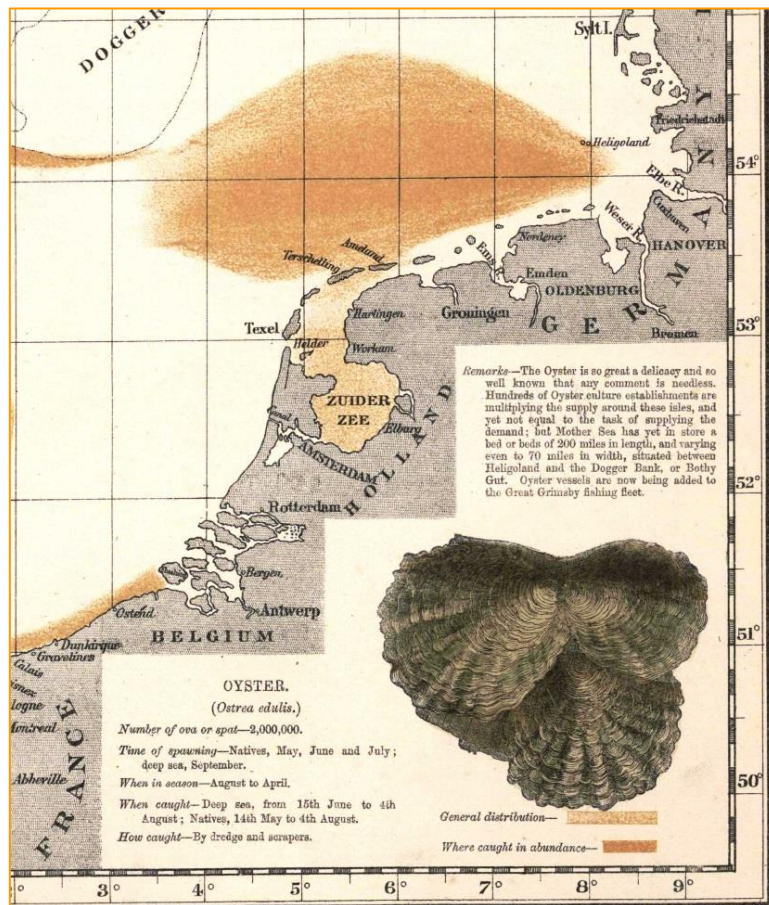


Jens Gercken and Andreas Schmidt

Current Status of the European Oyster (*Ostrea edulis*) and Possibilities for Restoration in the German North Sea

2014



Cover image: Excerpt from the map on the distribution of the oyster in the North Sea from Olsen's "Piscatorial Atlas" (1883)

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“The preservation of oyster beds is as much the role of the State as preservation of forests.”

(K. A. Möbius, 1877)

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1 Introduction and Definition of Objectives

The native European flat oyster (*Ostrea edulis* L.) represented an important source of food for coastal communities in Europe, even during prehistoric times. This is confirmed by excavations of Stone and Iron Age kitchen middens, which contained large quantities of oyster shells. In the remains of Viking settlements, oyster shells were also frequently found (NEUDECKER, 1990a; YONGE, 1960).

The historical importance of the oyster¹ is also demonstrated by the fact that the Romans cultivated oysters to satisfy the huge demand for this delicacy (YONGE, 1960). In the 12th and 13th centuries, the oyster fishery, in addition to the herring catch, were considered the first commercially operated fisheries (LOTZE, 2007). In later centuries, the harvest of oysters was often regulated through licensing some steps were also taken towards population management to conserve the coveted "oyster" resource.

Nevertheless, throughout the past centuries oyster stocks have been exploited much too intensively. Through the continuous removal of adult oysters, recruitment was greatly weakened. In addition, ever more efficient harvesting techniques allowed the takes to increase and simultaneously led to the destruction of biogenic hard structures. All this consequently led to a Europe-wide decline of the fishery during the course of the 19th century. The oyster fisheries in the North Sea were also affected. Accompanying the loss of oyster beds in the North and East Frisian Wadden Sea as well as the offshore areas of the German Bight were the losses of the biogenic reef habitats and their associated species-rich fauna and flora.

Because of their high ecological value, locations where today only the remains of mostly degraded oyster stocks or beds exist are now the focus of European conservation efforts. Thus, according to the Habitats Directive for the protected habitat type "reef", a favorable conservation status is to be preserved or restored. This requirement has led to the current situation, whereby population support measures take not only the concerns of oyster harvesting, but also conservation concerns into account. In the context of cooperation within the Oslo-Paris Commission (OSPAR), the oyster was identified as an especially endangered species and as a creator of habitat, and measures for its protection in their area of distribution were agreed to (OSPAR, 2008).

In view of the ecosystem-related benefits of oyster reefs, especially the high biodiversity of species found in reefs, the Federal Agency for Nature Conservation (BfN) is engaged with the possibilities of a potential reintroduction of native European oysters in the North Sea. The BfN commissioned the Institute for Applied Ecology Research GmbH (IfAÖ) to conduct a feasibility study on this type of restoration.

This report presents the results of this feasibility study. It focuses on different points of view that are to be considered as background information and as a basis for decision making with regard to restoration of the oyster.

¹For reasons of linguistic simplification, the word "oyster" always refers to the European oyster. If other species are meant, they will be designated as such.

2 Historical Distribution and Fisheries of *Ostrea edulis*

2.1 Decline of oyster fisheries in Europe

The natural range of the European oyster stretches along the coastline from the center of Norway to the Iberian Peninsula and south to Morocco. In addition, localized remnant populations of the oyster are found in the Mediterranean Sea, mainly along the northern coast and in the western part of the Black Sea to the Crimea peninsula.

Until about 1,000 years ago, the millennia-long use of the oyster as a food source was limited mainly to the collection of easily accessible oysters in the lower intertidal zone by individuals for their own needs. Only with the development of commercial harvesting and the marketing of the oyster as a commodity were oyster stocks increasingly exploited. The following examples outline the decline of the oyster in Europe.

In **France**, the region of Brittany and particularly the estuaries and sheltered coastline along the Bay of Biscay were originally very rich in natural oyster beds. The intensive exploitation of these banks led to a collapse in the stocks earlier than elsewhere in Europe. For example, during peak periods at the beginning of the 19th century, in excess of 100 million oysters were harvested. By the middle of the century, the stocks had been decimated to the point that commercial fishing was no longer profitable. Consequently, in 1858 in a region of Brittany, out of 23 formerly harvested beds, 18 had been completely destroyed (YONGE, 1960).

With the elimination of the use of wild stocks, measures were taken which represent the beginning of the French oyster culture. Inspired by Italian (most likely previously developed by the Romans) culture methods, "oyster parks" sprung up along the coast. Breeding oysters were applied together with large quantities of shells as an attachment substrate for the larvae. In addition, branch bundles (fascines), and later roof tiles, served as spat collectors. The vulnerable spat were then nurtured for a short duration in special wire-covered boxes to protect them from predators. With these measures, the basis for the later, successful French oyster culture was established (YONGE, 1960).

As it still is nowadays, the Arcachon Basin south of Bordeaux was already a center of shellfish farming in the 19th century. According to MÖBIUS (1877), the local topographic conditions are comparable with those in the Wadden Sea.

In **Great Britain**, where large natural oyster stocks were also located, overharvesting usually occurred until commercial exploitation was no longer profitable. In 1864, over 700 million oysters were consumed in London alone. One hundred years later, the national oyster production amounted to only 3 million. MÖBIUS (1877) mentioned that in Cornwall (Falmouth) originally 700 fishermen pursued a regulated oyster fishery. Even after the abolition of conservation measures, the number of fishermen was reduced within 10 years to just 40, due to reduced catch rates.

Another example of how oyster populations, not only in the UK, have been exploited for centuries to extirpation, is the fishing industry in Firth of Forth on Scotland's east coast. The local oyster beds once covered 166 km² and were maintained into the 19th century as the most important oyster fishery of Scotland. The oysters from the Firth of Forth were already being consumed in the 13th century, and widespread commercial exploitation of the stock began in the 16th century. For centuries, the oysters were harvested not only for the domestic market, but also exported to other countries for such purposes as refreshing the local, degraded stocks. Thus, large amounts of juvenile oysters were exported to replenish oyster beds in England and the Netherlands at the beginning of the 19th century. At the same time, the export of market oysters also increased. The unrestrained exploitation led to a 99% decrease in the harvest over the course of 60 years and by 1890 the fishery was no longer

profitable. Today, the oyster is considered to be extirpated from the Firth of Forth (THURSTAN et al., 2013; UNIVERSITY MARINE BIOLOGICAL STATION MILFORD, 2007).

Unlike France, no attempt was made in the UK to compensate fishery losses by the development of an intensive, state-supported oyster aquaculture program.

The French method of regeneration of oyster stocks, i.e., the distribution of shells, breeding oysters and spat collectors became widespread practice in Europe. For example, this method was used in the late 1930s to regenerate *O. edulis* stock in the Oosterschelde (KORRINGA, 1952). This method, however, also contributed to the depletion of donor stocks and ultimately couldn't prevent the collapse of the much-too-intensely managed fisheries (YONGE, 1960). Even today, it is definitely still recommended to regenerate remnant populations through the distribution of non-resident oysters (KENNEDY & ROBERTS, 1999; LAING et al., 2005).

The decline of oyster populations in Europe took place in the 19th century in many places during about the same period. With the development of machine-driven vessels which could employ larger harvesting gear, exploitation of stocks became even more intense than it already was (NEUDECKER, 1990a). Adding to this was a faster and more efficient transportation by railway, which led to an increased inland market for oysters.

Overall, it can be observed that the main reason for the loss of formerly widespread oyster populations was centuries-long overharvesting. In general, a stock was exploited to the point that the fishery became no longer economically viable. With the consequential loss of reef structures, intensified effects of other stressors, such as sedimentation, diseases and invasive species were observed.

2.2 Historical distribution of *O. edulis* in the German North Sea and reasons for its extirpation

The historical distribution of the oyster in today's German North Sea extended to the North and East Frisian Wadden Sea, Helgoland Oyster Bed and offshore oyster grounds of the German Bight.

The ***oyster fishery in North Friesland*** was the most important in the Wadden Sea; consequently the most information is available on this fishery. The local oyster beds had already been mentioned for the first time in 1241 (LOTZE, 2005). In 1587, the Danish King Frederick II placed the (at the time belonging to Denmark) oyster beds under royal prerogative. Regulated harvesting was only allowed for licensed tenants. The "Holstein oysters" were especially sought after due to their good quality. They were exported to the Danish court in Copenhagen and the Russian court in St. Petersburg, among other places (HAGMEIER & KÄNDLER, 1927; NEUDECKER, 1990a; NEUDECKER, 1990b).

Over time, oyster harvesting became an important economic factor that also led to violent clashes between Danish and German fishermen. Traditionally, the harvesting was done with one-masted sailing cutters that utilized iron drag nets (dredges) as harvesting gear (Figure 1). This method was probably used beginning in the 13th century (SEAMAN & RUTH, 1997).

Since the end of the 17th century, the destruction of oyster beds due to overfishing and the occurrence of ice winters was a constant problem, so that, for example, in 1695 ten banks between Rømø and Foehr were considered ruined. At times, the harvesting was interrupted by bans for several years. This was the case in 1703 - 1706 and 1882 - 1891. Additionally, unusually cold winters repeatedly caused huge stock losses. On several occasions, restock-

ing with oysters from France, the Netherlands and the UK was carried out to refresh the depleted stocks. The steady decline of oyster beds was also not prevented by these measures (NEUDECKER, 1990a).

During the 19th century, oyster stocks continued to steadily decrease. Even the stocking of oysters on impoverished banks could not stop the decline of oyster fisheries in the Wadden Sea, primarily caused by overharvesting. From 1894 to 1930, large amounts of spat from the Netherlands, France and Norway were distributed in the North Frisian Wadden Sea, in order to continue to permit commercial fishing. This was also achieved to some extent. On the other hand, the imported oysters turned out not to be as strong as their native peers. Some were also not able to reproduce themselves. The harvest industry at Sylt and Foehr was supported by the import of spat from the Netherlands until the 1930s (SEAMAN & RUTH, 1997).

In 1868, the Kiel zoologist Karl Möbius was commissioned by the Prussian government and the angling club to examine whether the standard oyster culture methods used in France and England could be applied to the situation in the German Wadden Sea, in order to revive the degraded North Frisian "fiscal oyster beds", fisheries regulated by state authorities. The results of his investigation were published in Möbius' classic writing: "The Oyster and the Oyster Industry" (MÖBIUS, 1877). The contents of the following paragraphs are derived from this publication.

Off the west coast of Schleswig-Holstein, 47 oyster beds of very different sizes were located over an area of 74x22 km. The largest bed was over 3 km long. Their preferred locations were the edges of narrow channels to deeper locations where coarse sand, stones and shells occurred (Figure 2). The beds were always located in the sublittoral zone at a maximum depth of 6 to 9 m. At low tide, they were covered by at least two meters of water. Only during the spring tide and upon the occurrence of easterly winds did the outlying areas become dry. Viewed in their entirety, the combined area of the oyster beds is very low, occupying less than 1% of the always-submersed tidal flats (Figure 3).

On the Schleswig-Holstein beds, 14 cutters operated with oyster nets and a dredge, the underside of which consisted of iron rings. In terms of shape, texture and taste the oysters displayed local differences. The largest number and best quality of oysters occurred on the banks on the east side of Sylt and near Amrum and Foehr.

The term "oyster bed" is often associated with a densely populated area of oysters. Möbius makes it clear that this was not the case: "At no point in the Wadden Sea are the oysters on rocky ground. Their best substrates are old oyster shells and shells of other mussels. Most occur in singles; oysters growing together in clumps are rare. The common opinion that they were rooted on the seabed is also false. On the better Schleswig-Holstein beds, the trawl must have a bed-area of 1 to 3 square meters, and often an even larger area, to harvest even a single full-grown oyster." To be considered along with this statement from Möbius is that the oyster beds found by him generally exhibited signs of very long overharvesting and were in a depleted state. This state probably differed significantly from a no-longer-existing, undisturbed "reference state".

MÖBIUS (1877) also dealt intensively with the environmental requirements of *O. edulis*. He asked himself the question, why oyster beds occurred only on such a small area of the Wadden Sea. He came to the conclusion that neither fertility nor salinity or temperature could be limiting factors. Sufficient food also appeared to be available. The only natural obstacle is the unfavorable properties of the sediment in most parts of the Wadden Sea. Despite tidal exchange, only a few areas are free of silt and always covered with water, making them suitable for the settlement of larvae. In all these areas, there were already oyster beds.

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For Möbius, it followed that the German oyster industry could only exploit the existing beds. He didn't consider the installation of new beds as being possible, at best, the area of individual beds could be expanded on hard ground from the spreading of oyster shells and from cultch of other mussel species.

The warning from Möbius that sustainable fisheries must take into account the biological requirements of the oyster, was not suppressed in fisheries policy. The methods of overexploitation with the use of paddle steamers in 1910, which could employ up to 6 dredges at the same time, were, however, ultimately more effective (NEUDECKER, 1990a).

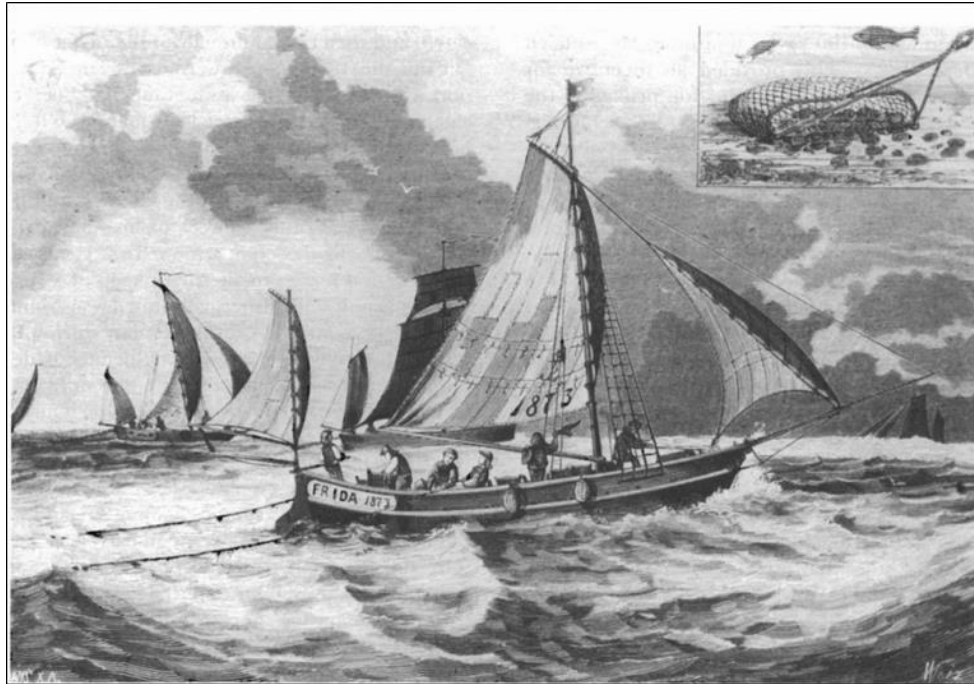


Figure 1: Typical oyster cutter that was utilized in the North Frisian Wadden Sea. The above right photo inset depicts an oyster drag net (dredge) (SEAMAN & RUTH, 1997).

In 1924-25, HAGMEIER and KÄNDLER (1927) studied the state of all 51 fiscal oyster beds located between Rømø and the Hallig Hooge / Süderau under Prussian administration. They released their findings in the extensive publication "New research in the North Frisian Wadden Sea and on the fiscal oyster beds". It contains the results of ecological and fisheries biology studies of oyster beds as well as data on their history. In the following sections, selected contents of this publication are summarized.

HAGMEIER and KÄNDLER differentiated three types of oyster beds on the basis of relative bed position. The *channel beds* were located on the hard substrate of tidal channels (large tidal creeks), which adjoin the sea channels. The strong tidal current provided them with large amounts of food, but also made settlement of oyster larvae difficult. Because of the greater water depths, the beds were not exposed to any danger of frost (Figure 2). The authors suggest that larval production of channel beds were of benefit to the flat and inland beds. For the *flat beds* located further toward the interior of the Wadden Sea, the water exchange was less than the channel beds. Because of the lower depths they were exposed to greater temperature fluctuations and possibly to frost damage. The oysters grew more slowly here than on the channel beds. They were also affected by strong fouling, competition from mussels and to some degree by siltation. Yet, under favorable conditions rich breeding took place

here, because larval drifting was reduced in comparison to the channel beds. The flat beds had a comparatively large surface area. The lowest surface area of all fiscal oyster beds was exhibited by the *internal beds* of the inner Wadden Sea. They lay on the slopes of the smaller, narrow channels. Due to the low water movement, larvae could settle well here. In the summer, high temperatures could occur, and in winter and there was a risk of frost, as in the flat bds. The oysters here suffered from a strong fouling and competition of mussels.

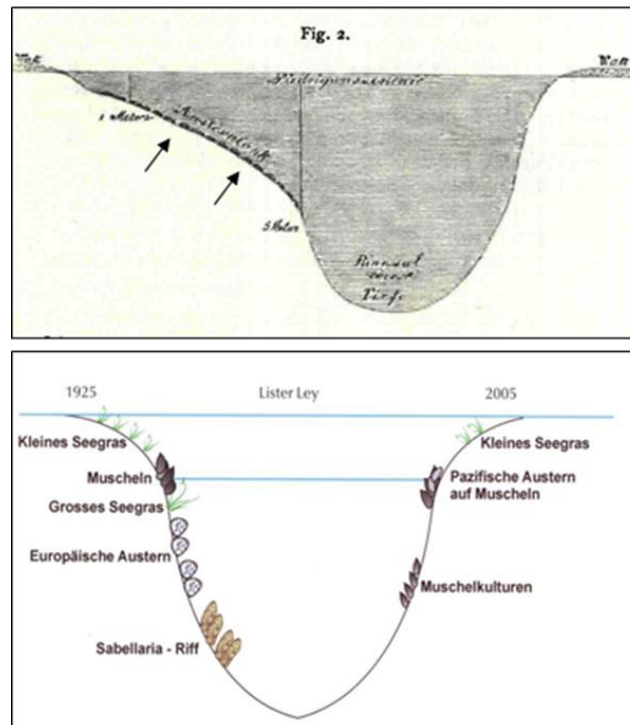


Figure 2: Top: cross section of a large tidal channel. The arrows show the location of oyster beds. (Figure from MÖBIUS, 1877). Bottom: Colonizing of a large channel at the time of the oyster beds (left) and present day (right) (acc. to REISE, 2005).

For the harvesting of the oyster beds with the paddle steamer “Gelbstern” (Yellow Star), HAGMEIER and KÄNDLER (1927) used a classic oyster iron (dredge), just as it was used by Möbius (1877) in his studies (Figures 4 and 5). It was shown that the beds were mostly in a completely decimated state. The few oysters which were present were heavily overgrown with epifauna, as well as shells and stones, so that there was hardly any substrate available for larval resettlement. Young oysters were virtually absent.

Based on relatively complete harvest statistics for the years 1891-1910 and 1910-1923, the income and stock densities for regularly harvested beds of the various bed positions were estimated. As a result, the average annual yields per hectare of bed area for the internal beds for the periods 1891-1910 and 1910-1923 were estimated at 806 and 848 oysters, respectively, for the channel beds at 283 and 503 oysters, respectively, and for the flat beds at 226 and 186 oysters, respectively.

The authors also describe the decline of the fiscal oyster industry based on historical documents. For large stock fluctuations that occur over long-term periods, especially the depletion of oyster beds, probable factors are identified by the authors: 1: persistent absence of optimal hydrographic factors; 2: damage caused by overabundance of food- and space-

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competitors; 3: catastrophic damage by winter frost or storm effects; 4: damage caused by overharvesting; 5: degeneration in the oyster itself. In relation to the decline of the fiscal oyster beds, the authors draw primary attention to factors 1 to 3.

Based on their investigation, HAGMEIER and KÄNDLER (1927) summarized that given the degradation, no improvement in the condition of the fiscal beds was to be expected without future human intervention. An economically-viable oyster fishery would not be possible given the conditions they encountered. They recommended transforming the utilization of natural beds into a Dutch-style oyster culture. For this, however, the beds needed to be cleaned of pests and spat needed to be imported from abroad. All this, ultimately, would be associated with high costs.

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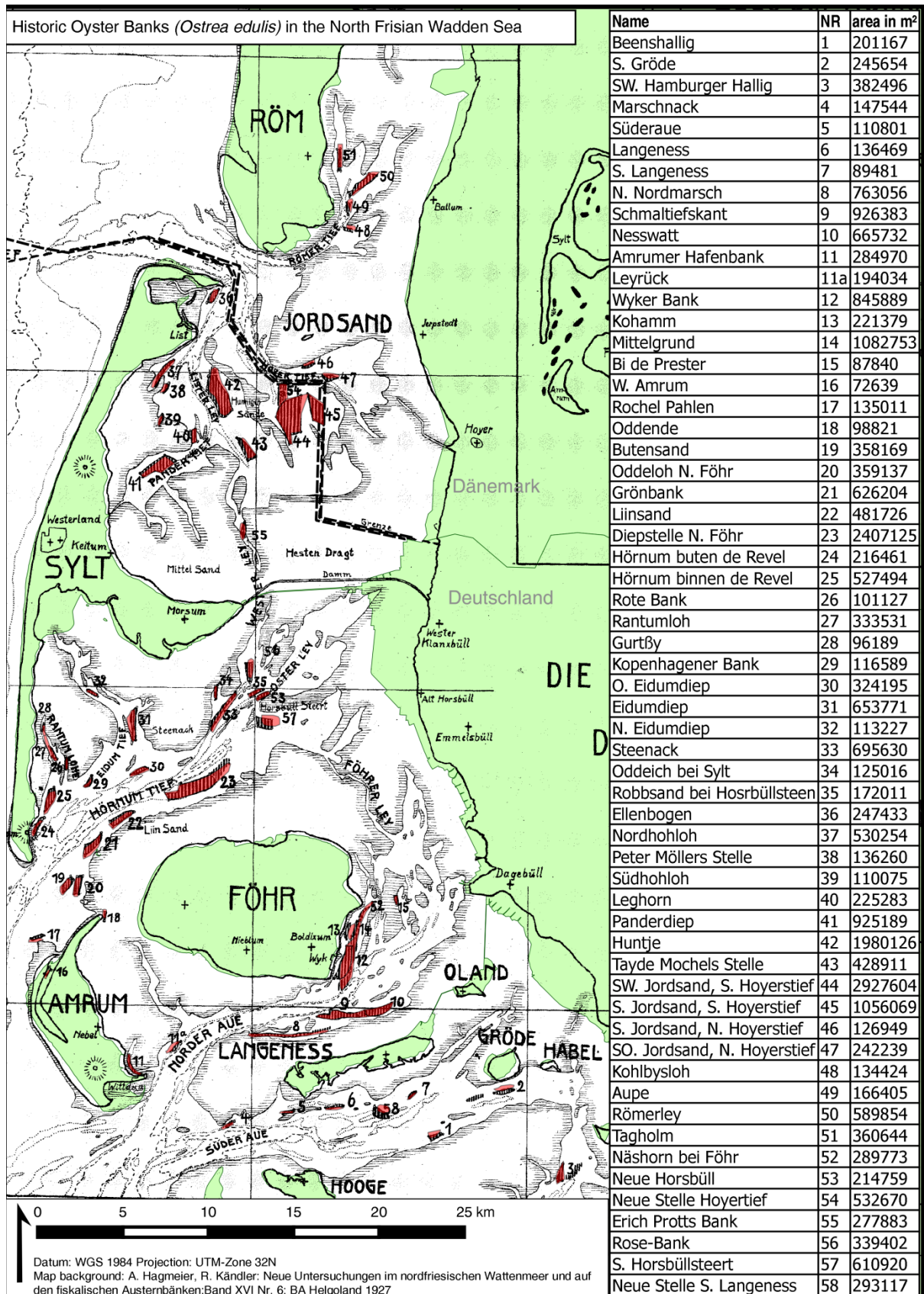


Figure 3: Historical distribution of oyster beds in the North Frisian Wadden Sea according to Hagmeier and Kändler (1927). The locations of the oyster beds (red) are based on surveys conducted from 1878 to 1890.

