster and Upper Tapes banks are 20-30%. For the Lower Tapes and Modern Littoral Shell banks 40-50%. The highest percentage of Lusitanian species is in Lower Tapes banks. This is remarkable because according to the ages obtained in this study the HTM is covered by the Upper Tapes Banks, so one would expect the proportion of Lusitanian species to be the largest in the Upper Tapes banks. Possibly these statistics are not right because the classification of Brøgger et al. (1900) is too imprecise.

Additionally, the trend shown in Figure 4.2 is not indicating a warm event, after which the Lusitanian species withdraw again. There is only a trend with an increasing percentage of Lusitanian species over time. It could be that the immigration of thermophilous species does not reflect the HTM but that it is part of a consistent trend that started after the last ice age, where more and more species penetrate northwards.

Summarizing, the categorisation of mainly the Lusitanian group has a large uncertainty, and even if the categories are not too imprecise, the trend found by Brøgger et al. (1900) is not likely to purely reflect the HTM, because the vast majority of thermophilous species arrived later.

4.2 Depositional environment

4.2.1 The outer Oslo fjord

According to the sea level curve for Halden (Sørensen, 1999) the sea level was 60 m higher around 7,800 years ago, so Hvaler 1 on Søndre Sandøy has a depositional depth of 50 m at the bottom of the section (Unit B). During the deposition of the oldest part of the section, Søndre Sandøy was not yet an island, since its highest peaks are about 40 m.a.s.l. The lower oyster bed was deposited around a depth of 40 m. A group of little islands was forming, with shallow, narrow waterways between them. The upper oyster bed has a depositional depth of ± 30 m (Fig. 4.3), so the island was rising further above sea level. Assuming the slightly dipped layers reflect paleotopography of a former marine setting, Hvaler 2 is the proximal one while Hvaler 1 is more distal. This is corresponding to the topography nowadays.

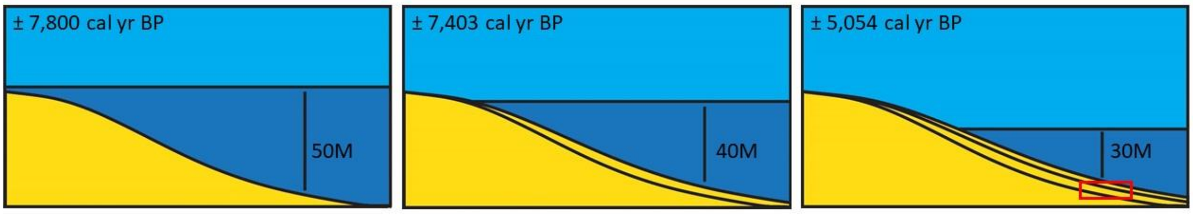

Figure 4.3 Model visualizing depositional depth over time for Søndre Sandøy. The red box in the right represents the section at Hvaler 1.

Sedimentation rate

Using the radiocarbon dates of the three shells in this section, two sedimentation rates can be given. In the ± 400 years covered by units B and C, 40 cm of sediment was deposited (i.e. average 1 mm/year). In contrast, in ± 2,400 years between the lower and upper oyster layer, only 20 centimetres of sediment were deposited (average 0.1 mm/year). The sedimentation rate is more than 10 times higher for the lower interval than for the upper interval. Unit D consists predominantly of shell fragments. That may look like a strong increase in amount of shells compared to the units below, but taking the low sedimentation rate into account the amount of molluscs per time unit might have stayed the same while the shells were deposited in a condensed section without much sand in between.

The dated shells could have been reworked and therefore be older than the layer where it is found, which could cause an error on the sedimentation rate. However, the two oysters from unit D are part of a continuous oyster bed, which make reworking unlikely. The *M. modiolus* in unit B is the only one of its species in that layer so it is more likely to be reworked and deposited in a younger layer. This would only make the difference in sedimentation rate higher, so reworking would not be an explanation for this observed change in sedimentation rate.

Sedimentation rate is affected by the availability of sediments and water energy. On a relatively short time span like this, assumed is that the hinterland area of the sediments did not change a lot. Given the fact that island were rising above the water, even more sediments were available from nearby sources, so a decrease in sediment supply is not expected. More likely is a change in water energy. There must have been either a longer time period with nearly non-deposition, or there must have been a shorter time period of erosion. In case of the latter, some stratigraphy is missing. That means there is a hiatus within unit D. At such a depth constant erosion by the surf of waves is unlikely, but oceanographic or tidal waves could have impacted the sediments (Bøe et al., 2009; Kuijpers et al., 1993). In addition, unit D disappears nearby (Fig. 3.7), so this discordant contact is also indicating erosive processes. Possibly deposition and erosion happened contemporaneous. After deposition the smaller sand particle could have been washed away while the bigger shell fragments remained on the sea bottom.

Grain characteristics

Several grainsize distributions in the section are bimodally distributed. This could be caused by seasonality, but distortion might have been caused by the presence of shell fragments, that are usually much larger than sand grains. Nevertheless there is a clear trend of two fining upward sequences (Fig. 3.2 and Fig. 3.3), indicating a slightly fluctuating water energy. The coastline could have been moving back and forth, or local currents could have fluctuated in strength.

Noteworthy is the local difference between Hvaler 1 and Hvaler 2. In Hvaler 1, many shells are found, but Hvaler 2 does not contain any. Instead, in unit D many cobbles and pebbles are deposited. Coarser sediments are mainly found in two marine settings, in the zone of wave-breaking and in the zone of maximum high tide (Kukal, 1971). Since this does not apply to a water depth of 40 m, coarse grained material as found in Hvaler 2 is unexpected. The cobbles are likely to originate from the Hvaler Moraine, deposited about 12,300 years ago. This moraine crossed the south-west of Søndre Sandøy (Sørensen, 1979). Even though this moraine is nearby, strong currents must have reworked the cobbles. The low sedimentation rate and the occurrence of cobbles and pebbles, indicate some strong currents as well. Although the units seem to continue between Hvaler 1 and 2, unit D transitions from a shell rich layer to a sandy layer with large cobbles, so some irregular processes must have been taken place. One option is that the layer is not deposited contemporaneous and that erosion and/or local channels disturbed the stratigraphy. The sediments at Hvaler 2 could have also been reworked a long while after deposition of the section, when the land rise had continued and the section had come closer to the water surface.

Since no clear explanation can be given, possibly wrong assumptions of this study should always be looked at. The interpretation of depositional depth is mostly done based on existing sea level curves. One possibility is that the sea level curve given by previous literature is wrong, but Sørensen (1999) used both radiocarbon dates on shells and isolation of lakes to substantiate the sea level curve. Especially the sea levels during the Atlantic stage and Subboreal stage are based on many measurements, so this is unlikely. Also mistakes in the dates are very unlikely, because as argued earlier, there is evidence against reworking of the dated oysters. The data obtained are not enough to conclude what exactly happened at and between Hvaler 1 and 2.

Relationship Hvaler 1, 2, 3 and 4.

Since Hvaler 3 and 4 are found at the same elevation, they might have the same age. The oysters found could have been part of the same contemporaneous colony, and they could have been occupying a large area. However, there is no evidence for this, and only dating the oysters could give a definite answer. Hvaler 3 and 4 are deposited 4 meters higher than Hvaler 1 and 2. Because no material from these localities is dated, it is uncertain whether this deposit is older or younger and thus deposited shallower or deeper. The composition of species occurring at Hvaler 4 is similar to at Hvaler 1, especially to the top of Hvaler 1, where *Arctica islandica* occurs. If this species migrated to the Hvaler area around 5,000 yr BP and not occurred earlier, it means that the section in Hvaler 4 is younger than Hvaler 1 and 2, and deposited shallower. An argument supporting this shallow depositional environment is the occurrence of *Rissoa membranacea* (Warén, 1996).

4.2.2 The inner Oslo fjord

In the inner Oslo fjord the sea level has dropped ± 40 m in the past 5,200 years. As Ski is slightly more south compared to Oslo, the relative sea level at Oslo could have been a few meters higher, but the deviation is probably small. Because of steep slopes along both sides of the fjord, the sea level drop since the middle Holocene has not affected the width of the inlet around Drøbak and the shape of the fjord so much. However, a waterbody that was 35 m deeper than nowadays must have had an impact on the water exchange between the inner and outer fjord.

The inner and outer Oslo fjord are separated from each other by a shallow threshold at Drøbak. As the sea level was 40 m higher, assuming the low-salinity lid had approximately the same thickness as today, more saline water could enter the fjord, the water would be mixed better, have a larger oxygen supply, and the inner Oslo fjord possibly had more fully-marine characteristics.

The deposits on Malmøya and in Slemmestad are both found at an elevation of 35 m. That means the sediments must have been deposited at a depth around 5 m, and probably slightly deeper for Slemmestad, since it is 500 years older. The current coastline of Malmøya is mostly rocky with some sandy beaches in between. The samples of this study are taken from a sandy layer on a steep rocky slope. *Littorina* snails, which are very common in the samples, live mostly on intertidal rocky shores (Hayward & Ryland, 2017).

The unconsolidated sediments at Heimansåsen in Slemmestad are surrounded by bedrock, and the shape is indicating a cave-like feature, where the thick deposits were possibly brought in by water currents. An apparent lack of stratigraphic layers on the pictures from 2002 (Fig. 2.11) could indicate that these sediments, including fauna, have been reworked into this cave-like feature. However, Slemmestad and Malmøya are located at topographic highs, meaning long-range transport is unlikely. Therefore it is assumed that the species living here reflect the faunal composition that lived here during the Atlantic.

4.3 Ecology

4.3.1 The outer Oslo fjord

Some species have a stable abundance throughout the Hvaler 1 section, but other species appear, disappear, increase or decrease over time. It is assumed that the found specimens are in situ or are transported only for a short distance. Variation in composition on local scale can be caused by changes of the depositional environment and depth. On a larger scale, the climate has an impact on the boundary of mollusc habitats. Biological factors also play a role, but this study focusses on the first two factors.

