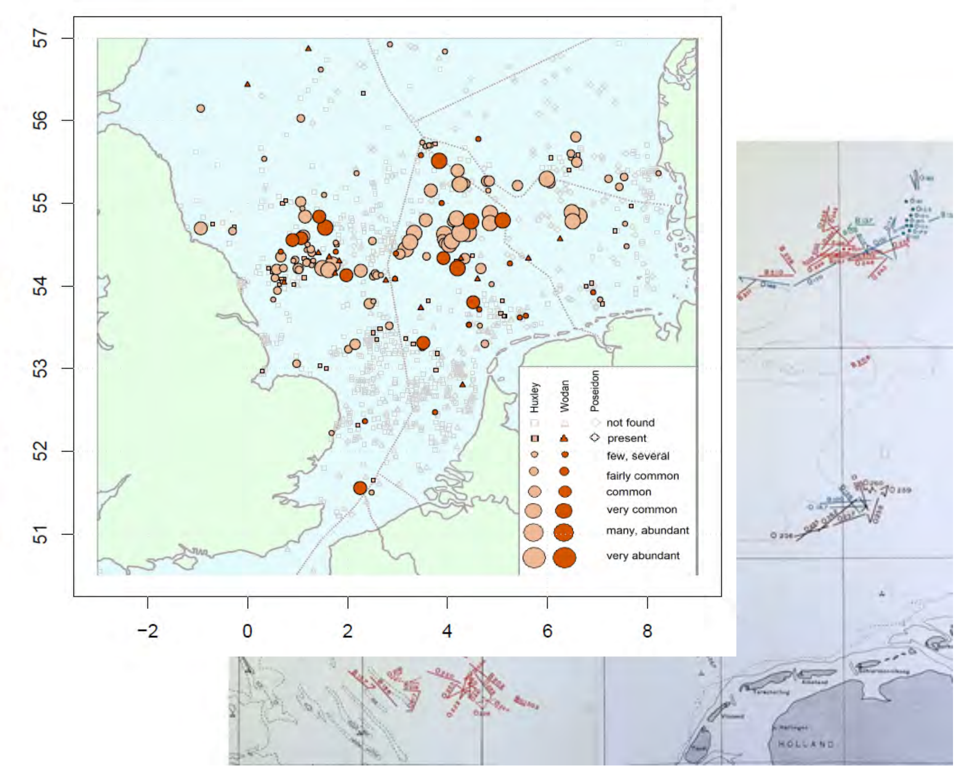
North Sea benthos 1902-1912 –
Distribution based on Huxley, Wodan and Poseidon surveys data

Second edition



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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.

Changes in the second edition

The second version was issued after detection of several faults in the digitalisation of the Huxley dataset. Statistics were adapted as well. In this version cluster analysis and β diversity analysis were restricted to species that were present in more than 5% of the hauls. This led to reduction of zeros in the dataset, which is beneficial to the analyses and led to a redescription of the distribution of clusters over the North Sea (§ 3.6.2).

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Contents

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.

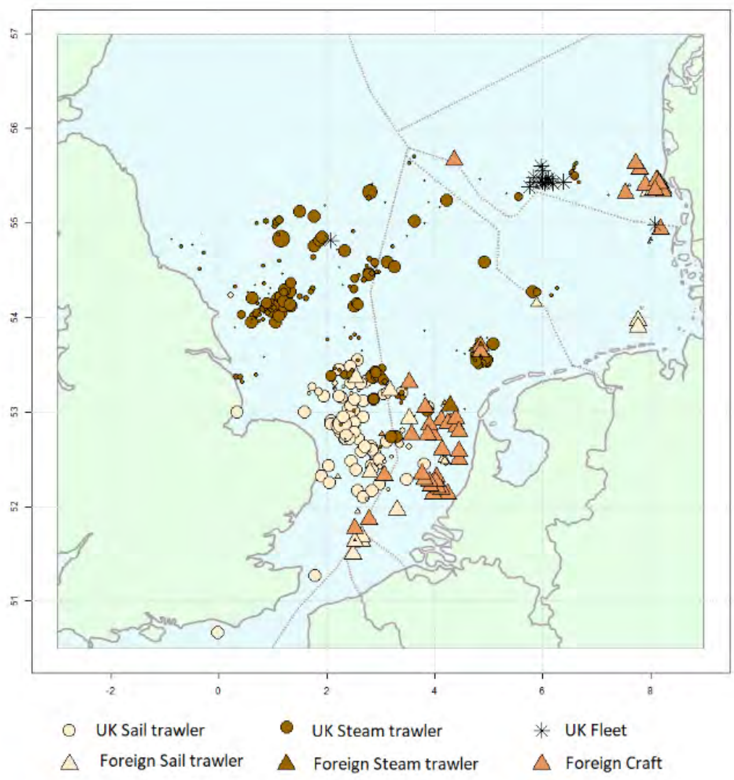


Figure 1. Fishing vessels observed by naturalists of the Huxley surveys 1902-1909. Fleets consisted of tens of sailing vessels. The definition of craft is unsure.

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 Vooys *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 m^2/h for the otter trawl, and 50.000 m^2/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).

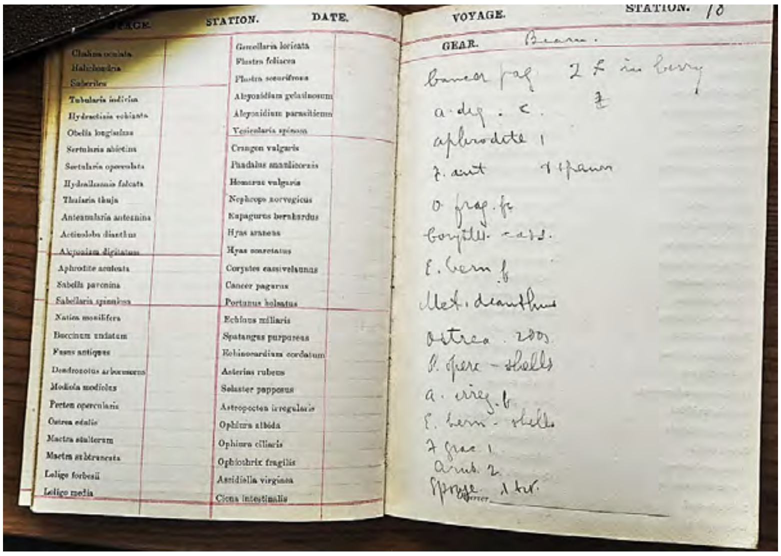


Figure 2. Invertebrates logbook page of the Huxley survey at station 111-18.

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. Scruff is a generalist term, it could comprise hydroids, bryozoans, ascidians, echinoderms and more. On some locations Huxley logbooks contain notes hoe many baskets full of scruff were hauled.
- *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 m^2/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 the value with the maximum coarseness 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

In calculations these sediment categories were given coarseness values from 1 to 6 (*max_bottom*).

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	-	*present*	several, few	fairly common	common	very common	abundant, much, many	very abundant, large quantities
Abbreviation		p	s	fc	c	vc	a	va
Wodan surveys	-	*aanwezig*	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 then in the Huxley data. 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 was less 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).

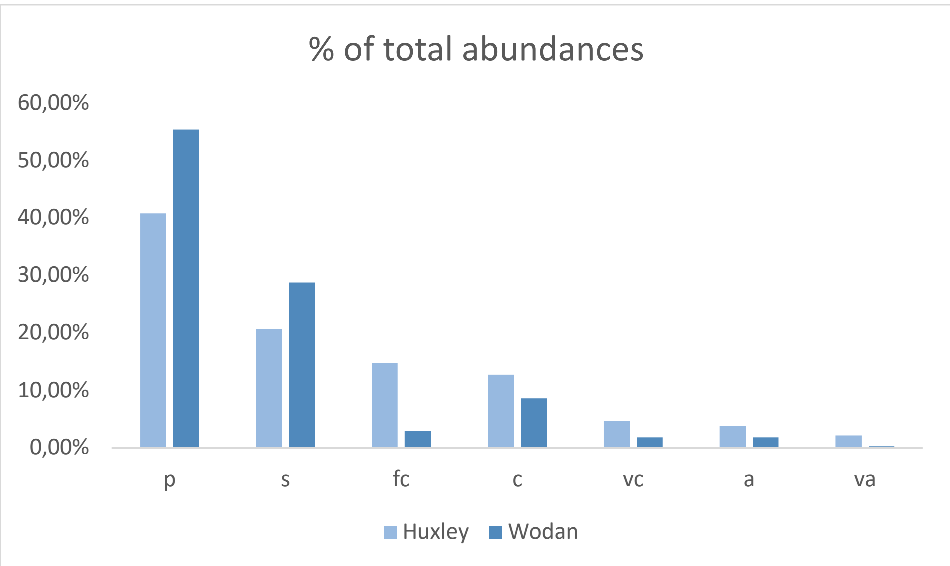


Figure 3. Frequencies of abundance categories (for abbreviations see text) in Huxley and Wodan data.

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 the introduction of this chapter (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 where benthos was collected per depth and sediment category

depth	n		Sediment*	abbreviation	n
<=20m	317		Stones	st	30
20-30 m	220		Gravel	gr	12
30-40 m	141		Coarse sand	cs	18
40-50 m	172		Sand	s	303
> 50 m	71		Fine sand (fs)	fs	271
			Mud and Muddy sand	m	67

* Shots were made when the net was and hauled. The coarsest sediment type of both was used in the statistics (max_bottom).

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.

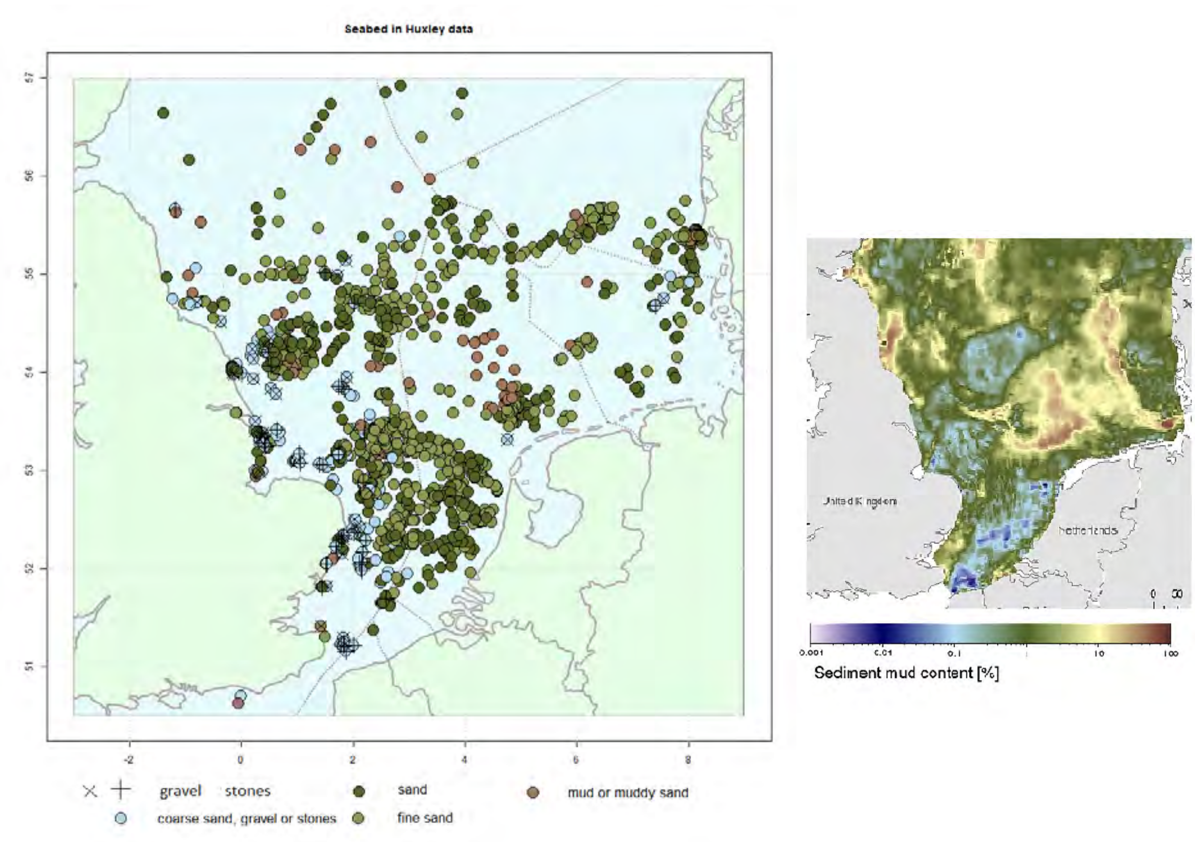


Figure 4. Left: average sediment grain size of samples taken during the Huxley surveys 1902-1909. The colours loosely matched to those in the mud content map (right) by of Bockelmann *et al*. (2018).

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.

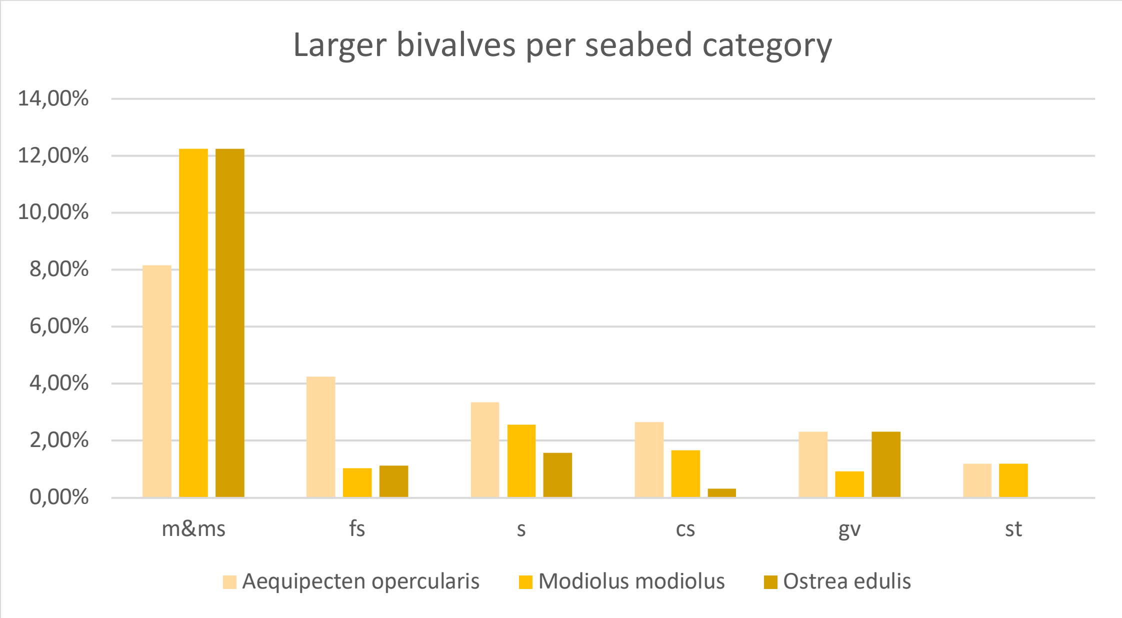


Figure 5. Huxley data. Presence of large bivalves per sea bed type. Each sediment grain size category, shows the percentage of hauls with species presence. For sea-bed categories see § 2.4.2.

The normalized Huxley data show that the large bivalve species occurred on sea bed of different compositions (Figure 5). Most species prefer muddy grounds. *Aequipecten opercularis* seems to be the most indifferent species.

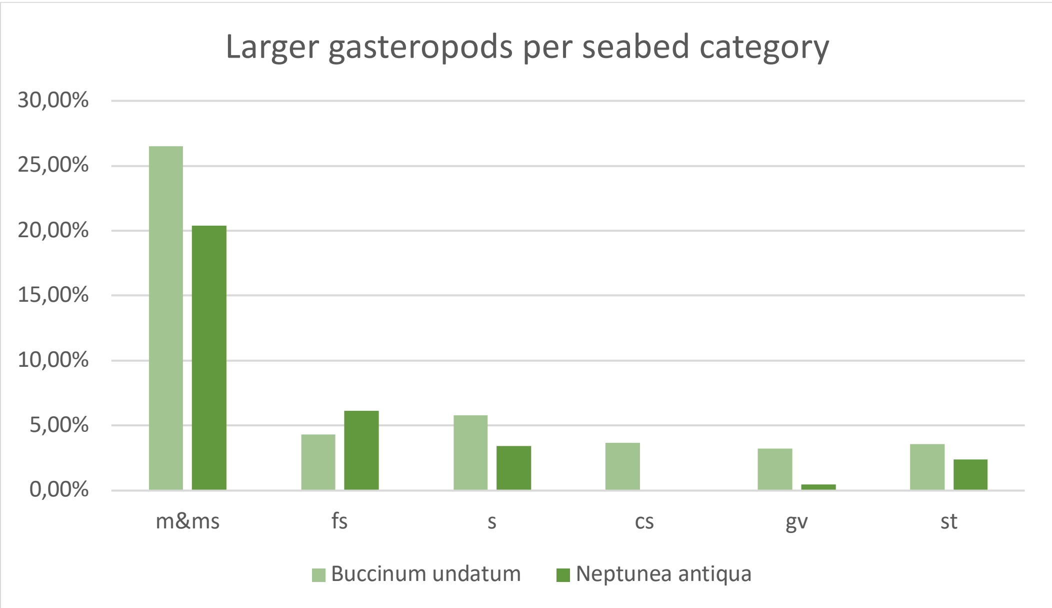


Figure 6. Huxley data on large gastropod presence per sea-bed type. Each sediment grain size category shows the percentage of hauls with species presence. For sea-bed categories see § 2.4.2.

In gastropods, red whelk *Neptunea antiqua* and *Buccinum undatum* prefer muddy grounds but occurred on a wide range of sediments (Figure 6)..

As a whole, larger molluscs were found in highest numbers in the northern part of the area (Figure 7 and 8). Most larger bivalves, except for *Ostrea edulis* were found north of a line from Flamborough Head 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 party due to the lack of samples north 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 high abundance of large molluscs continued more to the north, where the depth increases, cannot be judged from the 19[h] century data. However, Figure 7 and 8 show that they were present in a large part of the northern survey locations, mostly in lower densities. Noticeable is that the Flamborough Head - Esjberg line is highly recognisable in the occurrences of brittle stars *Ophiothrix fragilis* (Chapter 6).

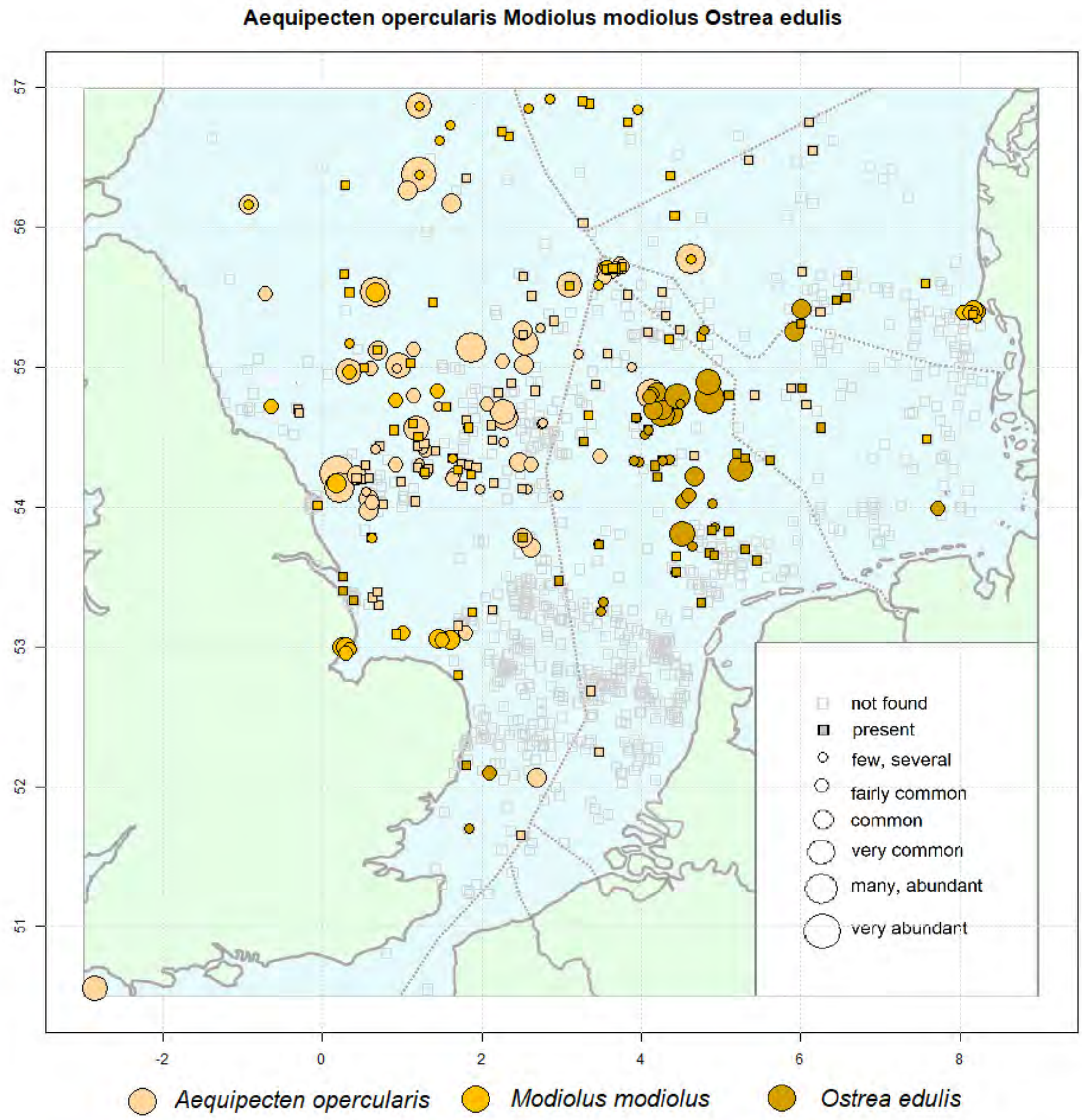


Figure 7. Distribution of four large bivalves in Huxley, Wodan and Poseidon survey data. Filled squares: only presence information provided.

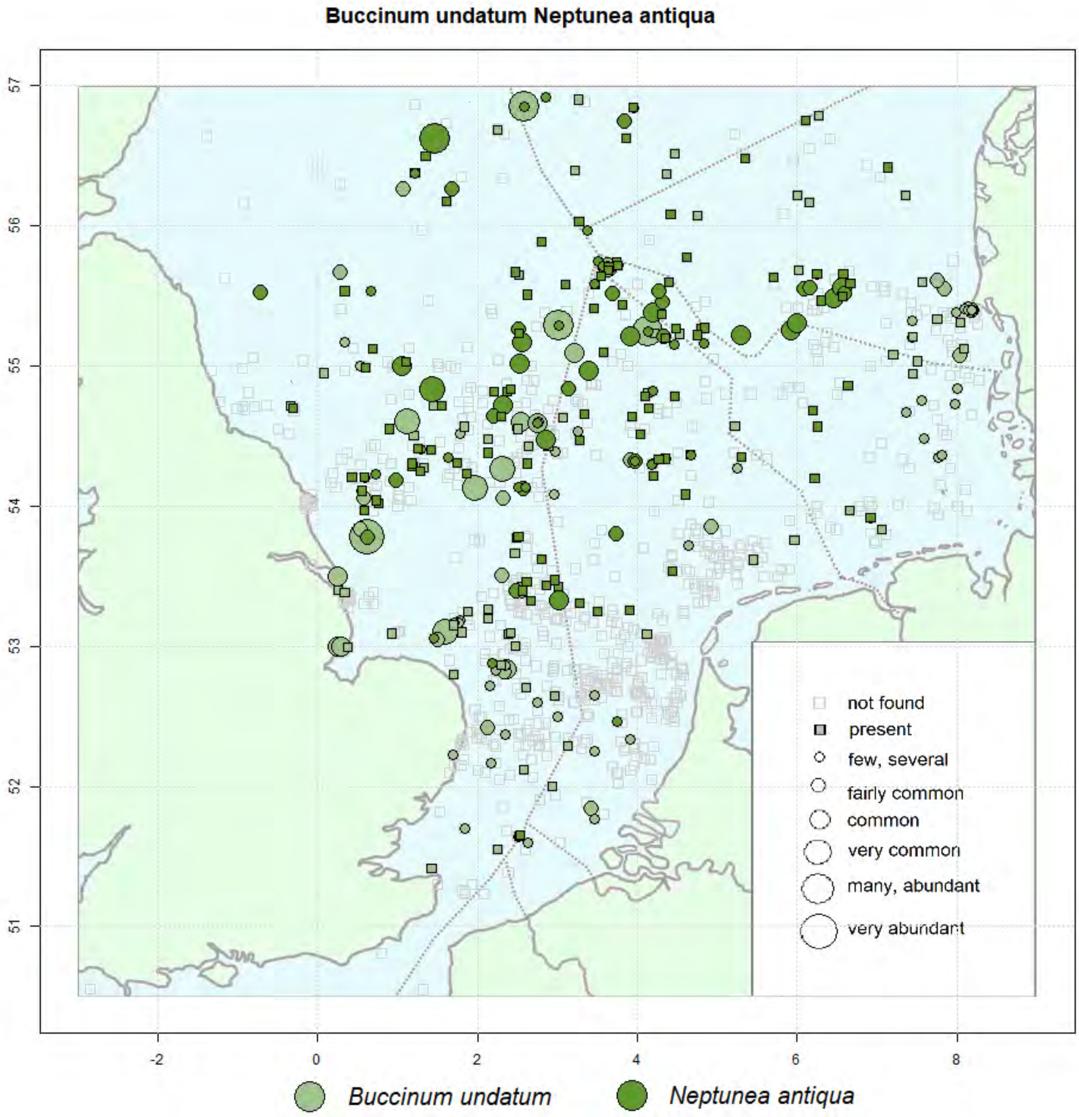


Figure 8. Distribution of three gastropods in Huxley, Wodan and Poseidon survey data. Maps on individual *Colus* species can be found in the maps section. Filled squares indicate that only presence information was provided.

3.2.2 Molluscs as primary bio-substrate

As many epizoic species settle directly on molluscs, they form a *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	*Buccinum undatum*	*Neptunea antiqua + Colus sp.*	Smaller gastropods	*Aequipecten opercularis*	*Arctica islandica*	*Modiolus modiolus*	*Ostrea edulis*	Smaller bivalves	‘ Shells’
Alcyonium digitatum on				1			4	1	
Actiniaria 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 Ascidians 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
Actiniaria 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 *surfroles* 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).

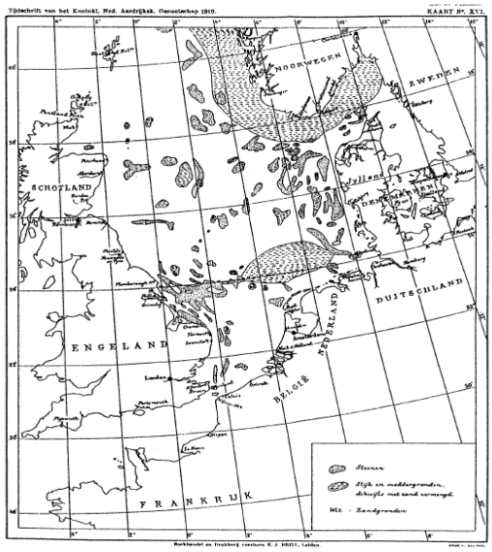


Figure 9. Stony and muddy areas in the North Sea (Tesch, 1910).

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.

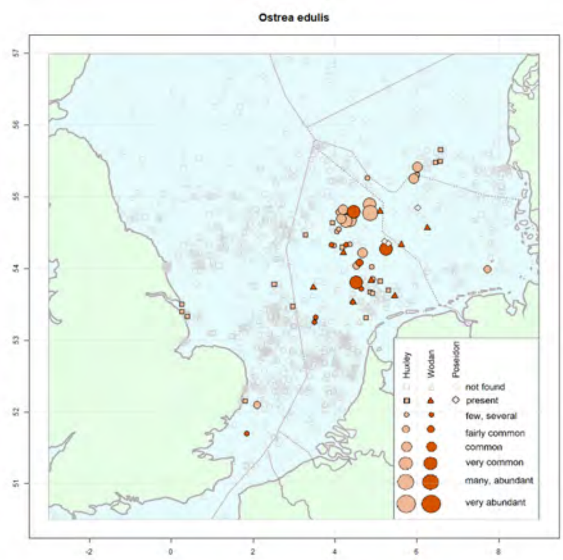


Figure 10. Flat oyster *Ostrea edulis* found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.

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

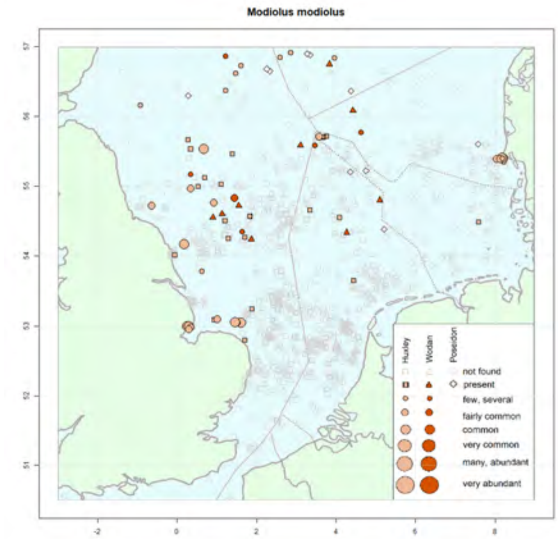


Figure 11. Horse mussel *Modiolus modiolus* found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.

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.

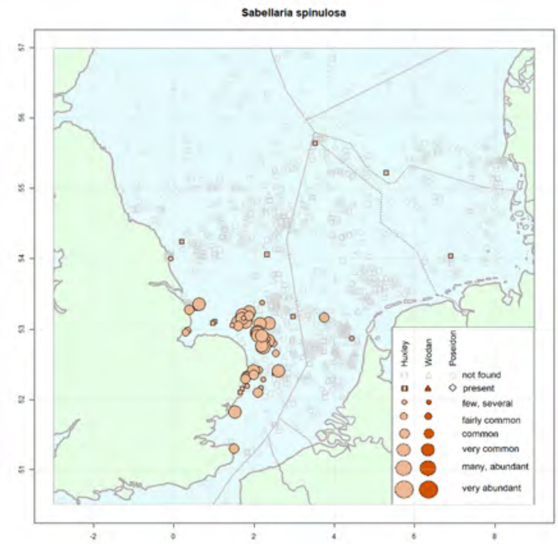


Figure 12. Ross worm *Sabellaria spinulosa* found by Huxley surveys. Chapter 6 provides a larger version of this map.

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.

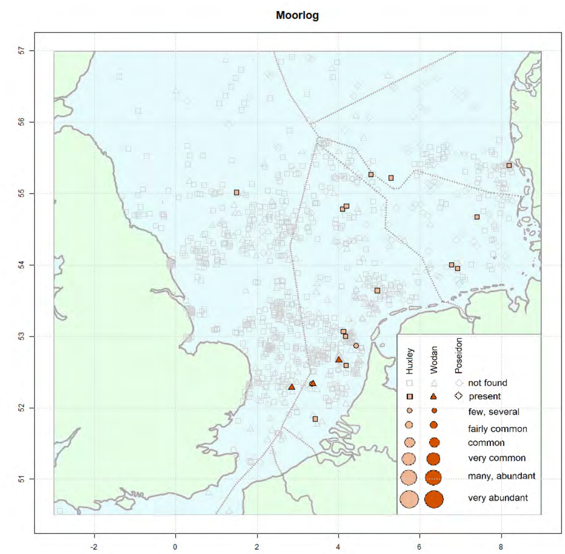
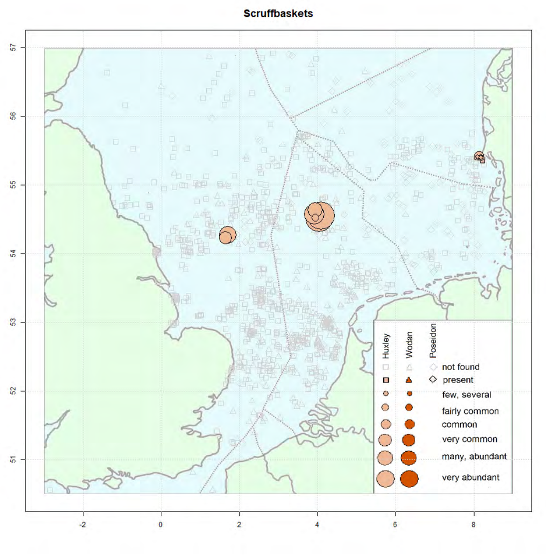


Figure 13. Moorlog found by Huxley and Wodan surveys. Chapter 6 provides a larger version of this map.

Places with much ‘scruff’ can be considered as rough grounds. At some locations Huxley logbooks mentioned the quantity of scruff in ‘baskets full’. Largest quantities where found in the *Ostrea edulis* area.

Figure 14. Scruff found by the Huxley 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 clustering resulted in clusters in more or less well defined regions in the area. (Figure 15).

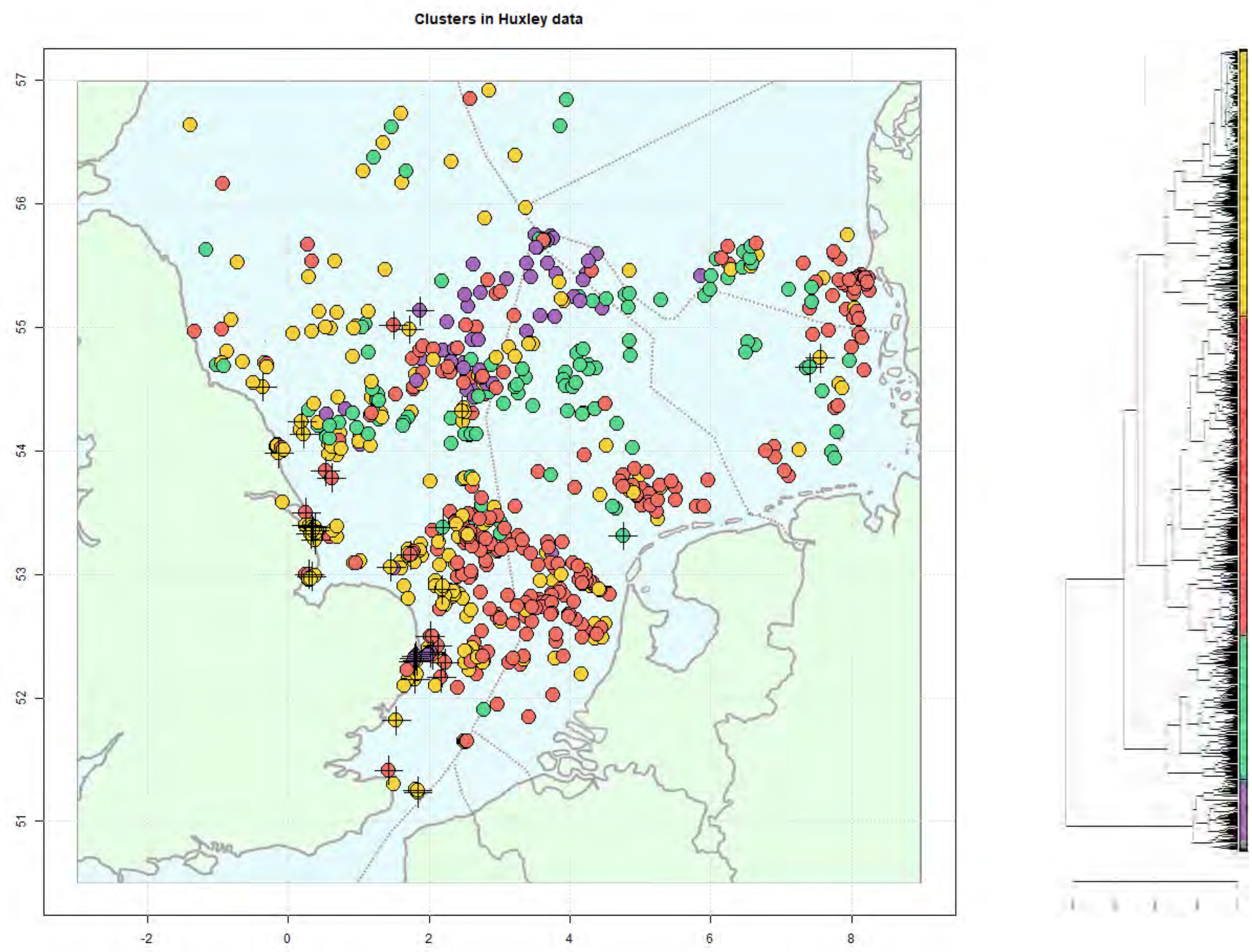


Figure 15. Distribution of epifauna according to cluster analyses based on Ward distances. Crosses are places were gravel or stones were found.

