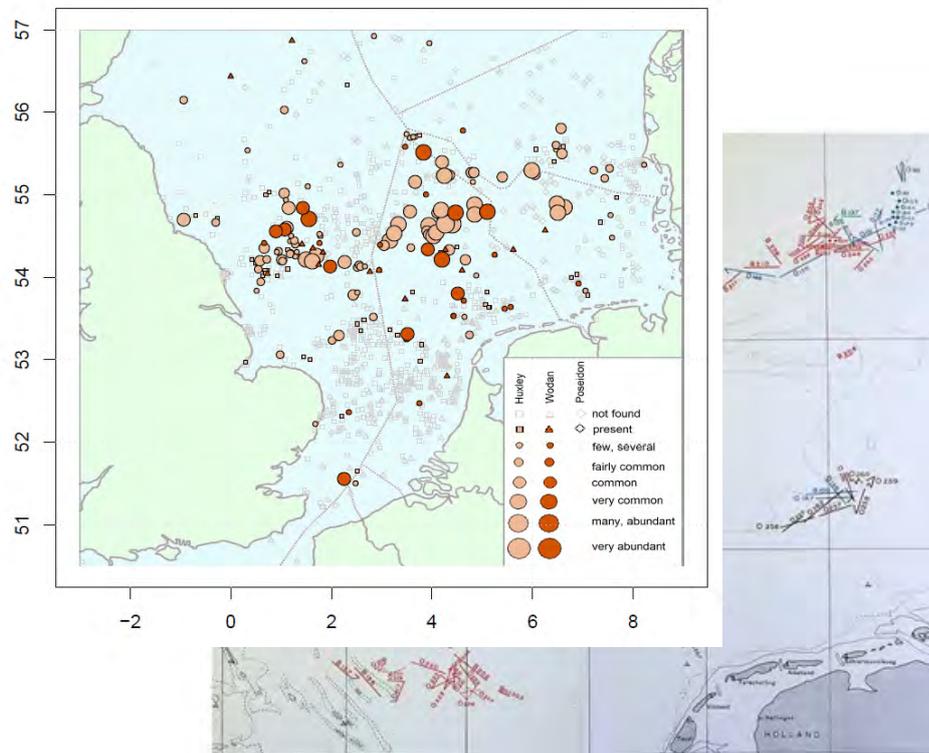


North Sea benthos 1902-1912 – Distribution based on Huxley, Wodan and Poseidon surveys data



Floris P. Bennema

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MARHIS

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Abstract

At the start of the 20th century, concern about depletion of fish stocks triggered North Sea fishery investigations by several countries. During these early trawl surveys, naturalists on board not only recorded fish but also invertebrates. The benthic data of the English RV Huxley and the Dutch SS Wodan bottom and otter trawl surveys were (partly) published, but hardly digitised. This report shows the preliminary results after digitalisation of the Huxley and Wodan epibenthos data. Simultaneously, German research on the RV Poseidon used a large variety of techniques to investigate North Sea benthos; these data were printed on paper in 1990.

Digitalisation of the Huxley and Wodan data resulted in the first dataset on invertebrates of the south and central North Sea. Distribution maps of 73 epibenthic species are presented integrating data of all three scientific programs. Ecological aspects of the early 20th century distribution of species and communities are discussed on basis of the Huxley data.

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1 Introduction

At the start of the 20th century, countries around the North Sea realised that fishery governance demanded sound fishery data. The UK equipped the steam vessel Huxley equipped as a fishery research vessel and the Dutch hired the paddle tugboat Wodan for the same goal. During their extensive trawling investigations commercial fish species were the main target, but epibenthic invertebrates were recorded as well. Several naturalists were on board of the Huxley most of the time; on the Wodan, invertebrates were analysed when times permitted. Most of these invertebrate data were published (Garstang, 1905; Redeke, 1905-1911; North Sea Fisheries Investigation Committee, 1909) but the 1906-1909 Huxley data are only available in handwritten logbooks, kept at Cefas in Lowestoft (Goodwin *et al.*, 2001).

German North Sea benthos investigations had a longer history; the most widespread research was undertaken on the research vessel Poseidon. This research used a great variety of sampling techniques and generated a large museum collection of crustaceans, echinoderms, molluscs and polychaetes. The species collected by these surveys were identified and linked to geographical data by Stein *et al.* (1990).

At the time these investigations took place, benthic life in the North Sea did no longer reflect a pristine situation. Intensive trawl fisheries under sail in the 19th century, and even more so, the use of steam power after 1880, already took its toll (Figure 1). We also have to take into account that the methodology of the researches was far from perfect. Nevertheless, the collective data represent the most comprehensive historical dataset on distribution of invertebrates in the North Sea south of the 57° N latitude.

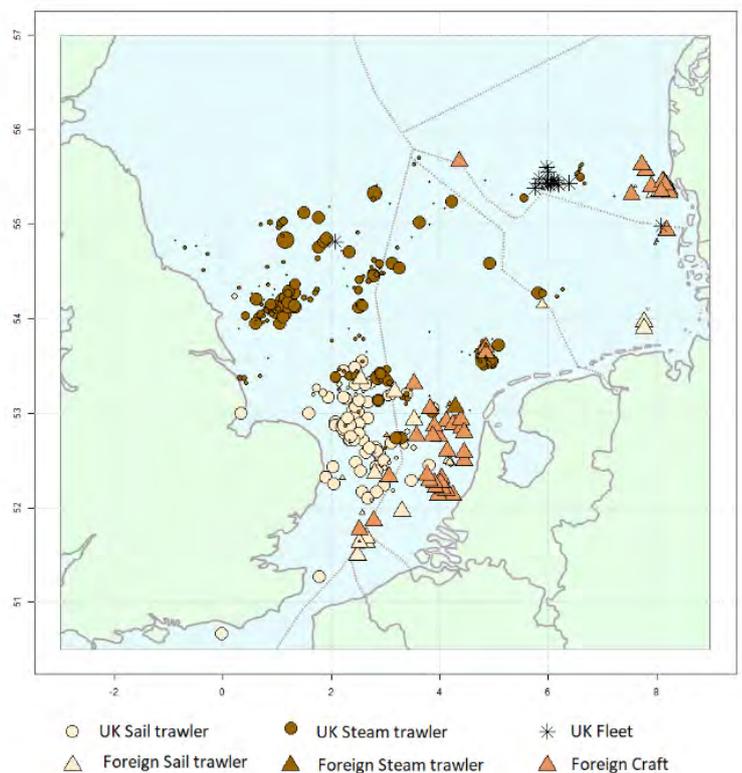


Figure 1. Fishing vessels observed by naturalists of the Huxley surveys 1902-1909. Fleets consisted of tens of sailing vessels. The definition of craft is unsure.

This report is the result of digitalisation of the published Huxley and Wodan data, added with an analysis of 12 of the 57 handwritten logbooks of the 1906-1909 Huxley surveys. Information on the choice of logbooks can be found in Bennema *et al.*, 2020.

Some of the digitised survey data were used already in earlier studies to compare early 1900 North Sea benthos with the current distribution. De Vooy *et al.* (2004) studied changes in the 52-56° N and 2-8° E area of the North Sea. Their study used a small part of the Huxley 1907 survey data (published in Walton (1908, ab)), a large part of the Wodan data, along with data from the German Brohan, Pommerania and Poseidon surveys. These results were compared with 1972-1976 beam trawl and more recent Triple-D and boxcore data. A number of species seemed to have changed their distribution patterns, but no general conclusion could be drawn.

Two other studies used the digitised, qualitative, Poseidon data. Rumohr and Kujawski (2000) compared data from 56 stations of the 1902-1912 Poseidon surveys with those from 40 stations the ICES Benthos surveys 1986. The area covered was between 52°30'-56°30' N and 0°30'-7°00' E. Callaway *et al.* (2007) compared the Poseidon 1902-1912 data with English 1982-1985 groundfish survey data and epibenthos from the 2000 International groundfish surveys. Comparisons were made for 48 species in 40 ICES rectangles.

Both studies concluded that there had been a decline in the occurrence of bivalves and a notable increase in crustaceans. In both studies, these benthic changes were attributed to trawling pressure.

The present report describes the Huxley and Wodan data and discusses ecological aspects of the distribution of the species on basis of the Huxley data. After adding data of the Poseidon survey, 73 maps were plotted showing the distribution of the most encountered early 20th century epibenthos species.

2 Methods

Huxley and Wodan surveys were principally targeted at fish, naturalists noted the invertebrate by-catch. Mesh sizes were rather large and it is not sure whether the observation effort remained constant among catches. As a result, more value may be given to 'present' than to 'absent' in the data.

2.1 Huxley 1902-1909

The RV Huxley used two types of netting, a 26.5 m headline otter trawl and a 13 m beam trawl. Mesh sizes of the cod end were 68 mm and 63 mm respectively. Haul duration varied from 0.5 to 9 hours. As trawling was executed at 2 miles/h the swept area was 60.000 m²/h for the otter trawl, and 50.000 m²/h for the beam trawl (Rijnsdorp *et al.*, 1996). Detailed information on invertebrates came from additional Agassiz trawls. Most invertebrates were identified on board, some were preserved and identified later.

Teams of 2 to 4 naturalists recorded invertebrate names in Naturalists notebooks on board and occasionally added more afterwards to the books. Huxley 1902 to 1905 invertebrate data were published in Fishery reports of the surveys (Garstang 1905, North Sea Fisheries Investigation Committee. 1909). Invertebrate data from 1907 to 1909 were never published but are kept in 57 handwritten logbooks kept at Cefas in Lowestoft (Goodwin *et al.*, 2001). Some of these books contain extensive information on the results of Agassiz trawls, these data were not added to the dataset. Some of the additional trawls and dredgings resulted in publications on sea anemones and nudibranchs (Walton, 1908ab).

STATION	DATE	SPECIES
		<i>Gammarus locifera</i>
		<i>Pluteus foliatus</i>
		<i>Pluteus senhousii</i>
		<i>Alpheididae gelatinosum</i>
		<i>Alpheididae parvicornis</i>
		<i>Yerkesia spinosa</i>
		<i>Crangon vulgaris</i>
		<i>Iludius multicornis</i>
		<i>Homarus vulgaris</i>
		<i>Nephrops norvegicus</i>
		<i>Scapargus herbstii</i>
		<i>Hyas araneus</i>
		<i>Hyas mantanus</i>
		<i>Corystes casvelanensis</i>
		<i>Clawer pagurus</i>
		<i>Portunus hibernicus</i>
		<i>Fohinus miliaris</i>
		<i>Squilla purpurata</i>
		<i>Polinoides cordatum</i>
		<i>Asterius rubrus</i>
		<i>Salaster papposus</i>
		<i>Astropecten irregularis</i>
		<i>Ophirura albida</i>
		<i>Ophirura ciliata</i>
		<i>Ophiodon fragilis</i>
		<i>Amidolia virginica</i>
		<i>Circa intestinalis</i>

VOYAGE	STATION	10
Beam		
		2 ♀ in berry
		a. det. c. ±
		aphrodite 1
		2 ant 1 ♀
		0 frag. fs
		Corp. det. - 1
		8. hem. f.
		Med. diaphus
		Ostrea 200
		8. spec. shells
		a. virg. b.
		8. hem. shells
		2 spec. 1
		2 spec. 2
		Sponge 1 det.

Figure 2. Invertebrates logbook page of the Huxley survey at station 111-18.

The resulting dataset consists of 154 invertebrate species and 99 additional entries on higher taxa, shells or egg capsules at 734 locations.

The Huxley reports on invertebrates use various vernacular names used by fishermen. In many instances an explanation was given.

- *Curly weed, amber weed, curly cabbage, sea chervil* – Used for some species of the bryozoan genus *Alcyonidium*. Sea chervil *Alcyonidium diaphanum* was very unpopular, it led to ‘Dogger bank itch’, an allergic reaction of the skin.
- *Scruff*– Rubbish in the nets. On the coarse English grounds the quantity could be enormous. Scruff is a generalist term, it could comprise hydroids, bryozoans, ascidians, echinoderms and more and is often used for dead flat oyster *Ostrea edulis* areas.
- *Oakum*– Hydroids. Originally oakum was a term for unraveled ropes, used to fill the seams between boards on wooden ships.
- *Teat* – Used for *Alcyonium* species, mostly dead man’s fingers *Alcyonium digitatum*.
- *Ross and white ross* – Used to indicate the firm congealed sand reefs produced by a polychaete: the ross worm *Sabellaria spinosa*.
- *White mud* – oaze (mud, probably with chalky remains of shells or foraminiferans).
- *White weed* – *Sertularia* species.

2.2 Wodan 1902-1911

Mostly, the Wodan used the same otter net as the Huxley surveys. Data on duration, speed and swept area were the same as well. The second net used was a 6 m otter net with a cod end mesh size of about 40 mm. With the small otter net the swept area was 15.000 m²/h (Rijnsdorp *et al.*, 1996). Invertebrates were collected and identified later in the laboratory, mostly by Dr. J.J. Tesch. Data on *Actiniaria*, *ascidians*, *Asteroidea* and *bryozoans* are often less specific in Wodan data, as they were lumped to higher taxonomic levels.

Wodan results were published in 6 issues of the Jaarboek Van Het Rijksinstituut Voor Het Onderzoek Der Zee (Redeke, 1905-1911).

The resulting dataset consists of 167 invertebrate species and 84 additional entries on higher taxa, shells or egg capsules at 199 locations.

2.3 Poseidon 1902-1912

The Poseidon survey visited fixed locations in the Baltic and the North Sea from 1902 to 1912. Between 1903 and 1906, other locations were visited as well. The survey used a great variety of gear to collect invertebrates on, and in, the sea floor. The invertebrate catches were collected in 7000 jars and kept at the Zoological Museum in Kiel.

Gears in use were:

- Dredge
- Austern dredge – strong oyster dredge
- Kurre – a small net used for small fish
- Granatkurre – a small net used to catch shrimps
- Helgoländer trawl – a fishery trawl
- Petersen trawl – An ‘otter drag-seine’ for use in deep water.

Stein *et al.* (1990) reconstructed the catch data and published the raw data using modern scientific names. Most of the species recorded belonged to the group of free-living epibenthos like molluscs, crustaceans, echinoderms and infauna like polychaetes. Sessile groups such as bryozoans, hydrozoans and sponges were not recorded. In contrast to the previous surveys only presence/absence information is available.

2.4 Data interpretation

2.4.1 Species

Many scientific species names used in Huxley and Wodan surveys changed over time. Interpretation and actualisation of these names was carried out by Godfried van Moorsel and Floris Bennema. The main source used was [WoRMS](#), next in order were [NEAT](#) and other sources.

The Bryozoa in the southern North Sea were checked by Hans de Blauwe.

A list of old and actualized names is given in supplements 7.1 (Huxley) and 7.2 (Wodan).

- ? means that the species was questioned by Huxley or Wodan naturalists.
- cf. means that doubts remained in our actualization of the old species name.

2.4.2 Position log data

The position of the survey hauls were recalculated to decimal coordinates. The Huxley data provides exact locations where the nets were shot and hauled. This study uses the middle position between these locations. Location data of trawls lacking naturalists on board to record invertebrates, were excluded from the dataset.

This study pays special attention on sediment composition data from the Huxley surveys, recorded in the form of average sediment grain sizes. Mostly the sediment categories at shooting and hauling was identical, in other cases an average was assigned. Sediment categories used in the Huxley surveys were aggregated to reduce their number. The resulting categories were:

- m mud
- ms muddy sand
- fs fine sand
- s sand
- cs coarse sand
- gr sand with gravel, gravel and stones

2.4.3 Qualitative abundance terms

Huxley and Wodan surveys used qualitative terms to indicate abundance. In this study, these terms were translated into 8 abundance categories (Table 1). In cases species were recorded without presence information, *present* (category 1) was used. The 'Number row' was used in the few cases where absolute numbers were given in the reports or logbooks.

Table 1. Qualitative abundance terms in Huxley and Wodan (in Dutch) surveys and conversion to abundance categories for this study.

Abundance category	0	1	2	3	4	5	6	7
Number		1	2-8	9-25	26-100	101-200	200-300	> 300
Huxley surveys	-	<i>present</i>	several, few	fairly common	common	very common	abundant, much, many	very abundant, large quantities
Abbreviation		p	s	fc	c	vc	a	va
Wodan surveys	-	<i>aanwezig</i>	enkele, weinig	vrij veel, tamelijk veel	gewoon	veel, talrijk	zeer veel, massa's	geweldige massa's, reusachtige hoeveelheden
Abbreviation		a	e	vv	g	v	zv	gm

In the Huxley data the categories *fairly common* and *common* were used more often, it seems that the naturalists on board were more inclined to leave out abundance information (now in *present*) when abundance was low.

In the Wodan data the *fairly common* and *common* categories were hardly used. (Figure 3). Probably, the naturalists were more inclined to leave out presence information (now in *present*) when the abundance was conform expected (fairly common or common).

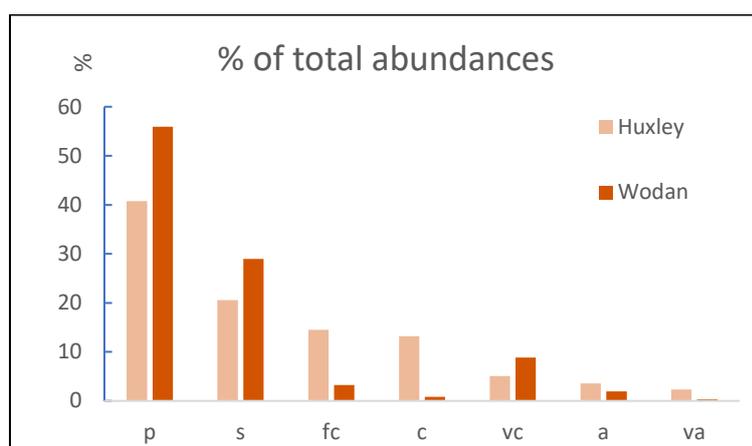


Figure 3. Frequencies of abundance categories (for abbreviations see text) in Huxley and Wodan data

2.4.4 Statistics and distribution maps

Statistics on community ecology were executed with the use of R packages Vegdist and Phylosec. The theoretical background came from the statistical roadmap described in Anderson *et al.* (2011). The distribution of communities was analysed by various statistical methods.

Hierarchical clustering (hclust) was used to detect the regional distribution of clusters in the studied area. In order to be able to use the Ward(.D2) minimum variance method, which enables to determine a low number of clusters, Huxley abundances were used. Abundances, because Ward's method is based on Euclidean distances. In Huxley data the category *present* seems to refer to low numbers (§ 2.4.3), but as this category is not exactly defined, there may be some noise in this analysis. SIMPER was used to find the most characteristic species of these clusters.

α and β diversity were analysed PERMANOVA, Pairwise adonis and PERMDISP. To exclude the noise by the category *present*, these analysis were based on presence and absence. As discussed in Methods (2), more value should be given to 'presence' than to 'absence' in this dataset. This leads to the choice of the "Jaccard" dissimilarity measure (Anderson *et al.*, 2011) in β diversity analysis. In order to avoid conclusions that were influenced by differences in α diversity, the "Raup-Crick" measure was used as extra check.

Ideally, statistics would be calculated using a balanced dataset. Especially when the data are split in sediment types, this is not the case (Table 2). This has to be taken into account, at the time that statistics lead to conclusions.

Table 2. Huxley haul locations divided by depth and sediment categories

depth	n		Sediment	abbr.	n
10-20 m	96		Gravel/ stones	gs	33
20-30 m	239		Coarse sand	cs	31
30-40 m	145		Sand	s	190
40-50 m	125		Fine sand (fs)	fs	327
> 50 m	62		Muddy sand	ms	54
			Mud	m	32

Species distribution maps in Chapter 6 were plotted directly from the data with use of the base plot function in R in addition with the tiff library. Circle sizes represent semi-quantitative abundance categories as shown in Table 1. Colours are used to present the data source. The category *present* is considered to be sizeless.

3 Results

3.1 Sediment

Both surveys took sediment samples at the survey locations. This gives the opportunity to compare the sediment data with species distribution at the time. Figure 4 shows that the simplified qualification of average sediment grain size of the Huxley survey (§ 2.4.1) greatly matches modern mud content data. Generally, fishery surveys avoid places with stones, like the Cleaver bank, to spare the nets.

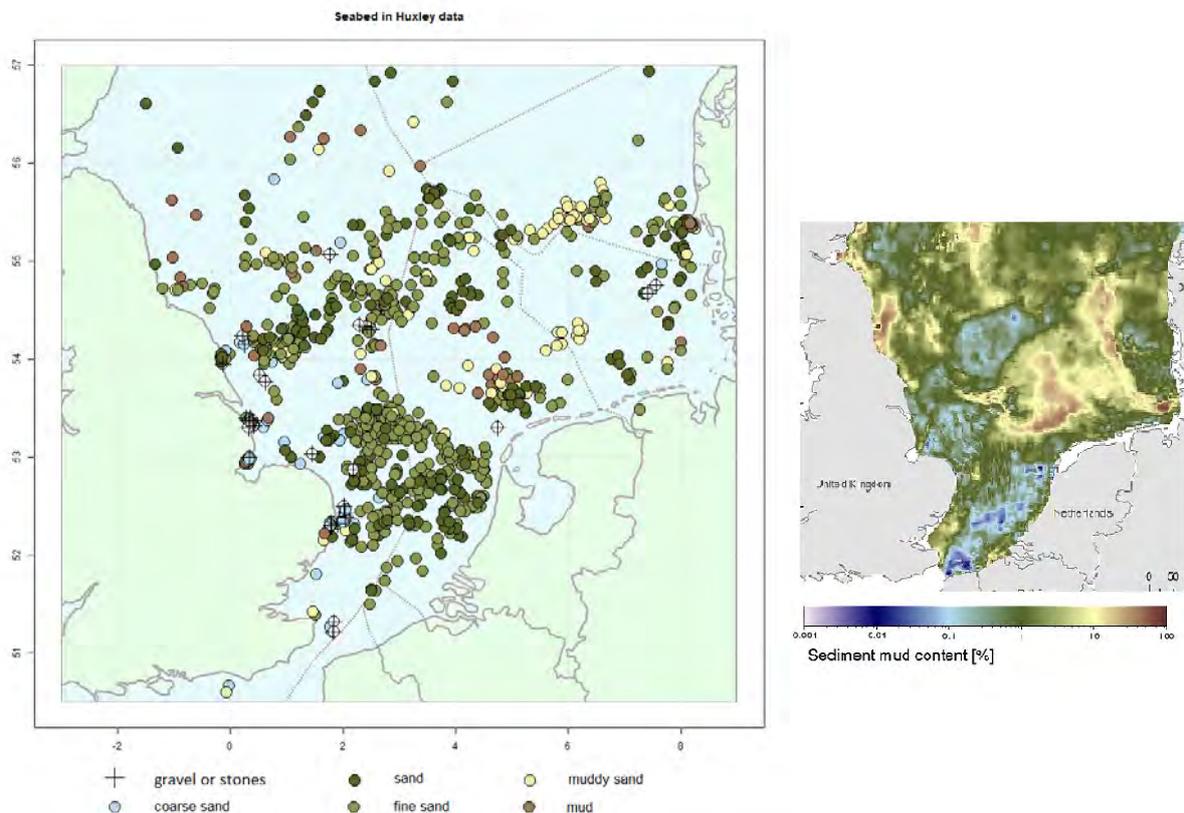


Figure 4. Left: average sediment grain size of samples taken during the Huxley surveys 1902-1909. The colours loosely match those in the mud content map (right) by of Bockelmann *et al.* (2018).

3.2 Biosubstrates

3.2.1 Distribution of large molluscs

Many epibentic species need hard substrates for settlement. As the North Sea is relatively poor in hard substrates as rocks, stones or pebbles, mollusc shells are important as bio-substrate. To understand the distribution of benthic communities we need to look at the preferences of large mollusc species. Figure 5 shows bivalve presence on sediments of different grain sizes.

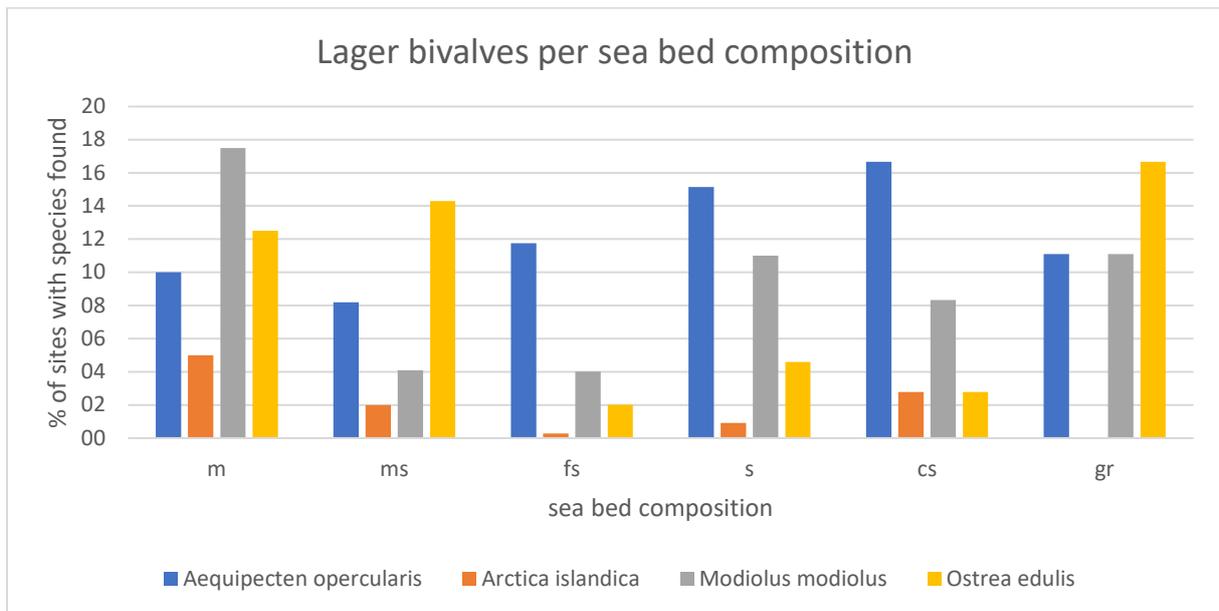


Figure 5. Huxley data. Presence of large bivalves per sea bed type. Each sediment grain size category, shows the percentage of hauls with species presence. For sea-bed categories see § 2.4.2.

The normalized Huxley data show that the large bivalve species occurred on sea bed of different compositions (Figure 5). Most species tend to avoid (unstable) sandy areas, Queen scallop *Aequipecten opercularis* seems to be the most indifferent species.

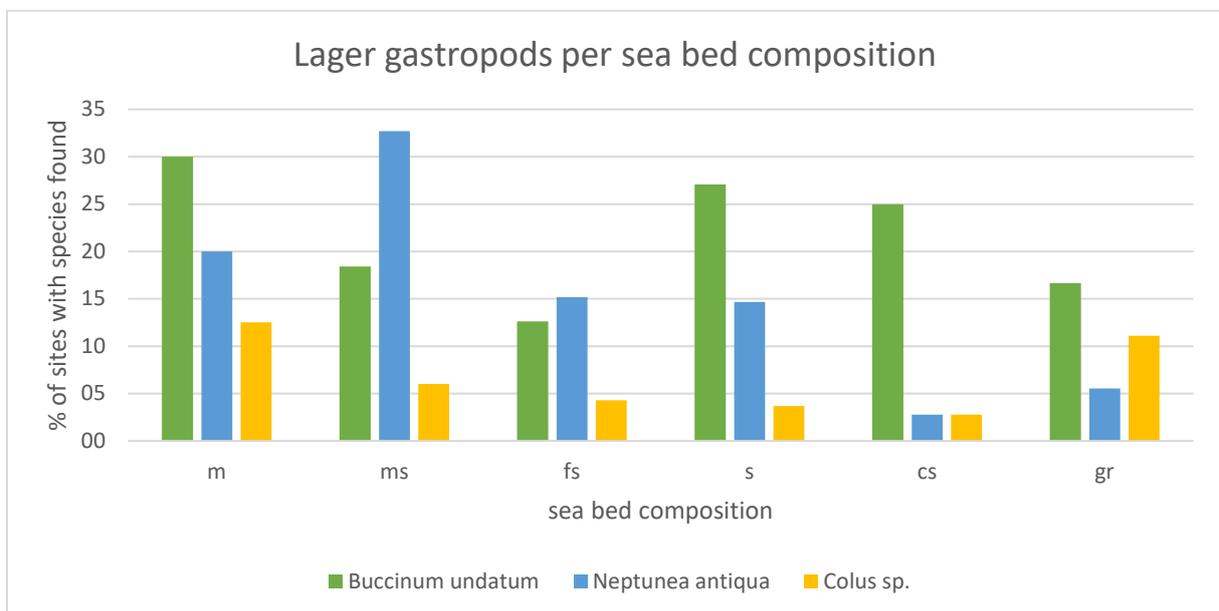


Figure 6. Huxley data on large gastropod presence per sea-bed type. Each sediment grain size category shows the percentage of hauls with species presence. For sea-bed categories see § 2.4.2.

In gastropods, the red whelk *Neptunea antiqua* shows the strongest tendency to live on muddy grounds while the common whelk *Buccinum undatum* seems rather indifferent (Figure 6). All in all, the large gastropods occurred on a wide range of sediments.

The most indifferent species (*Aequipecten opercularis* and *Buccinum undatum*) occupied large parts of the survey area (Figure 7 and 8). As a whole, larger molluscs were found in highest numbers in the northern part of the area. Most larger bivalves, except for *Ostrea edulis* were found north of a line from the Humber estuary in England to Esbjerg in Denmark (Figure 7). To a lesser extent, this also holds for gastropods (Figure 8). Possibly, the acute aspect of this line is partly due to the lack of samples south of it. However, more to the south in the Southern Bight, large-mollusc presence is low, especially in bivalves. Most *Ostrea edulis* were found on the Oyster Ground as discussed earlier in Bennema *et al.* (2020). Whether the abundance of large molluscs continued more to the north, where the depth increases, cannot be judged from the 19th century data. However, Figure 7 and 8 show that they were present in a large part of the northern survey locations.

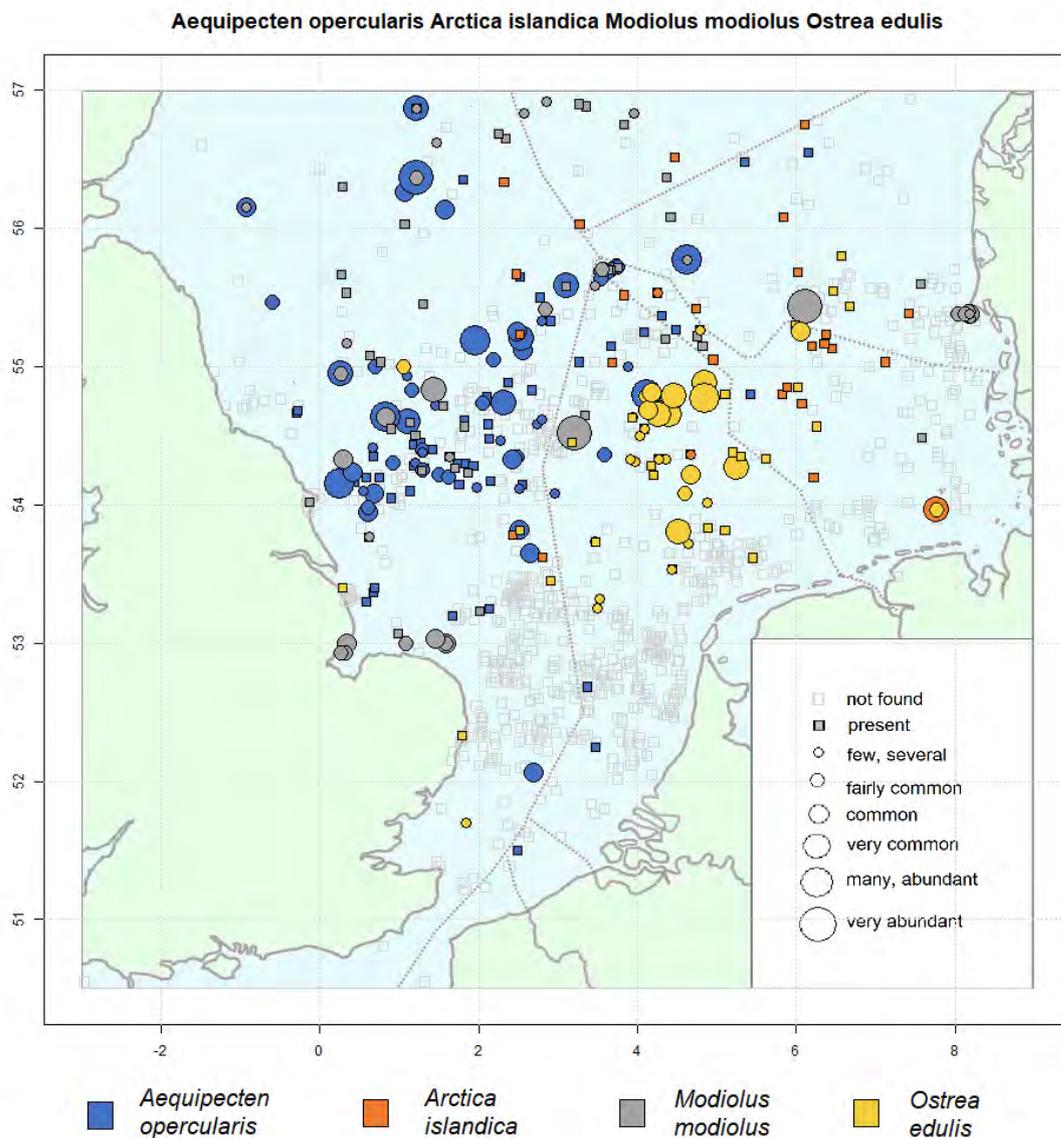


Figure 7. Distribution of four large bivalves in Huxley, Wodan and Poseidon survey data. Filled squares: only presence information provided.

Buccinum undatum *Neptunea antiqua* *Colus* sp.

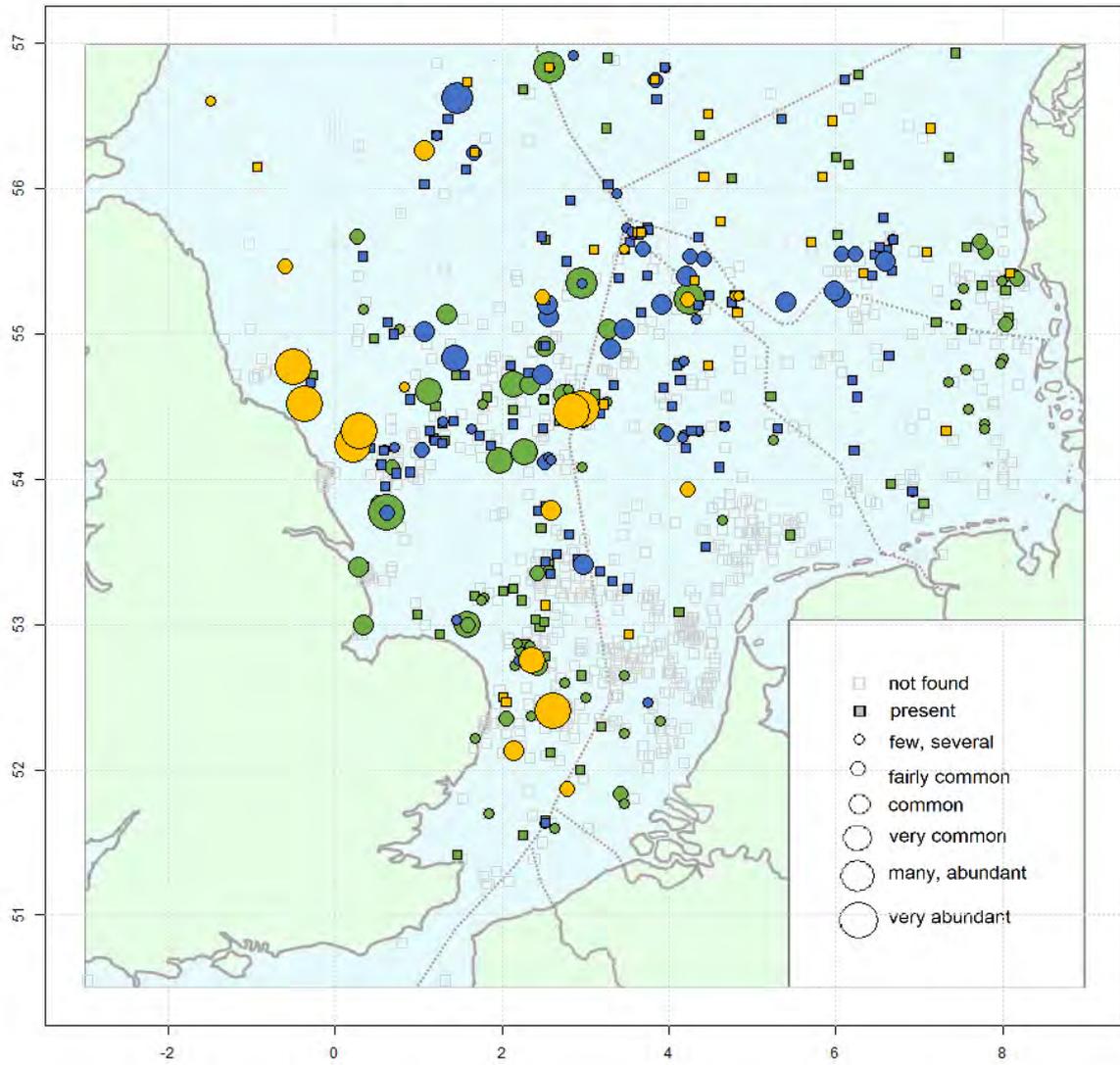


Figure 8. Distribution of three gastropods in Huxley, Wodan and Poseidon survey data. Maps on individual *Colus* species can be found in the maps section. Filled squares indicate that only presence information was provided.

3.2.2 Molluscs as primary bio-substrate

As many epizoic species settle directly on molluscs, they form a *primary bio-substrate*.

The dependence of several taxa on molluscs as a substrate is illustrated by notes in the Huxley reports and studied logbooks (Table 3).

Table 3. Species using mollusc shells as a substrate. The numbers represent the times the combination was mentioned in the Huxley data.

Substrate:	Gastropoda			Bivalvia					
Epizoan	<i>Buccinum undatum</i>	<i>Neptunea antiqua</i> + <i>Colus</i> sp.	Smaller gastropods	<i>Aequipecten opercularis</i>	<i>Arctica islandica</i>	<i>Modiolus modiolus</i>	<i>Ostrea edulis</i>	Smaller bivalves	' Shells'
<i>Alcyonium digitatum</i> on				1			4	1	
Actinaria on/in	3	4		1			1		
Hydrozoa on	2	4	1	1			2		
Bryozoa on					3			1	
Bivalvia on/in		1		1				1	
Serpulidae on				1					1
Porifera on							1	3	

3.2.3 Secondary bio-substrates

Species not only settle directly on mollusc shells but also on species that live on molluscs. The logbook notes illustrate the role of Ascidiaceans and Hydroids as secondary bio-substrates (Table 4).

Table 4. Species indirectly growing on mollusc shells. The numbers are the times the combination was mentioned in the Huxley data.

	Hydrozoa	Bryozoa	Ascidiacea
Actinaria on:			1
Hydrozoa on:		1	4
Bryozoa on:	5		5

3.3 Rafting species

Not all epizoic species stay in place, for instance a Huxley notebook recorded that some of the '*Alcyonidium diaphanum*' lived freely on the sea bed. Also *Alcyonium digitatum* and sponges are known to 'raft' over the sea bed. In four occasions the Huxley logbooks speak of *surfoles* of hydroids. *Alcyonidium diaphanum* is known to easily detach from the holdfast (Hayward and Ryland, 2017). In other occasions, the growing animal becomes too buoyant to keep the holdfast (pebble or shell) in place.

3.4 Gastropod shells for hermit crabs

Hermit crabs depend on gastropod shell for protection but need larger shells as they grow. In the Huxley logbooks, *Pagurus bernharus* was mentioned 6 times in a *Buccinum undatum* shell, 1 time in a 'Fusus' (*Neptunea antiqua* or *Colus* sp.) shell and 8 times in smaller shells like *Natica catena* and *Propebela turricula*. *Pagurus cuanensis* was mentioned one time in a 'Fusus' shell while the slightly larger *Pagurus pubescens* was mentioned 3 times in smaller shells.

3.5 Reefs

Rocky ground and gravel enable formation of special communities. In the North Sea, however, the hard substrates are restricted to certain parts of the surveyed area (Figure 9). Anecdotal information tells us that stones seem to be taken away by fishermen (Moons, 2020). Gravel is more widespread in the North Sea, but as a result of extraction, the distribution of this hard substrate decreased in the southern North Sea (De Groot, 1986). Several studies were made on the hard substrate communities in these areas (Tesch, 1910; Van Moorsel, 2003; Houziaux *et al.*, 2008; Coolen *et al.*, 2015).

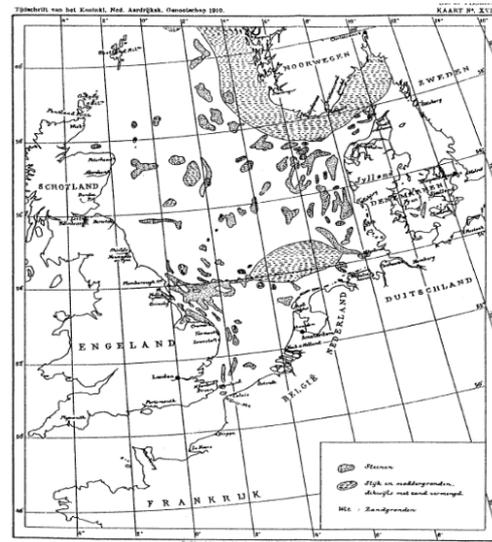
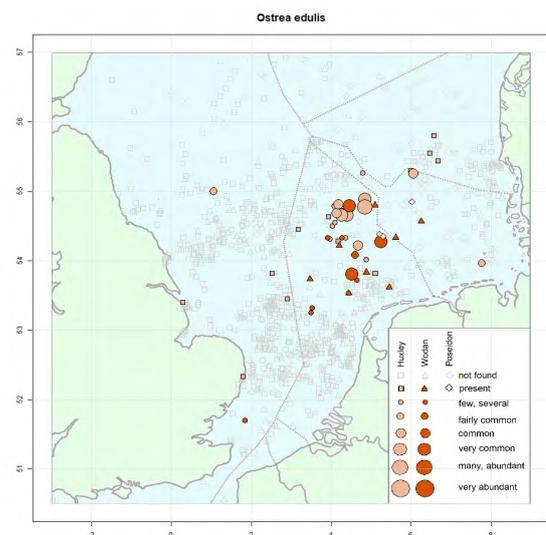


Figure 9. Stony and muddy areas in the North Sea (Tesch, 1910).

Flat oysters *Ostrea edulis*, ross worms *Sabellaria spinulosa* and horse mussels *Modiolus modiolus* are known to form biogenic reefs in the deeper parts of the North Sea.

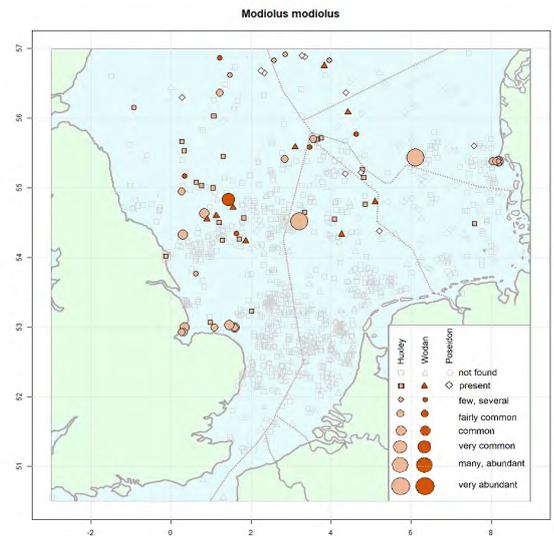
Although heavy dredging for *Ostrea edulis* took place from 1880 onward, the surveys still found many oysters on the Oyster Grounds. The area further to the east was hardly visited by the surveys. The former distribution of 'deep sea oyster' reefs on these muddy grounds is discussed in Bennema *et al.* (2020) and on gravel in Houziaux *et al.* (2008). These studies also give information on the rich epifauna in this oyster-bed biotope.

Figure 10. Flat oyster *Ostrea edulis* found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.



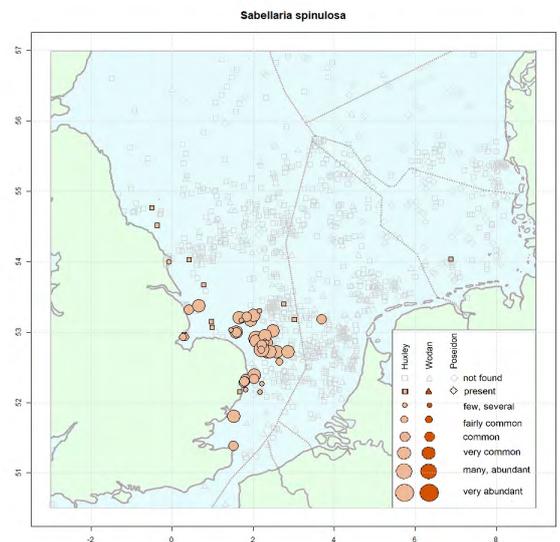
Horse mussels *Modiolus modiolus* were widespread. The surveys found several places where the species was noted as common or abundant.

Figure 11. Horse mussel *Modiolus modiolus* found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.



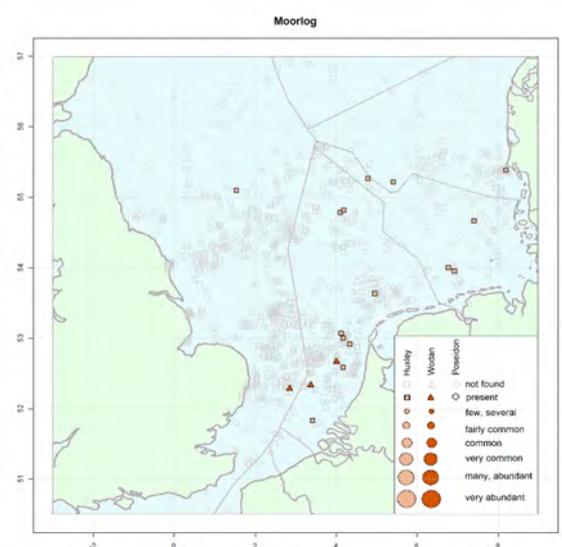
Crusts formed by tubes of the ross worm *Sabellaria spinulosa* form a holdfast for several benthic species (OSPAR, 2013). The Huxley survey trawled many pieces of “Ross” near the English coast, which shows the vulnerability of this biogenic reef. Occurrences on the Brown Bank (Van der Reijden *et al.*, 2019) and a former widespread distribution in the German Bight (Berghahn & Ruth, 2005) seem to be missed.

Figure 12. Ross worm *Sabellaria spinulosa* found by Huxley surveys. Chapter 6 provides a larger version of this map.



Moorlog may be considered as a special type of reef. Moorlog in English and ‘veenbanken’ (= peat banks) in Dutch is the term used for smaller or larger remains of early Holocene peat layers on the sea bed. Especially the Broad Fourteens area, named after the depth of approximately 14 fathoms, west of the Netherlands was feared for them. The pieces were large enough for nets to get stuck in them with the danger that the vessel could capsize. The surveys recorded moorlog as well as Great (or Oval) piddock *Zirfaea crispata*, a boring bivalve commonly found in moorlog. In recent times larger pieces of moorlog is rarely found due to intensive trawling.

Figure 13. Moorlog found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.



3.6 Community ecology

3.6.1 Introduction

The largest (Huxley) dataset was used to study the distribution of macrobenthic communities in the North Sea in early 20th century. Distribution of communities over the North Sea map was studied by hierarchical clustering. This is followed by a discussion of the factors that influenced this distribution. After addressing the relations between physical factors in the studied area, their influence on species assemblages will be analysed. The statistical methods used in these analyses are discussed in § 2.4.4.