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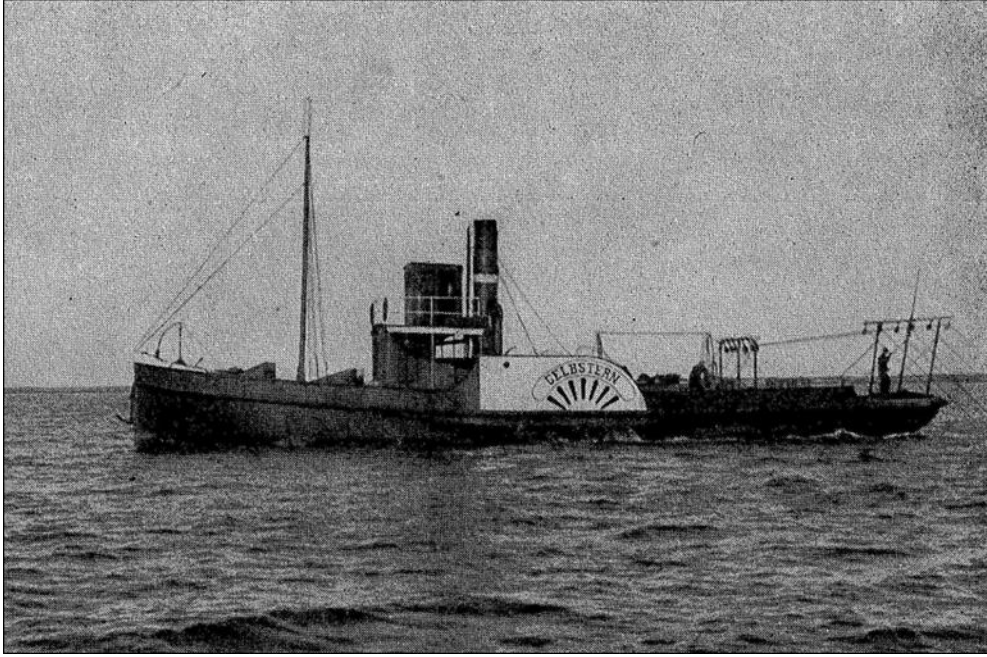


Figure 4: The 1911-christened oyster steamer “Gelbstern” (Yellow Star) during harvesting (Photo from HAGMEIER & KÄNDLER, 1927).

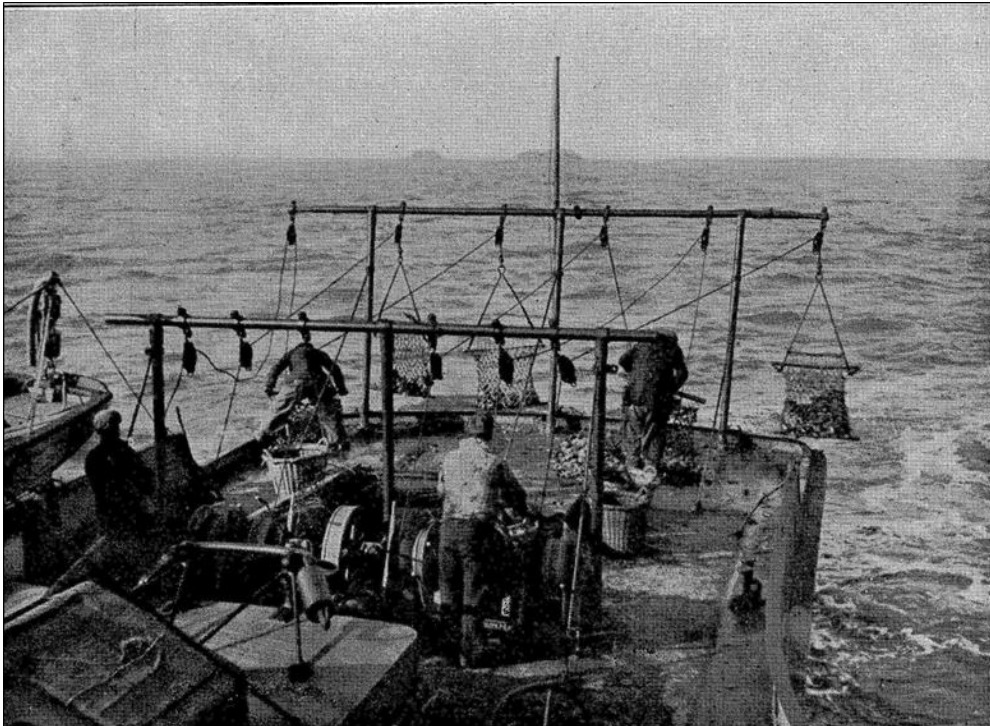


Figure 5: Harvesting oysters with the steamer “Gelbstern” (Yellow Star). The six dredges on the rear of the boat have been hauled up (Photo from HAGMEIER & KÄNDLER, 1927).

Oyster harvesting in the **East Frisian Wadden Sea** was economically less significant than that in North Frisia. The local oyster beds were first mentioned in 1642 in the county archives of Oldenburg. The fishery first developed at Borkum (1715) and later at Baltrum, Juist, Langeoog and Wangerooge. In 1728, the fishing rights were granted to Prince of Oldenburg. From this time there are no harvest figures; but it would likely have been more than 100,000 oysters per year. In 1740, an exceptionally hard winter damaged the oyster beds, so much so that a prohibition on harvesting was put in place until 1764. The ever-present illegal harvesting, in particular by Dutch boats, was not prevented by the prohibition. In 1772, the oyster fishery was officially awarded to a Dutch licensee and in the subsequent years to the end of the century the yield drastically decreased. Despite restocking measures in 1800 and closure of the fishery from 1816-1823, the excessively damaged stock did not recover and harvest income decreased continuously (NEUDECKER, 1990b).

As the following map depicts, the oyster beds lay along the inlets and on the mainland-side mudflats of the islands (Figure 6).

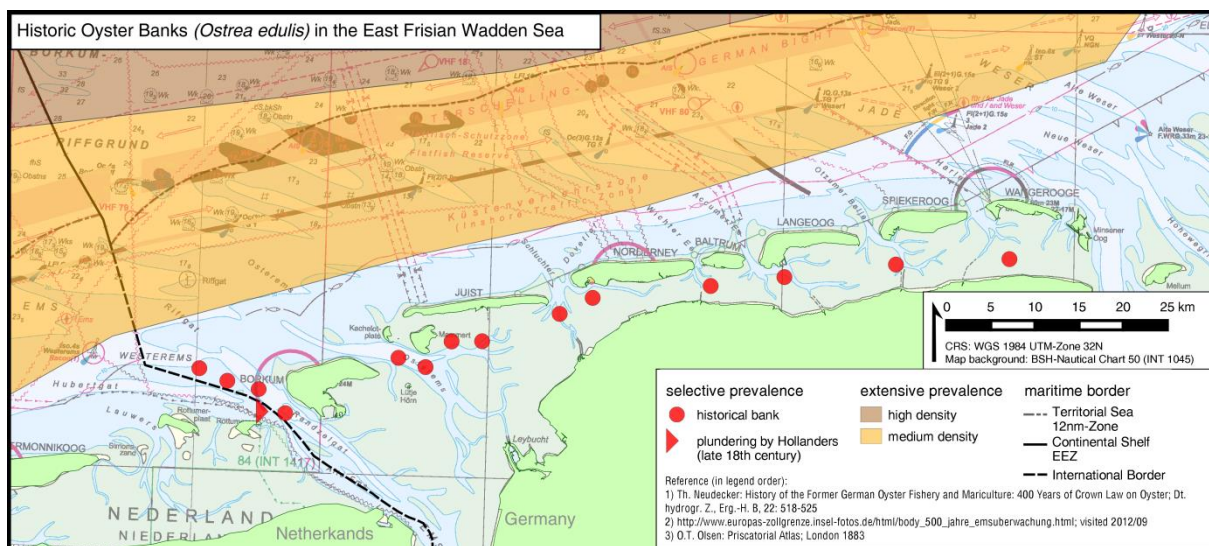


Figure 6: Historical distribution of oyster beds in the East Frisian Wadden Sea (red) (location of the beds obtained from NEUDECKER, 1990b).

The **Helgoland oyster bed** was located approximately 4 nm east-southeast of Helgoland on the northern slope of the Helgoland deep channel at a depth of 23 to 28 m. With an area of 0.8 km², it was comparatively small (BOOS et al., 2004).

For the main period of Helgoland oyster fisheries, CASPERS (1950) provides statistical harvest data, which is based on "Annual Report of the Commission for the Scientific Study of the German Seas" for the years 1873-1874 and based on records of Helgoland teacher Th. Schmidt for the years 1875-1886 (Table 1).

As can be gleaned from the harvest statistics, the oyster fishery was always only operated a few days a year. In doing so, the large mussels were harvested, while the smaller were thrown overboard. The highest yields in total numbers of oysters harvested, from 350,000 to 500,000, were achieved in the years 1875-1877. Beginning in 1878, a significant decline in yield began, resulting in the implementation of a closed season from 1879 to 1882. During the 1882-1884 harvest seasons, an intensive harvesting again took place, which again resulted in a higher harvest yields. In subsequent years, the oyster stock collapsed again. After

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1886 the use of oyster bed was leased and harvest statistics were no longer published (BOOS et al., 2004; CASPERS, 1950).

Table 1: Harvest statistics for the Helgoland oyster bed (adapted from CASPERS, 1950).

Harvest season	No. of harvest days	Total no. of boat trips	Highest daily no. of boat trips	Highest daily no. of oysters harvested	Avg. no. of oysters harvested by each boat per trip	Total no. of oysters Harvested
1872/73	5	-	-	35,000	-	160,000
1873/74	15	299	55	23,000	734	219,000
1874/75	-	-	-		-	166,600
1875/76	9	348	50	56,100	1,007	350,000
1876/77	16	515	56	58,800	775	399,000
1877/78	21	602	55	53,350	841	506,380
1878/79	9	232	50	33,500	402	93,275
1879/80	3	37	19	13,200	428	15,840
1882/83	9	312	72	36,300	565	170,190
1883/84	3	26	13	5,100	431	11,200
1884/85	1	1	1	550	550	550
1885/86	1	3	2	2,000	833	2,500

According to an estimate from the Biological Institute of Helgoland (BAH), the Helgoland oyster bed comprised about 1.5 million individuals in 1900. The stock was aging, with the majority of shells already 20 to 30 years old, while juveniles were missing. Added to this was the fact that half the oysters were attacked by the red boring sponge *Cliona ciliata*. In the period 1910-1923, the commercial fishery was discontinued. Ultimately, the stock was not able to rebound from the damage despite the interruption on the season caused by World War I (BOOS et al., 2004; CASPERS, 1950).

Overall, excessive harvesting is to blame for the collapse of Helgoland oyster population. As elsewhere also introduced here, the selective removal of the large, marketable oysters led to depletion of stocks.

Investigations by CASPERS (1950) in 1936-37 of the shellfish community in the Helgoland oyster bed showed that instead of the oyster, the nut clam *Nucula nucleus* seemed to be the dominant faunal element. Otherwise, the former species spectrum of the oyster bed was unchanged. As a comparative investigation from 2003 revealed, the faunal community documented by CASPERS no longer exists. For this condition, the intensive land-trawl fishing in the area is almost certainly responsible (BOOS et al., 2004).

The very large stocks of "**deep sea oysters**" or "**North Sea oysters**" of the southern **North Sea** were first discovered in the mid-19th century. Regarding the actual extent of the so-called, "oyster ground", no accurate data exists. According to MÖBIUS (1877), the area of the "deep-sea oysters" began as a narrow strip SE of Helgoland and then stretched as a 15 - 22 km wide strip WNW of Helgoland far to the west in the North Sea. The water depth in the area was 33-34 m.

In the "Piscatorial Atlas" published by OLSEN (1883), the range of these North Sea oysters extended from Helgoland northwest to the Dogger Bank and south along the East Frisian and Dutch island chain. As the map shows, there was also a large stock of "offshore oysters" in the English Channel (Figure 7).

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In any case, the oyster deposits in the southern North Sea were much larger than that in the Wadden Sea. Historical German fishing maps show large areas of oysters near Helgoland (oyster ground) and "oyster grounds" in the southern North Sea northwest of Helgoland to the Doggerbank. According to estimates by BERGHAIN and RUTH (2005), the oyster stock was at least 100 to 1,000 times as large as the North Frisian Wadden Sea stock, which had been documented for over 200 years. Its area is said to have amounted to approximately 21,000 km².

Just shortly after its discovery, the oyster ground in the open North Sea was not spared from harvesting. MÖBIUS (1877) writes: "Dutch and German fishermen operate here, especially in the oyster harvesting months of August, September and October, and pulling a trawl sometimes harvest around 1,000 oysters. Sometimes large clumps of oysters are caught in the net."

As elsewhere, North Sea oysters were not spared from overexploitation. No catch-regulating leases existed, and after a relatively short period of time, even these large stocks became so exhausted that the oyster fishery was no longer profitable.

Unfortunately, nothing definitive is known about the biogenic reefs formed by the sublittoral oyster. The high catch yield suggests, however, that they must have more or less covered the seabed. That the oysters to a certain degree grew together in clumps is mentioned in English publications using the term "coarse oysters". These coarse oysters did not comply with the requirements of the marketplace for well-formed individual oysters, such as those that were encountered from Wadden Sea cultivations.

The "deep sea oysters" were unloaded by Dutch and German fishermen in their home ports. In the 18th century, an area for intermediate storage of oysters caught in the open sea was established in Wangerooze.

In the fishing maps of the former German Naval Observatory and the German Hydrographical Institute (maps from 1915-1968) are several entries which indicate the presence of oysters in the maritime region of the central German Bight. Figure 8 depicts an excerpt of the fishing map from 1915 (Chart 112) with information on oyster deposits printed in red. In later editions of this fishing map until 1968, these notes on oysters can be found unchanged. Since the literature does not indicate a significant fishery for "offshore oysters" at the beginning of the 20th century, it may be assumed that even the local information listed in the fishing license from 1915 no longer depicted the usable oyster harvesting grounds for fisheries.

That a worthwhile oyster industry on the "oyster ground" in the North Sea midway through the first half of the 20th century apparently was no longer possible can be concluded from HAGMEIER and KÄNDLER (1927), who suggest in their notes (p. 70): "During the March trip of the Reich research steamer "Poseidon", observations were made of the oyster ground of the North Sea. While a 0.5 nautical mile long trawl with an oyster iron was entirely unsuccessful, a total of 42 oysters were caught in several short trawls, their dimensions are reported here: ... ". The mean positions of the two most profitable short trawls (25 and 14 oysters) were 54°24' N - 5°48' E and 54°21' N - 5°14' E. These positions are approximately 140 and 170 km WNW of Helgoland.

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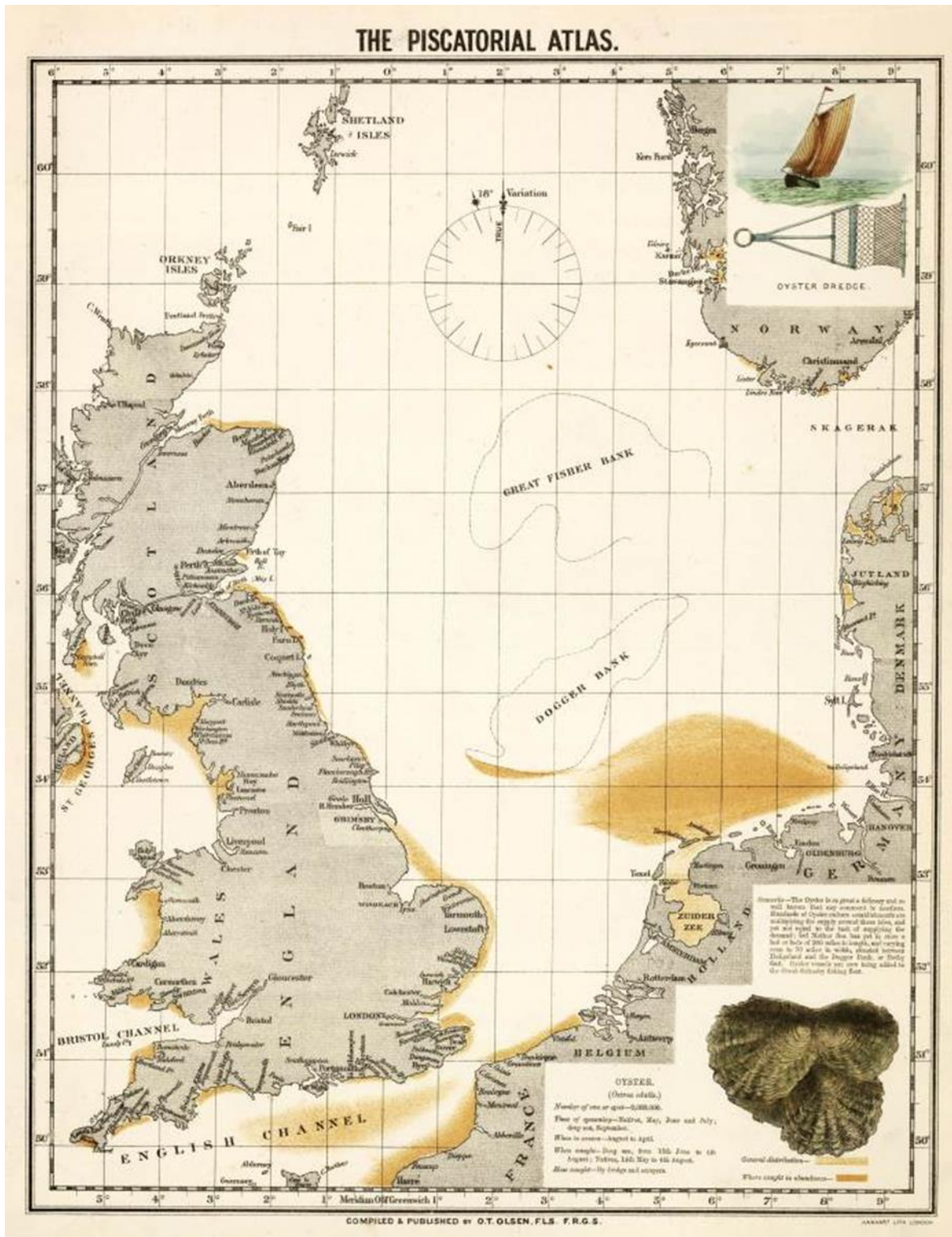


Figure 7: Map of oyster deposits in the North Sea and bordering countries from the “Piscatorial Atlas” by OLSEN (1883). In the southern German Bight, an extensive oyster stock, the so-called “oyster ground” is marked.

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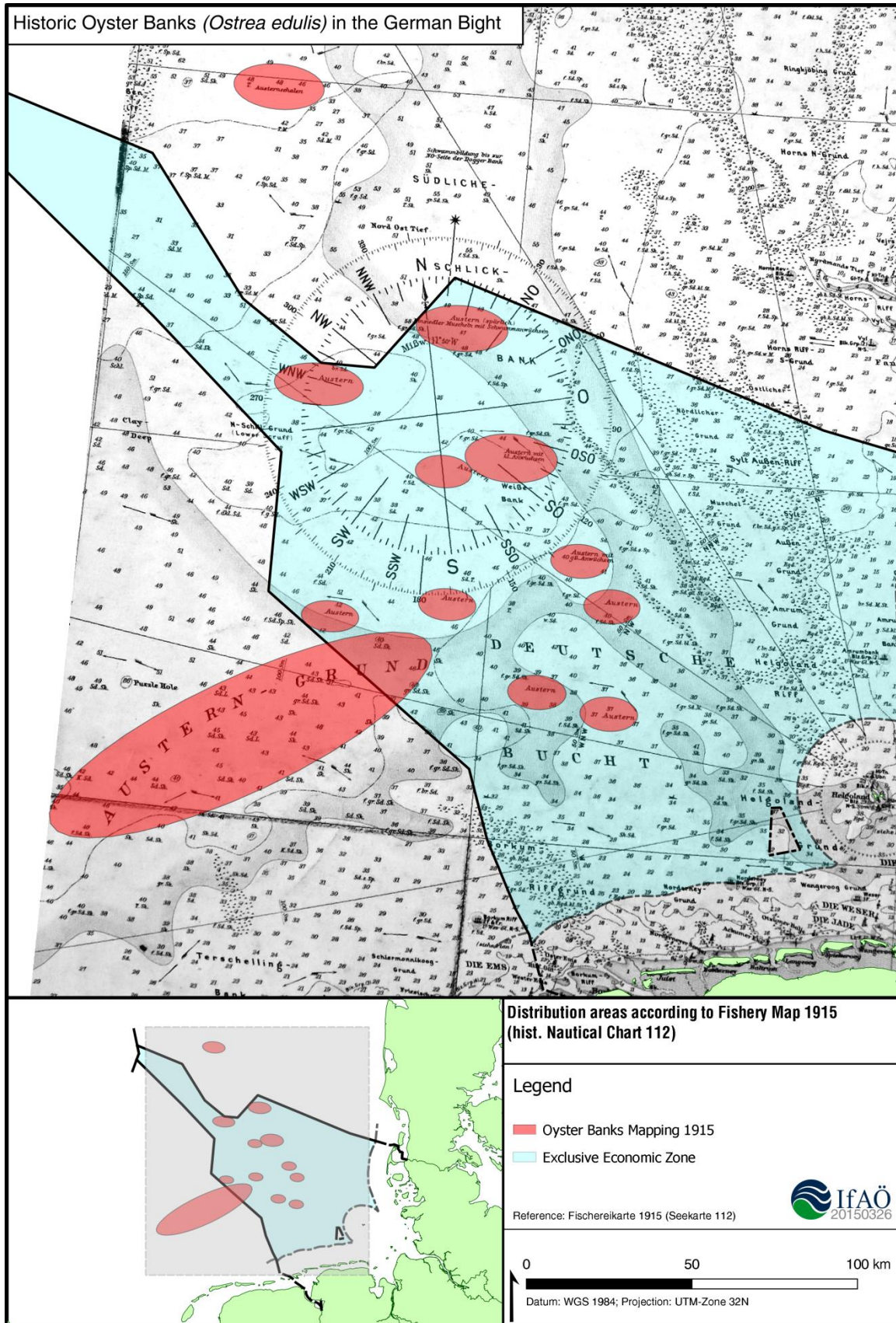


Figure 8: Excerpt from the 1915 fishing map with markings that indicate the presence of oysters.

In NEUDECKER (1990a) the timing of the harvest rates for the four mentioned harvest zones is shown (Figure 9). As already stated, the East Frisian oyster beds were exhausted in the first half of the 19th century, while oysters were still commercially harvested in the North Frisian Wadden Sea at the beginning of the 20th century. The curve for the Helgoland oyster bed is based on relatively accurate harvest statistics for the years 1872 to 1886. It shows that after an initial peak, the yields decreased drastically within a short time. After closing the season between 1879 and 1882, the yield increased again for a short time (Table 1). There are no reliable harvest statistics for the oyster ground fishery (BERGHAIN & RUTH, 2005). The route of the curve (C) depicted in the chart does not, at a minimum, match the information from BERGHAIN & RUTH (2005) according to whom harvest operations at the oyster ground steadily increased until the middle of the 19th century and was then further operated until about the end of the century.

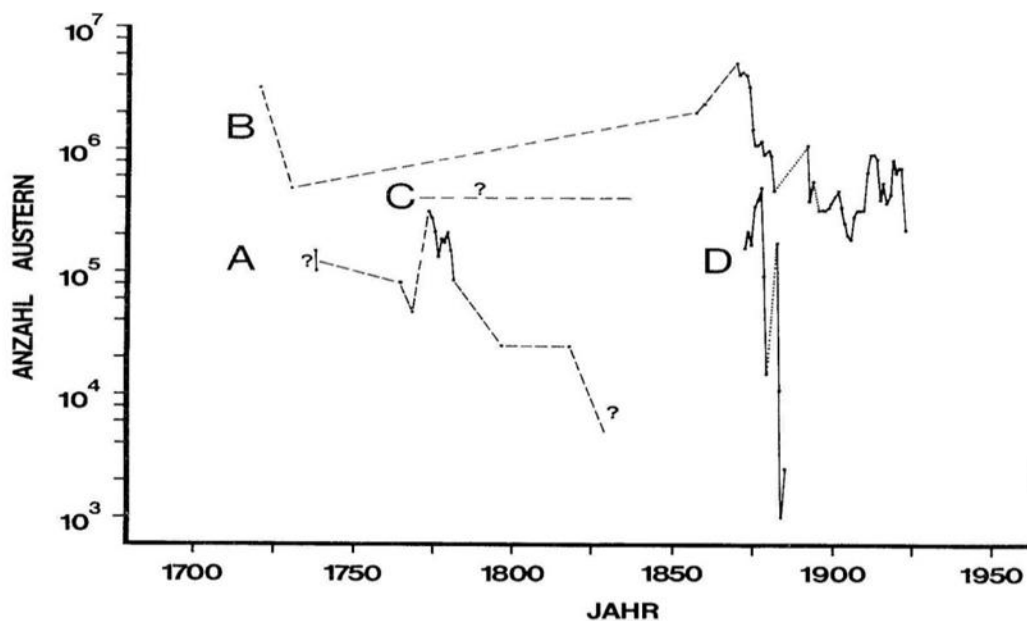


Figure 9: Harvest of the German oyster fishery from 1700 to 1950 acc. to literary sources. A: East Frisia, B: North Frisia, C: Oyster Ground, D: Helgoland (NEUDECKER, 1990a).

Regardless of which of the former "offshore" oysters deposits in the German North Sea is considered, extirpation of the native oyster, primarily a result of the centuries-long overexploitation from over harvesting, was already virtually complete about 100 years ago. In this respect, German oyster harvesting practices were not any different from those of other countries.