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 'yellow' cluster is characterised hornwrack *Flustra foliacea,* by reefs built by the Ross worm *Sabellaria spinulosa* and the hydroid species *Obelia longissima* and *Abietinaria abietina*. The last three species were mostly found off the English coast where the hydroids *Hydrallmania falcata* , *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 15).

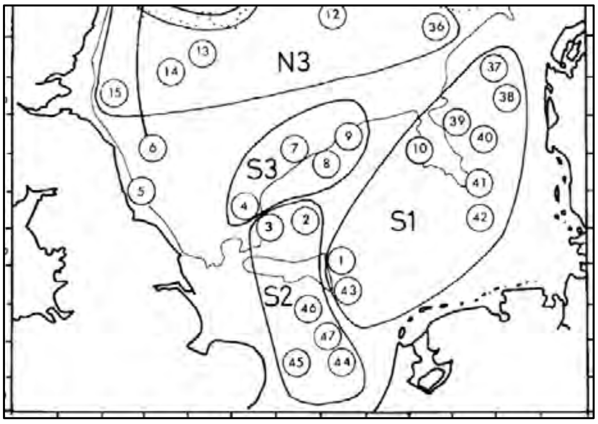
The ‘brown’ cluster is characterised by the echinoderms *Asterias rubens*, *Astropecten irregularis*, *Echinocarium cordatum* and *Spatangus purpureus* as well as and common whelk *Buccinum undatum*. These are widespread species that reached their highest abundances in the sandy areas in the Southern 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 green cluster is characterised by the cnidarians *Alcyonium digitatum* and *Metridium senile,* sponges Porifera, flat oysters *Ostrea edulis,* brittle stars *Ophiothrix fragilis* and red whelk *Neptunea antiqua.* Common whelk *Buccinum undatum* was also common in this area. 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, e specially *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).

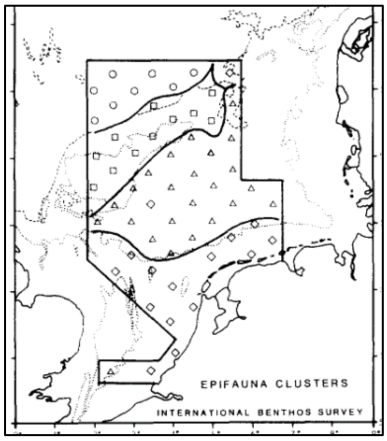
The ‘purple’ cluster is mainly concentrated on the sandy part of the Dogger Bank. The cluster is characterised by the bryozan *Alcyonidium diaphanum* (and perhaps some *A. condylocinereum*)*,* the hydroid *Obelia longissima* and narrow-leaved hornwrack *Securiflusta securifrons*. The first two species were found rafting on the seabed.

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^{o} NB, the delineation of the clusters varied (Figure 16). The six clusters found by Rees *et al.* (1999) in the North Sea are not depicted, their analyse also comprised data from southern and western England.

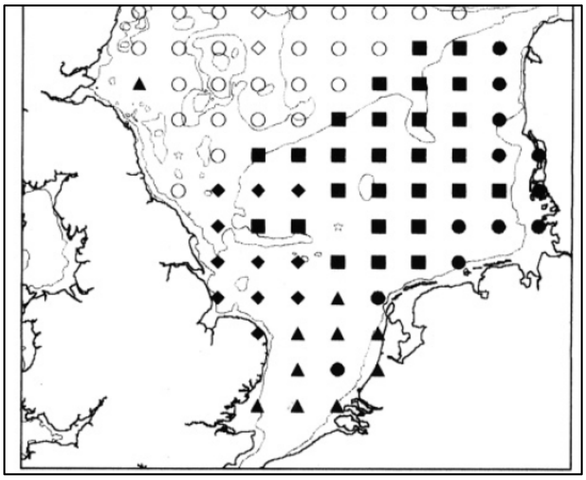
The most apparent differences in the early 20th century clusters are the former division of the Southern Bight in two clusters and the clearer distinction of the sandy part of the Dogger Bank. These differences will be addressed in the discussion. A north-west cluster in deeper water is missed in the 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.



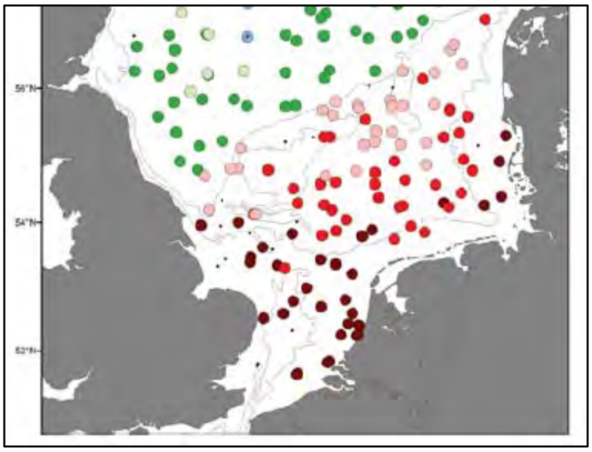
a. Dryer *et al*. (1983), based 1977-1981 otter trawls (Granton type).



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 16. Recent epibenthic clusters analysed from trawl data in four papers.

3.6.3 Relations between physical factors

Research of the factors that explain the distribution of communities in this area is complicated by the mutual relations between the physical factors. Important physical factors that may influence the distribution of marine benthos are depth, bottom temperatures, sediment composition, seabed stress and bottom movement. A mixture between Huxley and more modern ICES data on bottom temperatures show some of these mutual relations.

(Table 5).

Table 5. Correlations between physical factors in the area. Depth and max_bottom correlation were calculated from Huxley data. Correlations between depth and temperatures were calculated per ICES area, using average depths from Huxley data and 1997-2002 data from ICES, 2008.

Physical factor	depth	summer bottom temperature
max_bottom	$p=0.023$ $R^2=0.00625$	
summer bottom temperature	$p<2.2E-16$ $R^2=0.6724$	
winter bottom temperature	$p=0.0071$ $R^2=0.0961$	$p=0.0029$ $R^2=0.000008$

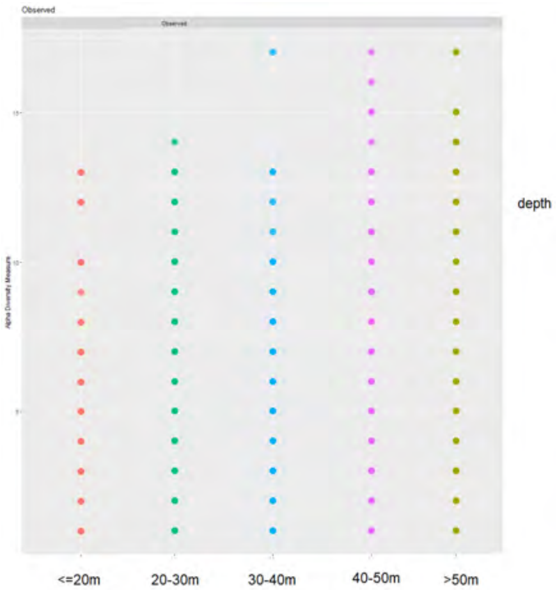
Fine sediments may be expected to accumulate in deep 'low energy areas'. The Huxley data on hauls indeed gave this relation for sediment coarseness (max_bottom, see 2.4.2), Pearson correlation $p< 0.005$. However, depth accounts for a negligible proportion of the variation in average sediment grain size ($R^2 = 0.00625$).

Temperatures are associated with latitude and depth. The relation between depth and summer bottom temperature is strong, helped by the fact that the North Sea is deeper at higher latitudes. The average winter bottom temperatures only varied from 6 to 8 °C between 51° and 57° NB (ICES, 2008). However, depth also accounts for a negligible proportion of the variation in average winter bottom temperatures ($R^2 = 0.0961$).

Bed sheer stress and bottom movement, factors that also have influence on species composition, are also interrelated with depth and seabed composition.

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. Lower number of haul locations may be responsible for the lower values on gravel/stones and coarse sand (Figure 17b).



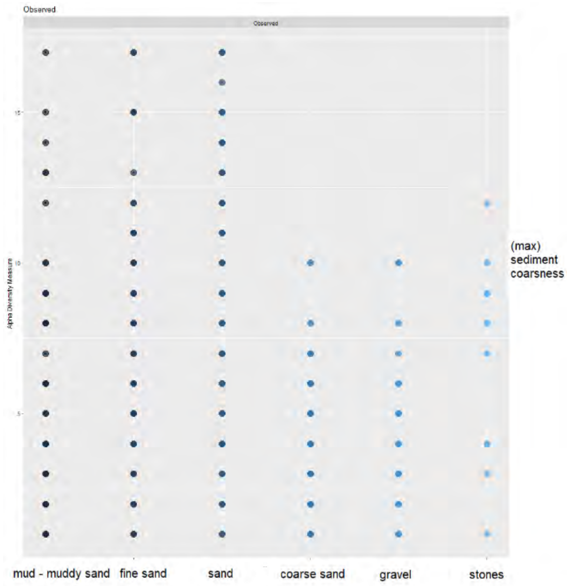


Figure 17. α diversity (species richness)
a. Species richness at several depths.

b Species richness on several sediments.

3.6.5 β diversity

Statistical packages in R were used to study the variation in community composition between Huxley samples, termed β diversity. The purpose was to analyse the physical factors that influence the community structure in the Huxley data. Communities could be differentiated on basis of all four studied factors (PERMANOVA results in Table1), while only the communities based on *depth* were found to lie on different locations (PERMDISP results in Table 1).

Table 6. Analysis of factors affecting community compositions based on Huxley presence absence data. Significant PERMANOVA values indicate that the communities that can be differentiated on basis of these factors differ in location or dispersion. Additional *unsignificant* PERMDISP values indicate the communities differ in location, while additional significant values indicate that they either differ in dispersion (i.e. the variability in the community composition) or in both location and dispersion.

p-values	PERMANOVA Jaccard	PERMDISP Jaccard	PERMANOVA Raup-Crick	PERMDISP Raup-Crick
depth	0.001	*0.173*	0.001	*0.3498*
max_bottom	0.001	0.0001	0.001	0.0001
wintemp4	0.001	0.0001	0.001	0.0001
sumtemp	0.001	0.0022	0.001	0.002

To analyse the influence of depth to more detail pairwise Permanova comparisons (pairwise adonis in R) using Jaccard and Raup-Crick distances were caried out between depth categories <=20m, 20-30m, 30-40m, 40-50m and >50m. In most comparisons statistical differences were found ($p<0.01$). The exception was the comparison between 20-30m and 30-40m. The depth-related differences in distribution are visualised in Figure 18.

The results of the PERMDISP statistics are confusing because biological speaking depth on its own does is not considered to be an important factor influencing marine communities.

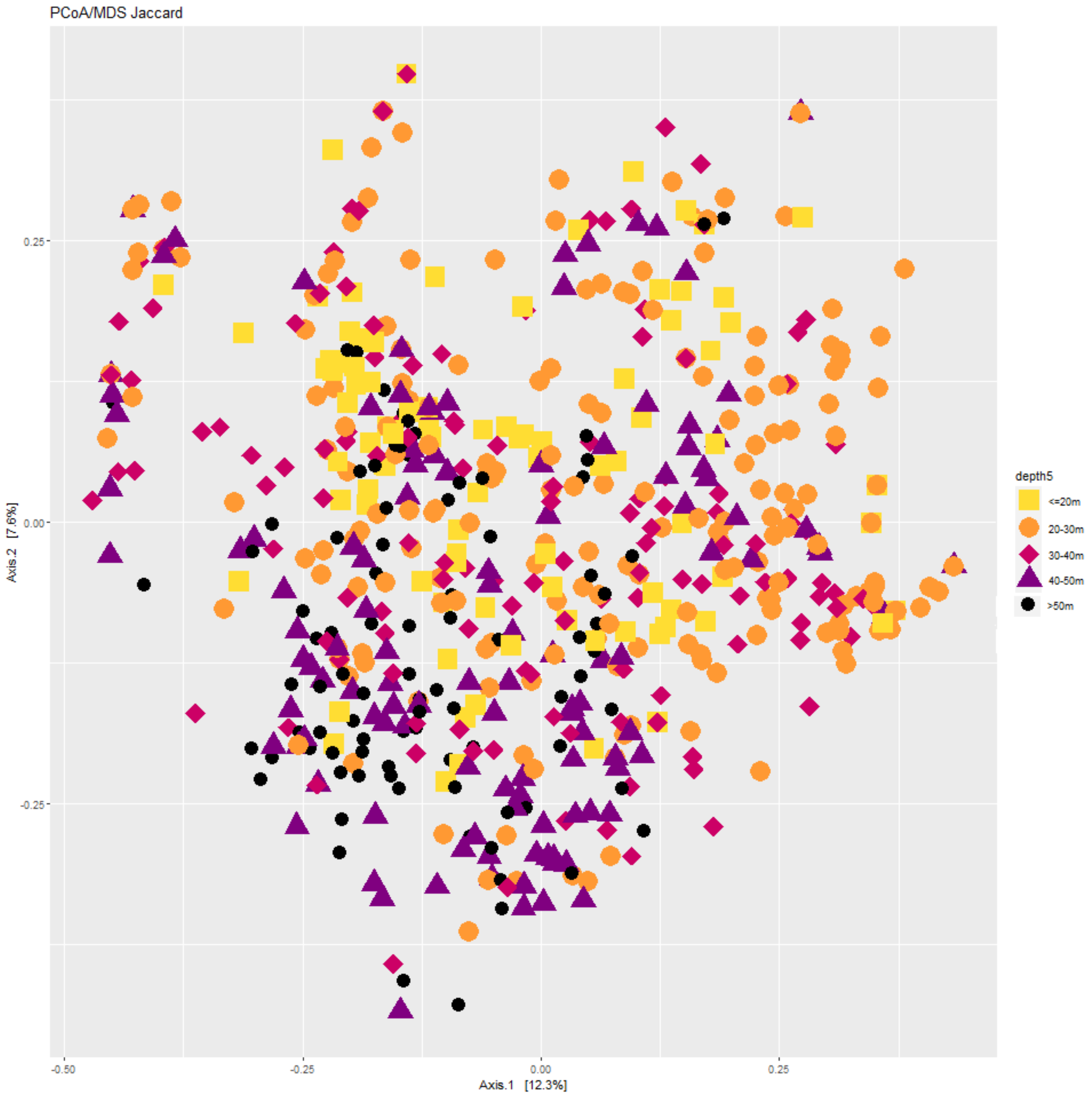


Figure 18. PCoA/MDS based on Jaccard distances of Huxley species data plotted with special shapes and colours for locations at different depths. Statistical R package Phylosec.

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-quantative 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 trajects 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

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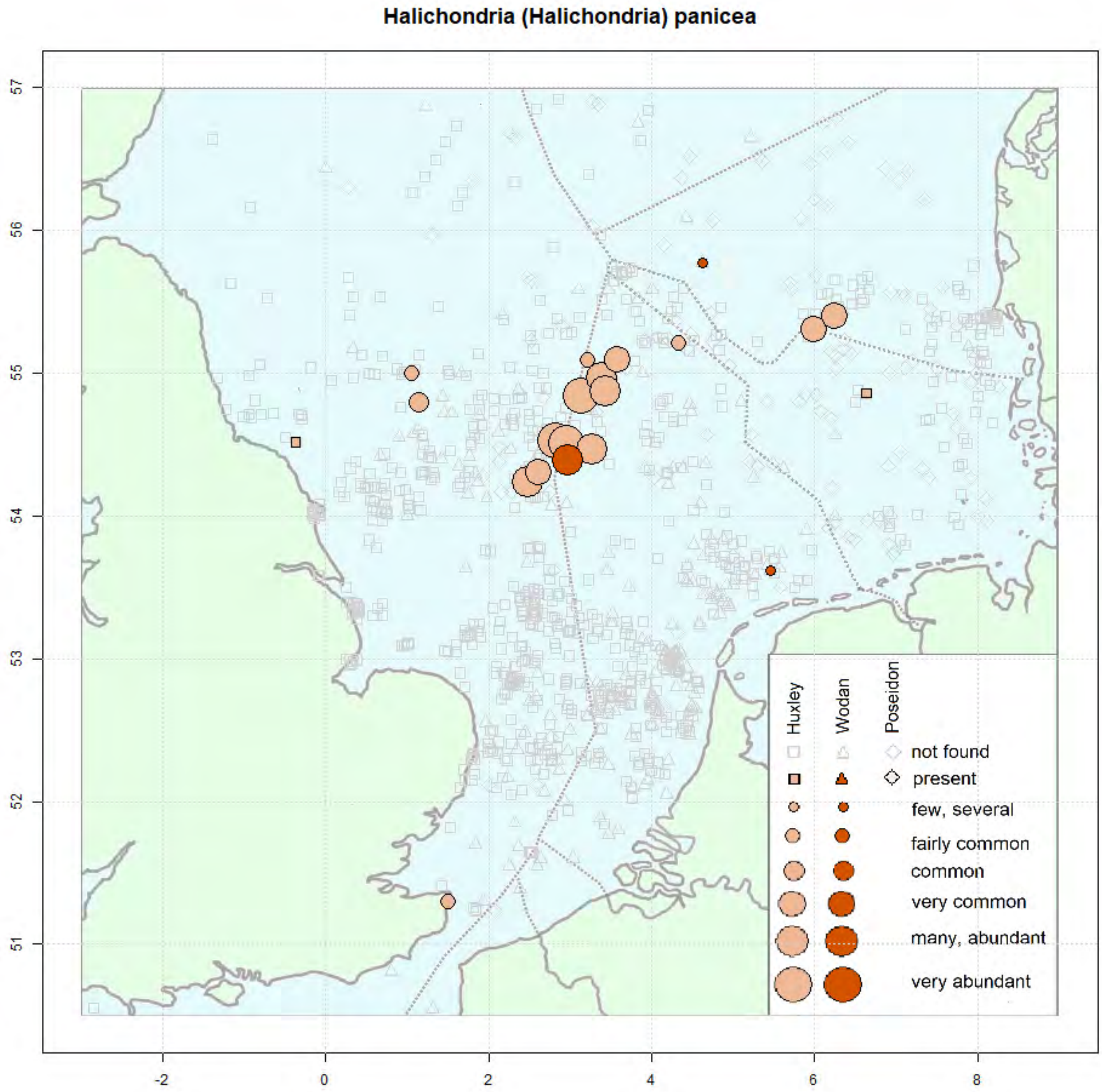
6 Species distribution maps

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

Haul locations were 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.

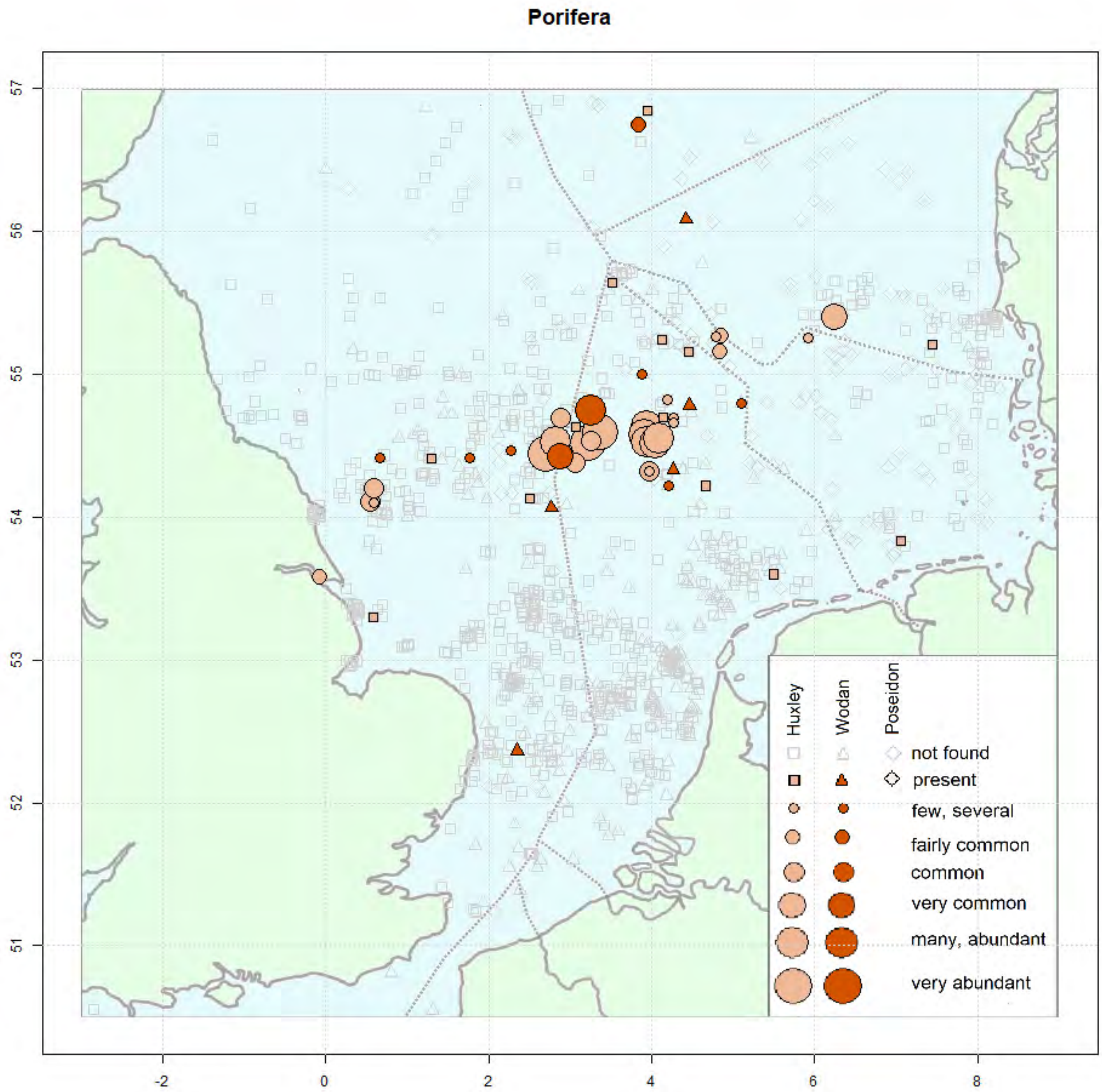
Porifera-Demospongiae



Halichondria (Halichondria) panicea Breadcrumb sponge

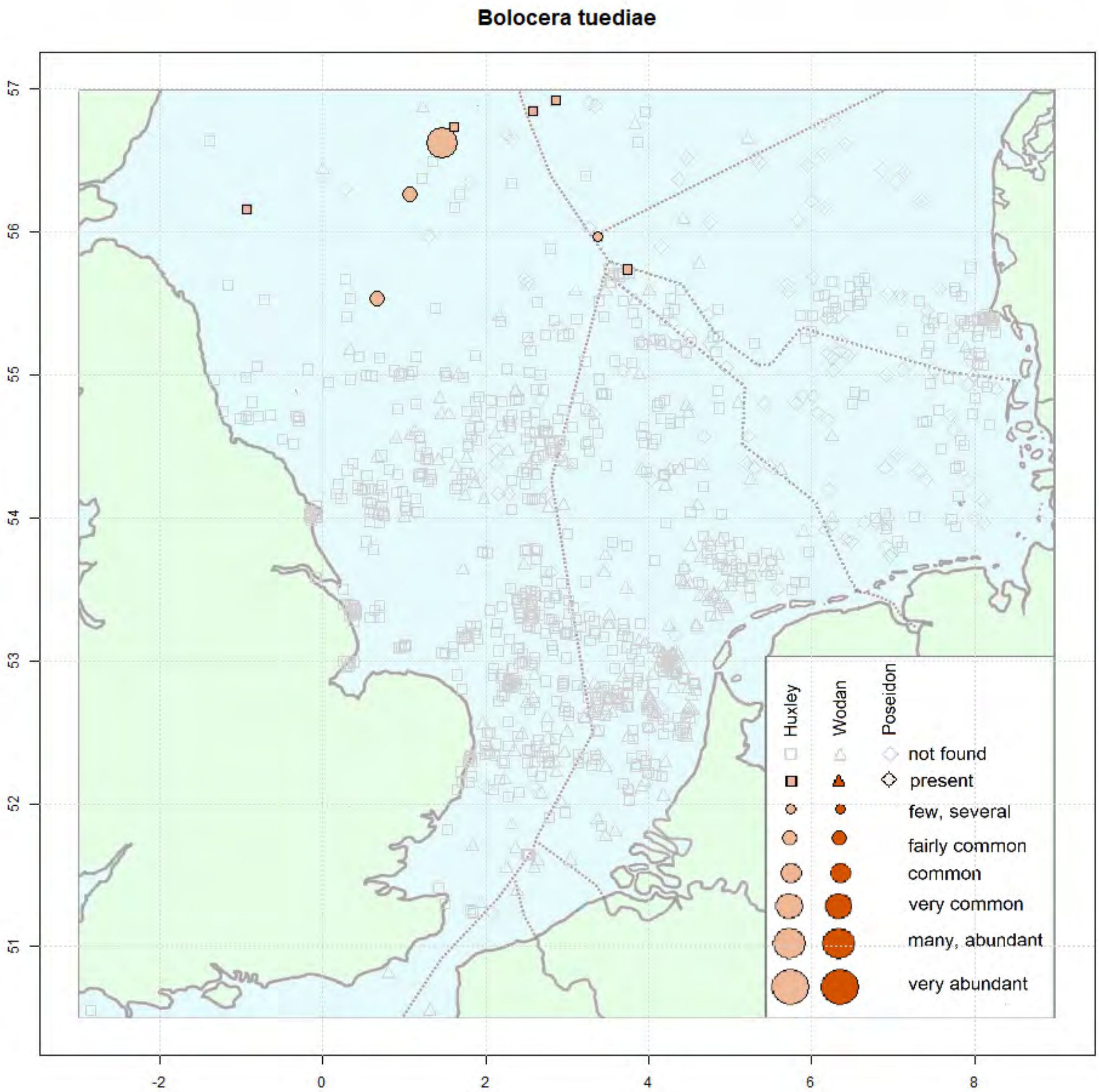
Breadcrumb sponge *Halichondria* (*Halichondria*) *panicea* at the South West rim of Dogger Bank could be floating like this individual at 54.077 N and 4.271 E.

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

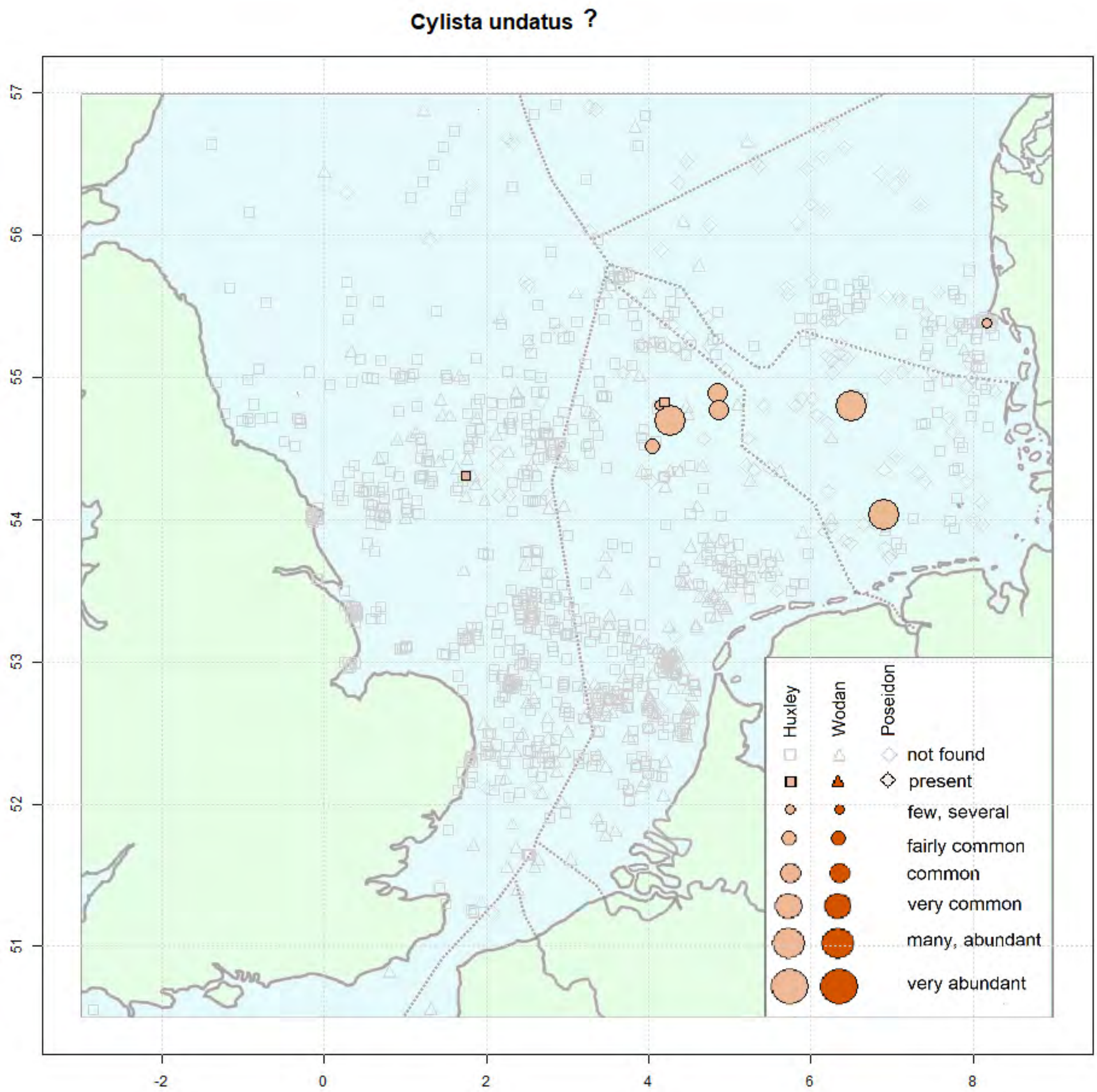


Unspecified Porifera   Sponges

Cnidaria-Anthozoa

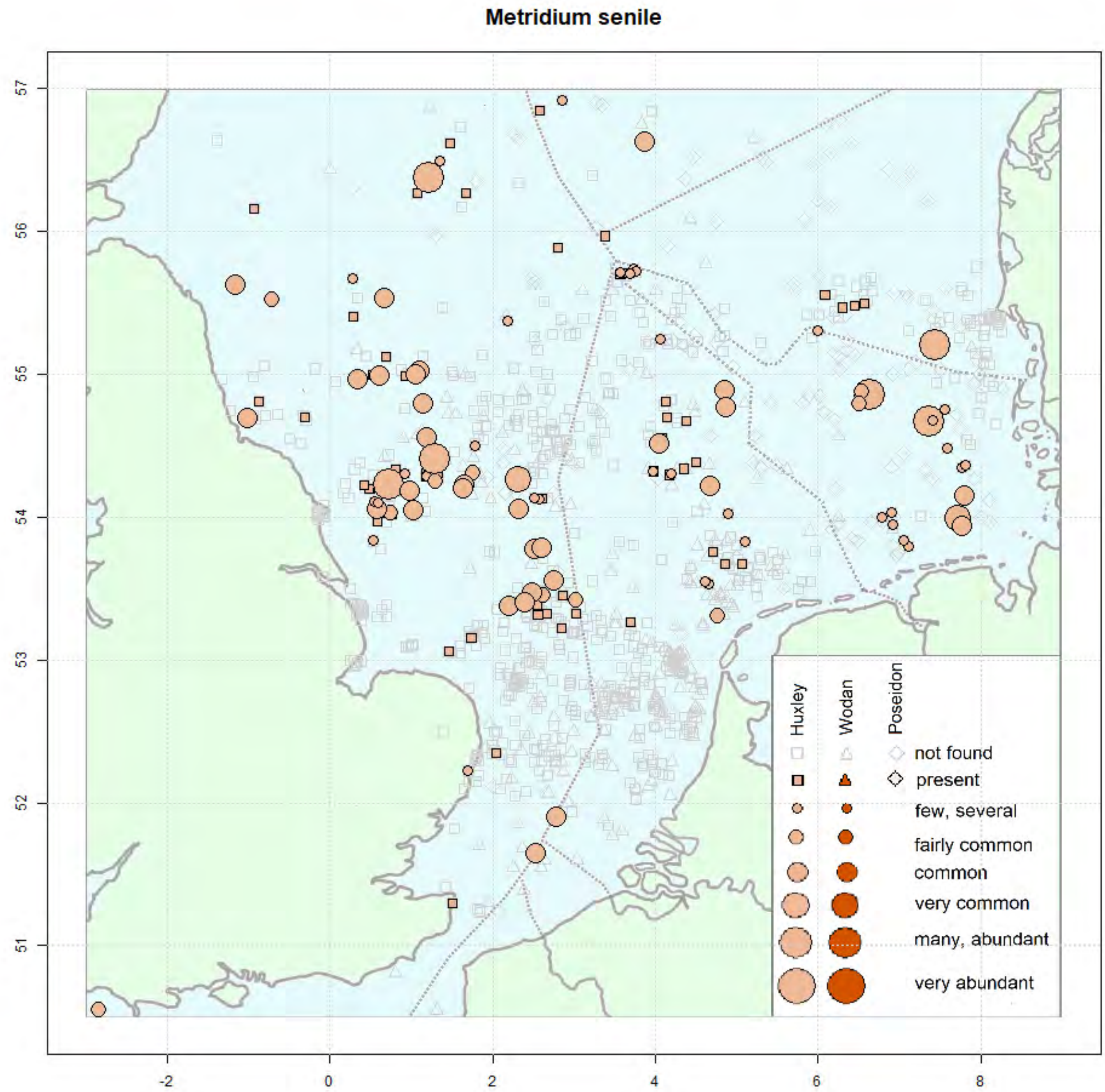


Bolocera tuediae Deeplet sea anemone



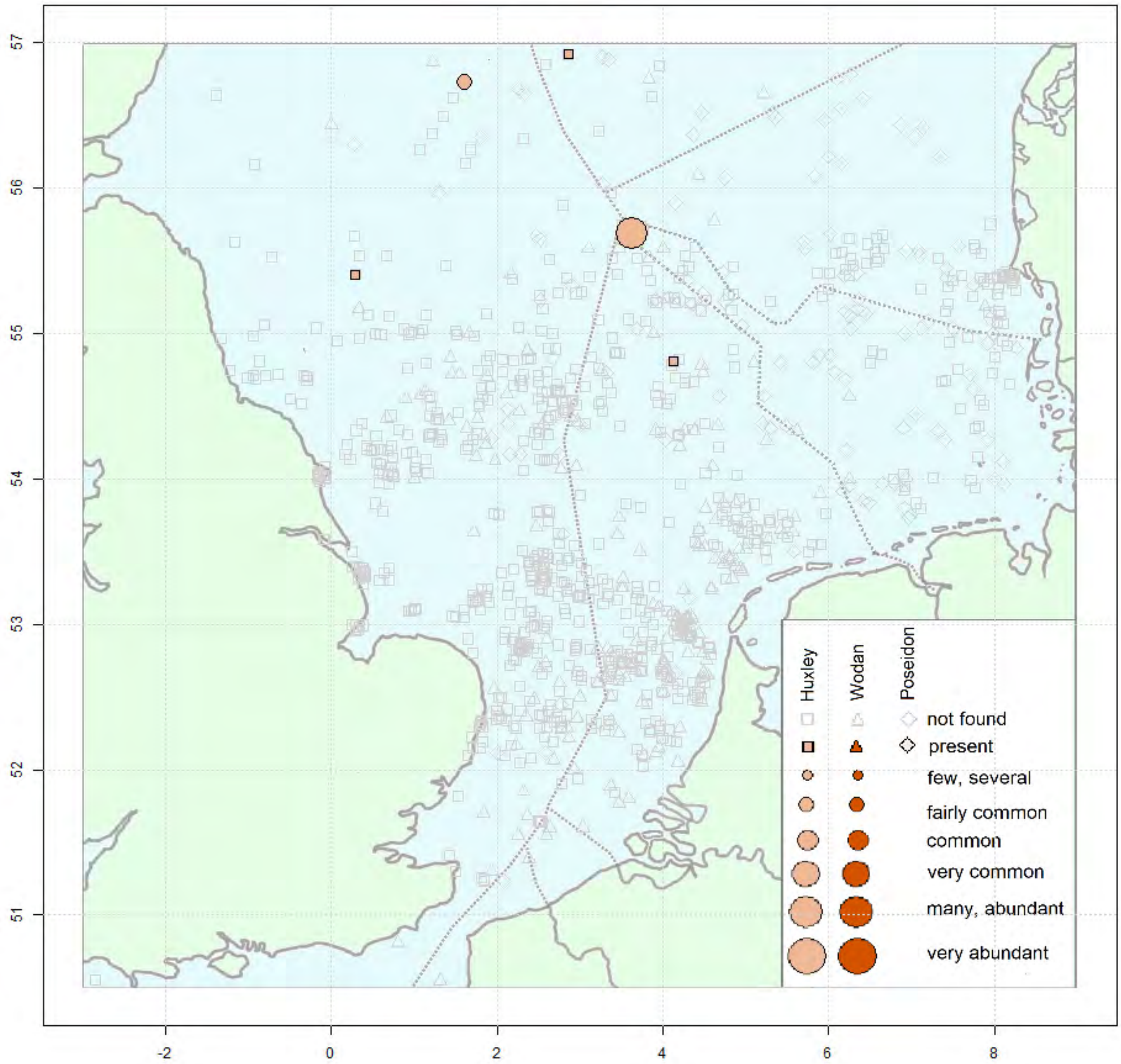
Cylista undatus? A sea anemone

? was added by the Huxley naturalist.