Common species and their habitats

In the ordination diagram (Fig. 3.6) the sample levels are divided into three groups. Group I is characterized by *Retusa truncatula, Alvania* sp*., Astarte montagui*, *Modiolus modiolus* and *Emarginula fissura. R. truncatula* can live from the lower intertidal down to 50 m, mostly shallower than 30 m (Hayward & Ryland, 2017; OBIS, 2022). *A. montagui* and *E. fissura* can live to deep offshore waters. A species staying common throughout the whole section is *Tectura virginea*. They can live at a water depth up to 100 m, but are most abundant at a depth shallower than 40 m. They are often found at the surface of boulders (Hayward & Ryland, 2017; Høisæter, 2009). In Hvaler it is noticed that they become less abundant with time, and so with decreasing deposition depth (Table 3.3). Boulders are not found at Hvaler 1, but cobbles are abundant in Hvaler 2. Even though the layer with cobbles at Hvaler 2 does not contain any molluscs, it shows that suitable hard substrate is close by. In spite of that, *Tectura virginea* is most likely not in situ here, but could have been transported from nearby.

Group II can be seen as a transition between the lower part and the upper part of the section. Species that become common are *Mytilus edulis*, *Ostrea edulis and Bittium reticulatum*. Usually, *Mytilus edulis* occurs in dense beds on hard substrate, in a range from upper shore to shallow sublittoral zone (Hayward & Ryland, 2017). In this section they become common at 50 cm and stay common throughout the shell rich layer. They are barely found as whole specimens, and in situ deposition is therefore questionable. Nevertheless, the coastline is coming closer over time and the water is getting shallower which could cause the change from low abundance in the lower beds to persistent presence higher up in the section. Areas densely populated by *Ostrea edulis* are found from the intertidal zone down to tens of meters of depth (Bennema et al., 2020; Hayward & Ryland, 2017). *Ostrea edulis* has a preference to settle on substrates rich in calcium carbonate (Fitt et al., 1990), which they did by settling on a thick shell layer at 60 and 80 cm in Hvaler. Very common up from 50 cm is *B. reticulatum,* which can live from the sublittoral zone to a depth of 250 m (Hayward & Ryland, 2017), but is mostly found shallower than 30 m (OBIS, 2022). There is no evidence for in situ deposition but this species could have been living here on the soft substrate, which is a preference for this gastropod.

Group III is characterized by *Arctica islandica, Polititapes aureus, Timoclea ovata, Tritia reticulata* and *Lucinoma borealis*. All these bivalves are burrowers in soft sediments from shallow sublittoral to offshore. Their burrowing life strategy could explain why they are found in situ here and they have not been reworked as much as many other molluscs. *L. borealis* can burrow down in the sand to a depth of 20 cm (Allen & Yonge, 1958; Dando et al., 1986). In case they were burrowing when they died, they are possibly younger than their surrounding sands and shells in this section. *T. reticulata* is a gastropod that can live offshore, but it is mostly found in shallow sublittoral waters between 10 and 20 m (Hayward & Ryland, 2017; OBIS). The increase of burrowing bivalves could indicate an environment with higher water energy, and thus a shallower, more proximal environment, but the habitat of these species alone does neither confirm nor disprove a shallowing trend.

The layer between 60 and 95 cm is very rich in molluscs compared to the lower part of the section, reflected by the counted amount of individuals (Table 3.2). The species richness and Shannon Wiener value do not increase much, so there is no indication for a surge in biodiversity, and the high amount of individuals is assumed to be caused by a condensed record due to a low sedimentation rate. Remarkable is that that many species have decreased in shell size, so for some reason life conditions have changed. In case there were periods of erosion, a higher flow speed could have affected the population. However, a change in water flow speed is affecting the growth of some molluscs in a positive way and others in a negative way (Grizzle et al., 1992). Also other biological factors could have played a role, and the reason for the decrease in body size remains unclear.

The boreholes in molluscs are most likely caused by predatory drilling gastropods, that ate the organism out of the shell (Nielsen, 2014). *M. modiolus* is an exception, since it contains many small borings. This is more likely to be caused by encrustation by other organisms.

Climatic response

Based on the age of the studied sections (± 7,800 to ± 5,000 cal yr BP) and previous studies (Davis et al., 2003; Velle et al., 2005; Antonsson & Seppa, 2007) one would expect this section to cover the peak of the HTM to near the end of the warm period in the upper part. In case there is an increase/decrease in Lusitanian/Arctic species, this could indicate a response of the ecosystem to the changing climate and help date the peak of the HTM in the Oslo region.

Since the timespan between the deposition of the oldest shells at 20 cm and the youngest ones at 95 cm is about 2,700 years, climate could potentially have affected the mollusc communities within the studied section. To investigate this, the species of the same ordination diagram as in the results section are now given colours (Fig. 4.4), where red dots represent thermophilous species (Lusitanian + Low Boreal) and blue dots for the "cold species" (Arctic + High Boreal) species. The yellow dots plot the species in between the categories, or cases where this information is uncertain. For this analysis the classification of Lusitanian, Boreal and Arctic categories have been waived. Only few true Lusitanian and Arctic species are found, and there was a clear distinction between low and high Boreal species that should not get lost. Therefore the low Boreal species are added to the Lusitanian group and the high Boreal species to the Arctic group.

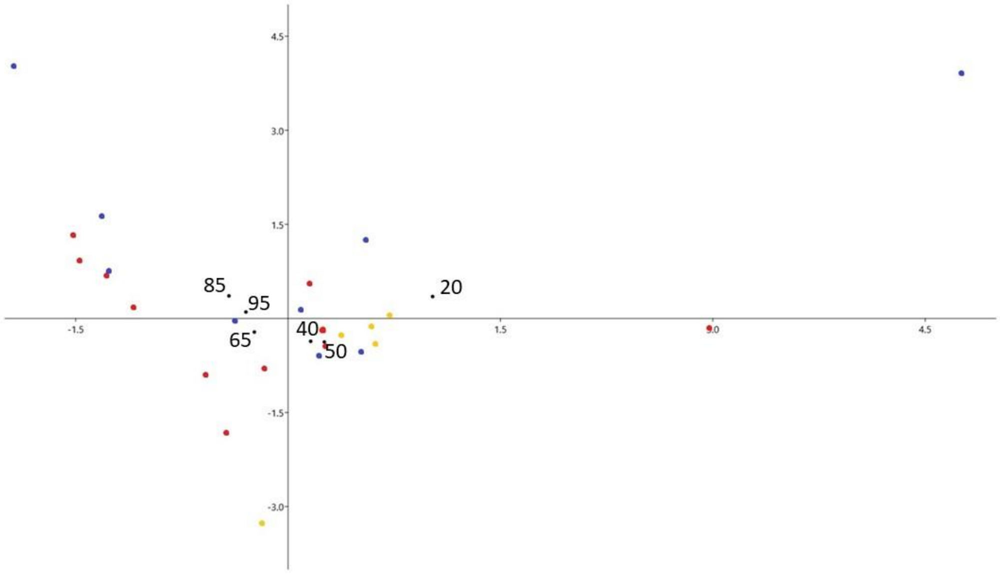

Figure 4.4 Correspondence analysis of Hvaler 1, identical to the one in figure 3.6, but now the species are categorized as thermophilous (red), cold species (blue) and other (yellow). The black dots with numbers represent the different sample levels.

The first axis seems to represent at least depositional depth, but the faunal composition could additionally also be affected by climate. In case of a warming trend during the deposition of the section, more thermophilous are expected in the left side of the ordination diagram. This seems to be slightly the case, but no clear warm or cold clusters are shown. Also, in the top of the section is richer in species in general. Simply counting the ratio between cold and warm species does not give reliable information because there is the problem regarding the fact that they are not excluding groups. The thermophilous species do live in warm regions and not live in cold regions, but the so-called cold water species do live in both cold and warm regions. To give an example of the problem: one of the cold species disappearing from the record is *Retusa truncatula (Fig. 3.6 and 4.4)*. This species appeared only in unit B, and disappeared above this level. Nevertheless, it is unlikely that *R. truncatula* disappeared because of rising temperature. Although it is a species tolerant to cold environments and its habitat extends to the Arctic, the species is also living in the Mediterranean. This indicates that the water in the Oslo fjord is not close to the upper lethal thermal limits of the Arctic species. A possible warmer climate during the Atlantic was therefore most likely not the reason for disappearance of the gastropod. The hypothesis of a warmer climate would therefore rather be supported by the appearance of thermophilous specious instead of the disappearance of cold water tolerant species.

An additional impeding factor is that the oldest shells lived in a depositional environment that was 20 m deeper and more distal than the youngest shells. So in case species arrive or leave, this might be because they follow their preferred depth and not because of a changing temperature.

Moreover, the division thermophilous and cold water species is complex. In the first place, the hard line between warm and cold does not do justice to the more nuanced habitats of mollusc. One should keep in mind that the colours are based on northern most limits of occurrences, which might give an oversimplified perspective, since the categories do not always represent the zone where the species is most common.

Summarized, there are slightly more thermophilous species at the top of the section than at the bottom. However, doubts about the way thermophilous and cold species are grouped, and the fact that the decrease in depth must have played a role, it is not concluded that this represents a warming climate.

4.3.2 The inner Oslo fjord: Malmøya & Slemmestad

Locality 1 on Malmøya was previously described by Brøgger et al. (1900), and belongs to the Upper Tapes banks. These banks had not been dated yet, so this study adds a timeline to the deposits and stages described by Brøgger. Species that are found in both this study and Brøgger's study are *Ostrea edulis, Littorina littorea, Tritia reticulata* and *Varicorbula gibba.* In addition, Brøgger et al. (1900) found *Anomia ephippium, Pododesmus pateliformis, Arctica* *islandica, Ruditapes decussatis, Polititapes rhomboides, Lucinoma borealis, Hiatella arctica* and *Rissoa membranacea.* The deposits are now heavily deteriorated, and probably were already in 1900, when Brøgger studied which species were present. Therefore it is possible that more species lived here. In Slemmestad many more species were found. It is probably more complete because it was not deteriorated since it was investigated directly after it was exposed while a road was being built.

In Figure 4.5 the fauna of the inner Oslo fjord (Malmøya + Slemmestad) and the outer Oslo fjord (Hvaler 1) are compared. In the inner Oslo fjord 33 species are found, and in the outer fjord 32 species. Regarding faunal composition, there is no large difference between these two areas. The areas show similar ratios of thermophilous and cold species, and the majority of the common species found on Malmøya and in Slemmestad is also found on Søndre Sandøy. One exception is the genus *Littorina*, which is not found in Hvaler at all. This could be explained by a difference in depositional environment. *Littorina* prefers hard substrate, usually littoral (Hayward & Ryland, 2017), which is found on the rocky coastline of Malmøya but not in the deeper sands of Hvaler. In addition, *Littorina* can handle brackish conditions which could have given them an advantage in the inner Oslo fjord. Another exception is *Astarte elliptica.* For this bivalve, the difference cannot be explained by depositional environment.