NEUDECKER (1990a) has shown that to enable the localized occurrence of the oyster in the Wadden Sea, several site-specific environmental conditions must be met. These special conditions were not significantly altered by early harvesting practices. However, through the introduction of ever-more-effective harvesting techniques, especially the motorization of ships and the simultaneous use of several dredges, oyster beds as a habitat for the resettlement of larvae were destroyed. The harvesting of marketable adult oysters not only reduced the number of larvae but also reduced the preferred substrate for settlement of larvae.

At this point, it should be emphasized that it is not known how the biogenic reef habitat formed by *O. edulis* looked before its early exploitation by humans. It is assumed that for at

least the last 1,000 years, the coastal oyster stocks suffered under a high and constant harvesting pressure by man and steadily degraded with respect to their natural state. An increasing depletion and also the "management" of oysters stocks in later centuries prevented the development of natural reefs. The removal of large food oysters, not only effected weakening of recruitment, but also eliminated settlement surfaces for larvae. This could not be compensated by the deployment of cultch as larval substrate. In addition, the traditional practice of spreading (relaying) isolated, juvenile oysters has prevented the formation of reef structures. The rationale was that oysters should grow in a solitary manner, since only then can they be effectively marketed.

Although it is not known how undisturbed oyster reefs in the North Sea would have looked in prehistoric times, it is assumed that the coastal relief had a significant influence on the structure of the reefs. Consequently, no reefs with a strong vertical structure would have formed along shallow coasts. Conversely, a rather steep coastal profile is required.

Only recently have immense *Ostrea edulis*-formed reef structures along the Bulgarian coast been described. The reefs are at a depth of 7-23 m. They form tower-like, biogenic structures with a height of 7 m, a length of 30-50 m, and a width of 10 m. Unfortunately, the reefs, which were documented in 2007-2008, no longer support live oysters. However, deposits of living oysters apparently exist at other locations along the coast, (TODOROVA et al., 2009).

The robust Bulgarian oyster reef probably represents an exception adapted to the unique circumstances of the particular location. It also displays the plasticity of biogenic structures that can be formed by the European oyster.

Although the oyster beds formerly existing in the German North Sea did not possess the possible reef status due to centuries of exploitation, they still constitute particularly species-rich habitats, such as described in the investigation by CASPERS (1950) on the of Helgoland oyster bed community. Species richness of former oyster beds also impressed Karl August MÖBIUS (1877), who introduced the term "biocenosis" to ecology, using the "living community" of the oyster bed as the example.

Interim Conclusions

- The loss of the oyster beds in the Wadden Sea in the southern North Sea is primarily a result of persistent overexploitation and the associated destruction of the original reef structure.
- The removal of marketable oysters weakened the reproductive proportion of the oyster stocks. Furthermore, this reduced the settlement area for the offspring and thus total recruitment.
- Extreme climatic events such as cold winters or the appearance of predators or competitors may have contributed to the further degradation of already depleted stocks, but are not responsible for their extirpation.
- The decline of the stocks began very early. Today's additional threat factors, such as invasive predators or epidemic diseases were then not yet relevant.

3 Biology of the Oyster

3.1 Biological description

Within the class Bivalvia (molluscs), the European flat oyster (*Ostrea edulis* L, 1758) is included in the taxonomic subclass Pteriomorpha and there to the family Ostreoidae (oysters). Morphologically, the approximately circular or slightly elliptical shells are relatively flat. The oyster grows on the substrate with the more curved left shell. The flat right shell serves as a type of cover. Both shells are only connected to each other via a ligament; a typical hinge is missing. Closing of the shells is performed via a single adductor muscle. The size of adult oysters is 10 to 12 cm. Occasionally, very large specimens of up to 20 cm are encountered.

3.2 Reproduction and growth

The oyster is a so-called protandric hermaphrodite that upon reaching sexual maturity first form functionally male gonadal tissue for the production of sperm. Following this, the female gonadal follicle is formed, within which eggs mature (KORRINGA, 1952). This sex reversal takes place during the entire living phase of the animal. The change from the female to male phase occurs relatively fast and is completed within a few days; the formation of the female stage, due to the greater metabolic burden of egg production, lasts significantly longer (YONGE, 1960). In the end, the rate of gender change is also heavily influenced by water temperature and food supply.

The frequency with which sex changes are carried out is generally related to the latitude and the duration of the reproductive period. Thus, in Scandinavia (the Limfjord included), *O. edulis* usually forms only one gender per year, meaning first the mature male gonads form and in the following year the female gonads. At UK latitude, one gender change within a year usually takes place while in the southern Bay of Biscay and the Mediterranean, gender changes may occur several times per year.

Functionally mature male sperm are produced in the form of sperm packets (spermatophores) into the surrounding area. In this form, the sperm remain viable longer and can be transported even further away from a female animal. If sperm packets are successfully transported via the inhalant siphon into the mantle cavity of a mature female animal, eggs are released into the cavity and fertilized there.

A special feature of *Ostrea edulis* and other species of the genus *Ostrea* is the so-called ovoviviparity. This means that the larvae develop initially for about 7 to 15 days, depending on the water temperature, in the mantle cavity of the oyster to the point that they can swim and ingest food. With the swarming out of the 170-180 µm-sized veliger larvae, the approx. seven to twelve-day planktonic larval phase (KORRINGA, 1952; YONGE, 1960) begins. As ovoviviparous species, the oyster produces comparatively fewer but larger eggs (approx. 150 microns) than, for example, the American oyster (*Crassostrea virginica*) (KAMPHAUSEN, 2012). The eggs are relatively large because sufficient yolk must be available for the initial development phase in the mantle cavity of the female animal.

Despite the "lavish" incubation period, a single oyster can produce one to two million larvae (WALNE, 1964). At optimal temperature and food conditions, oysters can also spawn several times a year.

In the plankton stage, the larva subsist of micro-plankton, which they direct into their mouth-opening with the help of a cilia wreath located around the velum. At the end of the planktonic phase, the larva form a foot, byssus gland and sense organs for perception of light and gravity. With the help of the foot, the pediveliger larvae (300 µm) can crawl about on surfaces in order to locate a suitable substrate for settlement. It is still able to float as needed in order to

change location to examine substrate until it finally has found a suitable substrate for the final adhesion process. For adhesion, the byssus gland is required, the contents of which are used as an adhesive for adhering the left shell half to the substrate.

The time required for attainment of sexual maturity varies depending on water temperature. In the Danish Limfjord and in the UK, reaching sexual maturity usually takes three to four years (COLE, 1941).

The number of eggs (fecundity), which an oyster produces depends less on the size of the animal, but rather on its age (KORRINGA, 1952). However, larger individuals generally contribute more to recruitment than smaller. In general, early in the year-spawning oysters produce more larvae than later in the year-spawning oysters. In this case, reserve materials were probably already consumed in the preceding male phase (KORRINGA, 1952).

In the Dutch Oosterschelde, spawning begins in early June and reaches its peak in late June / early July and then begins subsiding slowly in August (KORRINGA, 1952). In the former oyster stocks in the North Frisian Wadden Sea, the breeding season began in June and ended in August / September (MÖBIUS, 1877). In Limfjord, oysters spawn in the summer when the water temperature has reached 15 °C (MOODY MARINE LTD, 2012).

As with all marine invertebrates with high fecundity, mortality in *O. edulis* during the planktonic phase and the first juvenile period of life is very high. According to an estimate by KORRINGA (1946), from 1 million larvae only 250 reach spat stage. Of these, 95% die before winter.

The recruitment of a stock is significantly influenced by the density of individuals. Thus, the presence of mussel aggregates and synchronization of spawning are important for good fertilization success. If the density of individuals decreases below a threshold value, the chance of fertilization also decreases, as only a few isolated individuals will find a mating partner. Under these conditions, a loss of a stock's genetic fitness is likely.

Therefore, measures that increase the density of individuals are to be taken into account during the restoration of degraded oyster stocks. This can be accomplished by introducing non-local oysters or by the clustering of widely scattered individuals. For example, in Scottish Loch Ryan, oysters not intended for market (<70 g) were placed back in the oyster fishery at a high density of up to 100 oysters per m² to improve the conditions for high fertilization success (HUGH-JONES, 2003).

For a restoration of the oyster, a high population density of the founder population is also important because the gender ratio and the proportion of mature individuals within the distributed stock is not known.

Interim Conclusions

- The recruitment of oysters stocks is irregular and sporadic, thus the number of individuals in a population exhibit a relatively significant, yet natural fluctuation.
- Due to the variability of recruitment success, *O. edulis* stocks react very sensitively to over-exploitation. They generally require significant time to recover from drops in stock.
- A high population density within a stock is an important prerequisite for successful recruitment.

4 Abiotic Influencing Factors (for growth and survival)

4.1 Temperature

Temperature is one of the most important factors that influence the growth and reproduction of *O. edulis*. In particular, in the northern area of distribution, temperature is the primary factor influencing successful reproduction. Recruitment of natural oyster stocks is usually carried out only when the water temperature has reached at least 15-16 °C.

The larvae develop faster at higher water temperatures, so that the planktonic phase of life is shortened, provided that there is sufficient food available. According to LAING et al. (2005) both a short- and long-term increase in the water temperature lead to better recruitment and thus to a longer-term survival of oysters stocks.

There is ample historical supporting evidence that oysters stocks have suffered drastic losses from extremely cold winters. This especially affected oyster beds that were exposed to wind and cold air temperatures at low water levels. Thus, the former oyster beds in the Wadden Sea were seriously damaged by very cold winters in 1728-29 and 1829-30. The stock losses caused by extreme winter conditions are repeatedly cited as a major factor - in conjunction with overfishing – contributing to the decline of European oyster stocks (HAGMEIER & KÄNDLER, 1927; MÖBIUS, 1877).

Although in the literature water temperatures beginning at 15 °C are usually cited as the prerequisite for successful reproduction, there are apparently European populations that are adapted to colder climates. Otherwise, Scottish waters would not have once been considered among the best oyster grounds in Europe. The Norwegian wild stocks are also able to successfully reproduce. However, it is assumed that recruitment in higher latitudes occurs more slowly and irregularly than in lower latitudes.

The "deep sea oysters" the open North Sea also had, despite low summer water temperatures on the seafloor (Figure 10), presumably developed over a long period of time into a very large stock size. With the expected increase in water temperature due to climate change, potentially better living conditions for the oyster in the deeper sublittoral zone the North Sea may result.

Interim Conclusions

- Temperature is a critical environmental factor that significantly influences the recruitment and thus the survival of oyster stocks.
- Sites that are selected for restoration of oysters should not exhibit extremely cold water temperature conditions.
- Locations at shallow water depths of approx. 20 - 30 meters offer the advantage that warmer near-seafloor water temperatures occur earlier in the summer than in deeper marine areas.

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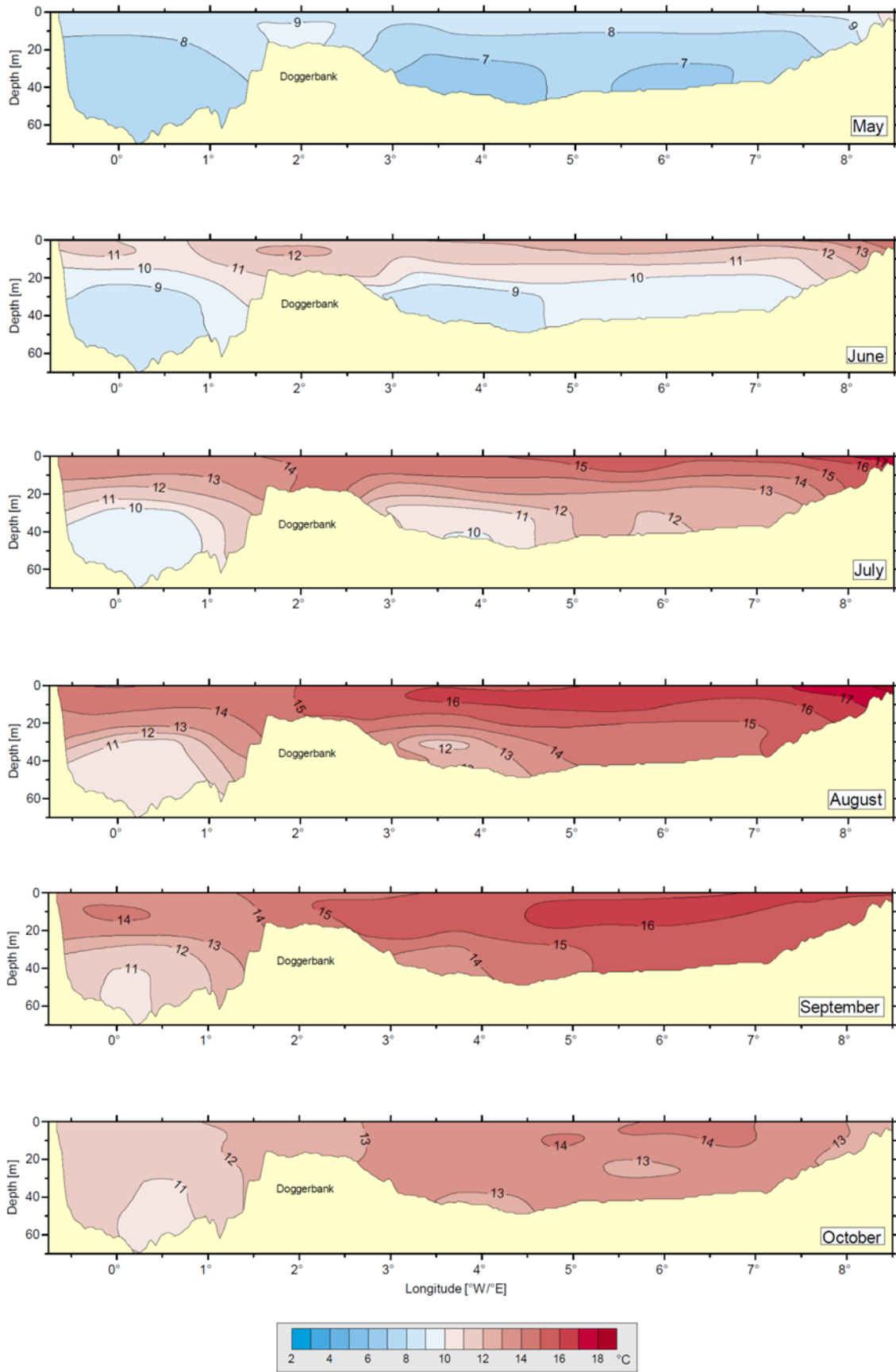


Figure 10: Average monthly temperature (1902 – 1954) of the North Sea along a section of 54°30'N (from TOMCZAK & GOECKE, 1964).

4.2 Salt content

The oyster occurs preferably in marine areas with a higher salinity (> 30 PSU). At low water temperature, it also temporarily tolerates lower salinities of 16-19 PSU. At a temperature of below 10 °C, metabolic activity is reduced and the oyster can survive in winter, for example, periods coupled with a supply of fresh water (HUTCHINSON & HAWKINS, 1992).

Interim Conclusions

- In the deeper sublittoral areas of the German Bight, the requirement of the oyster for a high salt content is always satisfied.
- A higher salinity in offshore sea areas also provides some protection against infection with the pathogen *Marteilia refringens*, which prefers a lower salinity.

4.3 Substrate

Generally speaking, oysters can settle on different types of hard substrate such as rock, gravel or muddy sand with cultch. They, however, quite clearly display a preference for certain substrates. Thus, oyster larvae settle preferably on the shells of living conspecifics or nearby cultch (Figure 11). This behavior promotes the formation of aggregates, which under favorable conditions over a long period of time may develop into a biogenic reef. This resulting spatial proximity of individuals is also an important requirement for high fertilization success. Vigorous oyster beds would thus promote their "self-preservation" by repeatedly settling new larvae in the same location.



Figure 11: Oyster shells on the beach at Oddesund Nord/Limfjord. Remains of young oyster shells which have settled on the strongly curved left shell of the adult oyster are visible (Photo: Gercken).

The preference of live oysters as a settlement substrate has been confirmed experimentally. Compared with cultch or roofing tiles, a greater presence of larvae was observed on the shells of living oysters (KORRINGA, 1952; KENNEDY, 1999).

The former German oyster beds were also closely linked to the presence of mussel shells as substrate. In the North Frisian Wadden Sea, the cultch in almost all beds consisted mainly of oyster shells. In addition, varying amounts of shells from other bivalves such as soft-shell clams, cockles and mussels were observed. HAGMEIER and KÄNDLER (1927) surmised "that

the now existing shells of many generations of living mussels and snails originated and in some cases have lain for decades on the oyster beds."

The Helgoland oyster bed also only occurred in the narrow belt where mussel cultch, namely oyster shells likewise occurred. Below this layer of cultch, the seafloor consisted of muddy sand (CASPER, 1950).

In aquaculture, the use of artificial substrates as "larvae collectors" (spat collector) is a common practice. Roof tiles were exposed in the sea at an early stage to produce spat for further breeding (YONGE, 1960) in France. In the Netherlands at the diked Lake Grevelingen, mussel harvesters distribute broken mussel shells in July to increase the settlement area for *O. edulis*. This method, however, has met with resistance from nature conservation organizations, since the introduction of foreign mussel shells is connected with the risk of unwanted introduction of alien species.

Collectors should ideally be effective, inexpensive, reusable and easy to deploy in the sea. In addition, the young spat should be able to be easily detached from the surface for further breeding. Within the framework of the EU project "Oysterecover", different types of shellfish collectors were evaluated based on literature data and *in-situ* experiments. The Dutch IMARES Institute tested the effectiveness of three types of collectors: 1) stacked, conically-shaped PVC discs with calcium oxide coating (Chinese hats), 2) bundles of plastic tubes with a rough outer surface and 3) with mussel shell-filled mesh bags. Because of their effectiveness, ease of use and low cost, the "Chinese hats" and shell bags were recommended as the most suitable collectors (VAN DEN BRINK, 2012).

As part of regeneration and resettlement activities, additional hard substrate will generally be introduced in order to promote the settlement of larvae. Since oyster shells are not usually available, shells of other bivalves such as mussels or scallops are used.

In future, the area of artificial hard substrates will increase significantly in in the German EEZ with the construction of numerous wind farms. The various types of foundations (monopile, jacket, and tripod) and the scour protection are known to be colonized fast by periphytic organisms. Among them is the blue mussel, from which one can assume that accumulations of shells will be formed over time. These shell agglomerates can then potentially serve as substrate for colonization by oyster larvae. During epibenthos investigations in connection with the 2002-erected Horns Rev wind farm along the Danish west coast, *Ostrea edulis* was documented in the scour protection zone of the monopile (ANONYMOUS, 2006). Also, at the 2006-erected Dutch offshore wind farm Egmond aan Zee, some specimens, likely the European oyster, were documented within the benthic community in 2011. The oysters settled there at the top of the monopile in the intertidal zone (BOUMA & LENGKEEK 2012). However, no oysters were found in the scour protection area.

The selection of an effective substrate is not only of importance in the larval settlement in the open water, but also under culture conditions in oyster farms. The substrate used should be as "attractive" as possible, so that a high percentage of larvae survive the critical period of settlement and metamorphosis. At the *Ostrea Sverige AB* oyster farm on the Swedish Koster Islands and at the breeding facility of the Danish Shellfish Centre (DSC) at Limfjord, the adhesion-competent larvae were offered finely-ground oyster shells (<1mm) as a substrate. These small shell fragments sufficed for the approx. 300 µm-large larvae to settle (Gercken, pers. observation).

The larval settlement and metamorphosis of *O. edulis* under farming conditions is still generally associated with large losses. In this respect, efforts are to be made to optimize the settlement of the larvae, this critical phase of artificial breeding, which is induced by chemical

factors and occurs in a synchronized manner. As recent studies have shown, the effectiveness of larval settlement is significantly improved by the administration of neuro-transmitting substances. Of various tested substances, the neurotransmitter GABA (gamma-aminobutyric acid) proved to be particularly effective in the induction and synchronization of larval settlement (MESIAS-GANSBILLER et al., 2013).

Interim Conclusions

- Oyster larvae preferably settle on the shells of their own species or autochthonous cultch. This behavior promotes reef structures formed by oysters.
- For a restoration experiment, it is necessary to distribute a large amount of hard substrate such as mussel cultch for larval settlement.
- Installation of larvae collectors in the context of a restoration site can serve to control the reproductive success and larval presence. Upon successful colonization they can contribute to increase of the founder population.
- With the increasing installation of wind farms in the German EEZ, the proportion of potentially-usable hard substrate for the settlement of *O. edulis* could increase.

4.4 Water depth, exposure and current

Oysters can form extensive reefs in the lower intertidal and deeper sublittoral regions. In general, the intertidal zone is less populated, since fluctuating environmental factors result in more pronounced stress. Oysters occur down to a depth of approx. 80 m in the lower sublittoral. An example are the aforementioned "deep-sea oysters" of the German Bight, which formerly populated large areas of the southern North Sea from Helgoland to the Dogger Bank until their discovery and extirpation due to overharvesting in the 19th century (NEUDECKER, 1990b; BERGHAHN & RUTH, 2005). In the fishing license of the North Sea from 1915, the offshore deposits of oysters to a water depth of approximately 40 to 50 m are listed (see Figure 8).

Water currents affect oysters in various ways. In exposed locations, it is important for the supply of food particles. For example, the former "current beds" in the Wadden Sea benefited from the continuous food intake maintained by the tidal current (HAGMEIER & KÄNDLER, 1927).

The local current conditions are also important for recruiting successes of a stock. A stronger current will cause the larvae to drift away from their original location during the planktonic phase and thus reduce autochthonous recruitment. On the other hand, oyster populations can also benefit from allochthonous larvae supply from other locations. It is suspected that the stocks in the oyster beds in the Wadden Sea were supported by the supply of larvae from the oyster ground in the southern North Sea (BERGHAHN & RUTH, 2005; HAGMEIER & KÄNDLER, 1927). In addition, the spawn produced in the exposed current beds of the Wadden Sea have likely benefited the oyster beds in the inner region of the Wadden Sea (HAGMEIER & KÄNDLER, 1927).

In areas with poor water exchange, such as the Oosterschelde, good recruitment success generally occurs. The larvae usually find sufficient substrate for settlement in their "home stock" (KORRINGA, 1952).

Interim Conclusions

- In the area of the German EEZ, the North Sea exhibits a water depth where oysters are protected from extreme climatic conditions. Compared to the intertidal zone, local hydrographic conditions fluctuate relatively little.
- When selecting a site for a restoration experiment, survey data and / or modeling data on the local current conditions should be taken into account.

5 Important Biological factors with regards to Restoration

5.1 Diseases

The occurrence of pathogens is an environmental factor that can be an existential threat for oyster stocks. With regard to the European flat oyster, this is especially true for the growing epidemic of protozoan parasites that in the worst case can cause mass mortality.

In 1920-21, the flagellate *Hexamita* caused such high losses to natural and cultivated oyster stocks in England, France, the Netherlands and Germany that some of the stocks have not recovered (YONGE, 1960). For several decades, however, the two pathogens *Bonamia ostreae* and *Marteilia refringens* have been the most serious threat to the native oyster.

The most dangerous disease is considered to be Bonamiosis, caused by *Bonamia ostreae*. For example, mortality rates of over 90% were recorded in Irish oysters stocks (CULLOTY et al., 2004). This one-cell parasite primarily infects the hemocytes (blood cells) (Figure 12) of the mussel and leads, after it has multiplied there, to the mussel's death, whereby new, infectious parasite stages are released. *B. ostreae* was also observed extracellularly in the gills and digestive gland (OIE, 2012a).

Young oysters to the age of two years are particularly susceptible to infection from *B. ostreae*. On the other hand, only older individuals exhibit severe disease symptoms. The soft body of a weak, infected oyster appears mostly normal, externally. Only in case of a severe attack can clear pathological symptoms such as yellowing of organs, damage to the connective tissue and gills as well as an overall poor condition occur (OIE, 2012a).

The life cycle of *B. ostreae* is not yet fully understood. What is certain is that the parasite can be transmitted directly from oyster to oyster; the route of entry is presumably via the gills. Whether intermediate hosts may act as possibly vectors of the disease is not known (OIE, 2012a). The presence of *B. ostreae* in the larvae of infected oysters has recently been demonstrated by molecular diagnostics. Oyster larvae could thus possibly contribute to dissemination of Bonamiosis during their planktonic phase (Arzul et al., 2011).

The standard method for detection of Bonamiosis is diagnosis by histological or cytological preparations. In recent years, the PCR technique was also developed as a particularly sensitive method for the detection of *B. ostreae* in tissue samples (OIE, 2012a).

B. ostreae was first detected in 1979 in Brittany (COMPS et al., 1980). In England, the first detection was in 1982 in Cornwall after unexplained mortality of the local oysters occurred (BUCKE & FEIST, 1985). According to LAING et al. (2005), Bonamiosis occurs in Britain along the south and the east coast, while Scotland, Wales and Northern Ireland are not affected. As part of recent research, however, *B. ostreae* was detected in smaller oysters stocks on the west coast of Scotland. In the oyster stock in Loch Ryan, the largest commercially exploited oyster stock in the southern west coast of Scotland, Bonamiosis does not occur. Ireland (MURRAY et al., 2012), Spain and the Netherlands are other countries where *B. ostreae* infection of local oysters is known. The countries of Denmark, Sweden and Norway are currently considered free of Bonamiosis. However, in 2008 a low prevalence of *B. ostreae* was detected in southern Norway in an oyster stock at Arendal. The disease did not spread and has no longer been observed during subsequent investigations conducted since 2009. The most recent monitoring of various Norwegian oyster stocks in 2012 resulted in no positive Bonamiosis detections (MEDHUS et al., 2013).

According to studies conducted at the University of Southampton, oysters that suffer from stress due to treatment in cultures and / or high stocking densities are particularly susceptible to *Bonamia* infection. Experiments have shown that with a lower population density, cel-

lular defense mechanisms were able to successfully combat the parasite. At higher population density, as e.g. is to be found with oyster baskets in the intertidal zone, this immune response was no longer present (LAING et al., 2005).