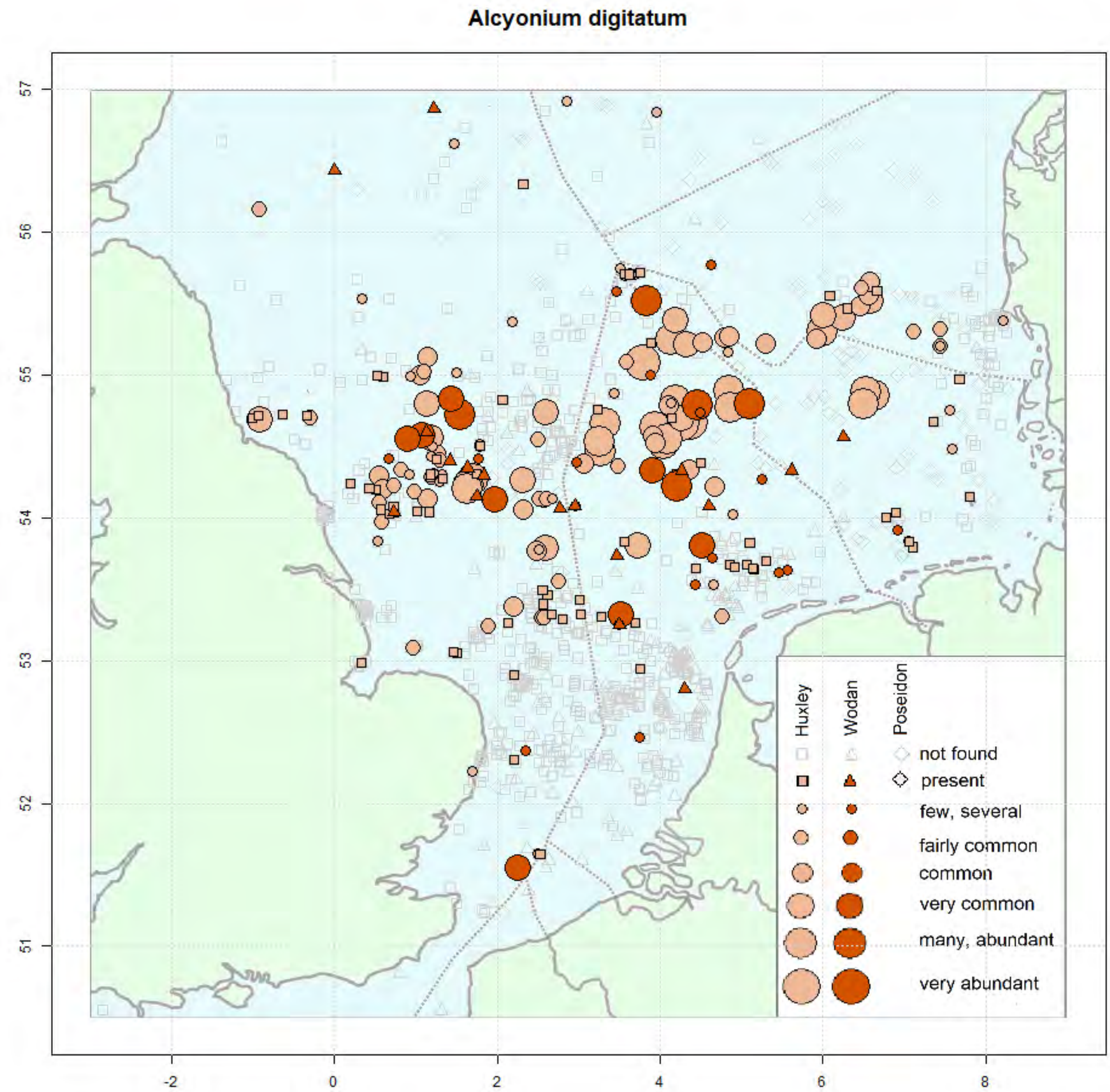
Metridium senile Plumose anemone

Urticina eques



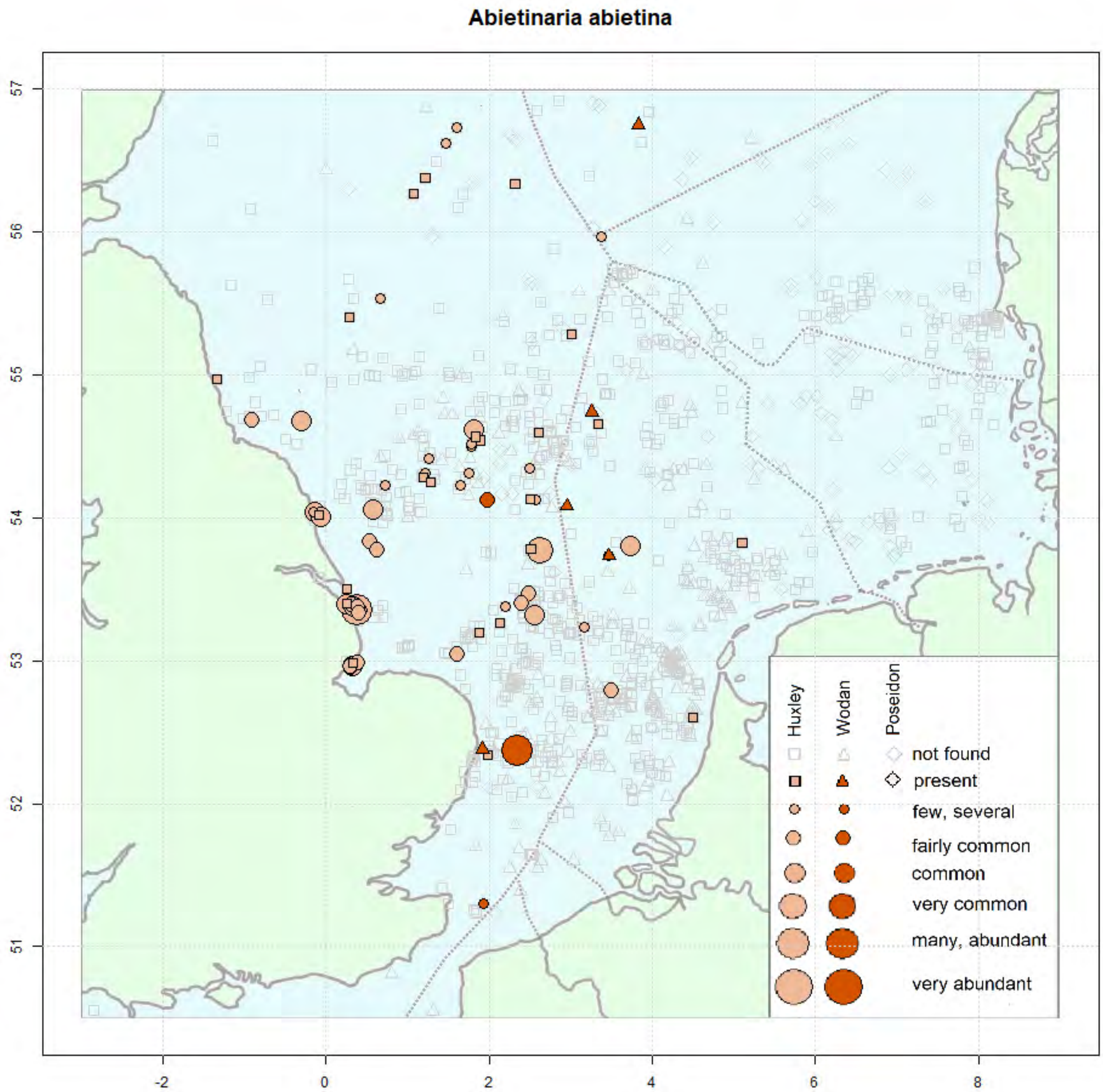
Urticina eques Horseman anemone

Cnidaria-Alcyonaria

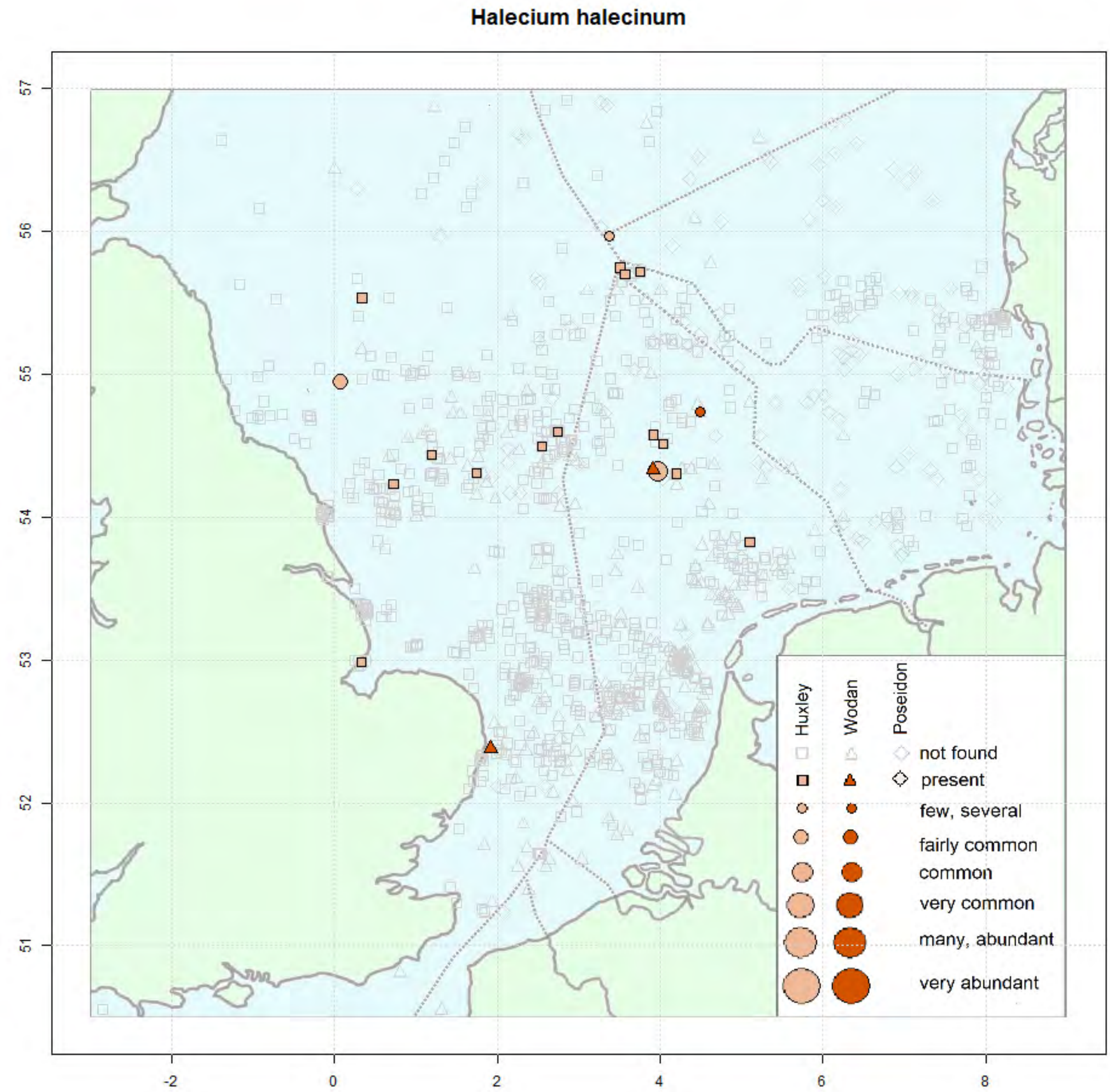


Alcyonium digitatum Dead men's fingers

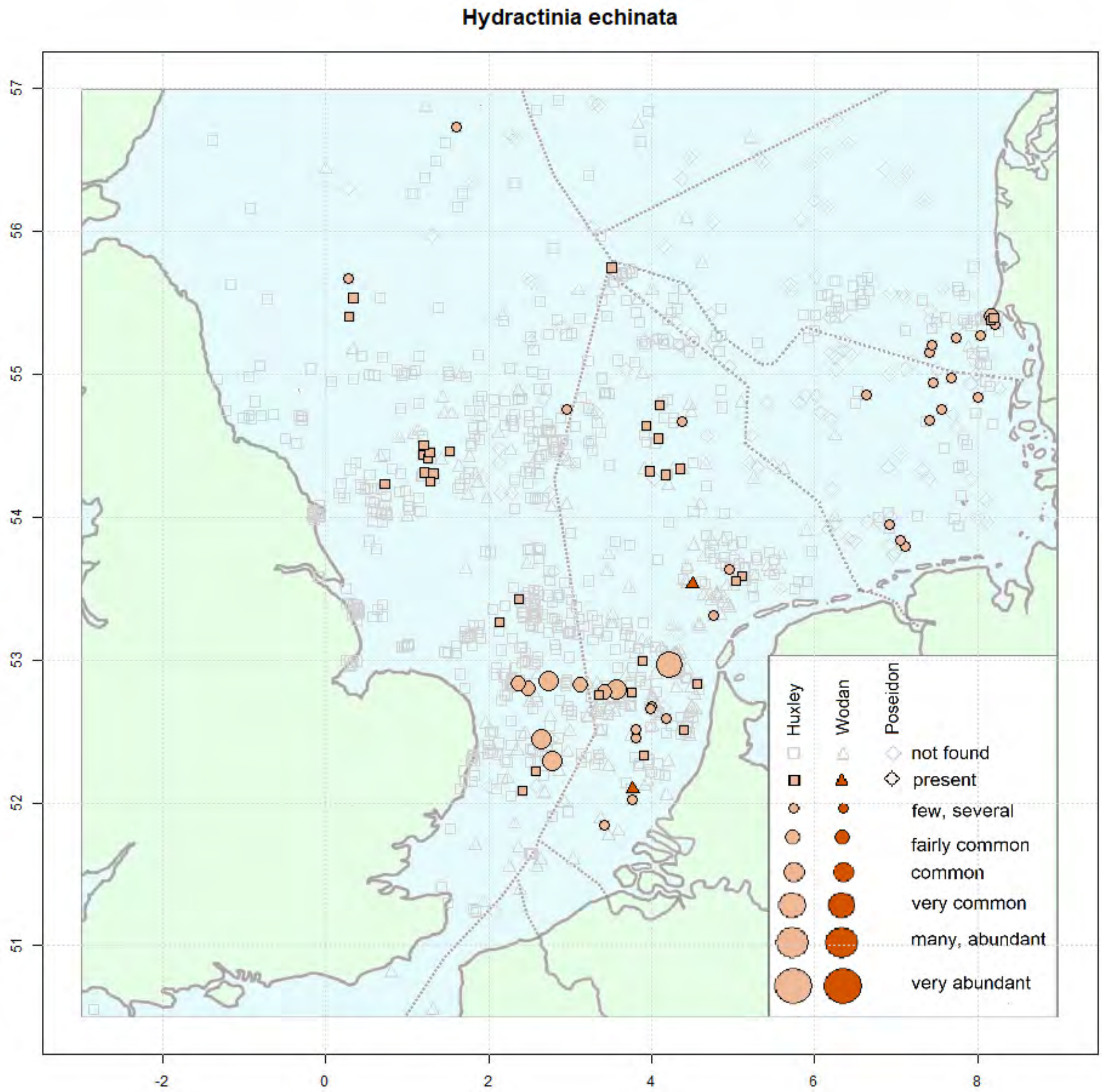
Cnidaria-Hydrozoa



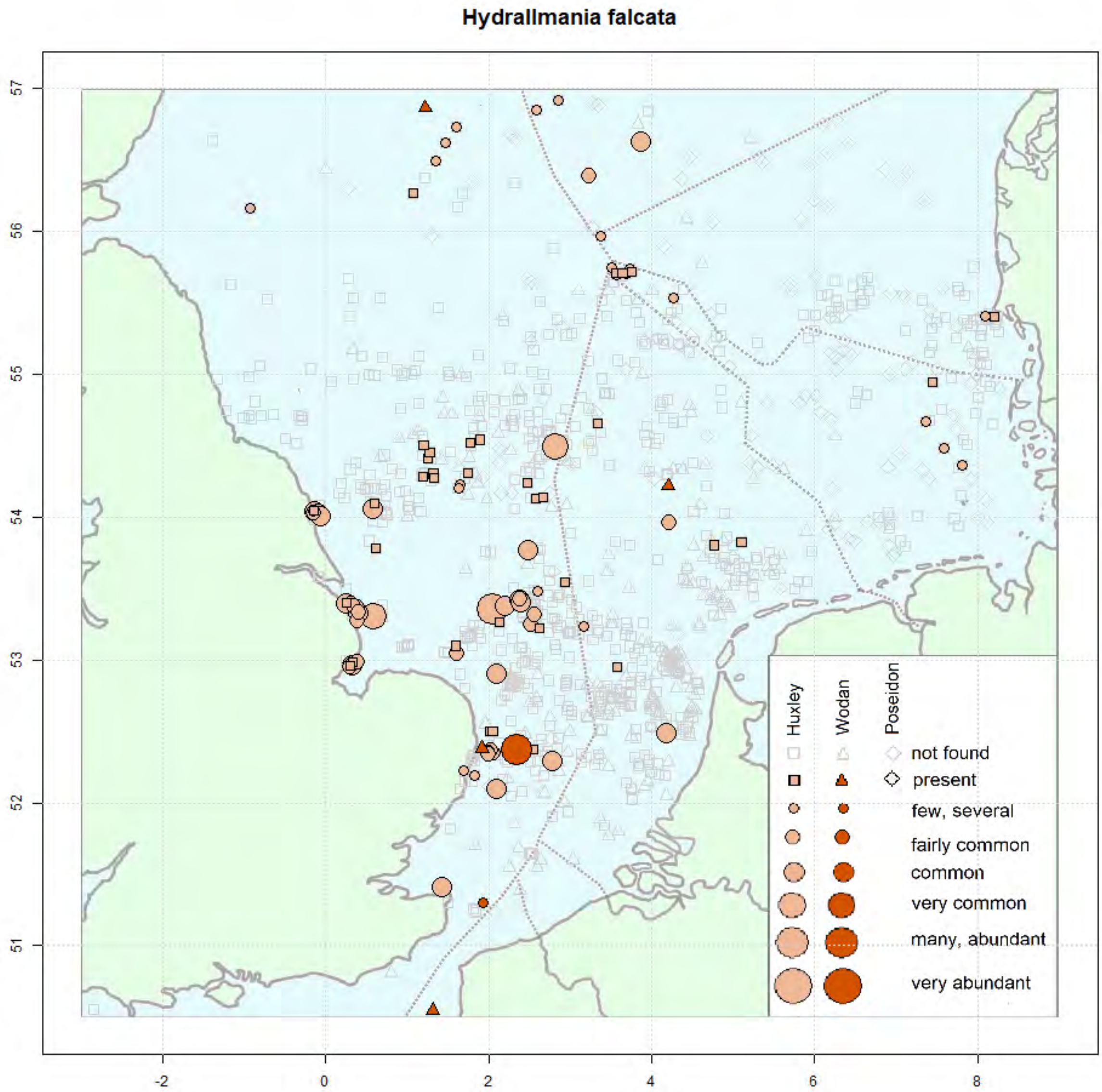
Abietinaria abietina Seafir



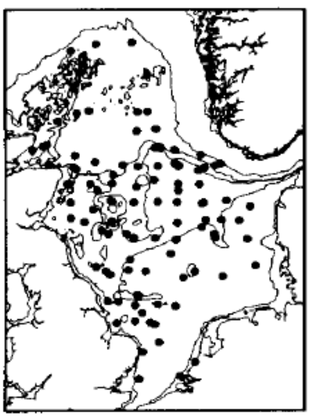
Halecium halecinum Herring bone hydroid



Hydractinia echinata Hermit crab fir

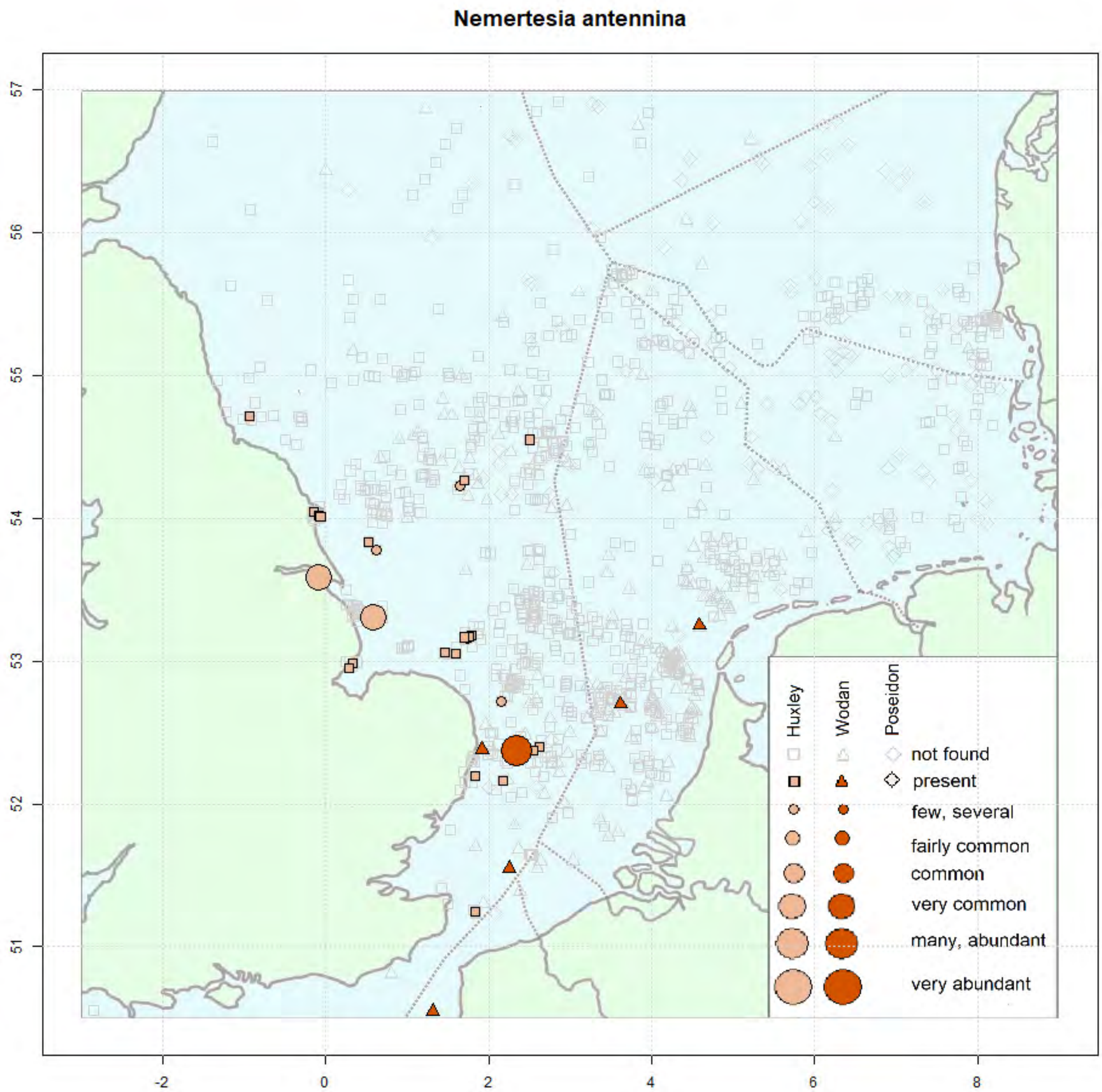


Hydrallmania falcata Sickle hydroid

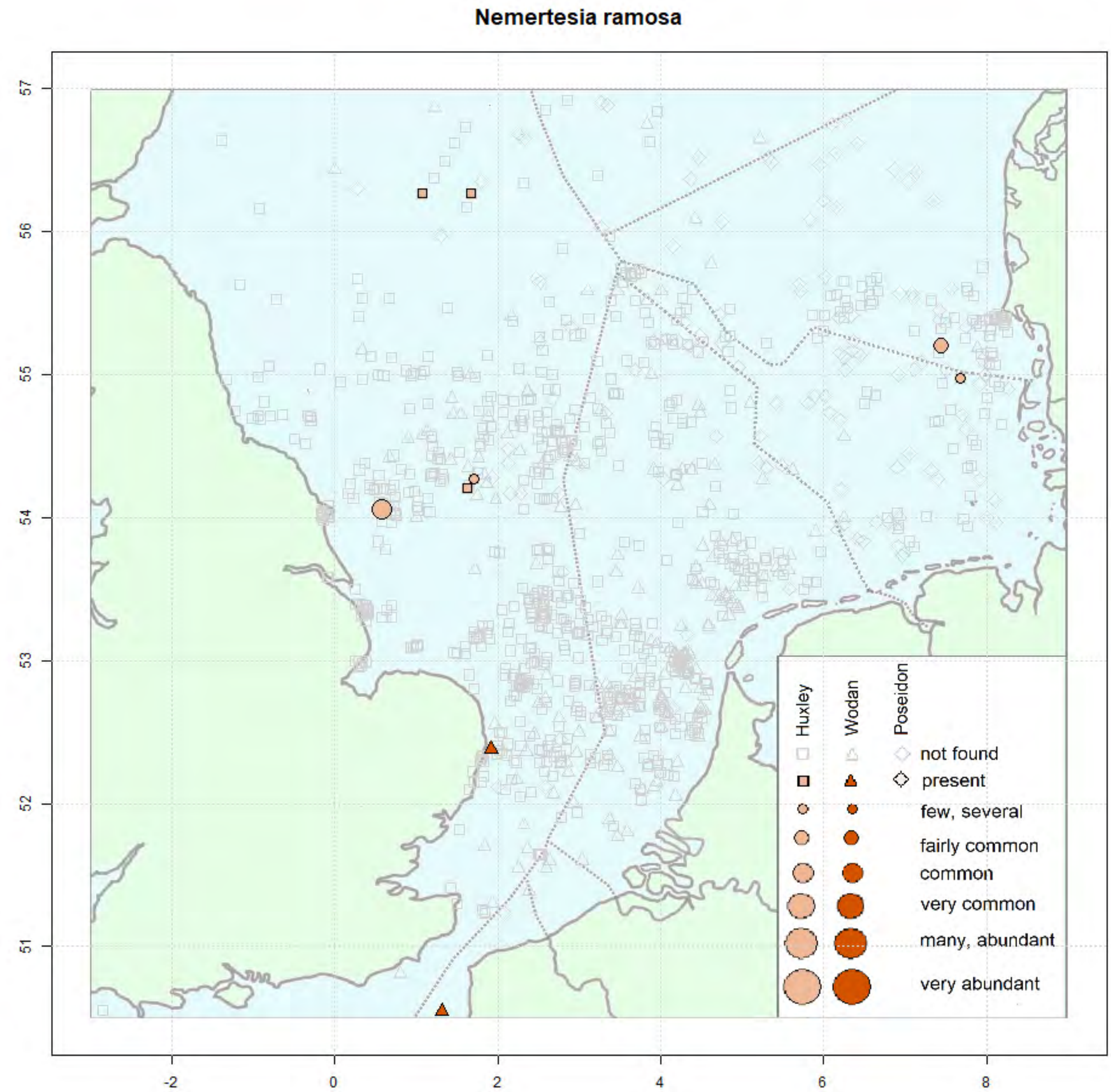


(i) *Hydralimania falcata*

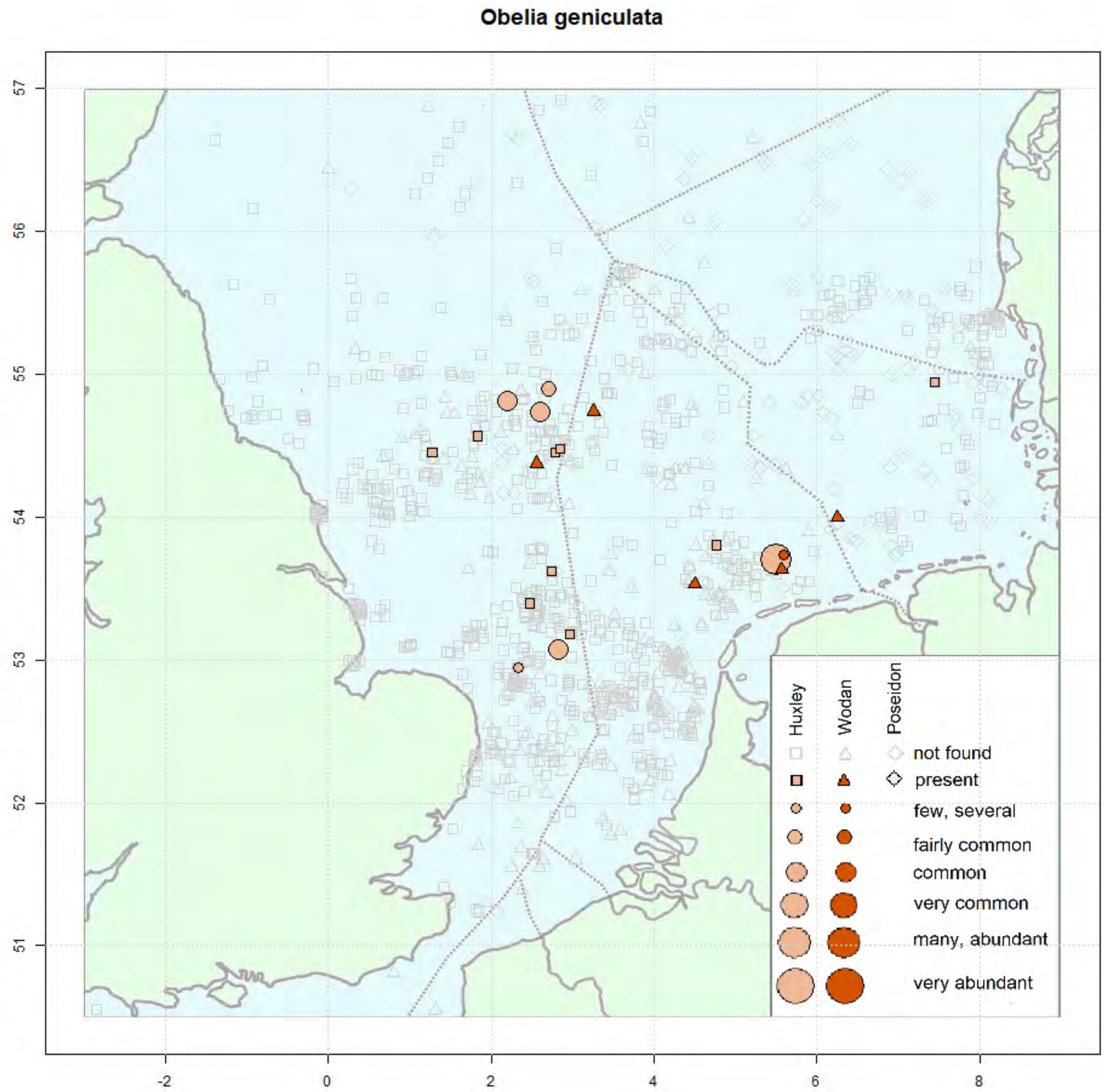
2000 distribution map (Callaway *et al.*, 2002).