3.6.2 Hierarchical clusters

Hierarchical clusterer resulted in clusters in more or less well defined regions in the area. (Figure 14).

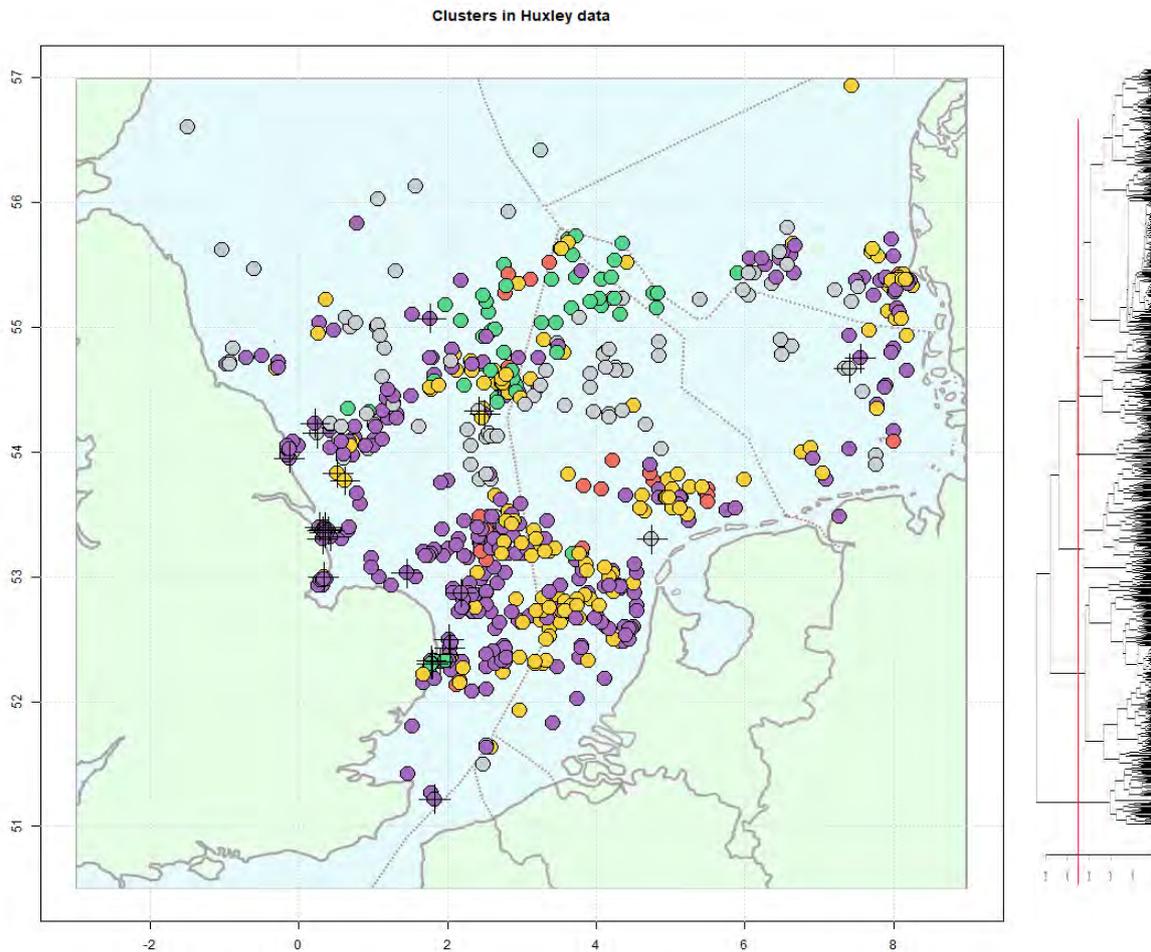


Figure 14. Distribution of epifauna according to cluster analyses based on Jaccard distances. Crosses are places where gravel or stones were found.

A Simper analysis was used to examine the most discriminating species in the clusters. Species in the top of the 'cluster contrast lists' discriminate more. And in case these species also have a considerable higher abundance in a cluster under consideration, they may be referred to as characteristic to that cluster. The distribution of these individual species can be studied further in the maps in Chapter 6.

The 'purple cluster' is characterised the bryozoan *Flustra foliacea*, by reefs built by the Ross worm *Sabellaria spinulosa* and the hydroid species *Abietinaria abietina* and *Hydrallmania falcata*. The last three species were mostly found off the English coast where the hydroids *Nemertesia antennina* and *Tubularia indivisa* also were common (Maps). These species require a holdfast that can partly be found here in the form of gravel or stones (Figure 4, 9 and crosses in figure 14). The 'purple' cluster points along the continental coast are harder to explain. Here the 'purple' points, in contrast to the 'yellow', seem to be identified by the lower abundance of the echinoderms *Asterias rubens* and *Astropecten irregularis*, and to a lesser extend, by the higher abundance of *Flustra foliacea*.

The 'yellow cluster' is characterised by the echinoderms *Asterias rubens*, *Astropecten irregularis* and *Echinocarium cordatum*. These are widespread species that reached their highest abundances in the sandy areas in the Southern Bight. As on the Dogger Bank, the logbook notes also mention 'surfroles' of *Obelia longissima* in this area. Another common species in this cluster was the burrowing crab *Corystes cassivelaunus*.

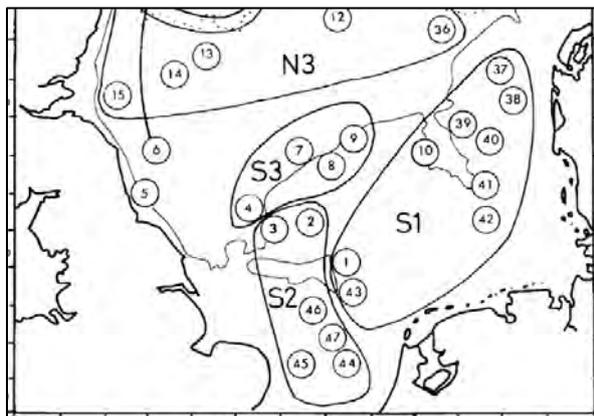
The grey cluster is characterised by the cnidarians *Alcyonium digitatum* and *Metridium senile* and the bivalves *Aequipecten opercularis* and *Ostrea edulis*. This cluster is positioned in the muddy sand to mud area in the German Bight and the area west of the Dogger Bank. At first sight it looks strange that these areas have something in common but the large numbers of the sea anemone *Metridium senile* and the soft coral *Alcyonium digitatum* suggests this is an area with a relatively high availability of hard substrate. The west side of the Dogger was known as 'rough', because of stones and dead oyster shells more to the north-west (Olsen, 1878 ; Tesch, 1910). In the German Bight, east of the Dogger Bank, especially *Alcyonium digitatum* is known to have lived in very large quantities on flat oysters *Ostrea edulis* in the German Bight (Tesch, 1910; Bennema et al., 2020).

The 'green cluster' is mainly concentrated on the sandy part of the Dogger Bank. The cluster is characterised by the bryozan *Alcyonidium diaphanum* (and perhaps some *A. condylocinereum*), the hydroid *Obelia longissima* and bread sponge *Halichondria (Halichondria) panicea*. The first two species were found rafting on the seabed. The bread sponge lived on the southeast rim of the area, possibly also rafting.

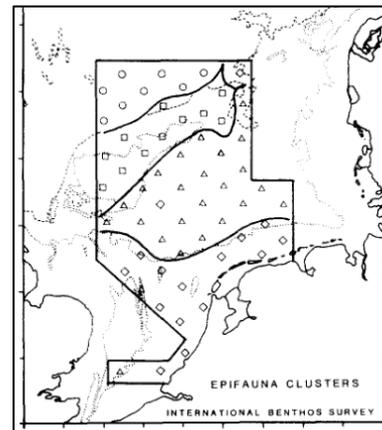
The 'orange cluster' is harder to interpret, characteristic species are the hydroid *Nemertesia ramosa*, the bivalves *Modiolus modiolus* and *Montacuta substriata*, and the echinoderm *Ophiura albida*. The first two species need some substrate to attach to, *Montacuta substriata* lives in association with sea urchins. This species aggregation indicates that they lived on a mixed substratum.

These clusters can be compared with more recent epibenthos clusters derived from otter or beam trawl data (Dyer *et al.*, 1983; Duineveld *et al.*, 1991; Callaway *et al.*, 2002; Reiss *et al.*, 2010). Although all authors found four epibenthic clusters in the North Sea area south of 57° NB, the delineation of the clusters varied (Figure 15). The six clusters found by Rees *et al.* (1999) are not depicted, their distribution over the area differed even more.

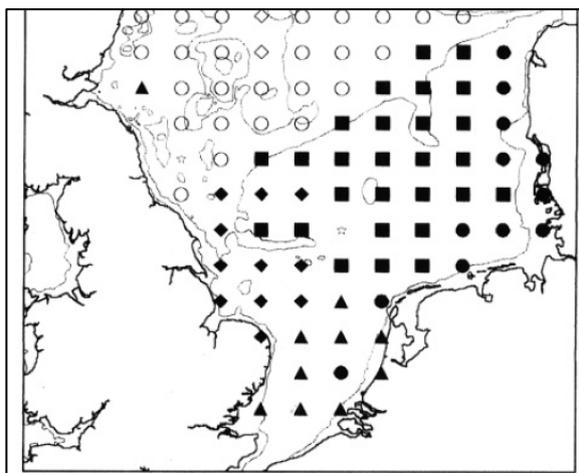
The most apparent differences in the early 20th century clusters are the former division of the Southern Bight in two clusters and the clearer distinction of the sandy part of the Dogger Bank. These differences will be addressed in the discussion. A north-west cluster in deeper water is missed in the Huxley data, probably due to a low number of hauls in this area. Nevertheless, the abundance of purple sea urchins *Spatangus purpureus* and the crab *Lithodes maja* was apparent here, these species were found at respectively 14 and 10 of the 26 locations at 50m or deeper. Together with the anemone *Bolocera tuediae* these seen to be characteristic species for this region.



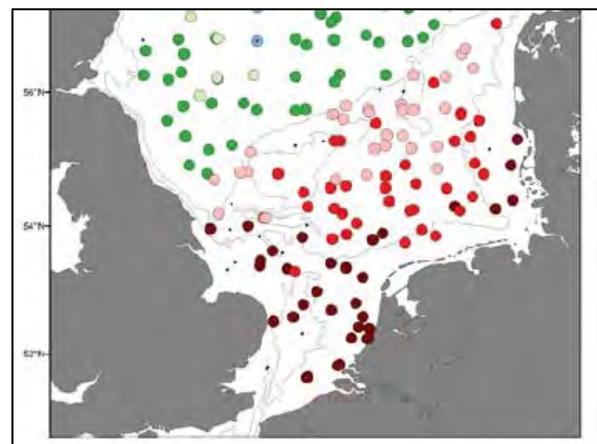
a. Dyer *et al.* (1983), based 1977-1981 otter trawls (Granton type).



b. Duineveld *et al.* (1991), based ICES North Sea Benthos Survey Trawls (beam) in 1986.



c. Callaway *et al.* (2002), based on International Groundfish Trawls (2 m beam) in 2000.



d. Reiss *et al.* (2010), based on International Groundfish Trawls (2 m beam) in 2000.

Figure 15. Recent epibenthic clusters analysed from trawl data in four papers.

3.6.3 Relations between physical factors

Important physical factors that may influence the distribution of marine benthos are depth, temperature and sediment composition. Depth is an ultimate factor, the other factors, as well as seabed movement and seabed stress are related with depth. Organisms are influenced by these proximate factors,

Temperature is associated with depth. In a 1997-2002 bottom temperatures in the studied area were investigated. The average summer bottom temperatures were correlated with depth (Figure 16). In the same period, the average winter bottom temperatures only varied from 6 to 8 °C between 51° and 57° NB (ICES, 2008).

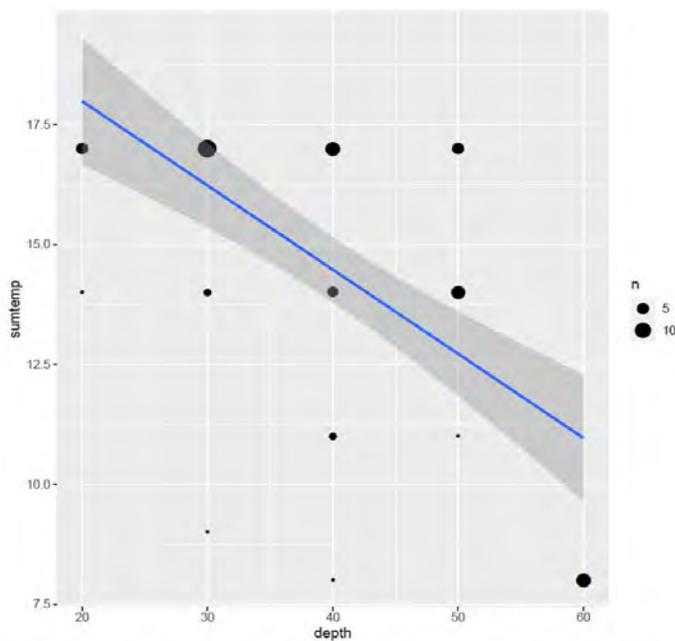


Figure 16. Relation between depth and summer bottom temperatures in the studied area (Pearson correlation $P < 0.001$; $R^2 = 0.407$). Points represent average values in ICES statistical rectangles. Bottom temperatures 1997-2002 (ICES, 2008).

Fine sediments may be expected to accumulate in deep 'low energy areas'. The Huxley data on hauls indeed gave this relation after the sediment categories (2.4.1) were given values from 1 to 6 (Pearson correlation $p < 0.001$) However, depth accounts for a negligible proportion of the variation in average sediment grain size ($R^2 = 0.045$).

3.6.4 α diversity

With presence-absence information it is not possible to calculate Shannon or Simpson diversities, only the number of observed species at locations can be used. Figure 17 gives an impression of species richness at different depths and on different sediment categories. There are no evident differences among depths or sediment types. Lower number of haul locations may be responsible for the lower values on gravel/stones, coarse sand and muddy sand (Figure 16b).

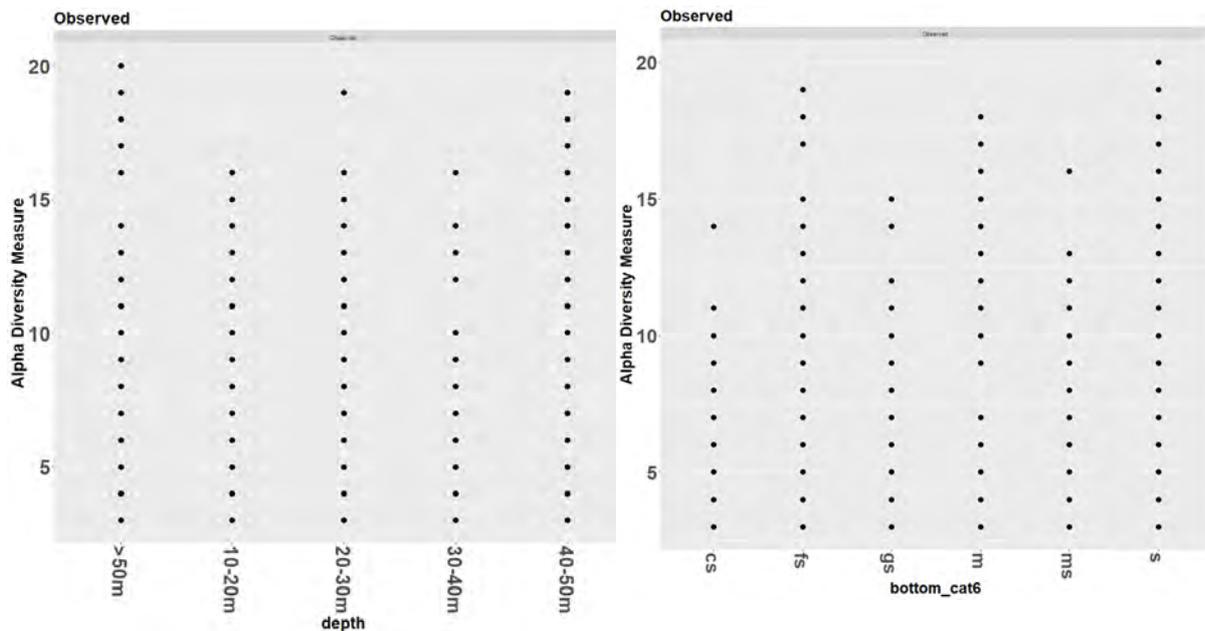


Figure 17. α diversity (species richness)
a. Species richness at several depths.

b Species richness on several sediments.

3.6.5 β diversity - influence of depth

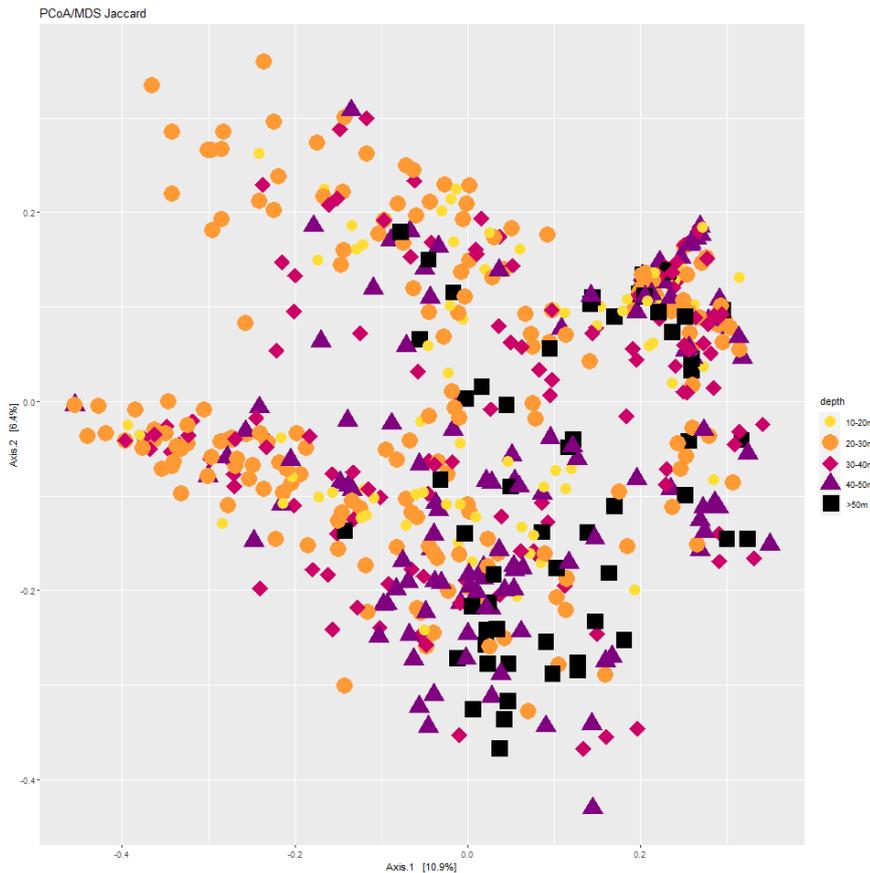


Figure 18. PCoA/MDS based on Jaccard distances of Huxley species data plotted with special shapes and colours for locations at different depths (10 m categories). Statistics by R package Phylosec.

Multidimensional scaling based on Jaccard distances did not result in clear separated clusters (Figure 18, ignoring shapes and colours). Adding depth information (shapes and colours) shows depth-related differences in distribution.

PERMANOVA results based on Jaccard and Raup-Crick dissimilarities both showed significant differences in community compositions at different depths ($p < 0.001$).

Pairwise Permanova comparisons between 10 m depth categories in most cases showed statistical differences ($p < 0.05$). The exception was the comparison based on Raup-Crick, in that case compositions deeper than 20-30m were not significantly different.

A successive PERMDIV evaluation showed no statistical significance for depth. The positive result for PERMANOVA and the negative for PERMSIV implies that the average community compositions differed with depth and was not influenced by dispersion (i.e. the variability in the community composition).

3.6.6 β diversity - Influence of sediment composition



Figure 19. PCoA/MDS based on Jaccard distances of Huxley species data plotted with special shapes and colours indicating the sea bed composition of the location. Statistics by R package Phylosec.

Adding sediment composition information to the same plot, also shows (sediment-) related differences in distribution (Figure 19).

PERMANOVA results based on Jaccard and Raub-Crick dissimilarities both showed significant differences in community compositions on different sediments ($p < 0.01$).

Pairwise Permanova comparisons in this case were less straightforward. Based on Jaccard distances, communities on most sediment categories differed significantly ($p < 0.05$) except those on muddy-sand vs. fine sand and on stones/gravel vs. coarse sand. When based on Raup-Crick distances, however, only communities on sand and coarse sand differed from those on all other sediment types.

The following PERMDISP, unlike in the case of depths, gave significant results for sediment compositions. This implies, that in this case, the PERMANOVA results are influenced by heterogenous dispersion (i.e. the variability in the community composition). However, unequal sample sizes may have influenced these results.

4 Discussion

The Huxley and Wodan datasets provide 734 and 199 locations respectively, where benthos was caught by beam or otter trawl and studied by naturalists. Semi-quantitative abundance data, and location information like depth, sediment composition and haul duration, add to the value of the datasets. Less favourable aspects of the datasets are abundances sometimes recorded as *present* only, and neglect of certain taxa. Although survey methodologies do not meet present standards, combined with the Poseidon survey data it forms the most comprehensive dataset on historical distribution of epibenthos in the North Sea. Comparison with the actual distribution of species will be carried out in near future. Digitalisation of pre-1900 German surveys is foreseen later.

For several decades, researchers have tried to line out epibenthic communities throughout the North Sea. In general, the zone >100 m is inhabited by cold-water species; the zone <50 m is inhabited by warm water species; and the intermediate zone between 50 and 100 m depth is inhabited by both (Künitzer *et al.*, 1992).

Dryer *et al.* (1983) and several other researchers (cited in Reiss *et al.*, 2010) pointed out that the factors that influence epifaunal assemblages depend on the spatial scale. Reiss *et al.* concluded: “For community structures on the scale of the whole North Sea the most influential environmental variables appeared to be hydrographic variables such as bottom water temperature, bottom water salinity, and tidal stress (for the infauna)”.

In the southern North Sea (< 50m), however, sediment characteristics are the most important variables affecting epifaunal community structure (Rees *et al.*, 1999; Callaway *et al.*, 2002).

The Huxley survey dataset provides information on depth and sediment composition of the locations. Contrary to the cited literature, depth appeared a better factor to describe differences in species aggregations than sediment type (§ 3.6). Depth is related to summer bottom temperatures, but this also holds for factors like current speed and sea bed stress. Data that lack so far back in time.

Cluster analysis of the Huxley data showed a clearer distinction of certain areas than comparable modern data (§ 3.6.2). In the Southern Bight along the English coast, reefs built by the Ross worm *Sabellaria spinulosa* were common. At certain locations they still exist (Pearce *et al.*, 2011), their existence along the haul trajectories of the surveys deserves a further analysis. The concentration of several hydroids and the erect bryozoan *Flustra foliacea* in the area confirms the supposition by Callaway *et al.* (2007) that their abundance was historically much higher in the southern North Sea. Changes in the other parts of the southern North Sea are less obvious. Especially here, we have to take into account that intensive sail trawling started already in the 1830's and that in the 1870's many fishing grounds already had lost their abundance of fish (Olsen 1878). However, the local species assemblage is undoubtedly selected by the highly dynamic quality of this area, known for its moving sand waves (McCave, 1971).

The distinction of the Dogger Bank in the cluster analysis, is also apparent. Comparison with modern data from Sonnewald & Türkay (2012) shows decreases of the hydrozoan *Obelia longissima* and the gastropod *Neptunea antiqua*, and increases of the crab species *Corystes cassivelaunus* and *Liocarcinus holsatus*. Comparison with Callaway (2002) shows that *Neptunea antiqua* and *Corystes cassivelaunus* nowadays have a more northern distribution. In these cases it is hard to separate the effect of higher seawater temperatures from trawling impacts. Apart from sand the Dogger Bank was also known for its stony areas that could act as a holdfast (Olsen 1878; Van Moorsel 2011). More hard substrate was provided by the bivalves *Aequipecten opercularis* and *Modiolus modiolus* and the gastropod *Neptunea antiqua* (§ 3.2.1).

Changes in the muddy-sand to mud region in the central-eastern North Sea were most prominent. Many flat oyster *Ostrea edulis* beds were already destroyed by dedicated trawling before the fishery surveys took place (Bennema *et al.* 2020). The abundance of the soft coral *Alcyonium digitatum* and hydrozoans like *Obelia longissima* can be explained by this substrate, as it is known that large quantities lived on individual and clustered oysters (Tesch, 1910). Nowadays, mainly echinoderms are the most characteristic species of this area (Reiss *et al.* 2010)

These results are in accordance with the results of studies that describe a decline in bivalves and an increase of crustaceans since the start of the 20th century (Rumohr and Kujawski, 2000; Callaway *et al.*, 2007). Both studies drew their conclusions from qualitative Poseidon data, demonstrating the value of such historic datasets to study the long-term effect of trawling on marine communities. The semi-quantitative Huxley and Wodan datasets gives a better impression of epibenthos distribution in the same period and seem to have the potential for further long-term comparisons.

4.1 Acknowledgements

Many thanks to Luna van Loos, Godfried van Moorsel, Jan van Dalftsen and Hans de Blauwe. Luna van Loos advised how to use β -diversity statistics, without her help the chapter on community could not have been written. Godfried van Moorsel helped with the actualisation of scientific species names and made some helpful comments that improved the manuscript. with suggestions and corrections of the text. Jan van Dalftsen also gave several suggestions that improved the text. Hans de Blauwe checked the identification of the bryozoans in the southern North Sea. I am also grateful for all the help with the collection of data and literature at Cefas in Lowestoft and at NIOZ on Texel.

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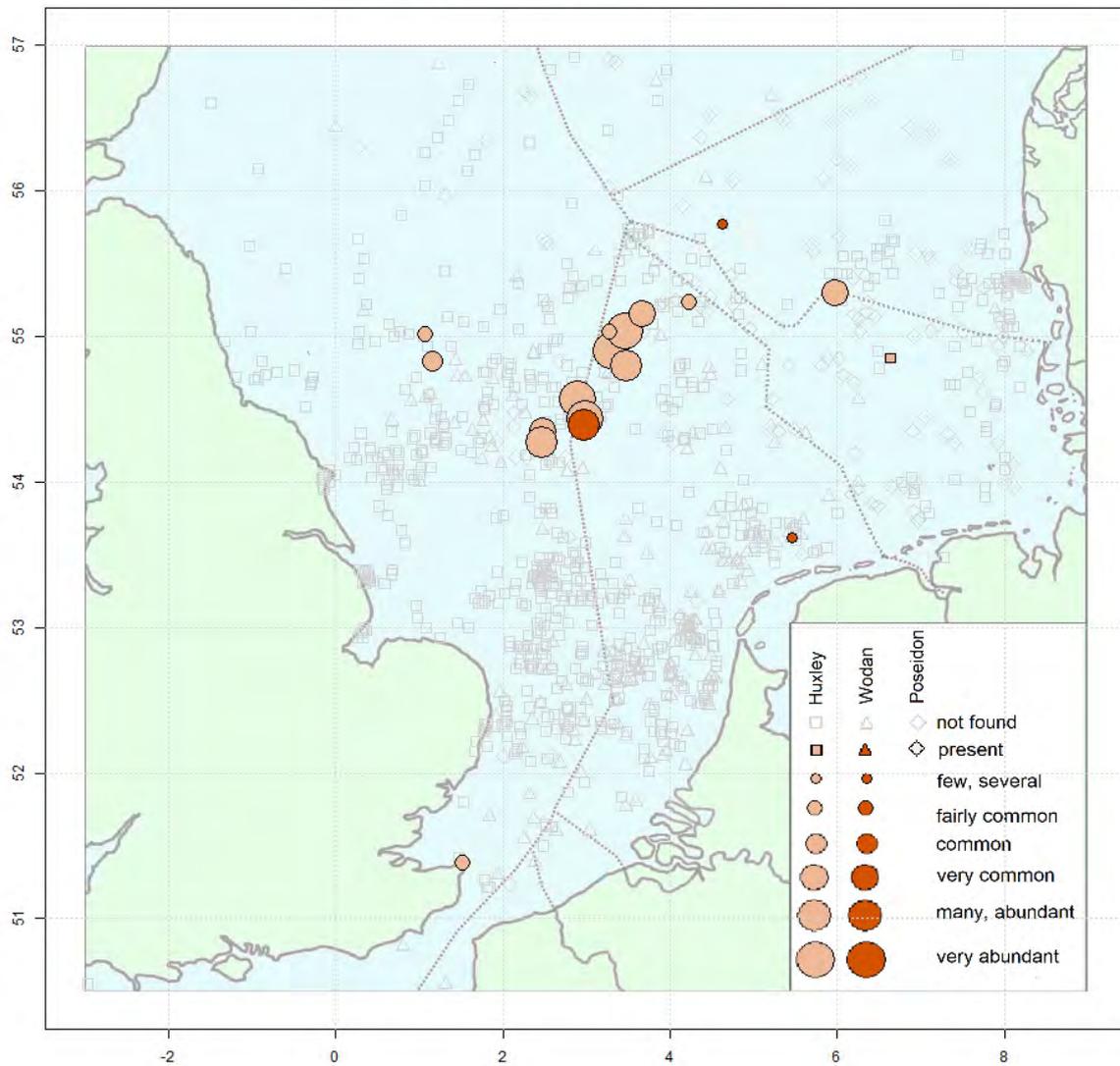
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6 Species distribution maps

Species distribution maps were plotted directly from the historical data. Species found at a low number of locations were not plotted.

Haul locations where the species weren't found, are depicted in grey. Circle sizes represent semi-quantitative abundance categories as shown in Table 1. Shapes and colours are used to indicate the data source.

Halichondria (Halichondria) panicea

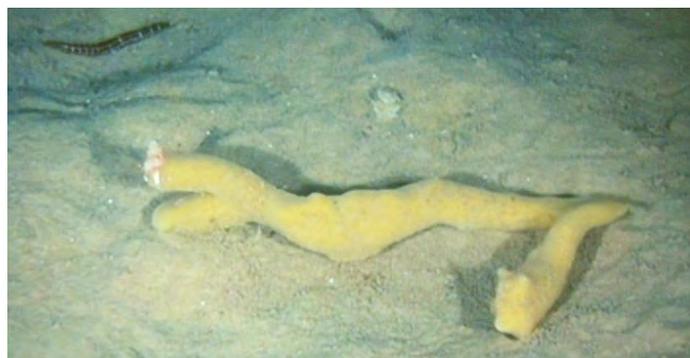


Halichondria (Halichondria) panicea

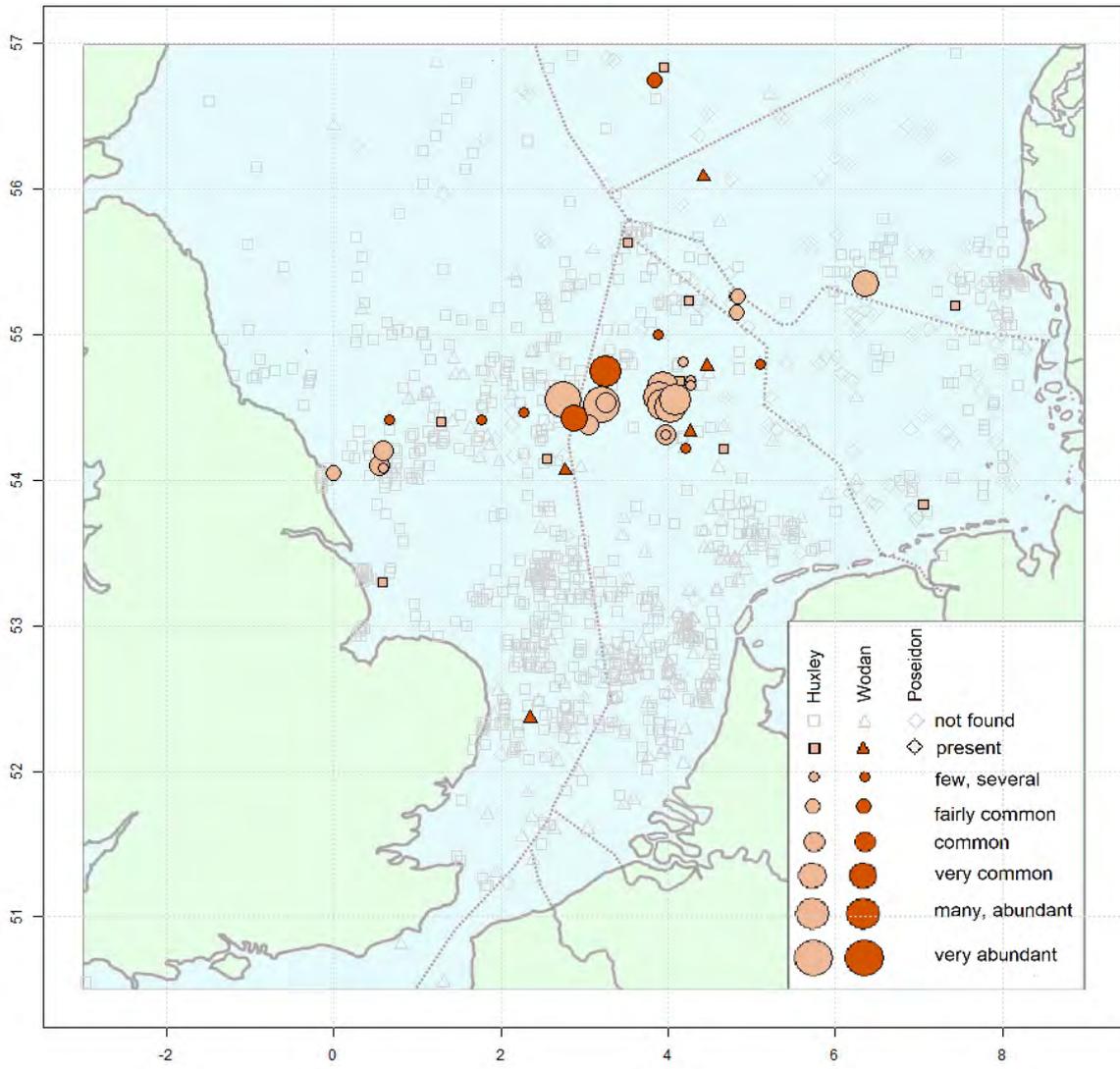
Breadcrumb sponge

Breadcrumb sponge *Halichondria (Halichondria) panicea* at the South West rim of Dogger Bank could be floating like this individual at 54.077 N and 4.271 E.

Oceana survey 25-8-2016, identification verified by Rob van Soest.



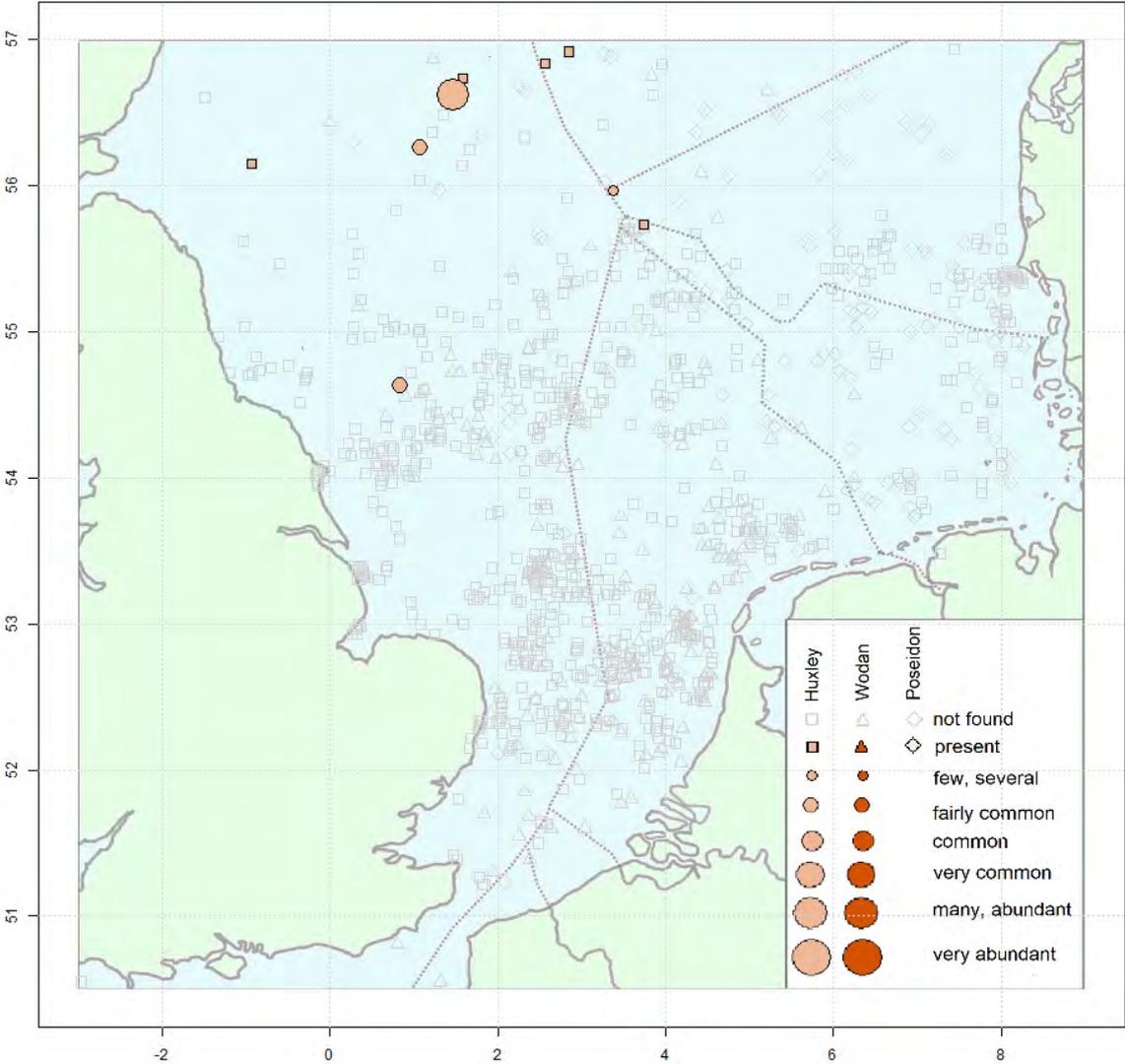
Porifera



Unspecified Porifera Sponges

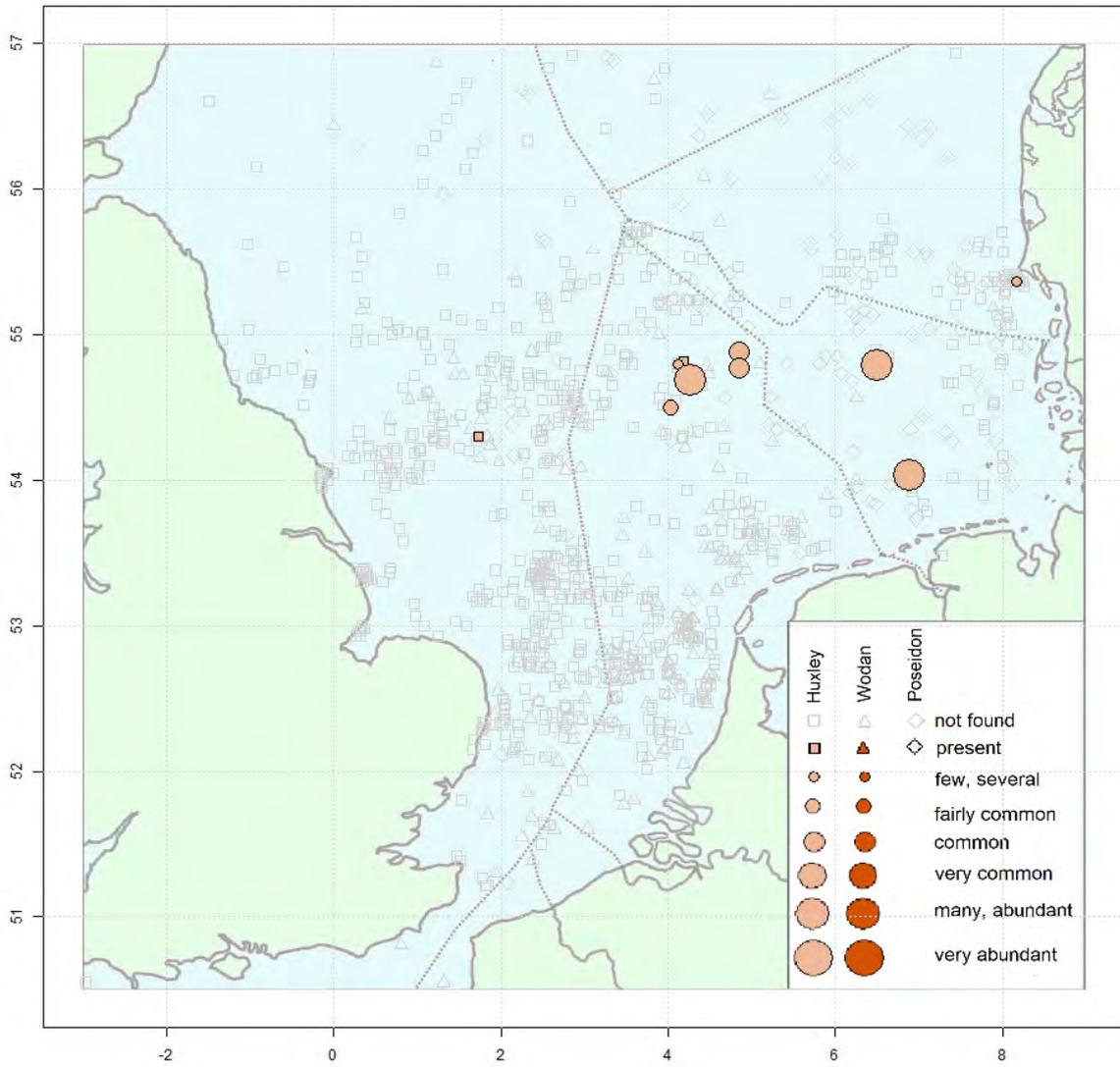
Cnidaria-Anthozoa

Bolocera tuediae



Bolocera tuediae Deeplet sea anemone

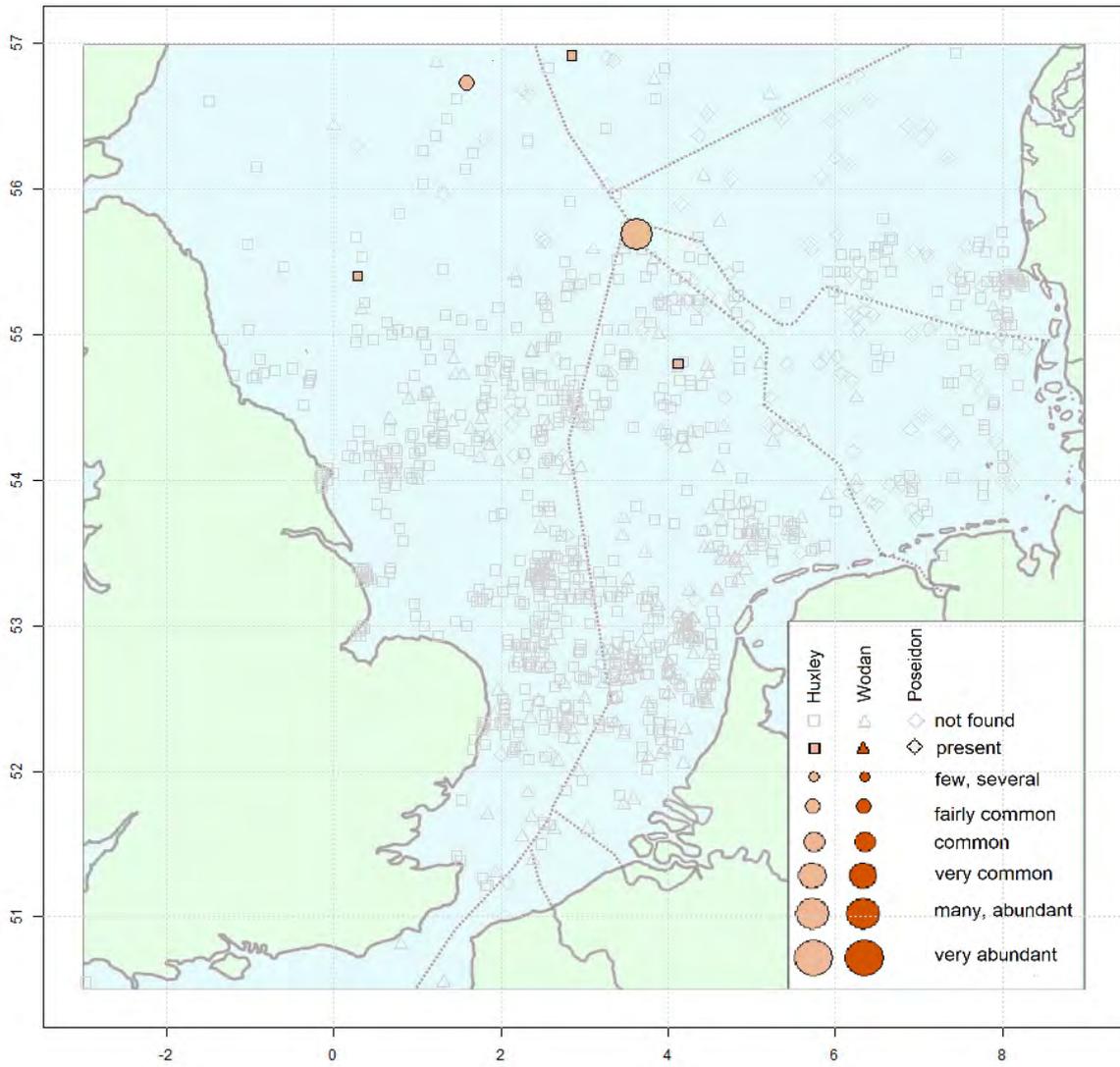
Sagartiogeton undatus ?



Sagartiogeton undatus? A sea anemone

? was added by the Huxley naturalist.