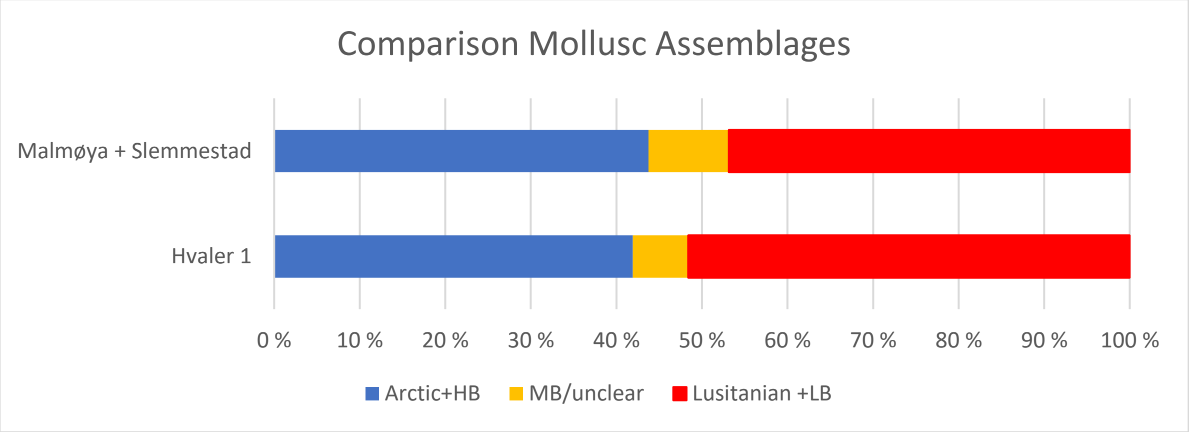

Figure 4.5 Distribution of warm and cold species in the Atlantic fossil assemblages in the inner and outer Oslo fjord

4.3.3 New localities compared to previous described banks

The faunal composition of the shell banks described by Brøgger et al. (1900) largely corresponds with the division of the different shell banks. There are some exceptions, and these localities should be further investigated. Differences between contemporaneous deposited sediments, can be caused by difference in geographical position, depositional depth or local environmental conditions. If these factors cannot explain the differences or similarities in faunal composition, it is questioned whether deposited during the same period. Remarkable results of the correspondence analysis of Brøgger's localities are discussed.

Previously studied localities

All Upper Oyster banks show very similar faunal compositions, with exception of Gjerpen. This sample contains only 14 species, considerably fewer than most other samples. The locality does not contain *O. edulis, T. reticulata, T. virginea* and *B. reticulatum*, typical species for the other Upper Oyster banks. Even though the faunal composition shows many similarities with the Upper Tapes banks, its high elevation makes it impossible to be deposited contemporaneous with the Upper Tapes banks. By then, the sea level had dropped to around 40 m, and these sediments are deposited 16.5 m above that sea level.

The faunal composition of the Upper and Lower tapes banks show some overlap with each other. Those localities in the overlapping zone could represent the transition between the two stages. However, one would expect the Upper Tapes banks to be plotted between the Upper Oyster Banks and Lower Tapes banks, because then the cluster would have shown a stratigraphic trend in species composition. Now, the youngest, Lower Tapes banks are plotted in the middle.

In addition, the correspondence analysis shows different clusters within the Upper Tapes banks. The localities at Trosvik and Smeiholmen, assigned to the Lower Tapes Banks, show similarities with the Upper Tapes banks of the red cluster. The red and blue clusters plot far away from each other. This seems to be mainly caused by the differences in species richness. All localities in the red cluster contain between 79 and 158 species, while the localities in the blue and green clusters contains between 9 and 29 species. In case this difference in species richness reflect the paleo environment, this is very important to further investigate. Because not all localities have been investigated in a systematic way, it is plausible that the record is incomplete, and no conclusions can be drawn before new systematic data from these localities is gathered.

The Upper Oyster and Upper Tapes banks show similar fauna in the inner and outer fjord. For the Lower Tapes banks, the two localities in the inner fjord do not cluster together with the rest of localities in the outer fjord. The two localities in the inner fjord, Engervannet and Vierviken contain 13 and 49 species respectively. The high amount of species in Vierviken can cause its position towards higher values on the first axis, but Engervannet does not contain any more species than the average Lower Tapes bank. Possibly the conditions in the inner fjord have developed differently than the conditions in the outer fjord. The Lower Tapes banks are the youngest banks, and the threshold at Drøbak was shallower compared to deposition of the older banks. Perhaps, the fauna in the inner fjord has differentiated from the fauna in the outer fjord as a result of more restricted circumstances later in the Holocene.

The Lower Tapes banks at Barholmen is mixed with deep-water species of an older, glacial age that are reworked. Brøgger et al. (1900) took this into account while making the faunal list that this study used for the correspondence analysis, and he left out the species he expected to be part of an older assemblage. Nevertheless, it is possible that some species assigned to the Lower Tapes banks do not belong to this stage. In addition, the localities at Barholmen contain a high number of species, 90 for the Upper Tapes banks and 123 for the Lower Tapes banks. These two factors differentiate Barholmen from the rest.

Newly studied localities compared to Brøgger's localities

In contrast with the other newly studied localities, Malmøya plots together with the other Upper Tapes banks. Malmøya must therefore have something in common with the other Upper Tapes banks that the other three new localities do not have. The only species occurring on Malmøya and not on the other three localities are *Pseudamussium peslutrae*. *P. peslutrae* is also occurring in multiple other banks, and does bring Malmøya slightly closer to the other Tapes banks. Findings from Hvaler that are not observed at the previously studied localities, are *Steromphala umbilicalis* and *Lacuna parva*. It is remarkable that these species are not found at other localities, and therefore it has been investigated whether species are misidentified in either this study, or by Brøgger et al. (1900) (see taxonomic notes, appendix). These species might affect the position of the Hvaler localities. Also the absence of *Littorina Littorea* in Hvaler is differentiating those 2 localities from the rest. The rare species *Marshallora adversa* from Slemmestad is not found in other previously described banks. Because the correspondence analysis is based on presence-absence data, some rare species can make the localities appear more different from each other than they actually are.

The Upper Tapes banks are divided over two clusters, at least partly caused by the difference in species richness. The amount of species in the three newly studied localities are similar to the banks in the blue cluster, so this is not expected to be the cause of the gap. Some other localities near Fredrikstad in the blue cluster are located close to Hvaler, so neither does the geographical position seem to create the gap.

The few findings at locality 2 on Malmøya are found at the same elevation as the closest Upper Oyster banks in Drammen and Nesodden. Therefore it is not unlikely that they belong to this stage, but more specimens should be found for further investigation.

4.3.4 Comparison present day fauna

Brøgger et al. (1900) reported a northward migration of southern species. In case species are migrating north and not disappear afterwards, this indicates a constant trend that started after the last ice age. In case the HTM affected the faunal composition, expected is that thermophilous species withdrew after the Thermal maximum, and that those species are not found in younger/recent deposits. Therefore the whole section at Hvaler 1 is as one mollusc HTM assemblage, and compared with modern fauna. The data set of modern molluscs covering a large area with many observations, and therefore comparisons should be done prudently. Nevertheless, the section from Hvaler is also including a large range of depositional depths (at least between 30 and 50 m). If a species is common in the large present day data-set, but not in our section, if that is due to the smaller and local sample of this study. However, if a species occur in the small Atlantic data set, but not in the large modern one, this is stronger evidence for changes.

Hiatella arctica and *Tectura virginea* are two of those species, common in the Atlantic sections of this study, but not so common in modern studies. They were not only abundant in Hvaler and Slemmestad. Including the previous studies, they are found at respectively 28 and 27 localities, so it is likely that those two species were generally more abundant in the area during the Atlantic.

Ostrea edulis is not especially counted very often, but is observed in large oyster banks characterizing many localities. Immigration of this species during the Atlantic is also observed in Denmark (Funder et al., 2002), and there is no indication that they left the area until recently. Until the 19th century, large oyster beds were spread out along the north western coast of Europe, but this amount has decreased significantly, due to overexploitation, introduction of new non-native species and diseases (Laing et al., 2006; Vera et al., 2019).

Steromphala umbilicalis[5], *Gari depressa* and *Polititapes aureus* are less common in the Atlantic section in Hvaler, but recently barely found in the Oslo fjord anymore (Artsdatabanken, OBIS, WoRMS). *S. umbilicalis* is observed only a few times along the Norwegian west coast and is absent along the Danish, German and Dutch coastline. It is often observed on the west coast of Great Britain, along the Atlantic coast further southwards. *Polititapes aureus* is observed in five localities described by Brøgger et al. (1900), and *Gari depressa* at six, both in the Upper and Lower Tapes banks. *P. aureus* is observed few times in Norway, and is more common along the British west coast and in the Mediterranean. *G. depressa* is barely present in Norway

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[5] See appendix for an extensive discussion about the identification of *Steromphala umbilicalis*

nowadays. No observations around the Oslo fjord have been reported. It is mostly observed along the British coasts, and also on the Normandy coast and in the Mediterranean (Artsdatabanken, OBIS, WoRMS). The most northern occurrences are on the Norwegian west coast (Tunberg, 1981).

Hiatella arctica and *Tectura virginea* are cold species that most likely decreased in abundance. *S. umbilicalis, G. depressa* and *P. aureus* are thermophilous species that left. The fossil record of the middle Holocene does not indicate a warmer climate during the HTM, compared to recent assemblages. The southern species migrating northwards during the middle Holocene did not leave after the HTM, and it is therefore likely that they continued a slow northwards migration during the HTM in the same way they did that in the previous millennia.

Enough evidence for a warming climate during the middle Holocene is found, so an effect on the marine ecology would be expected. Ecology is a combination of extrinsic factors and intrinsic factor. Extrinsic factors include the physical and chemical circumstances and intrinsic factors are biological. Shallow communities are more often affected by extrinsic factors than deeper communities (Rex et al., 2005). The extensively studied section at Hvaler has a depth between 50 and 30 m, and might therefore be too deep to be affected by the warming during the HTM. The studied sections in the inner fjord are shallower. Figure 1 shows that the annual temperature has a larger deviation than the summer temperature, which is indicating that mainly winter temperatures were higher. In shallow waters, less extreme winter conditions can result in a higher species diversity (Beukema et al., 1978). Perhaps the HTM only affected the shallower communities in the Oslo fjord, but not to the deeper water ecosystems.