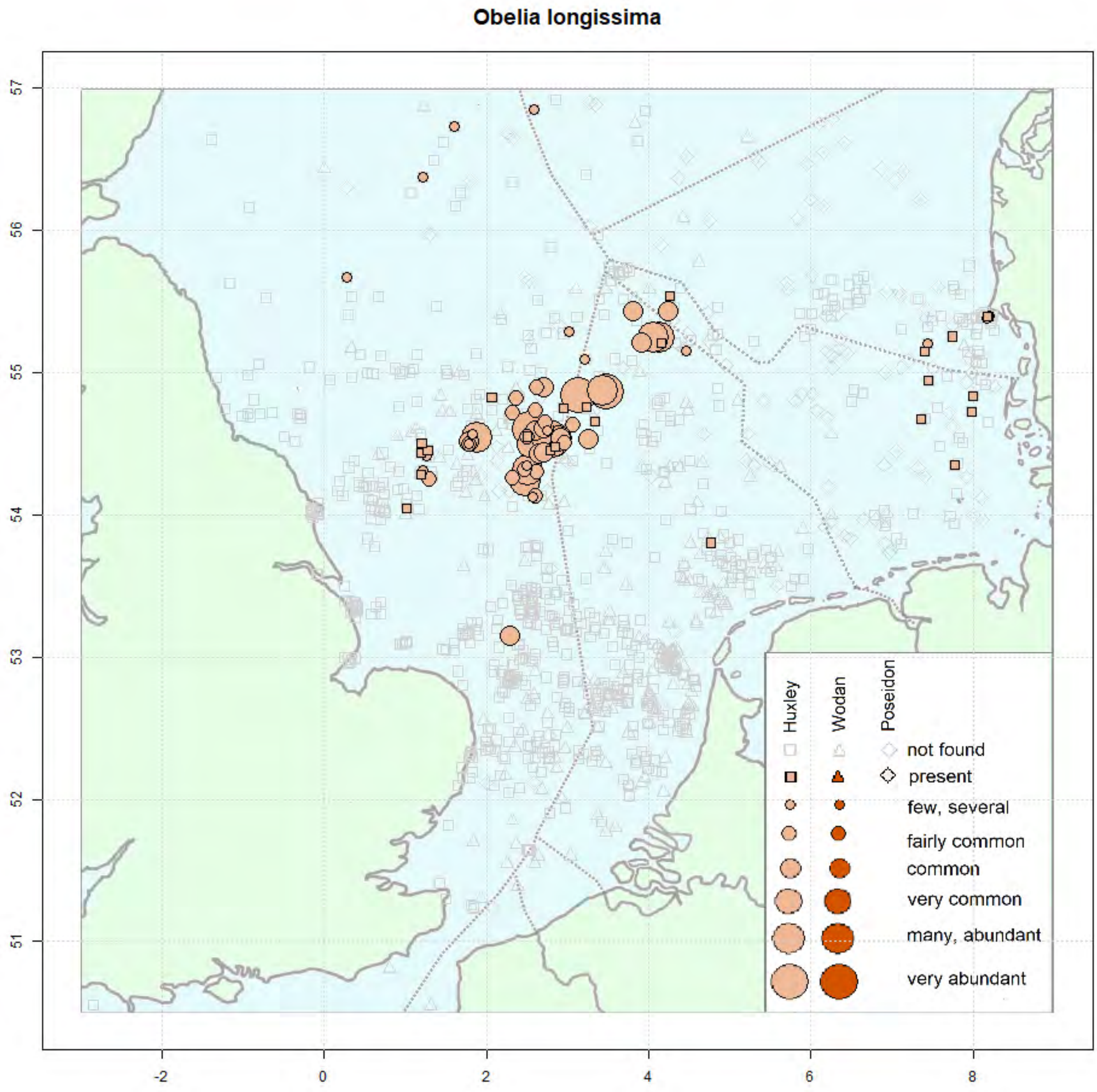
Nemertesia antennina Sea beard



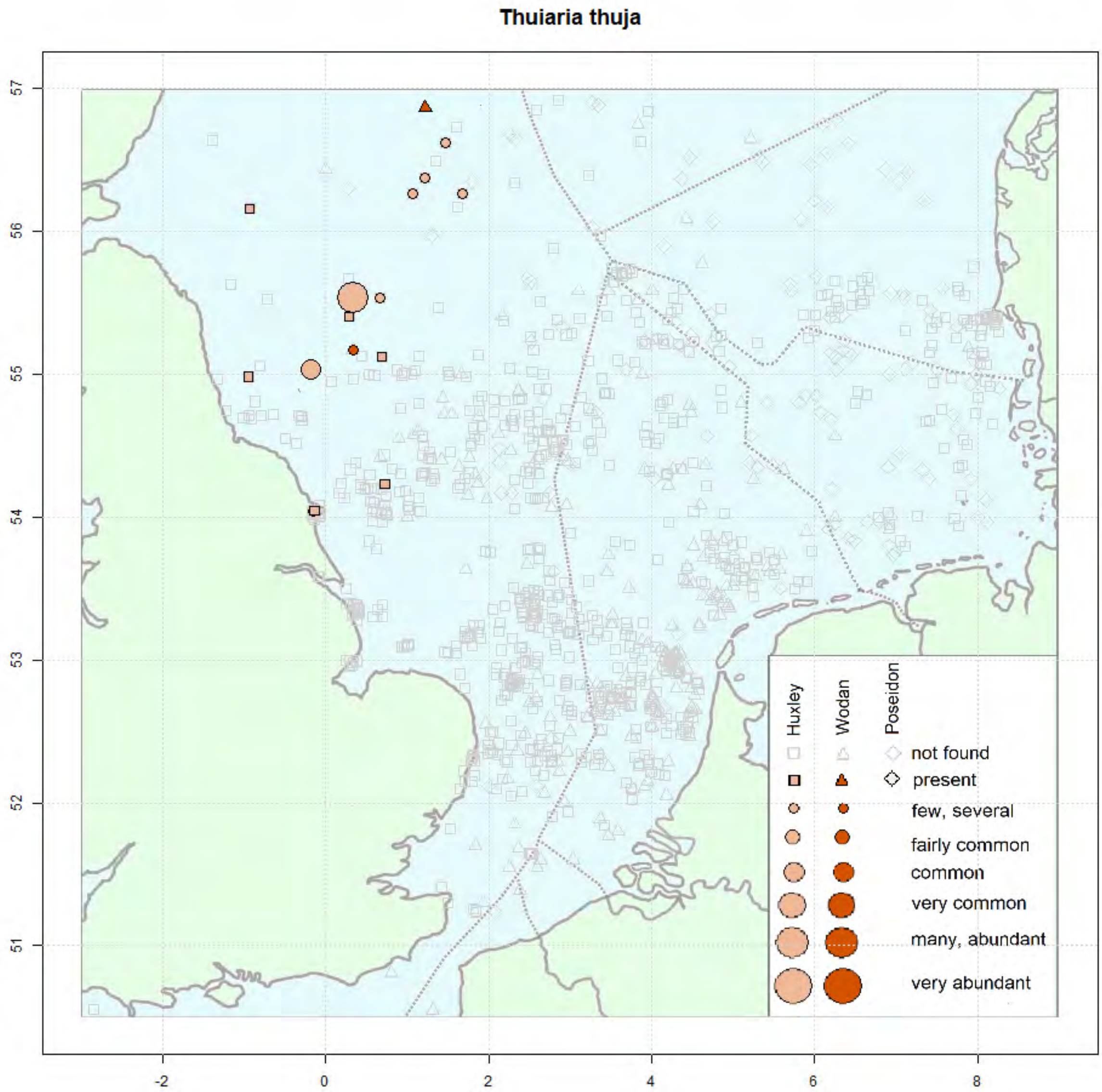
Nemertesia ramosa Branched antenna hydroid



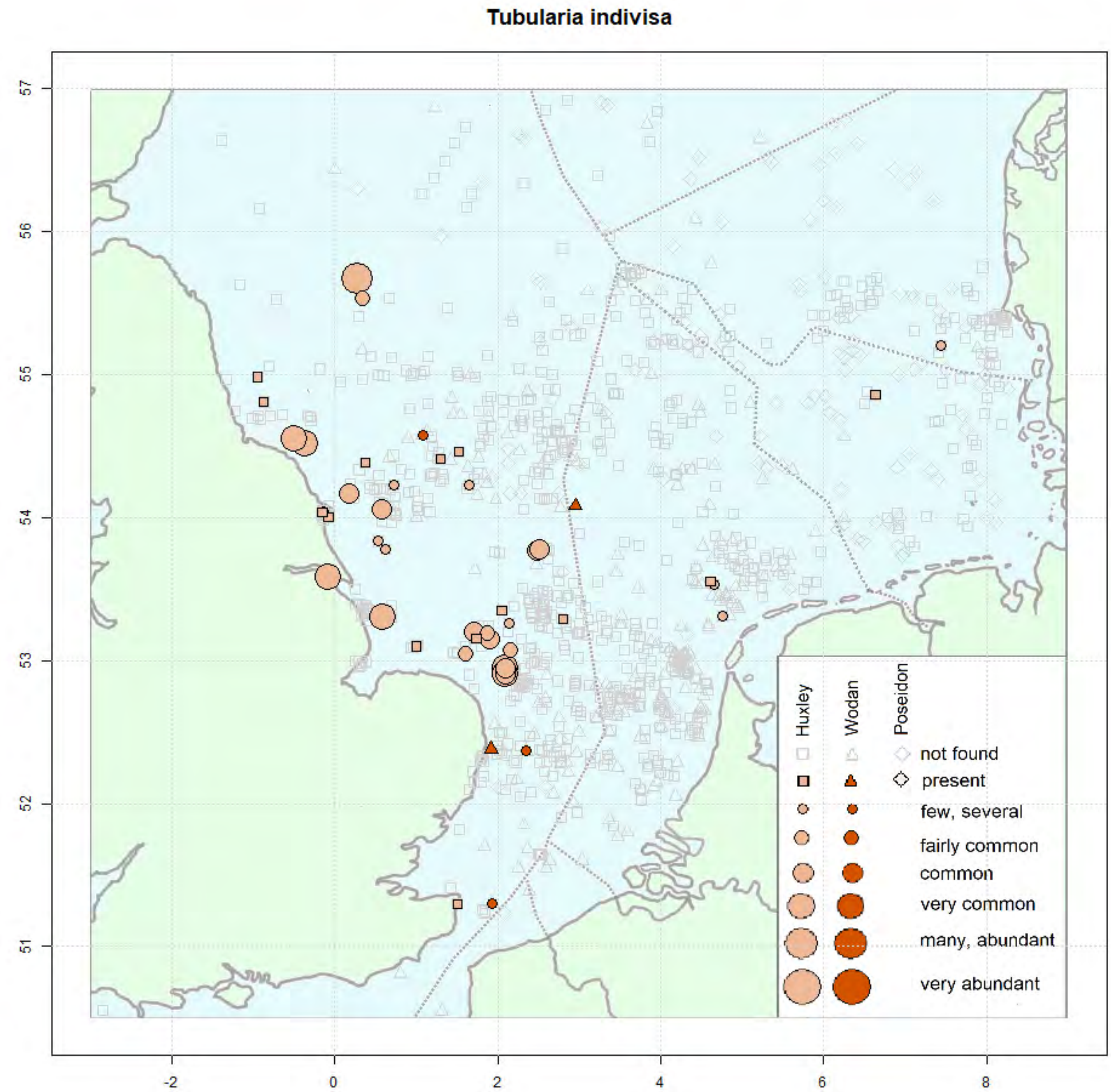
Obelia geniculata Kelp fir



Obelia longissima A hydroid

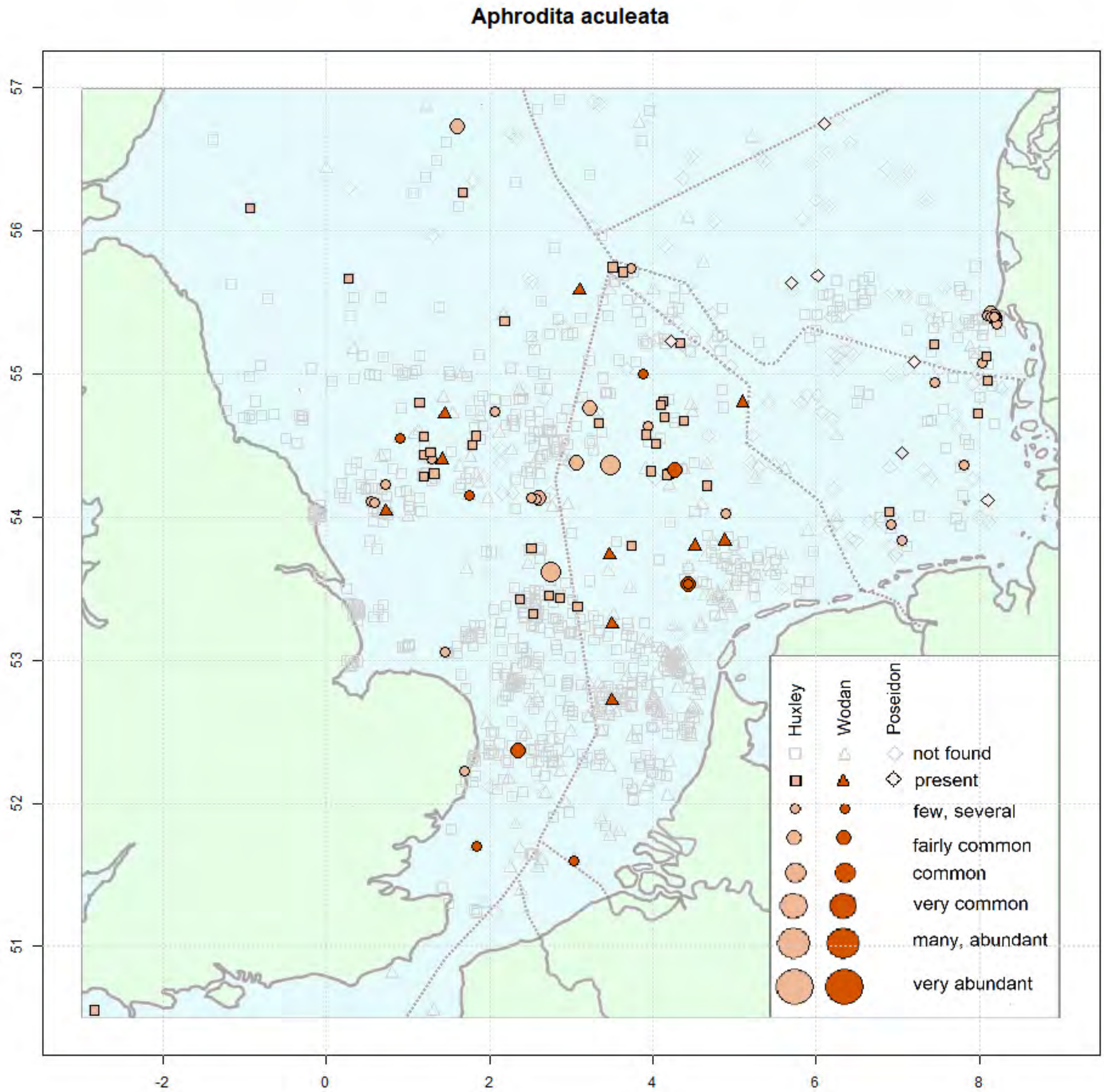


Thuiaria thuja Bottle brush hydroid

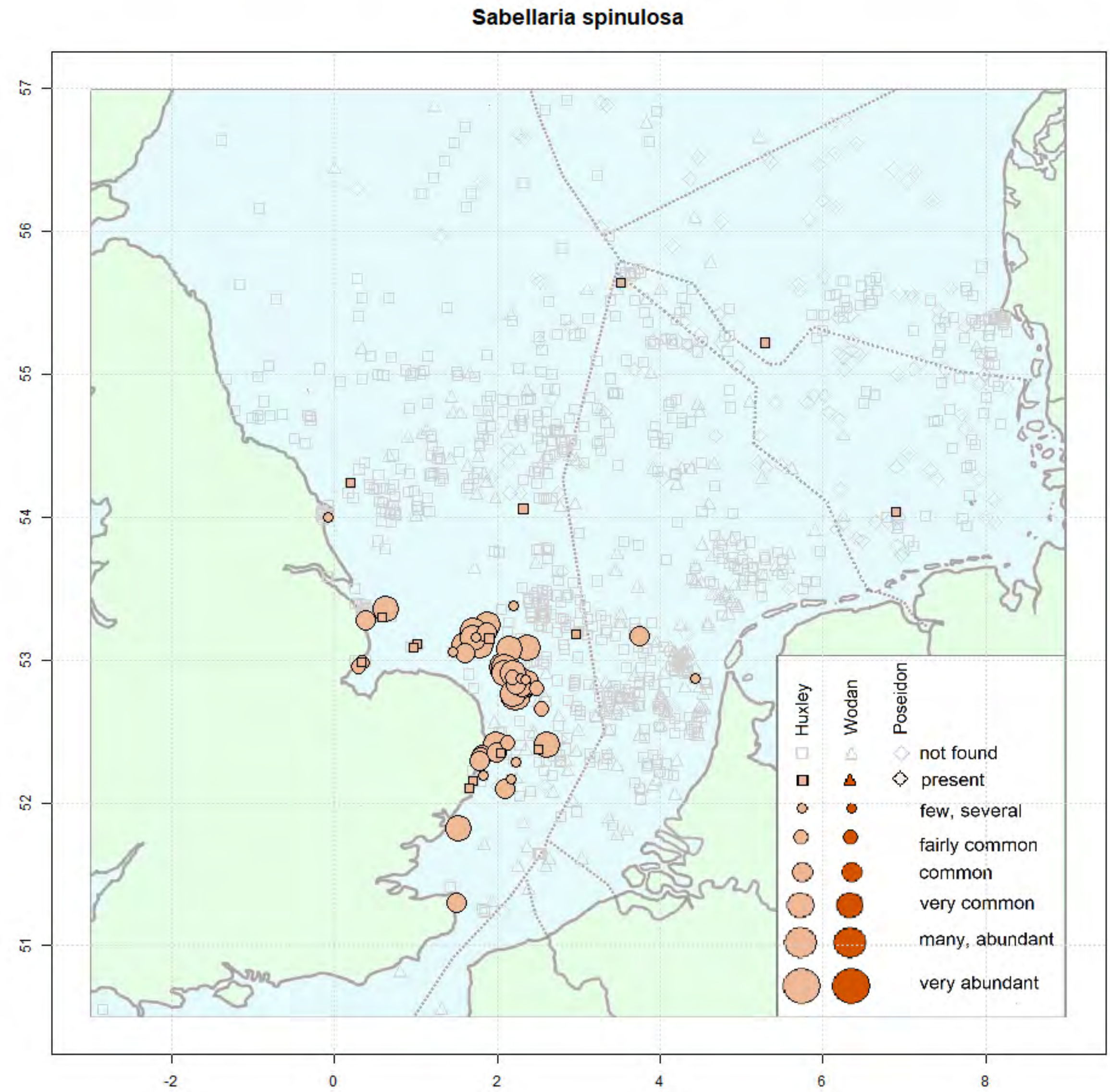


Tubularia indivisa Oaten pipe hydroid

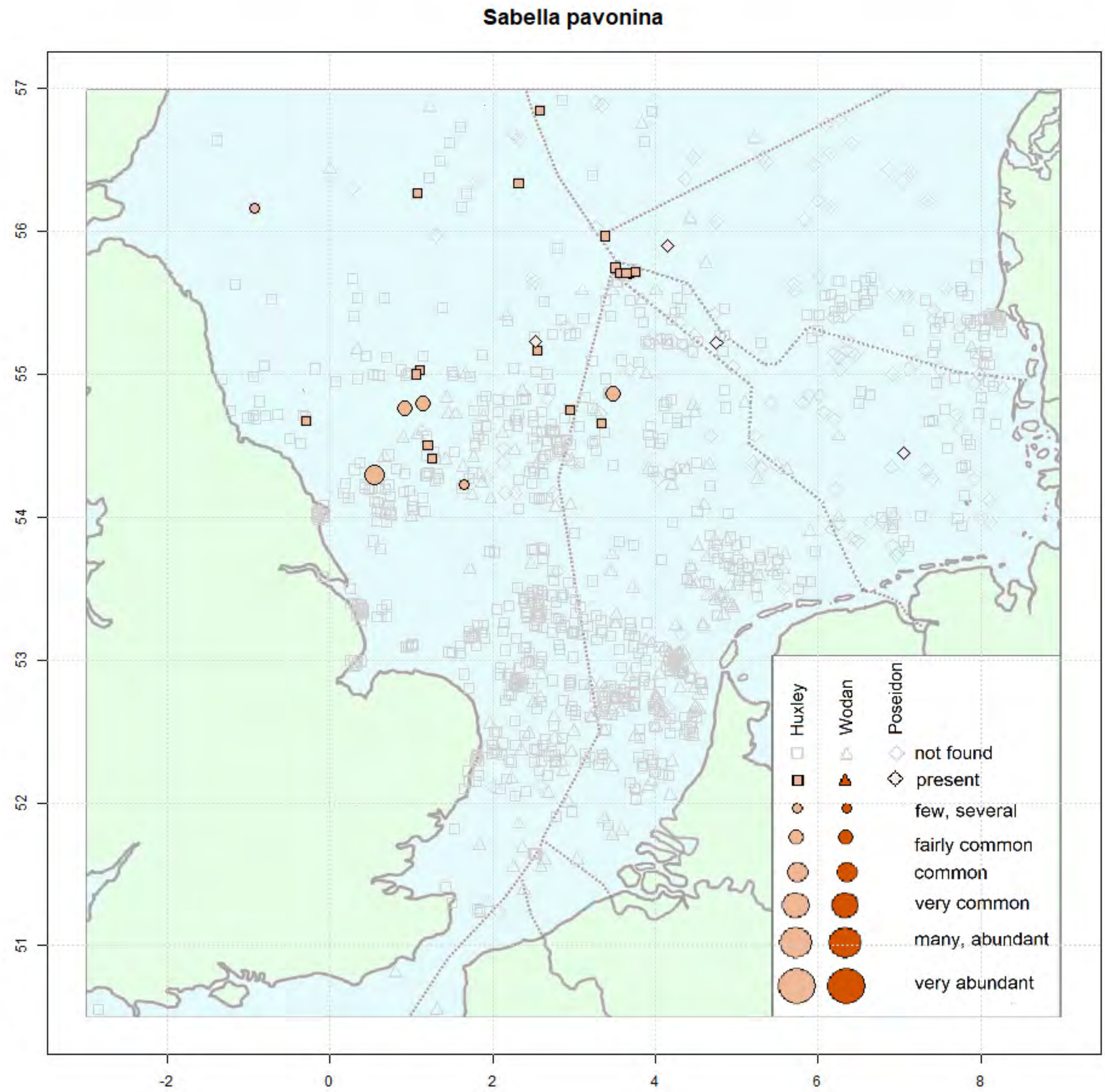
Annelida-Polychaeta



Aphrodita aculeata Sea mouse

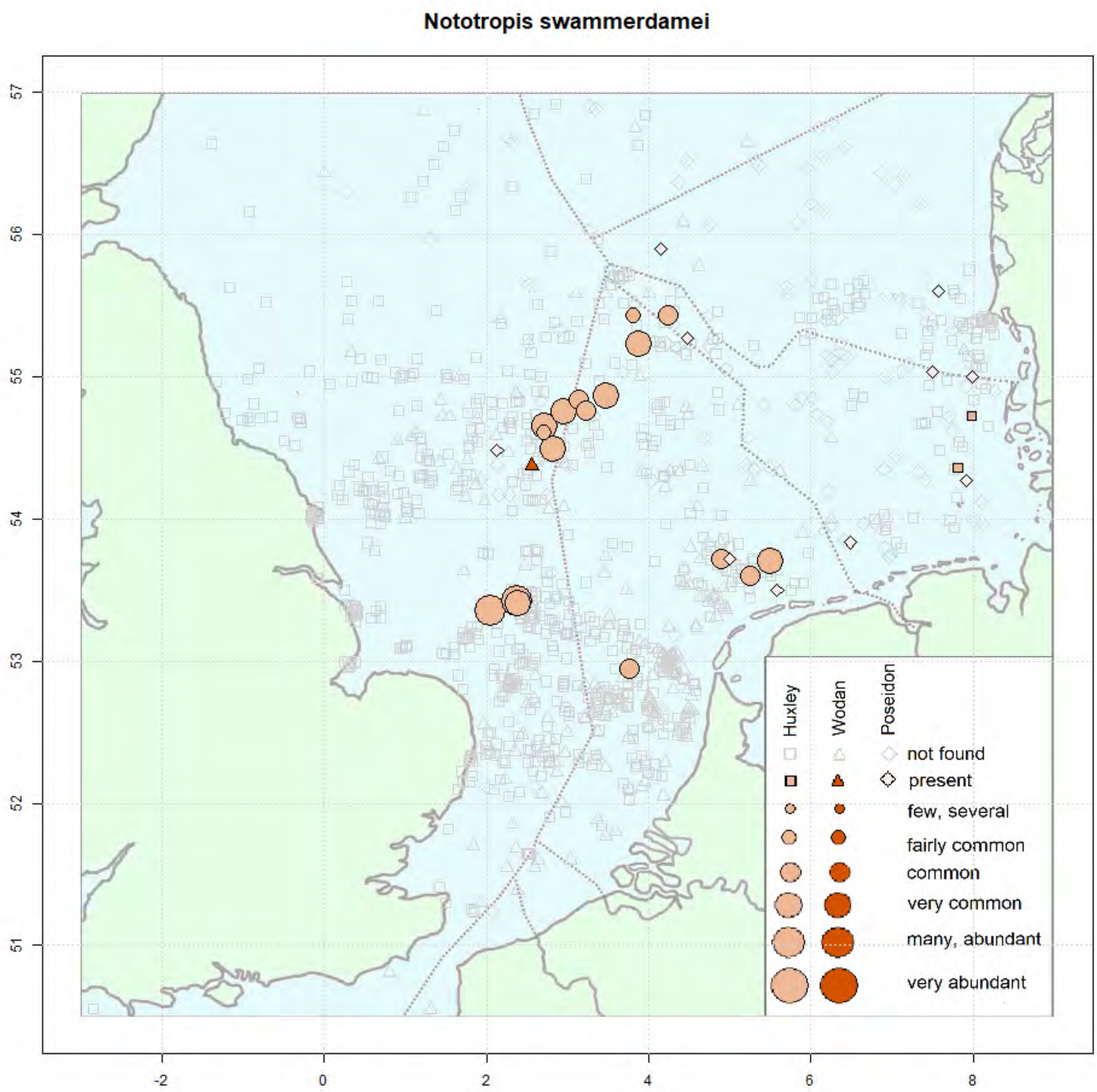


Sabellaria spinulosa Ross worm



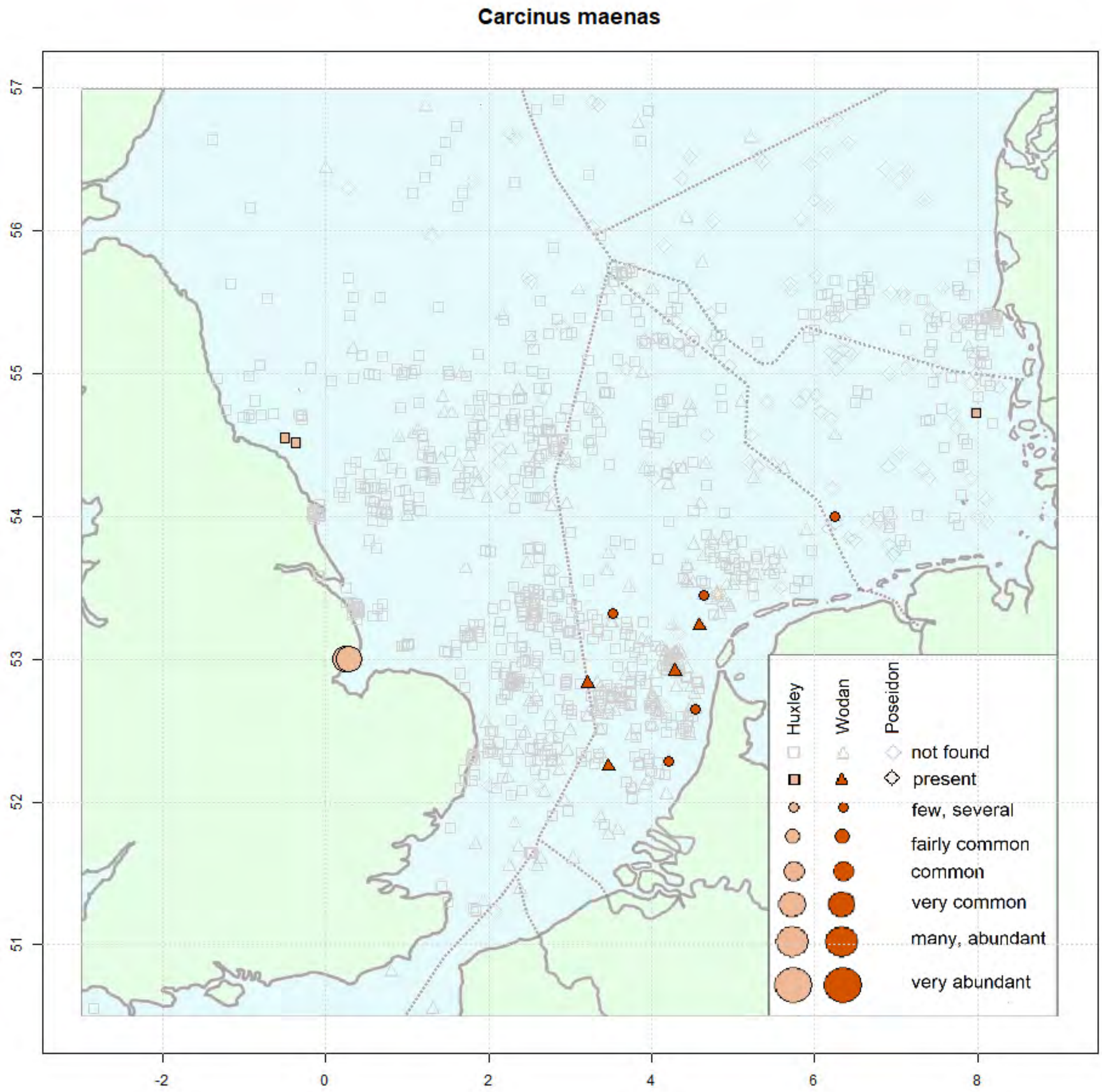
Sabella pavonina Peacock worm

Arthropoda – Malacostraca-Amphipoda



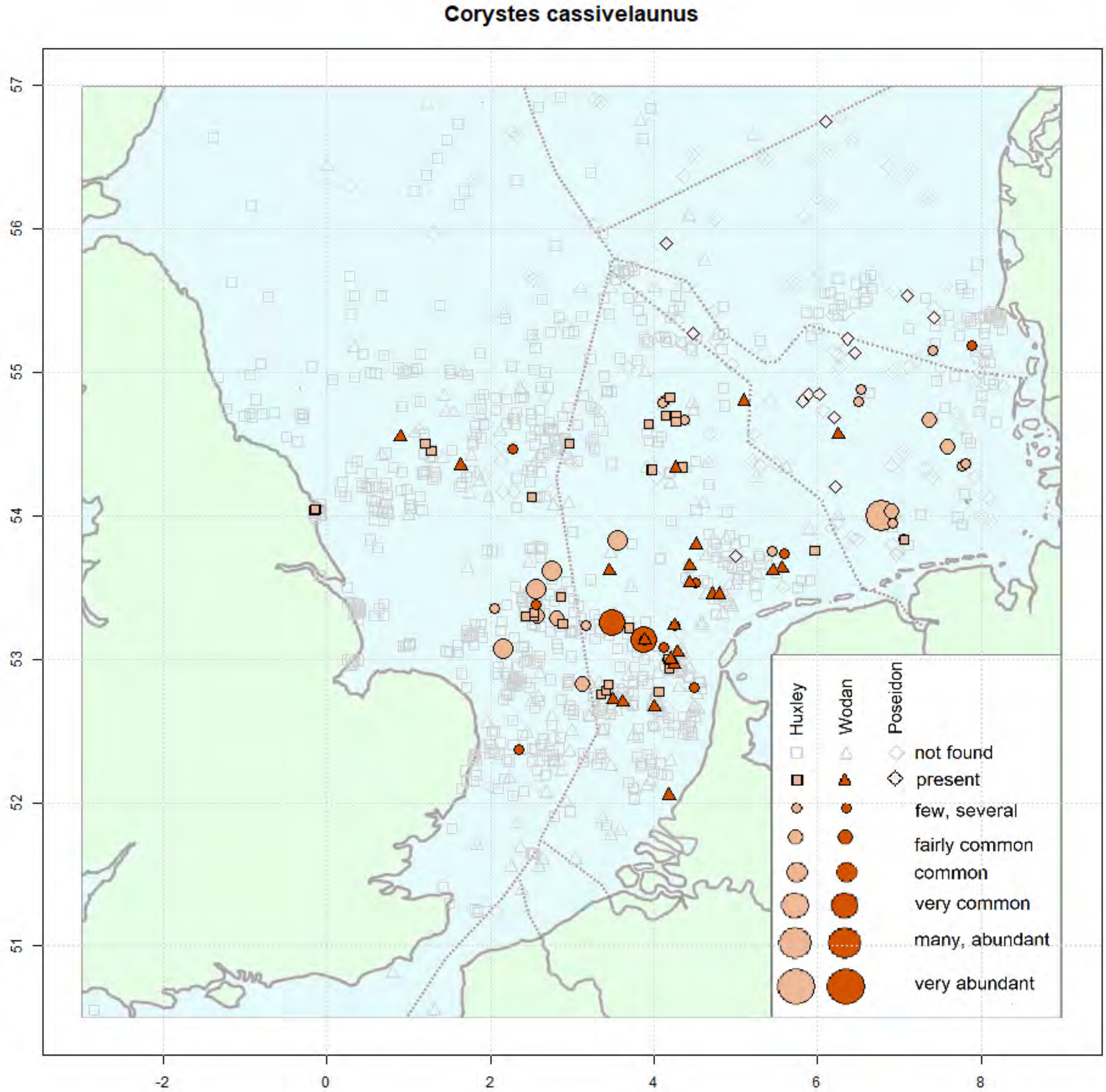
Nototropsis swammerdamei An amphipod crustacean