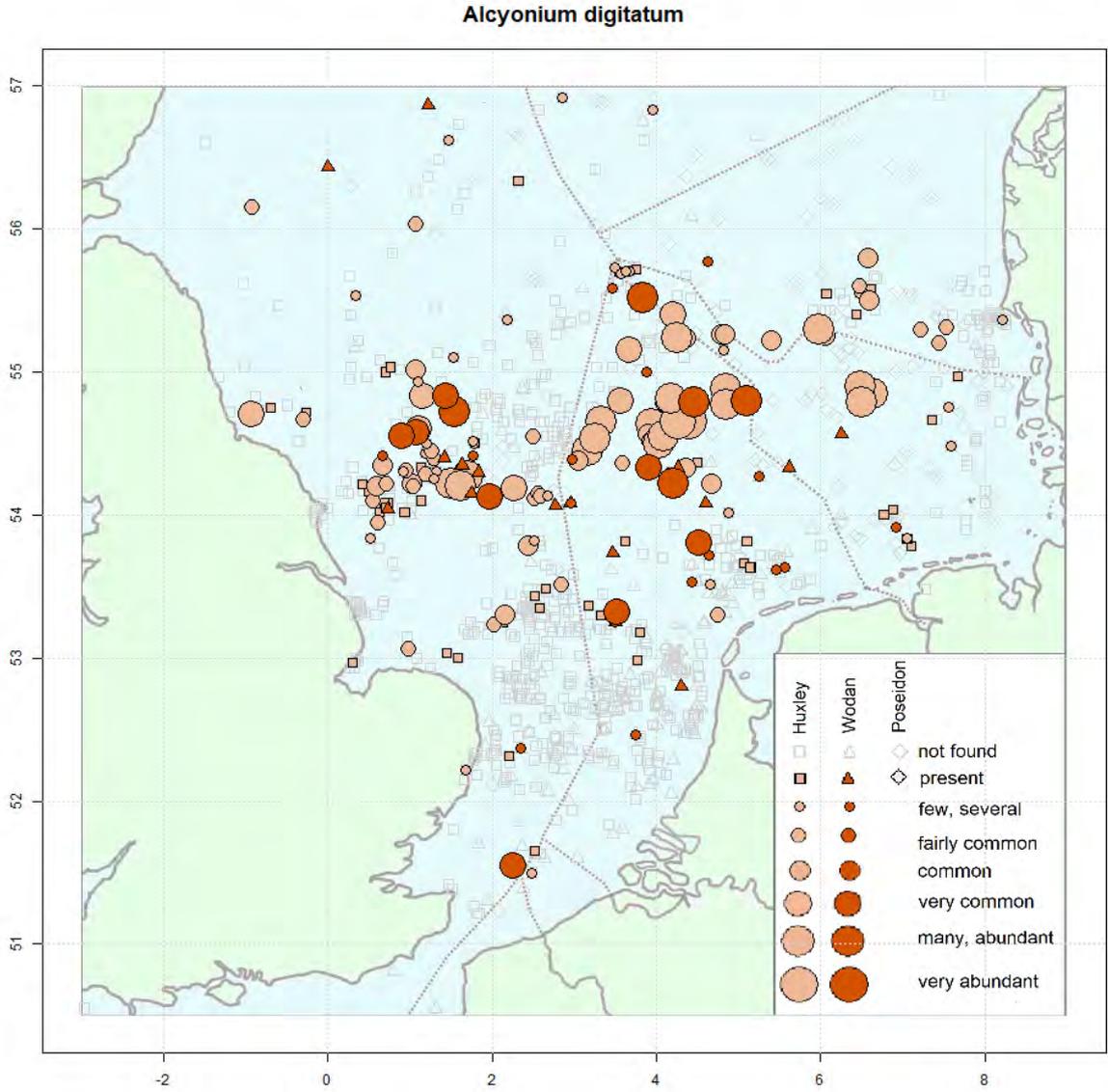
Urticina eques



Urticina eques

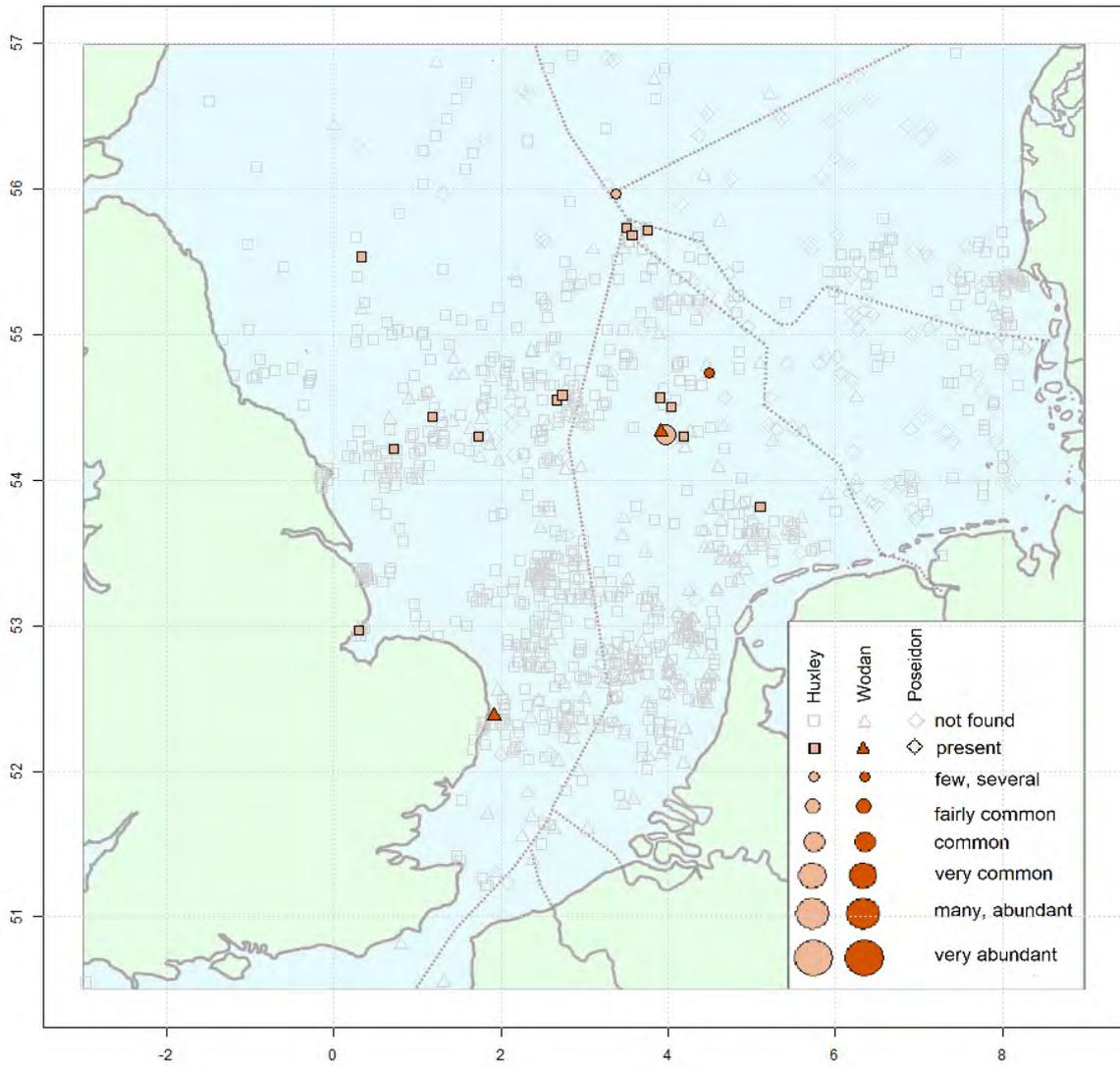
Horseman anemone

Cnidaria-Alcyonaria



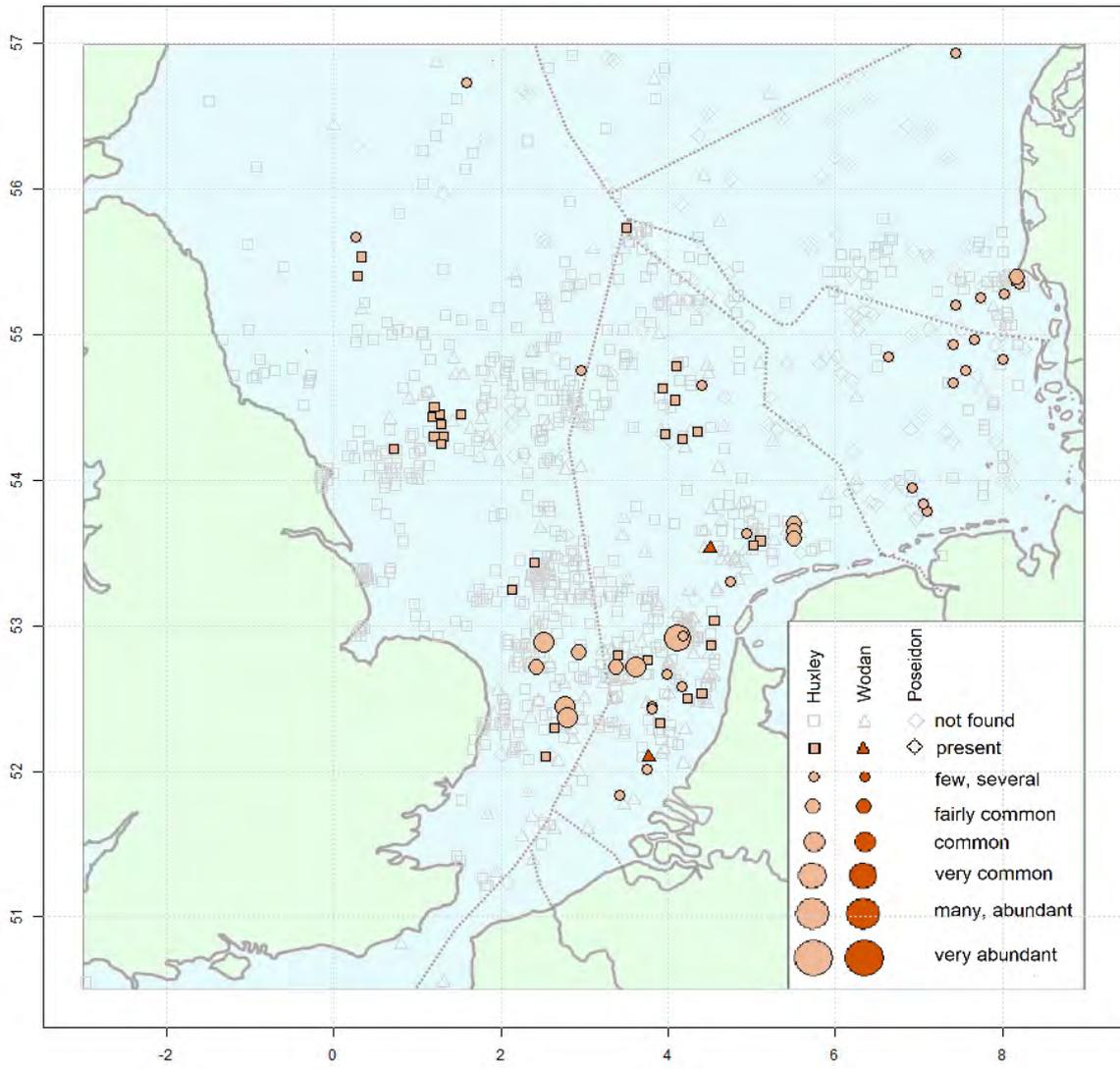
Alcyonium digitatum Dead men's fingers

Halecium halecinum



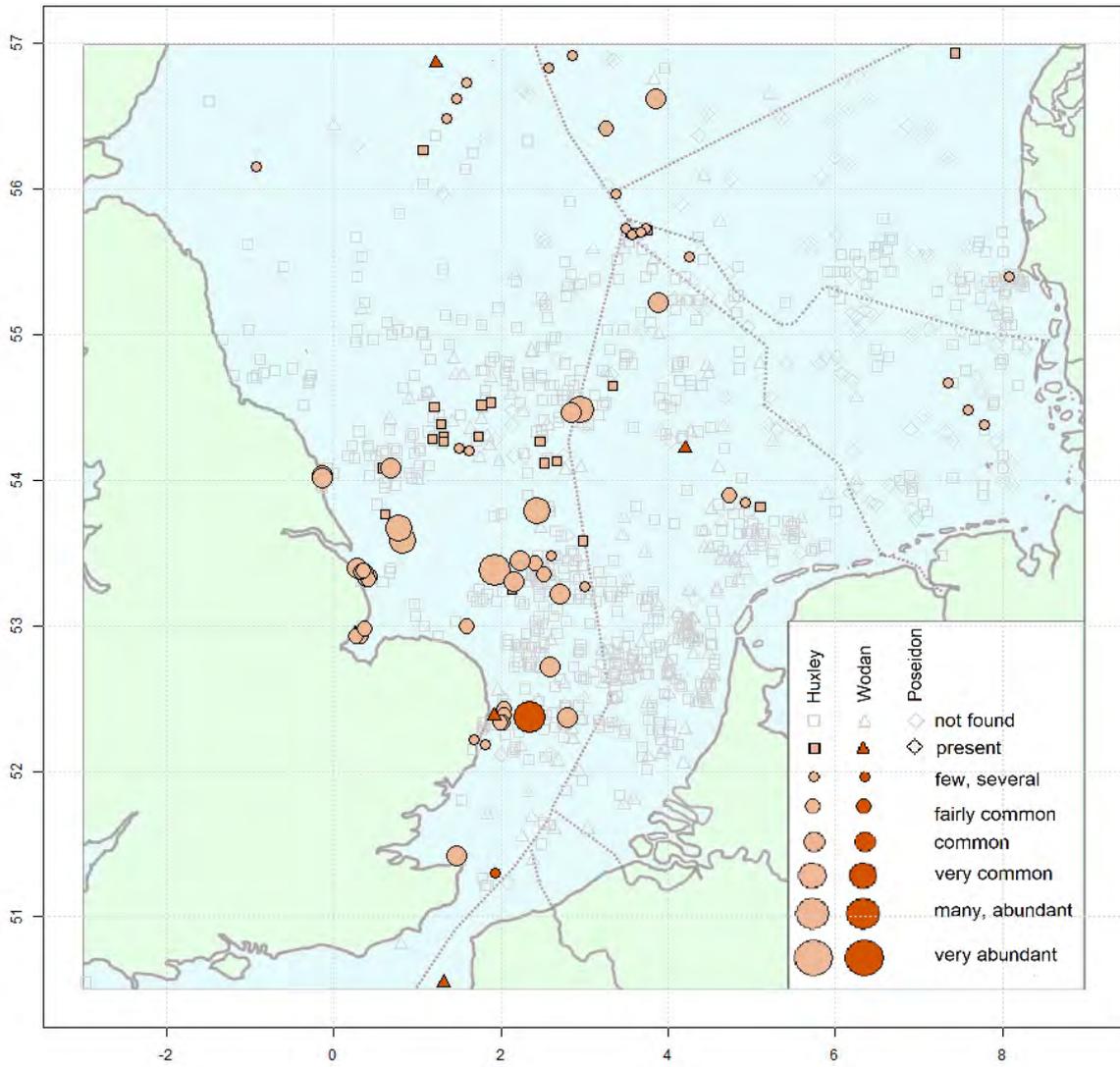
Halecium halecinum Herring bone hydroid

Hydractinia echinata



Hydractinia echinata Hermit crab fir

Hydrallmania falcata



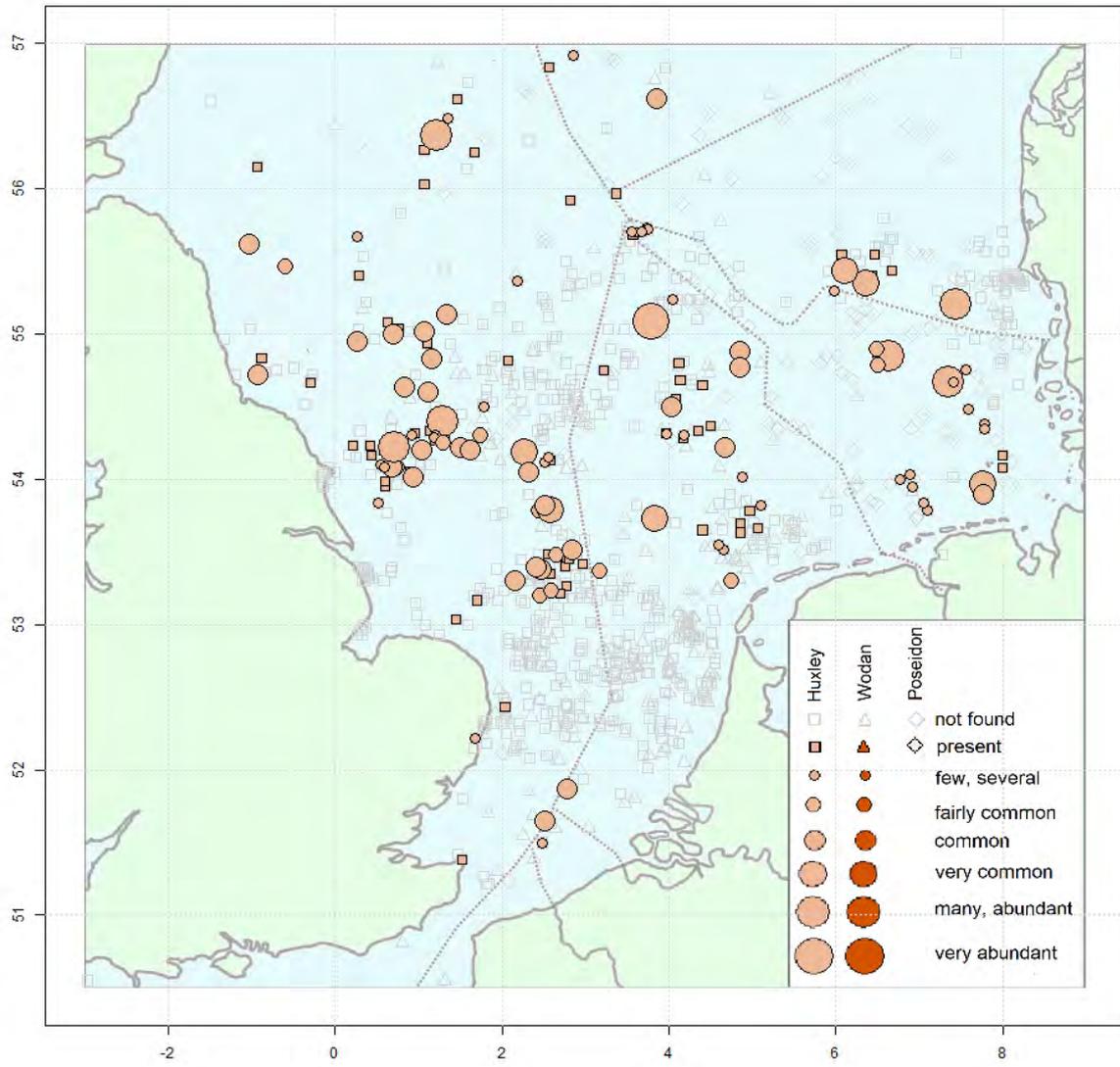
Hydrallmania falcata Sickle hydroid



(i) *Hydrallmania falcata*

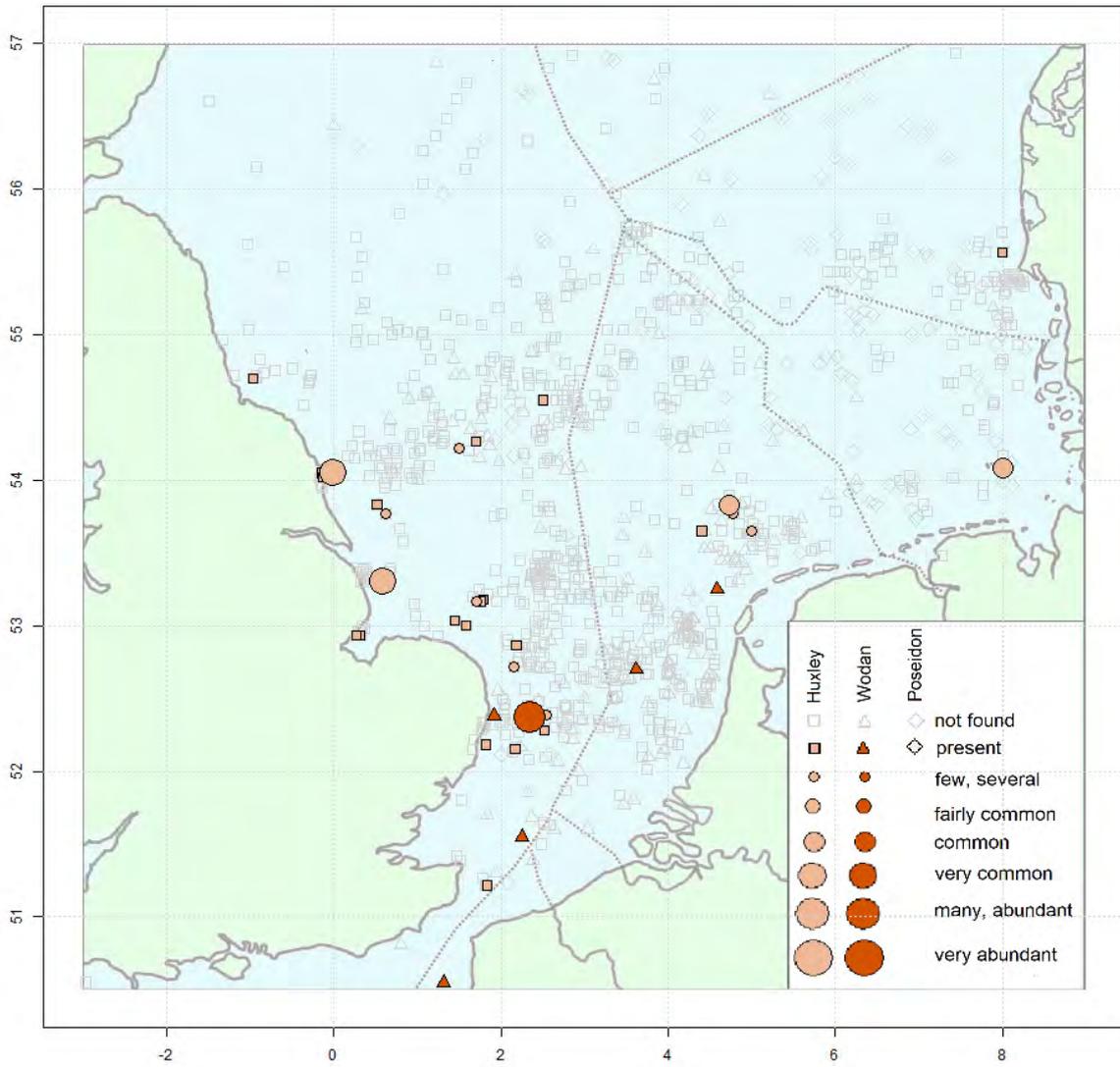
2000 distribution map (Callaway *et al.*, 2002).

Metridium senile



Metridium senile Plumose anemone

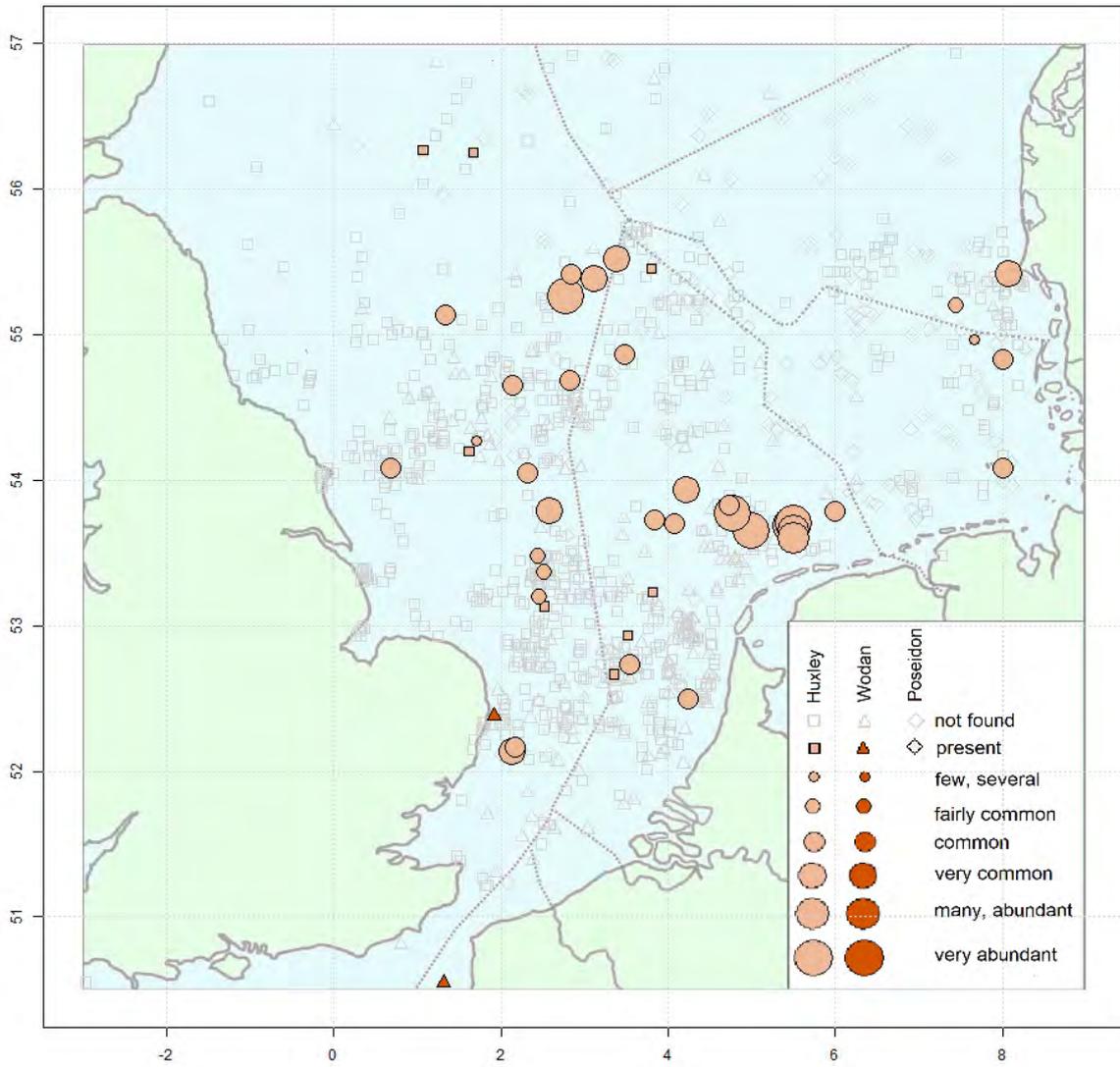
Nemertesia antennina



Nemertesia antennina

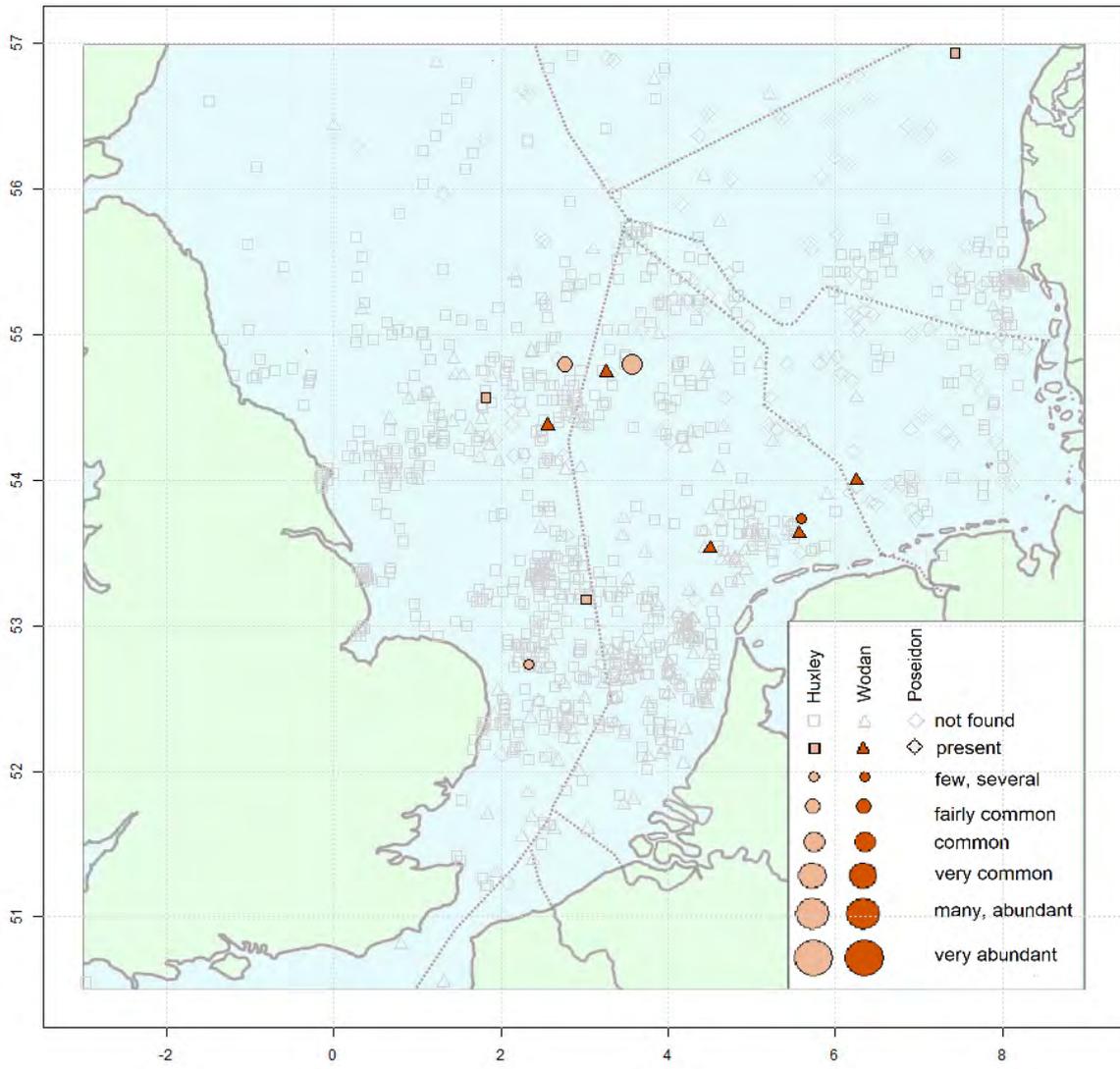
Sea beard

Nemertesia ramosa



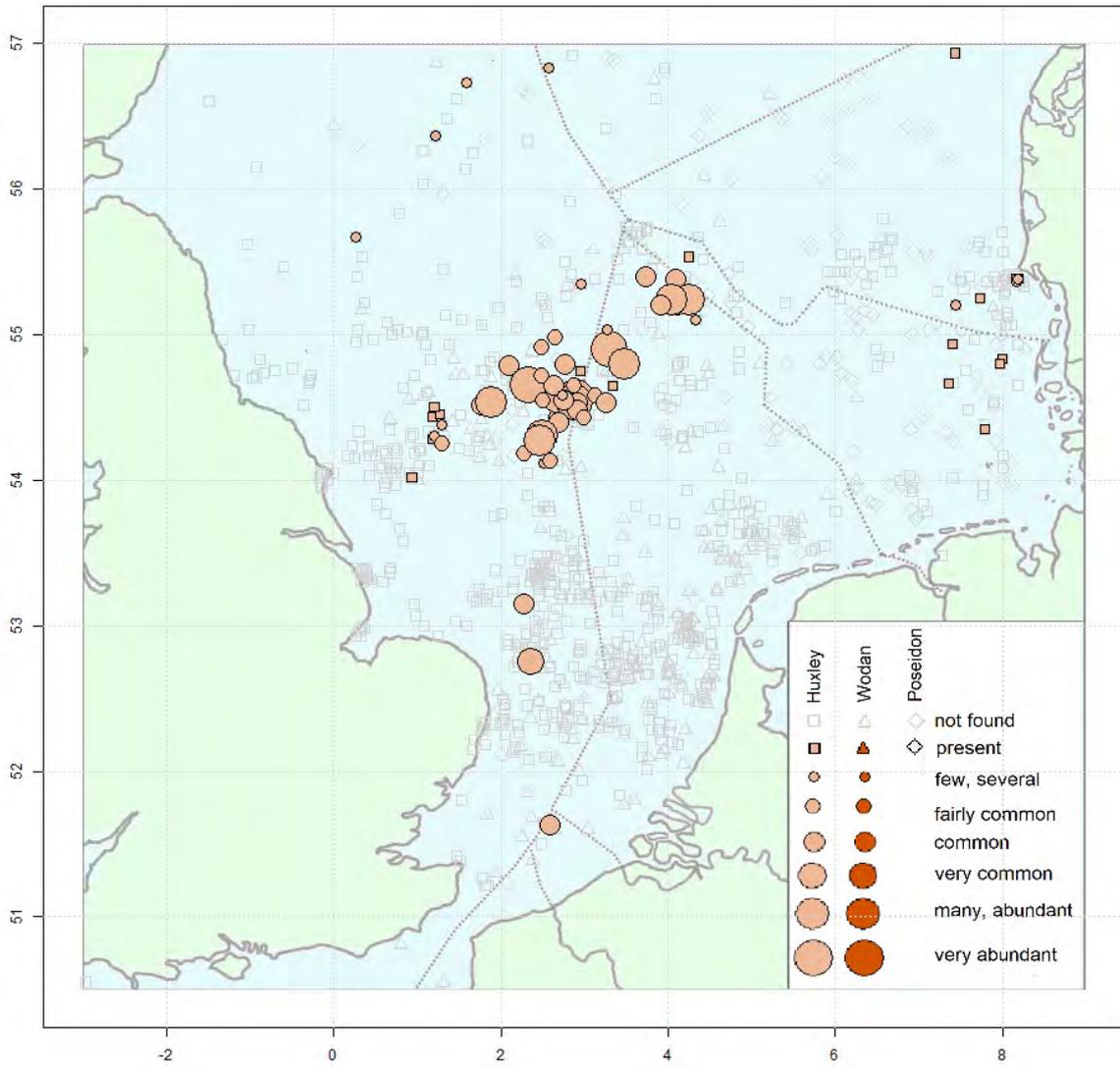
Nemertesia ramosa Branched antenna hydroid