The studied deposits on Malmøya and Slemmestad are shallower, but they show a faunal composition similar to Hvaler. Species common in Slemmestad but barely found in Hvaler 1 are *Littorina littorea, Rissoa membranacea* and *Varicorbula gibba*. These differences are explained by the depositional environment. *L. littorea* lives on rocky shores (Hayward & Ryland, 2017) and *R. membranacea* occurs mostly on sheltered coast shallower than 10 m (Warén, 1996). *V. gibba* a tolerant species thriving low oxygen concentrations (Brenko, 2006; Holmes, 2006), which is an advantage for living in the oxygen depleted inner fjord, and is still common in the Oslo fjord. Besides some differences caused by local factors, the inner and outer fjord show similar records, so neither shallower communities do show clear effect of the HTM.

5. Conclusion

The Upper Tapes banks as described by Brøgger et al. (1900) are dated between at least 7,800 and 5,000 yr BP, corresponding to the Atlantic period. The banks were assumed by Brøgger to be beach deposits but probably have a depositional depth of several tens of meters. The division of the bank stages is reconsidered, but correspondence analysis shows that the faunal composition is corresponding to this division. Nevertheless, dating the deposits is crucial for investigating the sedimentological and ecological development during the mid and late Holocene.

The study of the mollusc assemblages in the Oslo fjord shows that most species occurring in the Atlantic period are still living in the region. A species that disappeared is *Steromphala umbilicalis*. It has withdrawn to more southern waters and can be considered as a Lusitanian species. *Polititapes aureus* and *Gari depressa* appear for the first time in the region during deposition in the Upper Tapes banks. In the Upper and Lower Tapes banks they have been regularly found at several localities. Nowadays these species are barely found in the region and are mainly observed in the Lusitanian zone. This appearance and subsequent decrease of thermophilous species could indicate a response to the HTM. However, the signal is not unambiguous because also cold species like *Tectura virginea* and *Hiatella arctica* have decreased in abundance. Therefore, there is no clear evidence that the Oslo fjord hosted more thermophilic species during the Holocene Thermal Maximum compared to the current mollusc assemblage.

Recommendations for further research

The different stages, defined by Brøgger et al. (1900), are likely to be largely right. There are some remarkable features, such as the fact that the Lower Tapes banks show more similarities with the Upper Oyster banks than the Upper Tapes banks. Dating of some localities per cluster (Fig. 3.12) could add a better timeline to the development of the banks over time. This study links the Upper Tapes banks to the age of the HTM. In case the HTM affected the mollusc assemblage, expected is a decrease of thermophilous species in the subsequence Lower Tapes banks. However, Brøgger et al. (1900) reported an increase instead. Therefore investigation of the Lower Upper banks is needed. Some old localities need to be reinvestigated systematically in order to compare the deposits with the others. This involves obtaining more quantitative data of old and new localities. Ideally, these deposits show stratigraphic layers. Whereas this study compared the faunal composition of some specific Atlantic deposits with modern fauna from a large area, future research could take a fossil assemblage and modern assemblage from the same beach or island to directly investigate changes over time, without the need to consider large differences in depositional environment.

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Appendix

Taxonomy list

- Mollusca
  - Gastropoda
    - Caenogastropoda
      - Cerithiidae
        - *Bittium reticulatum* (da Costa, 1778)
      - Triphoridae
        - *Marshallora adversa* (Montagu, 1803)
    - Cephalaspidea
      - Retusidae
        - *Retusa truncatula* (Bruguière, 1792)
    - Lepetellida
      - Fissurellidae
        - *Emarginula fissura* (Linnaeus, 1758)
    - Littorinimorpha
      - Aporrhaidae
        - *Aporrhais pespelecani*
      - Littorinidae
        - *Lacuna parva* (da Costa, 1778)
        - *Littorina littorea* (Linnaeus, 1758)
        - *Littorina saxatalis* (Olivi, 1792)
      - Naticidae
        - *Euspira montagui* (Forbes, 1838)
      - Rissoidae
        - *Alvania* (Risso, 1826)
        - *Onoba semicostata* (Montagu, 1803)
        - *Rissoa parva* (da Costa, 1778)
        - *Rissoa membranacea* (J. Adams, 1800)
    - Lottidae
        - *Tectura virginea* (Müller, 1776)
    - Neogastropoda
      - Mangeliidae
        - *Mangelia costata* (Pennant, 1777)
      - Muricidae
        - *Boreotrophon truncatus* (Strøm, 1768)
      - Nassariinae
        - *Tritia reticulata* (Linnaeus, 1758)
      - Raphitomidae
        - *Leufroyia leufroyi* (Michaud, 1828)
      - Trochidae
        - *Steromphala umbilicalis* (da Costa, 1778)
  - Bivalvia

    - Adapedonta
      - Hiatellidae
        - *Hiatella arctica* (Linnaeus, 1767)
    - Arcida
      - Arcidae
        - *Tetrarca tetragona* (Poli, 1795)

Cardiida
    Cardiidae
        Parvicardium (Monterosato, 1884)
    Laevicardiinae
        Laevicardium crassum (Gmelin, 1791)
    Psammobiidae
        Gari depressa
    Semelidae
        Abra alba (W. Wood, 1802)
Cartitida
    Astartidae
        Astarte elliptica (T. Brown, 1827)
        Astarte montagui (Dilwyn, 1817)
        Astarte sulcata (da Costa, 1778)
Lucinida
    Lucinidae
        Lucinoma borealis (Linnaeus, 1767)
Myida
    Corbulidae
        Varicorbula gibba (Olivi, 1792)
Mytilida
    Mytilidae
        Modiolus modiolus (Linnaeus, 1758)
        Mytilus edulis (Linnaeus, 1758)
Nuculida
    Nuculidae
        Nucula nucleus (Linnaeus, 1758)
Ostreida
    Ostreidae
        Ostrea edulis (Linnaeus, 1758)
Pectinida
    Pectinidae
        Mimachlamys varia (Linnaeus, 1758)
        Pseudamussium peslutrae (Linnaeus, 1771)
Venerida
    Arcticidae
        Arctica islandica (Linnaeus, 1767)
    Veneridae
        Timoclea ovata (Pennant, 1777)
        Polititapes aureus (Gmelin, 1791)

Taxonomic notes

Most specimens have enough distinguishable characteristics to identify them down to species level. Species of which occurrence is remarkable and/or showing ambiguous characteristics are discussed in these taxonomic notes.

Rissoa parva

PMO 236.625 and PMO 236.610 (plate 2) are difficult to identify, and although they have a different appearance they are assumed to be the same species, *Rissoa parva. R. parva* can have various shell morphologies. The two basic forms both have an oval-conical shape and often has an angulate peripheral side of the aperture, but the whorls can be of the ribbed type or the smooth variation. Previously, some studies divided these into different species, the ribbed type and smooth variant are now both classified as *Rissoa parva* (Hayward & Ryland, 2017). The morphology of the ribs is dependent on environmental conditions, and populations contain both shell morphologies. The ribbed type is more often found in sheltered areas, and the smooth variation is more common along exposed shores (Wigham, 1975). This is in agreement with the findings in this study. The smooth variant is only found in Hvaler, and not in the more sheltered inner fjord.

Specimens found in Hvaler do not have very dark colours, possibly due to deterioration, but many of them do have a brown glow. There are also many that are dull white. *R. Parva* occur in different colours, varying from white to brown.

The Rissoidae family does contain many similar gastropods. The specimens found in this study all lack ornamentation in the uppermost whorls, which rules out the possibility for it to be *Pussilina sarsii*, where the ornamentation continues in the upper whorls. A species similar to this study's specimens is *Pussilina inconspicua*, but the ribs are finer than with *R. parva* (Hayward & Ryland, 2017). Because most specimens found in this study have coarser ribs, they are assumed to be all *R. parva*, but there is some variation within the ornamentation so there is a possibility that some of the specimens actually are *P. inconspicua*. *P. inconspicua* is nowadays observed in the Oslo fjord (OBIS, Artsdatabanken), but it is not mentioned by Brøgger et al. (1900).

Barleeia unifasciata is a gastropod in the same superfamily Rissooidea and has a smooth surface, similar to *R. parva interrupta*. It has up to five whorls, and the apex is blunt. It has a small umbilical groove and the aperture is oval-shaped. It can have either brown or red bands, or is totally red, white or crimson (Hayward & Ryland, 2017). Those characteristics are also seen in the specimens of this study. However, the body whorl left of the inner lip is slightly more concave than in Barleeia unifasciata and aperture is not angulate peripherally.

Another family with similar species is Hydrobiidae. One example is *Peringia ulvae*, a species observed regularly by Brøgger et al. (1900)[6] in other localities. However, the whorls of *P. ulvae* are more slender then *R. parva*.

Regarding these taxonomic notes, PMO 236.625 and PMO 236.610 are assumed to be the same species. Nevertheless, they are referred to as *Rissoa Parva* and *Rissoa parva interrupta* because given the fact that they reflect different depositional environments, distinguishing them can give additional useful information.

Steromphala umbilicalis

Steromphala umbilicalis (plate 2) is a gastropod found in Hvaler and Slemmestad, but not mentioned at the other localities described by Brøgger et al. (1900). They did identify *Steromphala cineraria*[7] on multiple localities, and possibly we are talking about the same species here. Distinguishing those two species is important because *S. umbilicalis* is a more southern species, which does currently not live in the north sea, Skagerrak or Oslo fjord , while *S. cineraria* does still live along the southern coast of Norway. The shells have a similar cyrtoconoid shape and same pattern, but *S. cineraria* has higher spire than *S. umbilicalis*. This high spire is not observed in specimens found in Hvaler and Slemmestad. Specimens from Kirkøy, found by Brøgger, preserved at the Natural History Museum in Oslo do show the same characteristics as the newly found specimens in Hvaler and Slemmestad, so are likely to be the same species. A factor impeding identification is morphological variation within the species. In more exposed waters, the gastropod has a larger relative aperture size and a shorter broader shell (Frid & Fordham, 1994). Taking this trend into account, the shells found in Hvaler should have a higher spire than the shells from Slemmestad. The newly found samples do not show this. Because there is no evidence for the species to contain specimens with high spires, this study appoint PMO 236.622 as *Steromphala umbilicalis.*

Lacuna parva

Lacuna parva is still living in the Oslo fjord, but not found at the other Tapes localities. The species can vary in morphology dependent on geography. The specimens in this study (PMO 236.652, plate 8) show similar characteristics to the selected morph from Jutland, Denmark, studied by (Jørgensen, 2002). In this variation the umbilical groove is not pronounced as much as in some other variations. Studying the drawings of the type collection by Brøgger et al. (1900), no similar species had been found. Possibly *L. parva* was not present at the other localities, but perhaps it had different morphology closer to the inner fjord.