Arthropoda – Malacostraca-Decapoda

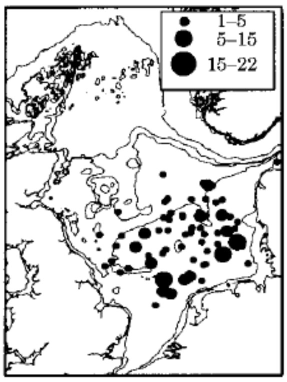


Carcinus maenas Common shore crab

Corystes cassivelaunus

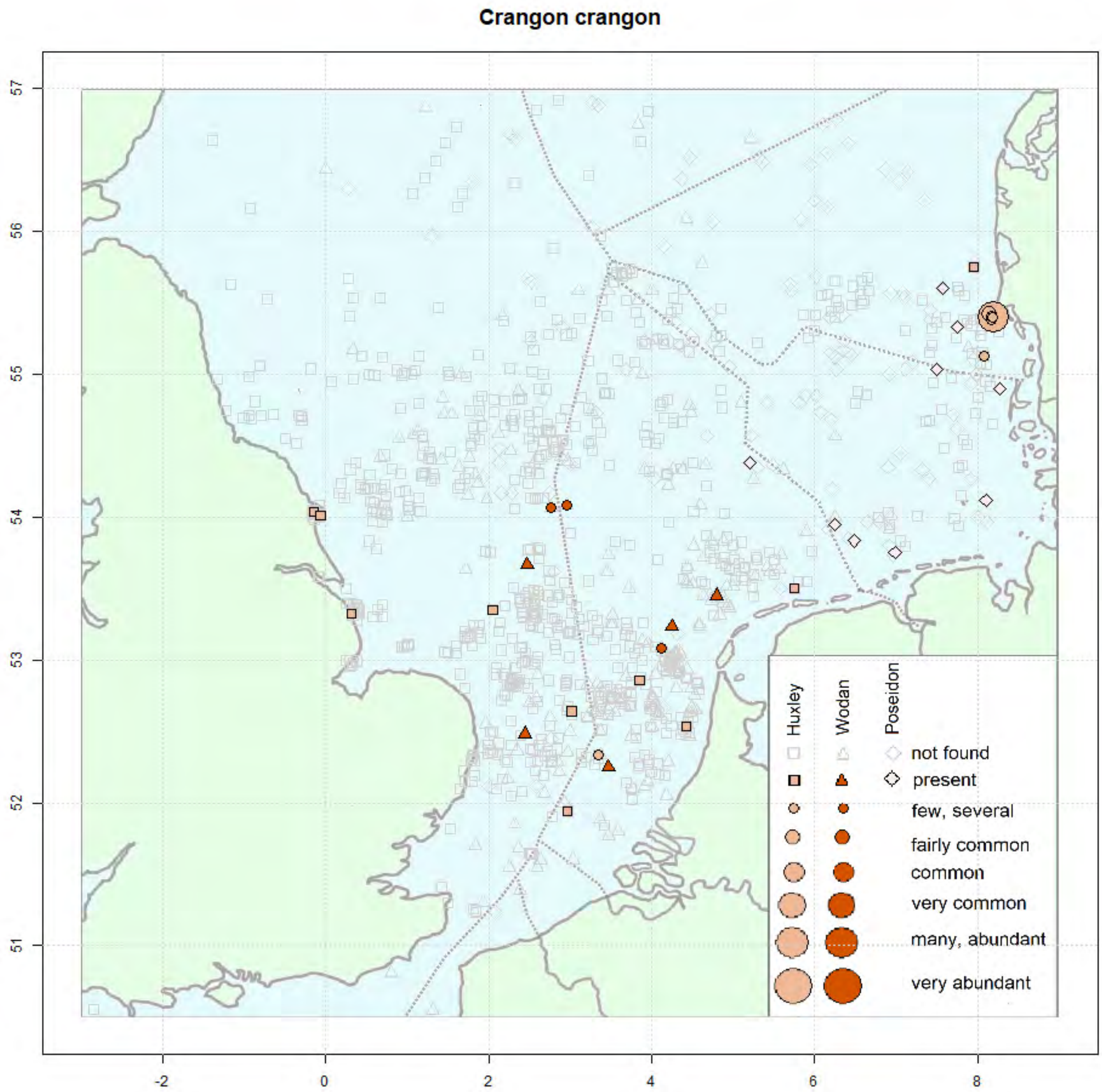


Corystes cassivelaunus Masked crab

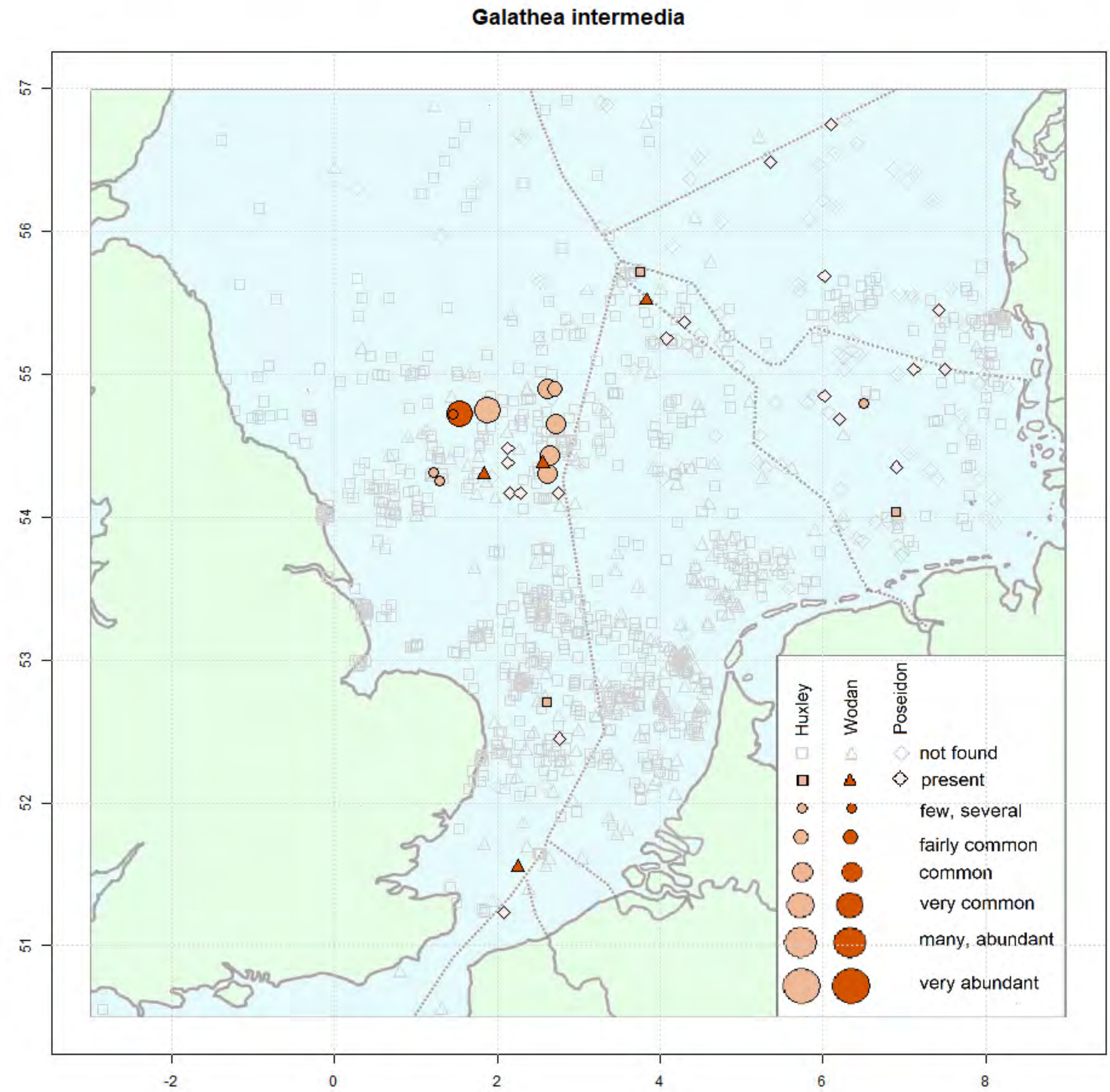


(c) *Corystes cassivelaunus*

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

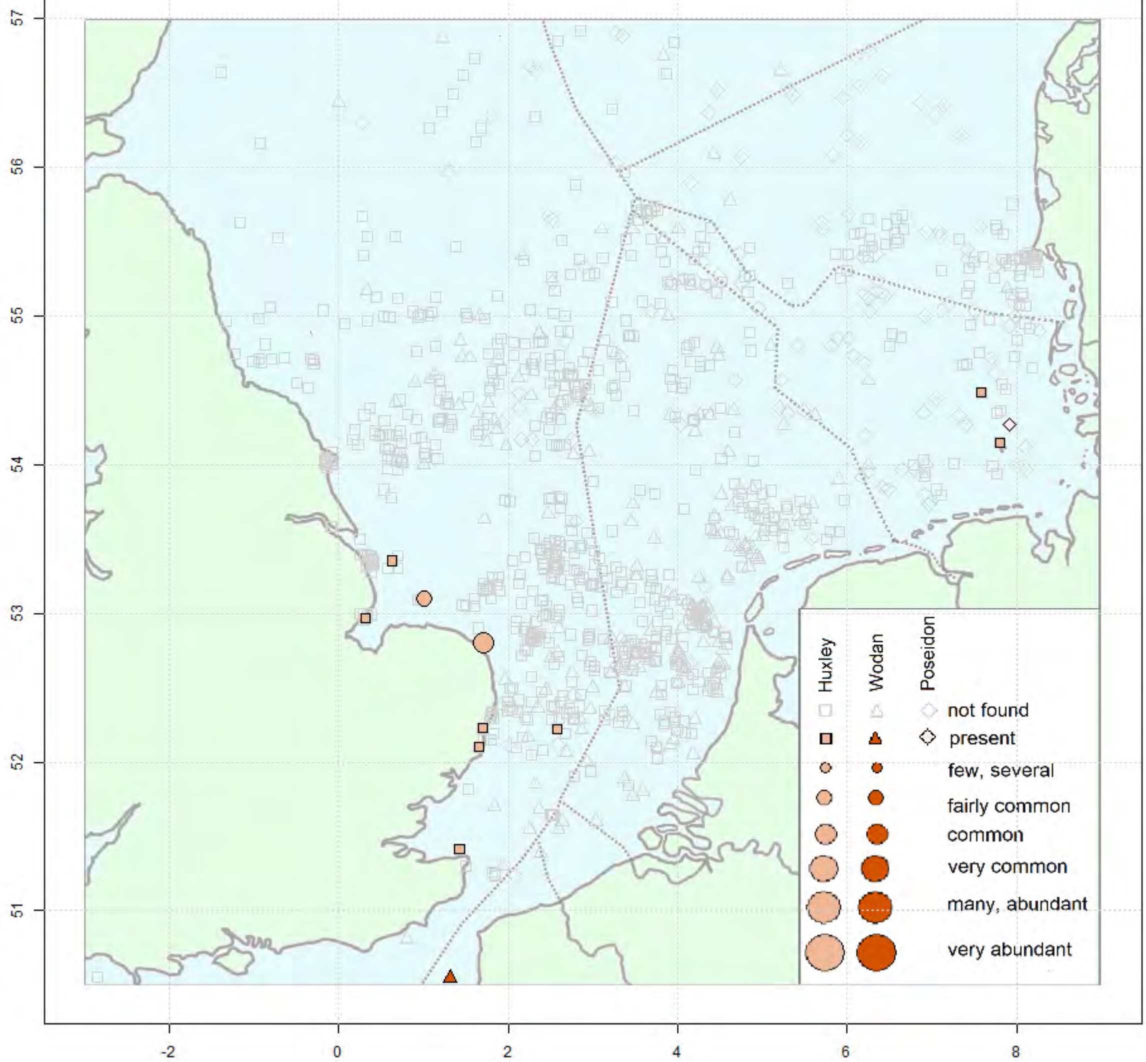


Crangon crangon Brown shrimp

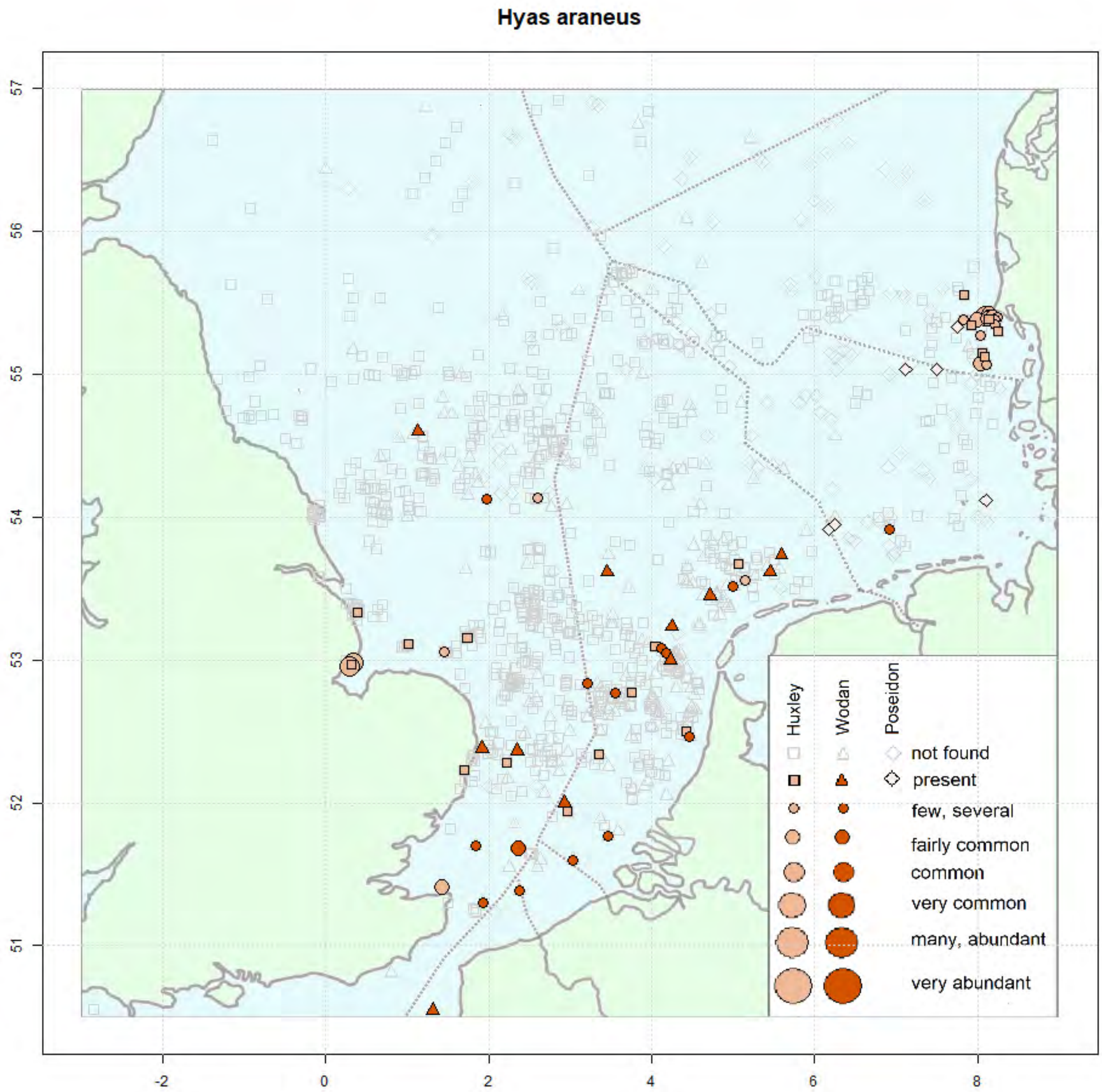


Galathea intermedia A squat lobster

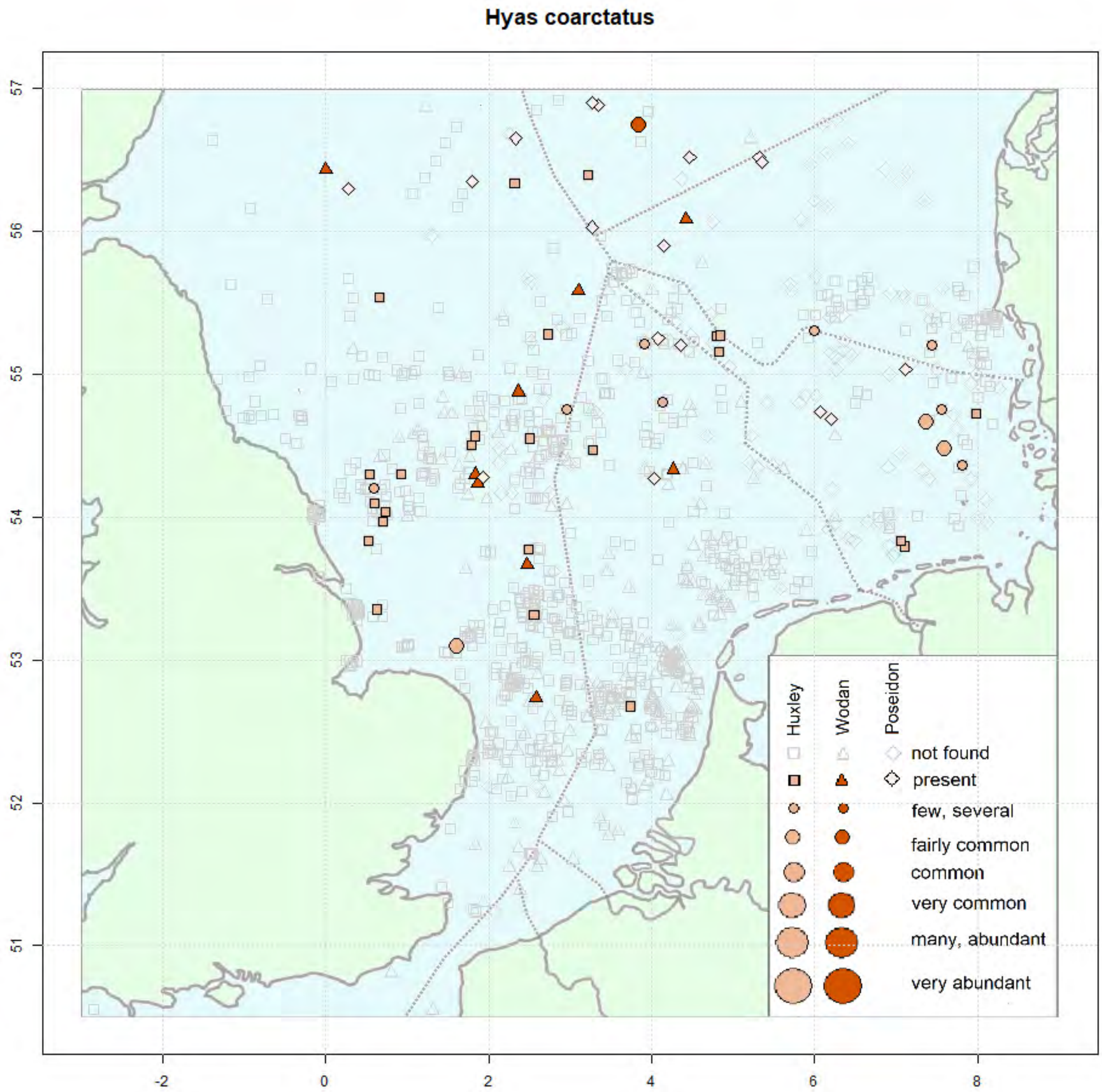
Homarus gammarus



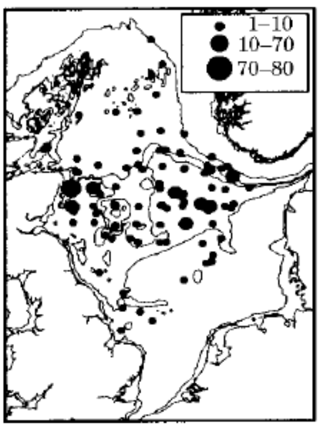
Homarus gammarus Common lobster



Hyas araneus Great spider crab

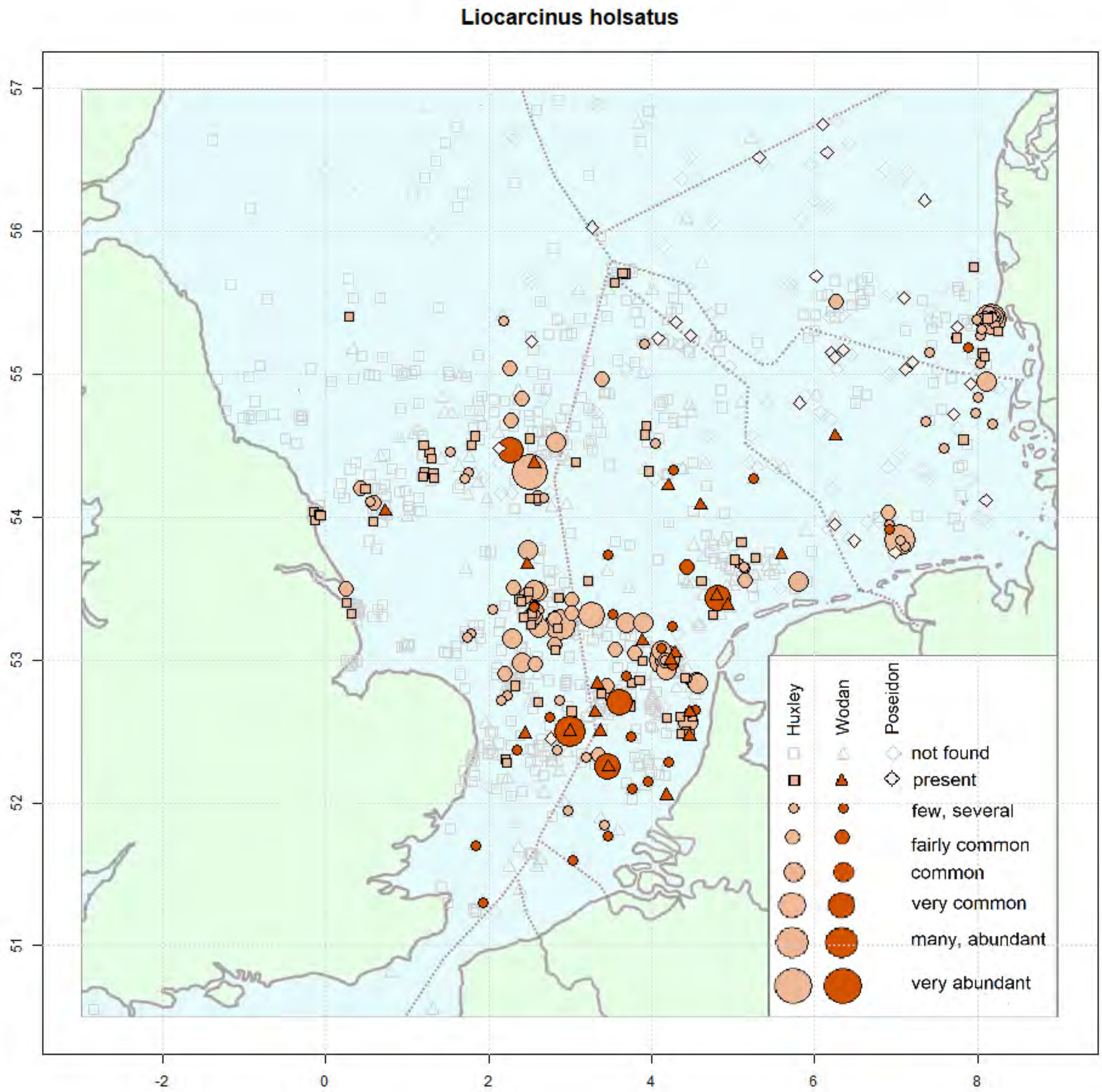


Hyas coarctatus   Toad crab

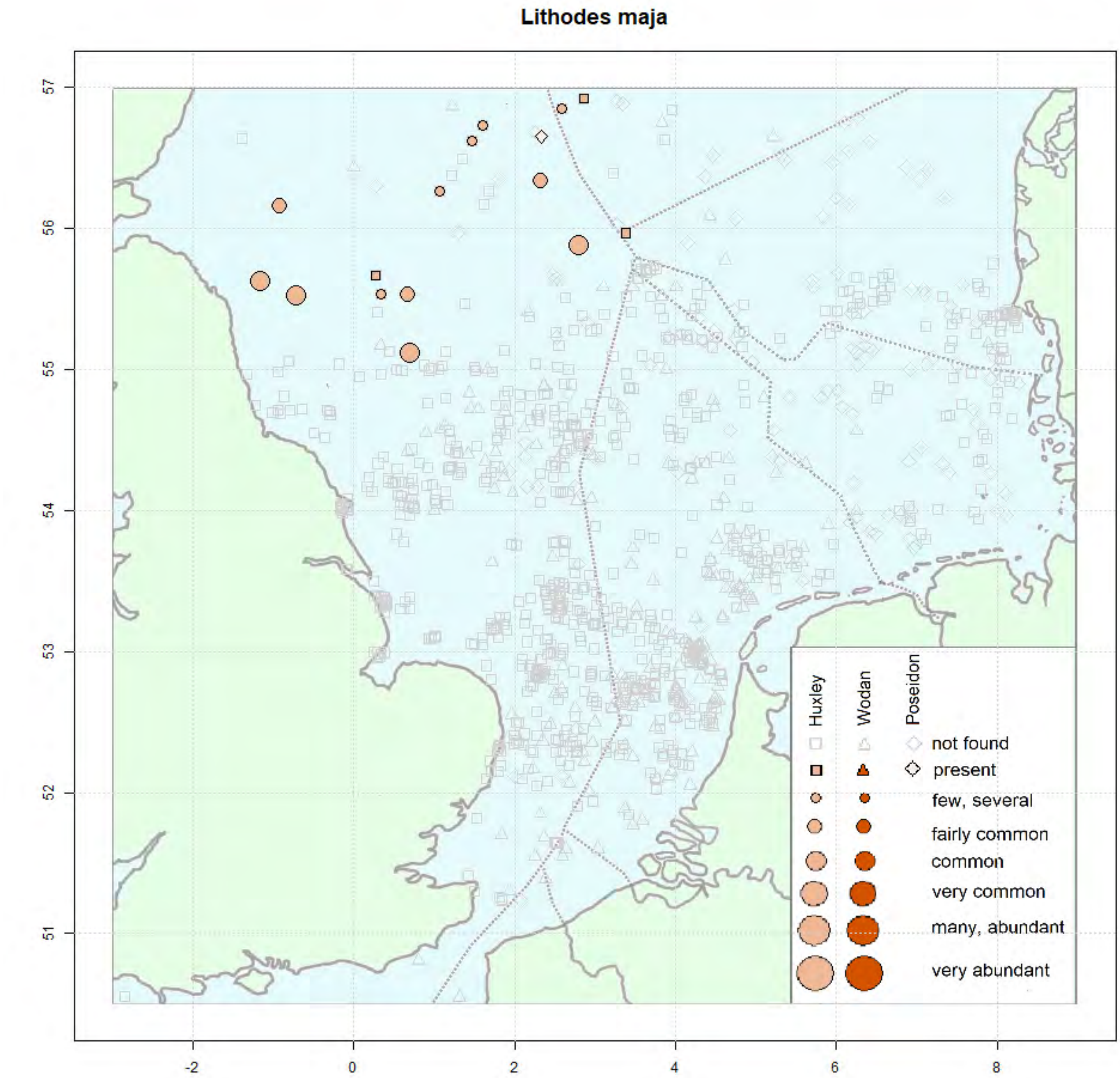


(e) *Hyas coarctatus*

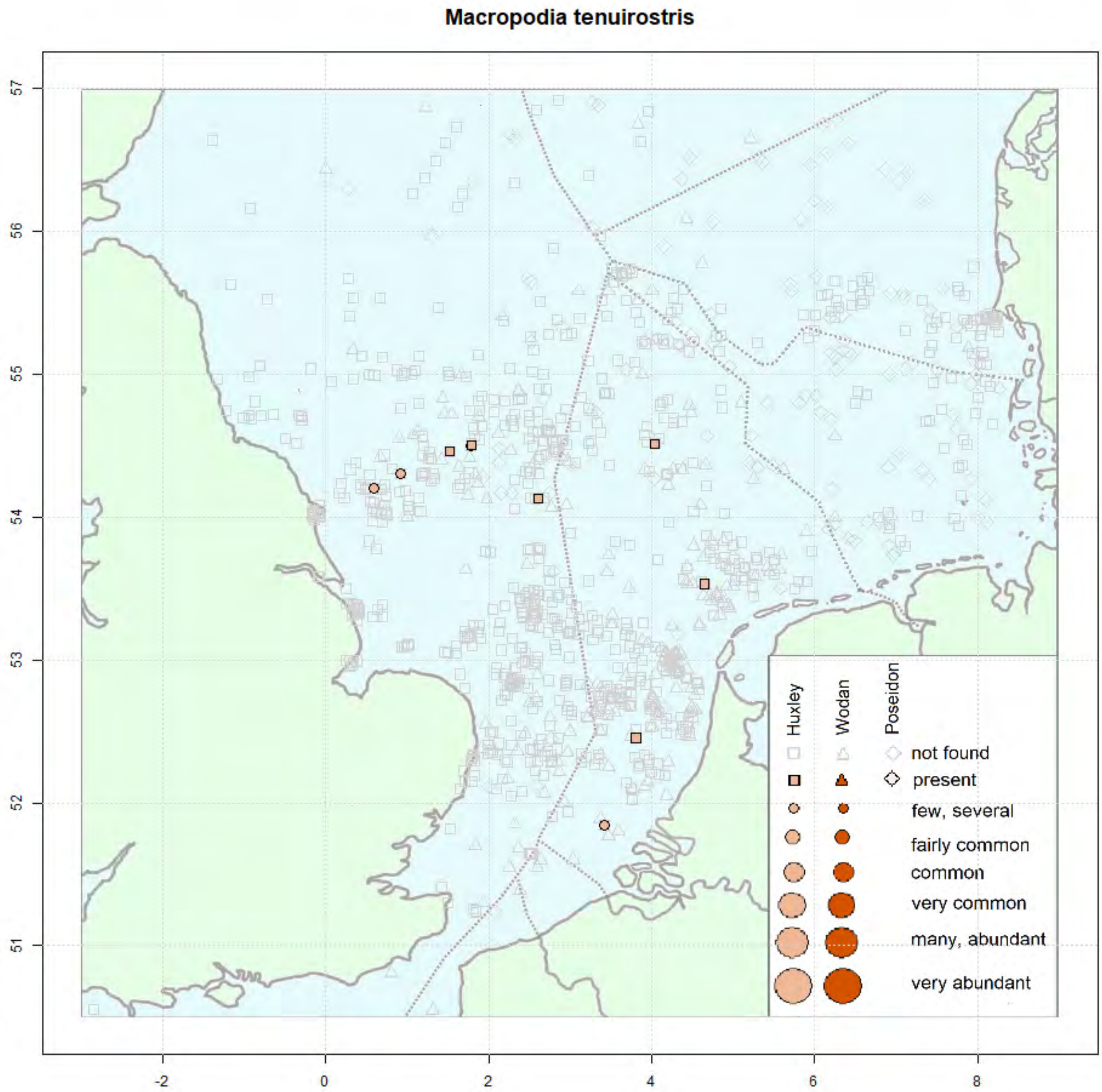
2000 distribution map (Callaway *et al.* , 2002).



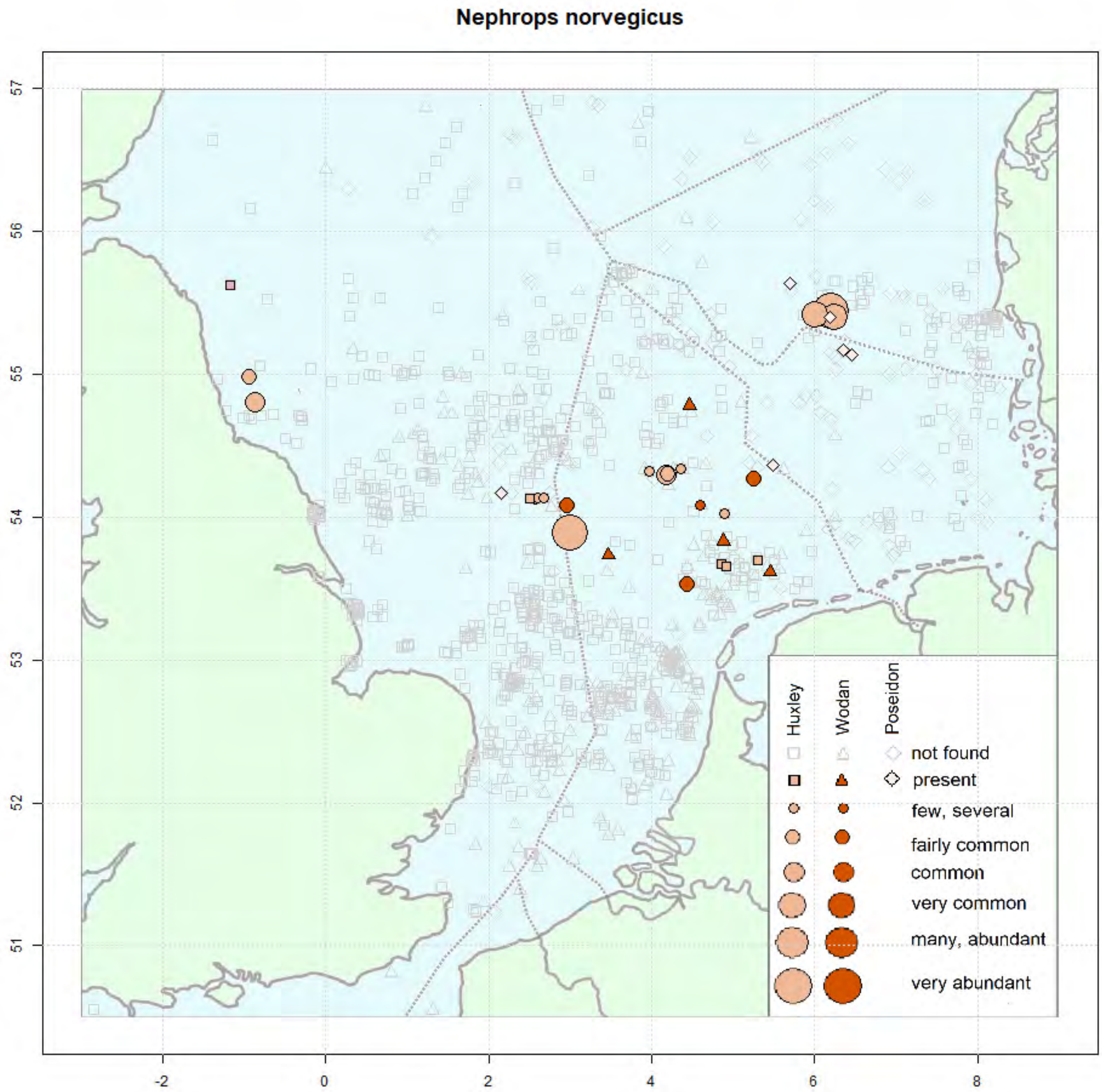
Liocarcinus holsatus Flying crab



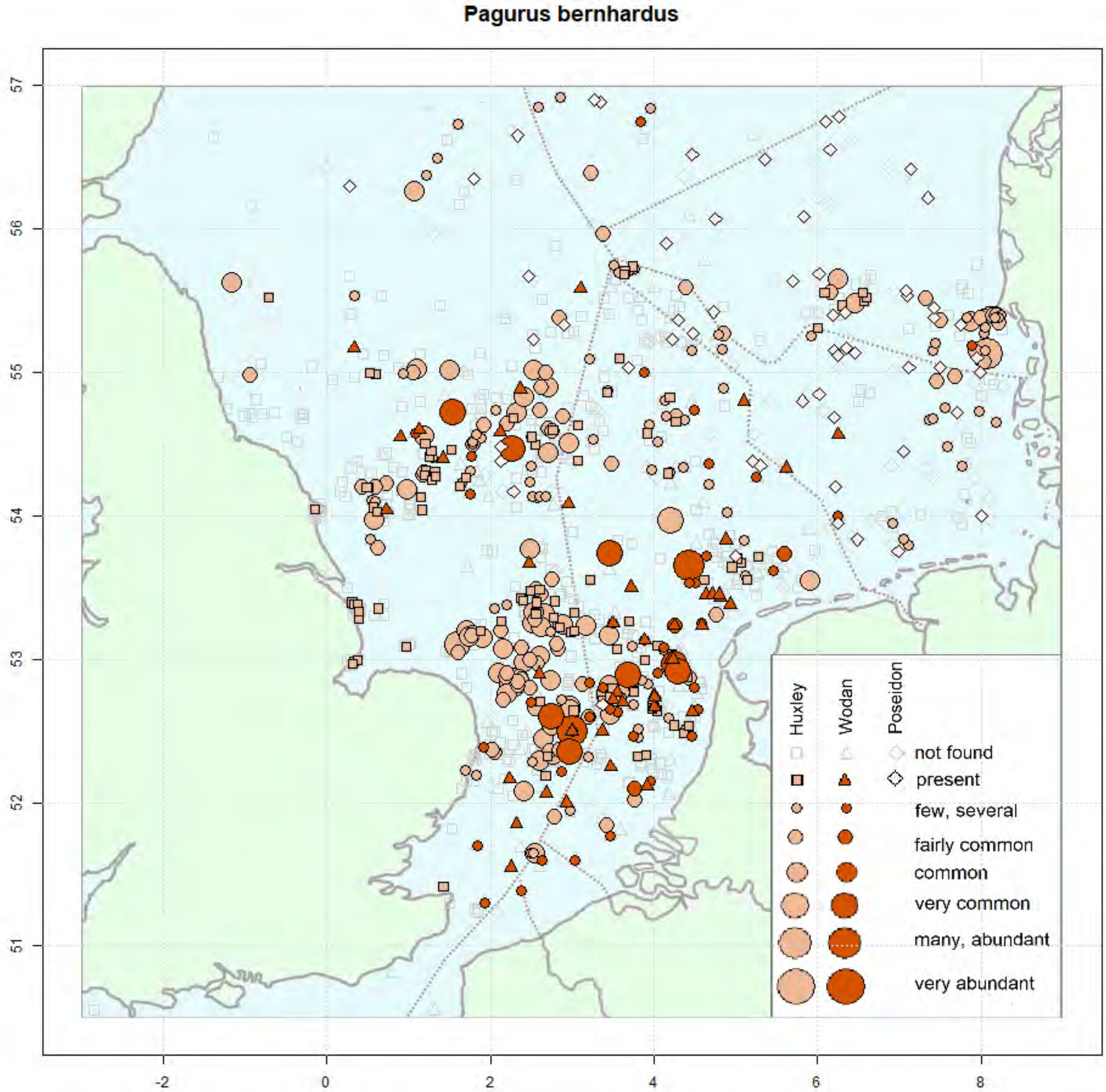
Lithodes maja Stone king crab



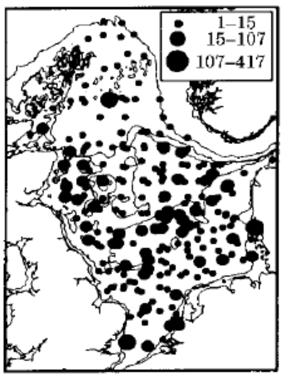
Macropodia tenuirostris Slender spider crab



Nephrops norvegicus Scampi (Norway lobster)