Obelia geniculata



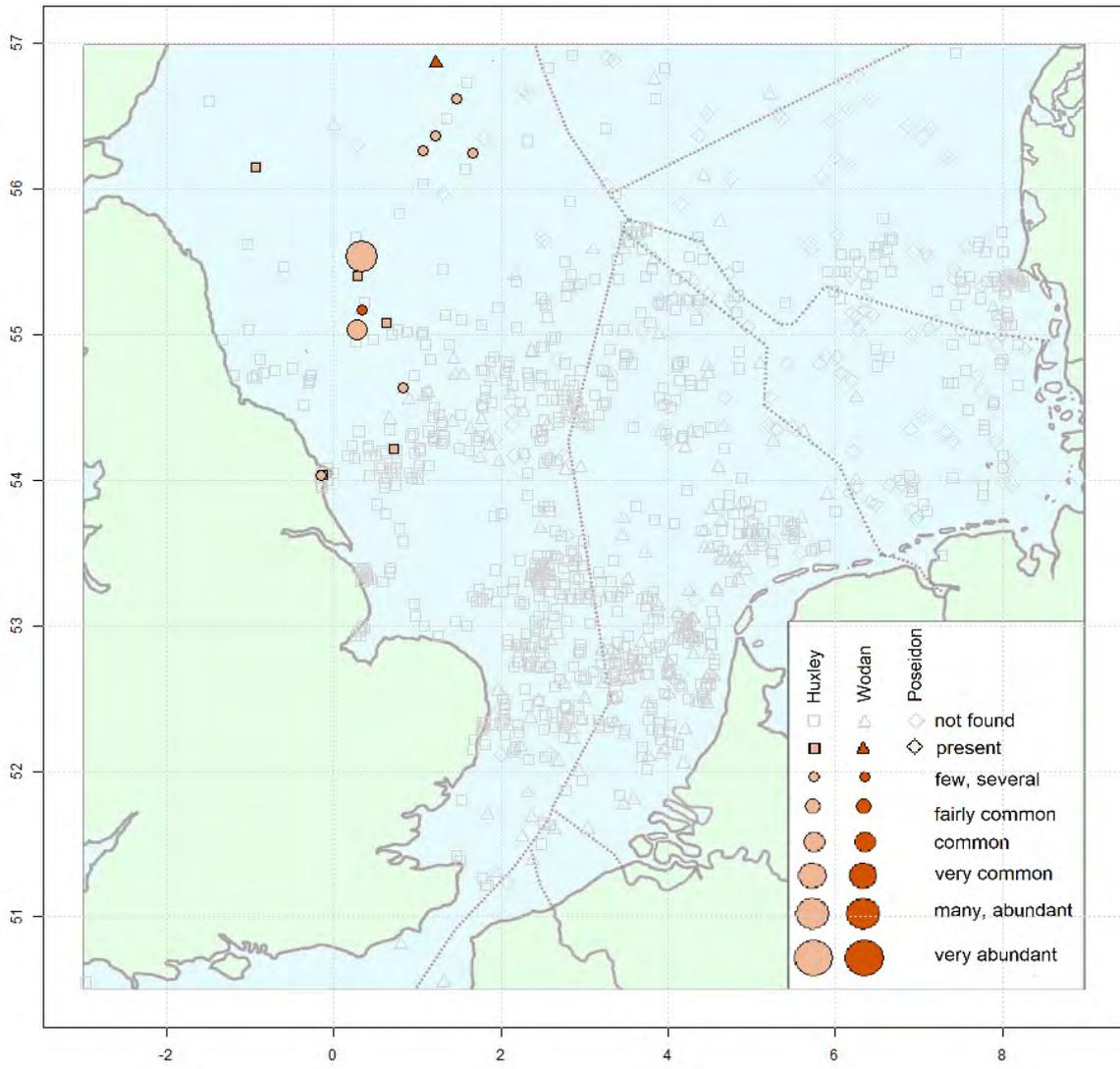
Obelia geniculata Kelp fir

Obelia longissima



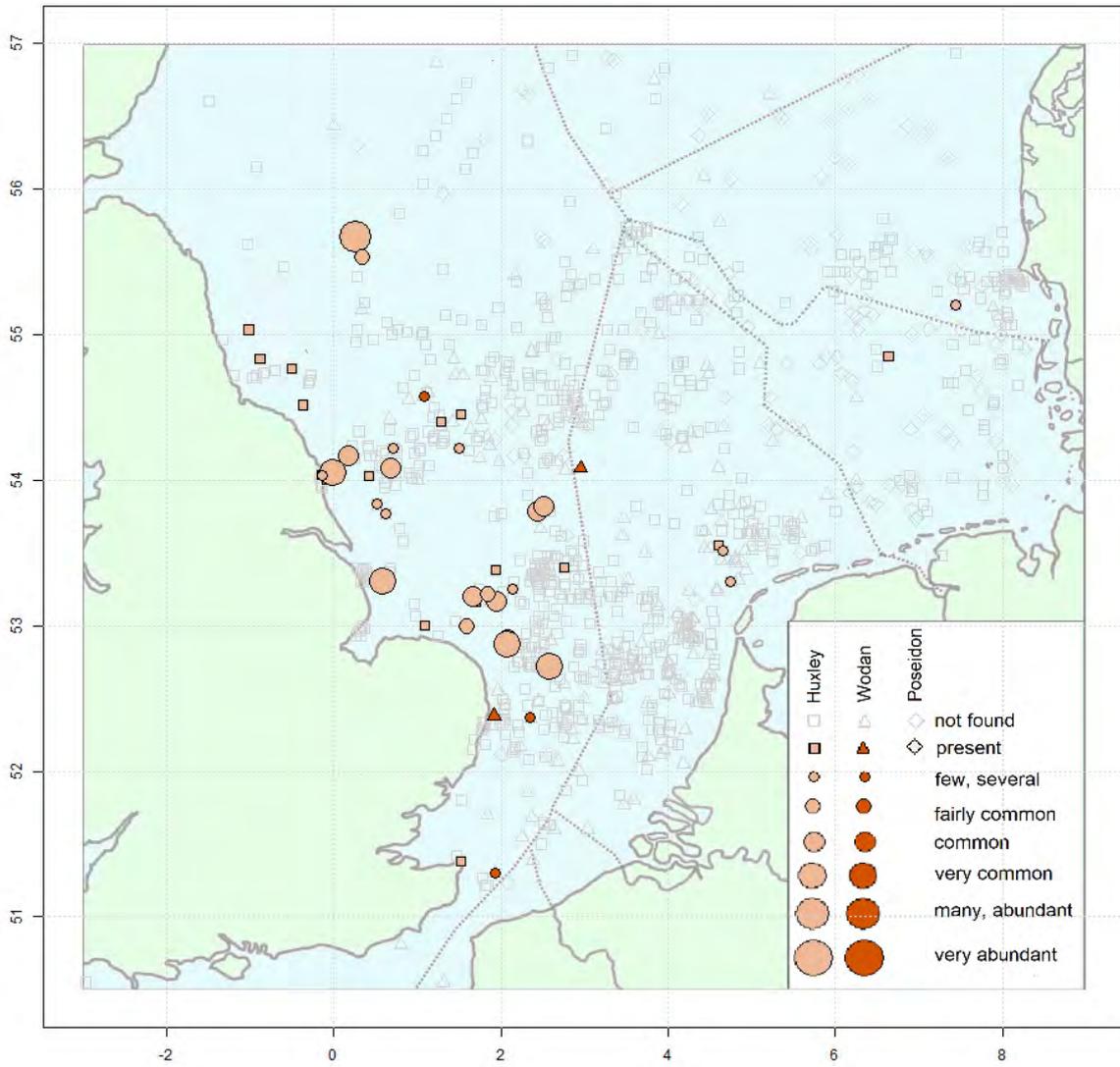
Obelia longissima A hydroid

Thuiaria thuja



Thuiaria thuja Bottle brush hydroyd

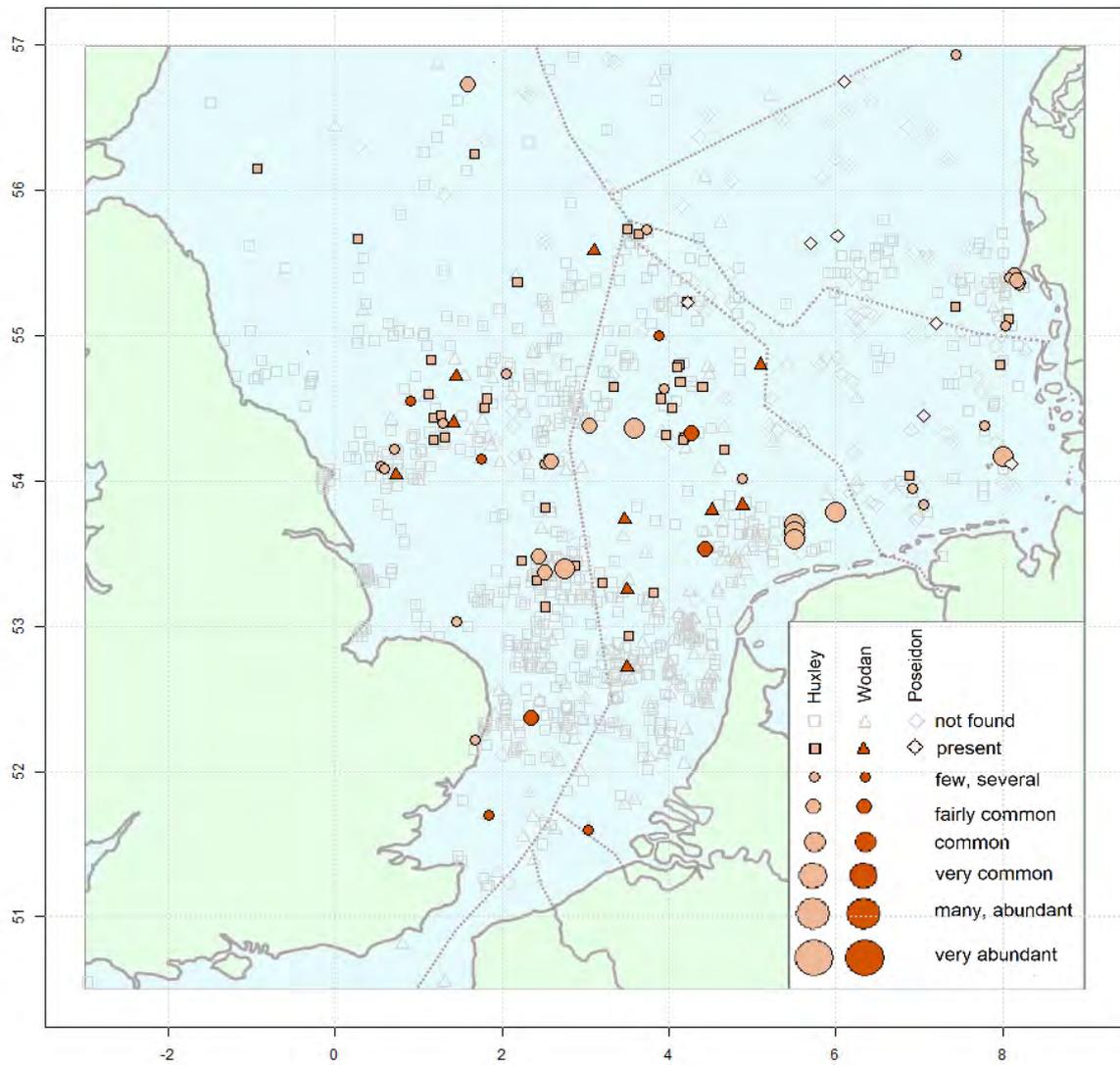
Tubularia indivisa



Tubularia indivisa Oaten pipe hydroid

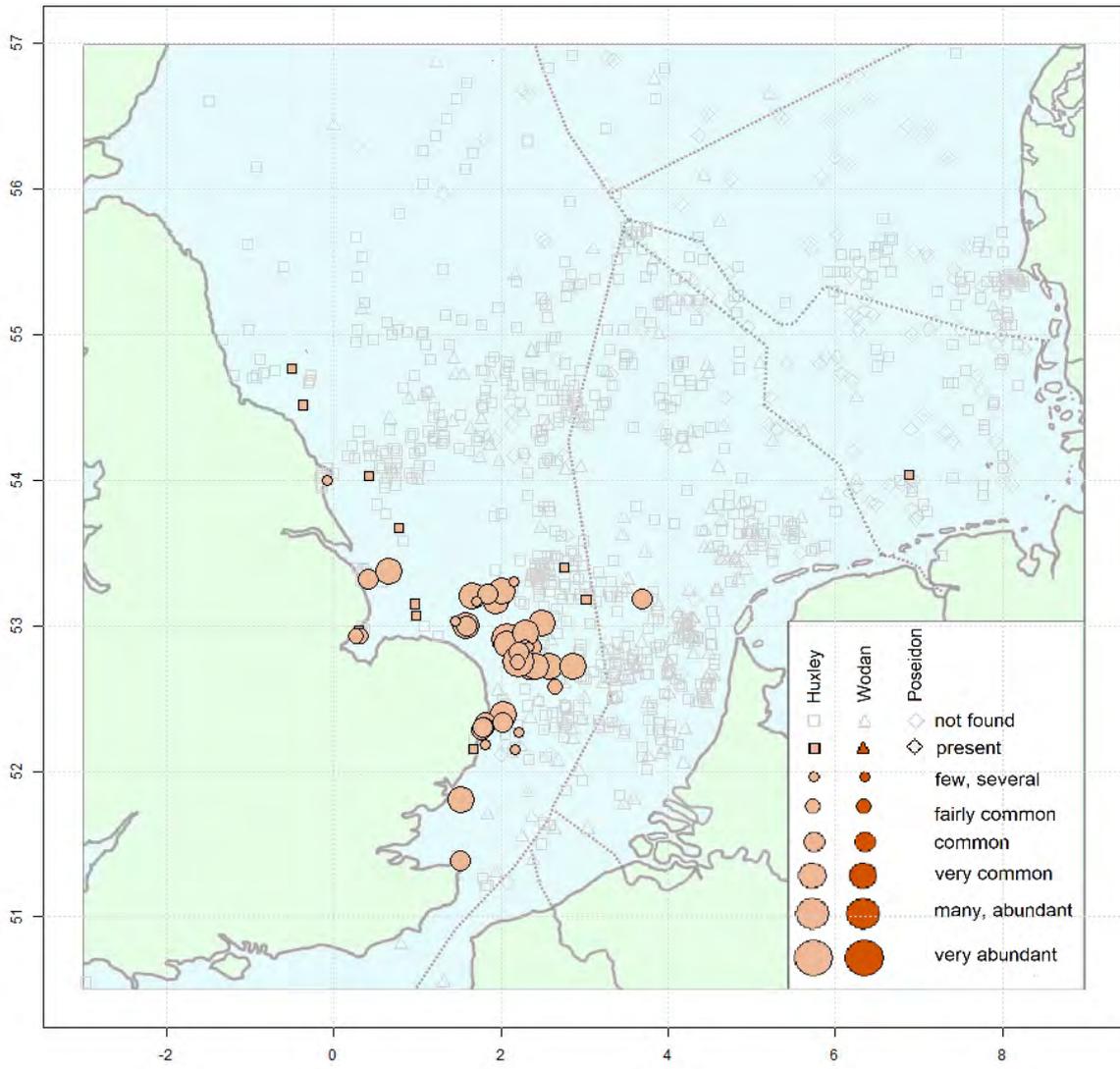
Annelida-Polychaeta

Aphrodita aculeata



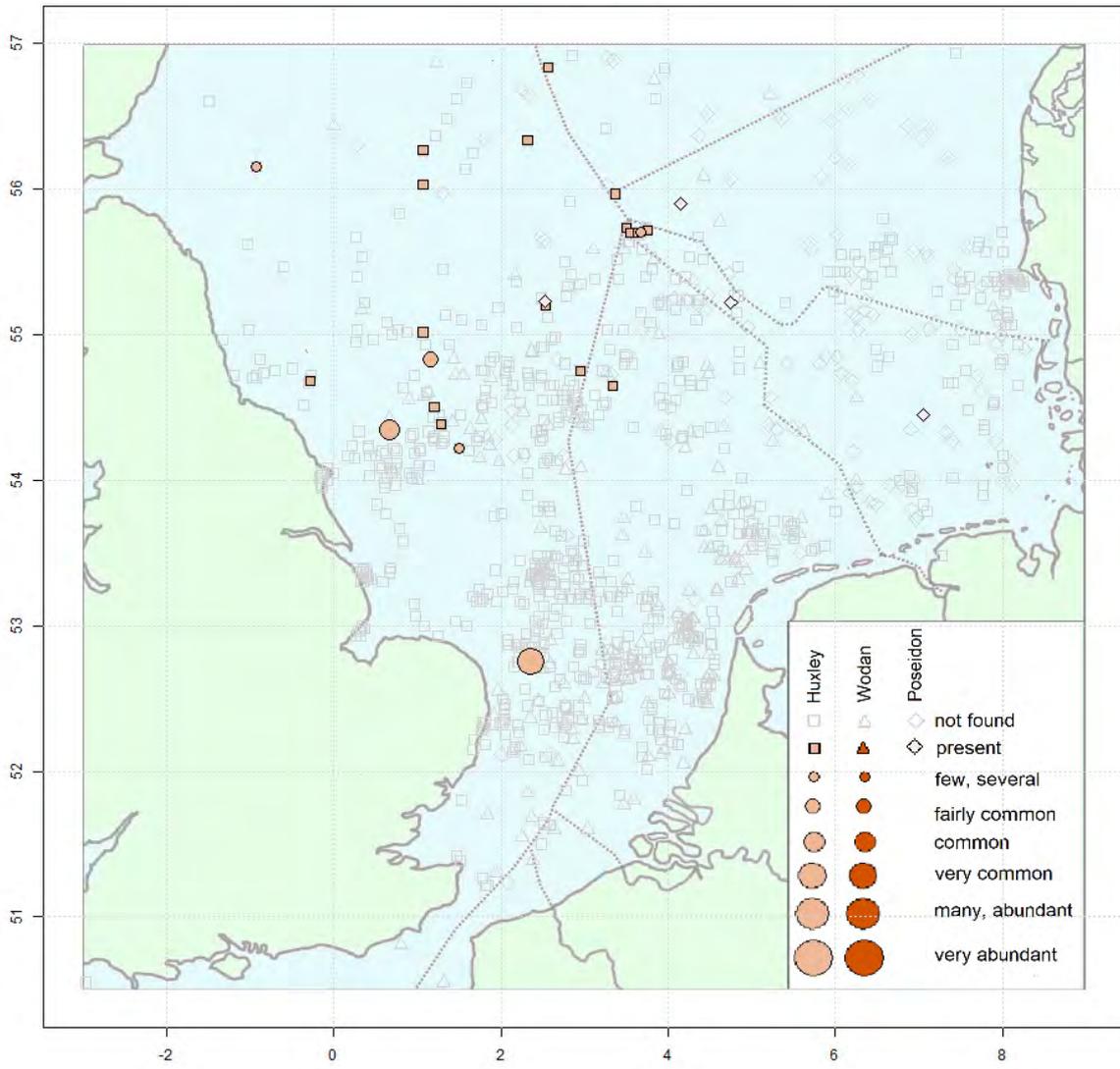
Aphrodita aculeata Sea mouse

Sabellaria spinulosa



Sabellaria spinulosa Ross worm

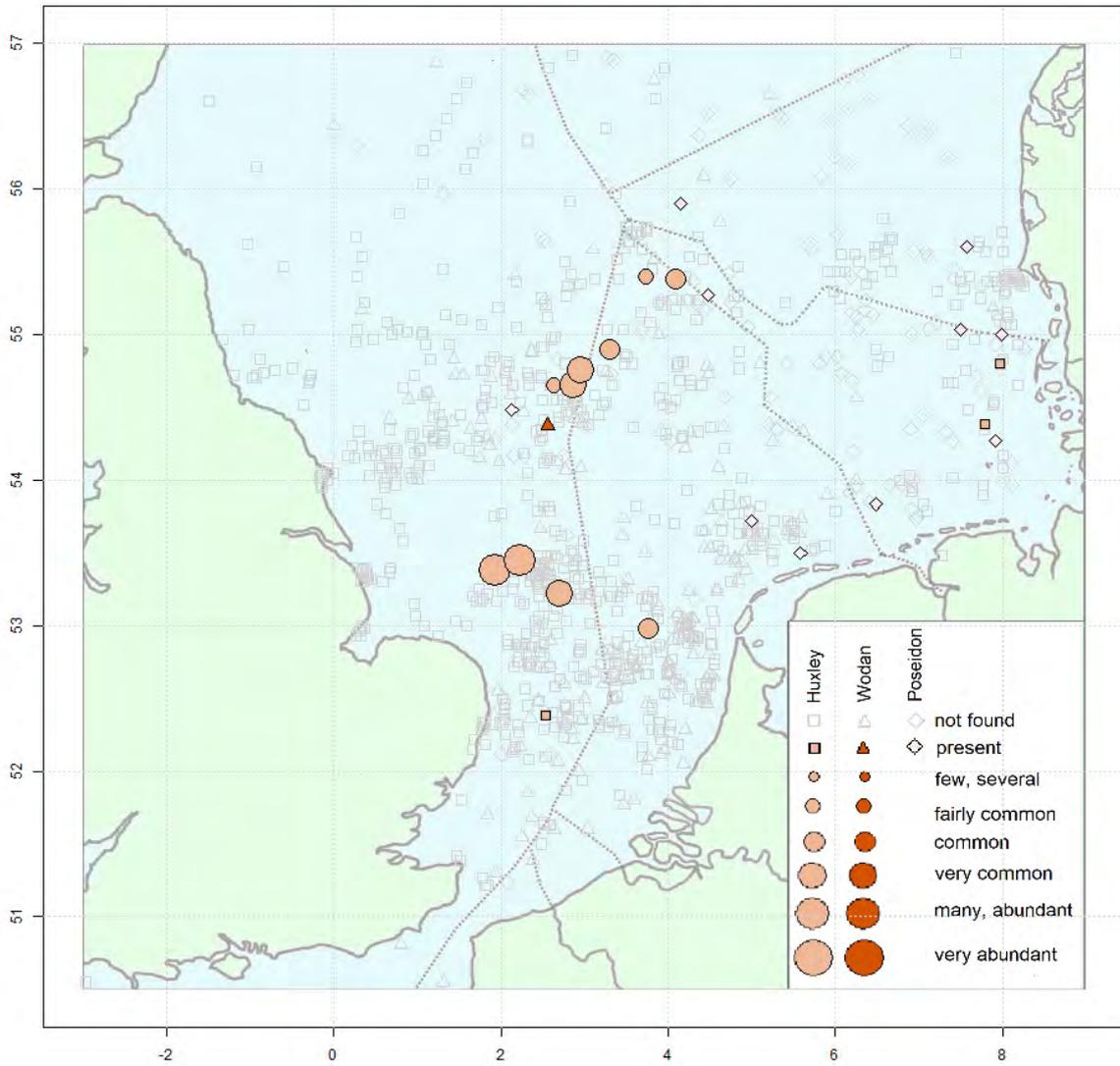
Sabella pavonina



Sabella pavonina Peacock worm

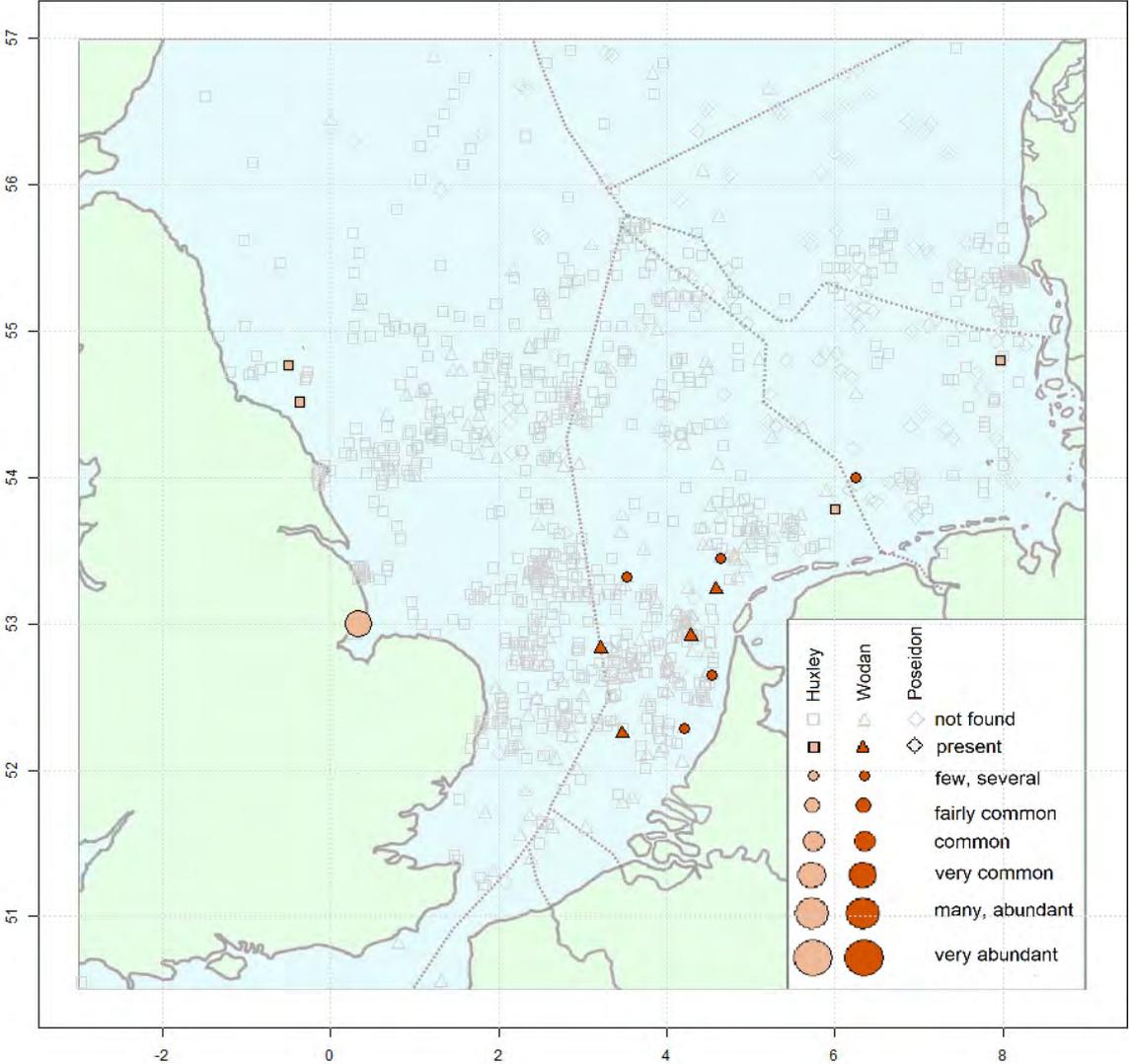
Arthropoda – Malacostraca-Amphipoda

Nototropis swammerdamei



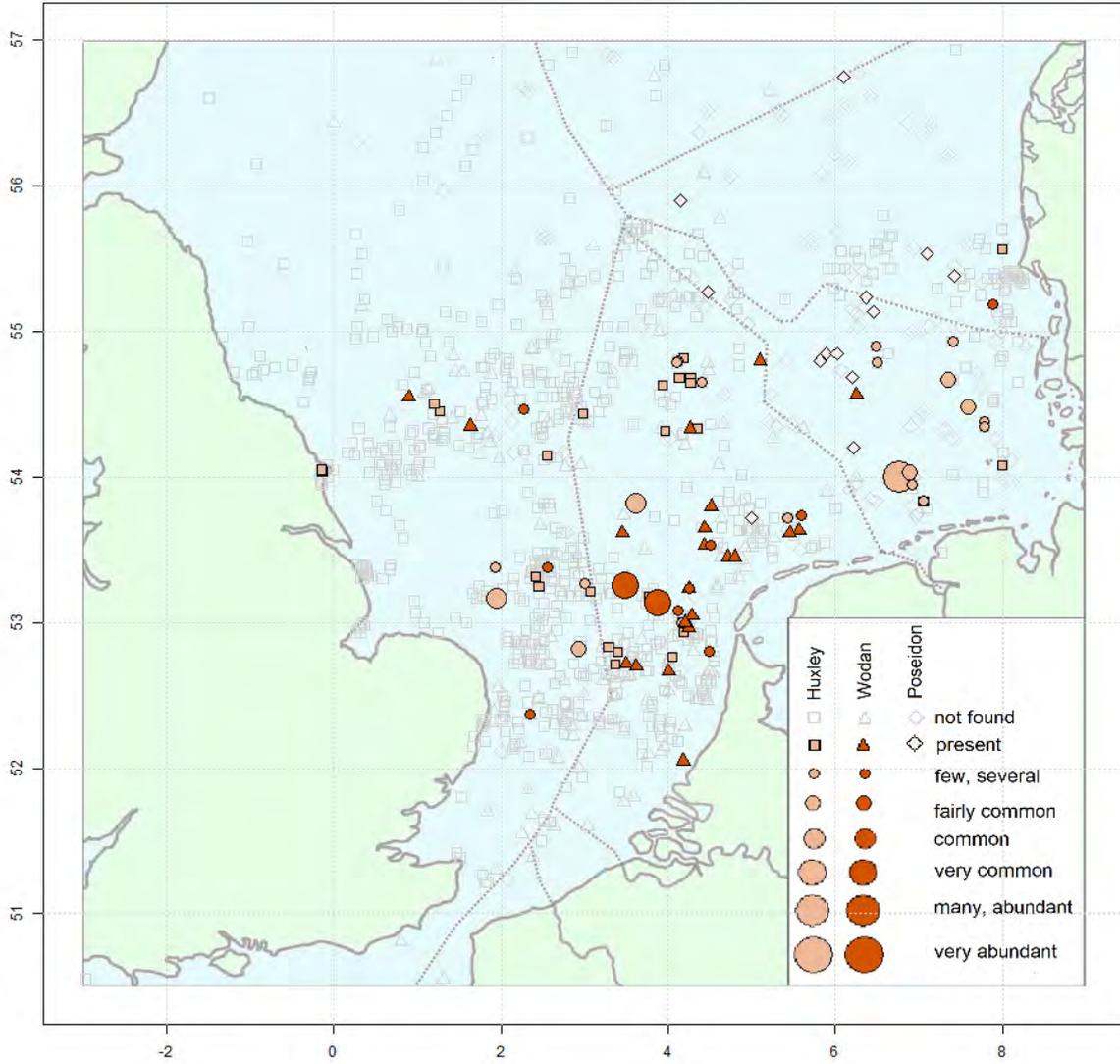
Nototropis swammerdamei An amphipod crustacean

Carcinus maenas



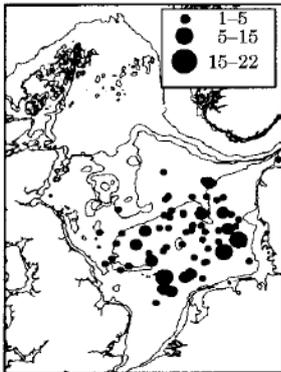
Carcinus maenas Common shore crab

Corystes cassivelaunus



Corystes cassivelaunus

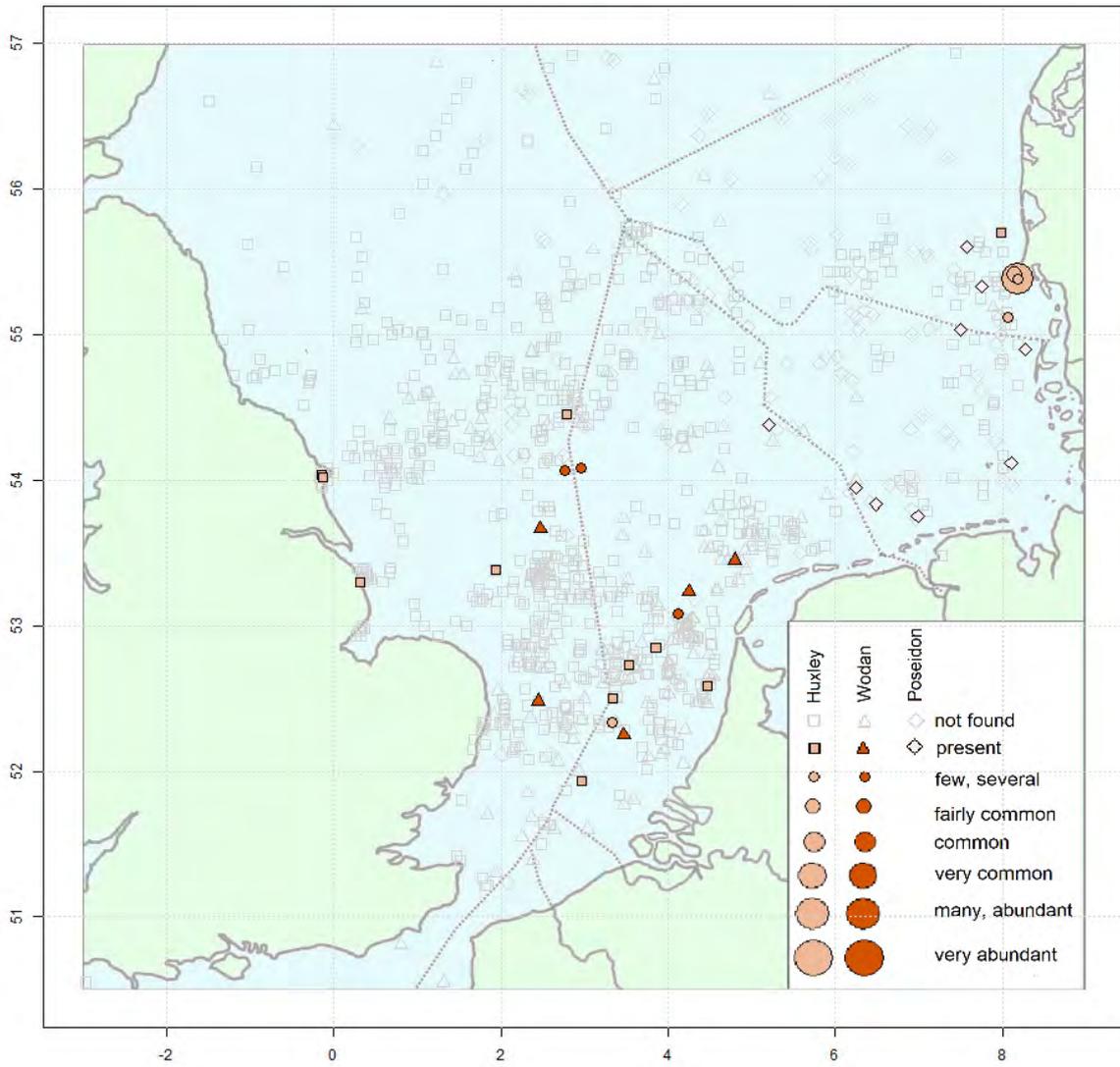
Masked crab



(c) *Corystes cassivelaunus*

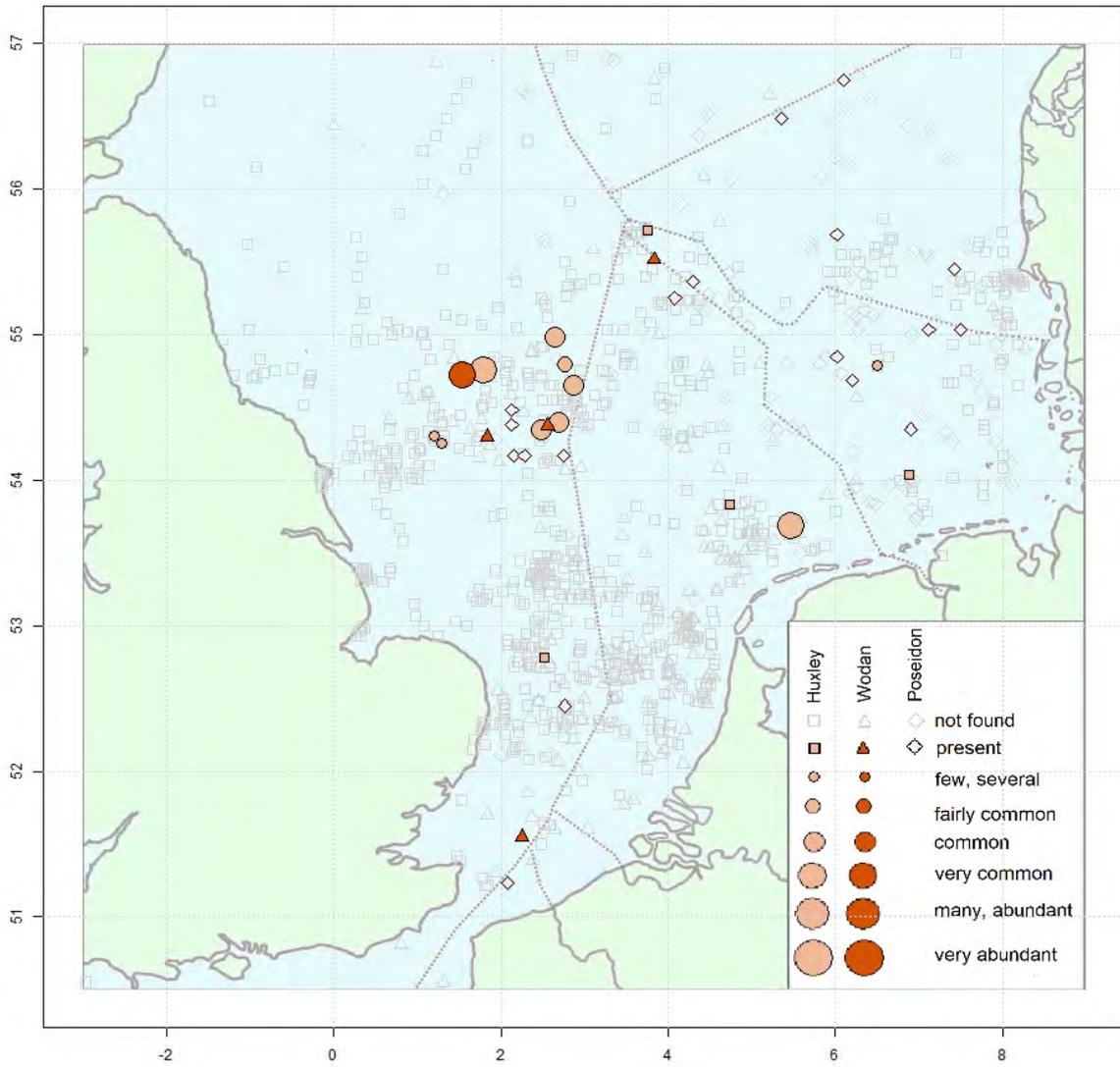
2000 distribution map (Callaway *et al.*, 2002).

Crangon crangon



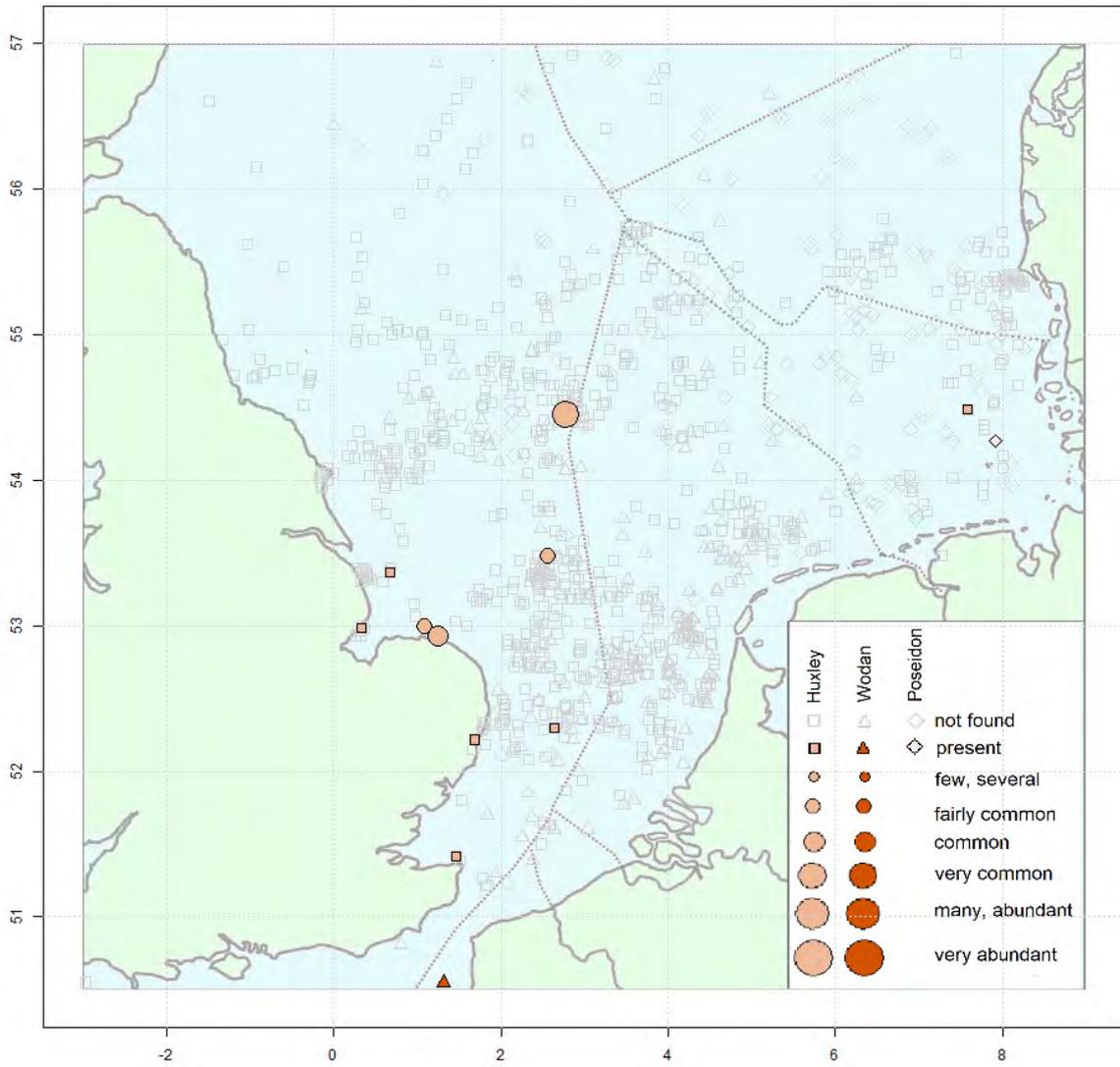
Crangon crangon Brown shrimp

Galathea intermedia



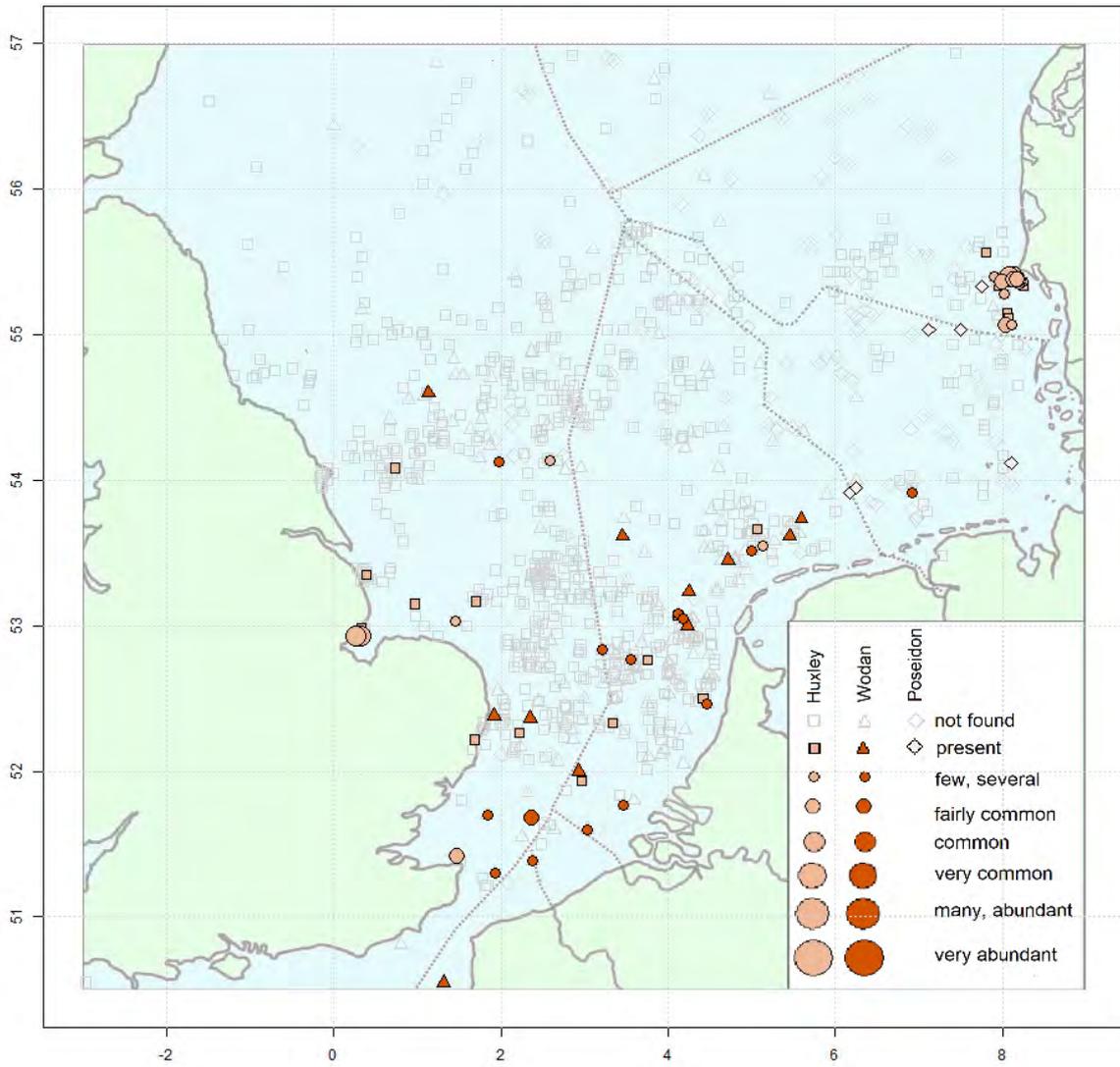
Galathea intermedia A squat lobster

Homarus gammarus



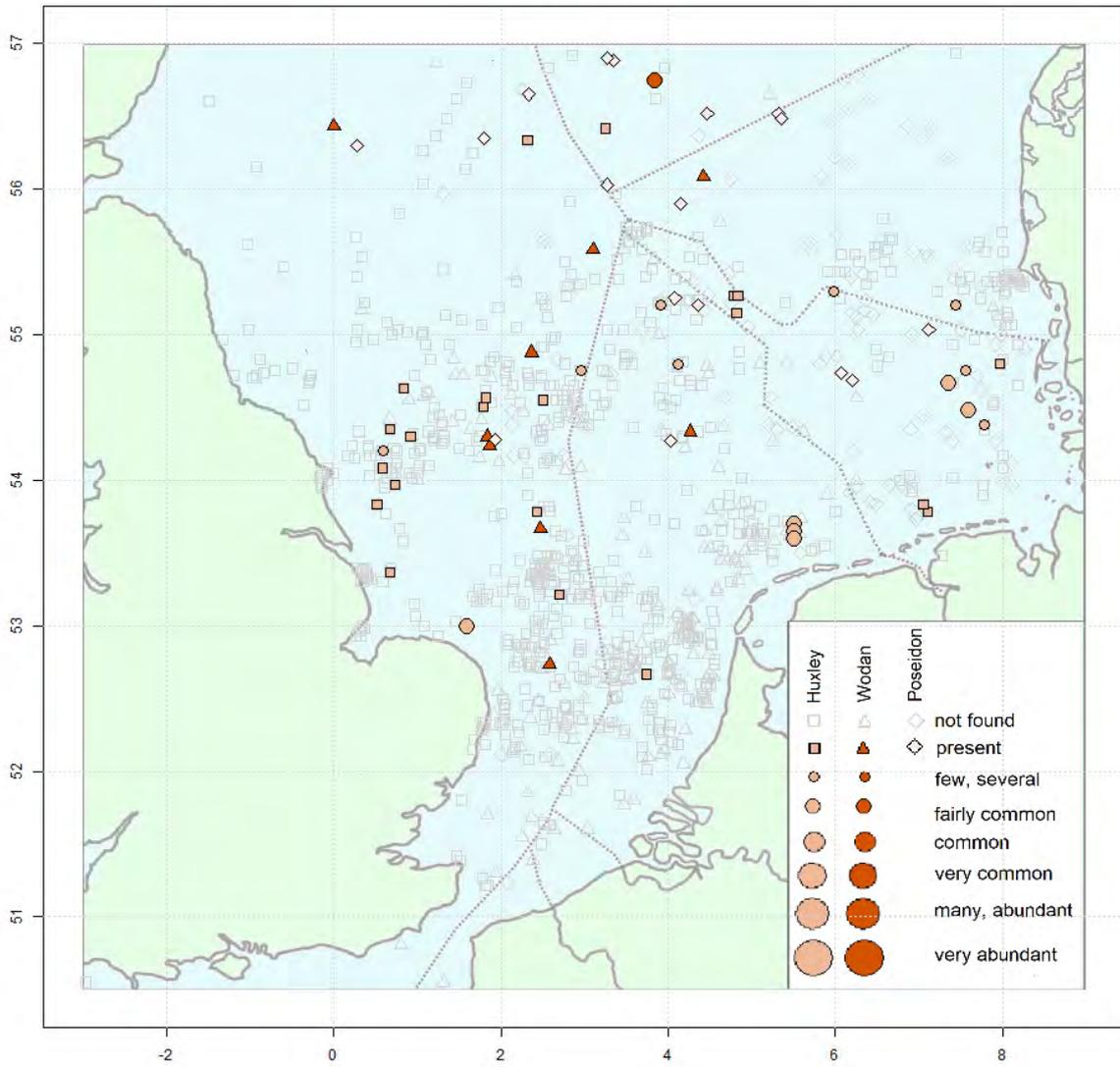
Homarus gammarus Common lobster

Hyas araneus

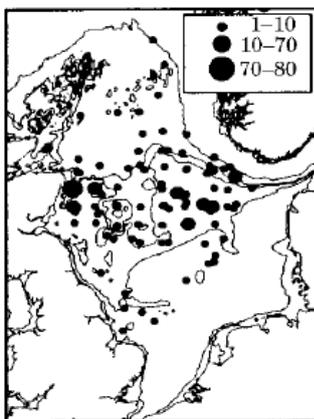


Hyas araneus Great spider crab

Hyas coarctatus



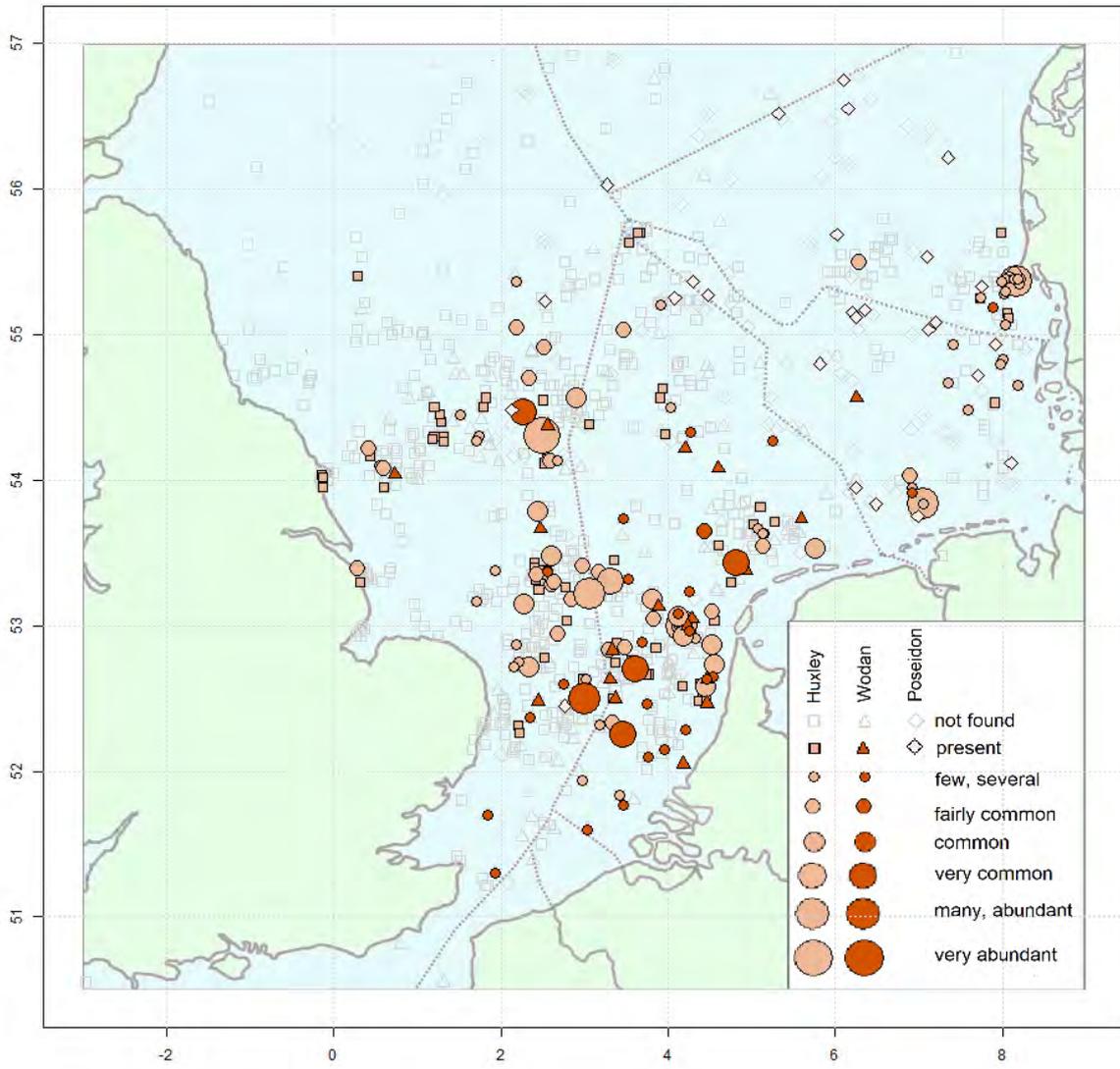
Hyas coarctatus Toad crab



(e) *Hyas coarctatus*

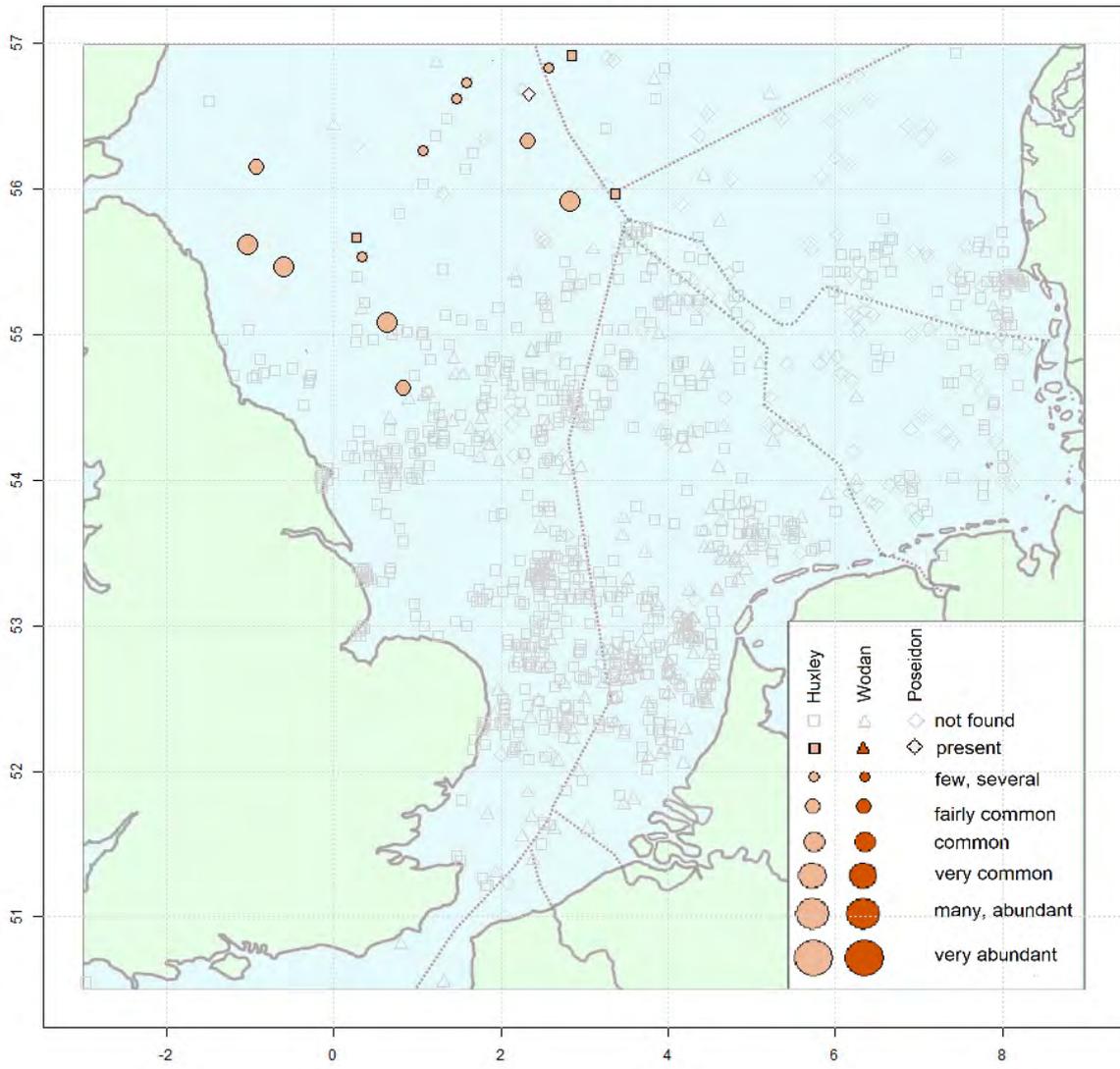
2000 distribution map (Callaway *et al.*, 2002).