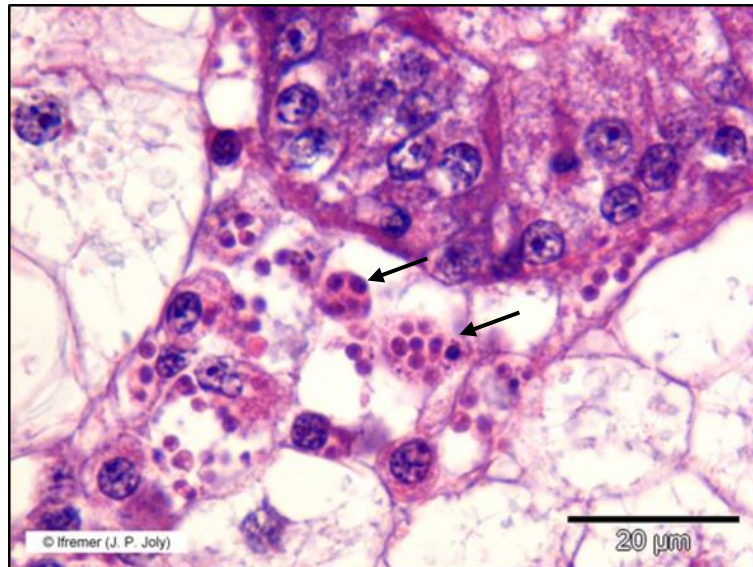


Figure 12: *Bonamia ostreae* in hemocytes and free in loose connective tissue at the periphery of the midgut gland of a European oyster (H&E staining). (European Reference Lab for Mollusc Diseases; www.eurl-mollusc.eu/Main-activities/Tutorials/Bonamia-sp).

In addition to *B. ostreae*, *Bonamia exitiosa* has been detected as another haplosporidium protozoa in European waters. It also attacks the hemocytes and causes the same symptoms as *B. ostreae*. In Europe, the parasite was first observed in Spain (Galicia) in *O. edulis* (ABOLLO et al., 2008). Further observations have been made in the Mediterranean (France, Adriatic) and England (Cornwall) (OIE, 2012b).

Another serious disease which threatens oyster stocks in European waters is Marteiliosis. The agent, the protozoan parasite *Marteilia refringens*, particularly affects the digestive tract of its hosts. In addition to *O. edulis*, mussels are among the organisms that are also affected by this disease, but the oyster has a significantly higher susceptibility to *M. refringens*.

The life cycle of the parasite is indirect. A direct transmission of the infection from oyster to oyster has not been demonstrated. Several lines of evidence suggest that zooplankton act as intermediate hosts. In experiments, *M. refringens* was transferred to the copepods *Paracartia grani* from *O. edulis* and *Mytilus galloprovincialis*. The reverse transmission path, however, could not be experimentally demonstrated (OIE, 2012c).

The geographical distribution of *M. refringens* ranges in Europe from the eastern Mediterranean (Adriatic, Greece) around the Iberian Peninsula, France and the UK to the Netherlands. In Sweden, *M. refringens* has previously only been detected in one mussel culture on the west coast. No infections of *O. edulis* are known in Norway (MEDHUS et al., 2013) and the Danish Limfjord (MOODY MARINE LTD, 2012).

Infections occur preferentially at higher water temperatures and low salinity. Depending on the environmental conditions, *M. refringens* can survive outside the host from a few days up to 2-3 weeks (ICES, 2012; OIE, 2012b).

Infected oysters display non-specific symptoms such as emaciation and discoloration of the midgut gland. Reliable diagnostic detection is accomplished either by histological tissue sections of the digestive tract and the gills or by molecular biological PCR diagnostics (ICES, 2012).

When planning a restoration of oysters, the disease-free status of the imported oysters is not the only factor which should be taken into account. Of utmost importance is whether there are other organisms living in the proposed restoration area which could act as potential intermediate hosts or as vectors of pathogens and thus could potentially infect the oysters. In terms of mussels from German coastal waters, the National Reference Laboratories for Mollusc Diseases at the Friedrich Loeffler Institute (FLI / Riems) has, however, found no evidence of the presence of *B. ostreae* and *M. refringens* (pers. Information Dr. Bergmann, November 2012).



Figure 13: Histological section through a digestive tubule of a European oyster with five *Martellia refringens* plasmodia in the digestive epithelium (H&E staining) (European Reference Lab for Mollusc Diseases; www.eurl-mollusc.eu/Main-activities/Tutorials/Martellia-refringens).

Interim Conclusions

- It can be interpreted from the present distribution of Bonamiosis and Marteilliosis that oysters from Scandinavian populations or from local farms would be best suitable for a restoration attempt in the German Bight.
- The Bonamiosis- and Marteilliosis-free status of the oyster population in the Limfjord is documented by an EU certificate.
- Oysters from the one Swedish breeding farm also have a Bonamiosis-free status. *Martellia refringens* has only been detected on the west coast of Sweden in one mussel culture.

5.2 Enemies

Apart from diseases, predators and competitors can present a threat to oyster stocks. These mainly come in the form of invertebrates, but some species of fish and birds are also included. In general, the thin-shelled spat are particularly vulnerable to predators. With increasing size and shell thickness, the level of predation decreases. From a size of about 3 cm shell diameter, oysters are no longer a prey for birds, crabs and fish.

The invertebrate predators include, for example, the common starfish (*Asterias rubens*), the common whelk (*Buccinum undatum*), the dog whelk (*Nucella lapillus*) and the green shore crab (*Carcinus maenas*).

In many stocks of the European oyster, members of the family of predatory sea snails (*Muricidae*) are the most dangerous enemies. These include the European sting wrinkle (*Ocenebra erinacea*), the Atlantic oyster drill (*Urosalpinx cinerea*) and the Japanese oyster drill (*Ocenebrellus inornatus*). While the sting wrinkle is native to Europe, the other two species have been introduced by the transport of oysters from the northeastern coast of the United States to Europe. All species feed on shellfish, including oysters, by drilling a hole in the shell of their victims with their toothed radula and thus reaching the mussel meat.

The mentioned predatory sea snails have no planktonic stage of life. They attach their egg capsules, which contain several eggs, on hard substrates such as oyster shells. Their natural propagation velocity is thus relatively low. Their current regional distribution in Europe is the result of extensive movement of oysters and other shellfish species from one sea to another (VAN DEN BRINK & WIJSMAN, 2010).

These representatives of sea snails are not obviously or appreciably spread in the German section of the North Sea. In the IfAÖ benthos database, no evidence has been recorded (R. Boensch, pers. comm). In a recent alert list of potentially invasive species for Germany, the status of *U. cinerea* is specified as "missing" (RABITSCH et al., 2013). Another member of *Muricidae*, the Asian rapa whelk (*Rapana venosa*), is listed in the alarm list as a potentially invasive species.

In the Netherlands, the invasive Atlantic and Japanese oyster drills were introduced with commercial clam transport to the Oosterschelde, the center of Dutch mussel farming. There, both adult snails and their egg capsules have been detected since 2007. For *R. venosa*, scattered evidence exists from the southern North Sea (Belgium, Netherlands) (FEY et al., 2010).

Apparently, these three predatory species have not yet been observed in the Dutch Wadden Sea. Since their spread there would pose a risk for the realization of protection objectives by the EU Habitats Directive, the IMARES Research Institute was commissioned to conduct a risk analysis to assess the probability of establishment of these three species in the Wadden Sea and its consequences. The experts came to the conclusion that the spread can be substantially prevented by the inhibition of shellfish transport in the Wadden Sea. However, once the three species have reached the Wadden Sea, they would encounter no problems settling and successfully reproducing. The extent to which native species may be harmed by their predatory activity is not known (FEY et al., 2010).

Once an occurrence of this invasive species in the Dutch Wadden Sea takes place, further spread eastward into the German Wadden Sea would only be a matter of time. For the Atlantic and Japanese oyster drills, the natural propagation speed would be lower due to the lack of planktonic phase, than the Asian predator snail with their planktonic larvae. However, if an intentional or unintentional transfer of mussels from the Oosterschelde into the Wadden Sea takes place, the risk of spread of these predatory snails and other invasive species

would exist (FEY et al., 2010). For this reason, there is a general prohibition of entry of shellfish from the Oosterschelde Delta into the Wadden Sea (BOS et al., 2012).

During benthos investigations in the Danish Limfjord, newly arrived gastropods were discovered. Among these was one which was originally described as a European sting winkle, but was later determined to be a Japanese oyster drill, *O. inornatus*. While in its native home this predator mainly fed on *C. gigas*, the European flat oyster occurs much more frequently in Limfjord. Currently, the spread of *O. inornatus* has been limited to a small area. However, since a reproductive population has been established, is expected to further spread. (LÜTZEN et al., 2012).

According to HAGMEIER and KÄNDLER (1927), accompanying predatory fauna including common whelk (*Buccinum undatum*), the hermit crab (*Eupagurus bernhardus*), the green shore crab (*Carcinus maenas*) and the common starfish (*Asterias rubens*) were present in the epifauna of the former North Frisian oyster beds, whereby the latter two were considered particularly strong enemies.

Interim Conclusions

- The presence of predatory enemies of oysters is a not-to-be-neglected impact factor which is to be taken into account both in the selection of a restoration site as well as in the origin of a donor population.
- By a potential import of oysters from the Limfjord, it is to be ensured that no adults or egg capsules of the Japanese oyster drill are introduced.
- For a restoration attempt, spat and juvenile oysters are particularly threatened by predators, while larger individuals are no longer threatened.
- Members of the predatory sea snail family are not, or do not seem to be, significantly distributed in the German sector of the North Sea. In the benthos database of IfAÖ, no evidence in this regard exists (R. Boensch, pers. comm).

5.3 Competitors

A number of invertebrate species compete with *O. edulis* for settlement area and in some cases also for food. These include, for example, tunicates (sea squirts) and barnacles. The presence of the common slipper limpet (*Crepidula fornicata*) can have a particularly negative effect on an oyster stock. This species was probably originally introduced through oyster imports (*C. virginica*) in the years 1887 and 1890 from the USA to southern England (ENO et al., 1997). Today, the range of the slipper limpet stretches from southern Norway to Spain.

In Germany, the slipper limpet was first detected in the 1930's in Sylt oyster beds, where they probably arrived with imported oysters from the Netherlands. They are now widespread throughout the Wadden Sea, where they are an integral part of the growths occurring on mussel beds (THIELTGES, 2003).

The slipper limpet grows very rapidly. In southern countries such as France, they can even form carpets and through the production of pseudofeces can alter the substrate such that the settlement of oyster larvae is prevented. In the Wadden Sea, the slipper limpet occurs at a significantly lower density. This is due to the recurring cold winter, which causes a high mortality rate among the limpets (THIELTGES, 2003). In the Danish Limfjord, where *C. fornicata* has been detected since 1934, they are also not found in great abundance, which is a testament to the negative influence of the cold climate.

According to the results of a query of the IfAÖ benthos database, the slipper limpet is also present in offshore regions of the EEZ in the German North Sea (R. Boensch, pers. comm.).

Another potential habitat and food competitor of the European oyster is the invasive Pacific oyster, which is now widespread. However, the two species primarily prefer different habitats. Thus, while the European flat oyster is mainly located in the sublittoral zone, the rival Pacific oyster prefers the littoral zone and has already developed extensive reefs in the Wadden Sea in this zone (TROOST, 2010; SCHMIDT et al., 2008) (see Figure 2.).

Interim Conclusions

- In the German Bight, the slipper limpet (*C. fornicata*) occurs both in the Wadden Sea as well as in deeper sublittoral zone. However, due to high mortality resulting from the cold winter, their abundance is so low that potential settlement areas for the larvae of *O. edulis* are not affected.
- Because of the preference for different water depths, competition between the European and Pacific oyster in habitat selection is small.

5.4 Genetic status

The genetic diversity of an oyster population is of central important for the ability to adapt to changing environmental conditions and to ensure long-term survival of the stock. The exchange of genetic material (gene flow) occurs naturally through the spread of larvae during the planktonic life phase. In the case of *O. edulis*, however, through centuries of transplants of oysters between different marine areas, humans have contributed to a noticeable mixing and alignment of the gene pool in Europe (LAING et al., 2005). Table 2 provides the example of Scotland, where the import of oysters and the domestic transplantation of oysters within the country has represents a common practice.

Although the genetic differences seen as a whole are not very pronounced, comparative studies of alloenzym polymorphisms in 19 samples from Norway to Greece resulted in significant differences between Atlantic and Mediterranean populations (SAAVEDRA et al., 1993, 1995). A subsequent study by LAUNEY et al. (2002) on samples from the Atlantic Ocean, the North Sea and Mediterranean demonstrated by means of repetitive DNA sequences (microsatellites) that the genetic difference between the samples also increased with increasing geographic distance. Within the Atlantic samples, the genetic variability was less than in the Mediterranean oysters. Another microsatellite analysis conducted as part of the Oysterecover project demonstrated that samples of populations from the Netherlands and Scandinavia displayed a particularly high genetic similarity (Paulino Martinez, Oysterecover project, pers. comm).

The Scandinavian populations have a comparatively lower genetic variability than populations from Spain, France and Ireland. One reason for this is that the extreme climatic conditions only allow for irregular reproduction and lead to overall stock losses. The genetic variability between the Scandinavian populations is thus relatively low (LAING et al., 2005).

Due to the low genetic variability in the Atlantic population and due to a low reproductive rate in the cooler northern regions, restoration could lead to a genetic bottleneck, i.e., leading to further genetic impoverishment. This can especially happen if the starting population is too small, resulting in the so-called "founder effect", which can lead to the consequence that the population is sensitive to extreme environmental conditions. This is due to a small number of alleles present in the founding population. A repetitive restocking during the restoration could

therefore reduce or prevent the founder effect. The influence of repetitive restocking is described by MOEHLER et al. (2011) for the Pacific oyster in the North Frisian Wadden Sea.

For restoration measures for degraded oyster stocks, large amounts of - mostly – spat or juvenile oysters will be needed. Healthy, natural wild stocks which could meet this requirement generally no longer exist. In addition, the transfer of donor oysters poses a potential risk of introduction of diseases and alien species. Against this backdrop, the use of farmed oysters as a potential source for restoration measures is gaining in importance. On the other hand, the use of spat from farms again harbors the danger of genetic depletion. In this context, LALLIAS et al (2010) posed the question to what extent oysters from breeding operations are, from a genetic point of view, suitable for restoration of wild stocks. They compared highly variable microsatellite loci in samples from spawn breeding farms (hatcheries), pond culture farms and natural stocks. The 12 samples collected were from Norway, Denmark, Great Britain, Ireland, France and Portugal. Genetic diversity was described by the parameters of allele frequency and heterozygosity.

The samples from wild populations exhibited the highest allele frequency and heterozygosity, therefore the highest genetic diversity. Oysters from spawn breeding farms displayed the lowest genetic diversity, while specimens from pond culture farms showed a mean diversity. With regards to oysters cultivated in ponds, the size of the pond played a role. In small pond cultures, genetic diversity was lower than in larger ones. In oysters from the large Norwegian ponds, genetic diversity was almost as great as in the wild stock.

The study has brought the problem of loss of genetic variability in hatchery-produced stocks to the forefront. The authors concluded: so long as hatcheries do not significantly change their production methods, the restoration of wild populations with breeding oysters (spat) may ultimately adversely impact the protection of the oyster and its sustainable use (LALLIAS et al., 2010).

With respect to a project to reintroduce the oyster in the North Sea, the transfer of individuals from a long-standing undisturbed wild stock would be the best course of action from a genetic point of view. However, due to the need to protect the relatively few still-surviving wild populations of *O. edulis*, it must be carefully examined whether this possibility is responsible from a conservation point of view.

In addition to oysters from a wild stock, farmed oysters should be used for restoration. Farms can primarily cover the great demand for spat and juvenile oysters. When choosing a breeding operation, it is to be ensured that the local breeding conditions produce progeny with the greatest possible genetic diversity.

Status of the European Oyster – Restoration in the North Sea

Table 2: Transplantation of oysters to and within Scotland (University Marine Biological Station Milport, 2007).

	Date	Details of translocation
A	1900s	Unknown quantities from Skye and Holland laid in unrecorded layings along west coast (Anon., 1885–1977).
	1950s	Thousands of oysters from Brittany (France) re-laid in 19 locations along west coast (Millar, 1961).
B	1990s	<i>O. edulis</i> from Loch Eriboll used to stock a hatchery in Orkney, which was used to stock a cultivation programme in the Kyle of Tongue (A. MacKay, pers. comm. 2003).
C	1800s	Unknown quantities from unknown locations re-laid in Long Hope Bay, St Margaret's Hope Bay and Widewall (Young, 1886).
	1912	800,000 oysters from an unknown location re-laid in Orkney (Millar, 1961).
	1920s	Oysters from Denmark re-laid in Orkney beds (Millar, 1961).
D	19 th century & 1990s	Loch Eriboll stock re-laid in Kyle of Tongue (A. MacKay, pers. comm. 2003).
E	20 th century?	Oysters from Loch Ainort removed to stock Broadford Bay (Millar, 1961).
F	1880s	Unknown quantities from Morbihan (France) re-laid in Loch Creran (Anon., 1885-1977).
	1894	Two consignments from Holland were re-laid in Loch Creran (Anon., 1885–1977).
G	From 1970s	Stock from Seasalter (England) layed in Mull (D. Wathen, pers. comm. 2003). Stock was also brought from the Orkney hatchery until early 2000.
H	1990s	Oysters moved from south Ulva to other locations around Ulva. <i>O. edulis</i> from the Isle of Colonsay also re-laid around Ulva (J. Howard, pers. comm. 2004).
I	1890s	40,000 oysters from Arcachon (France) <i>via</i> Whitstable (England) re-laid in Loch Sween (Smith, 1894; Millar, 1961).
	1947	Few thousand oysters from Brittany re-laid in Loch Sween (Millar, 1961).
J	1886	700,000 oysters from Loch Sween, the Hebrides and France re-laid in West Loch Tarbert (Anon., 1885–1977). Further restocking from unknown areas in the late 1800s (Millar, 1961).
	1950s	201,000 oysters translocated from Brittany to West Loch Tarbert (Millar, 1961).
K	1800s	Unknown quantities from France, Holland and Essex layed in Loch Ryan (Millar, 1961).
	1958–1960s	Thousands of oysters from Brittany re-laid in Loch Ryan (Millar, 1963).
L	18 th & 19 th centuries	Millions of oysters taken from the Firth of Forth and re-laid in England, France and Holland (Fulton, 1895; Millar, 1961; Anon., 1885-1977).
	1870s	30,000 oysters from an unknown source laid in unknown locations within the Firth of Forth (Fulton, 1895).

For artificial breeding of European oysters and mussels in general, one should endeavor to produce progeny with the highest possible genetic variability by "genetic management" or "selective breeding". This applies to all breeding methods, since only a small number of breeding pairs for the production of offspring can be used. In the case of *O. edulis*, several circumstances complicate a targeted production of offspring with high genetic diversity (JOYCE et al., 2013). With regards to development of gametes, there is no clear synchronization, and fertilization success during the reproductive period is very variable. Under breeding conditions, a possible synchronous spawning of gametes would be an important prerequisite for maximum "participation" of all breeding partners in the production of offspring. Another "obstacle" is often highly variable and shifted gender ratio. As a result, it is not considered which gender the selected breeding oysters currently exhibit and which phase of maturity the gametes have. Against this backdrop, research should strive to determine which environmental conditions determine, for example, the manifestations of the gender phases, and thus how a synchronous spawning of gender products can be induced (JOYCE et al., 2013).

Interim Conclusions

- Due to the relative genetic similarity of *O. edulis* populations in Europe, the geographical origin of potential donor mussels is not of primary importance.
- Other criteria, such as the absence of pathogens and the best possible ability for physiological adaptation to local environmental factors at the dispersal location are comparatively more crucial.
- However, the oysters selected for restoration should exhibit a high genetic variability in order to possess the greatest possible adaptability to stress factors in the new environment. A repeated distribution of the founder population could thereby improve genetic diversity.
- In breeding farms, brood batches should consist of a large number of animals (at least 50) so that the offspring exhibit a very high genetic variability. In addition, new brood batches with alternating parent animals from wild populations should be formed.
- For the release of breeding oysters as part of restoration measures, progeny from different brood batches should be used.

6 Ecosystem Services

Not only in Europe, but worldwide oyster reefs are included as one of the most degraded marine habitats. According to estimates, about 85% of the worldwide oyster reef habitats have been destroyed over the last 130 years (LOTZE et al., 2005; BECK et al, 2011). Along with the loss of the reefs, so-called ecosystem services, which are provided by vigorous oyster reefs, also become unavailable.

Ecosystem services refer to different types of direct and indirect benefits that humans obtain from ecosystems (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005). According to a UN study on the global state of ecosystems, four categories of services can be differentiated (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005):

- support services
- providing services
- regulatory services
- cultural services

All these categories apply to intact oyster reefs. They offer e.g. support services through their function as a food source and as protective habitat for juvenile stages of many fish species. As a providing service, they allow commercial fishing and aquaculture. Examples of regulatory services are improvements in water quality, coastal protection and stabilization of sediment. Cultural services such as tourism and environmental education are of importance in areas with a significant oyster culture such as in France.

According to COEN et al. (2007), measures for restoration and reintroduction of oyster stocks should keep all ecosystem services in mind. Their benefit is overall more valuable than the economic value of oyster harvesting alone.

According to COEN et al. (2007), ecosystem services of oyster reefs include:

- the provision of hard substrate
- the formation of vertical structures
- the provision of food
- regulation of water quality
- stabilization of coastal sediments

The economic value associated with mussel reef ecosystem services is strongly influenced by the reef's location and vicinity. Thus an intertidal reef already has a high value based solely on its coastal protection function. Another example is the filtration performance of a healthy reef, which can reduce water turbidity in the environment, which in turn provides better living conditions for macrophytes (GRABOWSKI et al., 2012).

If one considers the economic value of all services provided by oyster reefs, the investments associated with restoration measures can be viewed as economically efficient projects that generate a good return (GRABOWSKI et al., 2012).

Oysters are considered as "ecosystem engineers" or as "founder species". Due to their preference to settle on the own species, their ability to form reefs is inherent. Depending on the species and preferred habitat, the reefs and beds may be structurally different. For example,

Crassostrea virginica, native to the east coast of the United States, had in earlier times, inter alia, formed massive reefs in the littoral zone and thus made an important contribution to coastal protection. The current extensive activities in the United States related to restoration of degraded mussel reefs are dedicated not only to the recovery of *C. virginica* reefs, but also the restoration of reefs of other oyster species and their associated ecosystem services (BRUMBAUGH et al., 2006).

Basically, the domestic *O. edulis* also has the potential for reef formation, i.e., for flat to three-dimensional formation of biogenic hard structures. However, of the currently existing, anthropogenically-degraded wild populations, none form a biogenic habitat that would correspond to the "classic" reef. At most, smaller shell aggregates (mini reefs) exist, while the majority of oysters occur solitary. Also, in the "better beds" in the German Wadden Sea, the oysters were not found close together, but widely dispersed (HAGMEIER & KÄNDLER 1927).

The ecosystem services that could be provided over the long term from a restoration of the European oyster in the North Sea are, from a conservation perspective, primarily the creation of a structure-rich, biogenic hard substrate (reef) and the accompanying increase in biodiversity through a species-rich epibiontic fauna and flora. Even under optimal conditions, several decades would have elapsed until such time that a reef would exist. The first signs of reef formation to initially expect are clumpy oyster aggregates or "mini-reefs".

In contrast to the European oyster, the invasive Pacific oyster is a very effective reef builder. In a relatively short time, it has formed large reefs in its new home - the Wadden Sea (TROOST, 2010).

Interim Conclusions

- Important ecosystem services provided by oyster reefs include the provision of structure-rich hard substrate, an increase in food supply, an improvement in water quality and stabilization of sediments.
- Oysters must have opportunities for natural settlement on conspecifics and mussel cultch so that they can form reef structures over time.
- From conservation point of view, the most valuable ecosystem service of an oyster reef is the increase of biodiversity through provision of a richly-textured biogenic habitat that provides a living space for many invertebrates and fishes.

7 Current Status of European Oyster Stocks

As mentioned, of the many formerly large and widespread deposits of the European oyster, generally only a few small remnants exist. In some countries, there are still more or less natural wild stocks, but their existence is threatened by legal and illegal use. Other deposits are composed of regulated fisheries or managed populations. In addition, *O. edulis* is grown to a relatively small extent in aquaculture and mariculture.

Over the last 50 years, the aquaculture production of *O. edulis* has declined dramatically. While in 1961 a maximum of approximately 30,000 tons was still produced, by the 1990s, that amount had dropped to only 4,000 to 8,000 tons (Figure 14). This decrease is due to the occurrence of epidemic diseases and the resulting switch to aquaculture of the Pacific oyster, *C. gigas*.

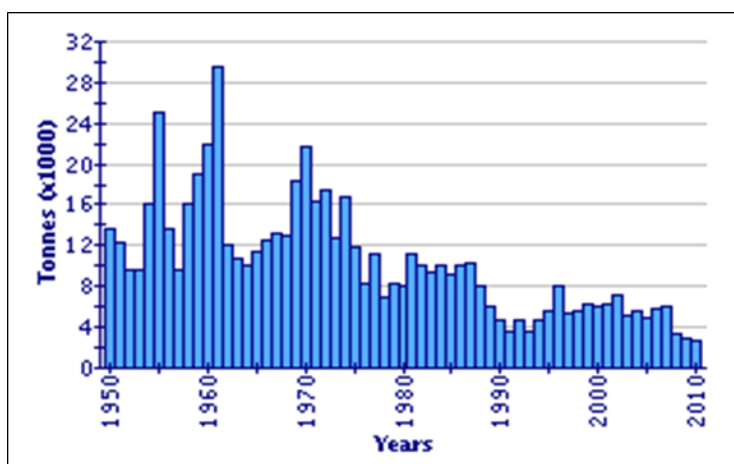


Figure 14: Progression of global production of the European oyster through aquaculture (FAO, 2004 - 2013).