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[6] Brøgger et al. (1900) used the synonym *Hydrobia ulvae*

[7] Brøgger et al. (1900) used the synonym *Gibulla cineraria*

Plates

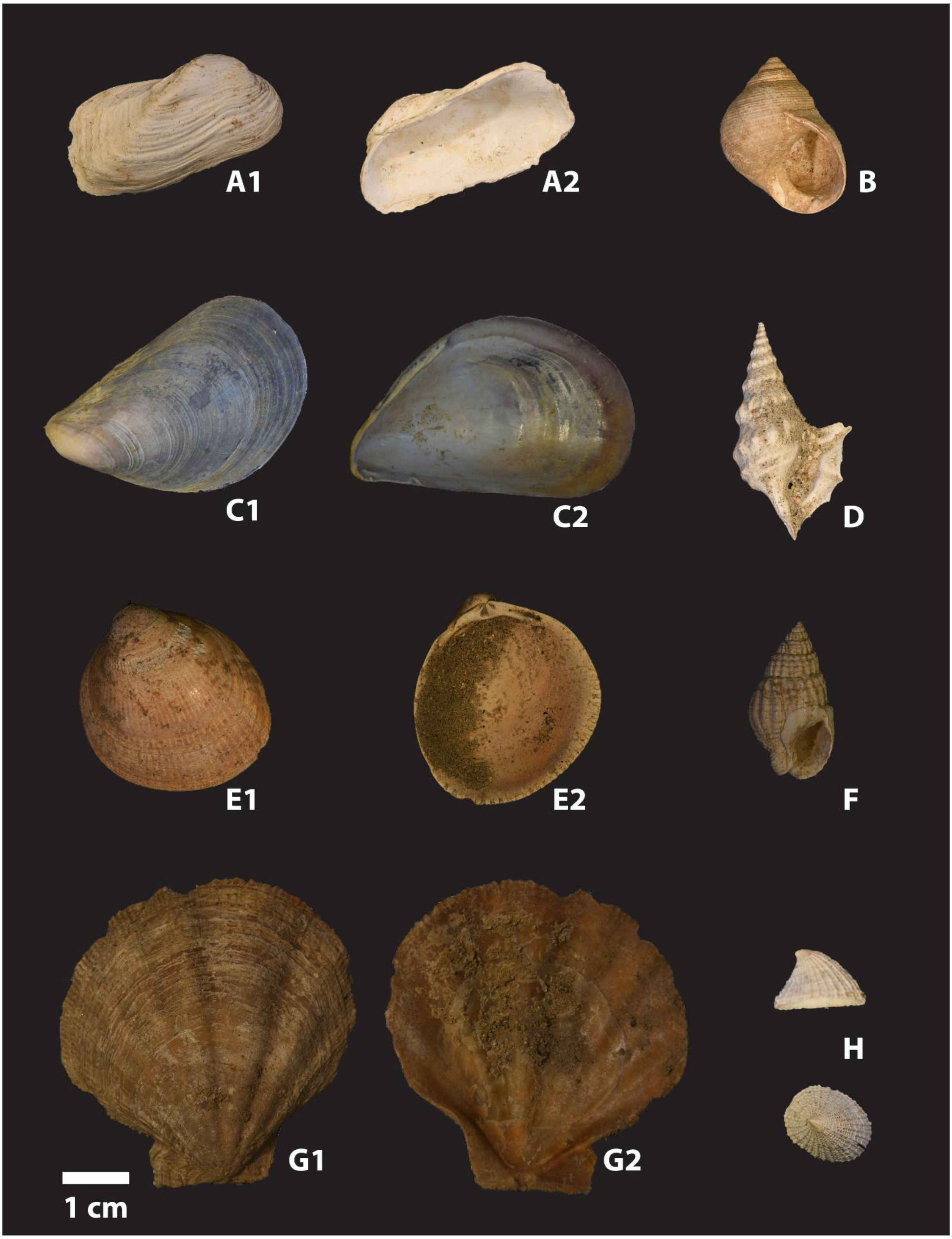

Plate 1 A Hiatella arctica (PMO 236.629); B Littorina littorea (PMO236.635); C Mytilus edulis (PMO 236.630); D Aporrhais pespelecani (PMO 236.627); E Laevicardium crassum (PMO 236.624); F Tritia reticulata (PMO 236.644); G Pseudamussium peslutrae (PMO 236.626); H Emarginula fissura (PMO 236.642)

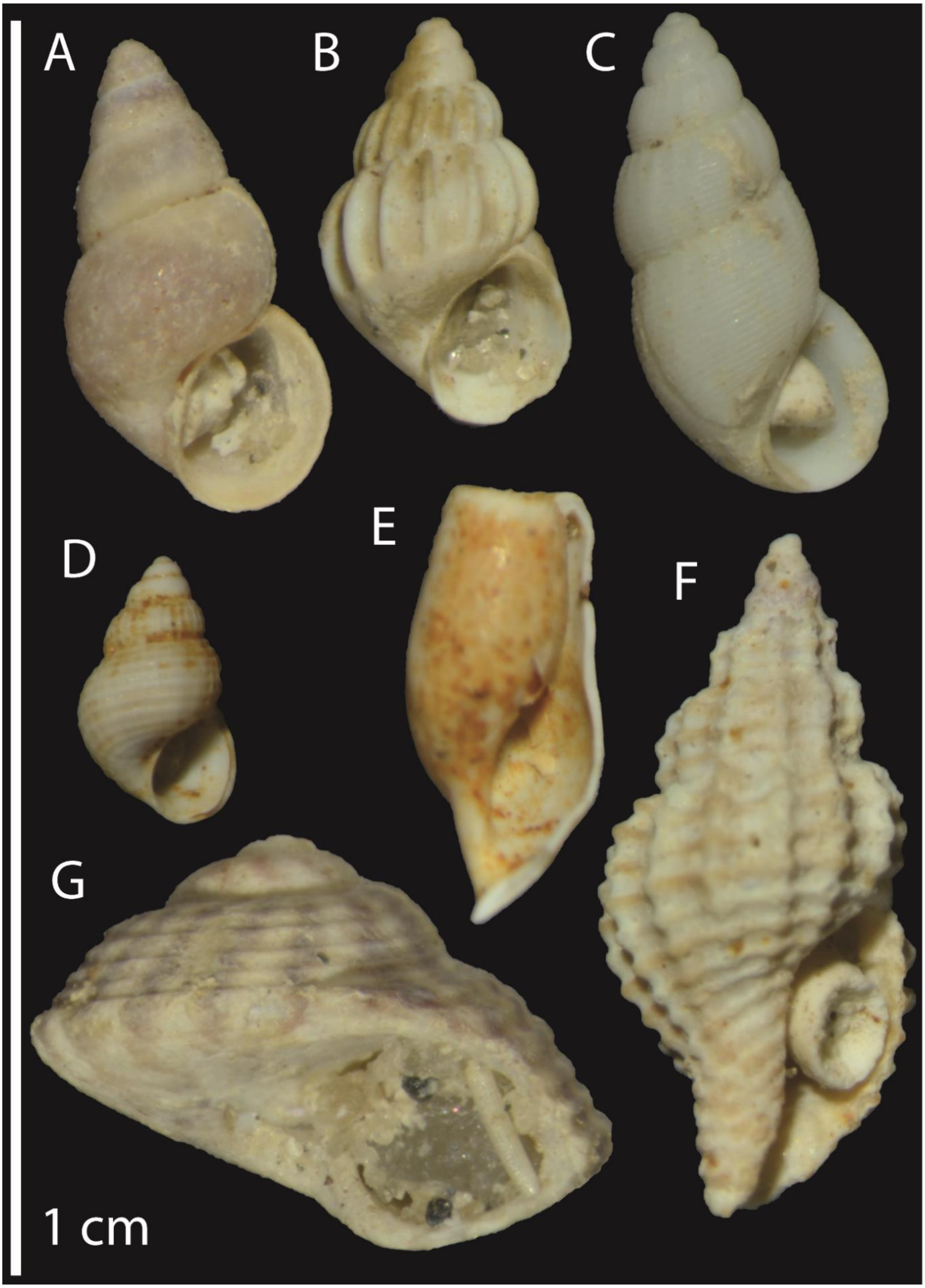

Plate 2 A Rissoa parva (var. interrupta) (PMO 236.625); Rissoa Parva (PMO 236.610); C Onoba Semicostata (PMO 236.637); D Alvania sp. (PMO 236.619); E Retusa Truncatula (PMO 236.612); F Leufroyia Leufroyi (PMO 236.646); G Steromphala umbilicalis (PMO 236.622).