Liocarcinus holsatus



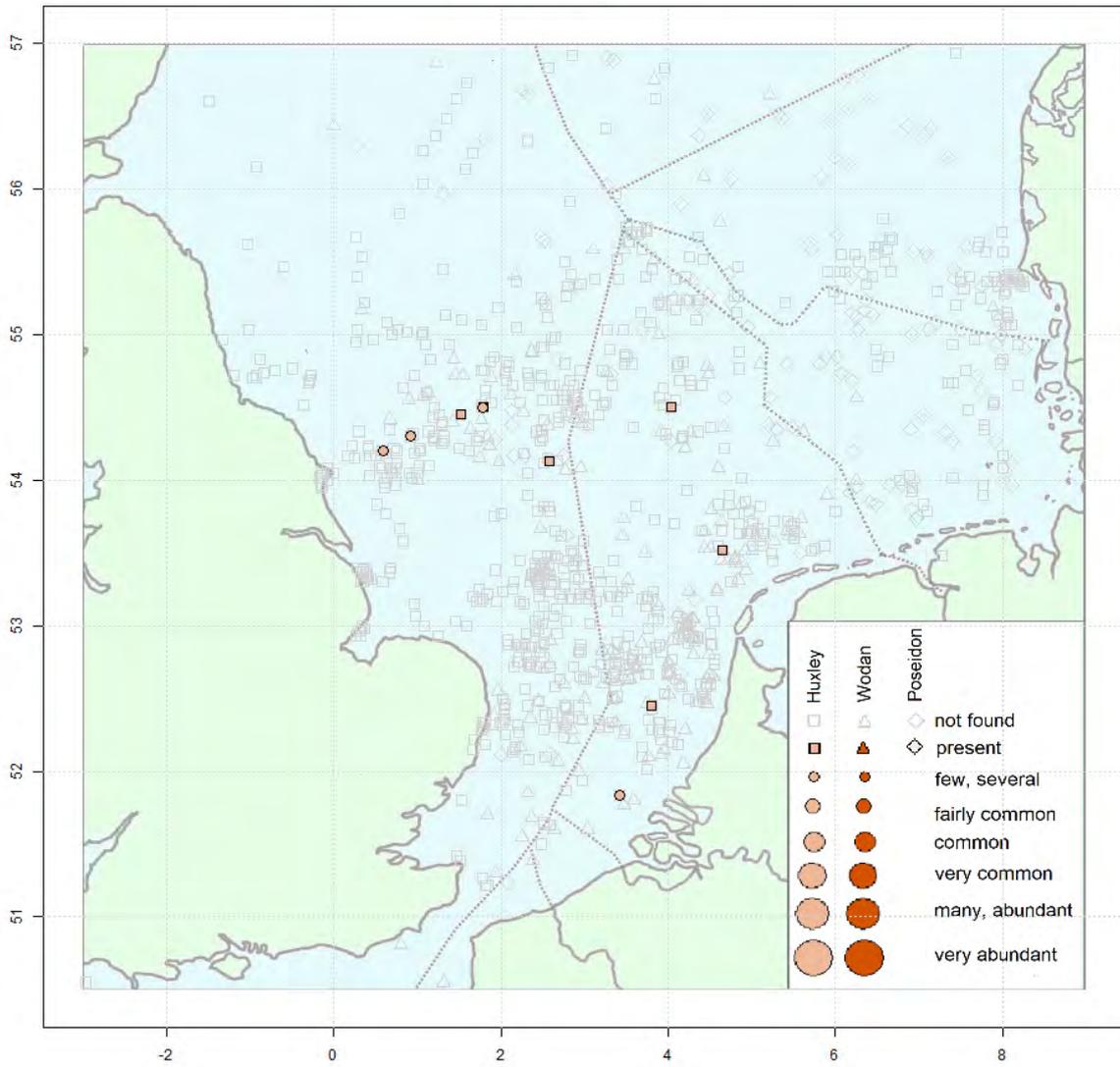
Liocarcinus holsatus Flying crab

Lithodes maja



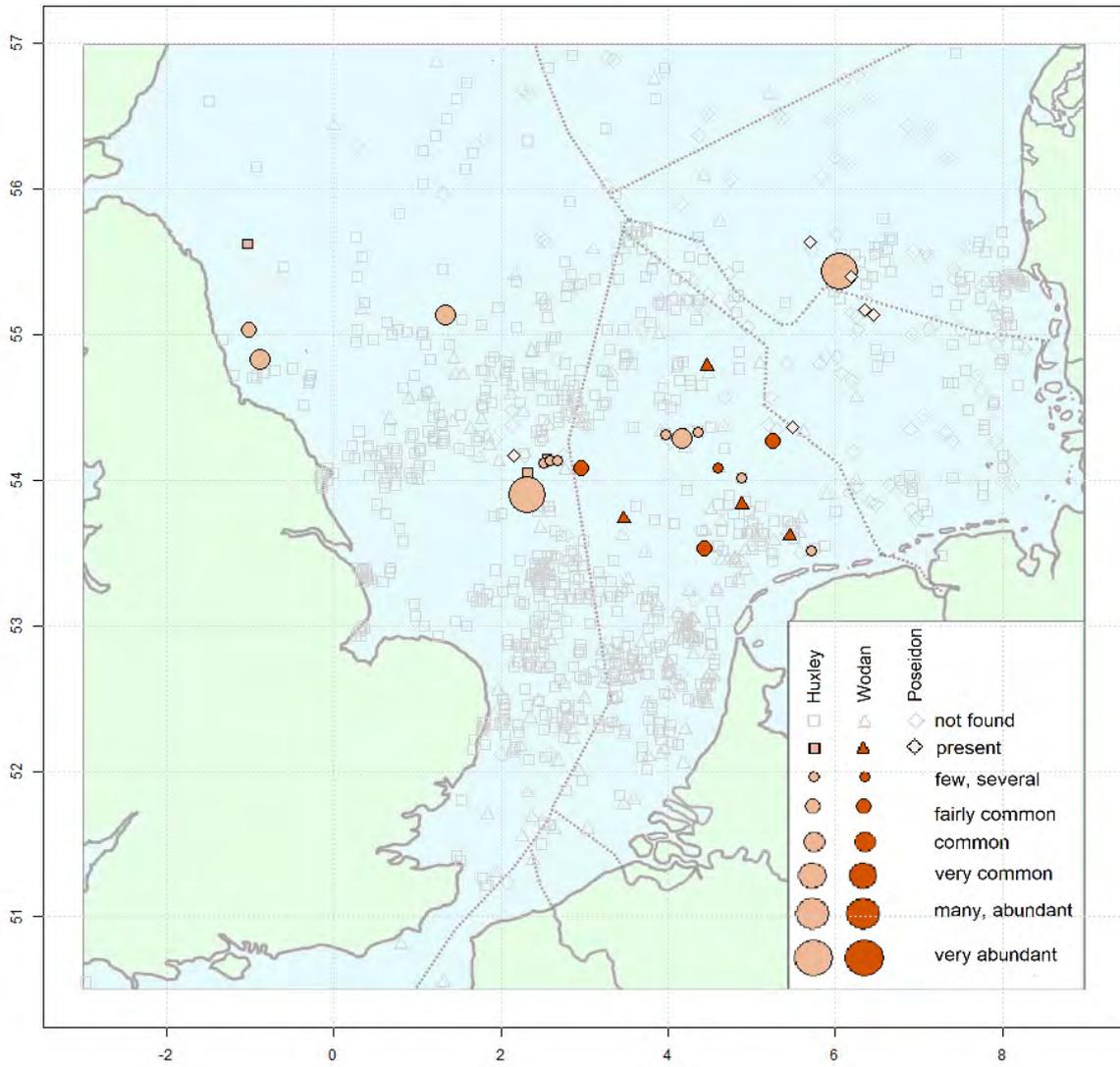
Lithodes maja Stone king crab

Macropodia tenuirostris



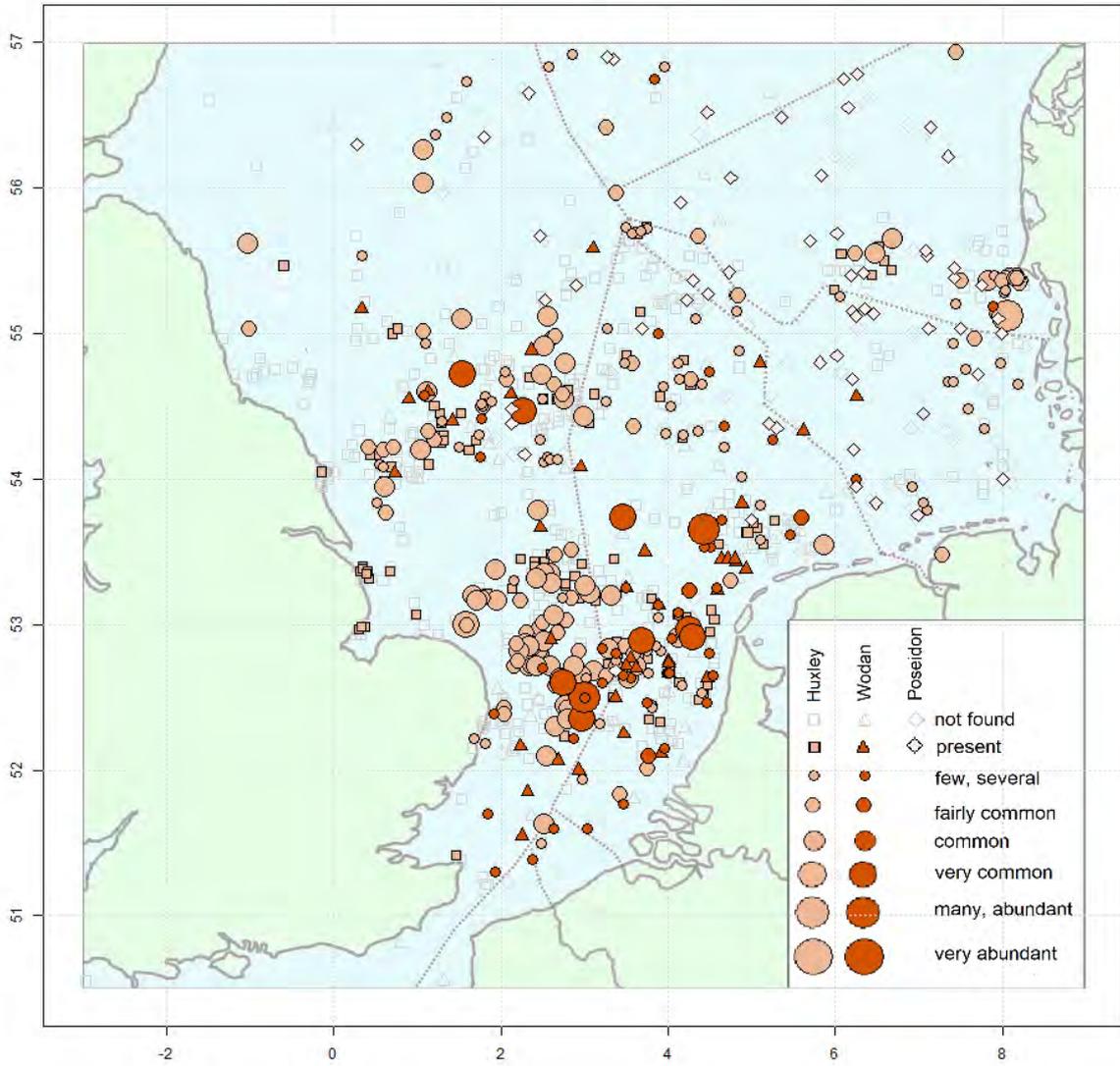
Macropodia tenuirostris Slender spider crab

Nephrops norvegicus

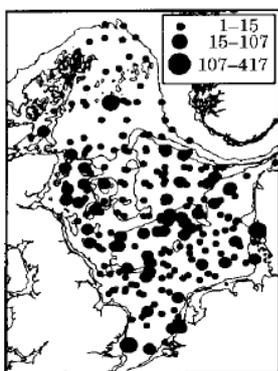


Nephrops norvegicus Scampi (Norway lobster)

Pagurus bernhardus



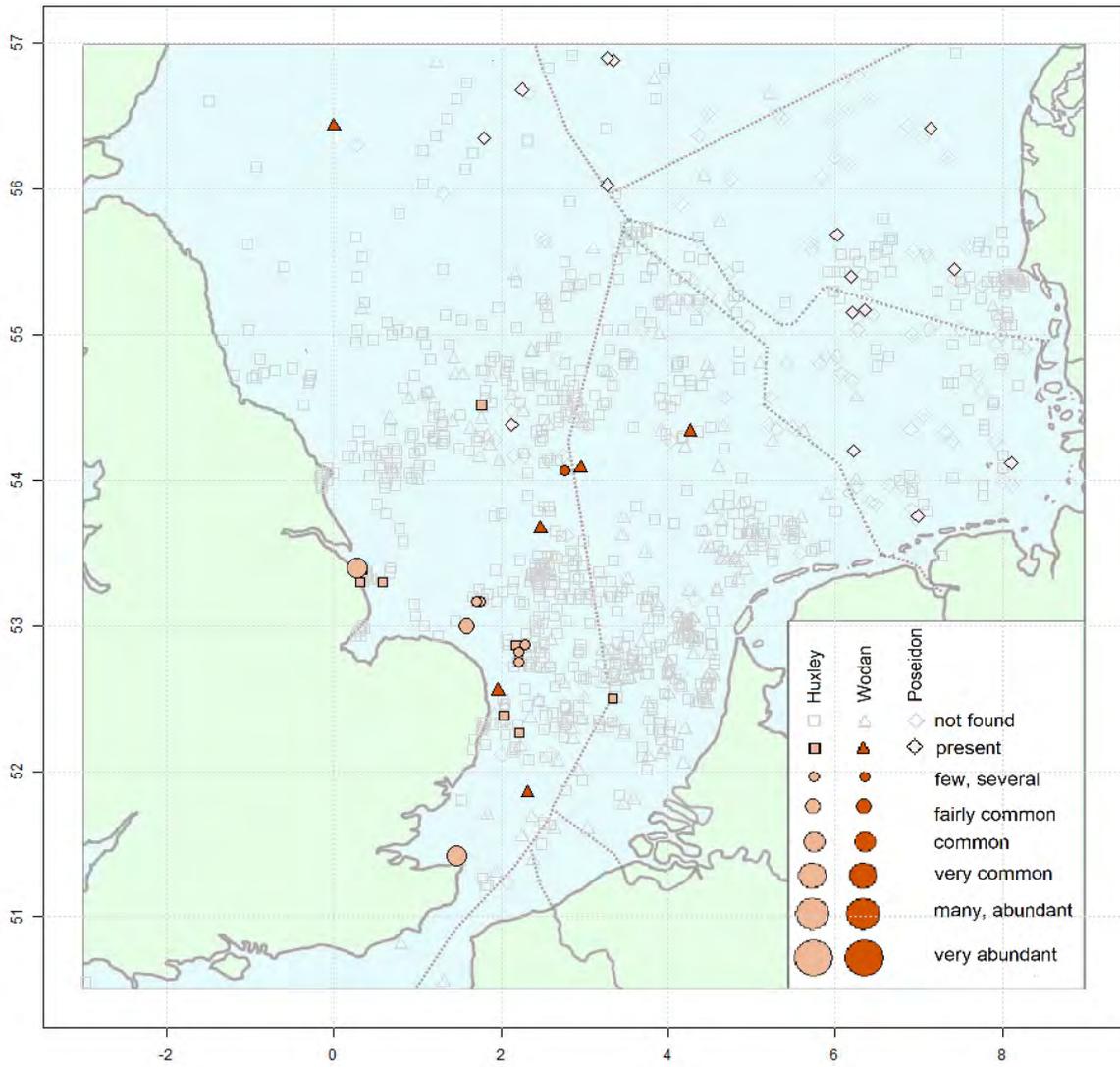
Pagurus bernhardus Common hermit crab



(a) *Pagurus bernhardus*

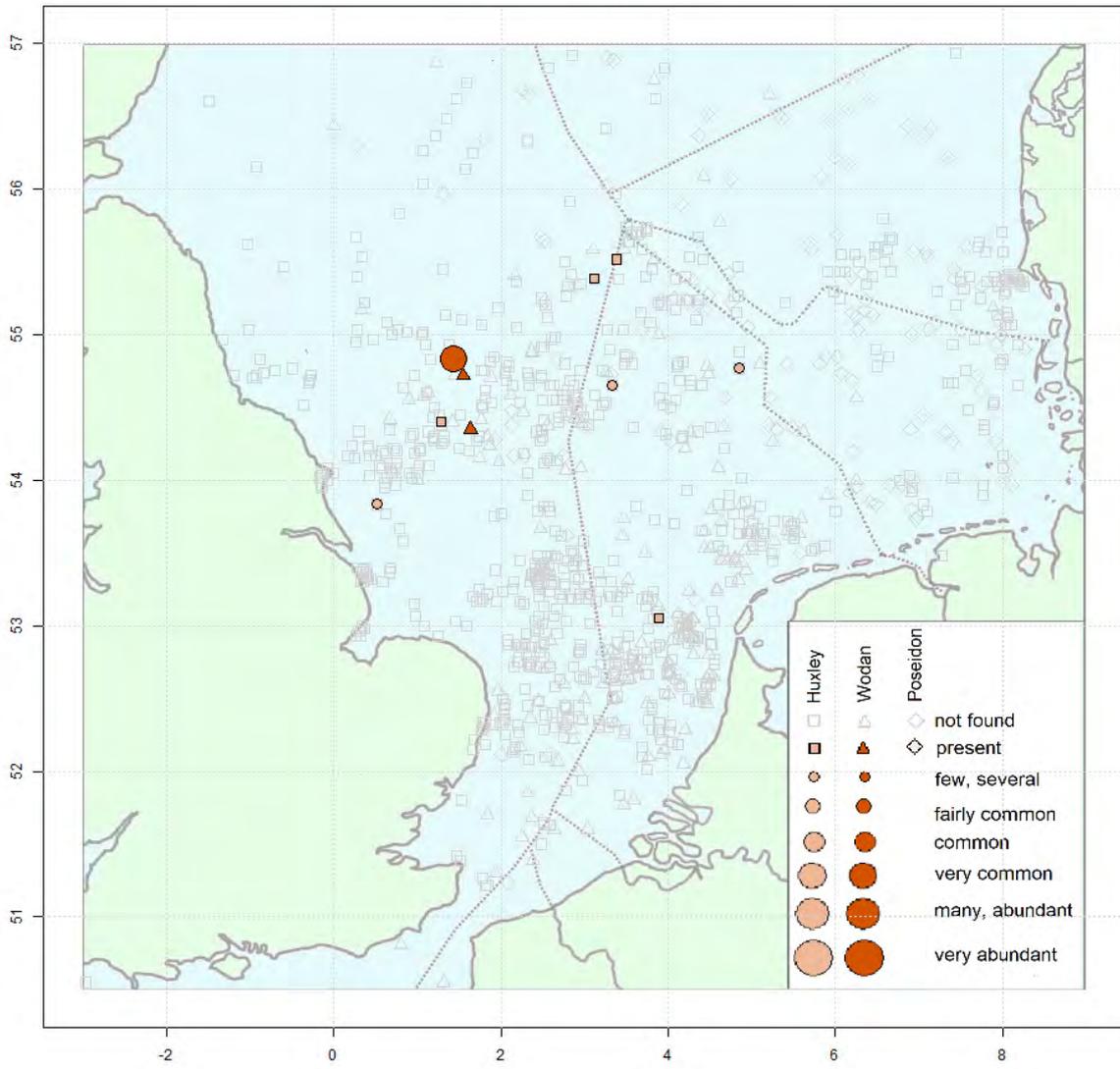
2000 distribution map (Callaway *et al.*, 2002).

Pandalus montagui



Pandalus montagui Humpback prawn

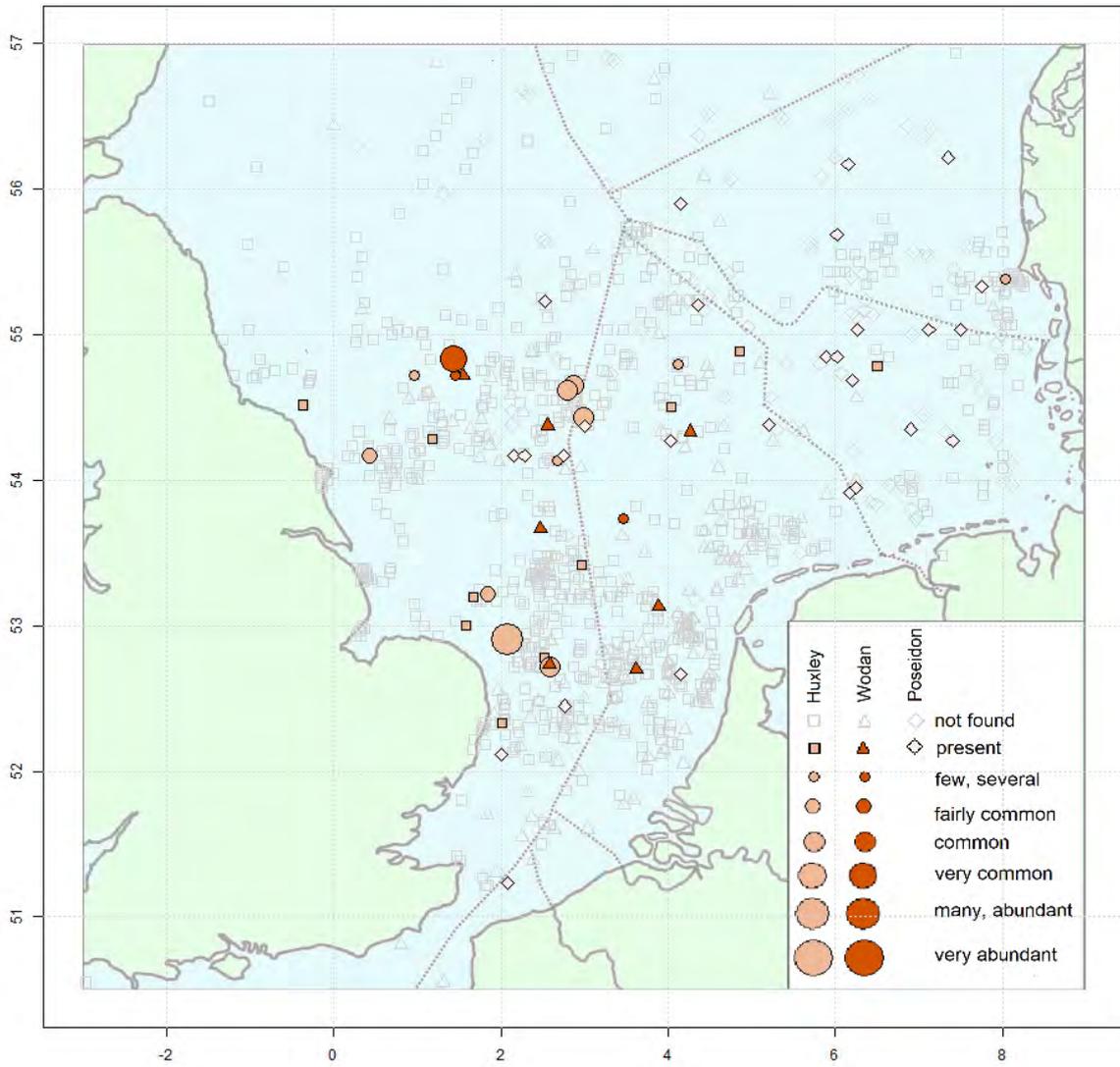
Pinnotheres pisum



Pinnotheres pisum Pea crab

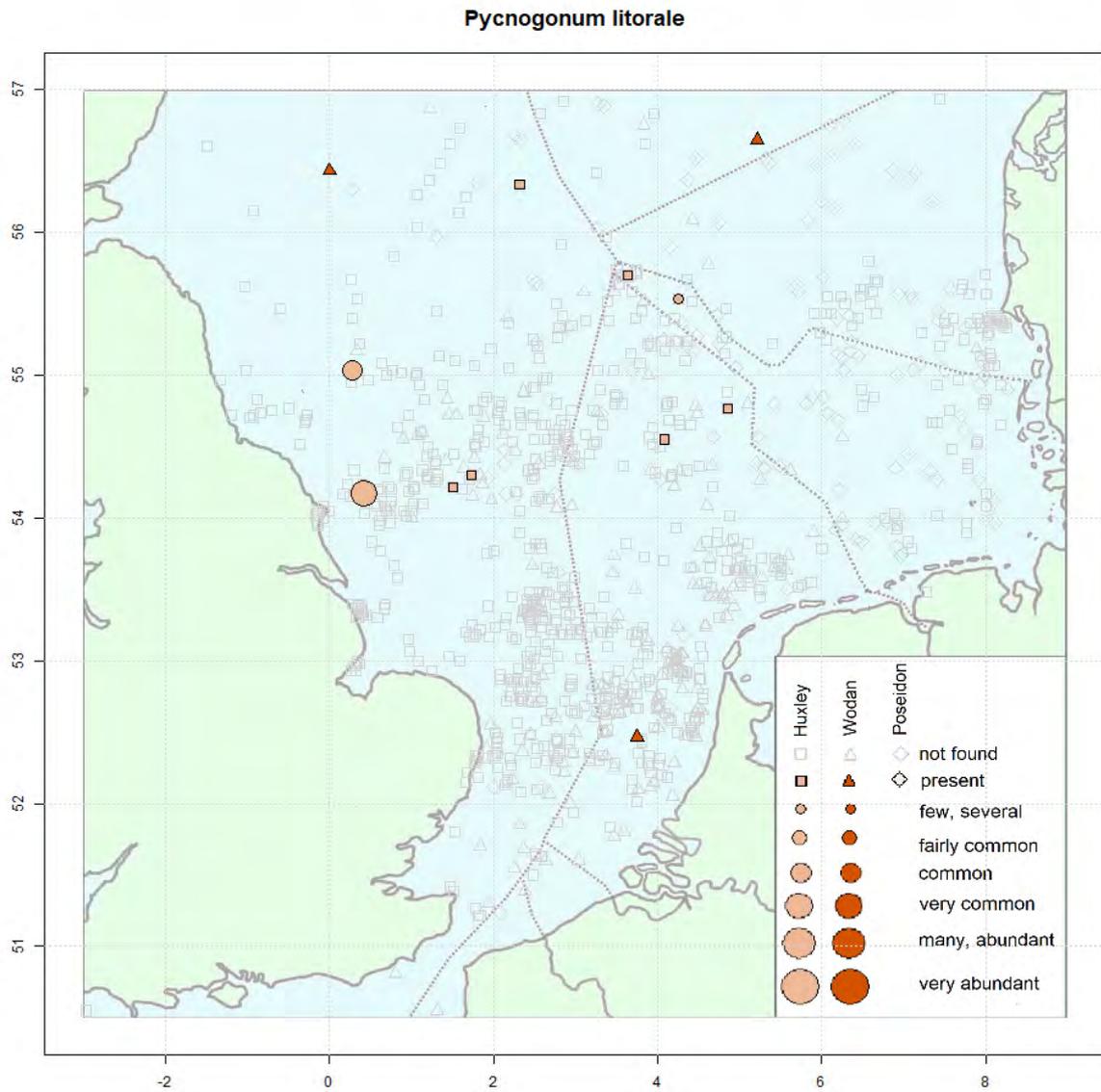
Found in *Modiolus modiolus*

Pisidia longicornis

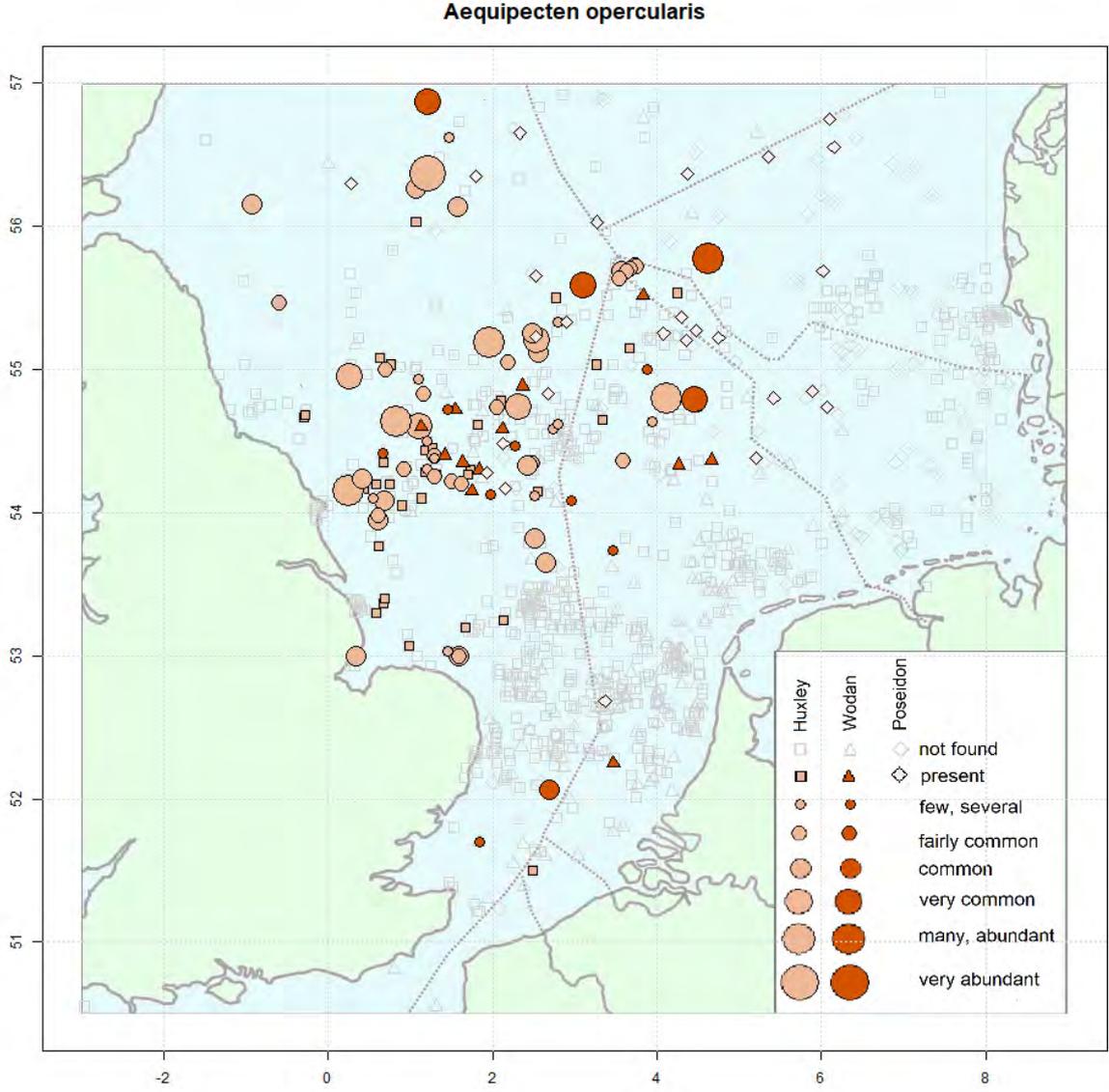


Pisidia longicornis Long-clawed porcelain crab

Arthropoda – Pycnogonida

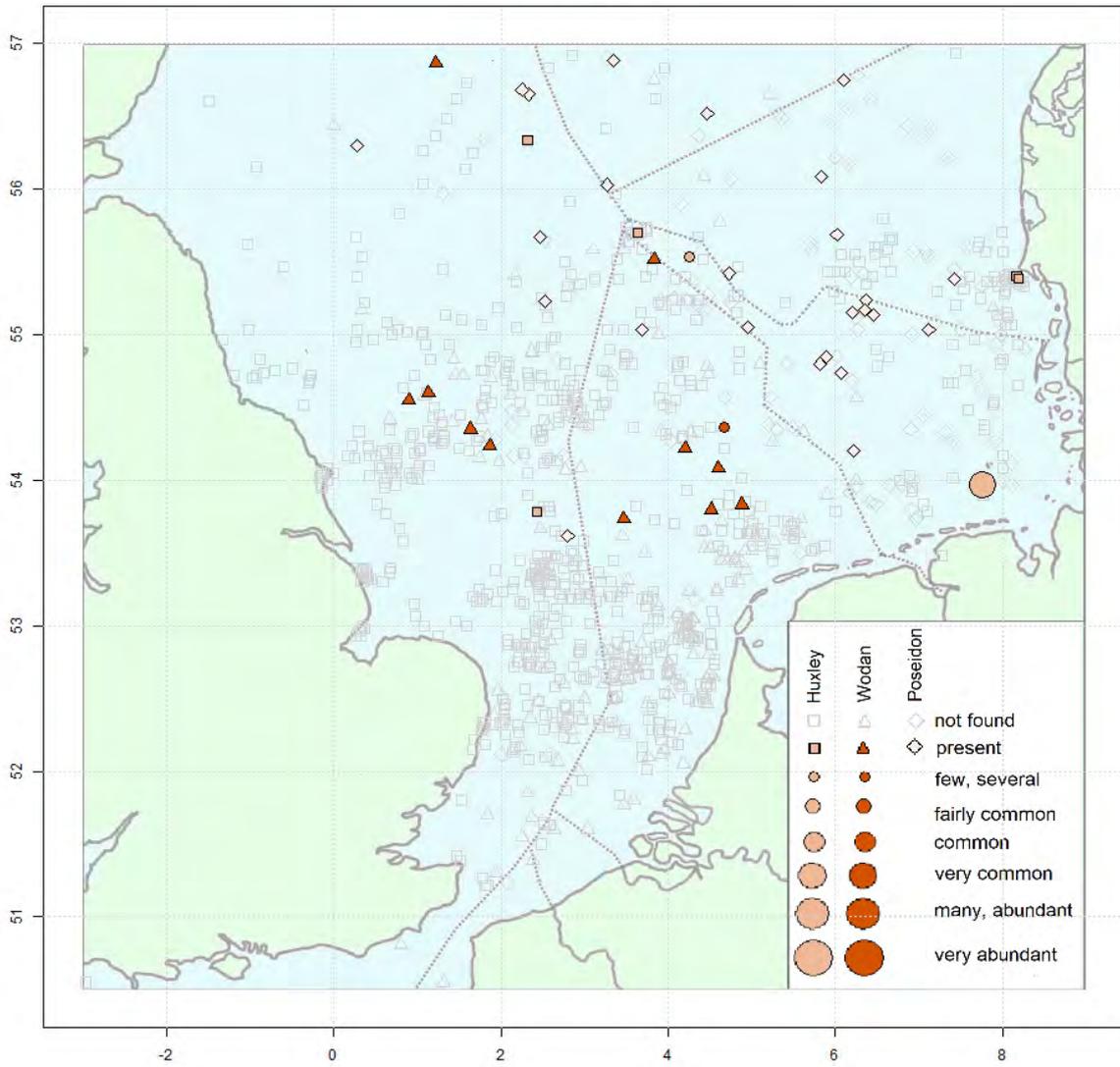


Pycnogonum littorale A sea spider



Aequipecten opercularis Queen scallop

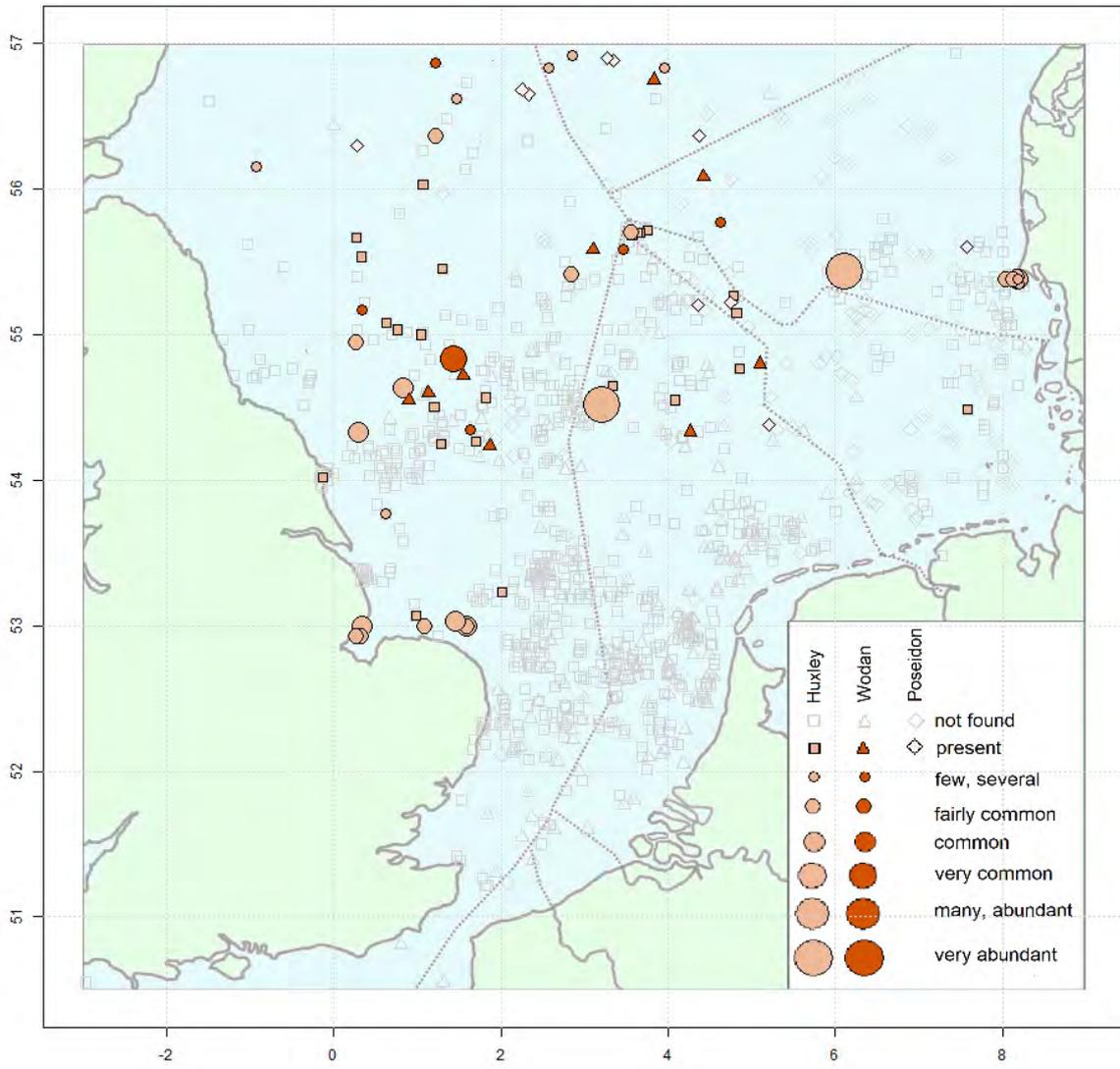
Arctica islandica



Arctica islandica

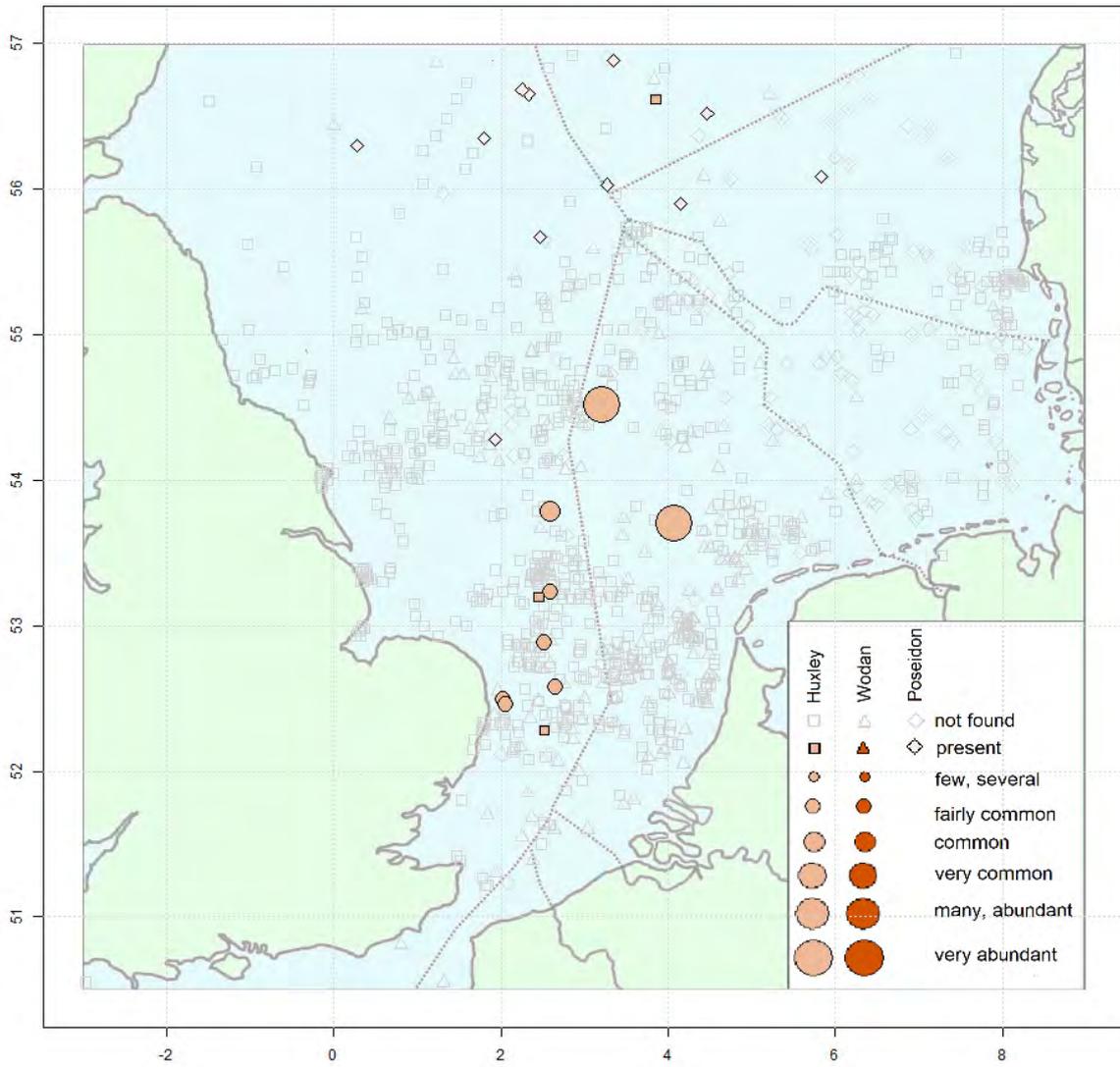
Icelandic cyprine

Modiolus modiolus



Modiolus modiolus Horse mussel

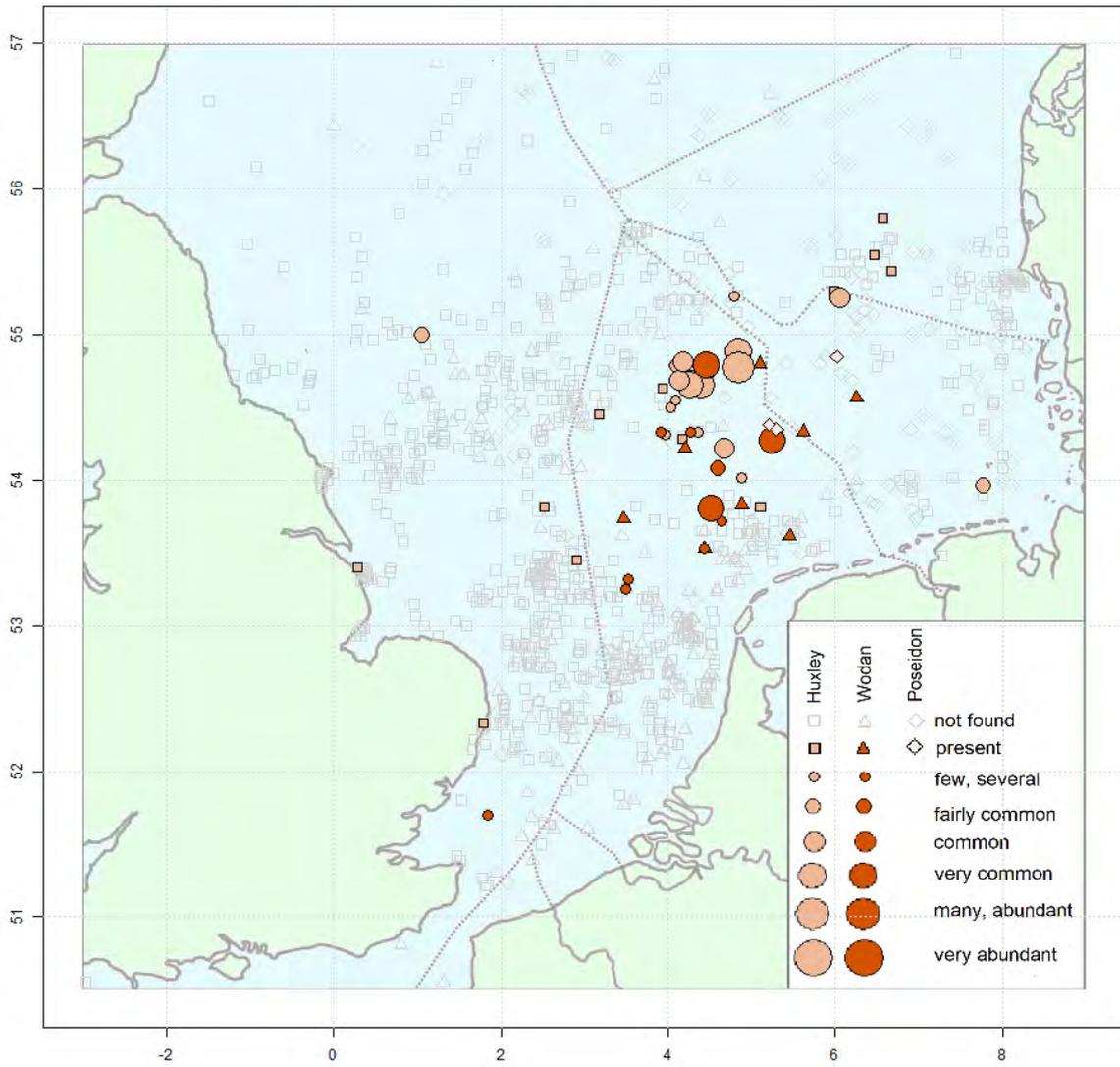
Montacuta substriata



Montacuta substriata

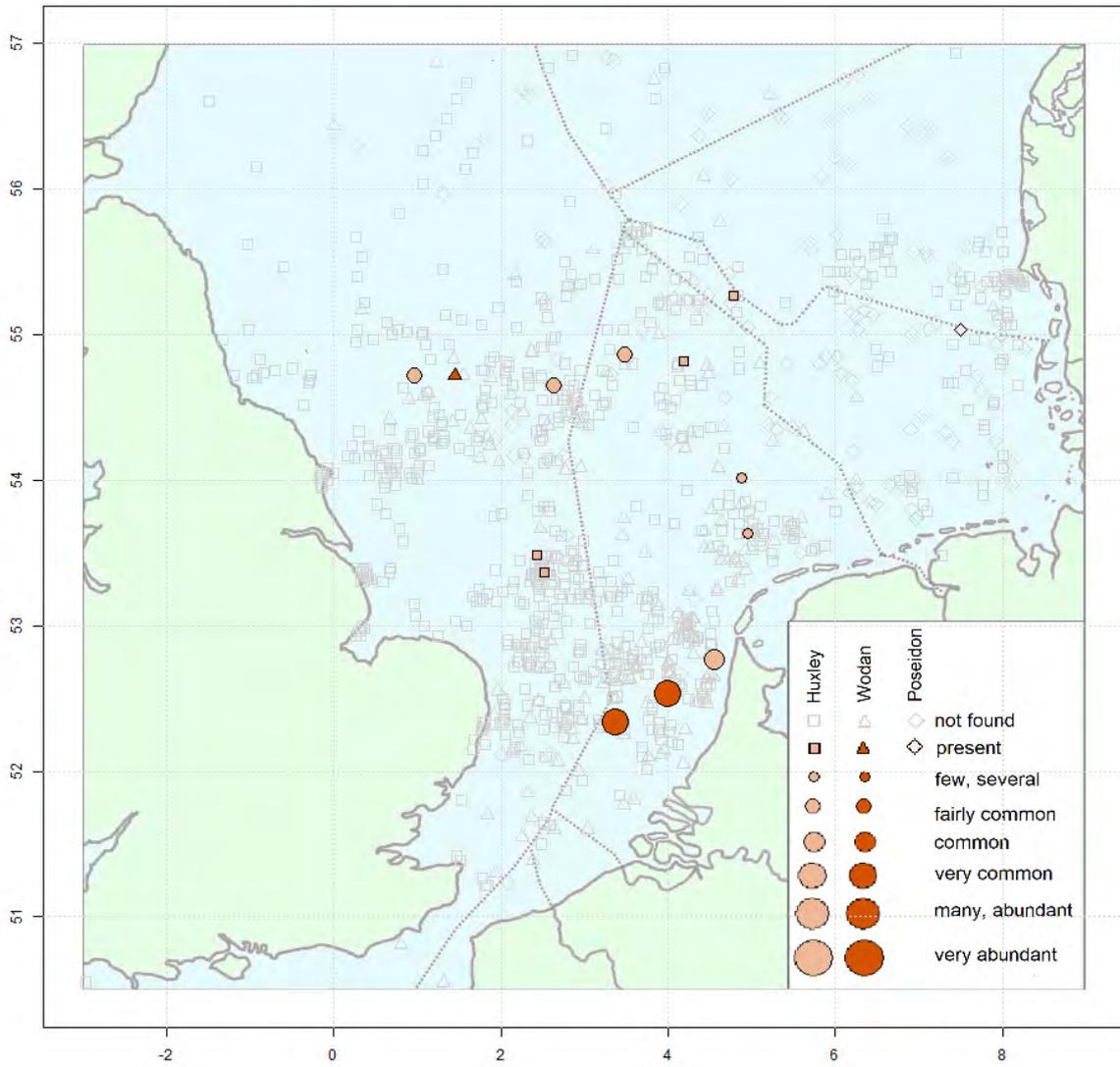
Substrated montacutid

Ostrea edulis



Ostrea edulis Flat oyster

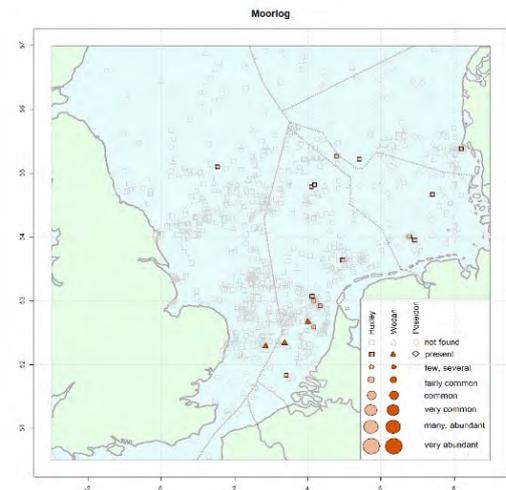
Zirfaea crispata



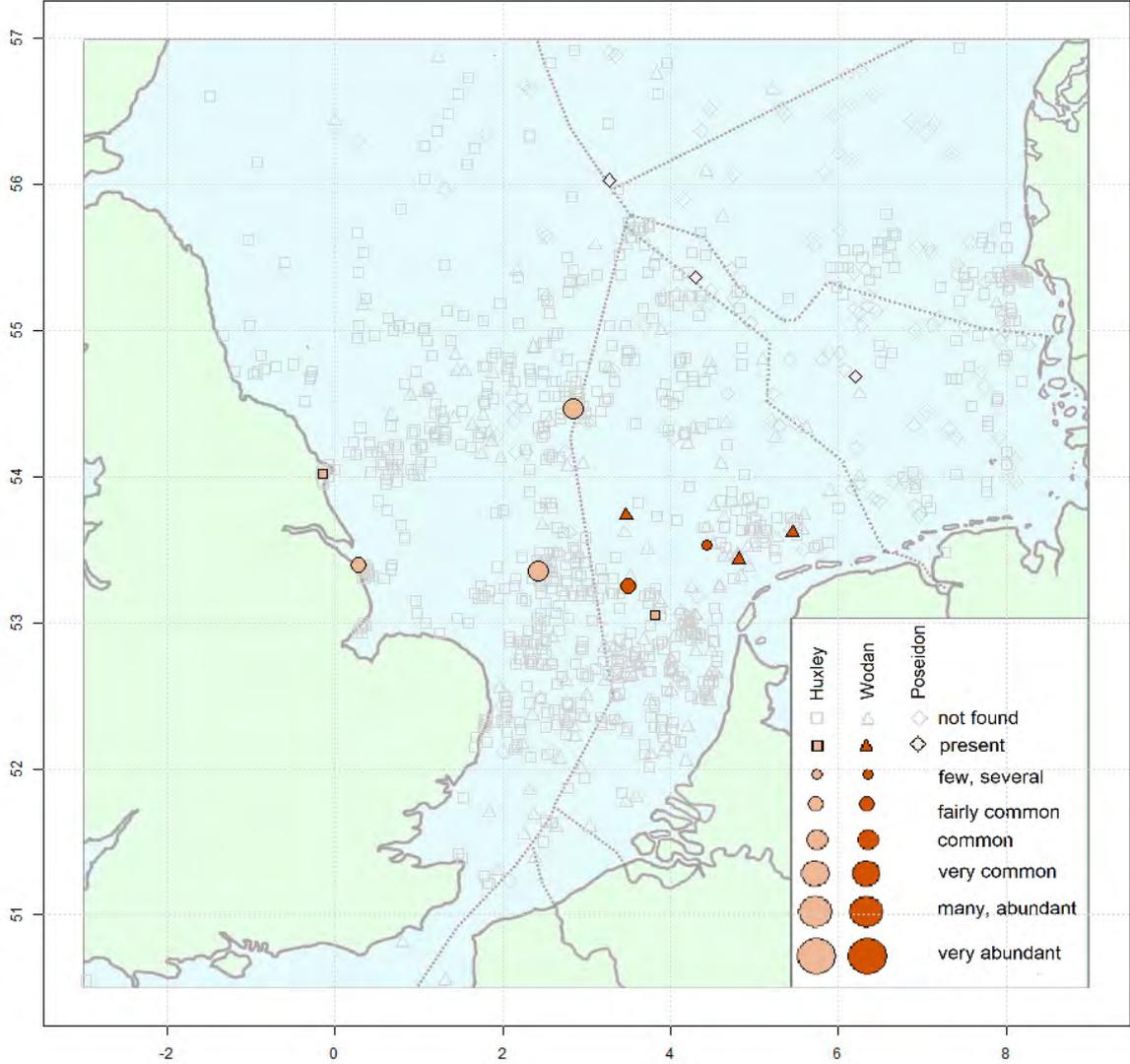
Zirfaea crispata

Oval piddock (found in moorlog)

Moorlog (peat).