The following statements contain information on the occurrence of wild stocks as well as oyster aquaculture and fisheries in some European countries.

In **Norway**, oysters occur from the Swedish border and north to the province of Helgeland. Their main area of distribution is, however, in the south along the coast of Skagerraks in the province of Aust-Agder. A mapping of the stocks was recently carried out there, which is to be extended in the future along more northern coastlines (BODVIN et al., 2011). The Norwegian stocks are still relatively original in terms of their genetic status. Several populations are likely to be of natural origin. Since 1934, there has been no systematic importation of oysters to Norway. Solely in 1964 were imported oysters distributed at a single site and possibly in 1999, when post-larval stages were illegally released. The Norwegian stocks are regularly inspected by the Veterinary Inspection Office and are certified as being free of pathogens (LAING et al., 2005).

The extent of aquaculture is low. Typically, the breeding of oysters takes place in so-called "polls". These are pond-like, separated fjord areas that offer distributed breeding oysters protection and also a slightly higher temperature than the ambient water. Since the substrate of polls tends to be muddy, the oysters and collectors for the settlement of oyster larvae in the water column are kept floating.

Norway, as other Nordic countries, aims at boosting domestic oyster aquaculture and conservation of wild stocks. Within the framework of the EU Interreg project entitled "Nord Ostron", universities and a marine innovation center are working together with similar facilities

in Sweden and Denmark to optimize aquaculture techniques and to strengthen Scandinavian cooperation.

In **Sweden**, oysters are naturally found along the West Coast in the province of Bohuslän from Gothenburg to the Norwegian border. These are mostly small and scattered deposits. Larger oyster beds are not found (Kent Berntsson, *Ostrea Sverige*, pers. comm.)

Relatively recently, a commercial oyster aquaculture operation was commenced by *Ostrea Sverige AB*. The Koster Islands-based company operates a hatchery facility and cultivates the spat in mariculture until they are ready for the market. The oysters produced are subject to a veterinary examination and are certified as free from *Bonamia ostrea*. *Ostrea Sverige AB* is a farm from which oysters for a restoration project can potentially be obtained (see 9.2, Selection of farms). For the previously mentioned Nord Ostron Project, the University of Gothenburg (project management) and *Ostrea Sverige AB* are participating from the Swedish side.

In **Denmark**, a larger oyster population is located exclusively at Limfjord. During a severe storm in 1825, a headland was broken in the west and a connection to the North Sea which hadn't existed for 600 years was restored. A few decades later, so many oysters were already present that a commercial fishery was possible. The population was continuously subject to severe fluctuations caused by natural factors and harvesting. In contrast to more southern populations, recruitment success is significantly influenced by the summer water temperatures.

Since 2000, the Limfjord population has increased significantly, as shown by the annual harvest data. With regards to diseases Bonamiosis and Marteiliosis, the oysters of Limfjord have a pathogen-free status. Exports to other pathogen-free areas are therefore allowed (LAING et al., 2005).

The oyster fishery in the Limfjord is the first in the world that has received a certificate from the Marine Stewardship Council (MSC) for sustainability and management (MOODY MARINE LTD, 2012). Harvesting occurs in the western areas of the Limfjord from May to October. Catch quotas are determined on the basis of an annual monitoring of the mapped oyster stocks.

The Danish Shellfish Center (DSC), situated in Nyköbing / Mors at Limfjord addresses such issues as sustainable use and measures to support the Limfjord population. It also maintains a spawning farm which deals with artificial spawning of *O. edulis*. The DSC was involved with several research projects related to the oyster, including the Nord Ostron project. As explained in more detail later, the DSC is a potential partner from which oysters can be obtained for a restoration attempt.

In the Danish Wadden Sea and in the EEZ, there appears to be no significant occurrence of *O. edulis*. At least, no information supporting their presence is available. A single source relates to Horns Rev 1 wind farm constructed in 2002 off of Blavands Huk. During 2003 - 2004 investigations of the marine growth (fouling) around the monopile foundations, specimens of the European oyster were detected in the area of the scour protection (ANONYMOUS, 2006).

In the **Netherlands**, the natural oyster beds in the Wadden Sea and in the province of Zeeland were harvested until 1860. Beginning in 1870, an oyster culture on the French model was developed in Zeeland, in the delta of the Schelde, Maas and Rhine (YONGE, 1960). After the loss of natural oyster beds in the Wadden Sea, there are currently still oyster stocks in Zeeland in the Oosterschelde (Yerseke bed) and in Greveling Lake. Both stocks are suffering from an infestation of *Bonamia ostreae*, which first appeared in 1980. No targeted ef-

forts will be made to stabilize the high disease-related losses due to restocking. However, there are indications that *O. edulis* has developed over time a certain resistance against *B. ostreae*.

In the Wadden Sea and in the Dutch EEZ, the European flat oyster has long thought to have been extirpated. In recent years, however, local evidence has been accumulating to the contrary. Most findings relate to offshore locations (STICHTING ANEMOON, 2013). This area was the home to the large oyster stock of the southern North Sea in the 19th century, which is depicted as a map in the OLSEN (1883) fishing Atlas.

Interestingly, *O. edulis* was also detected at the Egmon aan Zee wind farm built in 2006. The oysters were detected in September in the intertidal area of two monopiles during the study of fouling of three monopile foundations. However, no oysters were detected in samples collected at the scour protection. In addition to the European, the Pacific oyster had also settled on the monopile. During the initial fouling monitoring in 2006, no specimens of *O. edulis* were observed (BOUMA and LENGKEEK, 2012).

The waters around the **UK** are among the regions where in earlier centuries very large stocks of the European oyster existed. With the introduction of drag nets (dredges), the oyster industry maintained one of the largest fishing fleets of the mid-19th century.

Since the 1960s in **England**, a switch has occurred in oyster production from the fisheries-dominated production to oyster culture. With the loss of commercially-viable wild stocks, the oysters were now often cultivated in areas where natural oyster beds formerly existed. Especially in the estuaries of the County of Essex, juvenile oysters imported from other regions of England were raised in cultures (LAING et al., 2005).

The formerly large populations of oysters of the Wash as well as the English Channel and the North Sea are no longer present. Commercial harvesting of wild stocks only still occurs in a few areas. These are stocks in estuaries along the south coast of Cornwall, the River Thames and the County of Essex. In general, in the years leading up to 1950, there were oyster stocks in many locations that exhibited natural stock preservation (LAING et al., 2005).

In the Solent along the English Channel coast, intensive oyster harvesting was always traditionally operated. From 1972 to 2006, this was Europe's largest, self-sustaining oyster fishery. Today, after a series of unsuccessful stock recruitments beginning in 2006, the stock is practically extirpated (KAMPHAUSEN, 2012). An examination of the reproductive behavior should shed light on the cause of the collapse of the stock. It was found that the gender ratio was strongly shifted toward male reproductive status. The individual reproductive phases, however, did not appear disturbed, so that the potential for regeneration of the stock was still fundamentally present (KAMPHAUSEN, 2012).

Since the advent of *Bonamia*, the oyster industry has been dealing with measures to mitigate the damage caused by this disease. In addition, the robust Pacific oyster was increasingly cultivated.

In **Wales**, natural oyster beds in many coastal areas were intensively harvested by the end of the 19th century. The high demand for oysters in conjunction with a low recruitment led to a rapid decline of the oyster industry. Today, significant residual stocks only exist along the south coast at Milford Haven, Swansea and Porthcawl (LAING et al., 2005).

In 2002, dive studies were to provide more accurate information on the status of these remaining stocks. During the studies, live oysters were only detected in the estuary of Milford Haven. The maximum and minimum abundances found were 1.49 oysters / m² and 0.09 oysters / m². Elsewhere, the seafloor was also potentially suitable as oyster habitat. That no

specimens were found there is probably due to the overall low number of dive observations made (EMU LTD., 2002).

Along the east and west coast of **Scotland** and the coastal islands, numerous oyster deposits once existed. Until the beginning of the commercial fisheries in the 17th century, the oyster was only used by rural communities for their own use. Towards the end of the 19th century, most stocks had already been completely exploited. Thereafter, landings only occurred along the west coast (Loch Ryan, West Loch Tarbert) as well as the Orkney and Shetland Islands (UNIVERSITY MARINE BIOLOGICAL STATION MILFORD, 2007).

According to a study commissioned by Scottish Natural Heritage (SNH) on the status of *O. edulis*, populations present in Scottish waters are generally larger than those in other marine areas of the UK. As a comparative study of multiple microsatellite loci revealed, the populations also exhibit a relatively high level of genetic variability in the form of numerous allelic variants in combination with a high heterozygosity. This finding is an indication that the stocks have not reduced significantly in recent years. However, a current problem is the widespread practice of illegal harvesting of *O. edulis*. This can result in risk to the stock and nullification of restoration measures (UNIVERSITY MARINE BIOLOGICAL STATION MILFORD, 2007).

Currently, the largest commercially-operated Scottish oyster stock is the stock at Loch Ryan on the southwest coast. During the 20th century, the local fishing industry experienced phases of intensive production followed by periods of decline. Since 1988, the stock has been exploited with care and the annual production has ranged from 10 to 15 tons (UNIVERSITY MARINE BIOLOGICAL STATION MILFORD, 2007).

In **Northern Ireland**, oyster deposits are concentrated in fjord-like inlets, the so-called “sea loughs”, including Lough Foyle and Lough Strangford. The natural stocks are “refreshed” by spat from spawning cultures. In neither area are the oysters infected with *Bonamia* or *Marteilia*. In Lough Foyle, 80-200 tons (2005) of oysters are harvested annually. The regeneration of natural stocks should be accomplished through considerate and sustainable use. In Strangford Lough, measures to restore the original oyster beds were undertaken as part of an EU Interreg project.

Similar to the UK, the coasts of **Ireland** offer the physical conditions for widespread occurrence of the European oyster. Due to over-exploitation, the stocks are generally depleted. Nevertheless, traditional oyster harvesting is still conducted at several locations along the western and northern coasts. The annual harvest varies between 100 and 300 tons, depending on which quotas are enforced (TULLY & CLARKE, 2012). Unlike other countries, these are wild populations and not commercial oyster cultures. The harvesting takes place in autumn and winter with the help of dredges.

From 2010 to 2012, the status of the oyster at six locations along the west coast was recorded. As a result, very different biomasses of the existing stocks were determined. At 980-1330 tons, the inner Trallee Bay (County Kerry) exhibited the maximum and Lough Swilly in the north (County Donegal) at 100-124 tons exhibited the second highest biomass. At the other locations, the biomass was less than 50 tons. The density was typically <0.5 oysters / m². Maximum oyster density of up to 50 / m² was detected in the inner Trallee Bay. In addition to *O. edulis*, the Pacific oyster was often detected at all locations (TULLY & CLARKE, 2012).

In the Lough Foyle estuary, along which both the Republic of Ireland and Northern Ireland border, large quantities of oysters were previously harvested. Since *Bonamia* was detected there in 2005, harvest yields have been reduced (LAING et al., 2005).

France was the first country in Europe where, already in the middle of the 19th century, the populations of *Ostrea edulis* had collapsed due to overharvesting. Then, in comparison to other parts of Europe, methods of oyster culture were developed here very early. After the major stock losses caused by the epidemic outbreak of the pathogens *Bonamia ostreae* and *Marteilia refringens* in the 1970s, no measures to support the remaining wild stocks were undertaken. Given the persistent and widespread occurrence of Bonamiosis and Marteiliosis, the outlook for success of restoration measures were considered to be low. The epidemic occurrence of these diseases in the 1970's and 1980's led to the collapse in production of *O. edulis* from 20,000 tons to 1,000-1,500 tons currently (ROBERT et al., 2013).

In areas of former *O. edulis* deposits, such as in Brittany, the invasive Pacific oyster has since massively expanded.

Despite the current low level of economic importance, the European oyster is a relatively intensively studied research topic in France. This is evidenced by, for example, extensive comparative genetic studies conducted by the Ifremer Marine Research Institute to compare the genetic status of *O. edulis* in different regions of Europe. In addition, the selective breeding of *Bonamia*-resistant strains is being carried out at Ifremer. Other projects are dedicated to the development of genetic markers for targeted selection of desired properties. Ifremer also operates a research station with an oyster farm, with the aim to standardize and optimize culture conditions for artificial breeding of *O. edulis*.

In **Spain**, the decline of natural stocks began in 1778. It was only in the 1930's that experiments were first carried out in Galicia for the regeneration of the strongly depleted natural stocks. In the 1960's, the oyster industry was no longer profitable. Between 1974 and 1987, stocks shrank a further 80% after the occurrence of the pathogens *Bonamia* and *Marteilia*.

Recently, the domestic oyster is again being viewed as an economic factor. Various initiatives focusing on possible factors that would prevent the restoration of the oyster. In addition, a program for developing a *Bonamia*-resistant strain was initiated (LAING et al., 2005).

The breeding of the European oyster in Galicia is mainly operated on rafts. Each raft provides for the culturing of 200,000 - 300,000 spat.

Interim Conclusions

- Even though translocations of oysters were undertaken regularly and over centuries, in Northern Europe, namely in Ireland, Great Britain and Scandinavia, oysters stocks with relatively little impact from non-resident oyster populations still exist.
- In most regions in Europe, the value of still-existing oyster stocks is seen primarily in terms of economic and less in terms of ecological value. Most EU projects also primarily target the promotion of *O. edulis* aquaculture.
- Development opportunities for restoration and / or sustainable use exist only in areas that are free of pathogens. The success of restoration is also only possible if illegal taking of oysters is prevented.
- For a restoration of the European oyster in the German Bight, suitable donor populations are available. Due to their pathogen-free status, in particular concerning Bonamiosis, individuals from Scandinavian oyster stocks and / or farms are particularly suitable for import.
- Experience has shown that the process of recovery of depleted oyster stocks extends over a long period of time.

8 Current Efforts Towards Regeneration of Oyster Stocks

The regeneration or rejuvenation of degraded *O. edulis* stocks through the distribution of spat and / or mature animals has been common practice in Europe for centuries. Until recently, economic reasons alone drove the decisions. Thus, non-resident oysters were distributed into degraded stocks with the aim of continuing to ensure a rewarding local oyster industry (YONGE, 1960).

Only recently have nature and species-protection aspects played a role in regeneration programs. Ecosystem services such as habitat structure and biodiversity are, against the backdrop of international conventions and EU Directives such as the Habitats Directive and the Convention on Biological Diversity, becoming increasingly important.

Compared with other European countries, the most extensive measures to support depleted wild stocks have been carried out or are in planning in the UK and Ireland. Moreover, studies have been commissioned with the goal of examining the conditions for restoration of the oyster in areas of their former range. That management measures often have their origin in population support measures for the fishing industry does not rule out that they are also applicable for nature conservation issues.

In **Northern Ireland**, extensive measures to refresh the local oyster stocks were carried out in Strangford Lough as part of an EU-funded Interreg project (1997-1999), with the goal of enabling sustainable future harvesting. Initially, 75 tons of scallop shells (*Pecten maximus*, *C. gigas*) were distributed as substrate for oyster larvae in 1996 and 1997. In 1998 and 1999, 3,000 breeding oysters and 250,000 spat were then spread on the shells (KENNEDY & ROBERTS, 1999).

During the same period (1997/1998), KENNEDY & ROBERTS (2006) investigated the distribution of planktonic larval oysters in Strangford Lough. They found the highest densities in the vicinity of commercially exploited oyster cultures. These mariculture oysters, due to their high population density, represented a particularly effective source for larvae production. Based on their observations, the authors concluded that mariculture may have a positive effect on regeneration of oyster stocks in the vicinity.

In **Scotland**, locations with former oyster deposits on the Shetland Islands were examined for their current fitness for a reintroduction of *O. edulis*. In the littoral zone, most localities were determined to be suitable for settlement of *O. edulis* on the basis of their status as hard substrate, while the sublittoral localities, with the exception of two areas with harder substrate, were deemed inappropriate due to the presence of silt. The absence of live oysters in the Shetland Islands has demonstrated that a naturally recruiting population apparently does not exist (Shelmerdine & LESLIE, 2009).

Population support measures require a high logistical and financial effort. According to KORRINGA (1946), at least 10 million oysters are necessary in the summer in the Oosterschelde to ensure adequate larval presence during the spawning season. KENNEDY & ROBERTS (1999) demonstrated that stocking with 125,000 individuals at high density (> 82 m²) led to a 10-fold increase in recruitment in Strangford Lough within five years.

It is important to note that these figures represent only a rough indication and not a close relationship between the biomass of an adult breeding population and successful settlement of larvae produced there. Even at a constant spawning biomass, settlement success of larvae usually varies greatly from season to season. A small breeding population may well be associated with a high larval presence and a robust stock with low settlement success. Ultimately, the survival of the larvae and their successful settlement is as important as a high population density for the vitality of an oyster stock (LAING et al., 2005).

Several collaborative projects have been or will be funded by the EU which are primarily concerned with various aspects of *Ostrea edulis* aquaculture and partly of other mussel species. From the results of the issues addressed, future restoration and reintroduction projects can also benefit.

First and foremost, the "Oysterecover" project is cited. This project focuses exclusively on aspects of optimizing *O. edulis* aquaculture and measures to combat Bonamiosis. The primary objective of the project is a regeneration of depleted oyster stocks through effective control of Bonamiosis in coastal regions affected by the epidemic. Partners are research institutes and oyster farms from Spain, France, the Netherlands and Denmark (Oysterecover, 2013).

Another EU project entitled "SETTLE", deals primarily with the artificial breeding of *O. edulis*, especially with the conditioning of breeding oysters and the optimization of larval settlement. The results will lead to a set of "operating instructions", which will enable year-round artificial breeding of oysters (SETTLE PROJECT, 2013).

Compared to Europe, where regeneration of oyster stocks with respect to conservation and sustainability aspects has only just begun, the United States is in this regard already much further advanced and armed with practical experience. In the last 20 years, there have been numerous measures undertaken to support the restoration of degraded stocks or former oyster reefs. Initially, the primary goal of regeneration measures was the restoration of commercial oyster fisheries, as is still fairly common in Europe. However, with increasing knowledge of the direct and indirect ecosystem services of oyster reefs, the motivation for rebuilding of former reefs has changed. Instead of solely increasing harvest yields, ecological services such as water filtration, sediment stabilization and nutrient dynamics as well as the provision of biogenic reef habitats for a species-rich assortment of fauna and flora are also of importance for restoration measures (BECK et al., 2011). In addition, the function of oyster reefs in coastal protection and as a nursery area for juvenile fish plays an important role.

Often, the restoration work is carried out by local municipalities. These municipalities are supported by large conservation organizations such as The Nature Conservancy (TNC), by federal agencies such as the National Oceanic and Atmospheric Administration (NOAA) and by local non-profit organizations. The general public apparently assumes a considerable share in the restoration of oysters, as many sites on the internet attest to. Overall, the available information on the internet regarding the restoration of oyster reefs in the US is very extensive. It should be emphasized at this point, that only one guide published by TNC and NOAA provides background and practical information for the restoration of mussel reefs (BRUMBAUGH et al., 2006). Numerous references on the biology of oysters and the restoration of reefs can be found in the bibliography of COEN (2013).

Two examples from the US East Coast are considered representative for restoration projects in other parts of the United States. The east coast is home to the American oyster (*Crassostrea virginica*). In the Chesapeake Bay, where the oyster was once very numerous, less than 1% of the original stock remains today. In the course of extensive restoration measures, the stock should again significantly increase over the long term so that the originally-existing oyster reefs recur. (NOAA, 2013; WILBERG et al, 2013.)

Another area in which restoration measures have been carried out for years is the Hudson River in the port area of New York / New Jersey. Primary ecosystem services which are expected over the long-term in this area of future oyster reefs include a contribution to coastal protection by the protective function of the reef structure, and improvement of water quality

through increased filtration capacity (GRIZZLE et al., 2013; HUDSON RIVER FOUNDATION, 2010).

Interim Conclusions

- In Europe to this point, economic aspects have stood in the foreground for efforts to regenerate or resettle oyster stocks. EU projects are primarily intended to promote aquaculture and mariculture. More recently, however, the conservation aspect is increasingly becoming the focus.
- The recovery of depleted stocks is a slow process. A time frame of 25 years is quite realistic (LAING et al., 2005). New settlement of oysters would probably require even more time until a stable reproductive stock is able to be formed.
- The distribution of hard substrate, preferably in the form of shells, is an important component of restoration measures. Drifting of the shells due to bottom currents or over-sanding must be prevented.
- A high density of individual breeding oysters is an important prerequisite for optimal larval production.

9 Restoration of the Oyster in the German North Sea

In this report, general information was previously provided regarding abiotic and biotic parameters that are of importance as part of a planned restoration project. In the following sections, selected aspects with regard to potential restoration in the North Sea will now be directly addressed.

9.1 Genetic-based population analyses for determination of suitable *O. edulis* populations for restoration in the German North Sea

As mentioned in Section 5.4, the oyster populations in different parts of Europe usually exhibit no large genetic differences. Comparatively large differences occur only between the Atlantic (including the North Sea) and Mediterranean populations (LAUNEY et al., 2002; DIAZ-ALMELA et al., 2004).

To select a donor population, it is more crucial that the population itself displays a broad genetic variability (GAFFNEY, 2006. Lallias et al, 2010). In general, this applies more to wild stocks as to oysters originating from a breeding farm.

As part of this feasibility study, IfAÖ conducted studies of population genetics with the aim of selecting a potential area of origin of oysters for restoration. The focus has been placed on wild populations, as these display greater genetic variability (larger diversity of alleles) than oysters from farms (LALLIAS et al., 2010). Efforts were also made to acquire material from historical collections of oysters from the German Bight, in order to compare it with living populations. Unfortunately, the museums contacted had, at best, shell material, but not wet material (soft body) necessary for a possible genetic analysis (see below).

Population analysis

To investigate the possibility for restoration of potential populations from the North Sea area, the genetic distance of *Ostrea edulis* populations by calculated by comparing the cytochrome-c-oxidase-1 gene (COX1, Figure 15). The COX1 gene is also used for DNA barcoding, which is an established method for genetic identification of species.

In order to make confident conclusions regarding the distances of individual relatives of the same species, it is necessary to compare conservative genome segments of individuals with each other. The mitochondrial genome has a higher mutation rate than the nuclear genome. The mtDNA is present in more copies, which is an advantage, since PCR amplification and DNA sequencing is also possible with little and / or degraded tissue material. When selecting the gene segment to be used, it must be noted that the observed sequence length is not too short, and the genome section is representative. The COX1 gene offers the necessary prerequisites. As the complete mt genome sequence of *Ostrea edulis* is already known (NCBI GenBank Gene ID: 11341134), the primers for the desired gene sequence can be generated relatively easily.

The genetic studies were carried out in cooperation with the Department of Biology at the University of Rostock (Animal Physiology / Dr. R. Bastrop).

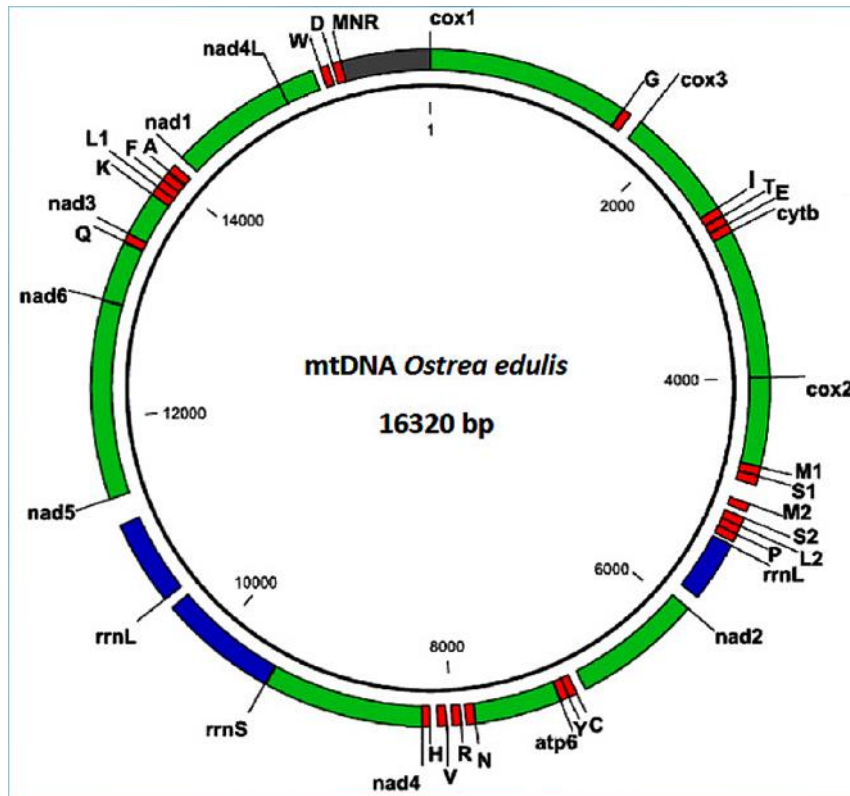


Figure 15: Map of the mitochondrial genome of *Ostrea edulis*. The gene sequences for proteins and rRNAs are green and blue, respectively (DANIC-TCHALEU et al., 2011).

Sample material

The oysters investigated were from wild populations from Loch Ryan in Scotland, from the Limfjord in Denmark, from the Koster Islands on the Swedish west coast and from Greveling Lake in the Netherlands (Table 3).

For a comparison of oyster populations originating from the German Bight, the acquisition of historical material was attempted. For this purpose, inquiries were made to the following museums and collections:

- Kiel Zoological Museum
- Hamburg Zoological Institute and Museum
- Senckenberg Museum
- King Bonn Zoological Research Museum
- Berlin Museum of Natural History

As mentioned, no collection possessed wet material from historic oyster stocks from the German Bight, which could have been included in the genetic comparison.

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Table 3: Origin of the samples for the genetic population comparison.