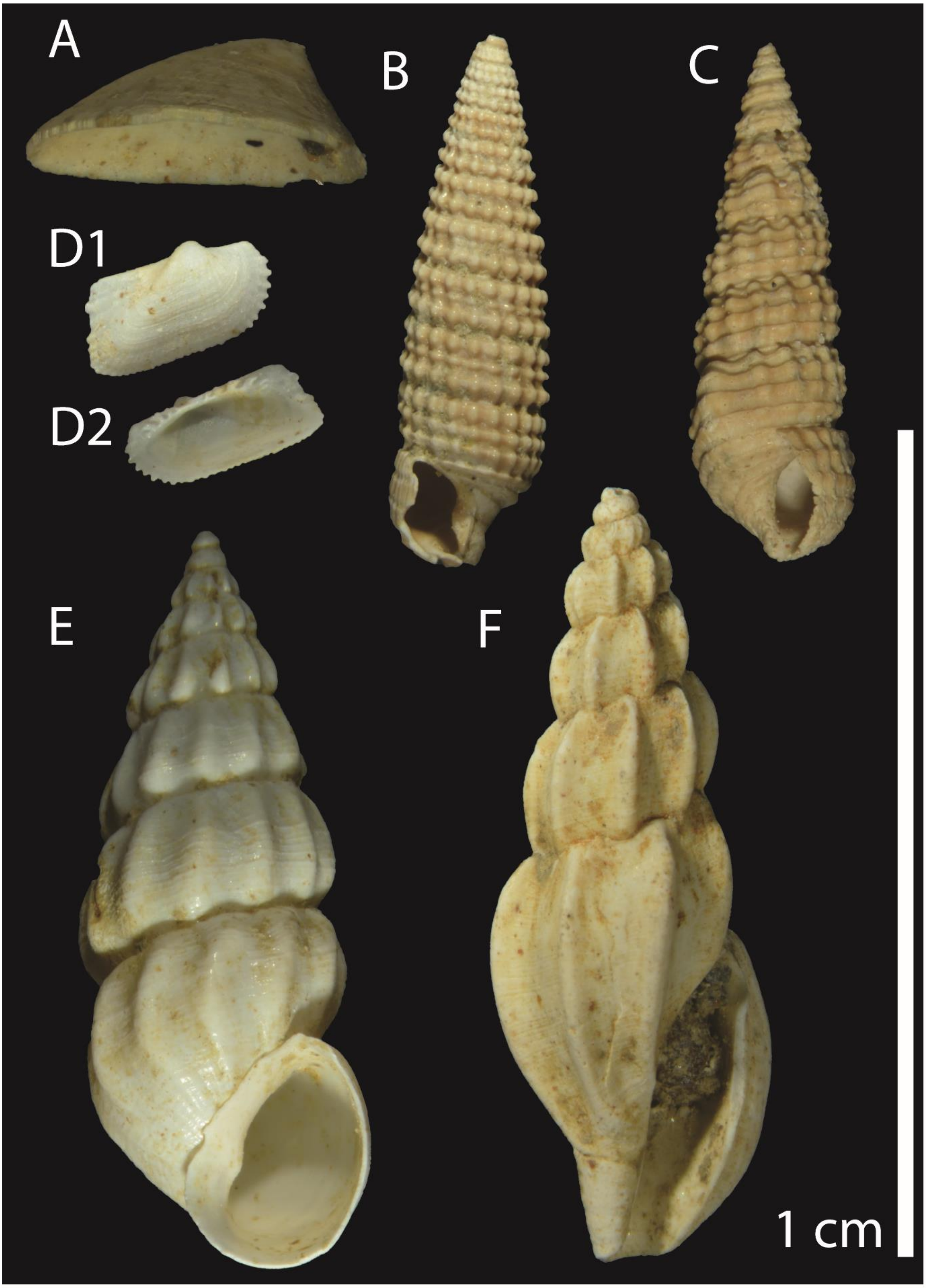

Plate 3 A Tectura virginea (PMO 236.631); B Marshallora adversa (PMO 236.613); C Bittium reticulatum (PMO 236.623); D Tetrarca tetragona (PMO 236.645); E Rissoa membranacea (PMO 236.614); F Mangelia costata (PMO 236.636)

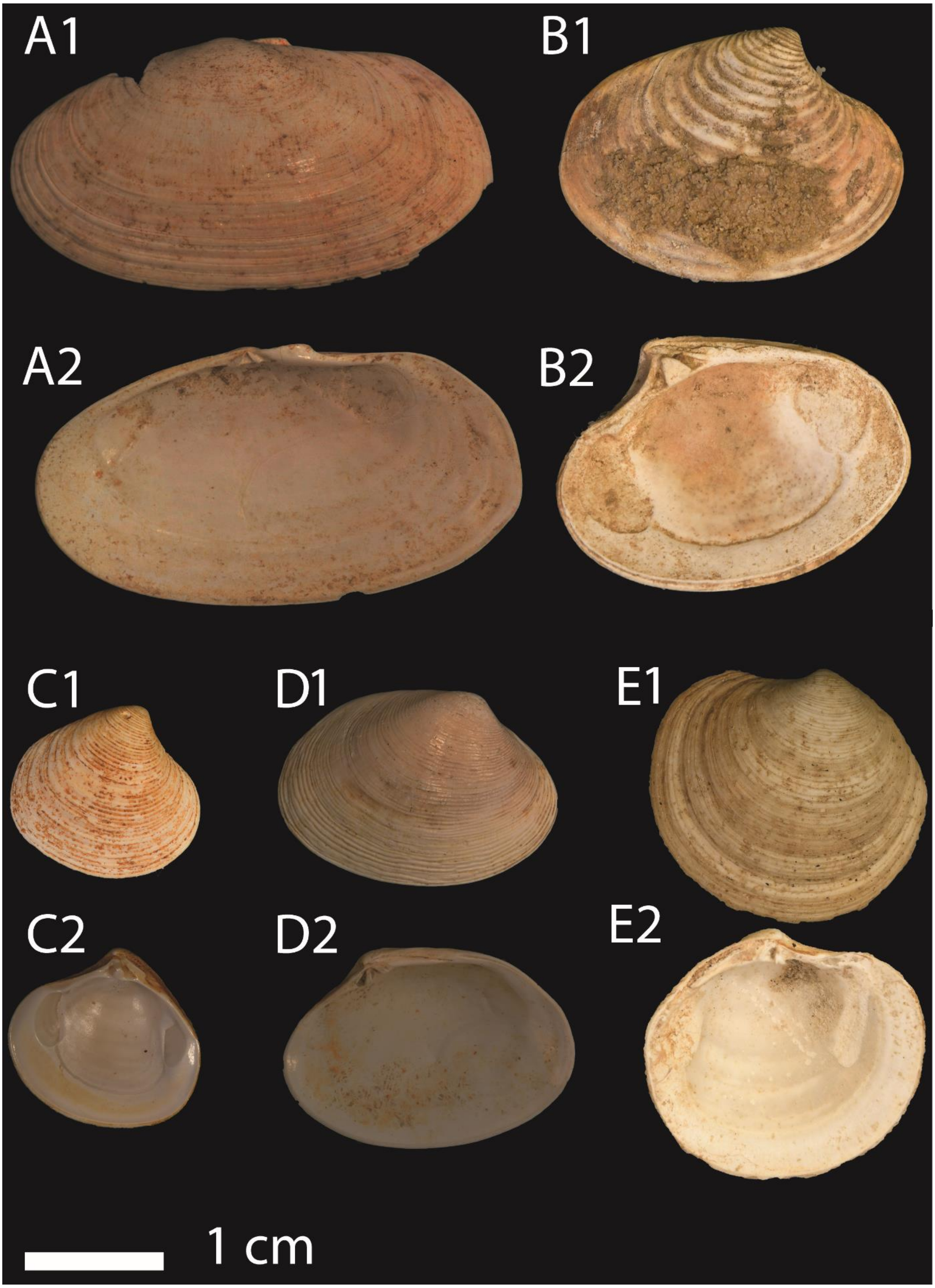

Plate 4 A Gari depressa (PMO 236.641); B Astarte elliptica (PMO 236.621); C Astarte montagui (PMO 236.617); D Politapes aureus (PMO 236.639); E Lucinoma borealis (PMO 236.632)

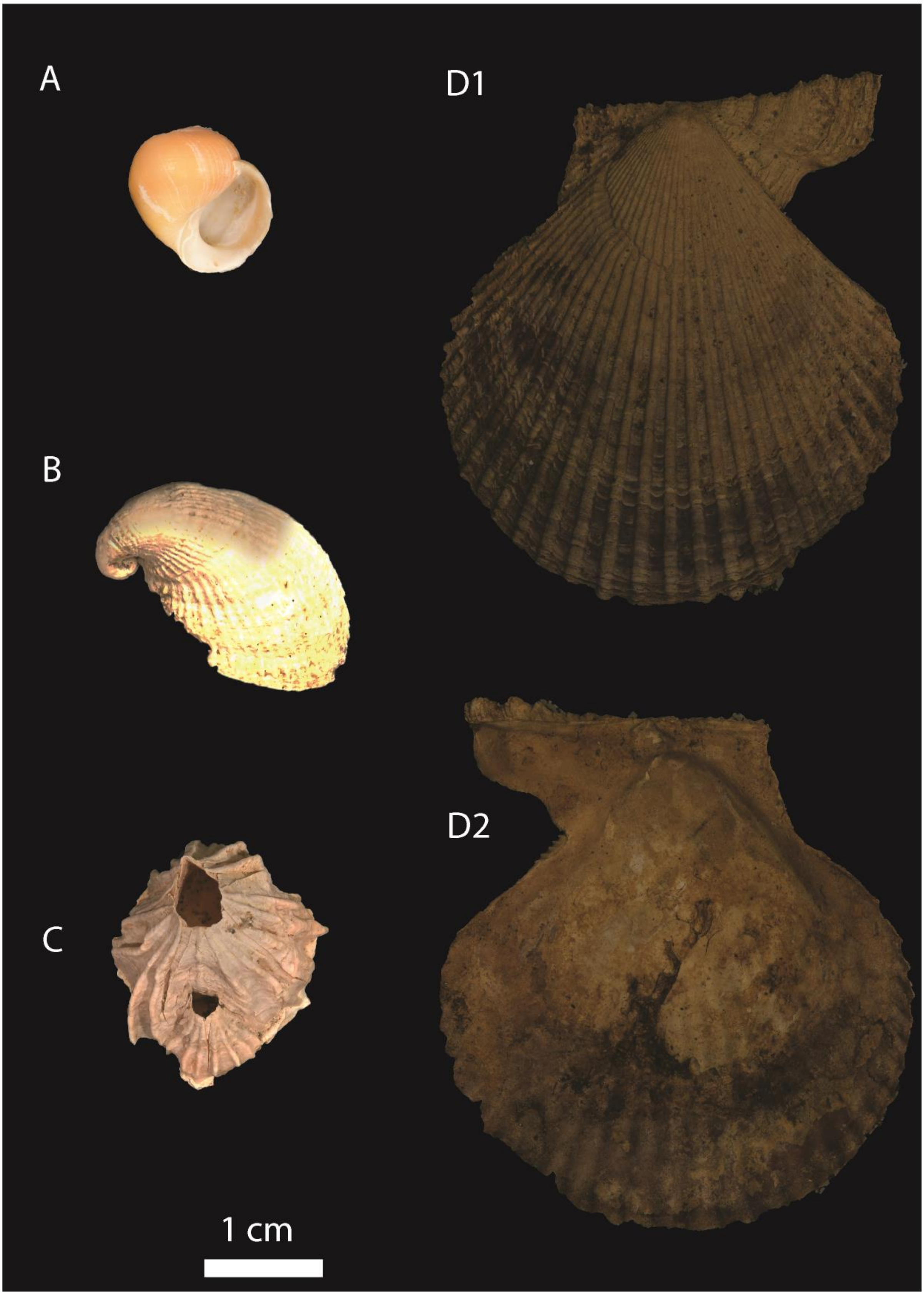

Plate 5 A Gastropod sp. *(PMO 236.634); B Glossus humanus (PMO 236.618); C Balanus* sp. *(PMO 236.640); D Mimachlamys varia (PMO 236.633)*