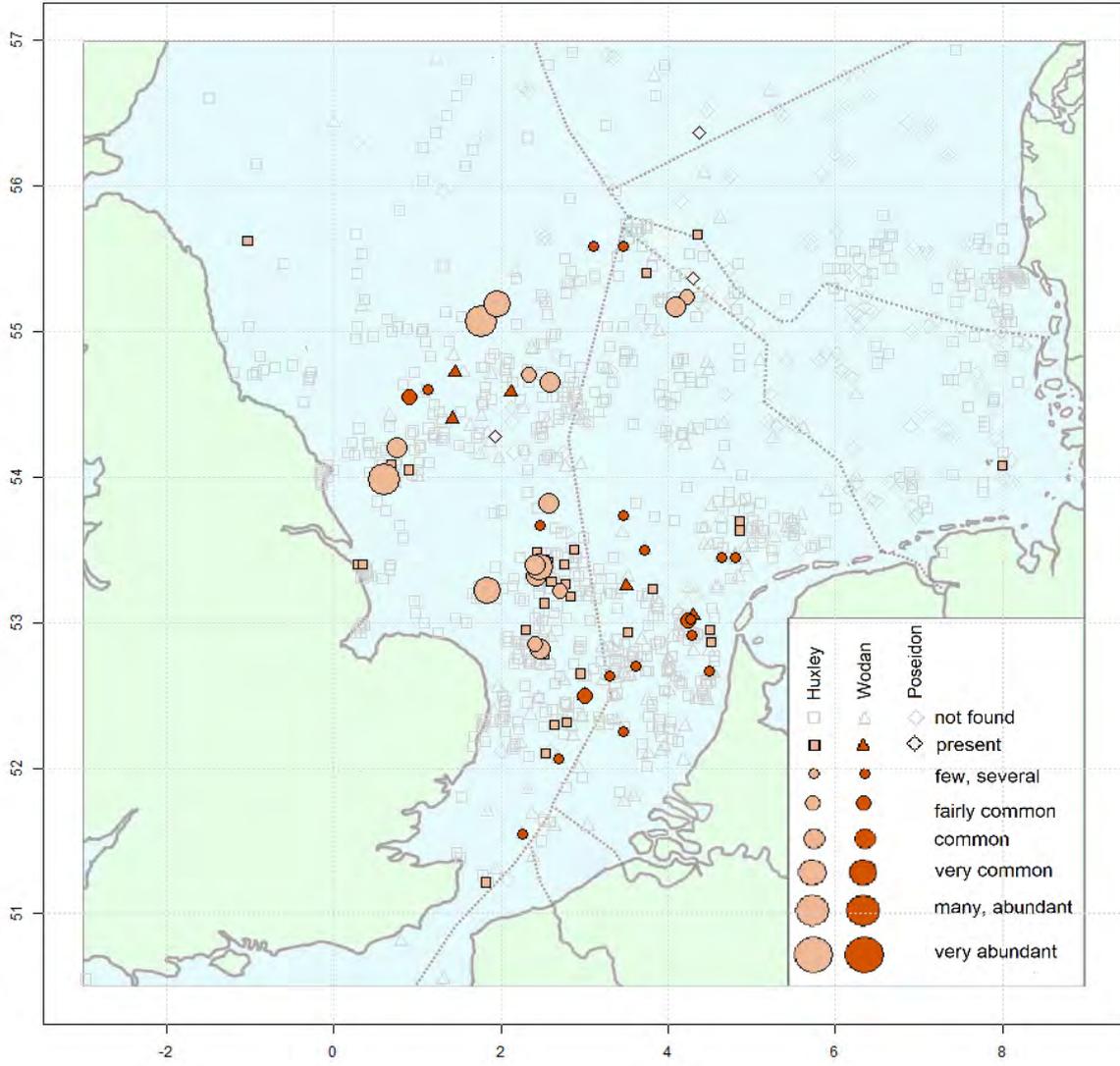


Alloteuthis subulata



Alloteuthis subulata Little squid

Loligo forbesii

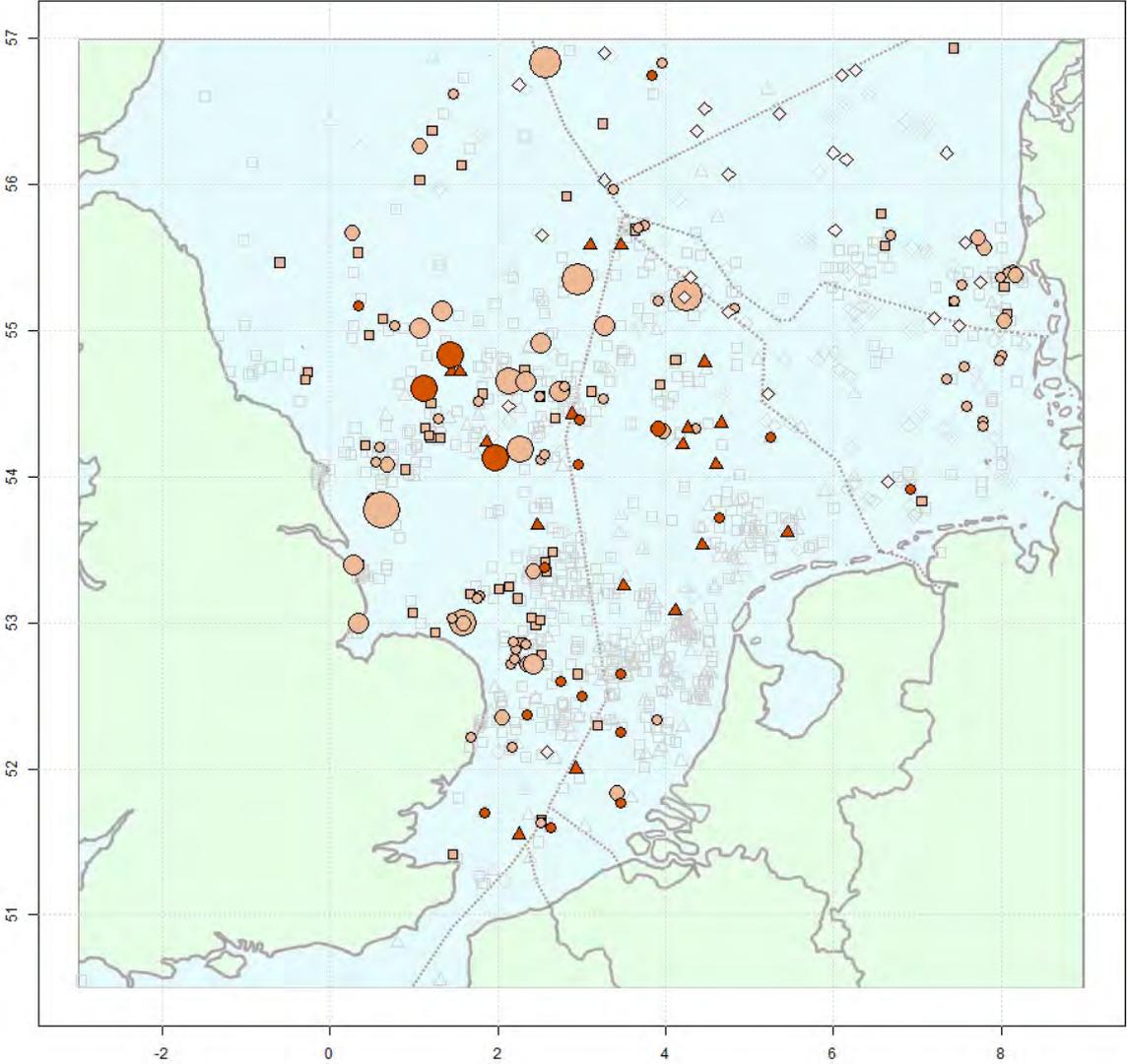


Loligo forbesii

Long finned squid

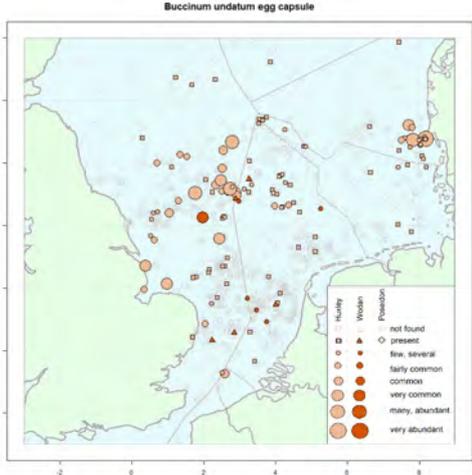
Mollusca-Gastropoda

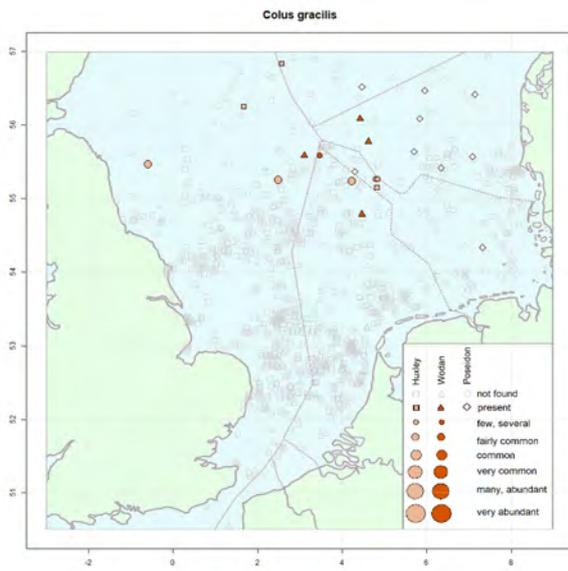
Buccinum undatum



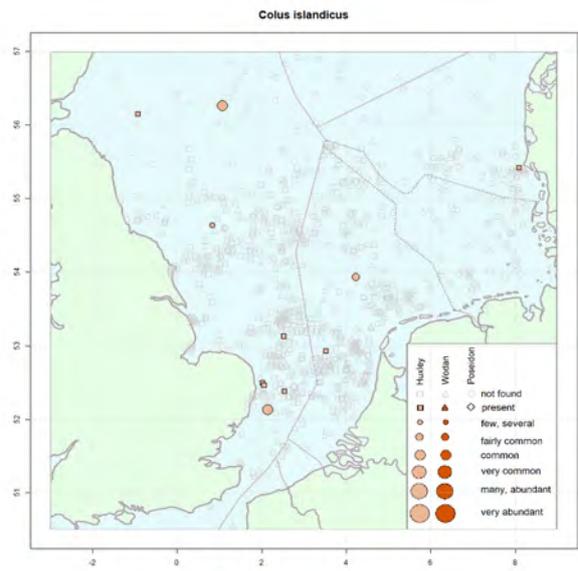
Buccinum undatum Common whelk

Buccinum undatum
egg cases.

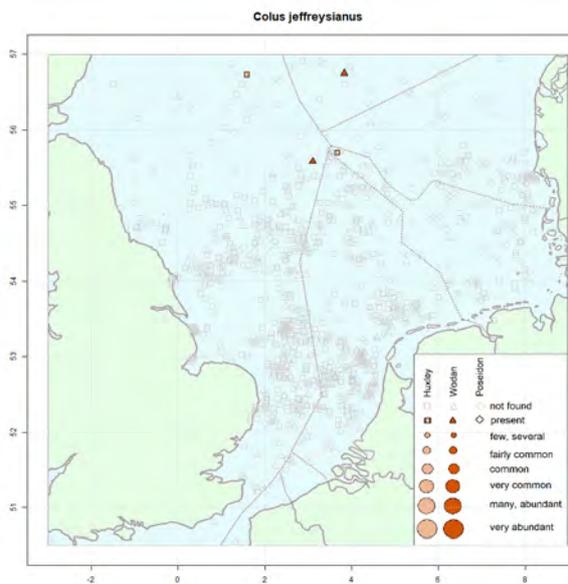




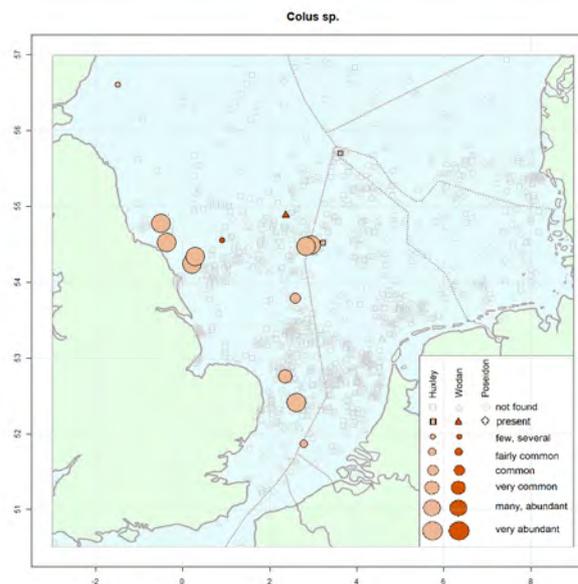
Colus gracilis Slender colus



Colus islandicus Islandic colus



Colus jeffreysianus Jeffrey's colus

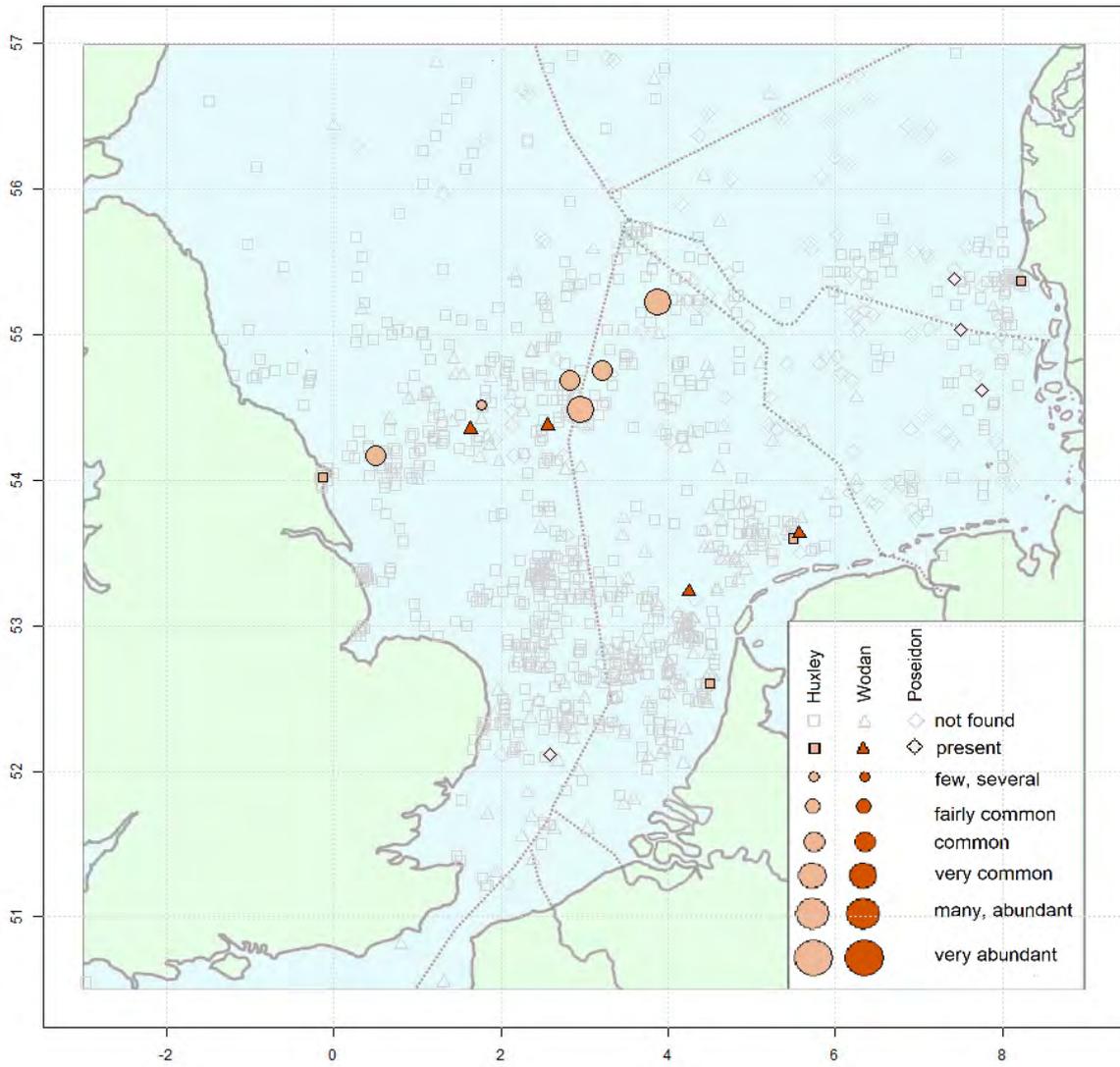


Colus sp. Colus

Colus sp. as indicated by Huxley naturalists.

Colus sp. in Figure 6 and 8 represents all the *Colus* species data joined.

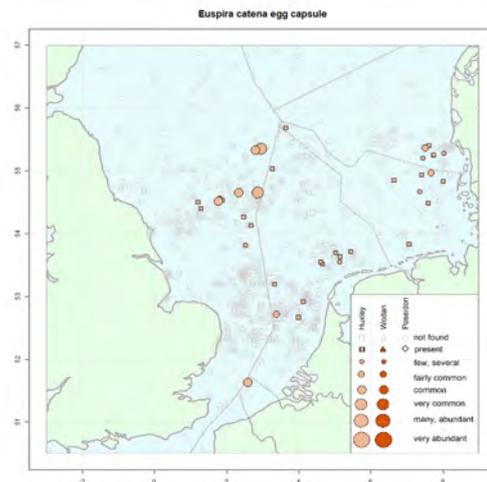
Euspira catena



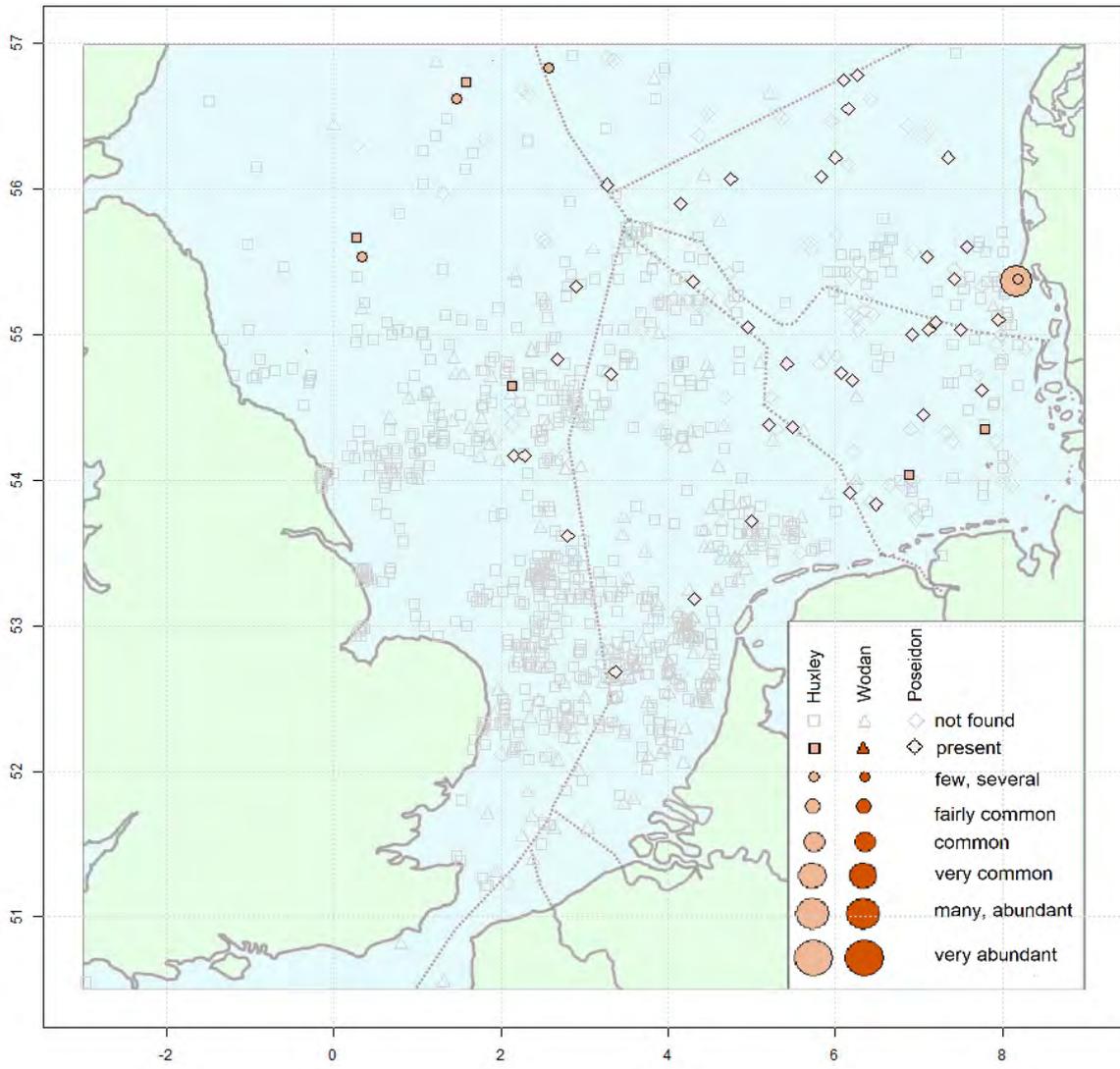
Euspira catena

Spotted necklace snail

Euspira catena egg capsules.

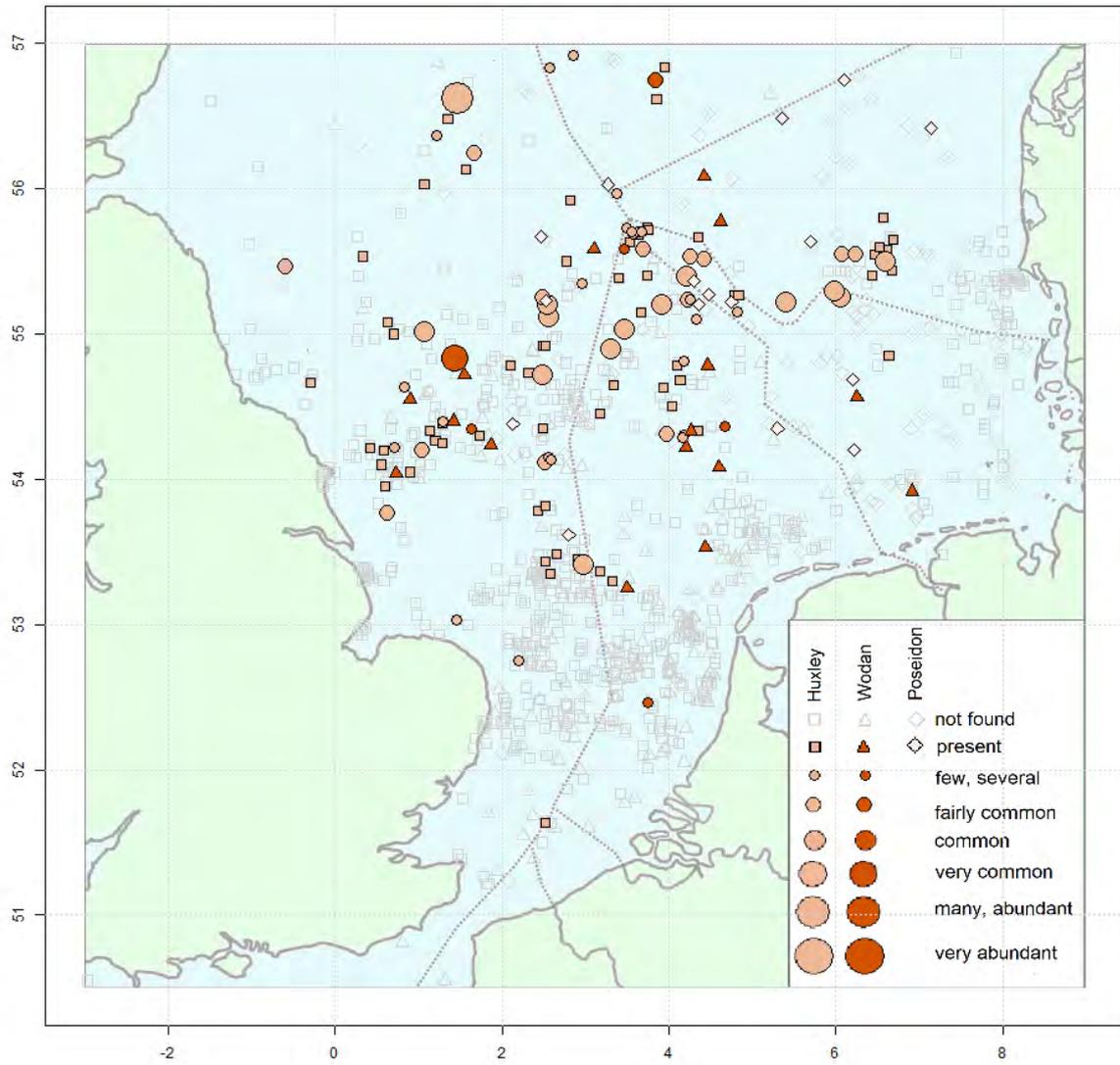


Euspira nitida

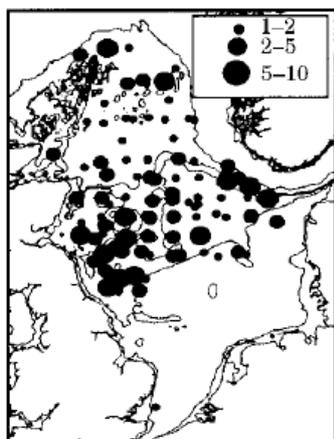


Euspira nitida Alder's necklace snail

Neptunea antiqua



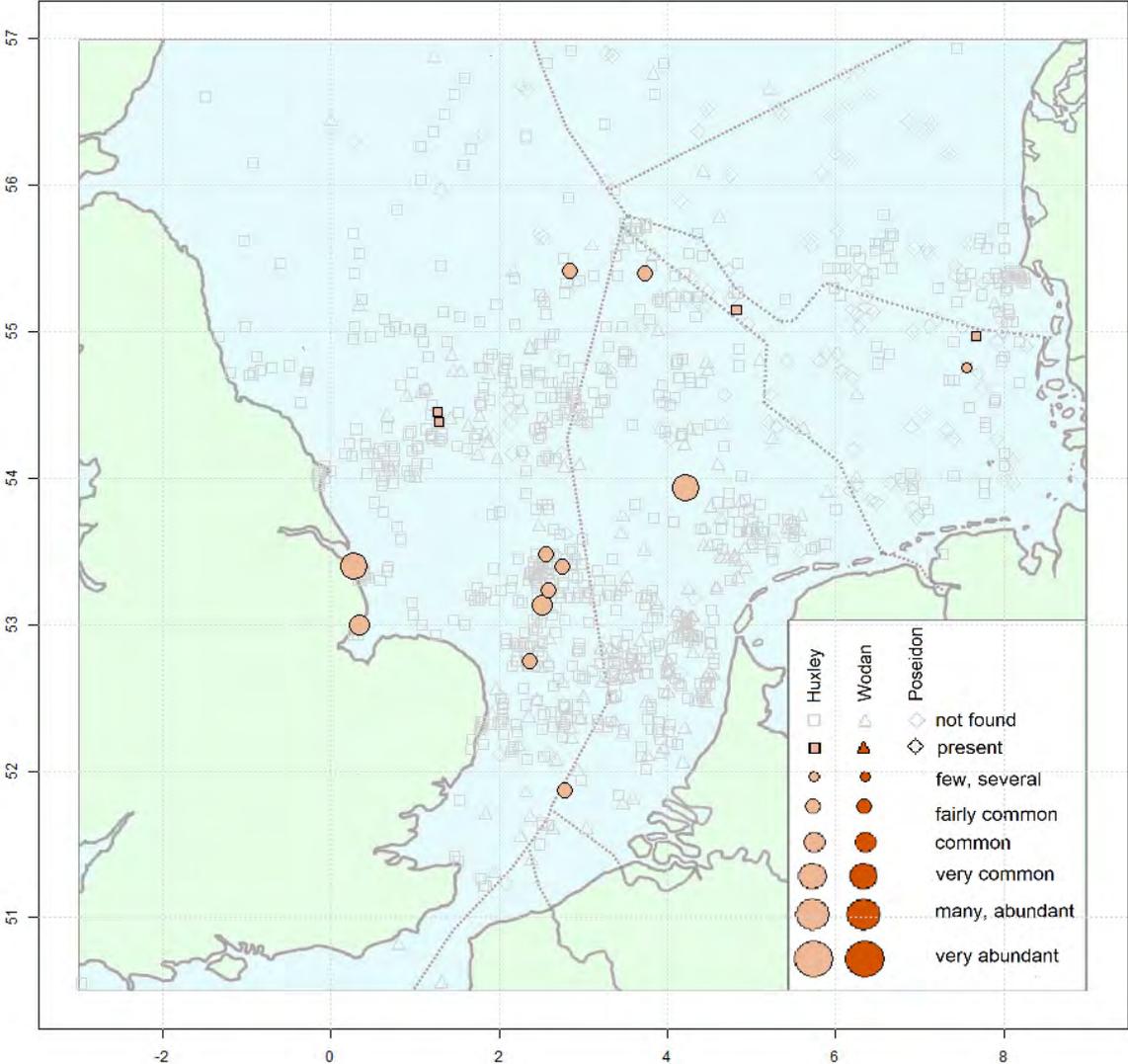
Neptunea antiqua Red whelk



(f) *Neptunea antiqua*

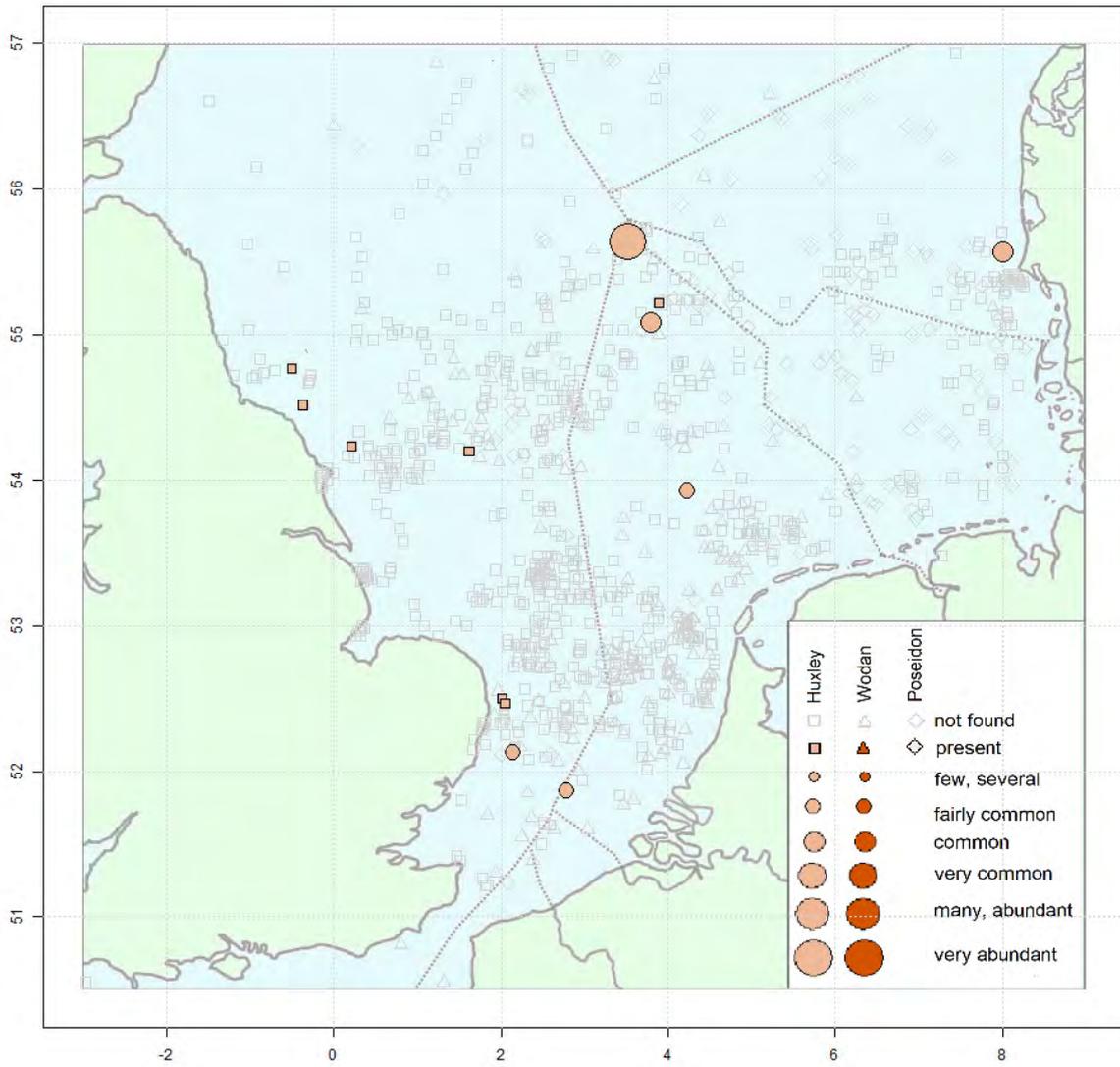
2000 distribution map (Callaway et al., 2002).

Acanthodoris pilosa



Acanthodoris pilosa Thorny doris

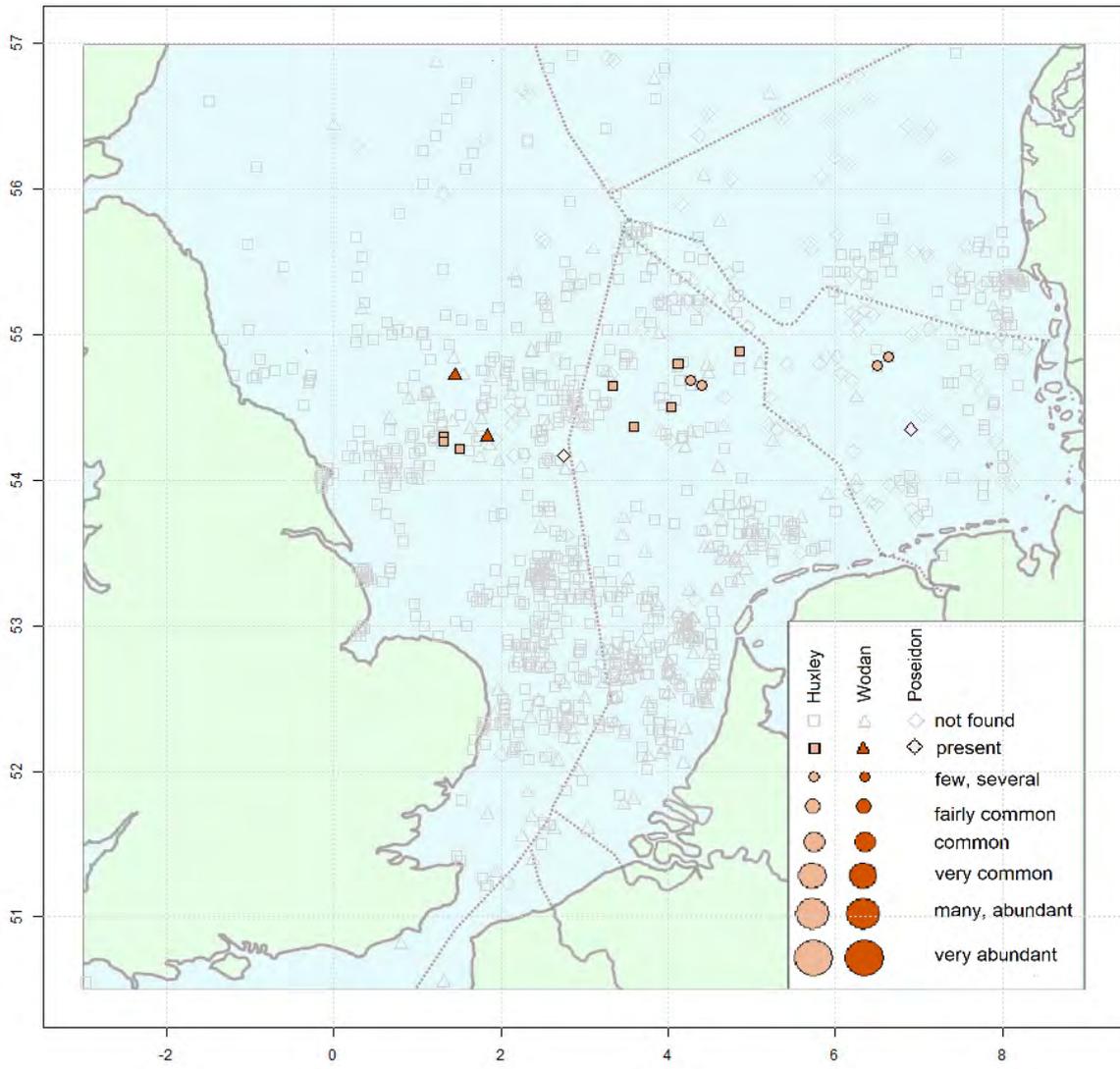
Doto coronata



Doto coronata

Crowned Doto

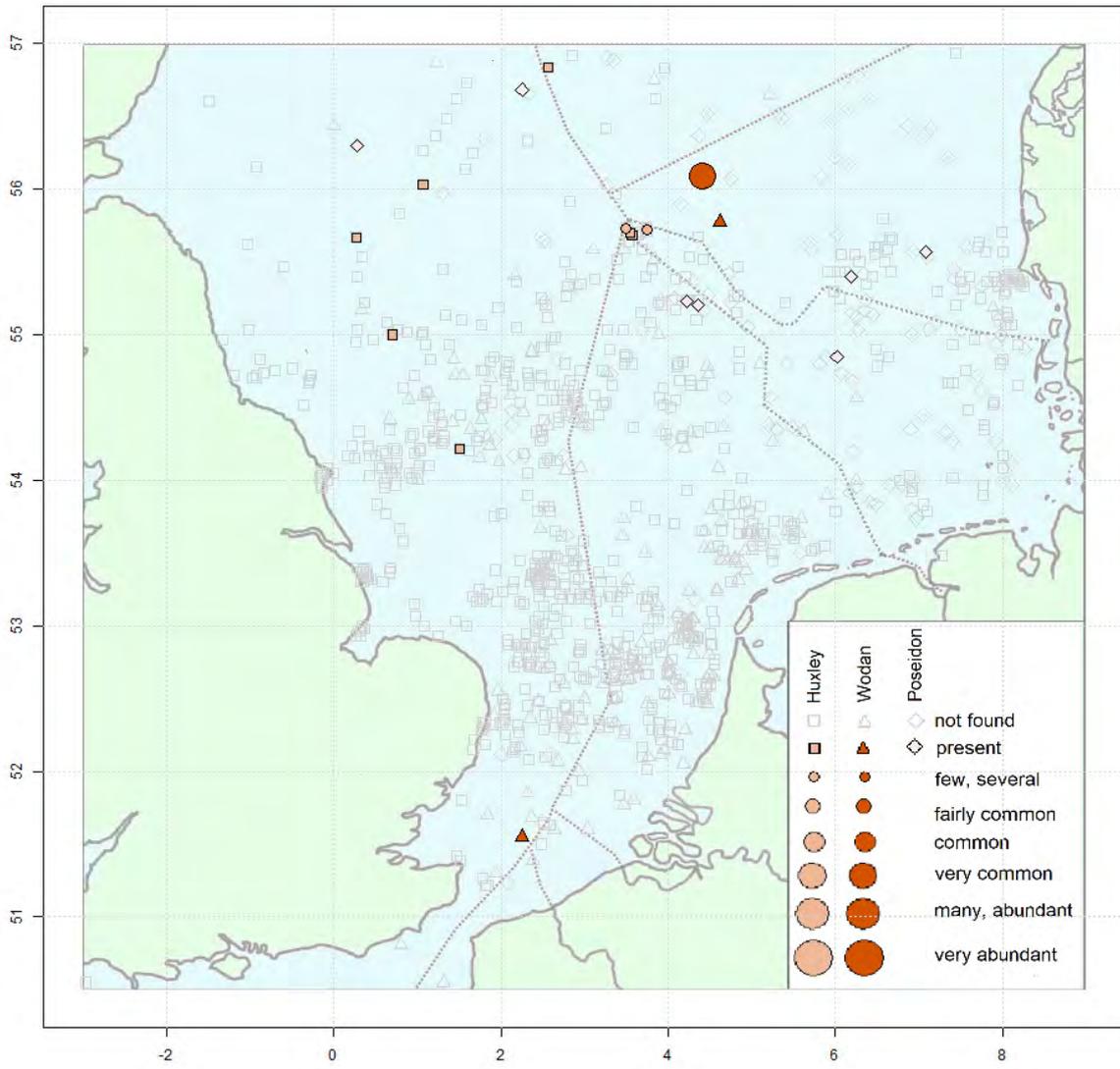
Duvaucelia plebeia



Duvaucelia plebeia

A sea slug

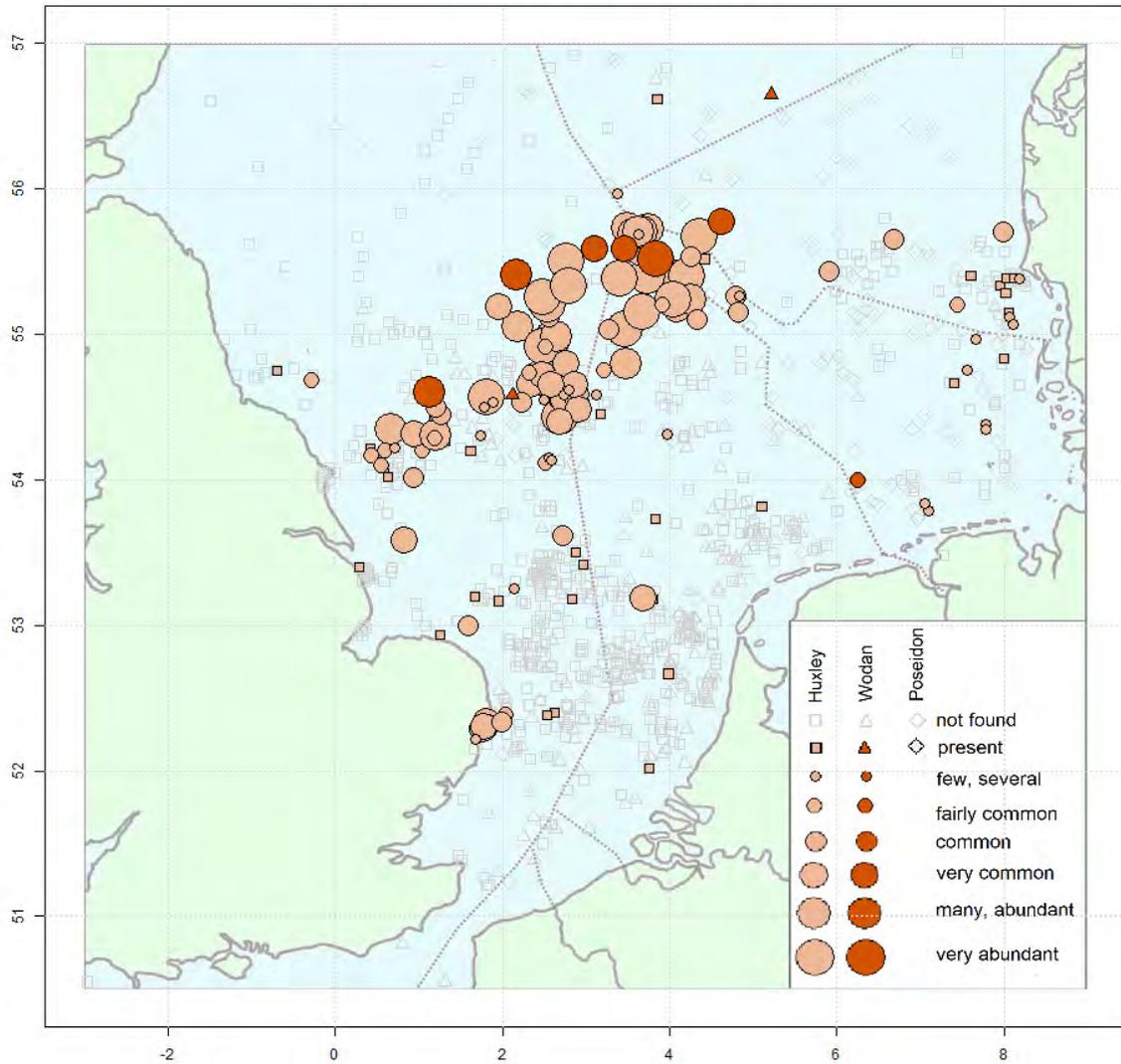
Tritonia hombergii



Tritonia hombergii Dead men's finger slug

Bryozoa- Gymnolaemata

Alcyonidium diaphanum or A. condylocinereum



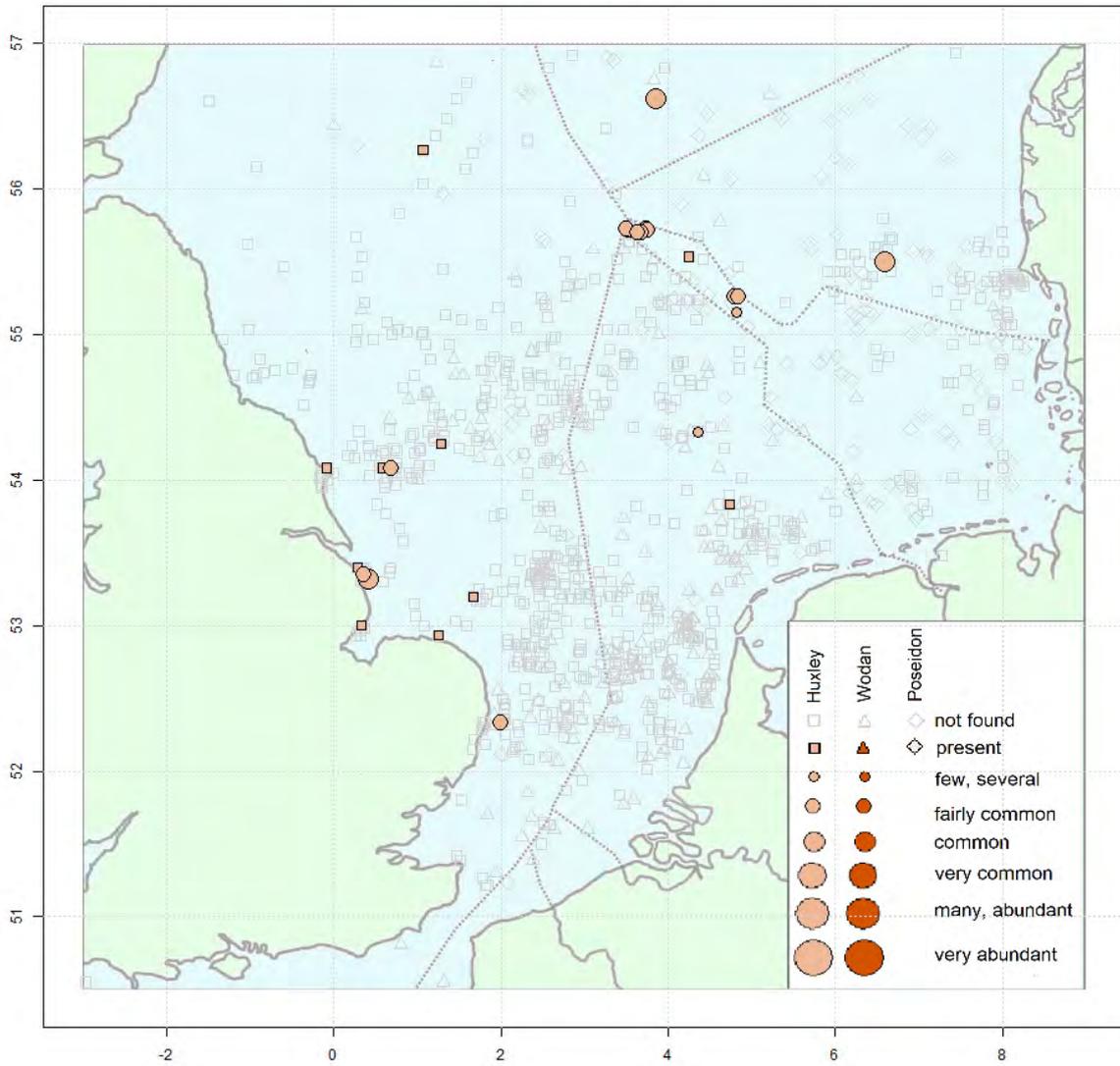
Alcyonidium diaphanum or *A. condylocinereum* Sea chevil and other Alcyonium bryozoan



(j) *Alcyonidium diaphanum*

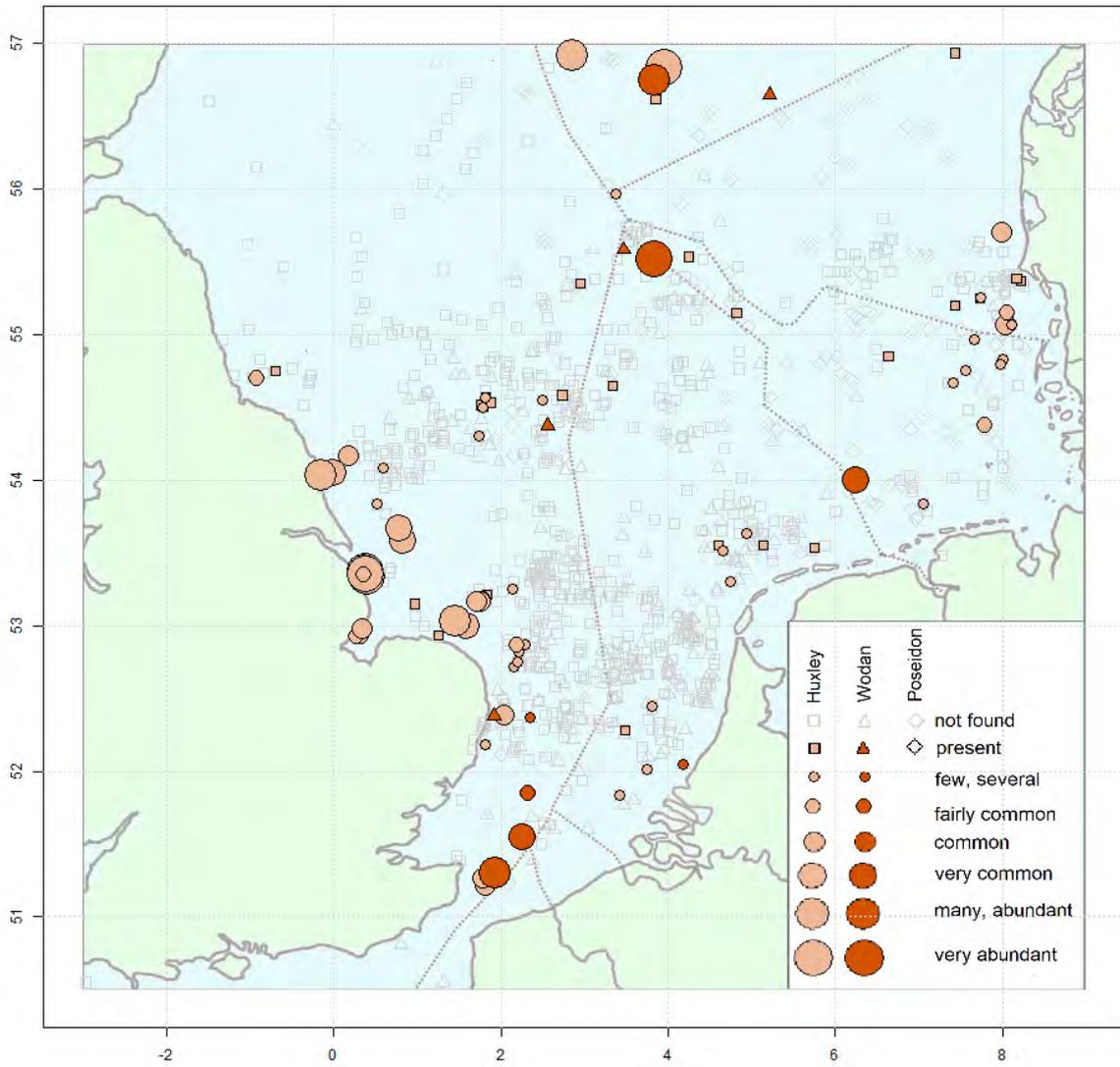
2000 distribution map (Callaway *et al.*, 2002).