Country	Region	Source	No. of Oysters
Scotland	Loch Ryan	Loch Ryan Oyster Fishery Co LTD.	30
Denmark	Limfjord	Danish Shellfish Centre	30
Sweden	Koster Islands	Ostrea Sverige AB	30
Netherlands	Greveling Lake	Hatchery Roem van Yerseke	30
France	Quiberon Bay, Brittany	Literature: Danic-Trechau et al., 2011	-

Laboratory methods

Of the sample material, each consisting of 30 animals, tissue samples were taken from adductor muscles and gills and an aliquot of each sample frozen (-20 °C) and set in ethanol. For the isolation of DNA, a kit from the firm Quiagan (DNeasy Blood & Tissue Kit) was selected. This procedure yielded DNA material sufficiently clean for subsequent amplification by PCR.

For the PCR, primers which were known to have been found to be suitable for the amplification of a COX1 gene segment in various invertebrate taxa were initially tested (HCO 2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' and LCO 1490: 3'-GGTCAACAAATCATAAAGATATTGG-5'; FOLMER et al., 1994). However, these primers yielded an unsatisfactory result, and as a result specific primers needed to be developed. As the complete mitochondrial DNA sequence of the oyster has been known since 2011 (Figure 15, DANIC-TCHALEU et al, 2011), specific primers for the section of *Ostrea edulis* COX1 gene could be constructed based from Genbank data (Oe fw_1: 5'-ATGGGACGATTTGATAGAGC-3' and Oe rev_4: 3'-AGTAAGACCACCAATCGTGAAAAGGGCAATAAACCC-5'). The PCR reactions carried out with the new primers yielded clean PCR products that were suitable for further sequence analyses. Figure 16 shows the result of an electrophoretic separation of PCR products, generated with the new specific primers.

The PCR products generated with the specific primers were transferred to the University of Rostock for further DNA sequence analyses.

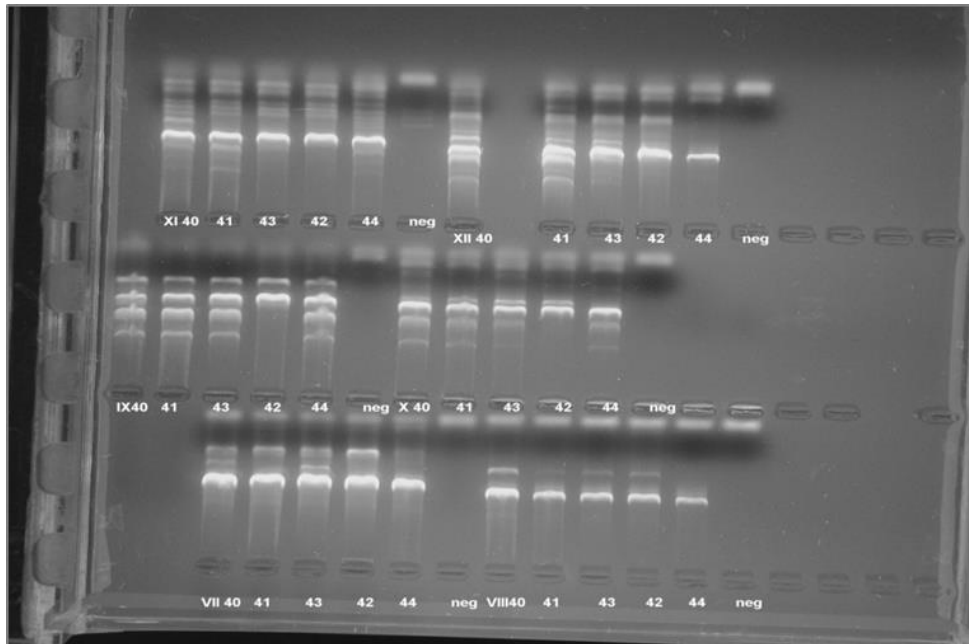


Figure 16: Electrophoresis of PCR products. The samples come from oysters from Loch Ryan (Scotland). Various primer combinations were tested.

Analysis of Data

For the determination of the familial relationship between the oyster samples from different origins, the creation or calculation of a phylogenetic tree is a suitable method.

In addition to the samples studied (Table 3), the COX1 sequence of French oysters on the basis of published genome MT (Danic-Trechau et al., 2011) was included in the comparison.

The first step in creating a phylogenetic tree was the cropping / editing of the sequencing products to create a usable alignment. For the identification of both the correct bases and the cutting to a representative sequence length, the Bioedit program was used. A representative base pair (bp = base pairs) length of 511 bp was chosen and all sequences in the selected section were cut. The complete sequence of *Ostrea edulis* with the included gene "Cox1" (Gene ID: 11341134), available in GenBank, served as reference. By using the ClustalW program, an alignment was constructed out of the existing sequences and transferred into FASTA format. The calculation of the family tree was performed using the MEGA 5.1 program (TAMURA et al., 2011). For the initial calculations, the Maximum Likelihood, or cluster method, was used. The result of the analysis showed a high similarity between all investigated *Ostrea edulis* populations. Also clearly visible is the wide gap to the two "outgroup" sequences used, *Crassostrea virginica* and of *Crasostrea angulata*, from the GenBank (Figure 17).

Status of the European Oyster – Restoration in the North Sea

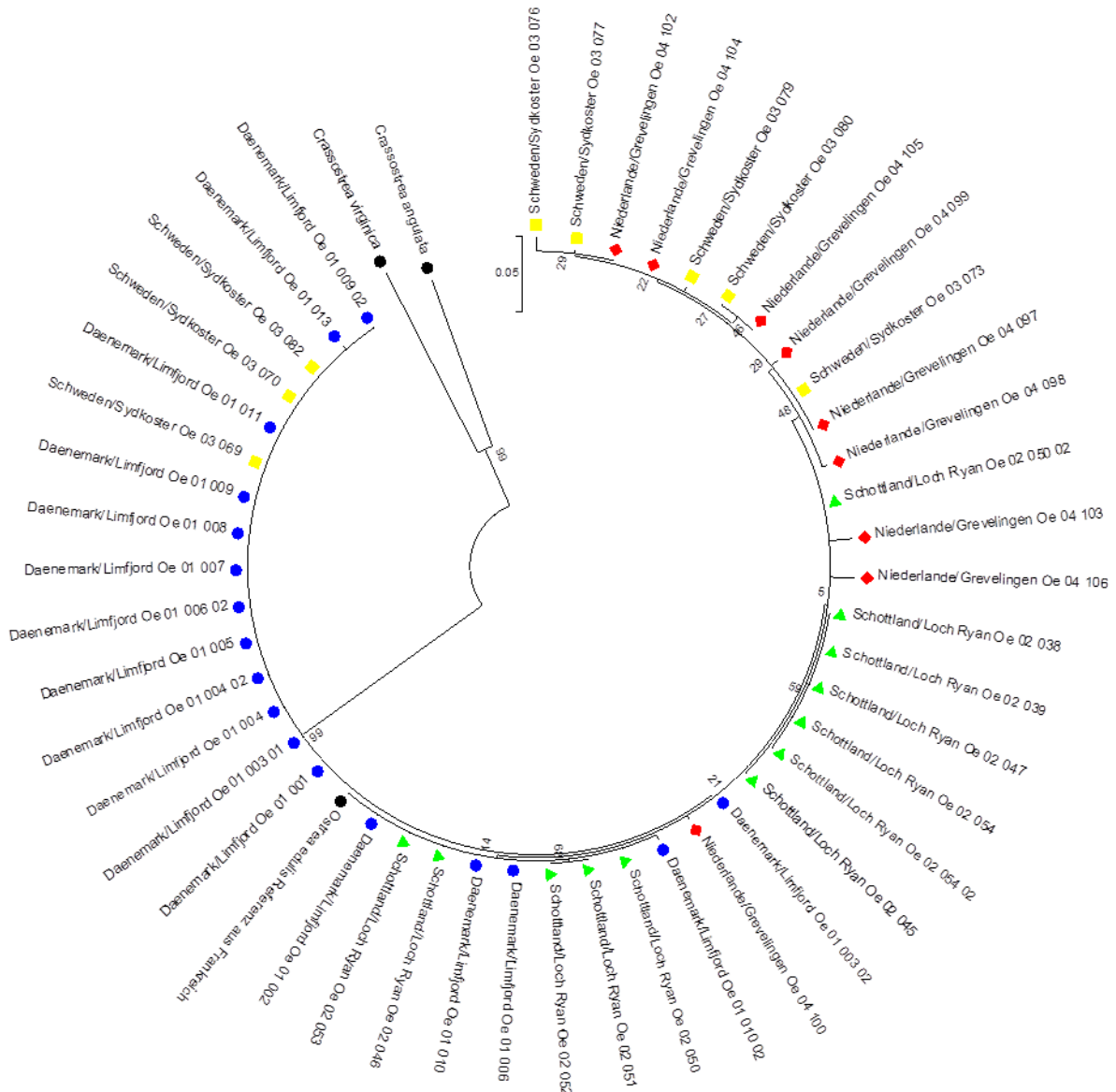


Figure 17: Family tree according to the Maximum Likelihood (● Limfjord / Denmark; ▲ Loch Ryan / Scotland, ■ Koster Island / Sweden; ◆ Greveling Lake / Netherlands).

The topology of the bootstrap consensus tree of the maximum likelihood method (Figure 18) shows no clear separation of the populations studied. The percentage difference in the main node is between 2% and 5%. The largest percentage difference occurred in samples from Scotland (Figure 19).

The fact that there is almost no genetic differentiation of populations in northern Europe was also demonstrated in the work of LAUNEY et al. (2002) and SOBOLEWSKA und BEAUMONT (2005). On the other hand, genetic differences between wild populations and oysters originating from a breeding farm were described by SOBOLEWSKA und BEAUMONT (2005) and LALLIAS et al. (2010), whereby the breeding farm oysters also displayed a lower genetic variability.

The low genetic differences between populations within the Atlantic metapopulations may be traced back to the historic "migration", in particular through aquaculture / restocking measures (LAING et al., 2005; SOBOLEWSKA & BEAUMONT, 2005).

Status of the European Oyster – Restoration in the North Sea

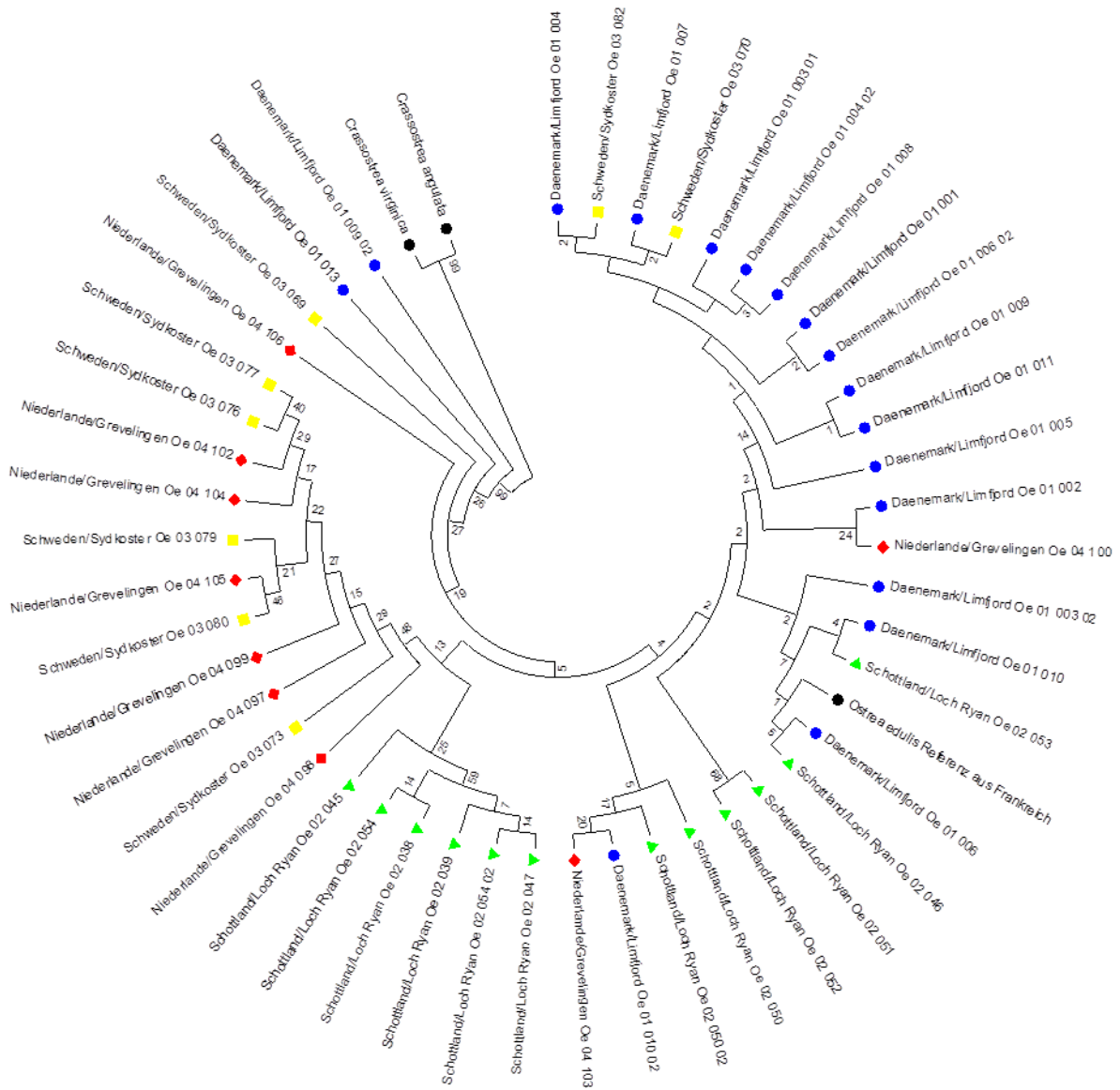


Figure 18: Bootstrap Consensus tree according to the Maximum Likelihood Method (cluster algorithm). Bootstrap values (in % of 500 repetitions) are provided at the nodes (● Limfjord / Denmark; ▲ Loch Ryan / Scotland, ■ Koster Islands / Sweden; ◆ Greveling Lake / Netherlands).

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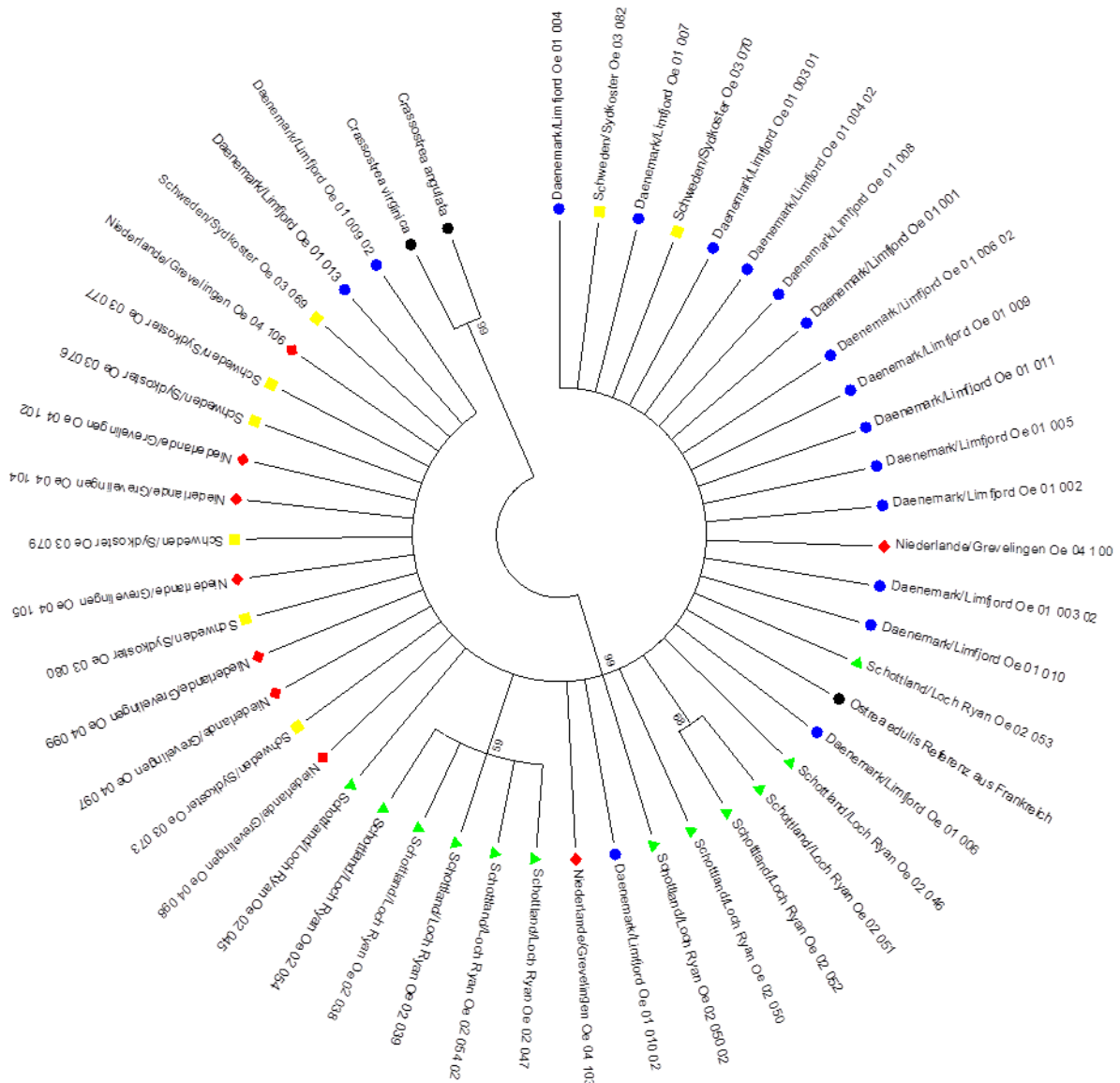


Figure 19: Condensed family tree (50% cut-off value) according to the Maximum Likelihood Method (cluster algorithm). Bootstrap values (in % of 500 repetitions) are provided at the nodes (● Limfjord / Denmark; ▲ Loch Ryan / Scotland, ■ Koster Islands / Sweden; ◆ Greveling Lake / Netherlands).

Conclusion

If one only considers the genetic status, the populations that occur along the southern and eastern North Sea from the Netherlands to Denmark / Sweden would work well for restoration of European oysters in the German Bight. An exchange of genetic material would be conceivable in the future without artificial stocking, if the settlement conditions for the European oyster, in particular in the German Bight, should improve, for example, through availability of hard substrate. That mussels or oysters can basically spread along the southern North Sea coast, was demonstrated in the work of WEHRMANN et al. (2000) and SCHMIDT et al. (2008), who described the spread of the Pacific oyster along the southern North Sea coast. A first indication that the European flat oyster could naturally return again to the German Bight, was presented by evidence of the European oyster in the Egmond aan Zee offshore wind farm off the Dutch coast (BOUMA & LENGKEEK, 2012).

For a restoration of the European oyster in the German Bight, oysters from the Limfjord would most likely work well, due to their availability and the absence of the pathogen *B. ostreae* and *M. refringens* (see sections 5.1 and 9.2). Since the oysters would also come from wild specimens, the genetic variability of the donor population would also be high. This would also facilitate the success of restoration and the sustainable development of the new founder population (LALLIAS et al., 2010). When using the Limfjord population as a donor population, the so-called "founder effect" could also be reduced (see Section 5.4), if the distributed oysters would mix with oysters that migrate naturally from the Netherlands. This would additionally increase the genetic variability of a newly-forming population in the German Bight.

Another possibility would be the use of oysters from Sweden and the Netherlands, whereas the oysters from Sweden which were available (see Section 9.2) would come from a single breeding farm, and not like those from the Limfjord, consisting also of wild harvested oysters. The genetic variability is therefore higher when stocking with oysters from the Limfjord. Oysters from the Netherlands should not be used due to the presence of pathogens there.

Interim Conclusions

- As the donor population for a restoration, populations with a high genetic variability within populations come closest in question, as is the case in wild populations.
- As almost no genetic differences exist between populations along the southern and eastern North Sea and along the coast of the Netherlands to Denmark, under appropriate conditions a genetic exchange in the future is possible even without artificial stocking. A donor population consisting of one of the still extant populations there would be most suitable.
- For a restoration of the European oyster in the German Bight, oysters from the wild population of the Limfjord or offspring from this population appear to be particularly well suited.

9.2 Selection of hatcheries and donor populations

In the course of this project, it became apparent quite early that oysters from Scandinavian countries would especially be taken into account as a donor population come because of their proven absence of diseases. From the Netherlands, it was also known that the local *O. edulis* stocks are not free from *Bonamia ostreae* in the Oosterschelde and in Greveling Lake. In this respect, the Netherlands dropped out as a possible source for *O. edulis*, even though there is an operation there which performs artificial breeding of the European oyster. In Scotland, with the oysters from Loch Ryan there is still a wild population that is not affected by Bonamiosis, but the larger (compared with Scandinavian oysters) geographical distance could indicate a poorer ability to adapt to the conditions of the German Bight. In addition, only marketable adult oysters and no spat can be obtained from Loch Ryan.

Against this backdrop, contact with one oyster hatchery each in Denmark and Sweden was undertaken. Both companies are also the only ones in their country which perform the artificial breeding of the European oyster. In Denmark, the Danish Shellfish Center (DSC), located on the Limfjord, is both a breeding station and research institute. It was and is involved in numerous research projects on aquaculture of shellfish. The Swedish company Ostrea Sverige AB does not conduct its own research, but works closely with research institutes. Both farms provided IfAÖ with oyster samples for the genetic population study. In order to be-

come acquainted with the production process as well as to explore the delivery conditions for oysters and willingness for cooperation within the framework of a restoration experiment, both operations were visited by Dr. Jens Gercken (IfAÖ). A separate report was submitted to BfN on the outcome of the visits.

In the following sections, the breeding farms and their production process for artificial breeding of oysters are presented.

Ostrea Sverige AB oyster farm

The Ostrea Sverige AB breeding farm was visited on 11 April 2013, and all production areas of artificial breeding of *Ostrea edulis* were observed. The company is the only company in Sweden that operates a commercial breeding with batches locally occurring as a wild population of the European oyster. The operation is located on the southern Koster Island in the town of Ekenäs, while their administration is located in Gothenburg (Figures 20 and 21). The waters around the Koster Islands, together with the Kosterfjord, form the first Swedish National Marine Sanctuary (NP Kosterhavet). The Koster Fjord is a trench that is connected to the Norwegian Trench and has a maximum depth of approx. 250 m. The availability of water with high and stable quality was a major factor in the selection of the Koster Islands as a location for the farm.

After completion of the hatchery facility in 2008, the breeding of *Ostrea edulis* began. Since the rearing of the larvae stage to marketable oyster takes several years, marketable oysters were first offered in 2013. According to the original plan, approximately 3 million oysters are involved.

Regarding production capacity, the company is still in the development phase. In the breeding facility, significantly more spat could be produced than is currently the case.

Address / Contact

- Ostrea Sverige AB, Hamnevägen 38, 452 05 Sydkoster, Sweden
- Dr. Kent Berntsson, kent.berntsson@ostrea.se

Production process

Water treatment: The production water is taken from a depth of 38 m from the Koster fjord. In the future, it is planned to extract the production water from an even greater depth of approx. 100 m. This water would be particularly rich in minerals and have less bothersome amounts of suspended solids and organic material.

The water pumped out of the fjord initially passes into two large circular pools on the top floor of the farm. After the passage through a protein separator and UV light for germ reduction, the water is transported to the ground floor where it passes a through fine gauze covered drum filter for separation of suspended solids. Finally, a brief heating (pasteurization) of the water to kill pathogens takes place. For the maintenance of algae stock cultures and small algae culture processing, the treated production water is additionally autoclaved.

Overall, the water treatment is relatively complex. The addition of antibiotics - such as in French farms - is not allowed.

Algae cultivation: All development stages of the oyster (brood oyster, larvae, spat) are fed with different types of microalgae. Starting material for the mass production of algae are strain cultures which are grown under sterile conditions. For mass production of feed algae, photobioreactors (from Biofence) are used (Figure 22). In the photobioreactors, higher densities of algae can be generated in comparison to plastic sacks, which are often used elsewhere for algae cultivation. To a small extent, culture of certain species of algae at Ostrea Sverige AB also takes place in plastic tubes.

Brood batches: On the coast of Bohuslän, the European flat oyster is found from the Norwegian border (Strömstad, Koster Islands) to Marstrand in the south. The stock consists of collections of mostly only a few square meters. Settlements of several hundred square meters are rare. Oyster beds or reefs appear to have never existed. The oysters are usually solitary and only seldom in small aggregates. According to fishermen, temperature conditions that permit reproduction occur on the coast of Bohuslän only once every five to seven years.

For breeding, oysters are collected from the wild stock of the Koster archipelago at shallow water depths (1-8 m). Oysters from other locations along the coast serve the breeding process by increasing the genetic variability of offspring.

The animals selected for breeding are conditioned in a separate tank for up to 1.5 months to induce spawning. A shorter conditioning with a daily 1 °C temperature rise is common (broodstock conditioning).

Each brood batch consists of approx. half of wild oysters and half of oysters from their own breeding (selective breeding). In the hatchery, several brood batches can be attended to simultaneously. Spawning larvae exhibit positive phototaxis and move into a container via an overflow. Since spawning of the larvae is not synchronized, a daily check of the collection tank is necessary (Figure 23). The offspring from different brood batches are not mixed, but rather separately reared through the following steps.

Larval culture: The planktonic larval stage is the most sensitive stage in the life cycle of the oyster. In this respect, the mortality is generally very high. If 2% of the larvae reach the stage of metamorphosis, that is already considered a good result for larvae handling.

The handling of larvae occurs in vertical plastic tubes that are perfused from the bottom with air. Microalgae are added as food. After approx. 10 days, upon reaching the eyespot stage, the larvae have reached the level of competence to adhere to a substrate (Figure 24).