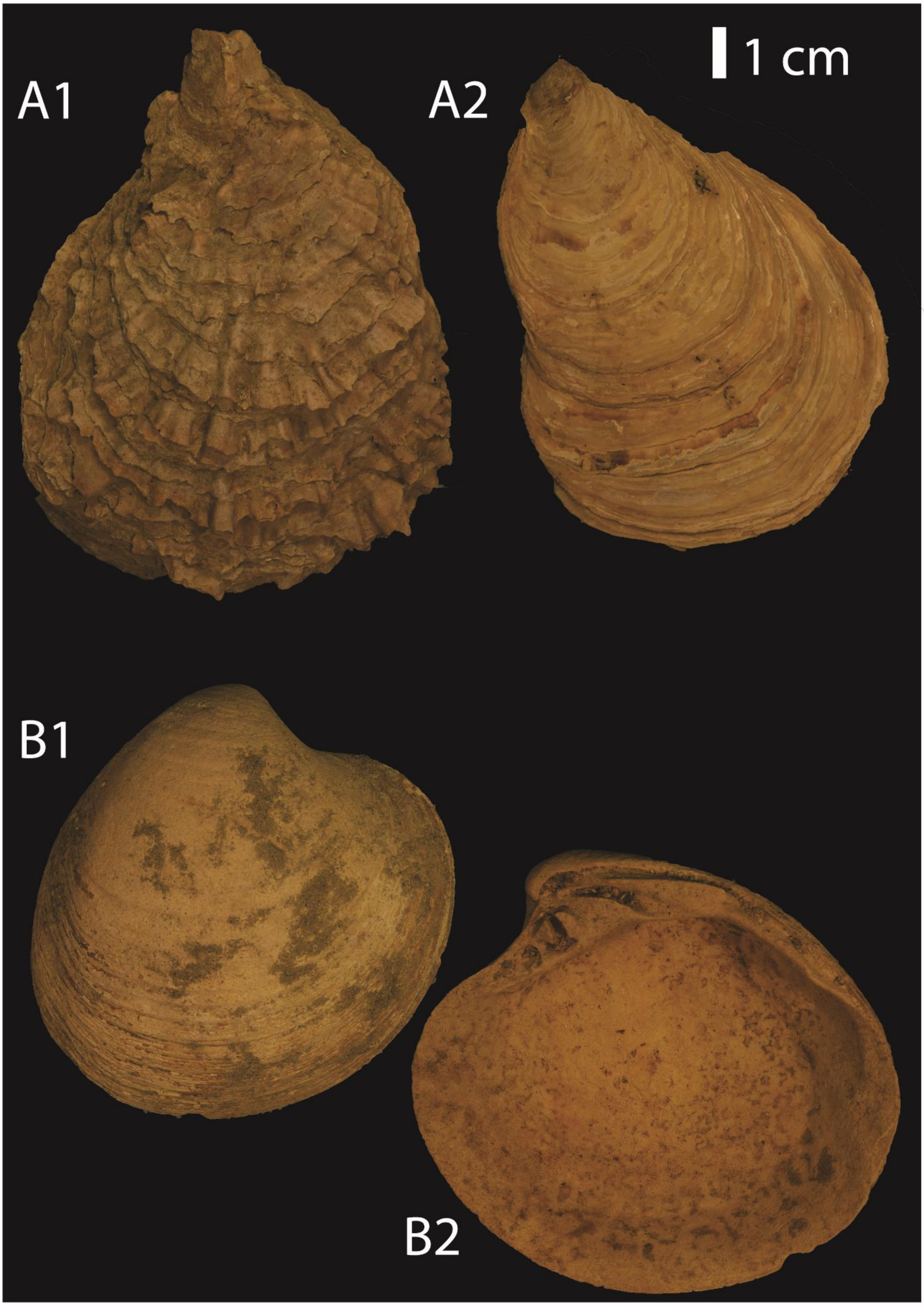

Plate 6 A Ostrea edulis (PMO 236.611); B Arctica islandica (PMO 236.615)

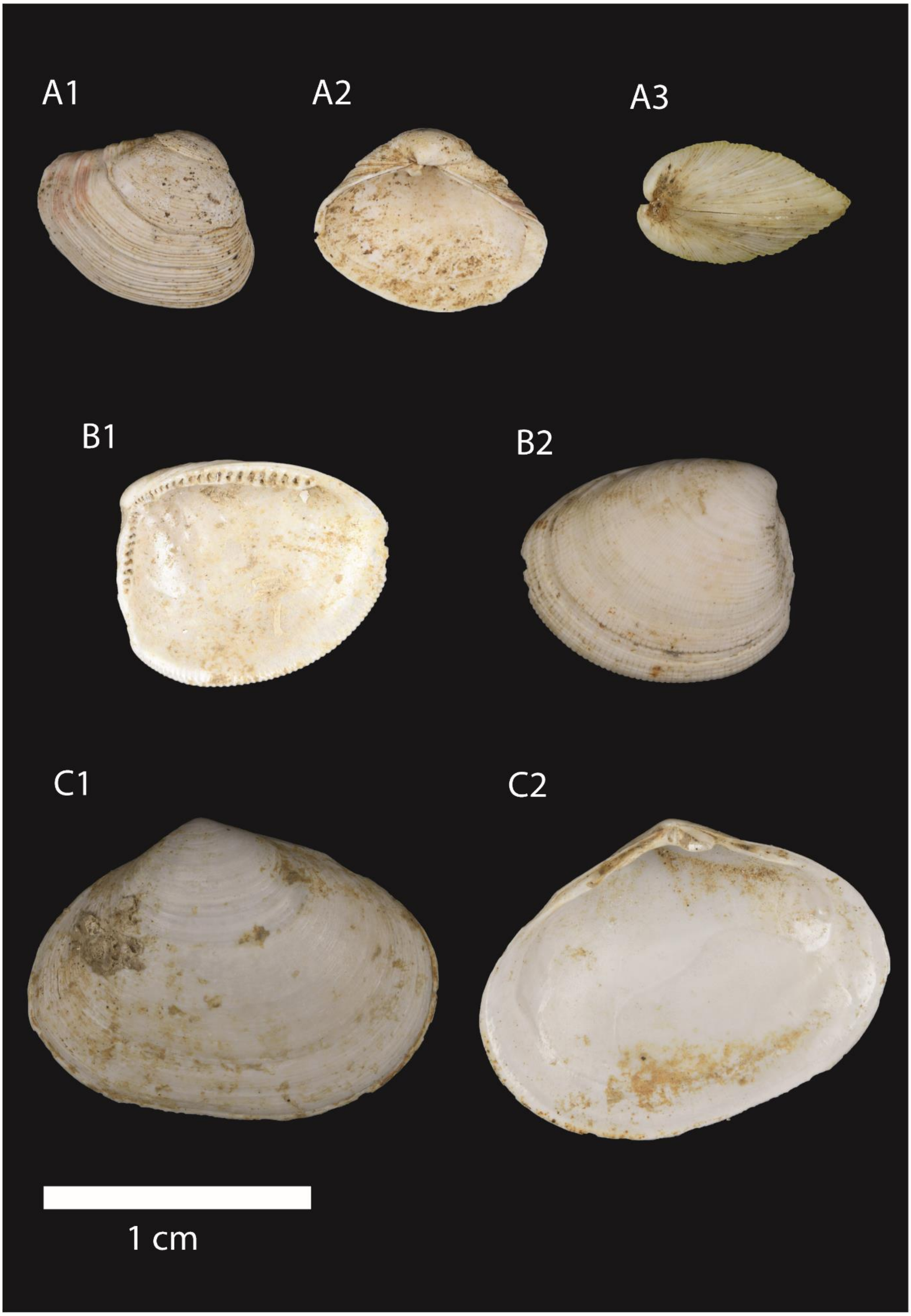

Plate 7 A Varicorbula gibba (PMO 236.638) ; B Nucula nucleus (PMO 236.647) ; C Abra alba (PMO 236.653)