Eucratea loricata



Eucratea loricata Paired bryozoan

Flustra foliacea

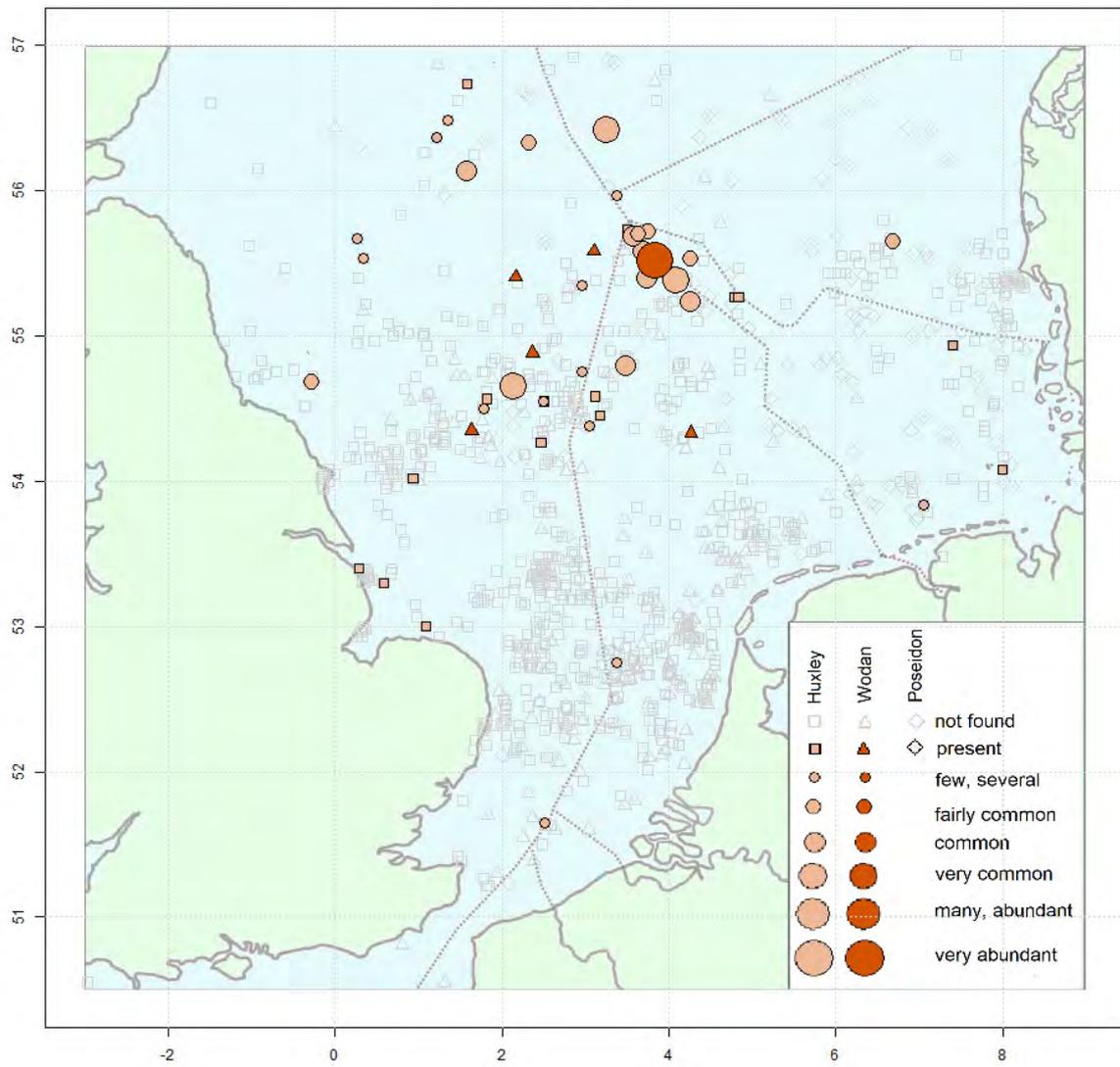


Flustra foliacea

Horn wrack

Abundance of this species at the North slopes of the Dogger Bank (55,5 N) and at the Fischerbank (56,5 N), were also reported by Tesch (1910).

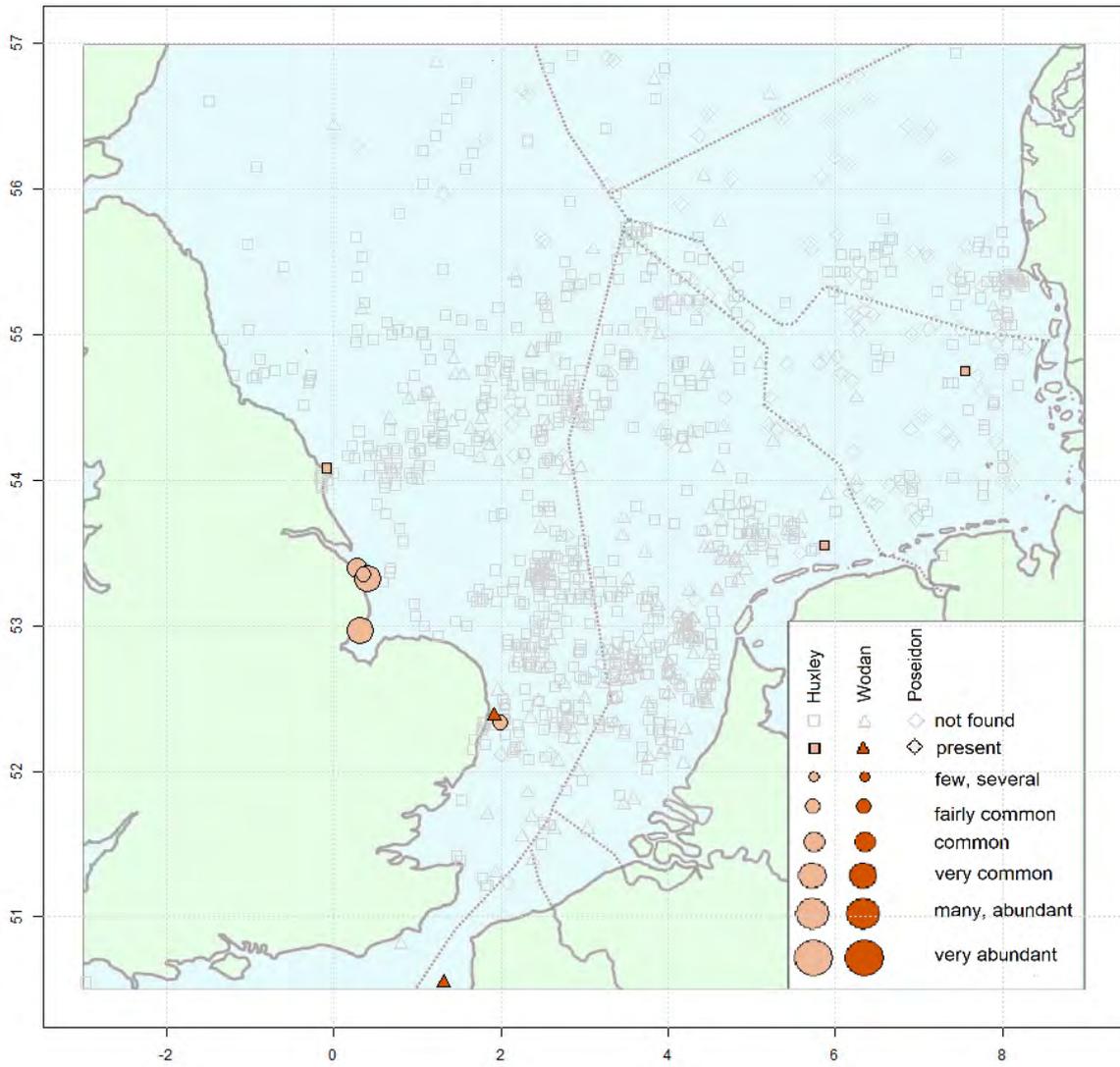
Securiflustra securifrons



Securiflustra securifrons Narrow-leaved hornwrack

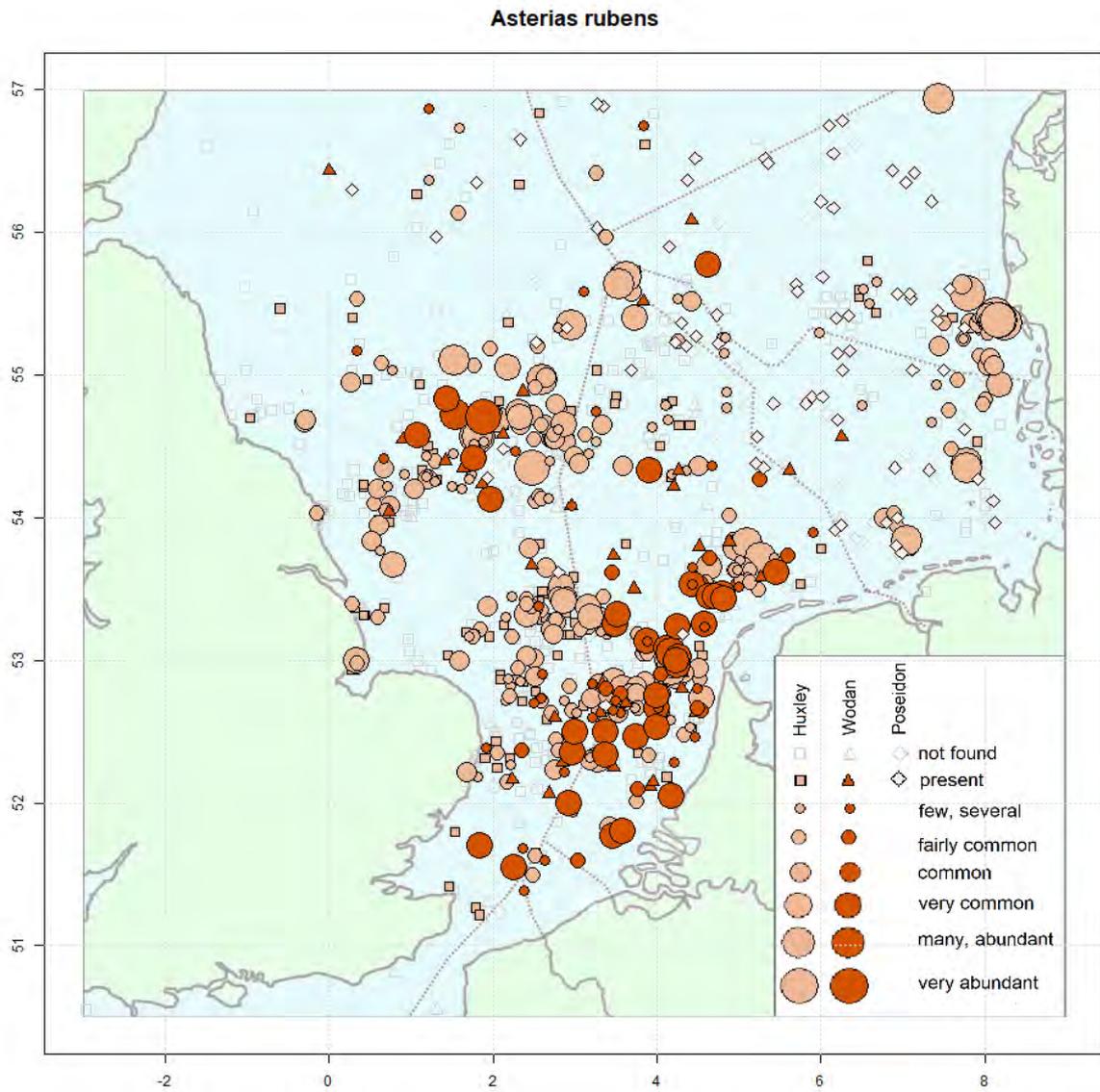
Concentrations of this species at the North slopes of the Dogger Bank (55,5 N) and at the Fischer Bank (56,5 N), were reported by Tesch (1910).

Vesicularia spinosa



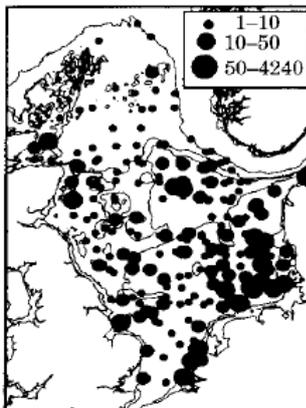
Vesicularia spinosa A bryozoan

Echinodermata-Asteroidea



Asterias rubens

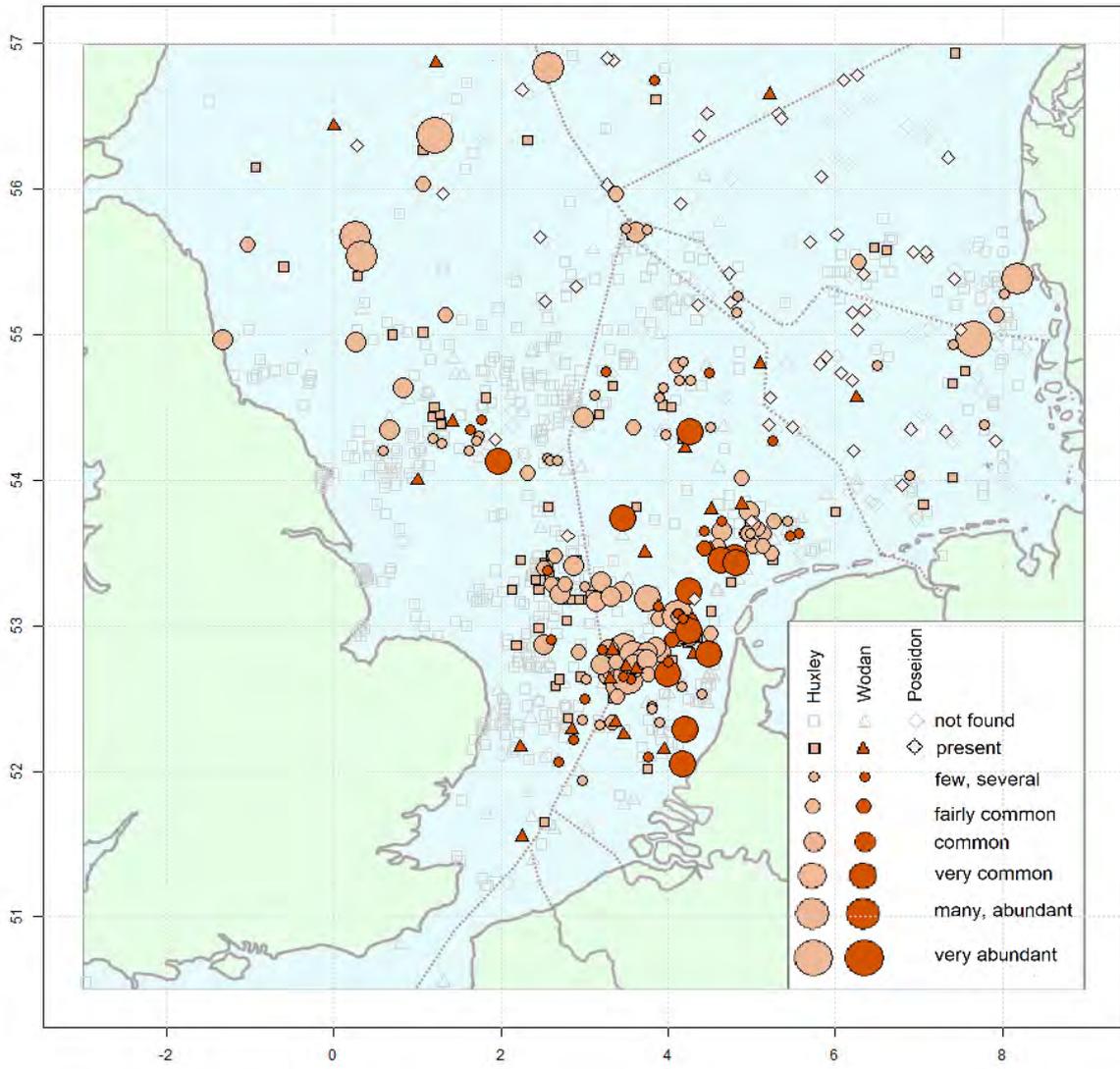
Common starfish



(b) *Asterias rubens*

2000 distribution map (Callaway *et al.*, 2002).

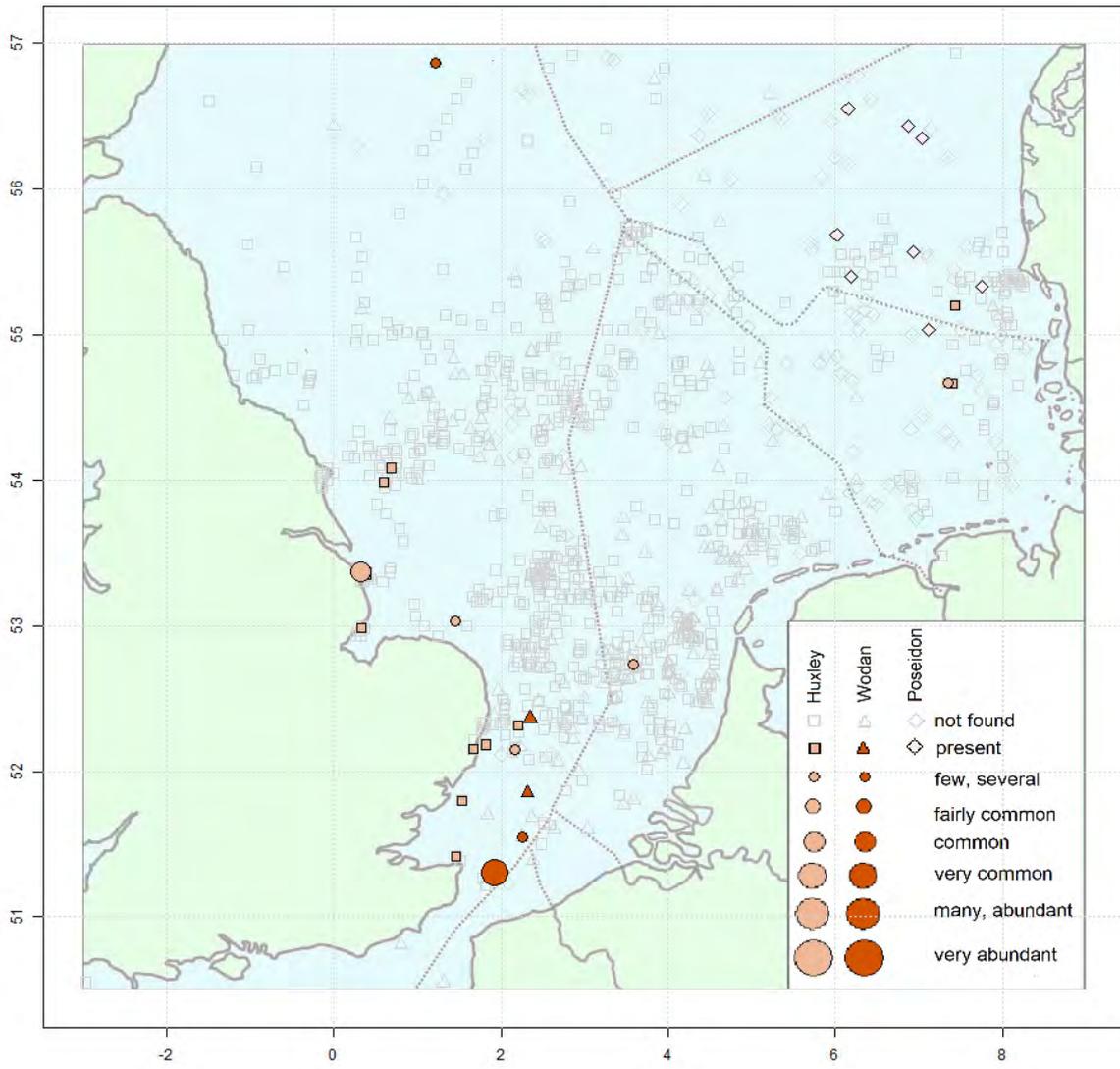
Astropecten irregularis



Astropecten irregularis

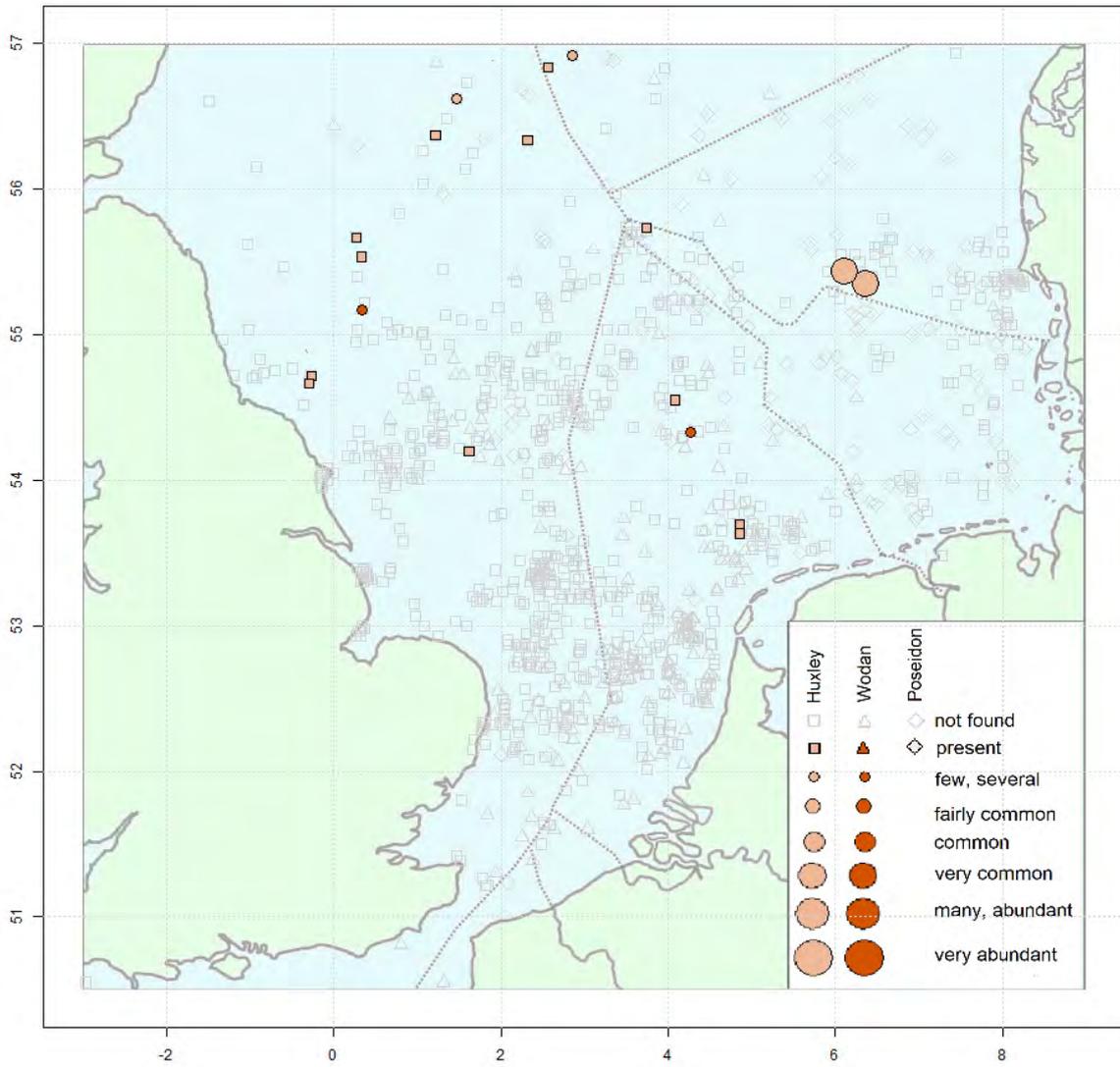
Sand star

Crossaster papposus



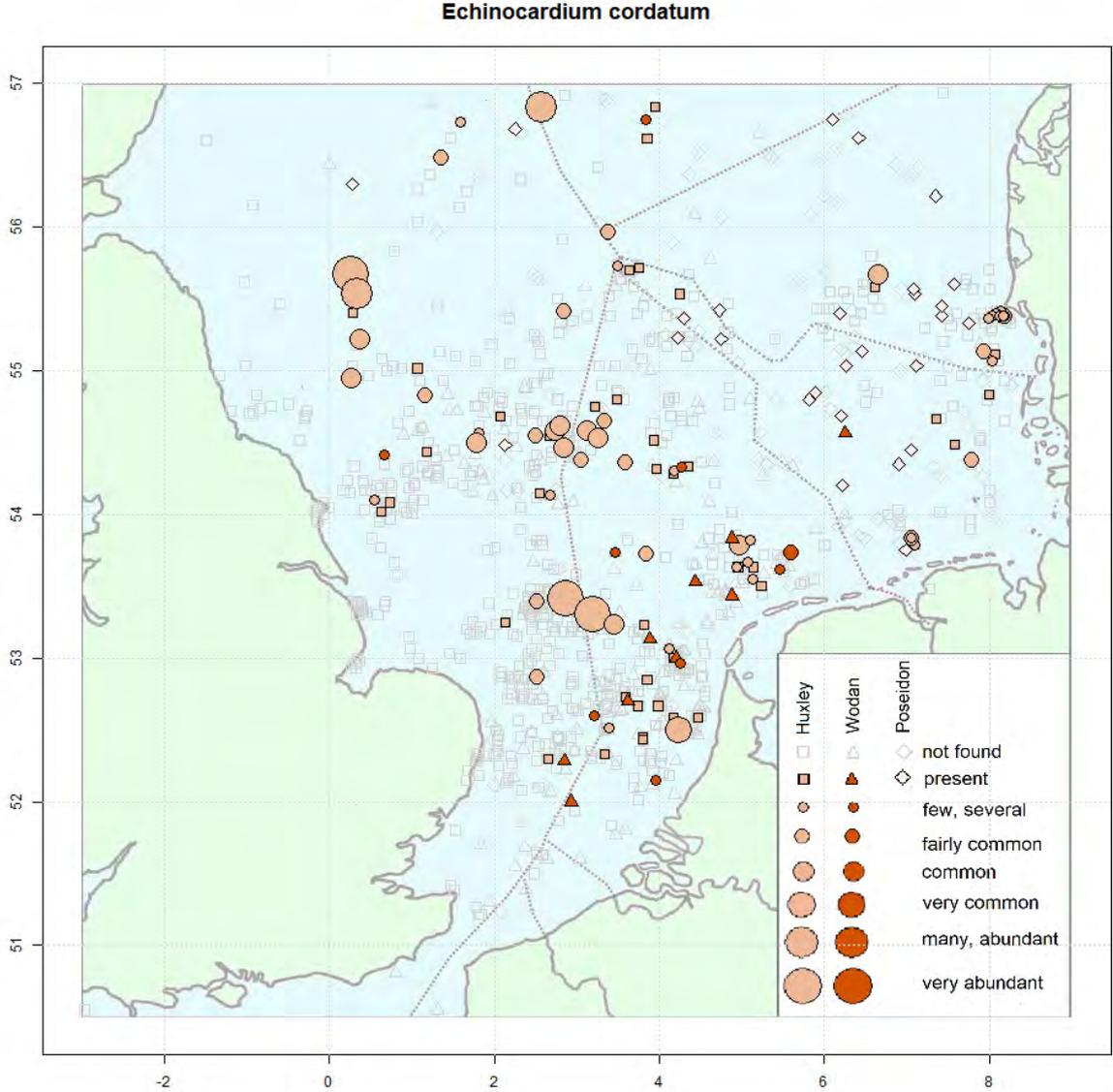
Crossaster papposus Common sunstar

Luidia sarsii



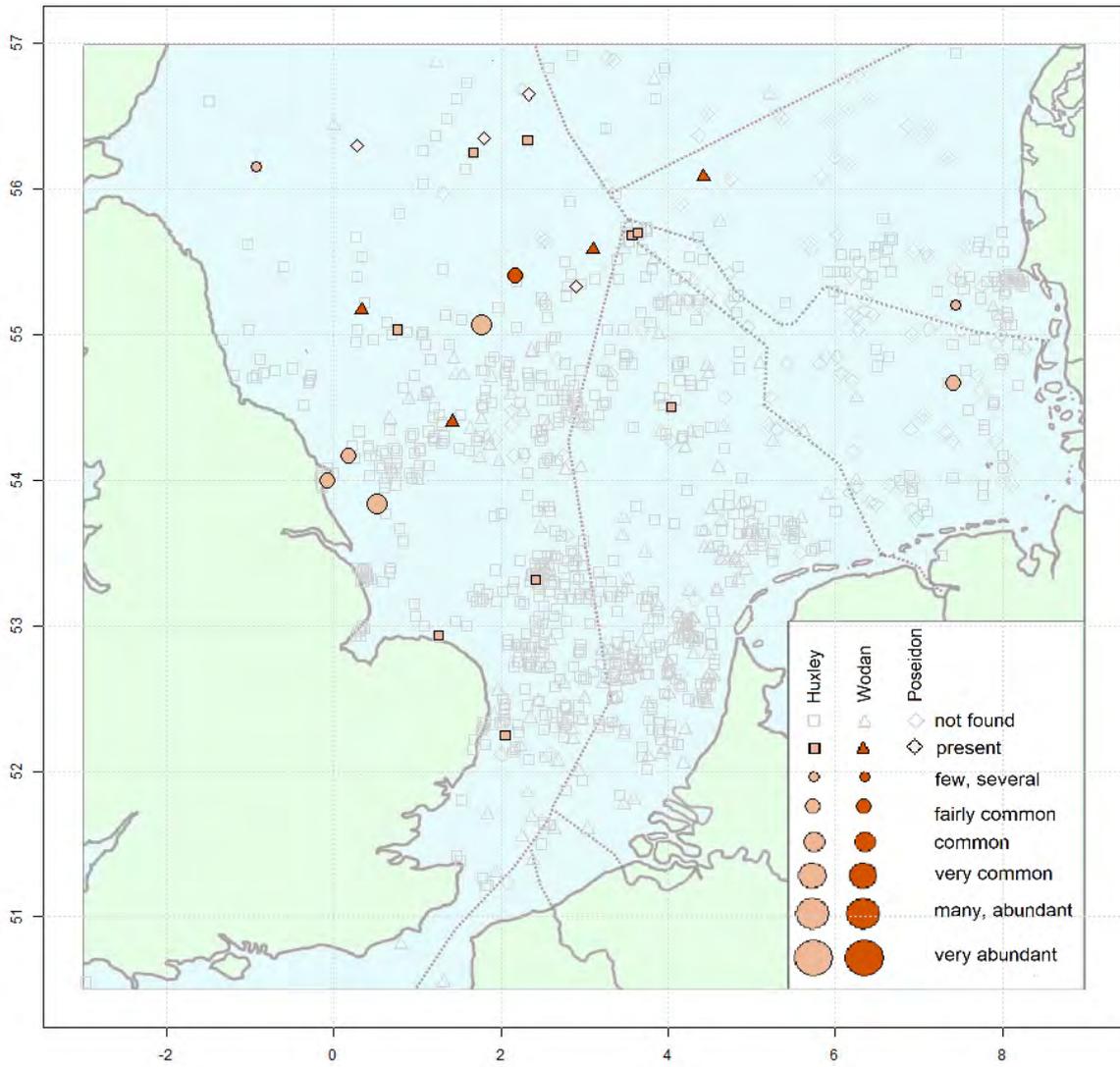
Luidia sarsii Seven armed starfish

Echinodermata-Echinoidea



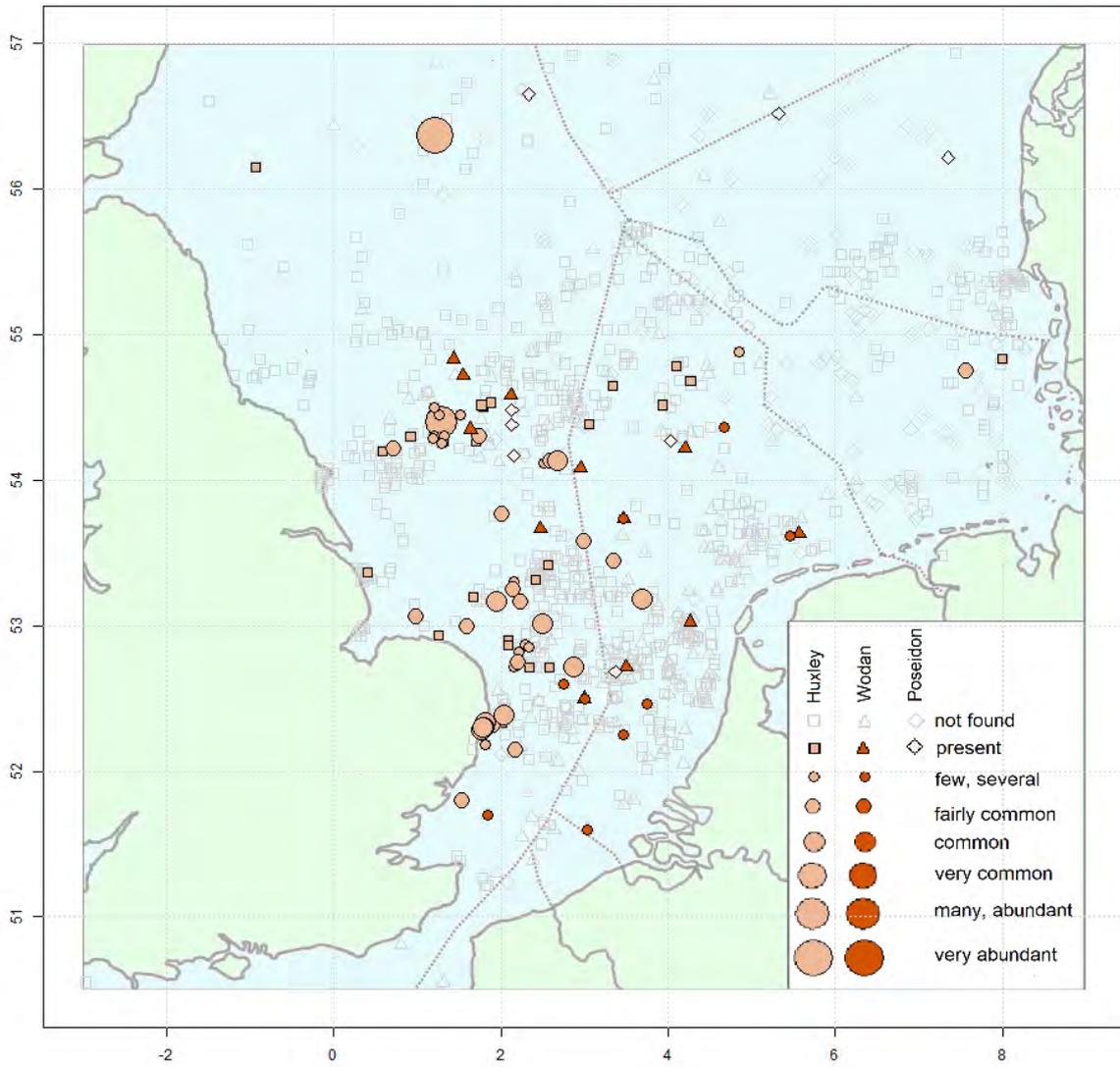
Echinocardium cordatum Common heart urchin