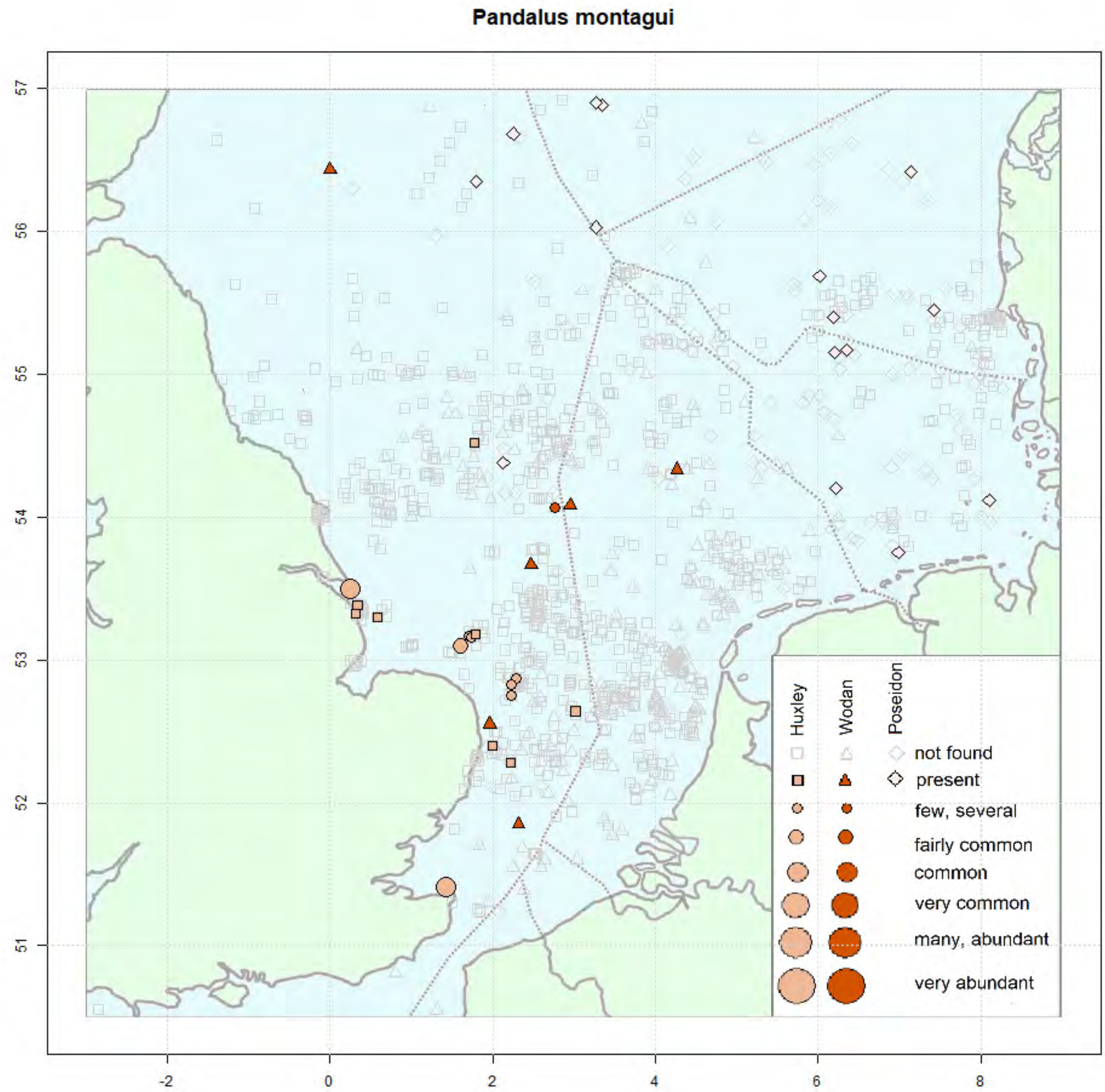


Pagurus bernhardus Common hermit crab

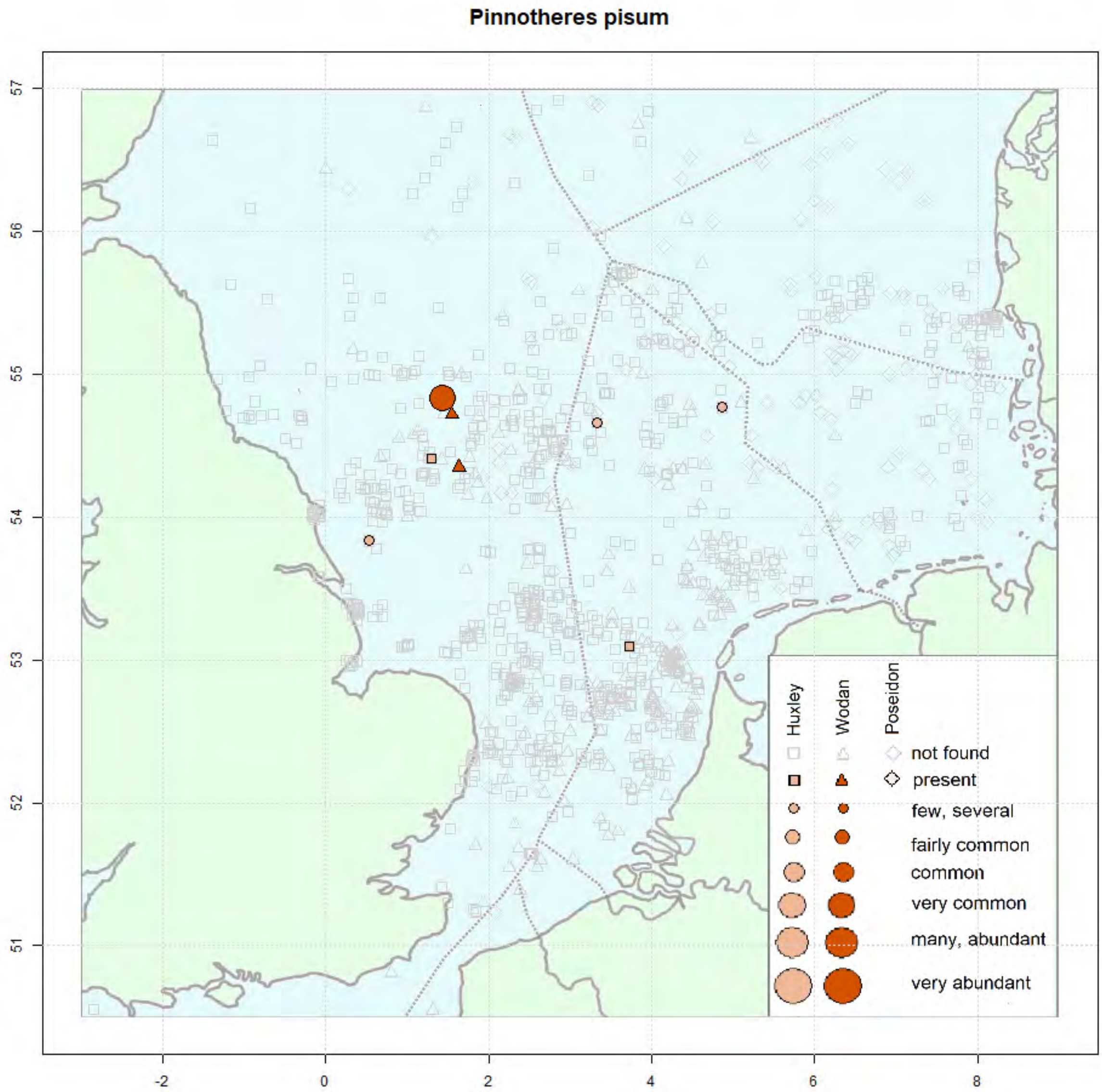


(a) *Pagurus bernhardus*

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

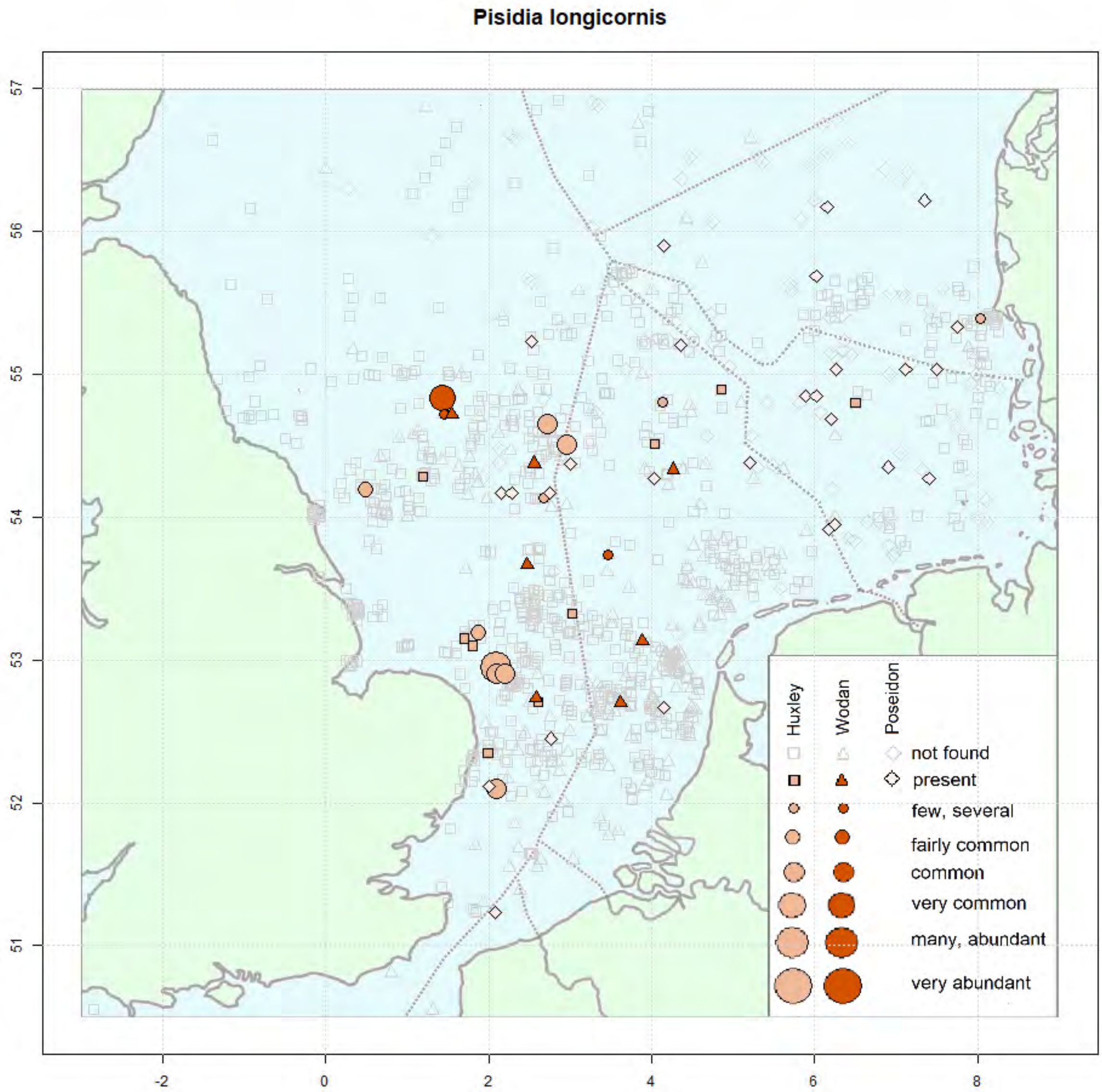


Pandalus montagui Humpback prawn



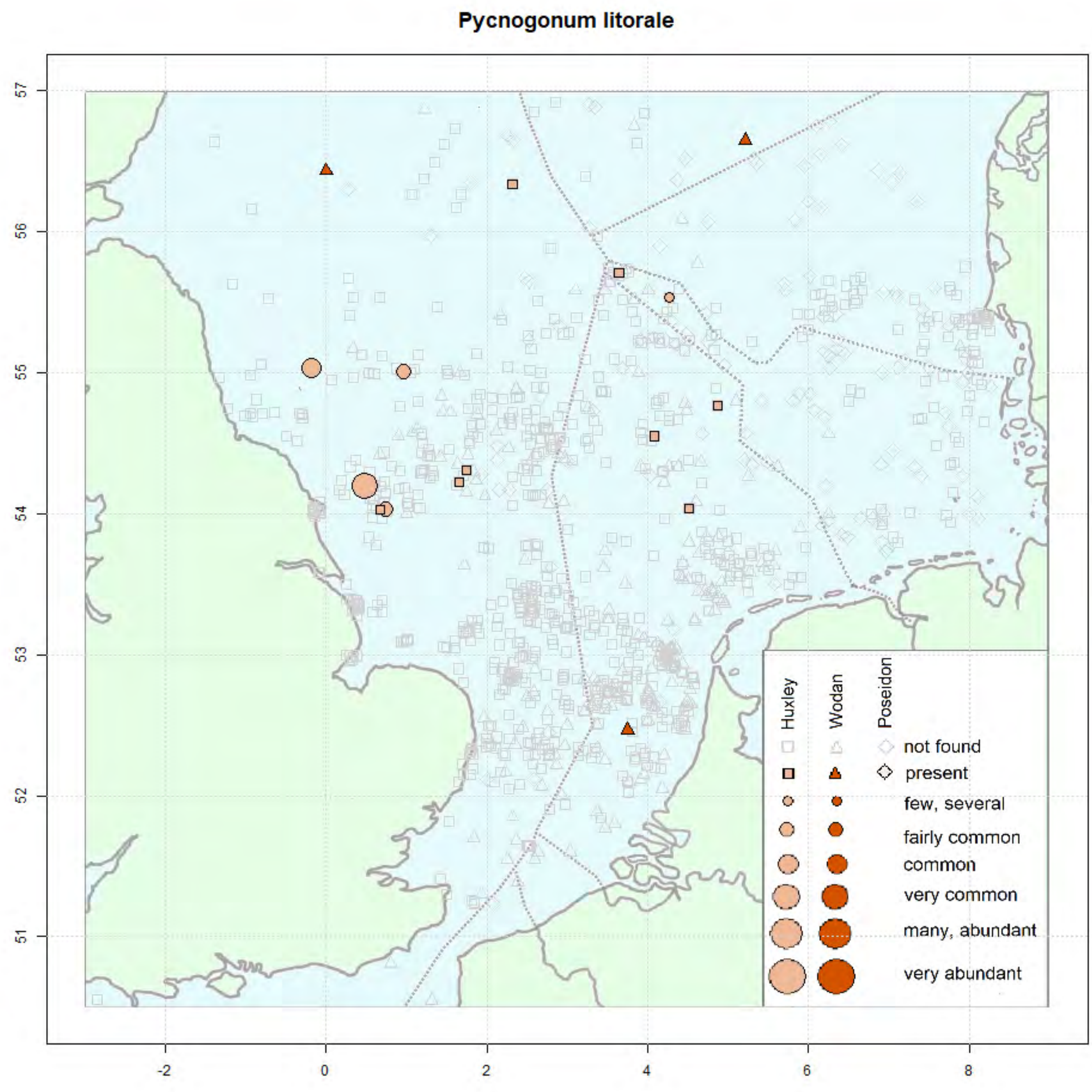
Pinnotheres pisum Pea crab

Found in *Modiolus modiolus*



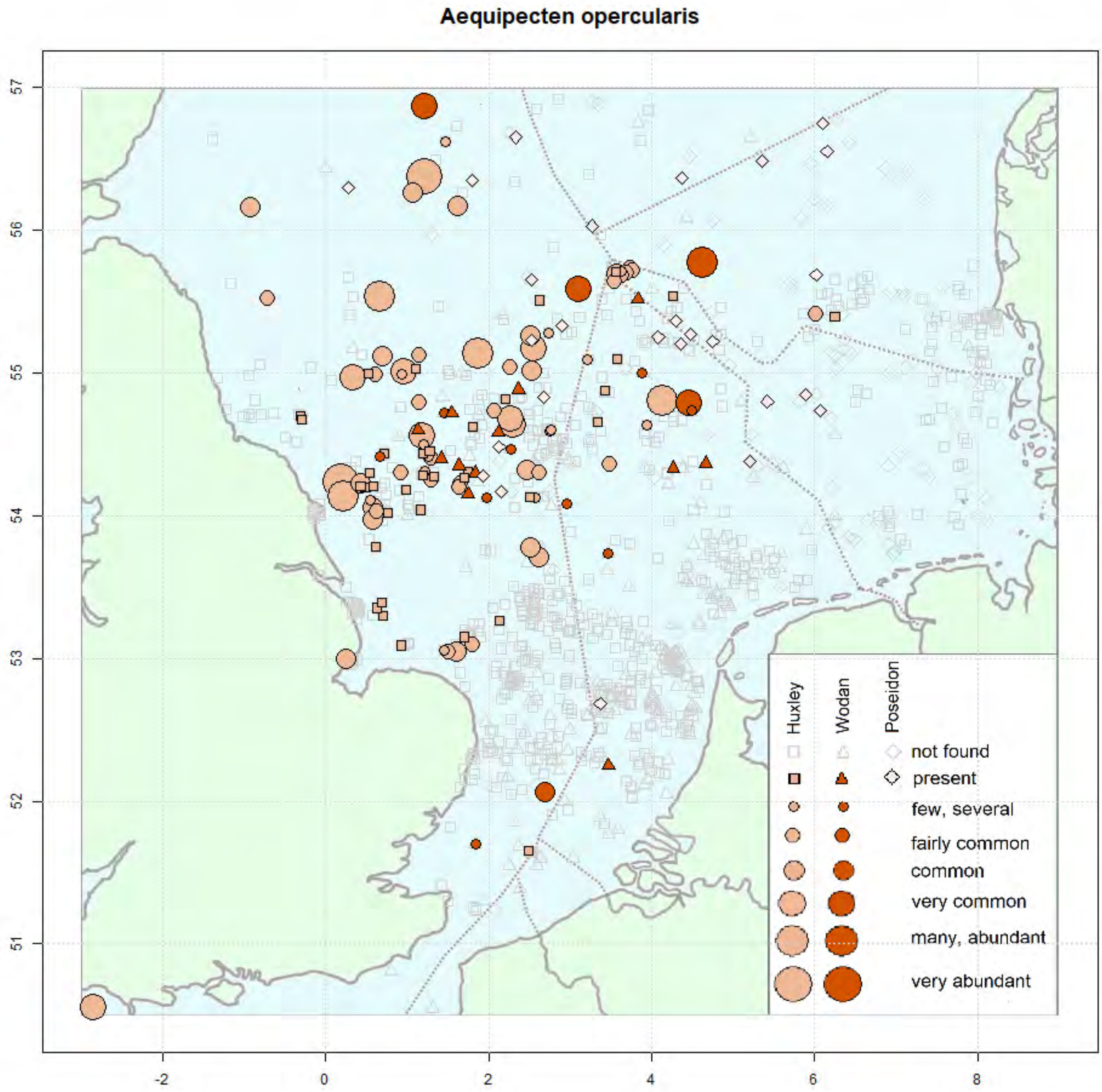
Pisidia longicornis	Long-clawed porcelain crab

Arthropoda – Pycnogonida

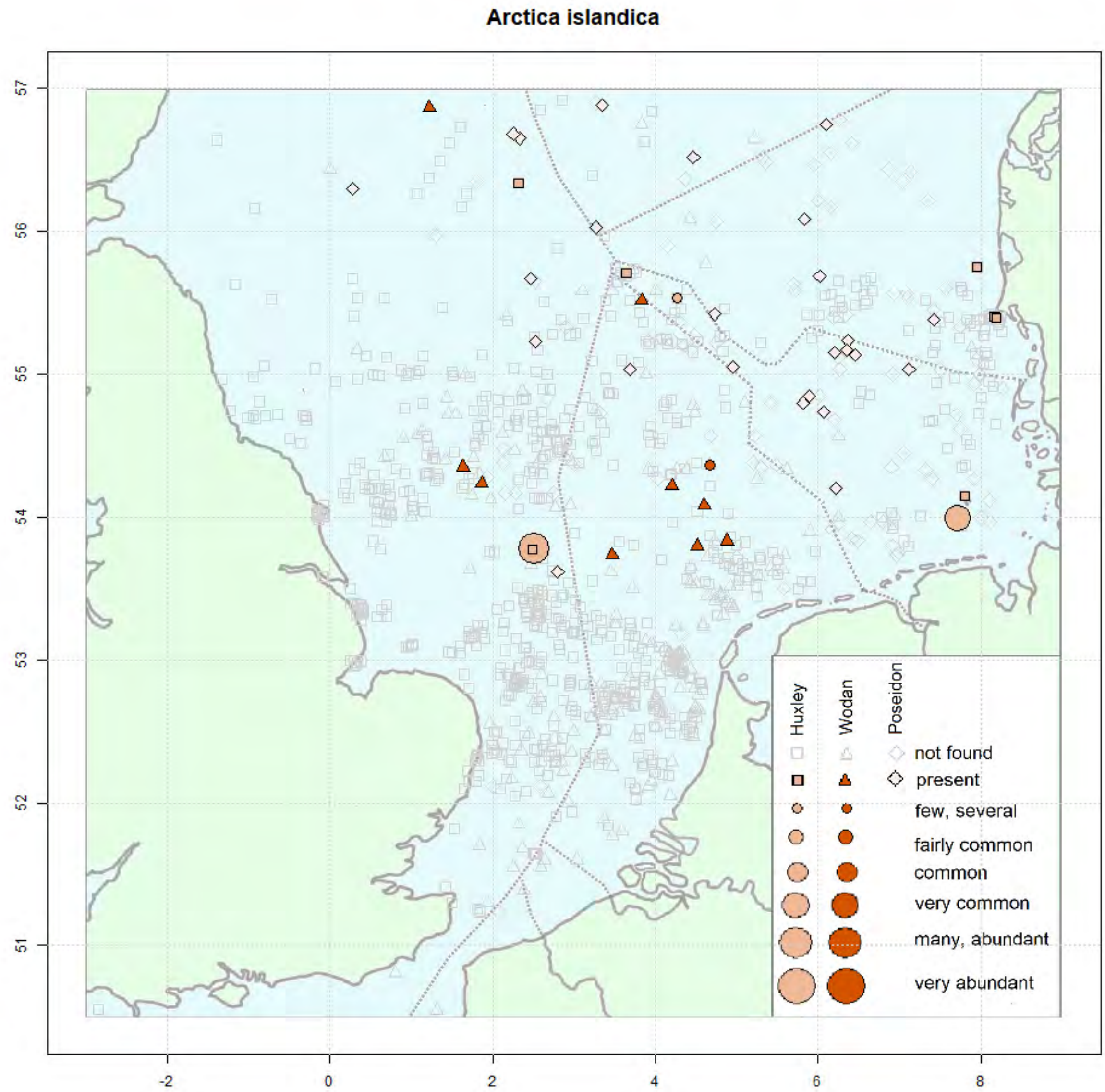


Pycnogonum littorale A sea spider

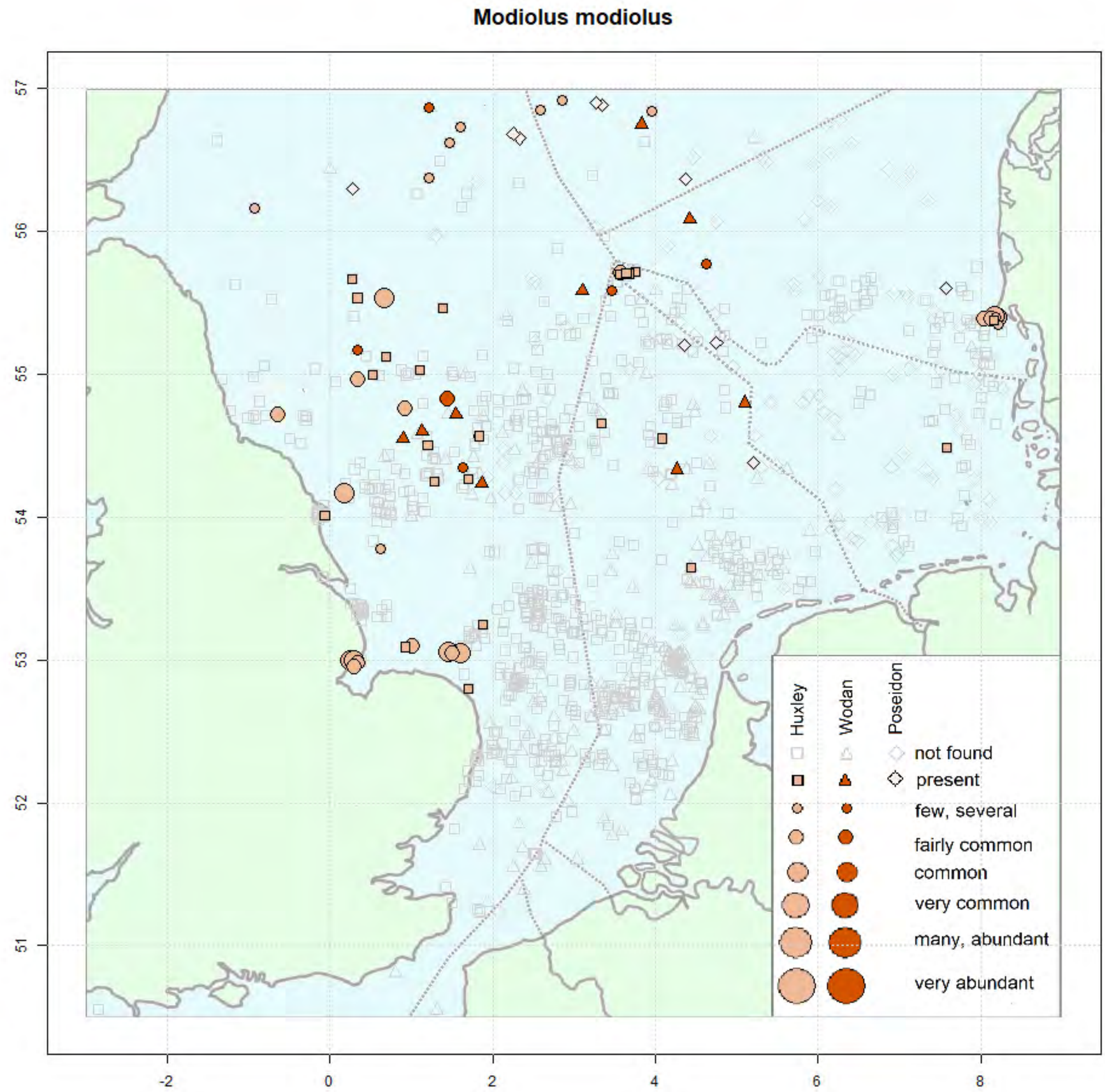
Mollusca-Bivalvia



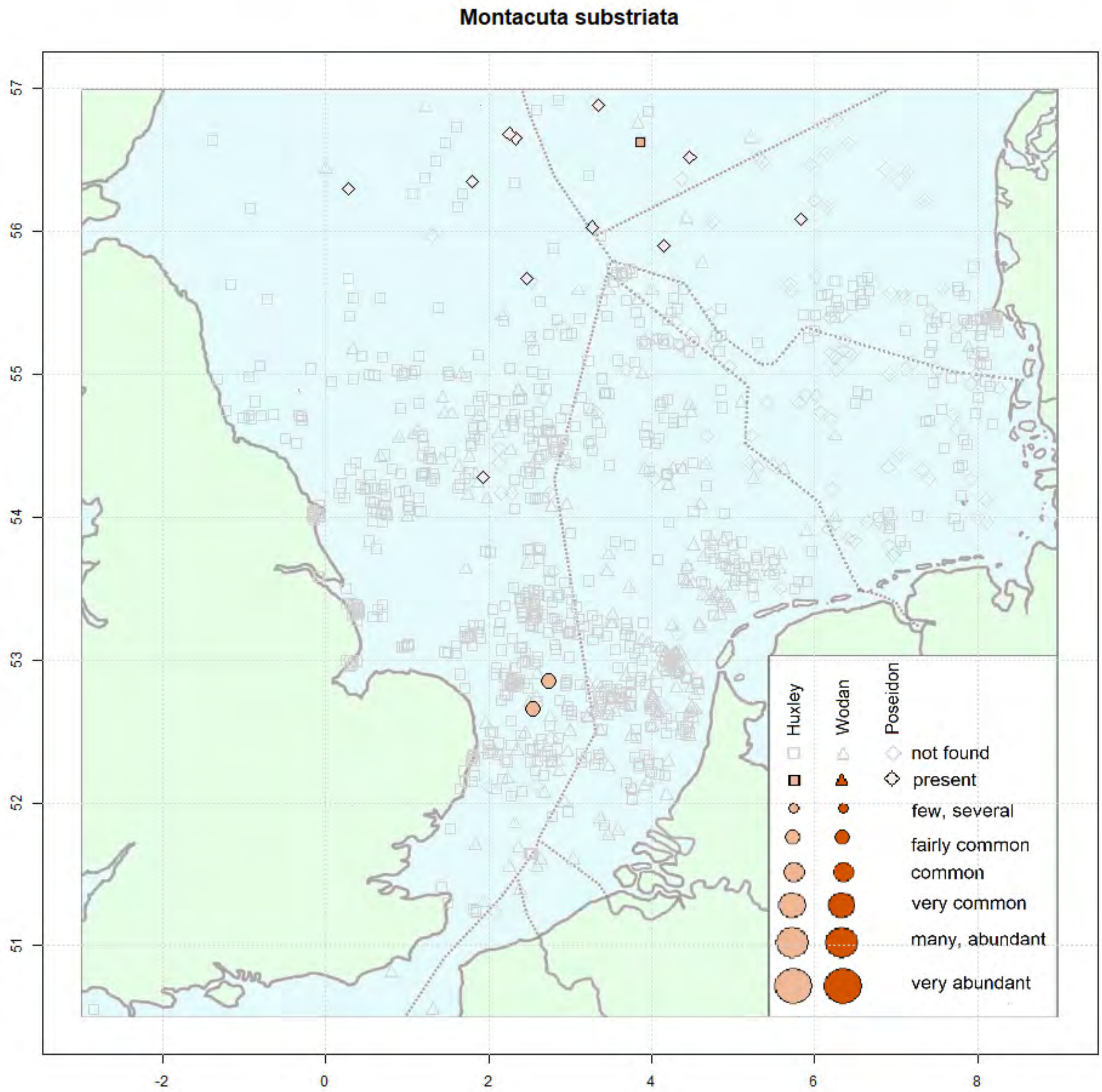
Aequipecten opercularis Queen scallop



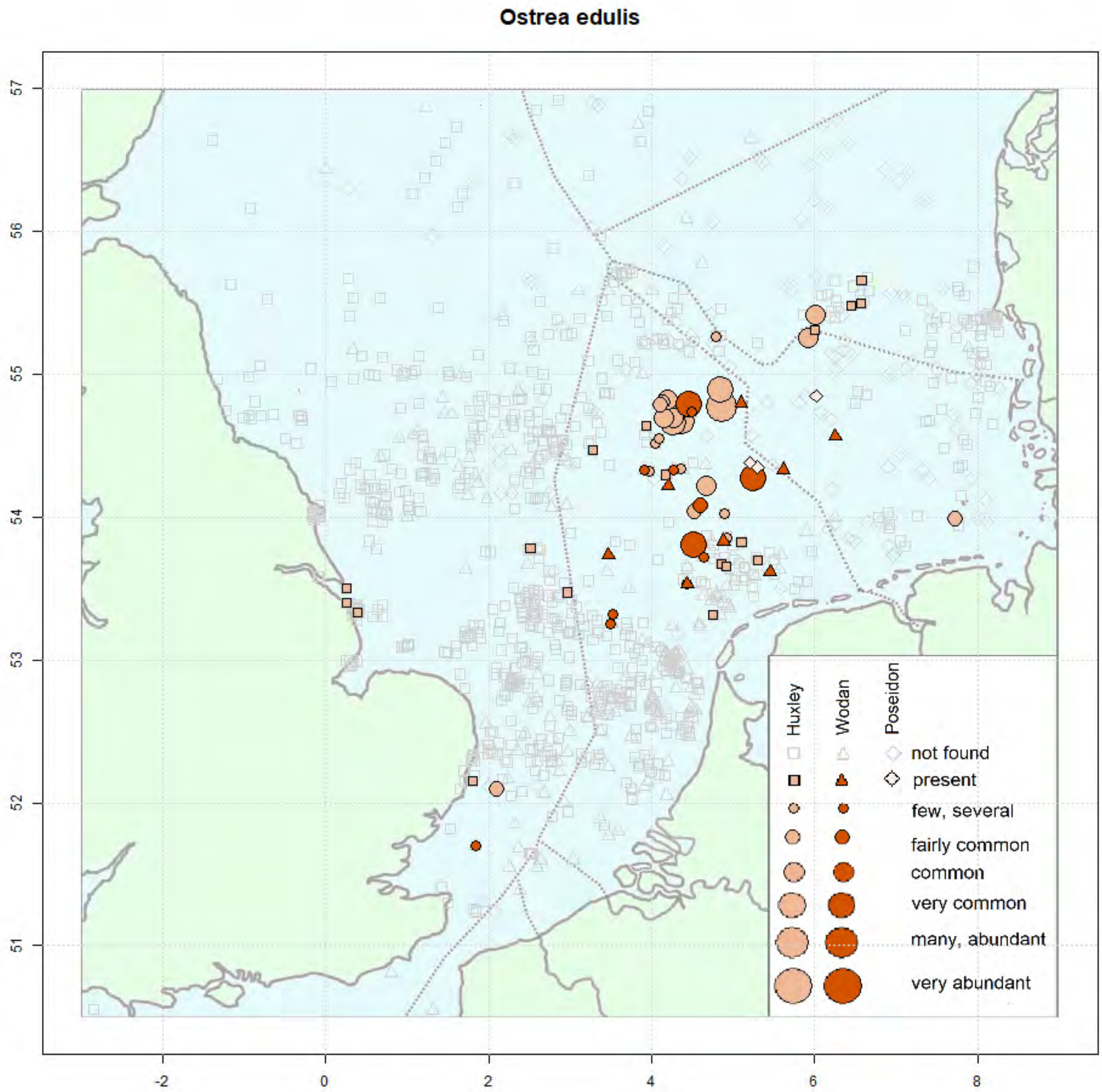
Arctica islandica Icelandic cyprine



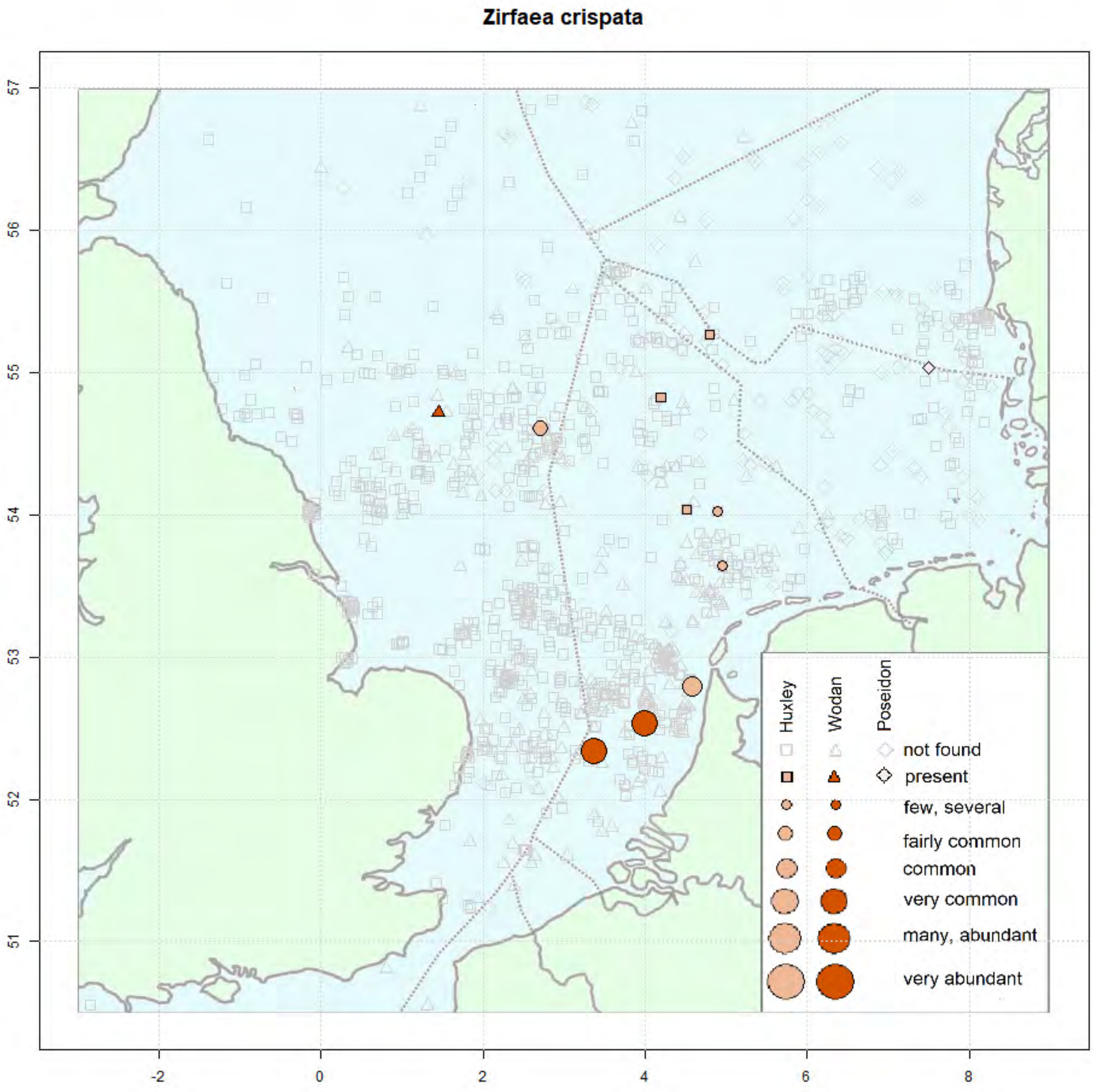
Modiolus modiolus Horse mussel



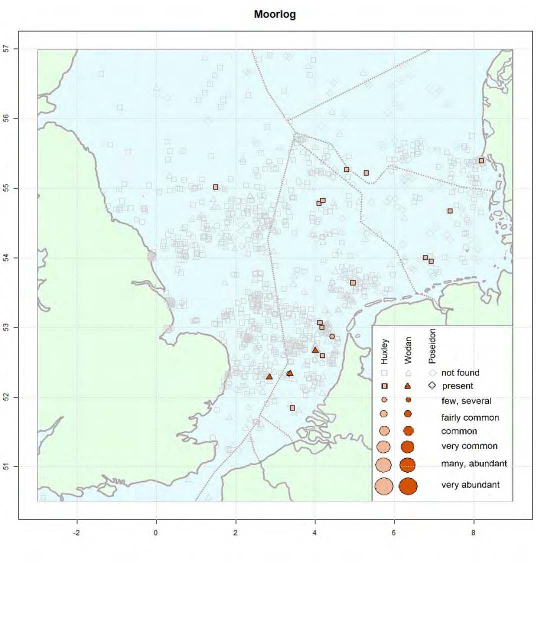
Montacuta substriata Substriated montacutid