Spat production: as adhesion substrate, the larvae (0.3 mm) are offered fine granules of ground oyster shell (<1 mm) in a vessel with a perforated bottom. After attachment to individual shell fragments, the larvae undergo their metamorphosis into an "actual" bivalve. The very small spat are now initially - as planktonic larvae - held in vertical, air-perfused tubes and supplied with micro-algae as food (Figure 26). Only when they have reached a size of just over a millimeter, the transfer into round containers with a perforated base takes place. These containers hang in troughs containing production water with algae as the food source. The "nursery" of Ostrea Sverige AB is dimensioned so that a maximum of approx. 12 million spat can be reared. At the time of the visit, only a small area was in use (Figure 25).

Once the spat have reached a size of 5-10 mm, further breeding in the wild takes place in a so-called FLUPSY system (Floating Upweller System), which is anchored as a raft near the port of Ekenäs. The oysters are now stacked in flat plastic baskets that allow upflow from the bottom with sea water. Via a motor-driven propeller, a strong sea water circulation is generated, so that large quantities of juvenile oysters can be supplied with food (Figure 27).

Mariculture: The final, multi-year growth of oysters to marketability takes place in plastic baskets that are deployed along the west coast of the southern Koster Island. Here, too, the oysters require intensive care. Thus, more or less frequently depending on the season, the baskets must be freed of fouling by organisms such as ascidians, barnacles and mussels. In addition, the number of ever-growing animals in the baskets must be regularly reduced. Since the cultured oysters under these conditions are also sexually mature and reproduce, the larvae spawned contribute to the general larvae presence in the region. After ca. 3 years of mariculture, the oysters have reached marketability.

Health Status

The oyster stock of the Koster Archipelago and breeding oysters are tested annually by the veterinary authorities. An infestation by *Bonamia sp.* and *Marteilia sp.* has not been demonstrated. Other occurring epidemic diseases have also not occurred on the coast of Bohuslän.

Production capacity and prices

Ostrea Sverige AB is a relatively young company and has not yet reached maximum production capacity. In 2013, a production of 3 million spat was announced. The capacity of the farm, however, is designed for 12 million spat. Planning target for 2015 is a production of 300 tons of marketable oysters.

Sufficient oysters at different development stages for a pilot project towards restoration of the oyster could already be made available from the current production. It makes sense that oysters should only be applied on a large scale in the German North Sea once it has been demonstrated, as part of a pilot project, that oysters develop well at the site and it is clear that they reproduce there.

The prices for individual spat (20 mm) are currently at 1 SEK (€0.12); the price for a market oyster is 10-15 SEK (€1.20 to €1.75).

Research

Ostrea Sverige AB does not have its own research department. However, there is close cooperation with research institutes and other farms in order to, inter alia, optimize particularly critical stages of oyster production. Close cooperation as part of joint research projects exists with the adjacent Sven Loven Center for Marine Sciences (formerly Tjärnö Marine Biological Laboratory) and the Danish Shellfish Center (DSC). In addition, an intensive exchange of experiences with other farms in Scandinavia exists. For example, the company was a partner in the "Nord Ostron" project, along with other oyster farms in Norway, Sweden and Denmark.

Interim Conclusions

- Ostrea Sverige AB can supply high quality European oysters from different developmental stages for a restoration attempt in the German Bight. On the part of the company, fundamental interest in a substantive cooperation within the framework of a pilot project for the restoration of the oyster also exists.
- The oysters of the Koster Islands are adapted to environmental conditions that would enable successful adaptation to the hydrographic conditions in the German Bight.

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- The oyster stock is free of the pathogens *Bonamia ostreae* and *Marteilia refringens*.
- In its corporate objectives, Ostrea Sverige AB has committed itself to environmentally-friendly oyster farming. Because of the location of the farm in a national marine sanctuary, strict constraints designed to prevent a negative impact of the farm on the marine environment are already in place (e.g. prohibition of antibiotics).

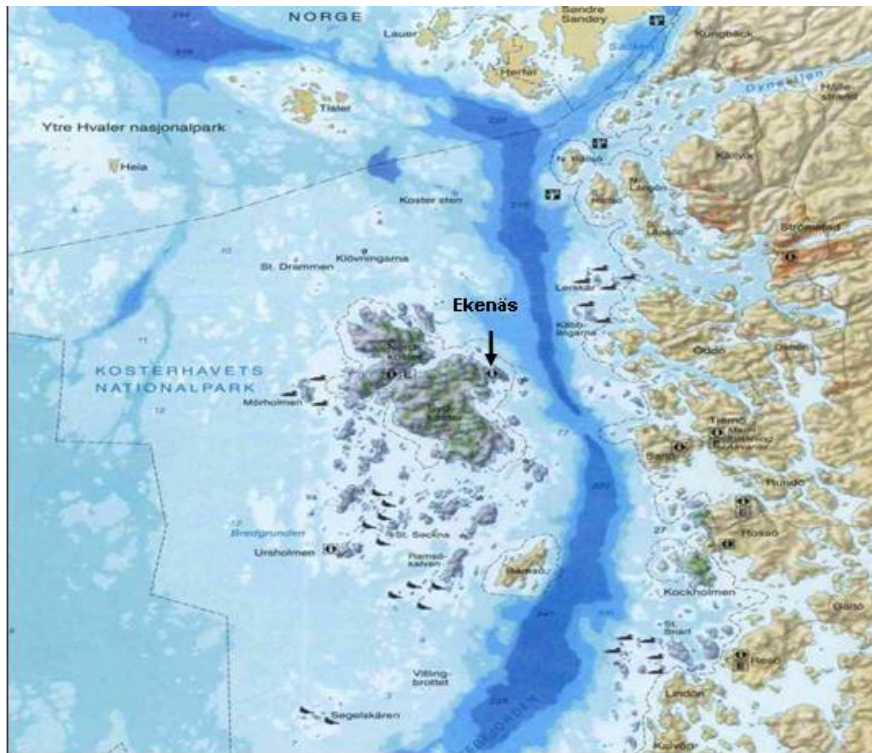


Figure 20: The Ostrea Sverige AB hatchery is located in the town of Ekenäs on the southern Koster Island. The nearby Koster fjord, an offshoot of the deep Norwegian Trench, enables the extraction of mineral-rich deep sea water for oyster breeding.



Figure 21: The Ostrea Sverige AB hatchery is located direct in the port of Ekenäs/ Sydoster.



Figure 22: Mass production of microalgae in a photobioreactor system (Biofence).



Figure 23: Brood batches with a group of oysters. The positive phototactic larvae pass through the overflow into a catch basin.

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Figure 24: The culture of oyster larvae or spat shortly after the adhesion phase takes place in vertical tube containers. The larvae or small spat are kept in motion by air escaping from the base.



Figure 25: Hall for growing spat. Early stages of spat are located in the round containers that are immersed in the trough-shaped tank.

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Figure 26: Handling of young spat in round containers with perforated bottom. The green water color is a result of the microalgae which serve as food for the spat.



Figure 27: Hanging baskets with spat on the raft. The FLUPSY system ensures a constant supply of water and therefore also of food.

Danish Shellfish Center (DSC)

The production area for artificial rearing of *Ostrea edulis* associated with the Danish Shellfish Center (DSC) was visited on 17 April 2013. The DSC was founded by local and regional authorities and the shellfish industry as a nonprofit and independent institute for research, technology and development in 2002. It is located in the western part of the Limfjord in the town of Nykøbing on the Island of Mors (Figures 28 and 29). Recently, the DSC became a part of the National Institute for Aquatic Resources at the Technical University of Denmark (DTU Aqua).

The overall objective of the DSC is sustainable use of coastal waters with emphasis on aquaculture and fisheries of shellfish. Participation in projects for basic research and applied research is one of the main activities of the DSC. In addition to laboratories, the DSC offers a facility for shellfish farming (hatchery) and equipment for longline culture of mussels. The breeding facility is mainly used for breeding of the European oyster (*Ostrea edulis*). Currently, the breeding of lobsters is also being conducted on a small scale.

Address / Contact

- Dansk Skaldyrcenter, Øroddevej 80, DK-7900 Nykøbing/Mors
- Dr. Jens Kjerulf Petersen (CEO), jkp@skaldyrcenter.dk

Production process

Water treatment: The production water is extracted from the Limfjord at a shallow depth of about 3 m in the vicinity of the DSC. It first passes into large circular tank to allow larger particles to settle. Then, the water is passed by UV light for microbial reduction and a sand filter. The pre-treated water is then fed to further processing facilities, each of which provide treated water for different production stages of the breeding facility (algae breeding, larvae culture, etc.). In these processing facilities, downstream water treatment is provided, including further treatment with UV light and removal of suspended solids in a drum filter covered with plankton gauze.

Algae cultivation: Different types of microalgae serve as food for all stages of oyster farming (brood oysters, larvae, spat). Source material for the mass production of algae is strain cultures grown under sterile conditions. For mass production of feed algae, plastic tubes or plastic pipes are used (Figure 30).

Brood batches: As source material for breeding, oysters are removed from the wild stock of the Limfjord. Approximately 50 animals of similar size form a brood batch. In the hatchery, several brood batches can be attended to simultaneously. Fluorescent lighting simulates a day-night rhythm (Figure 31).

Larval culture: At the time of the visit, no larvae were in the holding containers because the conditioning of brood oysters had just begun and no oysters had yet spawned. As in the natural environment, the planktonic larval phase is the most sensitive life stage and represents by far the highest mortality.

The handling of larvae occurs in vertical plastic tubes that are kept in motion by a stream of air from below, and contain a microalgae mix as a food source. Once the larvae have reached the eyespot stage, they have the ability to adhere to a substrate.

Spat production: Finely ground oyster shell (<1 mm, reference from Ostrea Sverige AB) serves as adhesion substrate. After adhesion to the shell particles and metamorphosis, the still very small spat are initially kept in vertical flow-through tubes and supplied with microalgal food. Only once they have reached a size of one to two millimeters, are they transferred into round containers with a perforated bottom. These containers hang in concrete channels that are traversed by microalgae-enriched production water. Here, the small spat grow into juvenile oysters (Figure 33).

Health status

The stock in the Limfjord has been regularly studied since the 1990s for the occurrence of diseases. An infestation by *Bonamia ostreae* and *Marteilia refringens* has never been documented. Since 2005, the absence of these epidemic pathogens has been confirmed by an EU certificate.

Production capacity and prices

The breeding success is subject to substantial fluctuations and it is generally not possible to selectively produce a certain number of spat from, for example, the known size of the brood pair batch. In contrast to the Ostrea Sverige AB farm, economic aspects are not priorities for the DSC. Upon good breeding success, however, commercial exploitation of the spat by, for example, international sale does occur.

In the case of a restoration project, the DSC could provide spat or juvenile oysters. Adult oysters should be harvested from wild stocks on the Limfjord (see below).

The price for individual spat (20 mm) is currently at 1 DKK (€0.13); the price of a kilo of adult oysters is 40-45 DKK (€5.40 - € 6.00) (August 2013).

Research projects

Since its founding in 2002, the DSC has been involved in numerous research projects for breeding and culture of shellfish and algae. The dissemination of research results to industrial users has played an important role.

With regard to the European flat oyster, the DSC was involved in three Danish national projects. These projects were concerned with the artificial breeding of oysters and with various systems for mariculture of spat under natural conditions.

Participation in the joint project "Nord Ostron" served as an exchange of experience between research institutions and oyster farms in Scandinavia. Good cooperation exists, for example, with the Ostrea Sverige AB farm.

Within the framework of the EU project "Oysterecover" (2010-2013), DSC tasks included the in situ production of spat by exposure of different adhesion substrates under natural conditions. In addition, the stock of oysters in the Limfjord was evaluated for sustainable commercial use with regards to its current size and in terms of restocking.

Interim Conclusions

- As a research institution with farm operations, the DSC represents both a highly-suitable cooperation partner for research projects as well as a potential supplier of European oysters for a pilot restoration project. Readiness for future cooperation is present on the part of the DSC.
- Although the breeding facility exhibits a rather "research" nature in terms of its size, it is capable of providing sufficient spat or juvenile oysters for a restoration project. The demand for oysters would not otherwise apply ad hoc, rather a restoration project would be preceded by a planning phase for which the supplier of oysters would be involved.
- The brood batches come from the Limfjord and are therefore free from infestation by *Bonamia ostreae* and *Marteilia refringens*. The absence of the pathogen is confirmed by an EU certificate, thereby one of the potential requirements for the transfer of oysters into other territories has been fulfilled.

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Figure 28: The Limfjord in northern Jutland. The oyster fishery is mainly operated in the western part of the Limfjord. Arrow: DSC in Nykøbing / Mors.



Figure 29: The Danish Shellfish Center (DSC) is located on a promontory at Nykøbing / Mors.



Figure 30: Mass cultivation of microalgae in various plastic tubes.



Figure 31: Tanks with different batches of brood oysters. The fluorescent lights simulate a day-night rhythm.

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Figure 32: Each brood batch consists of a large number of approximately equally-sized oysters.



Figure 33: The concrete troughs containing microalgae-enriched production water. Inside hang the sieve-like round containers with the spat.

The Limfjord oyster stock as potential donor population

As part of a project to restore the European oyster in the German Bight, spat or juvenile oysters and adult oysters should be used. While the former can be obtained from the mentioned Swedish and Danish farms, the latter can be provided from wild stocks in the Limfjord.

As the largest Danish fjord, Limfjord is connected in the west to the North Sea and in the east by the Baltic Sea. After the connection to the North Sea was closed for several centuries, it reopened in 1825 following a severe storm. The Limfjord is a shallow body of water. The average water depth is 7 m; large areas are less than 5 m deep.

Ostrea edulis was detected in the Limfjord relatively shortly after the opening 1825. The stock evolved so quickly and to such an extent that their exploitation was stipulated early under state supervision. As records show, the oyster stock always exhibited significant fluctuations. The peak in stock that has occurred in the last decade and the related increase in the harvest rate is primarily due to an exceptionally successful recruitment in conjunction with a good food supply as a result of eutrophication of the Limfjord. Often, the water in the Limfjord does not reach the required temperature for successful reproduction.

The oyster fishery in the Limfjord is the only one in northern Europe where wild stocks of *Ostrea edulis* are fished on a larger scale. In addition, the oyster fishery is the first worldwide that has received a certificate from the Marine Stewardship Council (MSC) for their good management and sustainability. As an example, the oyster stock is examined annually by scientists from DTU Aqua (Danish Technical University) with respect to its abundance and based on the results, adjusted quotas for local harvesting are set (MOODY MARINE LTD, 2012).

Harvesting occurs from October to May in the western part of the Limfjord. The maximum 12-meter-long cutters use very light drag nets (dredges; 1 m width; <35 kg) (Figures 36 and 37). Oysters cannot be harvested from shallow areas with a water depth of less than 3 m. In the main harvesting area, Nissum Bredning, the catch is only allowed below a water depth of 4 m. Through these harvest limitations, the possibility of oyster recruitment in deeper water by the unused stock exists. The total biomass of the oyster harvest in 2005-2006 was 3,500 tons according to an estimate by KRISTENSEN & HOFFMANN (2006).

The Nissum Bredning (Figure 34 and 35) and other large areas of the Limfjord enjoy protected status as Natura 2000 sites. Fisheries and conservation agencies work closely together to enforce environmental regulations and to ensure that the mussel industry (mussel, oyster) does not run contrary to nature conservation objectives.

Overall, a well-established fisheries and conservation management ensures the sustainable maintenance of the oyster stock in the Limfjord, while safeguarding the interests of environmental protection. Because of its geographical proximity to the German Bight, Limfjord oysters are expected to display good adaptability to the hydrographic conditions in the North Sea. Furthermore, the absence of pathogens such as *Bonamia* and *Marteilia* is another positive aspect that speaks for Limfjord oysters as favorable candidates for a restoration project in the North Sea.

Seen as a whole, between the wild oysters from the Limfjord and the breeding oysters from the Danish and Swedish farms, suitable sources of *Ostrea edulis* for restoration in the North Sea are available. One reason to favor the oysters from the Limfjord is the fact that they may be better adapted to the environmental conditions in the German Bight due to their geographical proximity in comparison to oysters from distant locations.

Interim Conclusions

- As part of a restoration experiment, adult breeding oysters should be applied in addition to juvenile oysters. These should preferably come from the wild stocks of the Limfjord. These oysters are adapted to the changing environmental conditions in nature. In addition, one may assume that a sample taken from the wild stock has a higher genetic variability than oysters from a farm.
- From a conservation perspective, the MSC certification of sustainably managed fisheries in the Limfjord is a criterion that speaks for an import of oysters from the area.
- The oysters in the Limfjord and thus also those from the DSC farm are free from infestation by *Bonamia ostreae* and *Marteilia refringens*. The absence of these pathogens is confirmed by an EU certificate. Thus, one of the possible requirements for the transfer of oysters to other destinations has been adhered to.
- Even if the oysters produced by the Danish and Swedish farms can be recommended without limitations for a restoration project, a strong argument towards a preference of the oysters from the Limfjord is provided by the presumption that they may be better adapted to the environmental conditions in the German Bight due to their geographical proximity, when compared to oysters from the more distant Swedish breeding stock.

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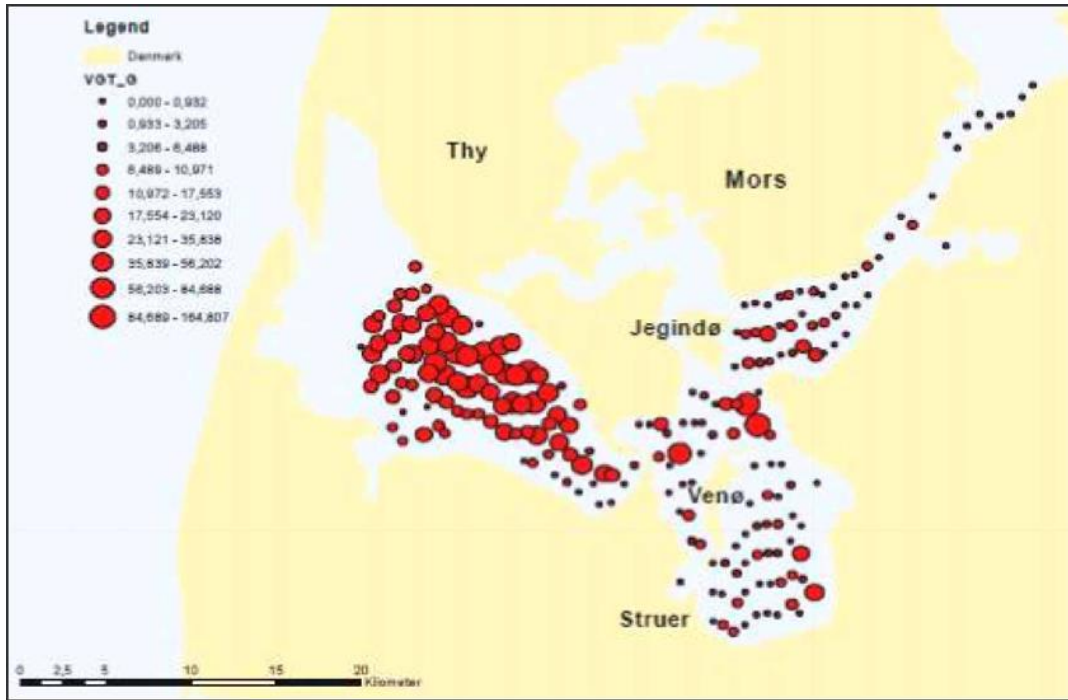


Figure 34: The oyster industry is only operated in the western part of the Limfjord. This map shows the location and abundance (g/m²) of oyster stocks on the basis of a monitoring study carried out in 2005 (from: KRISTENSEN & HOFFMANN, 2006).



Figure 35: Oyster shells on the beach of Oddesund Nord near the local harbor.

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Figure 36: Mussel cutters in the harbor at Nykøbing. Most fishermen harvest both mussels and oysters.



Figure 37: For the oyster harvest, the use of smaller and lighter dredges (max. 35 kg) is mandated.

9.3 Site selection in the German North Sea

When selecting a site for the restoration of the European oyster, both the needs for a suitable habitat as well as existing and planned future uses are to be taken into account.

As for the Wadden Sea, no restoration is feasible given the current fishing practices. The territories of the former oyster beds in the Wadden Sea are now used extensively by the shrimp fishery. Even if oyster larvae were present in the plankton, they would have no chance to settle at their former sites, let alone grow there, for lack of a suitable settlement substrate (NEUDECKER, 1990a). In addition, the prevailing strong fluctuations of abiotic environmental factors and the tidal currents are likely to reduce the chances of a successful re-settlement and recruitment from the outset.

In addition, the protected status of the Wadden Sea (National Park and World Heritage Site) might not allow for an import or reintroduction of mussel species into this area. A judgment of the Federal Administrative Court (BVG, Az.: 4 B 18.12) has now confirmed the decision of the Higher Administrative Court of Schleswig (Az.: 1 LB 19/10, December 2011) which places a ban on the import of mussel spat from areas outside the Schleswig-Holstein Wadden Sea as stock mussels for cultures in the national park.

Basically, the deeper and offshore areas of the German Bight offer better starting conditions for a restoration attempt. The important abiotic factors of temperature and salinity exhibit less variation than in the coastal sea region.

When choosing a location, it is generally assumed that the former distribution areas of oysters in the open North Sea exhibit a different condition today than in historical times. The changes were already set in motion with the destruction of oyster beds by oyster harvesting. The present state of the historic oyster beds areas is likely to be influenced mainly by fishing, which has been operated there since the exploitation of the oyster deposits. The fact that no oysters are currently found in the deeper sublittoral zone, in the area of the former, extensive oyster beds, can be ascribed with a high probability to the ongoing, massive disruption posed by fishing with benthic trawls.

Due to the diverse usage requirements, it is difficult to select areas that are not subjected to any use. Overall, the focus should be directed to areas that already have some level of protected status. But even in these areas, for example, bottom trawling is allowed. An important prerequisite for a successful reintroduction of the oyster, however, is the presence of areas that are free from trawling that disturbs the seafloor.

Potential restoration sites should exhibit no major fluctuations in relation to water temperature and salinity. This condition is most likely present in the deeper sublittoral zone, preferably at water depths greater than 10 m.

Furthermore, the presence of hard substrate and low sedimentation rates are of fundamental importance to successful settlement of oyster larvae. In this case, the current conditions in a region of sea are of importance with regard to the settlement of larvae on a suitable hard substrate. On the one hand, the larvae should not drift too far away from the founder population, on the other hand a stronger current also carries with it a favorable supply of food and provides a "clean" hard substrate for settlement. Existing local current data and / or hydrodynamic models should be consulted to estimate the potential for larval drifting

The offshore oyster stocks were mostly located in areas designated as predominantly fine sandy seabed in the sediment map of FIGGE (1981) (Figure 38). Sandy seabed does not generally stand in the way of oyster bed development. Pre-requisite for their development is

a base of mussel cultch, which in natural oyster beds forms over a long period, primarily from autochthonous shells.

Due to the widespread occurrence of sandy sediment, many opportunities for restoration of the oyster are apparently offered. The areas of former oyster beds may not necessarily have a priority, since it can be assumed that the former hard "oyster bed" substrate is certainly no longer available. The reef structures of oyster beds have already been destroyed in the course of oyster harvesting. Thereafter, intense fishing with bottom trawls determined the state of the seabed.

Marine areas with proven hard substrates such as gravel and stones are not places where oysters preferably settle. Oyster larvae tend to avoid these substrates and clearly prefer shells, as field studies in Scotland have demonstrated (UNIVERSITY MARINE BIOLOGICAL STATION MILFORD, 2007). That hard substrate is not, per se, populated by *O. edulis*, is also demonstrated by the fact that no oysters are present in many areas of the EEZ in which hard mineral substrate occurs.

A restoration of the oyster in the German EEZ can only have a chance of success if the site selected is completely protected from disruptive interventions. This raises the question of whether for individual areas of the former oyster deposits, there is already a certain protection status resulting from the designation of protected areas. In Figure 39, the historic oyster deposits are displayed together with existing Natura 2000 sites (SCI and SPA). Of the four protected areas (MPA) reported in the German EEZ, only the "Borkum Riffgrund" (Borkum Reef Ground) area lies in an area of former oyster deposits. At least this protected area extends into the extensive oyster ground in the southern German Bight documented in the Piscatorial Atlas of OLSEN (1883). The areas of the offshore oyster deposits listed in the fishing map from 1915 do not coincide with any of the other protected areas. However, some of the oyster beds were near the "Sylter Außenriff" (Sylt Outer Reef) reserve, which projects the furthest into the central region of the EEZ.

Protected areas would really only offer oyster's protection if it were to involve no-take zones, through which bottom trawl harvesting would be completely banned. However, this is not the case in the existing areas. On the contrary, the use of mobile, ground-disturbing equipment is allowed.

With the increasing amount of offshore wind farms, virtual "no-take zones" are forming since fishing is either banned or at a minimum no mobile equipment may be used. In this respect, wind farms meet an important site selection criterion for the restoration of the oyster.

This is and will increasingly be the case with the expansion of offshore wind farms. Figure 40 shows which wind farms are already in operation, under construction or are planned in the German Bight and the vicinity of the historic oyster deposits. There are numerous overlaps here with regard to the location of the near-shore, southern wind farms and the wind farms projected further north or northwest.

With the expansion of offshore wind farms, these will represent an extensive, dominant use of the EEZ in the future. In addition to offshore wind farms, marine spatial planning presents additional claims for use that are also to be considered as part of a restoration project (Figure 41).

Interim Conclusions

- The Wadden Sea is not an appropriate area for the restoration of the European oyster. The deeper, offshore areas of the German Bight offer better conditions for potential restoration.
- During site selection, a special focus should be placed on existing protected areas. Protection of the oysters would only be provided, however, if ground-trawl harvesting would be prohibited there.
- In the vicinity of offshore wind farms, the use of mobile, ground-disturbing harvesting equipment is prohibited. This aspect should be considered when choosing a location for a restoration project.