Echinus esculentus



Echinus esculentus Common sea urchin

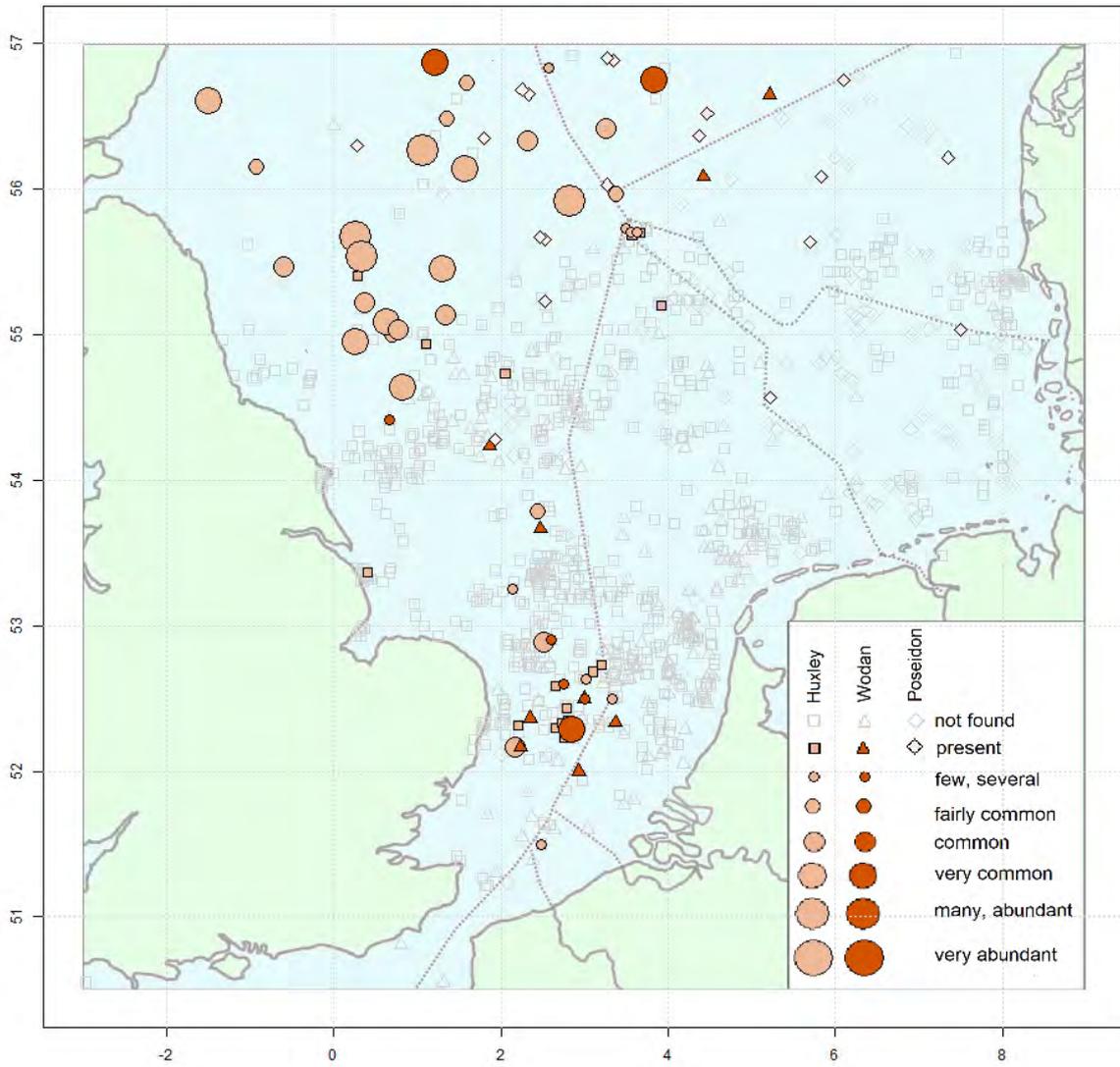
Psammechinus miliaris



Psammechinus miliaris

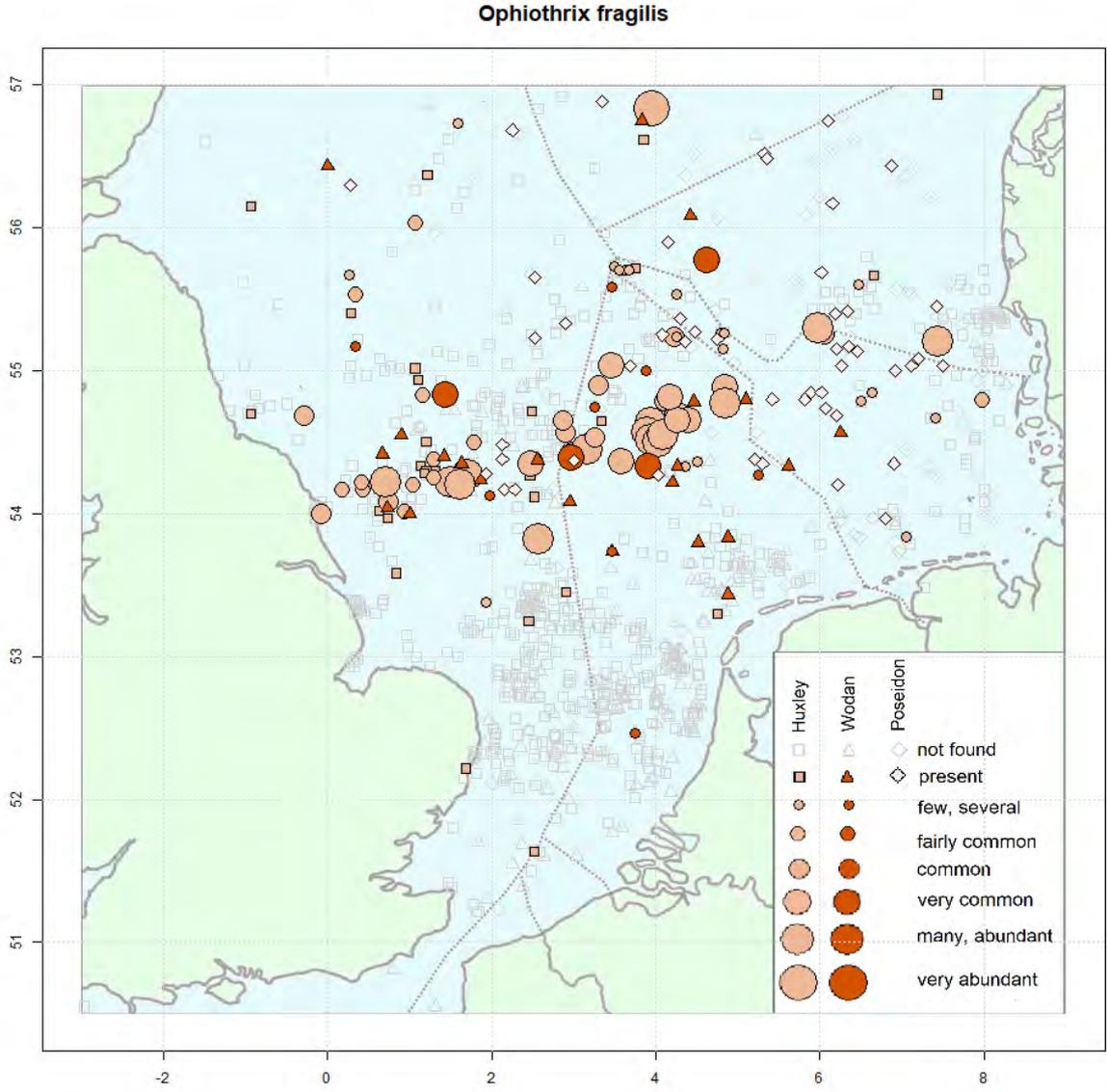
Shore sea urchin

Spatangus purpureus



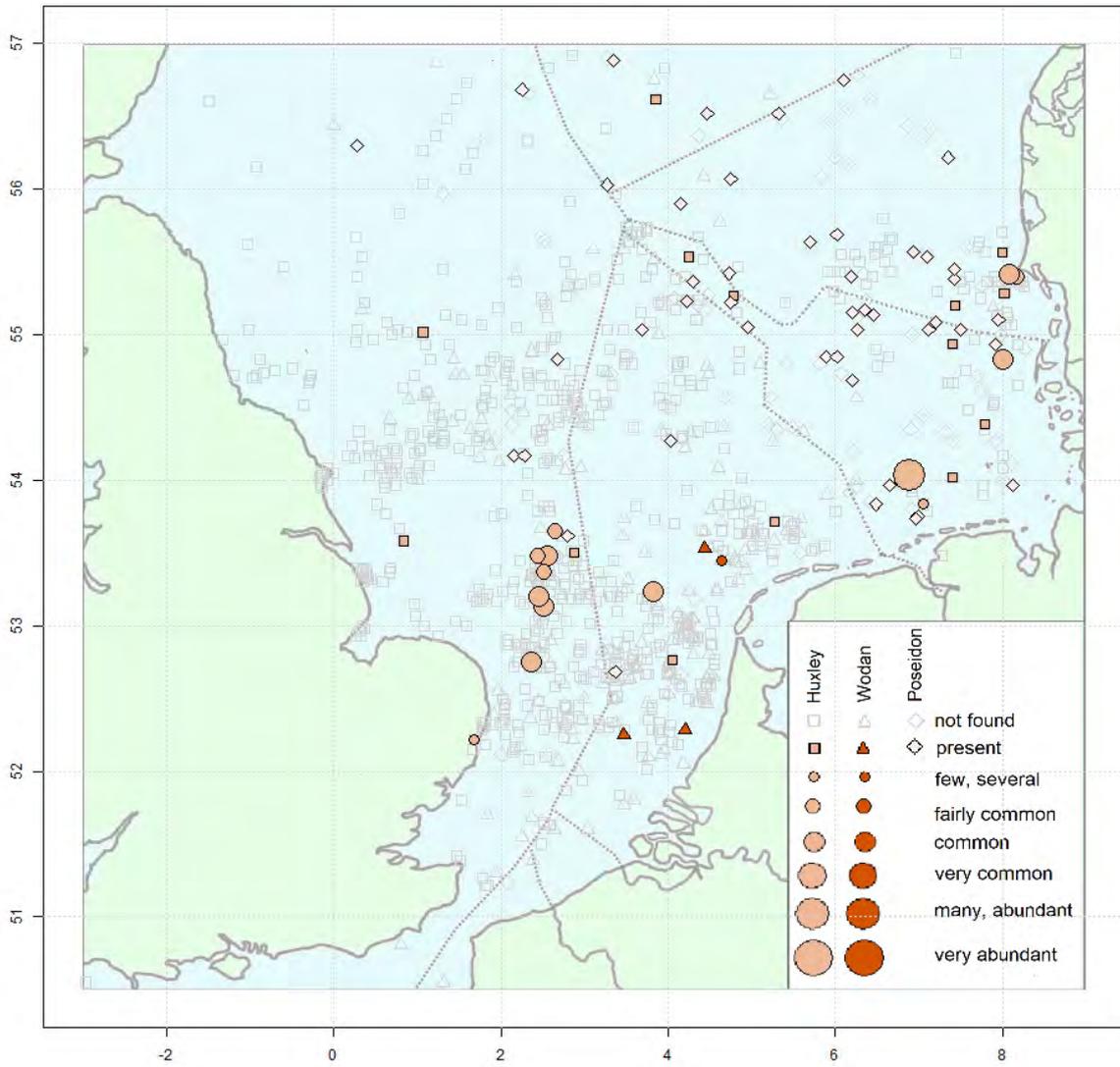
Spatangus purpureus Purple heart urchin

Echinoderma-Ophiuroidea



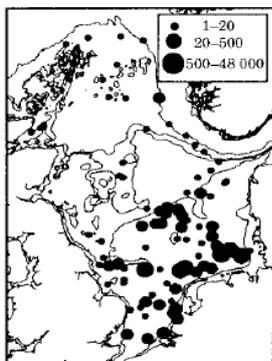
Ophiothrix fragilis Common brittle star

Ophiura albida



Ophiura albida

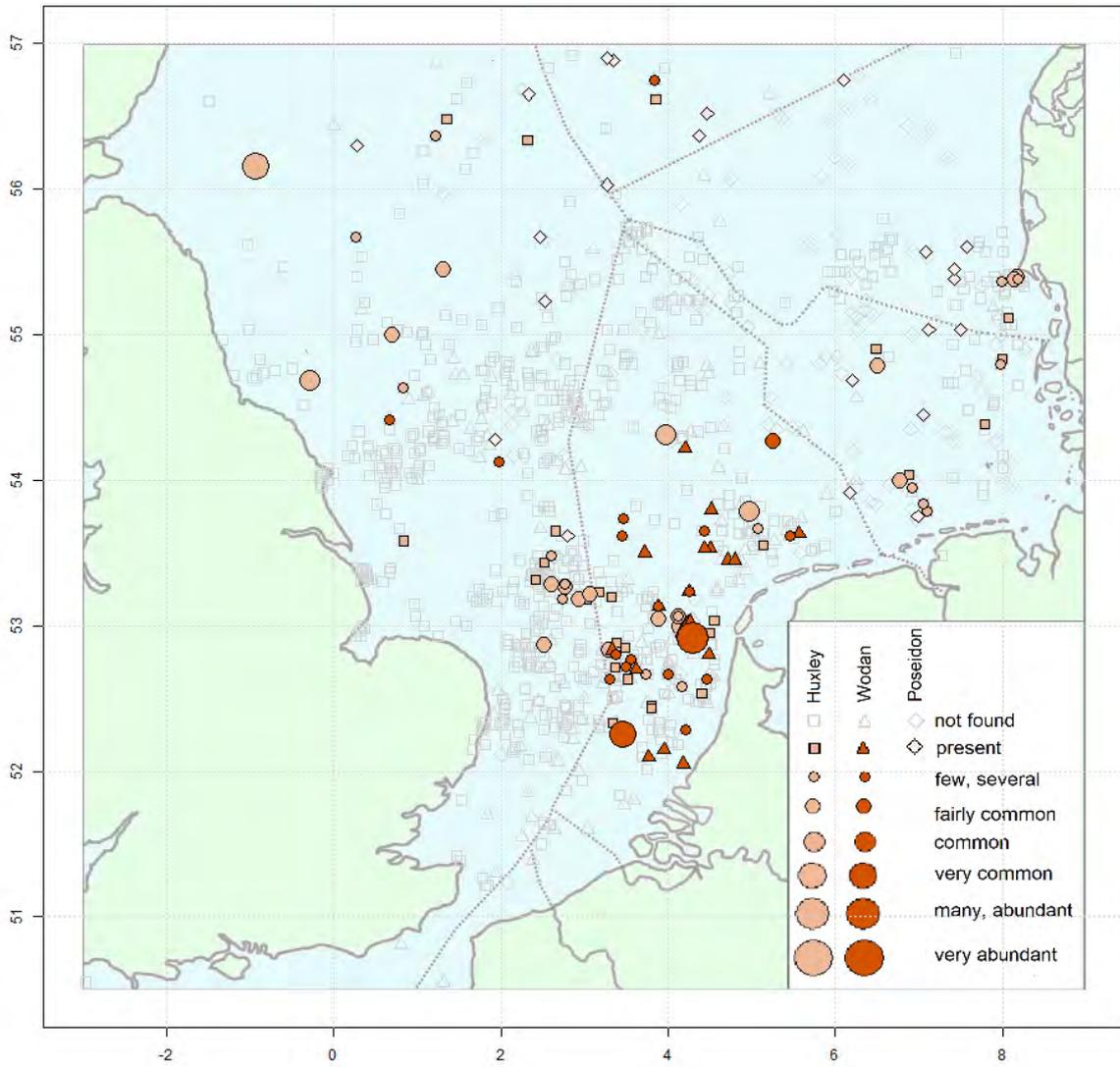
Serpent's table brittle star



(d) *Ophiura albida*

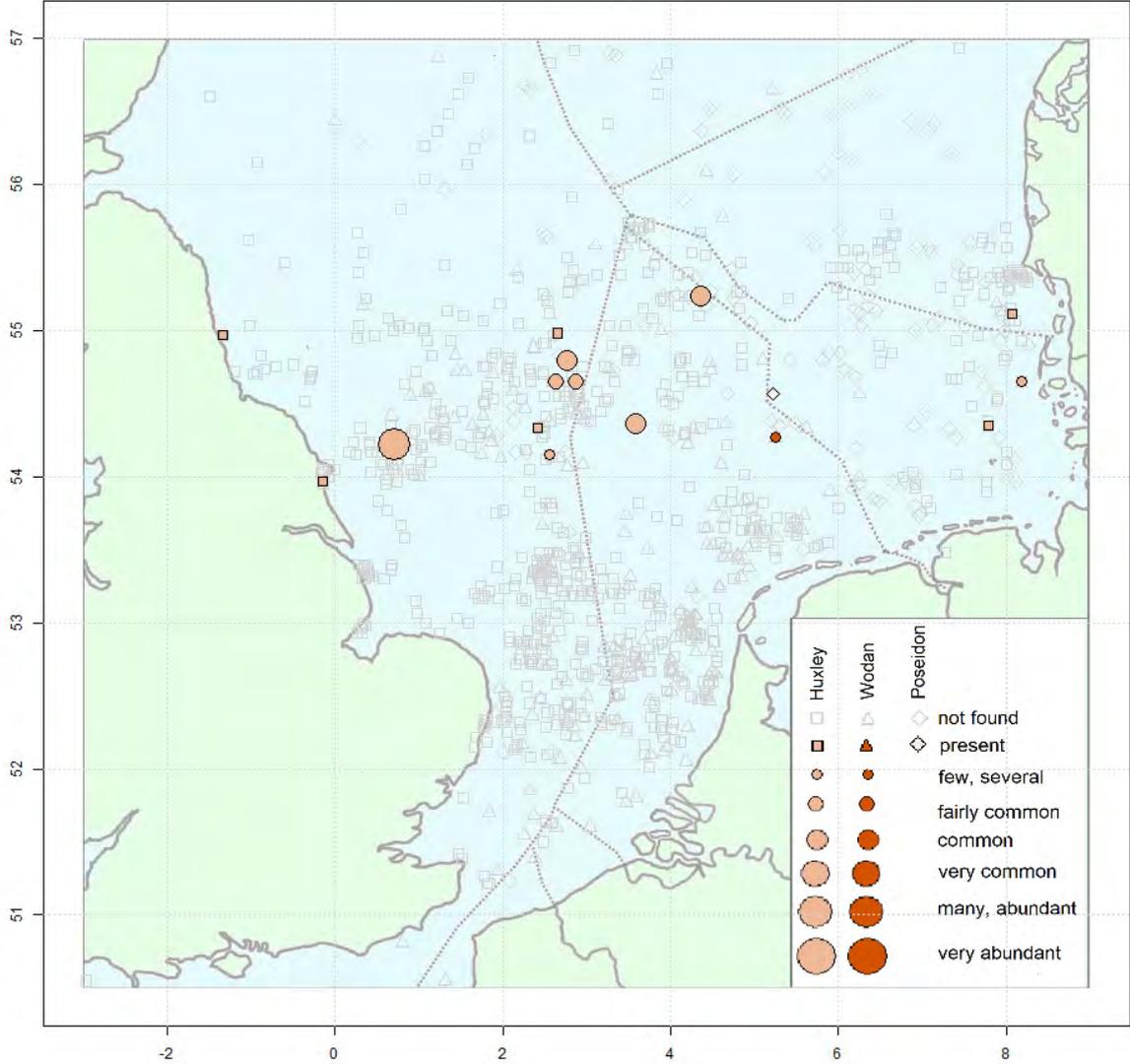
2000 distribution map (Callaway *et al.*, 2002).

Ophiura ophiura



Ophiura ophiura Sand brittle star

Ascidia virginea



Ascidia virginea

A sea squirt

7 Supplement: species names

7.1 Huxley species

Huxley

Acanthodoris pilosa
Actiniloba senile
Actinozoa
Acquorea sp.
Acteon tornatilis
Aeolidia papillosa
Aeolidella alderi
Aeolis sp.
Alcyonidium gelatinosum
Alcyonidium hirsutum
Alcyonium digitatum
Alcyonium parasiticum
Anomia pattelliformis
Anomias, *Anomia* sp.
Antennularia antennina
Antennularia ramosa
Aphrodite aculeata
Artemis lincta
Ascidians
Ascidiella virginea
Astarte
Astarte borealis
Astarte compressa
Asteroids
Asterias rubens
Astropecten irregularis
Aurelia aurita
Balanus hameri
Beanii
Bolocera teudiae
Bolocera longicornis
Botryllus sp.
Brittle-stars
Brissopsis lyrifera
Buccinum undatum
Bugula murrayana
Callisoma kroyeri
Calycella syringa
Campanularia verticillate
Caprella linearis
Cancer pagurus
Carcinus maenas
Cardium aculeatum
Cardium echinatum
Cardium edule

Modern name

Acanthodoris pilosa
Metridium senile
Cnidaria_or_Ctenophora
Scyphozoa
Acteon tornatilis
Aeolidia papillosa
Aeolidiella alderi
Aeolidiidae
Alcyonidium diaphanum or (less) *A. condylocinereum*
Alcyonidium diaphanum or (less) *A. condylocinereum*
Alcyonium digitatum
Alcyonidium parasiticum
Pododesmus patelliformis
Anomia sp.
Nemertesia antennina
Nemertesia ramosa
Aphrodita aculeata
Dosinia lupines lincta
Ascidiacea
Ascidia virginea
Astartidae
Astarte borealis
Astarte montagui
Asteroidea
Asterias rubens
Astropecten irregularis
Aurelia aurita
Chirona hameri
Beania or *Dendrobeania*
Bolocera tuediae
Bolocera tuediae
Botryllus sp.
Ophiuroidea
Brissopsis lyrifera
Buccinum undatum
Dendrobeania murrayana
Scopelocheirus hopei
Calycella syringa
Rhizocaulus verticillatus
Caprella linearis
Cancer pagurus
Carcinus maenas
Acanthocardia aculeata
Acanthocardia echinata
Cerastoderma edule

Huxley species

<i>Cardium pennanti</i>	<i>Laevicardium crissum</i>
<i>Cardium</i>	<i>Cardiidae</i>
<i>Carinella</i> sp.	<i>Tubulanus</i> sp.
<i>Chaetopterus variopedatus</i>	<i>Chaetopterus variopedatus</i>
<i>Cirripedia</i>	<i>Cirripedia</i>
<i>Cellepora pumicosa</i>	<i>Cellepora pumicosa</i>
<i>Chalina oculata</i>	<i>Haliclona (Haliclona) oculata</i>
<i>Chondractinia digitata</i>	<i>Hormathia digitata</i>
<i>Chrysaora</i>	<i>Chrysaora</i> , cf. <i>C. hysoscella</i>
<i>Ciona intestinalis</i>	<i>Ciona intestinalis</i>
<i>Clione</i>	cf. <i>Cliona</i> sp.
<i>Clytia Johnstoni</i>	<i>Clytia haemispherica</i>
<i>Copinia arcta</i>	<i>Filellum serpens</i>
<i>Corystes cassivelaunus</i>	<i>Corystes cassivelaunus</i>
<i>Crabs (small)</i>	<i>Brachyura</i>
<i>Crangon vulgaris</i>	<i>Crangon crangon</i>
<i>Crangon allmani</i>	<i>Crangon allmanni</i>
<i>Cribrilina punctata</i>	<i>Cribrilina punctata</i> or <i>Collarina balzaci</i>
<i>Crisia eburnea</i>	<i>Crisia eburnea</i>
<i>Crustacea</i>	<i>Crustacea</i>
<i>Cyanea capillata</i>	<i>Cyanea capillata</i>
<i>Cyanea lamarcki</i>	<i>Cyanea lamarckii</i>
<i>Cyprina islandica</i>	<i>Arctica islandica</i>
<i>Dendronotus arborescens</i>	<i>Dendronotus frondosus</i>
<i>Dentalium entails</i>	<i>Antalis entalis</i>
<i>Diastopora patina</i>	<i>Plagioecia patina</i>
<i>Dicoryne conferta</i>	<i>Dicoryne conferta</i>
<i>Diphasia pinaster</i>	<i>Diphasia margareta</i>
<i>Doris exigua</i>	<i>Eubranchus exiguus</i>
<i>Doris pilosa</i>	<i>Acanthodoris Pilosa</i>
<i>Doto fragilis</i>	<i>Doto fragilis</i>
<i>Doto coronata</i>	<i>Doto coronata</i>
<i>Echinoids</i>	<i>Echinoidea</i>
<i>Echinocardium cordatum</i>	<i>Echinocardium cordatum</i>
<i>Echinocardium</i> sp.	<i>Echinocardium</i> sp.
<i>Echinus acutus</i>	<i>Gracilechinus acutus</i>
<i>Echinus esculentus</i>	<i>Echinus esculentus</i>
<i>Echinus milliaris</i>	<i>Psammechinus miliaris</i>
<i>Eledone cirrhosa</i>	<i>Eledone cirrhosa</i>
<i>Eolis exigua</i>	<i>Eubranchus exiguus</i>
<i>Eupagurus bernhardus</i>	<i>Pagurus bernhardus</i>
<i>Eupagurus pubescens</i>	<i>Pagurus pubescens</i>
<i>Filograna implexa</i>	<i>Filograna implexa</i>
<i>Flustra carbacea</i>	<i>Carbacea carbacea</i>
<i>Flustra foliacea</i>	<i>Flustra foliacea</i>
<i>Flustra securifrons</i>	<i>Securiflustra securifrons</i>
<i>Fusus antiquus</i>	<i>Neptunea antiqua</i>
<i>Fusus gracilis</i>	<i>Colus gracilis</i>
<i>Fusus islandicus</i>	<i>Colus islandicus</i>
<i>Fusus norvegicus</i>	cf. <i>Volutopsius norvegicus</i>
<i>Fusus propinquus</i>	<i>Colus jeffreysianus</i>
<i>Fusus</i>	<i>Colus</i> sp.

Huxley species

<i>Galathea intermedia</i>	<i>Galathea intermedia</i>
<i>Galathea</i> sp.	<i>Galathea</i> sp.
<i>Gammarus locusta</i>	<i>Gammarus locusta</i>
<i>Gemellaria loricata</i>	<i>Eucratea loricata</i>
<i>Goniaster equestris</i>	<i>Hippasteria phrygiana</i>
<i>Halecium halecium</i>	<i>Halecium halecinum</i>
<i>Halecium</i> sp.	<i>Halecium</i> sp.
<i>Halichondria panicea</i>	<i>Halichondria (Halichondria) panicea</i>
<i>Henricia sanguinolenta</i>	<i>Henricia sanguinolenta</i>
<i>Hermit crabs</i>	Paguroidea
<i>Hippasteria phrygiana</i>	<i>Hippasteria phrygiana</i>
<i>Hippolyte varians</i>	<i>Hippolyte varians</i>
<i>Hippolyte spinus</i>	<i>Hippolyte</i> sp.
<i>Homarus vulgaris</i>	<i>Homarus gammarus</i>
<i>Hyas areaneus</i>	<i>Hyas araneus</i>
<i>Hyas coarctus</i>	<i>Hyas coarctatus</i>
<i>Hydractinia echinata</i>	<i>Hydractinia echinata</i>
<i>Hydrallmania falcata</i>	<i>Hydrallmania falcata</i>
<i>Hydroids</i>	Hydrozoa (polyp)
<i>Idmonea serpens</i>	<i>Tubulipora liliacea</i>
<i>Janira maculosa</i>	<i>Janira maculosa</i>
<i>Kellia</i> sp.	<i>Kellia</i> sp.
<i>Kellia suborbicularis</i>	<i>Kellia suborbicularis</i>
<i>Lafoea Dumosa</i>	<i>Lafoea dumosa</i>
<i>Lamellaria perspicua</i>	<i>Lamellaria perspicua</i>
<i>Lobsters</i>	<i>Nephropidae</i>
<i>Loligo</i> sp.	<i>Loligo</i> sp.
<i>Loligo media</i>	<i>Alloteuthis subulata</i>
<i>Loligo forbesi</i>	<i>Loligo forbesii</i>
<i>Lacuna crassior</i>	<i>Lacuna crassior</i>
<i>Lamellidoris bilamellata</i>	<i>Onchidoris bilamellata</i>
<i>Lanice conchilega</i>	<i>Lanice conchilega</i>
<i>Lepralia foliacea</i>	<i>Pentapora foliacea</i>
<i>Lithodes maia</i>	<i>Lithodes maja</i>
<i>Luidia sarsi</i>	<i>Luidia sarsii</i>
<i>Lutraria</i>	<i>Lutraria</i> sp.
<i>Mactra</i>	<i>Mactra</i> sp.
<i>Mactra subtruncata</i>	<i>Spisula subtruncata</i>
<i>Mactra stutorum</i>	<i>Mactra stultorum</i>
<i>Maia squinado</i>	<i>Maja squinado</i>
<i>Mangelia turricula</i>	<i>Propebela turricula</i>
<i>Medusae</i>	Hydrozoa (medusa)
<i>Melita obtusata</i>	<i>Abludomelita obtusata</i>
<i>Membranipora unicornis</i>	<i>Tegella unicornis</i>
<i>Metridium senile</i>	<i>Metridium senile</i>
<i>Modiolaria nigra</i>	<i>Musculus niger</i>
<i>Modiolus modiolus</i>	<i>Modiolus modiolus</i>
<i>Molluscs</i>	<i>Mollusca</i>
<i>Montacuta substriata</i>	<i>Montacuta substriata</i>
<i>Mya truncata</i>	<i>Mya truncata</i>
<i>Mytilus edulis</i>	<i>Mytilus edulis</i>
<i>Myxicola?</i>	<i>Myxicola</i> sp.?

Huxley species

<i>Natica alderi</i>	<i>Euspira nitida</i>
<i>Natica catena</i>	<i>Euspira catena</i>
<i>Natica monifilera</i>	<i>Euspira catena</i>
<i>Nephrops norvegicus</i>	<i>Nephrops norvegicus</i>
<i>Nereis pelagica</i>	<i>Nereis pelagica</i>
<i>Nucula nucleus</i>	<i>Nucula nucleus</i>
<i>Nudibranchs</i>	<i>Nudibranchia</i>
<i>Nymphon</i>	<i>Nymphonidae</i>
<i>Obelia</i> sp	<i>Obelia</i> sp.
<i>Obelia geniculata</i>	<i>Obelia geniculata</i>
<i>Obelia longissima</i>	<i>Obelia longissima</i>
<i>Ophelia limacina</i>	<i>Ophelia limacina</i>
<i>Ophiurids</i>	<i>Ophiuroidea</i>
<i>Ophiopholis aculeata</i>	<i>Ophiopholis aculeata</i>
<i>Ophiothrix fragilis</i>	<i>Ophiothrix fragilis</i>
<i>Ophiura albida</i>	<i>Ophiura albida</i>
<i>Ophiura ciliaris</i>	<i>Ophiura ophiura</i>
<i>Ostrea edulis</i>	<i>Ostrea edulis</i>
<i>P. crispata</i>	<i>Zirfaea crispata</i>
<i>P. pinnata</i>	<i>Kirchenpaueria pinnata</i>
<i>P. pusillus</i>	<i>Liocarcinus pusillus</i>
<i>Pandalus</i> sp.	<i>Pandalus</i> sp.
<i>Pandalus annulicornis</i>	<i>Pandalus montagui</i>
<i>Pandalus montagui</i>	<i>Pandalus montagui</i>
<i>Panopea norvegica</i>	<i>Panomya norvegica</i>
<i>Paratylus swammerdami</i>	<i>Nototropis swammerdamei</i>
<i>Pecten, Pecten purio</i>	<i>Pecten</i> sp.
<i>Pecten opercularis</i>	<i>Aequipecten opercularis</i>
<i>Pecten striatus</i>	<i>Palliolum striatum</i>
<i>Pecten varius</i>	<i>Mimachlamys varia</i>
<i>Philine aperta</i>	<i>Philine quadripartita</i>
<i>Pholas crispata</i>	<i>Zirfaea crispata</i>
<i>Pinnotheres pisum</i>	<i>Pinnotheres pisum</i>
<i>Pleurophillidia loveni</i>	<i>Armina loveni</i>
<i>Pleurotoma turricula</i>	<i>Probela turricula</i>
<i>Plumularia</i> sp	<i>Plumularia</i>
<i>Podocoryna carnea</i>	<i>Podocoryna carnea</i>
<i>Pomatocerus triqueter</i>	<i>Spirobranchus triqueter</i>
<i>Polynoids, Polynoe</i> sp.	<i>Polynoidae</i>
<i>Polyzoa</i>	cf. <i>Bryozoa</i>
<i>Porcellana longicornis</i>	<i>Pisidia longicornis</i>
<i>Portunus</i> sp.	<i>Polybiidae</i>
<i>Portunus depurator</i>	<i>Liocarcinus depurator</i>
<i>Portunus holsatus</i>	<i>Liocarcinus holsatus</i>
<i>Portunus puber</i>	<i>Necora puber</i>
<i>Pycnogonum littorale</i>	<i>Pycnogonum litorale</i>
<i>Rhodactinia crassicornis</i>	<i>Urticina eques</i>
<i>Sabella pavonina</i>	<i>Sabella pavonina</i>
<i>Sabellaria spinulosa</i>	<i>Sabellaria spinulosa</i>
<i>Sabellaria tubes</i>	<i>Sabellaria</i> sp.
<i>Sagartia minuata</i>	<i>Sagartia elegans</i>
<i>Sagartia pallida</i>	<i>Metridium senile</i>

Huxley species

<i>Sagartia viduata</i>	cf. <i>Sagartiogeton undatus</i>
<i>Saxicava rugosa</i>	<i>Hiatella rugosa</i>
<i>Saxicava (Hiatella) arctica</i>	<i>Hiatella arctica</i>
<i>Scrupocellaria reptans</i>	<i>Cradoscrupocellaria ellisii</i> or <i>C. reptans</i>
<i>Schistomysis ornata</i>	<i>Schistomysis ornata</i>
<i>Sepia</i> sp.	<i>Sepia</i> sp.
<i>Serpula tubes</i>	<i>Serpula</i> sp.
<i>Sertularella polyzonias</i>	<i>Sertularella polyzonias</i>
<i>Sertularia abietina</i>	<i>Abietinaria abietina</i>
<i>Sertularia argentea</i>	<i>Sertularia argentea</i>
<i>Sertularia distans</i>	<i>Amphisbetia distans</i>
<i>Sertularia operculata</i>	<i>Amphisbetia operculata</i>
<i>Sertularia rosacea</i>	<i>Diphasia rosacea</i>
<i>Solen pellucidus</i>	<i>Phaxas pellucidus</i>
<i>Solen</i>	cf. <i>Ensis</i> sp.
<i>Solaster endeca</i>	<i>Solaster endeca</i>
<i>Solaster operculata</i>	Solaster or Crossaster
<i>Solaster papposus</i>	<i>Crossaster papposus</i>
<i>Spatangus purpureus</i>	<i>Spatangus purpureus</i>
<i>Spirorbis</i>	Spirorbidae
<i>Sponge</i>	Porifera
<i>Starfish</i>	Asteroidea
<i>Stenorhynchus longirostris</i>	<i>Macropodia longirostris</i>
<i>Stenorhynchus phalangium</i>	<i>Inachus phalangium</i>
<i>Stenorhynchus tenuirostris</i>	<i>Macropodia tenuirostris</i>
<i>Stylifer</i>	<i>Pelseneeria stylifera</i>
<i>Suberites domuncula</i>	<i>Suberites domuncula</i>
<i>Syncoryne gravata</i>	<i>Sarsia tubulosa</i>
<i>Syndosmya</i>	<i>Abra</i> sp.
<i>Tealia coriacea</i>	<i>Urticina felina</i>
<i>Tealia crassicornis</i>	<i>Urticina crassicornis</i>
<i>Teredo</i> sp.	Teredinidae
<i>Thelepus cincinnatus</i>	<i>Thelepus cincinnatus</i>
<i>Thelepus</i> sp.	<i>Thelepus</i> sp.
<i>Thuiaria thuja</i>	<i>Thuiaria thuja</i>
<i>Triticella pedicellate</i>	<i>Triticella pedicellata</i>
<i>Tritonia hombergi</i>	<i>Tritonia hombergii</i>
<i>Tritonia plebeia</i>	<i>Duvaucelia plebeia</i>
<i>Tubularia coronata</i>	<i>Ectopleura larynx</i>
<i>Tubularia indivisa</i>	<i>Tubularia indivisa</i>
<i>Tubularia</i> sp.	Tubulariidae
<i>Tunicates</i>	Tunicata
<i>Turritella</i>	Turritellidae
<i>Velutina laevigata</i>	<i>Velutina velutina</i>
<i>Venus exoleta</i>	<i>Dosinia exoleta</i>
<i>Venus gallina</i>	<i>Chamelea gallina</i>
<i>Venus lincta</i>	<i>Dosinia lupinus lincta</i>
<i>Venus striatula</i>	<i>Chamelea striatula</i>
<i>Vesicularia spinosa</i>	<i>Vesicularia spinosa</i>

Wodan species

7.2 Wodan species

Wodan

Acanthodoris sp.?
Aeolis (*papillosa*?)
Aurelia aurita
Alcyonidium albidum
Alcyonidium gelatinosum
Alcyonidium hirsutum
Alcyonium digitatum
Amathia lendigera
Amphioxus lanceolatus
Amphiura filiformis
Anneliden
Anomia ephippium
Anomia patelliformis
Antennularia antennina
Antennularia ramosa
Aphrodite aculeata
Aplidiopsis pomum?
Aporrhais pes pelicanae shell
Artemis exoleta
Artemis lincta
Ascidien
Ascidiella virginea
Ascidiella adpersa
Ascidiella scabra
Ascidiella sp.?
Astacilla longicornis
Astarte compressa
Asteriden, Zeesterren
Asterias glacialis
Asterias rubens
Asterias mulleri
Astropecten irregularis
Atelecyclus heterodon
Aurelia aurita
Balanus porcatus
Balanus hameri
Bryssopsis lyrifera
Buccinum undatum
Buccinum undatum shell
Bugula murrayana
Campanularia johnstoni
Campanularia (Gonothyraea) gracilis
Campanularia sp.
Cancer pagurus
Carcinus maenas
Cardium echinatum
Cardium edule
Cardium edule shell

Modern name

Acanthodoris sp.
cf. *Aeolidia papillosa*
Aurelia aurita
Alcyonidium albidum
Alcyonidium diaphanum or (less) *A. condylocinereum*
Alcyonidium diaphanum or (less) *A. condylocinereum*
Alcyonium digitatum
Amathia lendigera
Branchiostoma lanceolatum
Amphiura filiformis
Annelida
Anomia ephippium
Pododesmus patelliformis
Nemertesia antennina
Nemertesia ramosa
Aphrodita aculeata
Synoicum pulmonaria?
Aporrhais pespelecani shell
Dosinia exoleta
Dosinia lupinus lincta
Ascidacea
Ascidia virginea
Ascidiella aspersa
Ascidiella scabra
Ascidiella sp.?
Astacilla longicornis
Astarte montagui
Asteroidea
Marthasterias glacialis
Asterias rubens
Leptasterias (Leptasterias) muelleri
Astropecten irregularis
Atelecyclus rotundatus
Aurelia aurita
Balanus balanus
Chirona hameri
Brissopsis lyrifera
Buccinum undatum
Buccinum undatum shell
Dendrobeania murrayana
Clytia haemisphaerica
Campanularia gracilis
Campanularia
Cancer pagurus
Carcinus maenas
Acanthocardia echinata
Cerastoderma edule
Cerastoderma edule

Wodan species

<i>Cardium norvegicum</i>	<i>Laevicardium crassum</i>
<i>Carinella annulata</i>	<i>Tubulanus annulatus</i>
<i>Chaetonymphon hirtum</i>	<i>Nymphon hirtum</i>
<i>Chrysaora hysocella</i>	<i>Chrysaora hysocella</i>
<i>Chrysaora isosceles</i>	<i>Chrysaora hysocella</i>
<i>Clytia johnstoni</i>	<i>Clytia haemisphaerica</i>
<i>Coppinia</i> sp.	<i>Filellum</i> sp.
<i>Corystes cassivelaunus</i>	<i>Corystes cassivelaunus</i>
<i>Crangon vulgaris</i>	<i>Crangon crangon</i>
<i>Crangon</i> sp.	<i>Crangon</i> sp.
<i>Cribrella sanguinolenta</i>	<i>Henricia sanguinolenta</i>
<i>Crisia eburnea</i>	<i>Crisia eburnea</i>
<i>Crisia eburnea fragment</i>	<i>Crisia eburnea fragment</i>
<i>Crossaster papposus</i>	<i>Crossaster papposus</i>
<i>Cultellus pellucidus</i>	<i>Phaxas pellucidus</i>
<i>Cyanea</i> sp.	<i>Cyanea</i> sp.
<i>Cyanea capillata</i>	<i>Cyanea capillata</i>
<i>Cyanea lamarcki</i>	<i>Cyanea lamarckii</i>
<i>Cyprina islandica</i>	<i>Arctica islandica</i>
<i>Dentalium entalis</i>	<i>Antalis entalis</i>
<i>Diphasia rosacea</i>	<i>Diphasia rosacea</i>
<i>Diphasia tamarisca</i>	<i>Tamarisca tamarisca</i>
<i>Dentalium entalis</i>	<i>Antalis entalis</i>
<i>Donax anatina</i>	<i>Donax vittatus</i>
<i>Donax trunculus</i>	<i>Donax vittatus</i>
<i>Donax vittatus</i>	<i>Donax vittatus</i>
<i>Doris tuberculata</i>	<i>Doris pseudoargus</i>
<i>Doris</i> sp.	cf. <i>Doris</i> sp.
<i>Echiniden</i>	Echinoidea
<i>Echinocardium cordatum</i>	<i>Echinocardium cordatum</i>
<i>Echinocardium flavescens</i>	<i>Echinocardium flavescens</i>
<i>Echinocyamus pusillus</i>	<i>Echinocyamus pusillus</i>
<i>Echinus esculentus</i>	<i>Echinus esculentus</i>
<i>Echinus miliaris</i>	<i>Psammechinus miliaris</i>
<i>Emplectonema neesi</i>	<i>Emplectonema neesii</i>
<i>Eupagurus benhardus</i>	<i>Pagurus bernhardus</i>
<i>Eupagurus laevis</i>	<i>Eupagurus laevis</i>
<i>Eupagurus pubescens</i>	<i>Pagurus pubescens</i>
<i>Eupagurus</i> sp.	<i>Pagurus</i> sp.
<i>Facelina coronata</i>	<i>Facelina auriculata</i>
<i>Flustra foliacea</i>	<i>Flustra foliacea</i>
<i>Flustra membranacea</i>	Bryozoa
<i>Flustra securifrons</i>	<i>Securiflustra securifrons</i>
<i>Flustra</i> sp.	Bryozoa
<i>Filigrana implexa</i>	<i>Filigrana implexa</i>
<i>Filigrana</i> sp.?	<i>Filigrana</i> sp.?
<i>Fusus antiquus</i>	<i>Neptunea antiqua</i>
<i>Fusus gracilis</i>	<i>Colus gracilis</i>
<i>Fusus propinquus</i>	<i>Colus jeffreysianus</i>
<i>Fusus</i> sp.	<i>Colus</i> sp.
<i>Galathea intermedia</i>	<i>Galathea intermedia</i>
<i>Galathea strigosa</i>	<i>Galathea strigosa</i>

Wodan species

<i>Galathea</i> sp.	<i>Galathea</i> sp.
<i>Halecium halecium</i>	<i>Halecium halecinum</i>
<i>Halichondria cervicornis</i> ?	<i>Haliclona (Haliclona) oculata</i> ?
<i>Halichondria panicea</i>	<i>Halichondria (Halichondria) panicea</i>
<i>Halodactylus</i> sp.	Alcyonidiidae
<i>Halodactylus gelatinosus</i>	<i>Alcyonidium diaphanum</i> or (less) <i>A. condylocinereum</i>
<i>Halodactylus mytili</i>	<i>Alcyonidioides mytili</i>
<i>Holothuriden</i>	Holothuroidea
<i>Homarus vulgaris</i>	<i>Homarus gammarus</i>
<i>Hyas araneus</i>	<i>Hyas araneus</i>
<i>Hyas coarctatus</i>	<i>Hyas coarctatus</i>
<i>Hydractinia echinata</i>	<i>Hydractinia echinata</i>
<i>Hydrallmania falcata</i>	<i>Hydrallmania falcata</i>
<i>Halodactylus mytili</i>	<i>Alcyonidioides mytili</i>
Hydrozoen	Hydrozoa
<i>Hippasterias phrygiana</i>	<i>Hippastria phrygiana</i>
<i>Inachus dorsettensis</i>	<i>Inachus dorsettensis</i>
<i>Inachus dorsettensis</i> ?	<i>Inachus dorsettensis</i> ?
<i>Inachus leptochirus</i>	<i>Inachus leptochirus</i>
<i>Idmonaea serpens</i>	<i>Tubulipora liliacea</i>
Kokerwormen/kalkkokerwormen	Serpulidae
<i>Lafoea (Filellum) serpens</i>	<i>Filellum serpens</i>
<i>Lafoea dumosa</i>	<i>Lafoea dumosa</i>
<i>Lamellibranchiate schelpen</i>	Bivalvia shells
<i>Littorina littorea</i>	<i>Littorina littorea</i>
<i>Loligo forbesii</i>	<i>Loligo forbesii</i>
<i>Loligo media</i>	<i>Alloteuthis subulata</i>
<i>Loligo</i> sp.	<i>Loligo</i> sp.
<i>Lolligo</i> sp. egg cases	<i>Lolligo</i> sp. egg capsules
<i>Lichenopora verrucaria</i>	Lichonoporidae
<i>Lithodes maia</i>	<i>Lithodes maja</i>
<i>Luidia sarsi</i>	<i>Luidia sarsii</i>
<i>Mactra solida</i>	<i>Spisula solida</i>
<i>Mactra stultorum</i>	<i>Mactra stultorum</i>
<i>Mactra subtruncata</i>	<i>Spisula subtruncata</i>
<i>Membranipora membranacea</i>	Bryozoa
<i>Membranipora pilosa</i>	<i>Electra pilosa</i>
<i>Membranipora</i> sp.	Bryozoa
<i>Modiola modiolus</i>	<i>Modiolus modiolus</i>
<i>Modiolaria nigra</i>	<i>Musculus niger</i>
<i>Mya arenaria</i>	<i>Mya arenaria</i>
<i>Mya truncata</i>	<i>Mya truncata</i>
<i>Mytilus edulis</i>	<i>Mytilus edulis</i>
<i>Natica</i>	<i>Natica</i> sp.
<i>Natica alderi</i> shell	<i>Euspira nitida</i> shell
<i>Natica catena</i>	<i>Euspira catena</i>
<i>Natica islandica</i>	cf. <i>Euspira</i> sp.
<i>Natica sordida</i>	<i>Euspira fusca</i>
Nemertea	Nemertea
<i>Nephrops norvegicus</i>	<i>Nephrops norvegicus</i>
<i>Neptunea antiqua</i>	<i>Neptunea antiqua</i>
<i>Nereis pelagica</i>	<i>Nereis pelagica</i>

Wodan species

<i>Nereis</i> sp.	<i>Nereis</i> sp.
<i>Nimphon grossipes</i>	<i>Nimphon grossipes</i>
<i>Nimphon mixtum?</i>	cf. <i>Nimphon grossipes</i>
<i>Nucula nucleus</i>	<i>Nucula nucleus</i>
<i>Nudibranchia</i>	<i>Nudibranchia</i>
<i>Obelia geniculata</i>	<i>Obelia geniculata</i>
<i>Obelia</i> sp.	<i>Obelia</i> sp./ <i>Laomedea</i> sp.
<i>Octopus vulgaris</i>	<i>Octopus vulgaris</i>
<i>Ophelia limnacia</i>	<i>Ophelia limacina</i>
<i>Ophioglypha albida</i>	<i>Ophiura albida</i>
<i>Ophioglypha albida?</i>	<i>Ophiura albida?</i>
<i>Ophioglypha lacertosa</i>	cf. <i>Ophiura ophiura</i>
<i>Ophioglypha texturata</i>	<i>Ophiura ophiura</i>
<i>Ophioglypha</i> sp.	<i>Ophiura</i> sp.
<i>Ophiopholis aculeata</i>	<i>Ophiopholis aculeata</i>
<i>Ophiopholis</i>	<i>Ophiopholis</i> sp.
<i>Ophiothrix fragilis</i>	<i>Ophiothrix fragilis</i>
<i>Ophiuriden</i>	<i>Ophiuroidea</i>
<i>Ostrea edulis</i>	<i>Ostrea edulis</i>
<i>Pagurus cuanensis</i>	<i>Pagurus cuanensis</i>
<i>Pagurus laevis</i>	<i>Anapagurus laevis</i>
<i>Pagurus</i> sp.	<i>Pagurus</i> sp.
<i>Pandalus annulicornis</i>	<i>Pandalus montagui</i>
<i>Pandalus montagui</i>	<i>Pandalus montagui</i>
<i>Paratylus swammerdamii</i>	<i>Nototropis swammerdamei</i>
<i>Parechinus miliaris</i>	<i>Psammechinus miliaris</i>
<i>Patella vulgata</i>	<i>Patella vulgata</i>
<i>Pecten opercularis</i>	<i>Aequipecten opercularis</i>
<i>Pecten varius</i>	<i>Mimachlamys varia</i>
<i>Pecten</i> sp.	<i>Pecten</i> sp.
<i>Pectinaria belgica</i>	<i>Pectinaria belgica</i>
<i>Perigonimus (repens?)</i>	<i>Leuckartiara octona?</i>
<i>Phalusia</i> sp.	cf. <i>Asciadiela</i> sp.
<i>Pilumnus hirtellus</i>	<i>Pilumnus hirtellus</i>
<i>Pinnotheres pisum</i>	<i>Pinnotheres pisum</i>
<i>Pleurotoma turricula</i>	<i>Propebela turricula</i>
<i>Pholas crispata</i>	<i>Zirfaea crispata</i>
<i>Pholas</i>	<i>Pholadidae</i>
<i>Polyclinum ficus</i>	cf. <i>Polyclinum aurantium</i>
<i>Polynoe squamata</i>	<i>Lepidonotus clava</i> or <i>L. squamatus</i>
<i>Polynoe</i> sp.	<i>Polynoe</i>
<i>Porcellana longicornis</i>	<i>Pisidia longicornis</i>
<i>Porifera</i>	<i>Porifera</i>
<i>Portunus holsatus</i>	<i>Liocarcinus holsatus</i>
<i>Portunus pusillus</i>	<i>Liocarcinus pusillus</i>
<i>Portunus marmoreus</i>	<i>Liocarcinus marmoreus</i>
<i>Portunus</i> sp.	<i>Polybiidae</i>
<i>Psammobia feroensis</i>	<i>Gari fervensis</i>
<i>Pycnogonum littorale</i>	<i>Pycnogonum littorale</i>
<i>Rhizostoma octopus</i>	<i>Rhizostoma octopus</i>
<i>Srupocellaria reptans</i>	<i>Cradoscrupocellaria ellisii</i> or <i>C. reptans</i>
<i>Scrupocellaria scruposa</i>	<i>Scrupocellaria scruposa</i>

Wodan species

<i>Scalaria trevelyana</i>	<i>Epitonium trevelyanum</i>
<i>Sepia officinalis</i>	<i>Sepia officinalis</i>
<i>Sepiola atlantica</i>	<i>Sepiola atlantica</i>
<i>Serpula</i>	Serpulidae
<i>Sertularella polyzonias</i>	<i>Sertularella polyzonias</i>
<i>Sertularia abietina</i>	<i>Abietinaria abietina</i>
<i>Sertularia argentea</i>	<i>Sertularia argentea</i>
<i>Sertularia cupressina</i>	<i>Sertularia cupressina</i>
<i>Sertularia filicula</i>	<i>Abietinaria filicula</i>
<i>Sertularia operculata</i>	<i>Amphisbetia operculata</i>
<i>Sertularia polyzonias</i>	<i>Sertularella polyzonias</i>
<i>Sertularia</i> sp.	<i>Sertularia</i> sp.
<i>Solaster papposus</i>	<i>Crossaster papposus</i>
<i>Solen ensis</i>	<i>Ensis ensis</i>
<i>Solen siliqua</i>	<i>Ensis siliqua</i>
<i>Solen vagina</i> shell	<i>Solen marginatus</i> shell
<i>Spatangus purpureus</i>	<i>Spatangus purpureus</i>
<i>Spatangus</i> shell	<i>Spatangus purpureus</i> shell
<i>Stenorrhynchus phalangium</i>	<i>Inachus phalangium</i>
<i>Stenorrhynchus rostratus</i>	<i>Macropodia rostrata</i>
<i>Stenorrhynchus</i> sp.	<i>Macropodia</i> sp. or <i>Inachus</i> sp.
<i>Strongylocentrotus drobachiensis</i>	<i>Strongylocentrotus droebachiensis</i>
<i>Tealia crassicornis</i>	<i>Urticina</i> sp.
<i>Tellina crassa</i>	<i>Arcopagia crassa</i>
<i>Tellina fabula</i>	<i>Fabulina fabula</i>
<i>Tellina tenuis</i>	<i>Macomangulus tenuis</i>
<i>Thia polita</i>	<i>Thia scutellata</i>
<i>Thracia papyracea</i>	<i>Thracia phaseolina</i>
<i>Thuiaria articulata</i>	<i>Thuiaria articulata</i>
<i>Thuiara thuia</i>	<i>Thuiaria thuja</i>
<i>Tritonia hombergii</i>	<i>Tritonia hombergii</i>
<i>Tritonia plebeia</i>	<i>Duvaucelia plebeia</i>
<i>Trochus tumidus</i>	<i>Gibbula tumida</i>
<i>Trochus occidentalis</i>	<i>Calliostoma occidentale</i>
<i>Trochus</i> sp.	<i>Gibbula</i> sp.
<i>Trochus</i> sp. shell	<i>Gibbula</i> sp. shell
<i>Tubularia indivisa</i>	<i>Tubularia indivisa</i>
<i>Tubularia</i> sp.	Tubulariidae
<i>Tunicaten</i>	Tunicata
<i>Turritella terebra</i>	<i>Turritella terebra</i>
<i>Velutina laevigata</i>	<i>Velutina velutina</i>
<i>Venus gallina</i>	<i>Chamelea gallina</i>
<i>Verruca stromii</i>	<i>Verruca stroemia</i>
<i>Vesicularia spinosa</i>	<i>Vesicularia spinosa</i>
<i>Zirphaea crispata</i>	<i>Zirphaea crispata</i>
<i>Zeeanemonen</i>	Actiniaria
<i>Zeerozen</i>	Actiniaria
<i>Ascophyllum</i>	<i>Ascophyllum nodosum</i>
<i>Chorda filum</i>	<i>Chorda filum</i>
<i>Fucus</i>	<i>Fucus</i> sp.
<i>Zostera</i>	<i>Zostera</i> sp.