Ostrea edulis Flat oyster

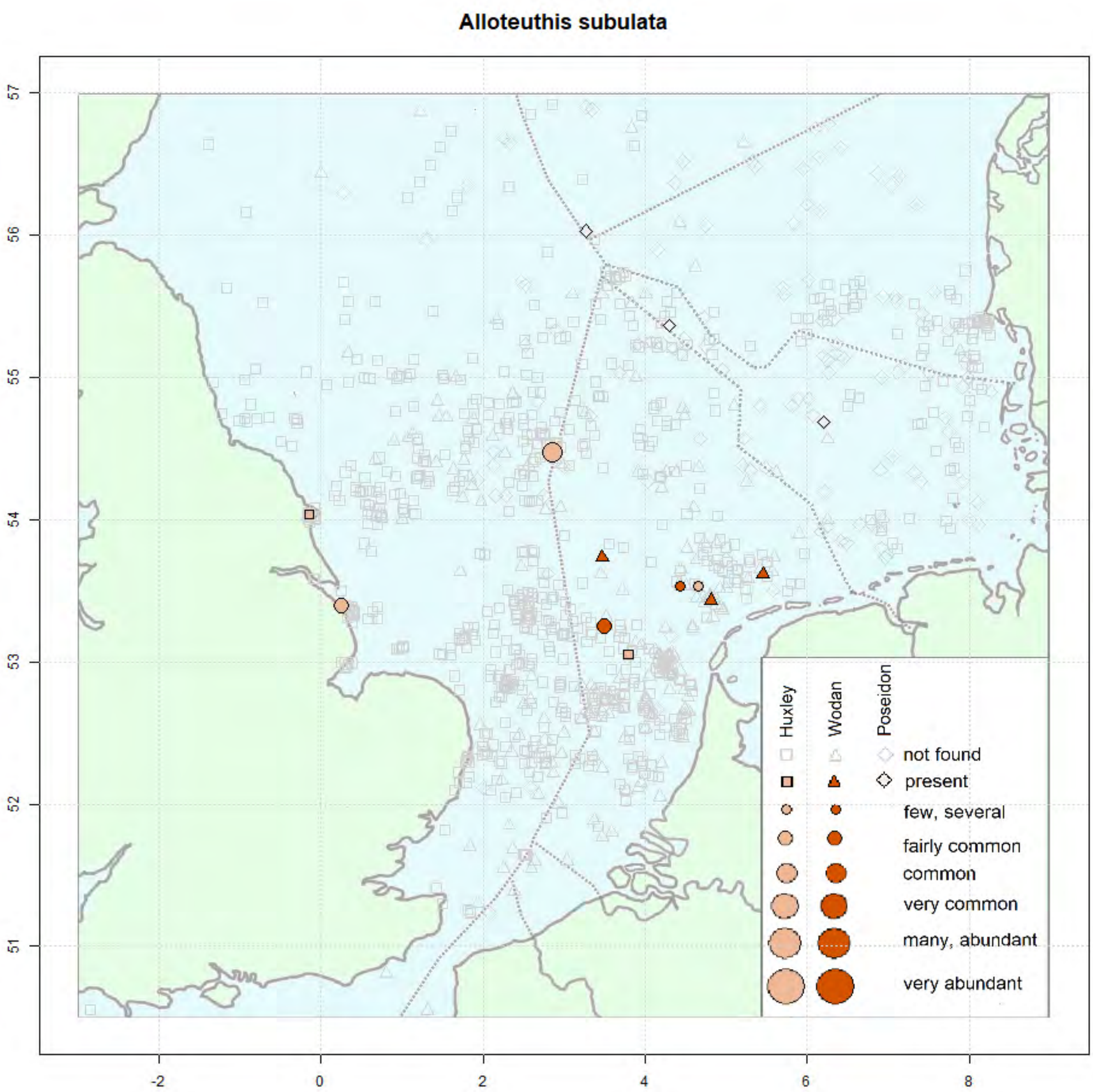


Zirfaea crispata Oval piddock (found in moorlog)

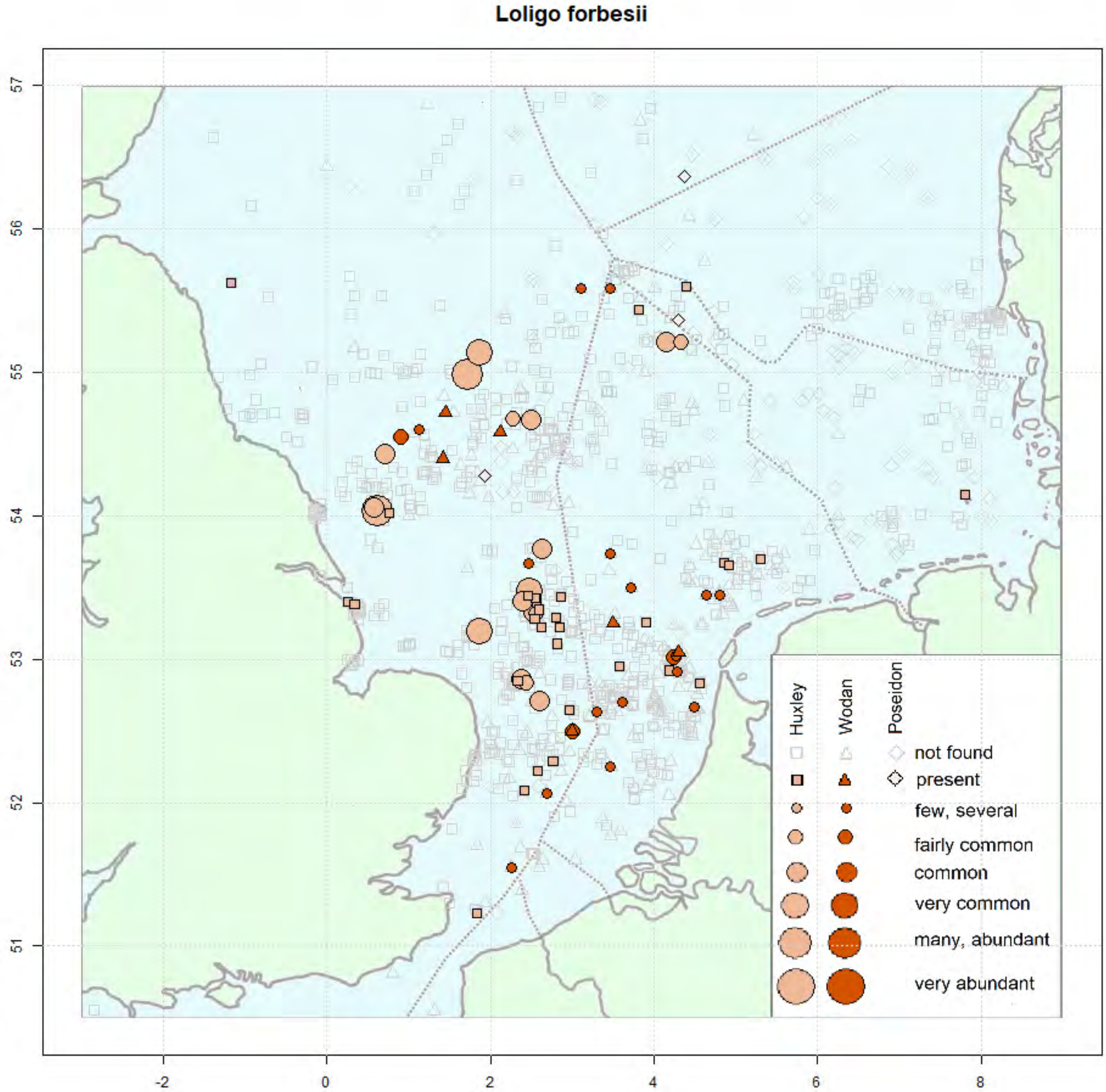


Moorlog (peat).

Mollusca-Cephalopoda

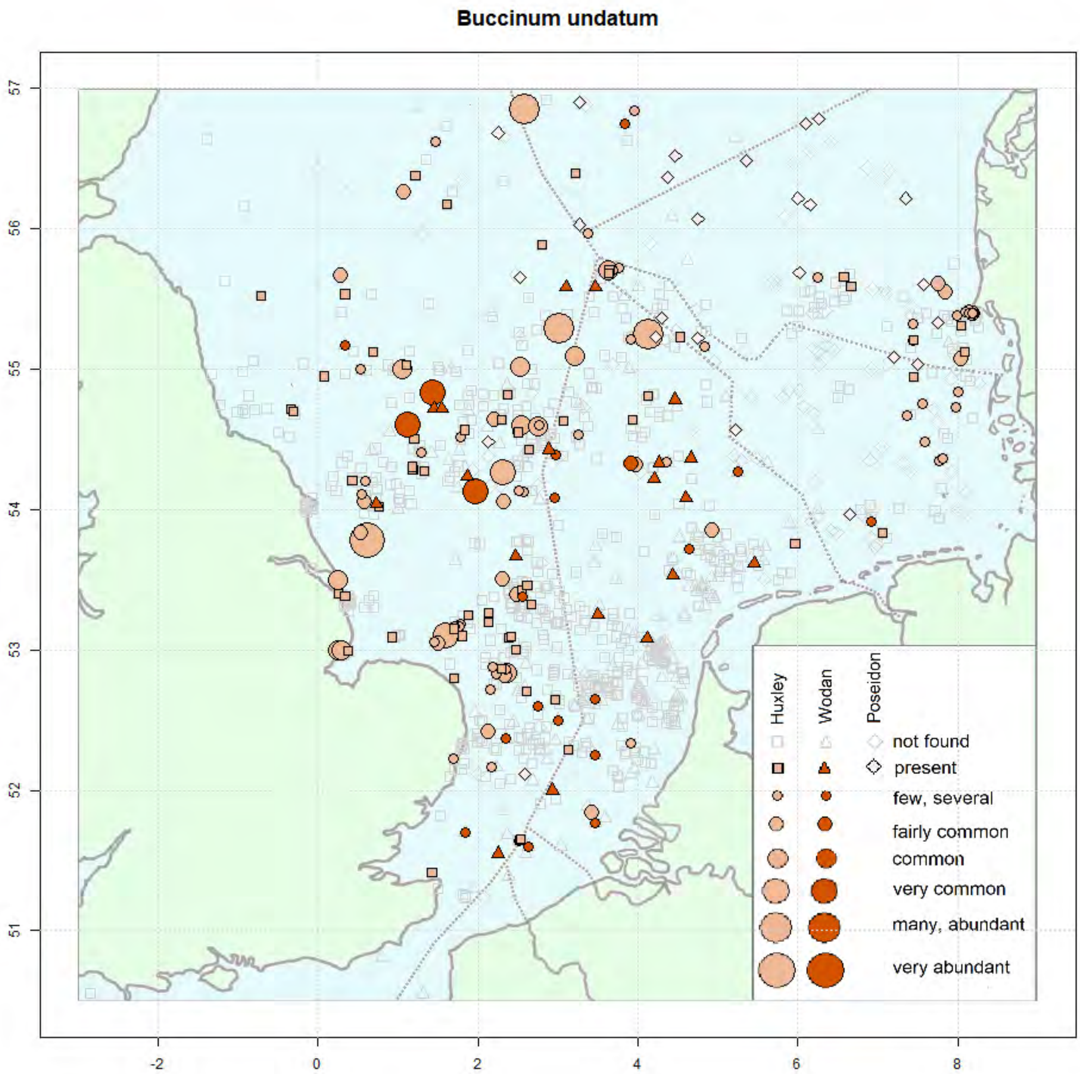


Alloteuthis subulata Little squid



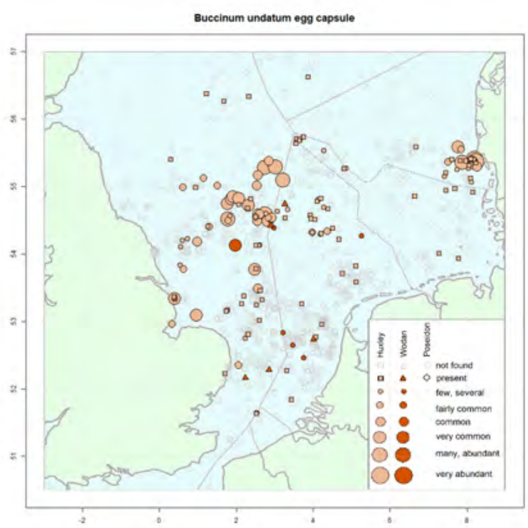
Loligo forbesii Long-finned squid

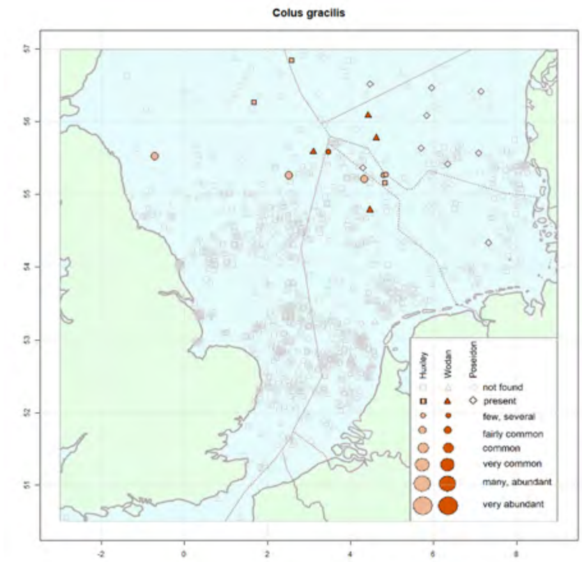
Mollusca-Gastropoda



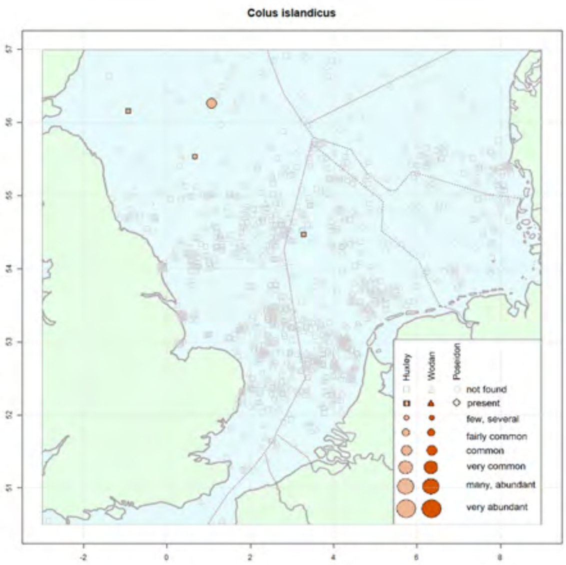
Buccinum undatum Common whelk

Buccinum undatum egg cases

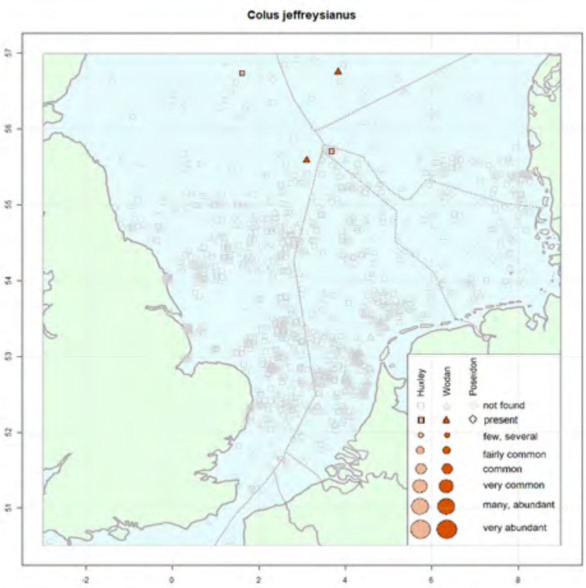




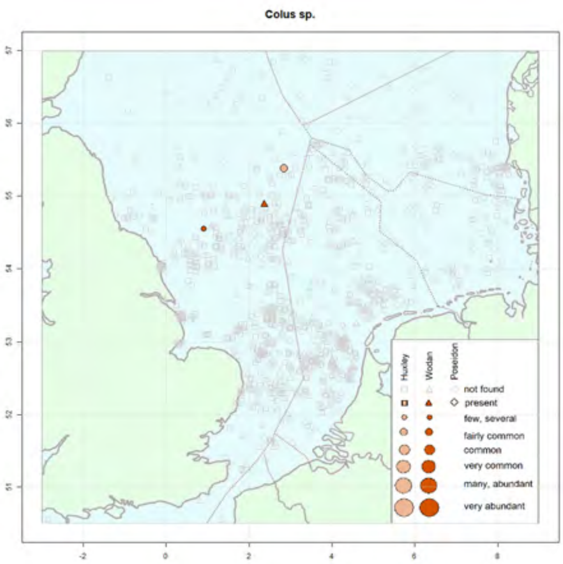
Colus gracilis Slender colus



Colus islandicus Islandic colus



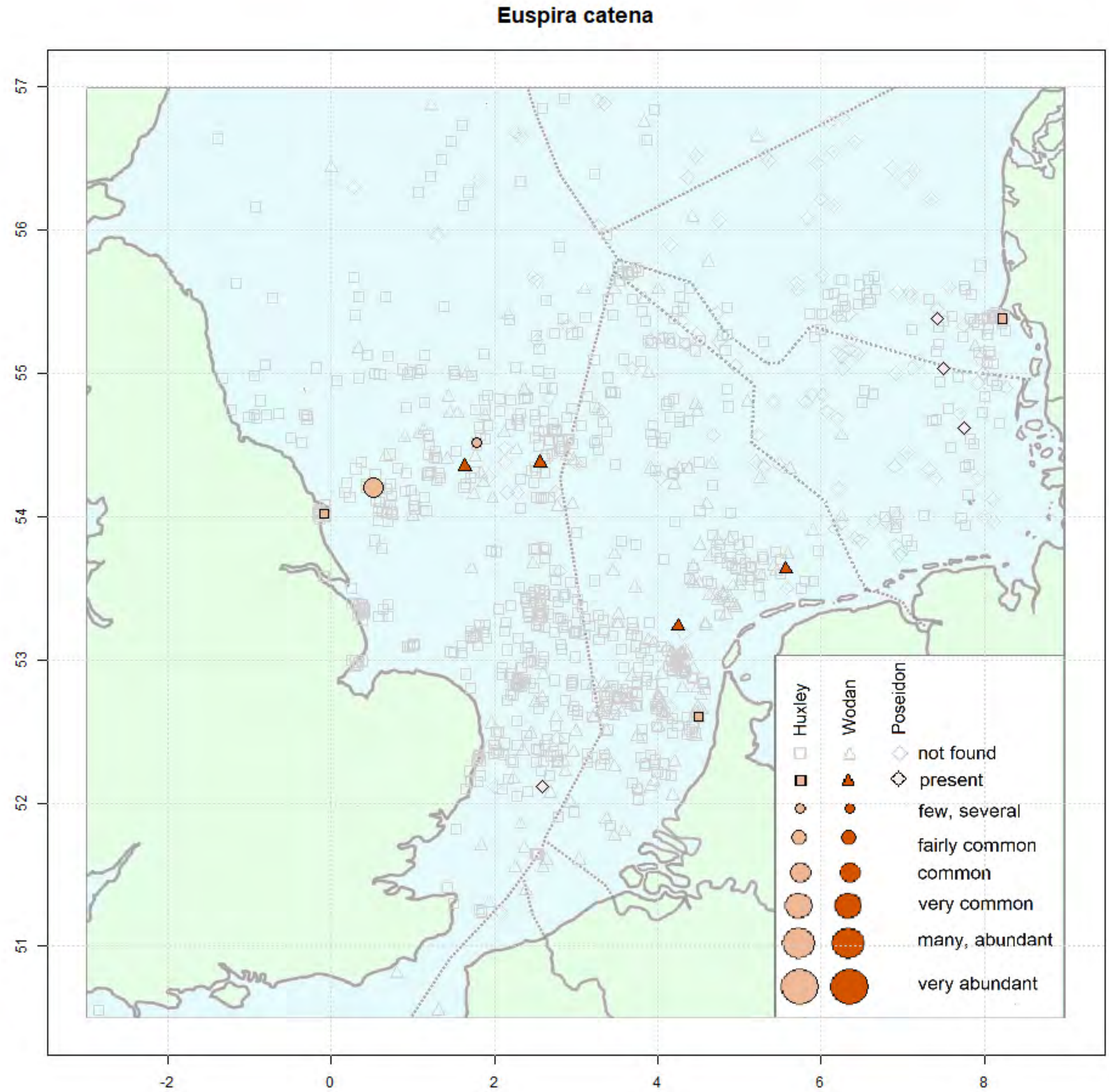
Colus jeffreysianus Jeffrey's colus



Colus sp. Colus

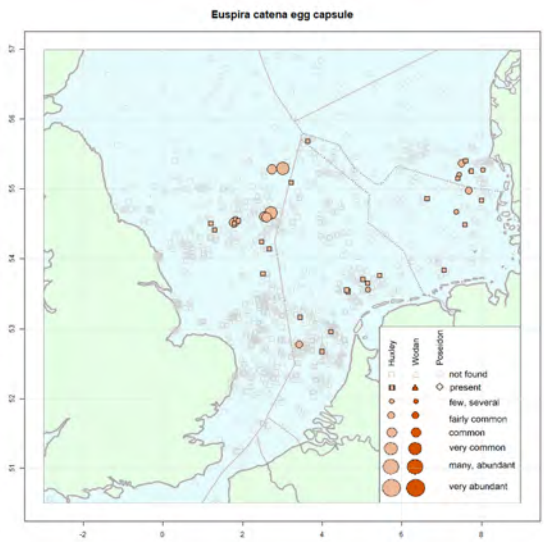
Colus sp. as indicated by Huxley naturalists.

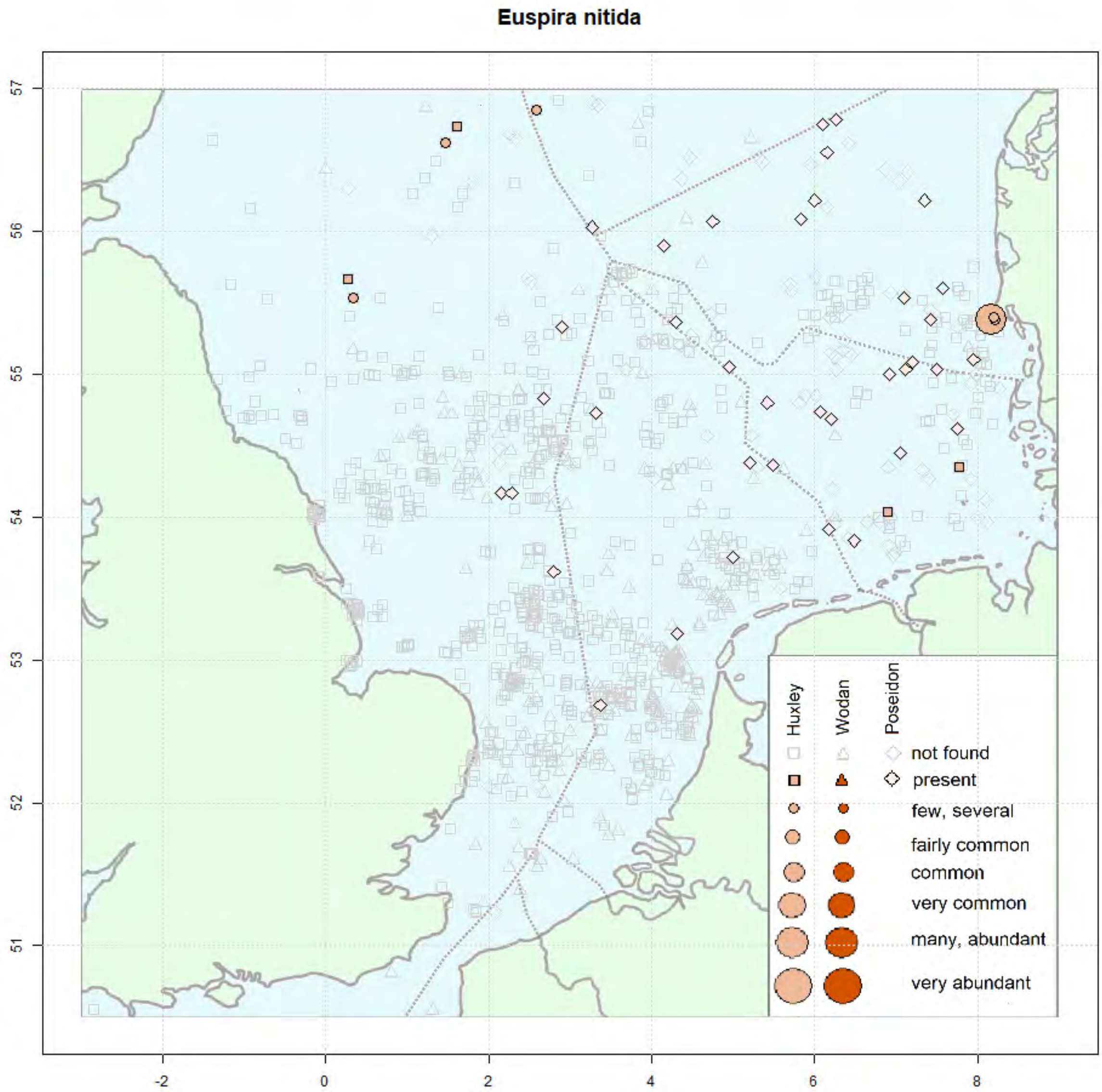
Colus sp. in Figure 6 and 8 represents all the *Colus* species data joined.



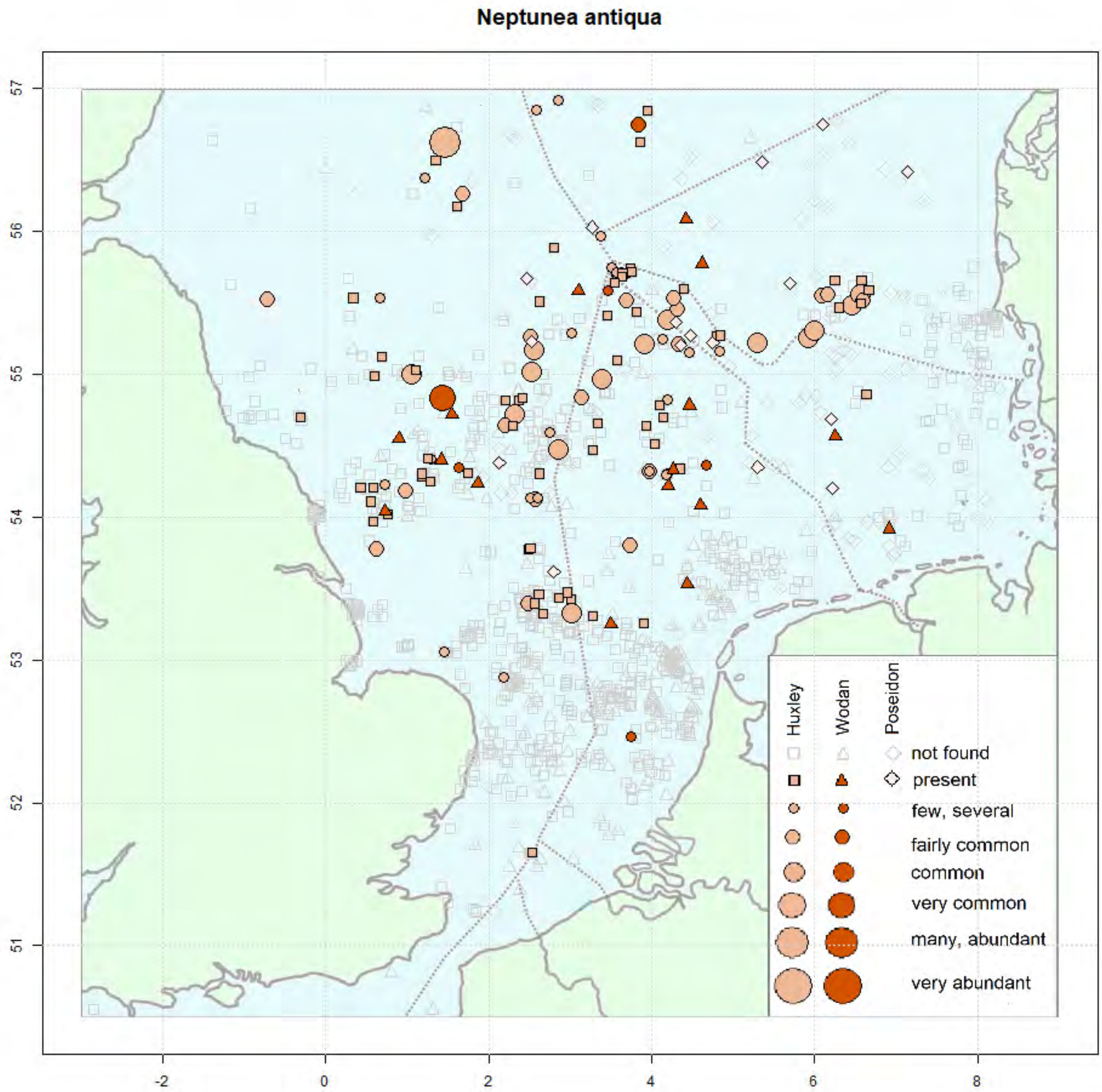
Euspira catena Spotted necklace snail

Euspira catena egg capsules.