Status of the European Oyster – Restoration in the North Sea

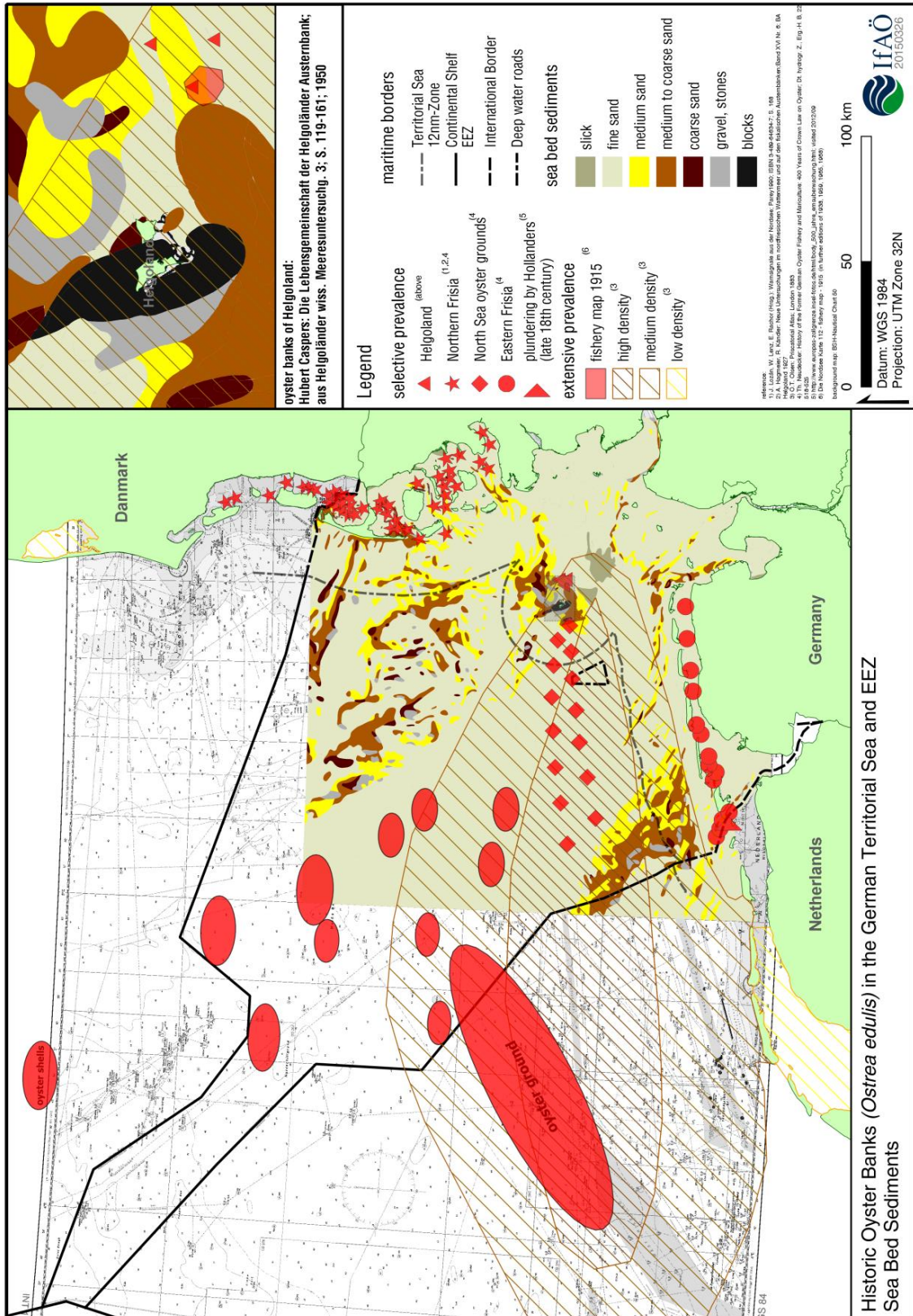


Figure 38: Location of historical oyster beds and distribution of sediment types [Seabed Sediments of German Bight (Classification acc. to FIGGE, 1981), Source: BSH].

Status of the European Oyster – Restoration in the North Sea

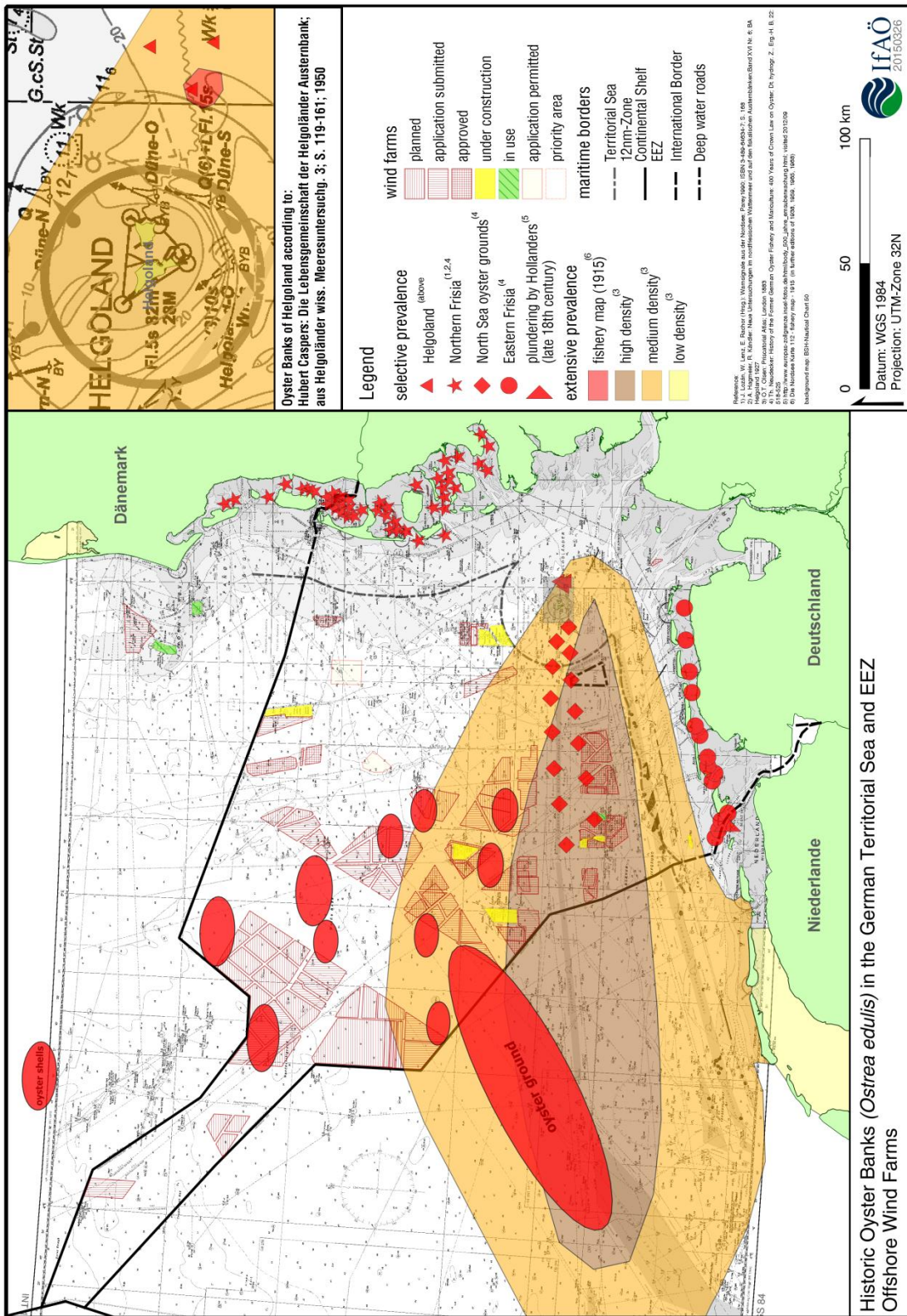


Figure 40: Location of historical oyster beds and offshore wind farms [Status: 1 May 2013, Source: BSH CONTIS].

Status of the European Oyster – Restoration in the North Sea

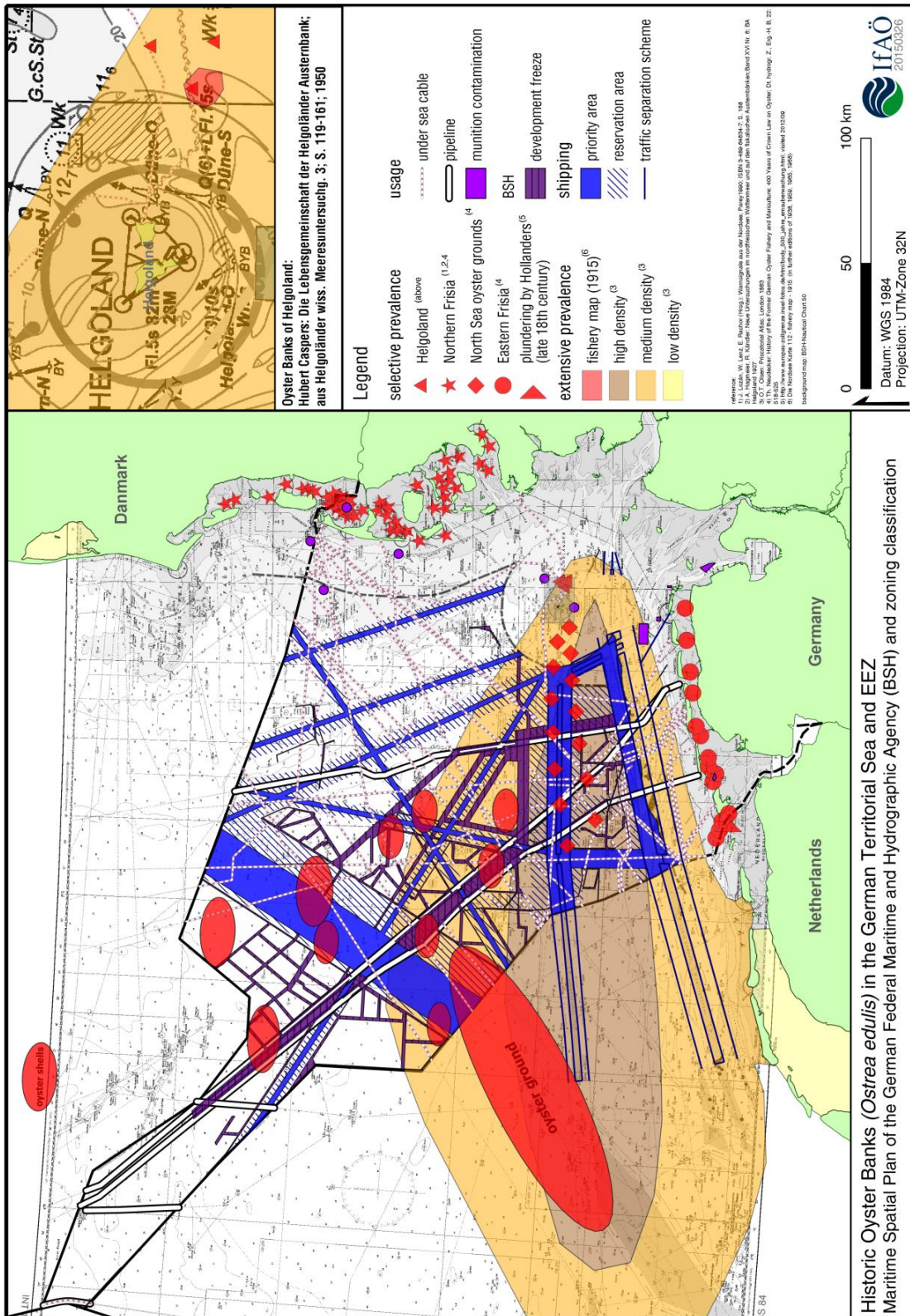


Figure 41: Location of historical oyster beds as well as regional planning and claims to use in the German EEZ [Status: munition (1 May 2013), marine cables / pipelines (1 May 2013), shipping lanes (Sept. 2009), development freezes (15 Jun. 2012), Source: BSH CONTIS].

9.4 Legal regulations and recommendations of international bodies

During restoration activities of the European oyster in the German North Sea, various legal requirements as well as guidelines and technical recommendations should be followed. Some of these are discussed briefly below.

With regard to the possible introduction of disease through the transfer of mussels, Directive 95/70/EG is of importance. It deals with the "setting of minimum measures by the community for the combating of certain diseases affecting molluscs." The measures are to ensure effective disease diagnosis and combat and prevent its spread.

In terms of Bonamiosis and Marteilliosis, the areas that have been designated with "disease free" status are listed in the European Commission's decision of 15 February 2007 (2007/104/EG). The certification as a disease-free area takes place at the request of the Member States on the basis of "Directive 2006/88/EC of the Council related to health and hygiene requirements for animals and products of aquaculture and on the prevention and control of certain diseases in aquatic animals". As mentioned, the Danish Limfjord is declared as *Bonamia*- and *Marteilia*-free area.

In addition to the introduction of the disease pathogens, the risk that unwanted alien species are also introduced into the target area is always associated with the transplanting of shellfish and other organisms. Moreover, it is also common practice to intentionally introduce non-resident mussels for the purpose of aquaculture (e.g. *Crassostrea gigas*).

In § 40, "Non-native, alien and invasive species", the Federal Nature Conservation Act of July 2009 regulates the problem of intentional and unintentional translocation of alien species. Paragraph 4 states:

"The application of alien plant and animal species in the wild is subject to the approval of the competent authority. Artificially-propagated plants are not considered non-resident if they have their genetic origin in the area concerned. The license shall be denied if a risk to ecosystems, habitats or species of the Member States cannot be excluded. The requirements of a permit do not cover:

Paragraph 3 on the establishment of animals not considered to be alien species that are subject to hunting or fishing rights,

Article 22 of Directive 92/43/EWC must be considered. "

The above-mentioned Article 22 of the Habitats Directive (92/43/EWC) discusses in Paragraph "a", the restoration of formerly native species, while pursuant to Paragraph "b", the Member States should ensure that habitats as well as animal and plant species are not harmed by the introduction of non-native species.

Invasive species and pathogens can be introduced not only by the transplantation of live oysters, but also potentially through the application of shells as a substrate for larval settlement. In this context it is to be fundamentally considered whether from a legal point of view the London Convention of 1972 on the prevention of marine pollution by dumping of wastes is affected. As can be seen in the updated protocol from 1996, the dumping of organic material of natural origin is generally allowed. However, an official permit is to be obtained for such introduction (LAING et al., 2005).

In addition to legal requirements, various international organizations and conventions have published multiple policy recommendations to minimize the environmental risk associated with translocation of native and non-native species.

The International Council for the Exploration of the Sea (ICES) wrote in this regard a "Code of Practice" (COP) (ICES, 2005). The COP provides practical recommendations to reduce the risk of introduction of alien species during intentional translocation of marine organisms. The individual sections provide, for example, instructions on how to proceed before and after the release of a species. In addition, various annexes address questions relating to risk assessment, quarantine and monitoring. In the preparation of the COP, the Working Group on the Introduction and Transfers of Marine Organisms (WGITMO) of ICES played a significant role. In the annual meeting minutes of the working group, current information on the translocation of organisms and associated environmental risks can be found.

The International Union for the Conservation of Nature (IUCN) recently published updated guidelines for the translocation of species with respect to nature conservation (IUCN/SSC, 2013). The report was prepared by the IUCN expert committees that deal with issues of restoration and invasive species. The guidelines relate in particular to the translocation of species within the framework of conservation measures. The IUCN distinguishes different types of translocations, depending on the intention behind it. Transplanted organisms may e.g. involve individuals from a wild or breeding stock. These can be used to support a degraded population or to establish a new population in the former area of distribution. In principle, conservation-related translocations should only be undertaken if they have a positive effect on the conservation status of a population and / or functions of an ecosystem. A restoration of the oyster in the German EEZ would meet these basic requirements.

In the IUCN report, aspects such as objectives, scheduling, exit strategy and social acceptance are addressed. In addition, a monitoring program as an integral part of a transplantation project is promoted. Overall, the IUCN report represents a current guideline that should be consulted for the potential restoration of the oyster.

With a reintroduction of *O. edulis* in the EEZ, the objectives of the OSPAR Convention on Protection of the Seas and the EU's Flora-Fauna-Habitat Directive (FFH Directive) (92/43/EEG) and the Marine Strategy Framework Directive (MSFD) will be followed.

In Annex V of the OSPAR Convention, the signatory states commit to protect and conserve marine ecosystems and their biodiversity. This includes restoration measures intended to restore marine areas to their original state. With a focus on habitat protection and biodiversity, OSPAR created a list of threatened species and habitats (OSPAR, 2008), in which the endangered European flat oyster and oyster beds are listed as worthy of special protection (OSPAR, 2009). For this purpose, a recent OSPAR Recommendation 2013/4 was adopted with measures for registration and protection of existing *Ostrea edulis* stocks. In the recommendation, restoration of the oyster in suitable marine areas is recommended (OSPAR, 2013).

The OSPAR activities on species and habitats are directly related to the FFH Directive. There, the habitat type "reef" (No. 1170) is listed as a particularly-protected habitat. For reefs, whether of mineral or biogenic origin, a favorable conservation status is, according to the Habitats Directive, to be preserved or restored. Maintaining or restoring the ecological functions of healthy reefs is also of importance in relation to the MSFD. For the implementation of this directive, the EU Member States committed to producing a good environmental status of the seas by 2020. In the draft program relating to German measures, *Ostrea edulis* is listed.

Interim Conclusions:

- When planning a restoration attempt, the legal requirements of the German Federal Nature Conservation Act are to be especially complied with.
- It must be determined which permits are necessary for a restoration of the oyster in the EEZ and from whom they are to be obtained.
- The current guidelines of the IUCN for translocation of species with regards to nature conservation provide a suitable guide when planning a project to restore the oyster (IUCN/ SSC, 2013).
- In the OSPAR list of threatened and/or declining species and habitats, the European oyster and the habitat "oyster" is listed. OSPAR adopted objectives and measures to protect the domestic oyster. Included therein, restoration in former areas of distribution is recommended as long as the necessary protective measures exist.
- In the Habitats Directive and the MSFD, biogenic reefs are highlighted as particularly sensitive habitats and in this respect actions are called for.

10 Final Assessment and Recommendations

This report deals with various aspects that are important in the context of a planned restoration of the European oyster in the North Sea. Each thematic block closes at the end with a brief interim conclusion.

In the following paragraphs, the criteria that are particularly relevant to the implementation and feasibility of an oyster restoration are once again briefly highlighted. These are mainly issues of site suitability and availability of suitable donor oysters.

Site selection in the German North Sea

When choosing a location in the German EEZ, the territories of the former oyster deposits offer no obvious location advantage, with the exception of the historical reference. As a result of intensive harvesting with bottom-disturbing equipment, these areas today offer just as little suitable hard substrate (mussel cultch) for oyster settlement as adjacent areas of the German Bight.

Without the artificial application of bivalve shells (cultch) as settlement substrate for oyster larvae, a locally-concentrated accumulation of oysters to serve as a nucleus of an oyster bed will not be able to develop. As in historical times, a sandy seabed presents a suitable basis for the remains of bivalve cultch. The sand-fine sand sediment type is extensively available in the offshore area of the German Bight, so that with regard to "base substrate", relatively few spatial limitations exist. Locally existing cultch grounds can provide a site advantage over purely sandy localities.

Compared with coastal areas or the Wadden Sea, the major abiotic environmental factors of water temperature and salinity in the deeper sublittoral zone are always in a range that does not limit the survival of the oyster. Regarding water temperature, it is advantageous if restoration in shallower water (20 m) occurs, as the required temperature for reproduction (approx. 15 ° C) is reached earlier in the year.

Pathogens, predatory enemies and competitors apparently do not present an existential problem in the offshore area of the EEZ. At a minimum, the epidemic pathogens *Bonamia ostreae* and *Marteilia refringens* have not previously been detected in mussels from German marine areas. *M. refringens* also occurs in the other European sea areas primarily in coastal areas with higher water temperatures and lower salinity. The predatory sea snails (Muricidae) are practically nonexistent in the German North Sea. While the invasive slipper limpet *Crepidula fornicata* competes for space with the oyster in other regions of Europe, it only displays a low incidence in the German Bight.

Restrictions on a suitable settlement location also result in terms of competition for space, as existing and planned future uses may also have an impact on a potential location.

Another question is whether the existing Natura 2000 protected areas overlap with the occurrence of former oyster beds. This is mostly not the case. Only the "Borkum Riffgrund" (Borkum Reef Ground) partially overlaps with the large-scale historical "oyster ground" in the southern North Sea, the exact location of oyster deposit is not documented, however.

The current status as protected areas is not adequate protection for newly settled oysters, as ground-contacting trawling is not prohibited. However, the designation of a no-take zone for mobile ground-contacting harvesting gear as well for the sand / gravel mining in the area of restoration is an essential prerequisite for the development of oyster stocks. Since the areas open to fishing are being reduced more and more, the designation of an area as a no-take

zone will at minimum be ripe for conflict. A no-take zone with respect to fisheries, however, is already in place in the vicinity of offshore wind farms. The current planning of offshore wind farms represents in the future a large-scale use of the EEZ. Wind farm areas are relatively common in areas where historic oyster beds once were. The indirect protection provided in this way by wind farms can be an important criterion for the choice of location. Wind farms also offer the additional advantage that the foundations of the wind turbines together with the scour protection can potentially provide primary (the foundation itself) and secondary (shells of mussel fouling) hard substrate for the settlement by oyster larvae.

Origin of oysters for restoration

As another important result of this study, breeding farms and oyster stocks were identified, from which oysters could be obtained for restoration. Due to the disease-free status with regard to the dangerous oyster disease, Bonamiosis, only Scandinavian oyster stocks come into question.

In the form of the Danish Shellfish Center (DSC), located on the Limfjord, and Ostrea Sverige AB, located on the Swedish Koster Islands, two breeding farms for the supply of oysters are available. Both farms strive for a high level of genetic variability in their breeding oysters. It would make sense to initially compare the state of the Danish and Swedish oysters in terms of fitness and reproductive behavior with respect to the intended environmental conditions as part of a pilot experiment. The use of oysters from both stocks could also lead to higher genetic variability of the founder population.

In addition to breeding oysters, adult oysters can also be obtained from the local wild stock at the Limfjord. The local mussel industry is subject to strict environmental and harvest management and is therefore logical that it is MSC certified. The oysters of the wild stock at Limfjord are also free from infestation by *Bonamia ostreae* and *Marteilia refringens*.

Speaking to a preference of the oysters from the Limfjord is the fact that they may be better adapted to the environmental conditions in the German Bight due to their geographical proximity, when compared to oysters from the more distant Swedish (breeding) stocks.

In summary, it can be concluded from site selection considerations and based on the presence of suitable sources of oysters that the conditions for a proposed restoration of the European oyster in the North Sea are in principle present.

Recommendations

So far, there are no experiences in Europe with the restoration of *O. edulis* in areas where the population has already been fully extirpated. In all previous projects for the settlement of the oyster, the focus was placed on population support measures with the objective of improving recruitment of the stock as a whole. The experience gained from these efforts demonstrates in particular that a large logistical, human and financial effort is needed in order to ensure that restoration measures have the prospect of success.

To minimize the risk of failure of a resettlement project, a thorough preliminary investigation should be carried out before undertaking an extensive translocation of oysters. Thus, a pilot study should initially determine whether the site selected also offers the prospect of a successful settlement of oysters. For this study, oysters from the areas of origin intended for translocation are to be used. These should therefore involve oysters from the Limfjord (farm and wild population) and / or from the breeding farm on the Swedish Koster Islands.

A pilot study should be designed to answer questions that are relevant to a decision. So, it is important to obtain, for example, information on the mortality rate during the different stages of development of the oyster. In addition, the fitness, possible occurrence of pathogens (*B. ostreae*, *M. refringens*) and reproductive capacity are to be identified. Furthermore, a pilot study should also provide any information on the occurrence of predatory enemies.

After positive conclusion of a pilot study that primarily examined fitness, reproductive capacity and absence of disease, essential pre-requisites for the implementation of a restoration project have been met. For the following phase of the project, current guidelines of the IUCN on reintroduction of organisms offer suitable support, for example (IUCN/SSC, 2013).

The actual design of a restoration project was not the subject of this report. In the following paragraphs, however, some general recommendations or comments are included.

- A restoration action must be undertaken in "large scale". The more suitable hard substrate as well as juvenile and adult oysters that are distributed, the greater the chance of a successful settlement. As to a favorable number of oysters to distribute for a founder population, there is not a direct example where one could orient to with respect to restoration. During measures carried out in the UK to freshen still existing oyster stocks, several hundred tons of cultch were often used as hard substrate. On top of this, several thousand to one hundred thousand adult oysters or spat were applied, depending on size (LAING et al., 2005). Another study identifies a number of 10 million oysters as being required for successful larval production and thus for the establishment of a self-sustaining population (KORRINGA, 1946). Due to the circumstances in the German Bight (such as the tidal current), a very large number of oysters is likely to be necessary.
- Oyster shells as hard substrate would provide optimal settlement area for oyster larvae. Since shells of *O. edulis* are either barely or not at all available, shells of the Pacific oyster are the second best choice. They are much heavier than mussel shells and thus do not easily drift as a result of a bottom current. Due to their size, they also offer settlement area for more oyster larvae, which would promote the formation of aggregates (mini-reefs).
- Scientific monitoring is an essential part of a restoration project. First, in advance of the restoration measure, documentation of the status of the community of species in the vicinity of the restoration site should be done to detect changes that may take place during the course of the restoration. After distributing the oyster, it is the task of monitoring to assess the health and development of the founder population. A subsequent, multi-year support monitoring can also provide knowledge as to whether further measures to support the population are necessary, or whether the attempt must be declared a failure.
- In the vicinity of the distribution site, larval collectors should be installed at appropriate times. They can provide valuable information about reproductive success, recruitment and distribution of larvae.
- If the restoration attempt is to be carried out in the area of a wind farm, there would be several ways to install the larvae collectors. The foundation can also function as collectors. At a minimum, the biological fouling should be investigated with regards to potential settlement of *O. edulis*.
- It is assumed that a successful restoration of the oyster would probably take decades. LAING et al. (2005) refers to a period of 25 years, which would be necessary to evaluate the success of a population support measure.

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