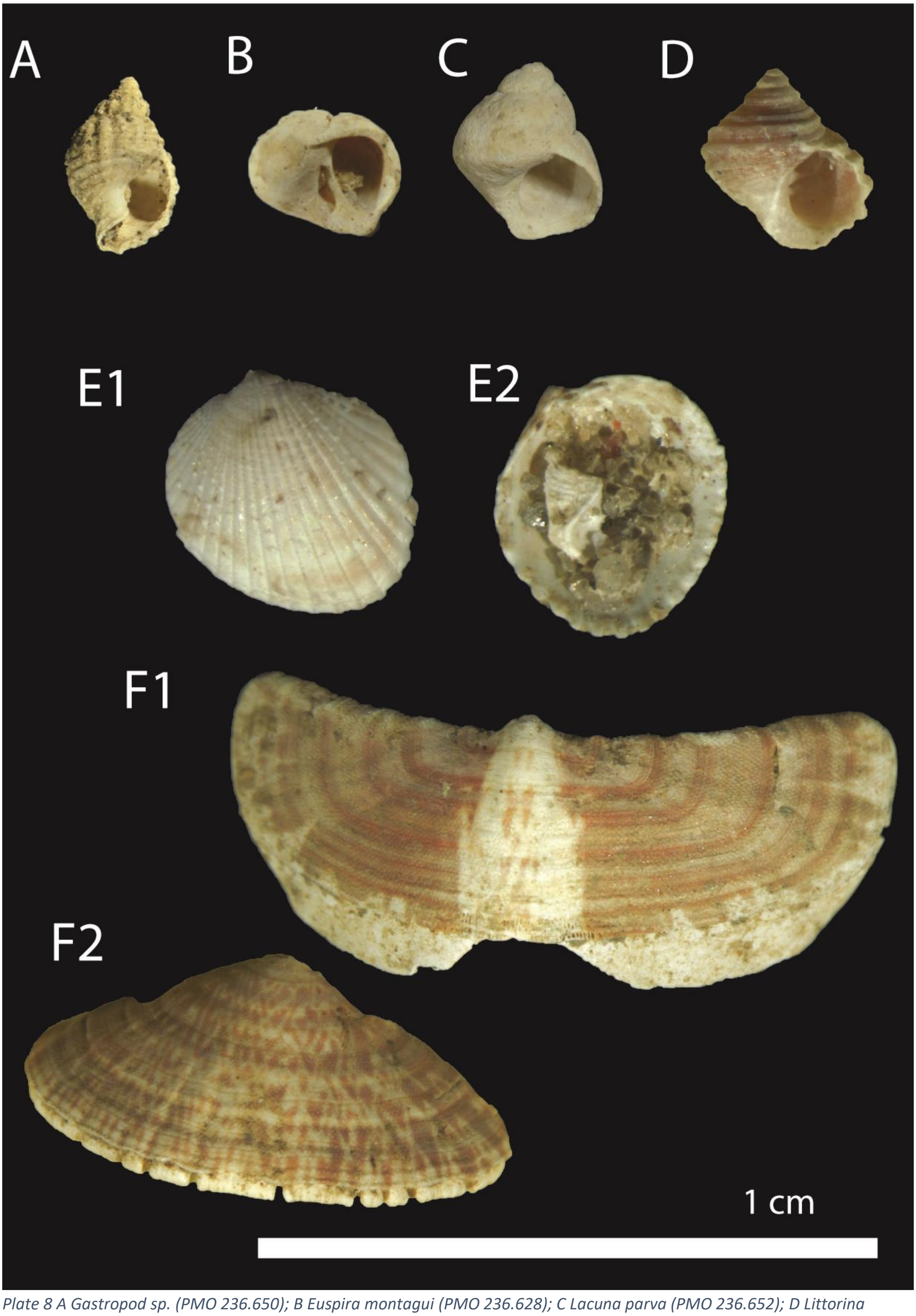

Plate 8 A Gastropod sp. (PMO 236.650); B Euspira montagui (PMO 236.628); C Lacuna parva (PMO 236.652); D Littorina saxatalis (PMO 236.651); Parvicardium sp. (PMO 236.643); Lepidopleura sp. (PMO 236.649)

PMO Numbers	**Species**	**Location**	**Synonym Brøgger et al. (1900)**
PMO 236.610	*Rissoa parva*	Søndre Sandøy, Hvaler 1	*Rissoa parva, R. interrupta*
PMO 236.611	*Ostrea edulis*	Heimansåsen, Slemmestad	
PMO 236.612	*Retusa truncatula*	Heimansåsen, Slemmestad	*Utriculus truncatulus*
PMO 236.613	*Marshallora adversa*	Heimansåsen, Slemmestad	
PMO 236.614	*Rissoa membranacea*	Heimansåsen, Slemmestad	
PMO 236.615	*Arctica islandica*	Søndre Sandøy, Hvaler 1	*Cyprina islandica*
PMO 236.616	*Timoclea ovata*	Søndre Sandøy, Hvaler 1	
PMO 236.617	*Astarte montagui*	Søndre Sandøy, Hvaler 1	
PMO 236.618	*Glossus humanus*	Heimansåsen, Slemmestad	
PMO 236.619	*Alvania* sp.	Søndre Sandøy, Hvaler 1	
PMO 236.620	Corals	Søndre Sandøy, Hvaler 1	
PMO 236.621	*Astarte elliptcia*	Høyboveien, Malmøya	
PMO 236.622	*Steromphala umbilicalis*	Søndre Sandøy, Hvaler 1	
PMO 236.623	*Bittium reticulatum*	Søndre Sandøy, Hvaler 1	
PMO 236.624	*Laevicardium crassum*	Søndre Sandøy, Hvaler 1	
PMO 236.625	*Rissoa parva (interrupta)*	Søndre Sandøy, Hvaler 1	
PMO 236.626	*Pseudamussium peslutrae*	Høyboveien, Malmøya	*Pecten septemradiatus*
PMO 236.627	*Aporrhais pespelecani*	Søndre Sandøy, Hvaler 1	
PMO 236.628	*Euspira montagui*	Søndre Sandøy, Hvaler 1	*Lunatia montagui*
PMO 236.629	*Hiatella arctica*	Heimansåsen, Slemmestad	*Saxicava arctica*
PMO 236.630	*Mytilus edulis*	Heimansåsen, Slemmestad	
PMO 236.631	*Tectura virginea*	Søndre Sandøy, Hvaler 1	
PMO 236.632	*Lucinoma borealis*	Søndre Sandøy, Hvaler 1	*Lucina borealis*
PMO 236.633	*Mimachlamys varia*	Søndre Sandøy, Hvaler 4	*Pecten varius*
PMO 236.634	*Gastropod* sp.	Heimansåsen, Slemmestad	
PMO 236.635	*Littorina littorea*	Høyboveien, Malmøya	
PMO 236.636	*Mangelia costata*	Heimansåsen, Slemmestad	
PMO 236.637	*Onoba semicostata*	Søndre Sandøy, Hvaler 1	*Onoba striata*
PMO 236.638	*Varicorbula gibba*	Heimansåsen, Slemmestad	*Corbula gibba*
PMO 236.639	*Polititapes aureus*	Heimansåsen, Slemmestad	*Tapes aureus*
PMO 236.640	*Balanus sp.*	Heimansåsen, Slemmestad	
PMO 236.641	*Gari depressa*	Søndre Sandøy, Hvaler 1	
PMO 236.642	*Emarginula fissura*	Heimansåsen, Slemmestad	
PMO 236.643	*Parvicardium sp.*	Søndre Sandøy, Hvaler 1	
PMO 236.644	*Tritia reticulata*	Søndre Sandøy, Hvaler 1	*Nassa incrassata*
PMO 236.645	*Tetrarca tetragona*	Søndre Sandøy, Hvaler 4	*Arca tetragona*
PMO 236.646	*Leufroyia leufroyi*	Søndre Sandøy. Hvaler 1	
PMO 236.647	*Nucula nucleus*	Heimansåsen, Slemmestad	
PMO 236.648	*Modiolus modiolus*	Søndre Sandøy, Hvaler 1	*Mytilus modiolus*
PMO 236.649	*Lepidopleurida* sp.	Heimansåsen, Slemmestad	
PMO 236.650	*Gastropod* sp.	Søndre Sandøy, Hvaler 4	
PMO 236.651	*Littorina saxatilis*	Søndre Sandøy. Hvaler 1	*Littorina rudis*
PMO 236.652	*Lacuna parva*	Søndre Sandøy. Hvaler 1	
PMO 236.653	*Abra alba*	Heimansåsen, Slemmestad	

Previously described localities by Brøgger et al., 1900

Locality	Old name/notes	Longitude	Latitude	Elevation (m.a.s.l.)	Bank stage
Mellemdahl Gård, Nesodden	Mellemdal	59.74339	10.69582	55	Upper Oyster banks
Gjerpen, Drammen	Skalstad	59.70355	10.23952	56	Upper Oyster banks
Barkås	Exact location not found, Holmestrand,	59.48532	10.3115	55	Upper Oyster banks
Karlsrud, Våle		59.44954	10.20476	42	Upper Oyster banks
Goksjø (33m)		59.17582	10.1458	33	Upper Oyster banks
Heistad, Brevik		59.07488	9.68831	37	Upper Oyster banks
Ørstveitmyra, Porsgrunn	Versviksmyren	59.1012	9.66835	33	Upper Oyster banks
Versvikdammen (35 m.o.h)		59.10203	9.65989	35	Upper Oyster banks
Løveid, Nordsjøen, Skien		59.19715	9.58768	39	Upper Oyster banks
Berg, Kragerø		58.88345	9.38296	37	Upper Oyster banks
Høvik, bærum		59.89409	10.58204	40	Upper Tapes Banks
Nedenfor Ravnsborg		59.86031	10.4759	40	Upper Tapes Banks
Hofstadveien		59.84893	10.47418	35	Upper Tapes Banks
Barholmen	Bergholmen, Drøbak	59.67727	10.58712	31	Upper Tapes Banks
Kirkeøy, Hvaler	Kirkeø	59.05737	11.0317	16	Upper Tapes Banks
Brandstorp, hunnebotn		59.20845	11.08223	35	Upper Tapes Banks
Gunnarstorp, skjebergkilen	Kårhonæs, Gunnarstorp	59.20507	11.13755	30	Upper Tapes Banks
Ekeberg løkke		59.89366	10.76036	44	Upper Tapes Banks
Lunde		59.08393	9.69603	24	Upper Tapes Banks
Rydningen		59.06517	9.69163	28	Upper Tapes Banks
Jette gryderne		59.05319	9.6911	20	Upper Tapes Banks
Isdammen		59.06129	9.68363	15	Upper Tapes Banks
Askum, Sweden		58.41718	11.32875	30	Upper Tapes Banks
Engervannet, Sandvika	Engervand	59.89628	10.5324	6	Lower Tapes banks
Bergholmen	Håøya and Bergholmen, Drøbak	59.67709	10.58709	31	Lower Tapes banks
Barkevik maskinehuset Hallen	location uncertain	59.01518	9.85431	23	Lower Tapes banks
Barkevik Ishuset	exaxt location not found	59.00488	9.85471	11	Lower Tapes banks
Ødegårdsbukta	Ødegårdsbugten	59.01279	9.85132	6	Lower Tapes banks
Ødegården		59.01767	9.84806	4	Lower Tapes banks
Vierviken	location not found	59.01387	9.85191	3	Lower Tapes banks
Hallem	location uncertain	59.01485	9.85379	1	Lower Tapes banks
Dåvøen	Dåvøya	59.01521	9.84374	1	Lower Tapes banks
Smeiholmen		59.06346	9.7329	9	Lower Tapes banks
Trosvik		59.05481	9.68847	3	Lower Tapes banks