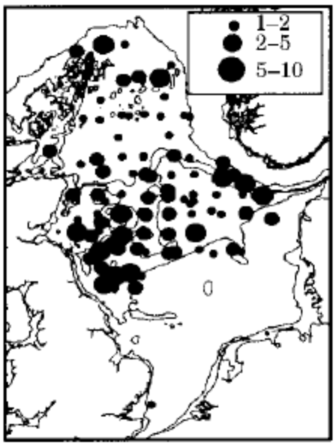




Euspira nitida Alder's necklace snail



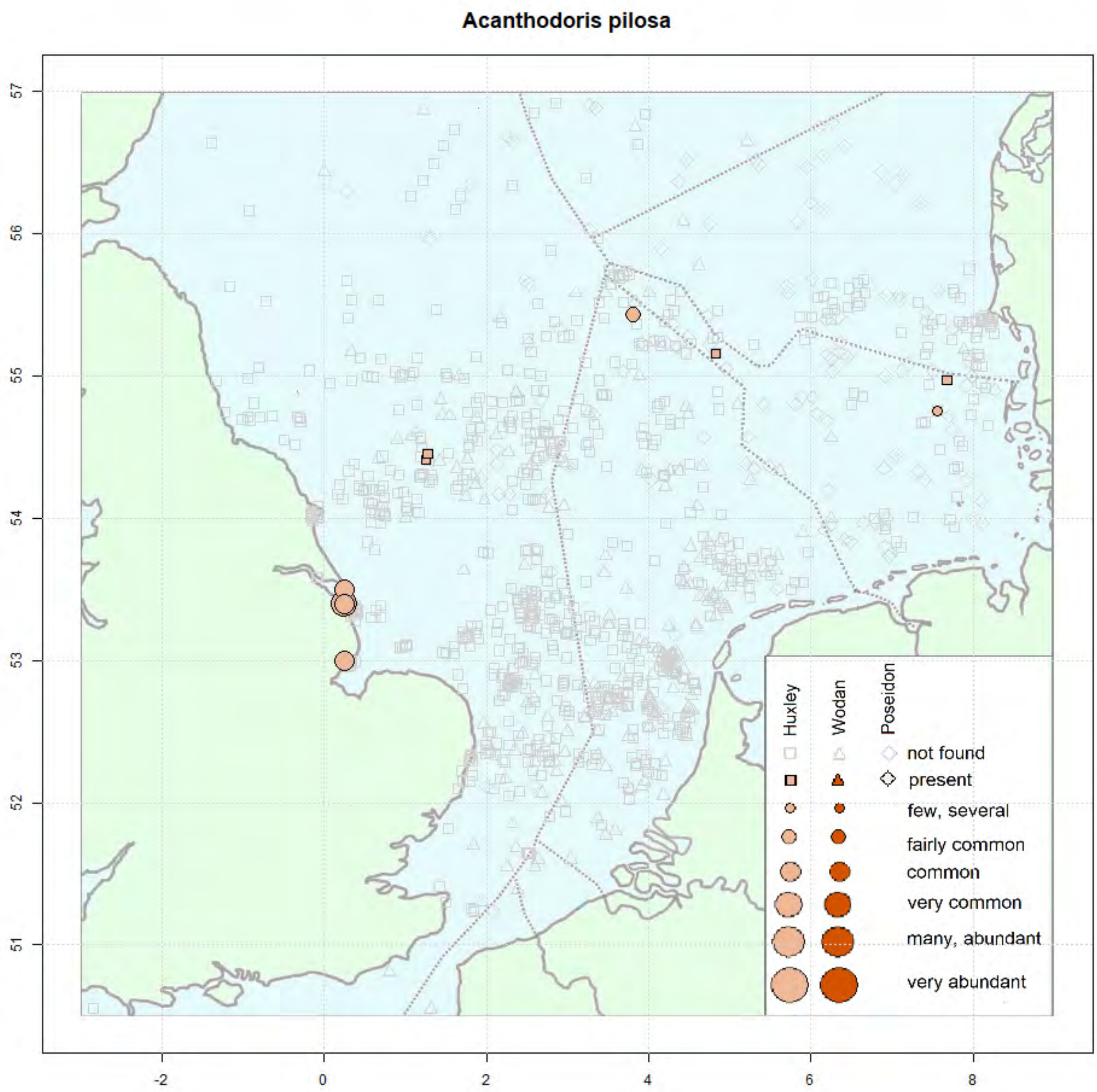
Neptunea antiqua Red whelk



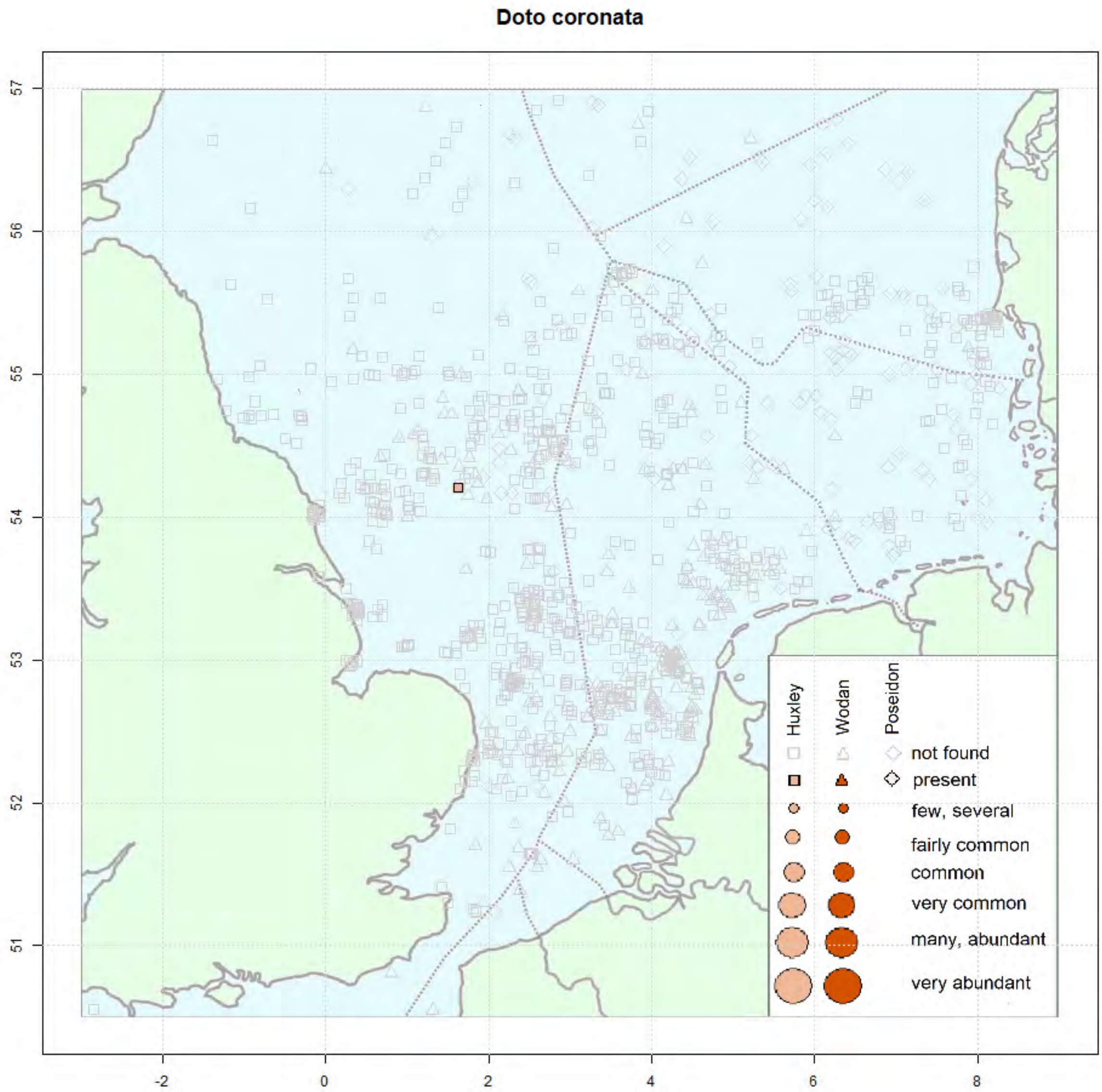
(f) *Neptunea antiqua*

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

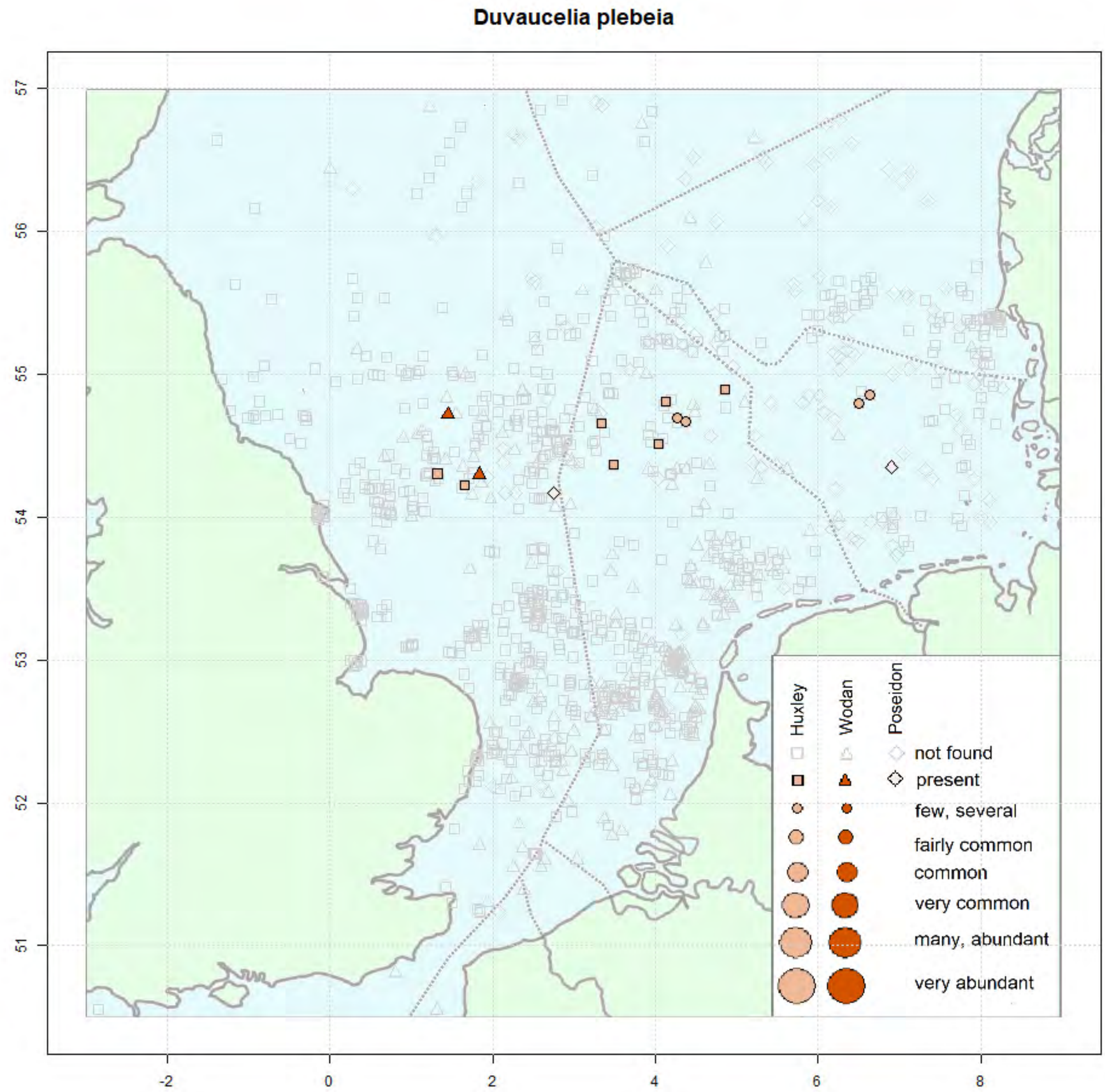
Mollusca-Gastropoda-Nudibranchia



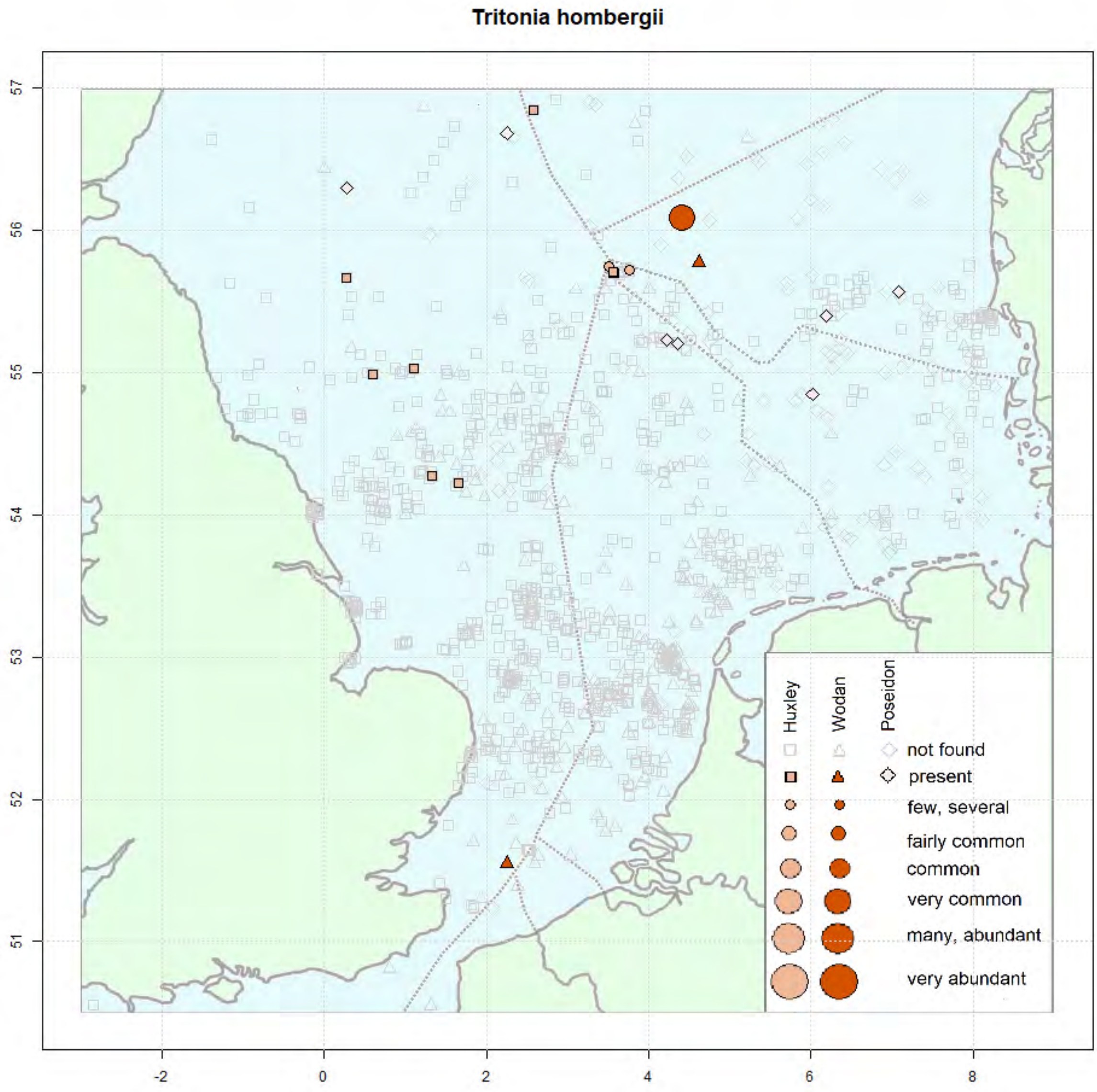
Acanthodoris pilosa Thorny doris



Doto coronata Crowned Doto

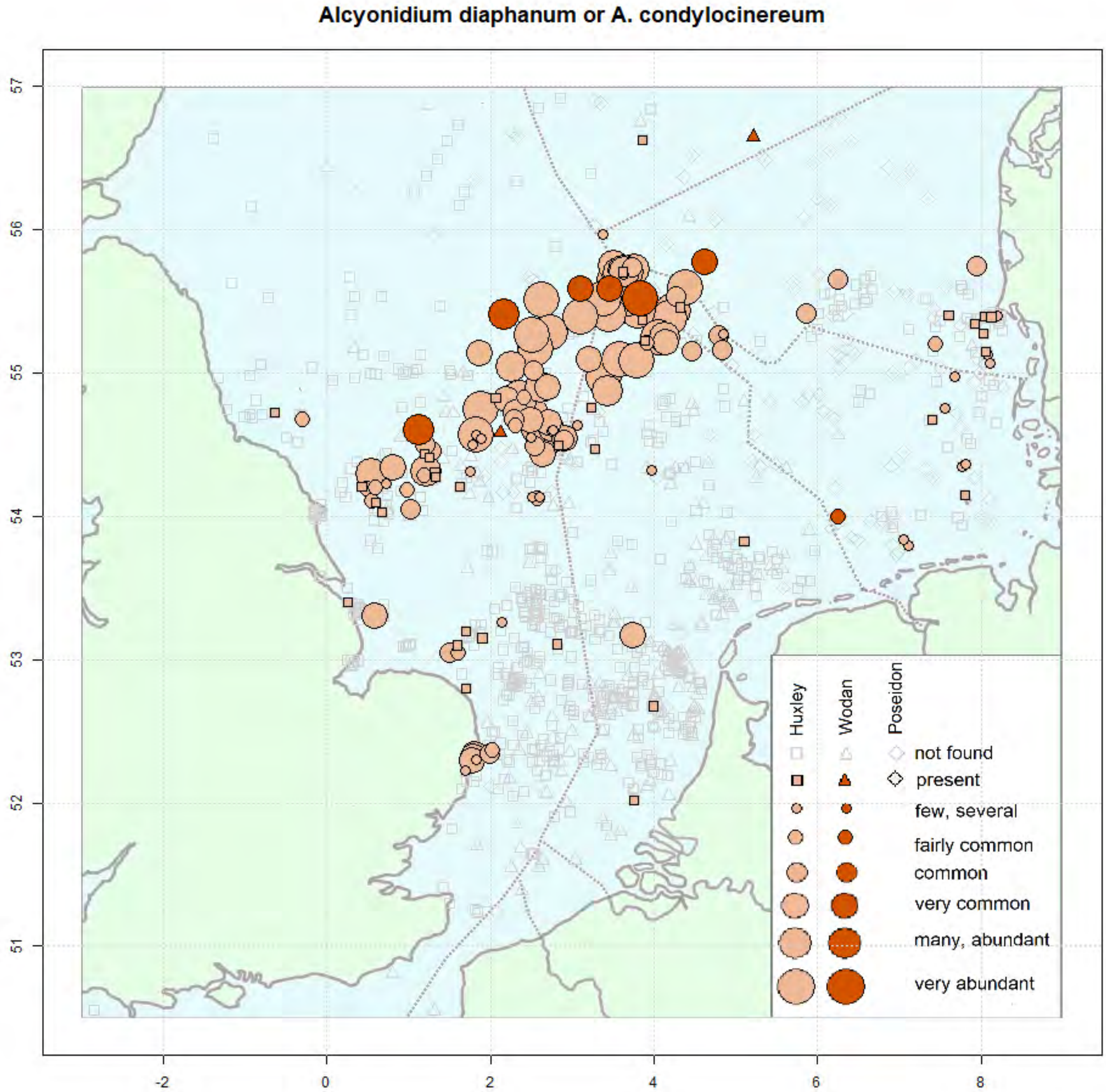


Duvaucelia plebeia A sea slug



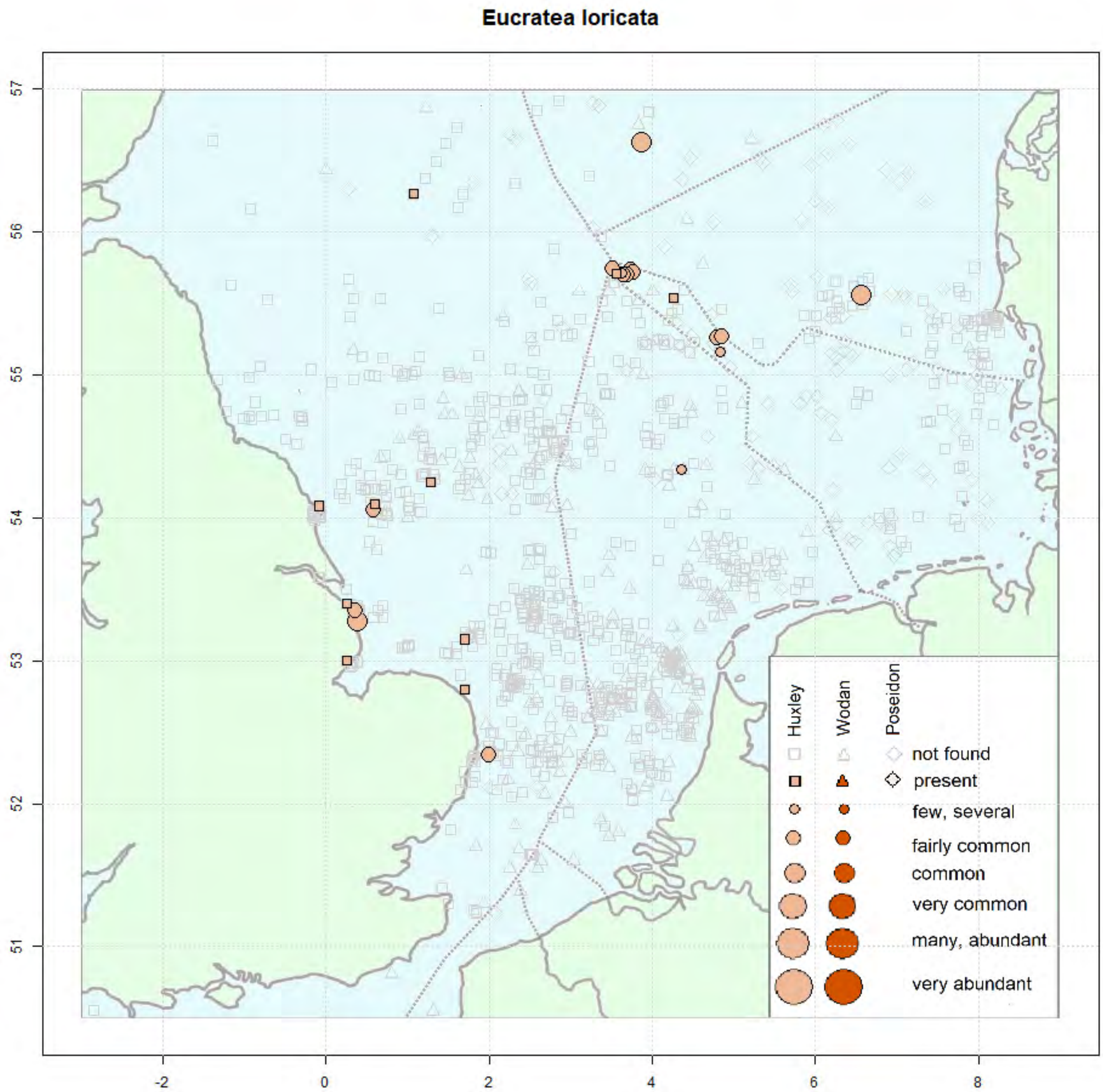
Tritonia hombergii Dead men's finger slug

Bryozoa- Gymnolaemata

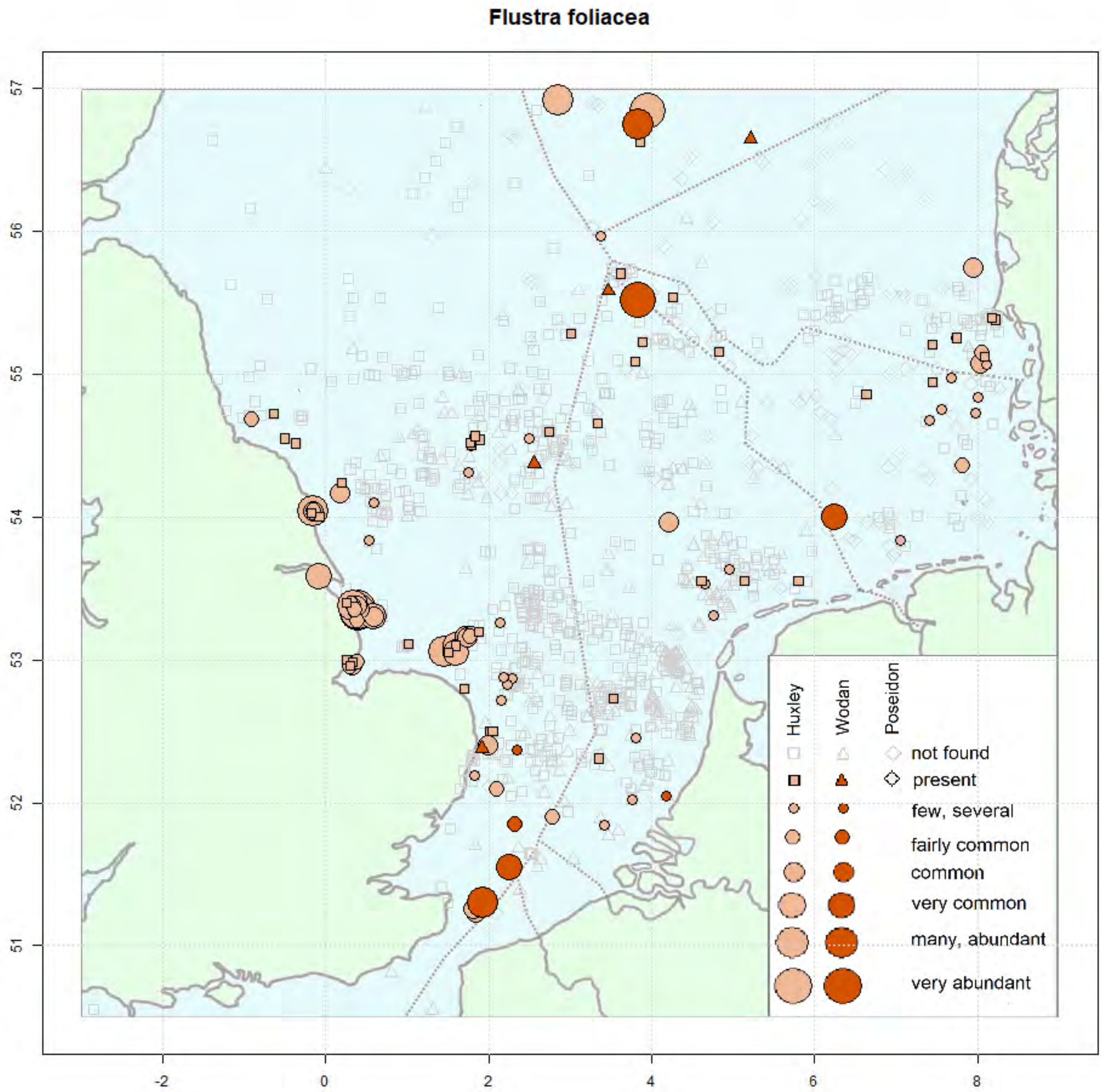


Alcyonidium diaphanum or A. condylocinereum Sea chevil and other Alcyonidium bryozoan

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

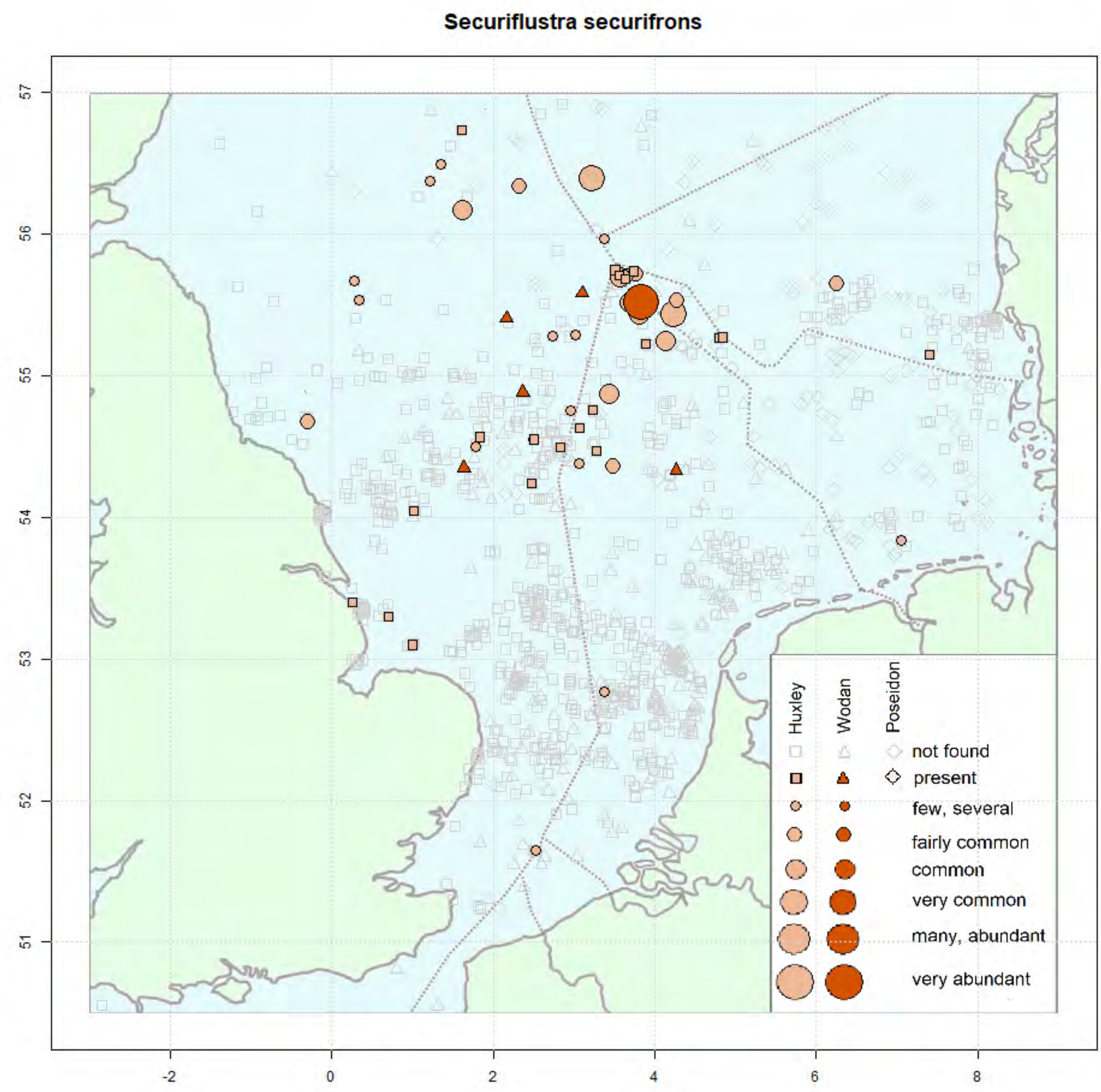


Eucratea loricata Paired bryozoan



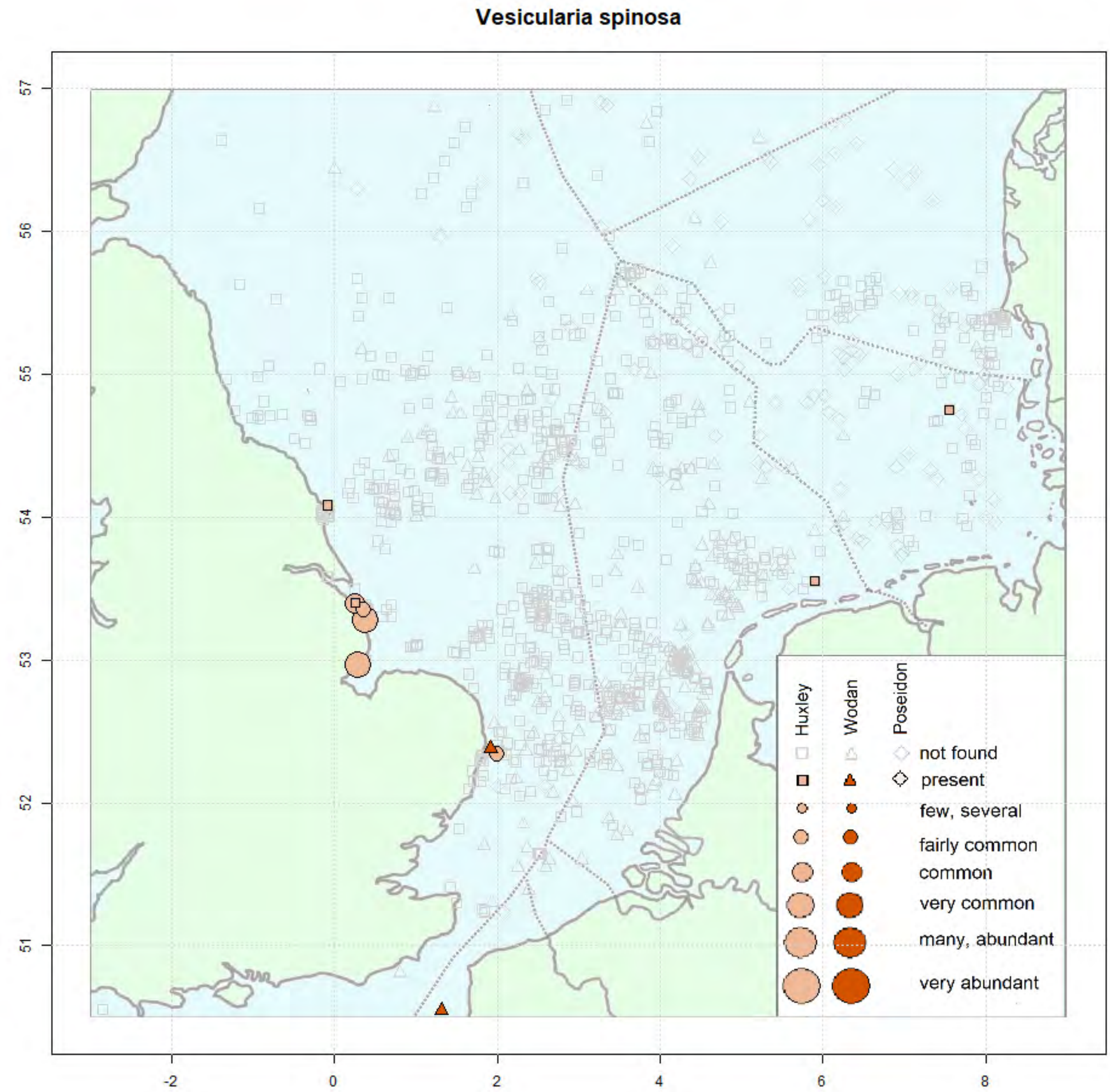
Flustra foliacea Horn wrack

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).



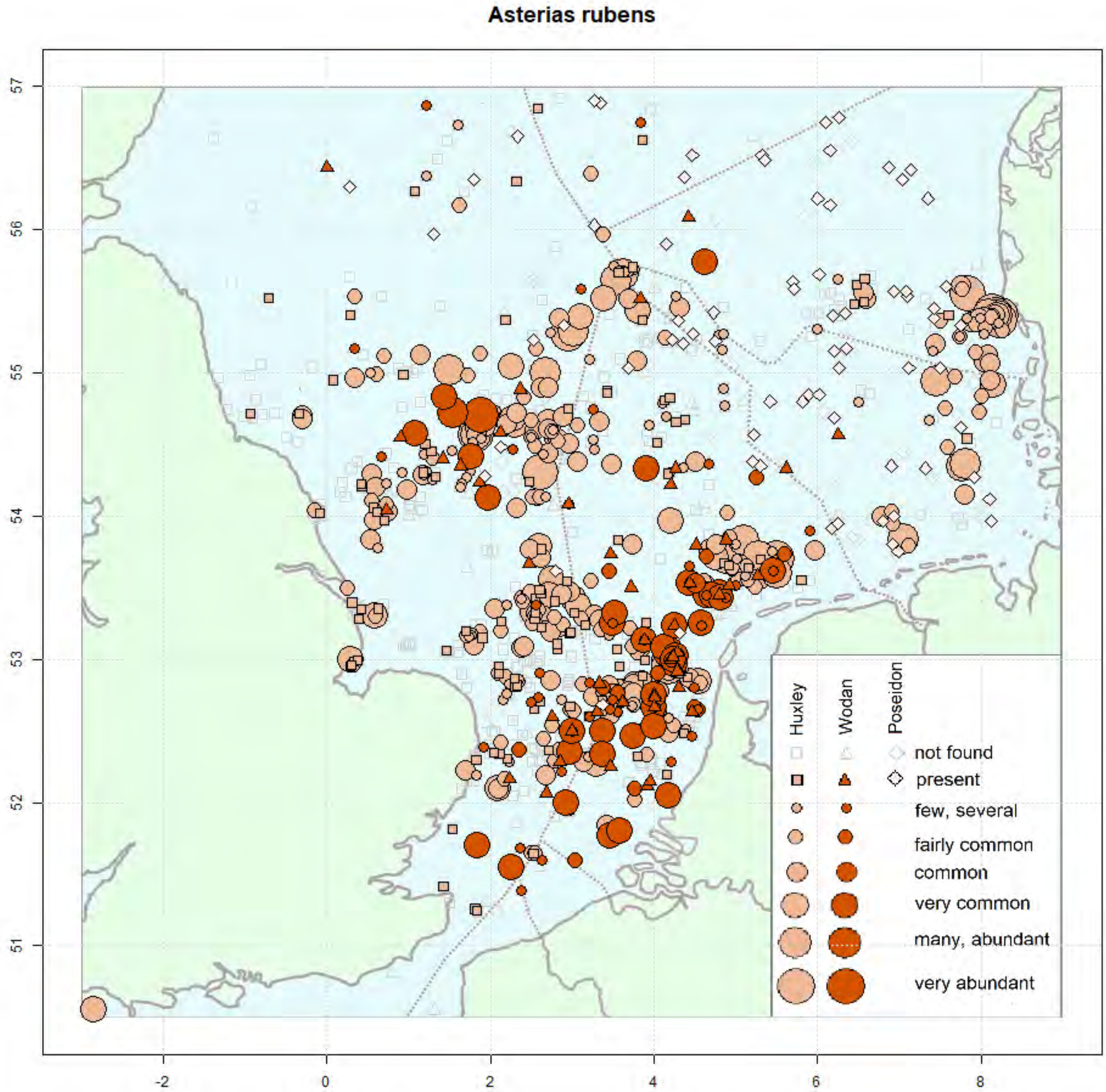
Securiflustra securifrons Narrow-leaved hornwrack

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).

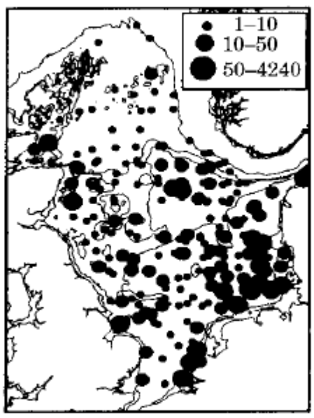


Vesicularia spinosa A bryozoan

Echinodermata-Asteroidea

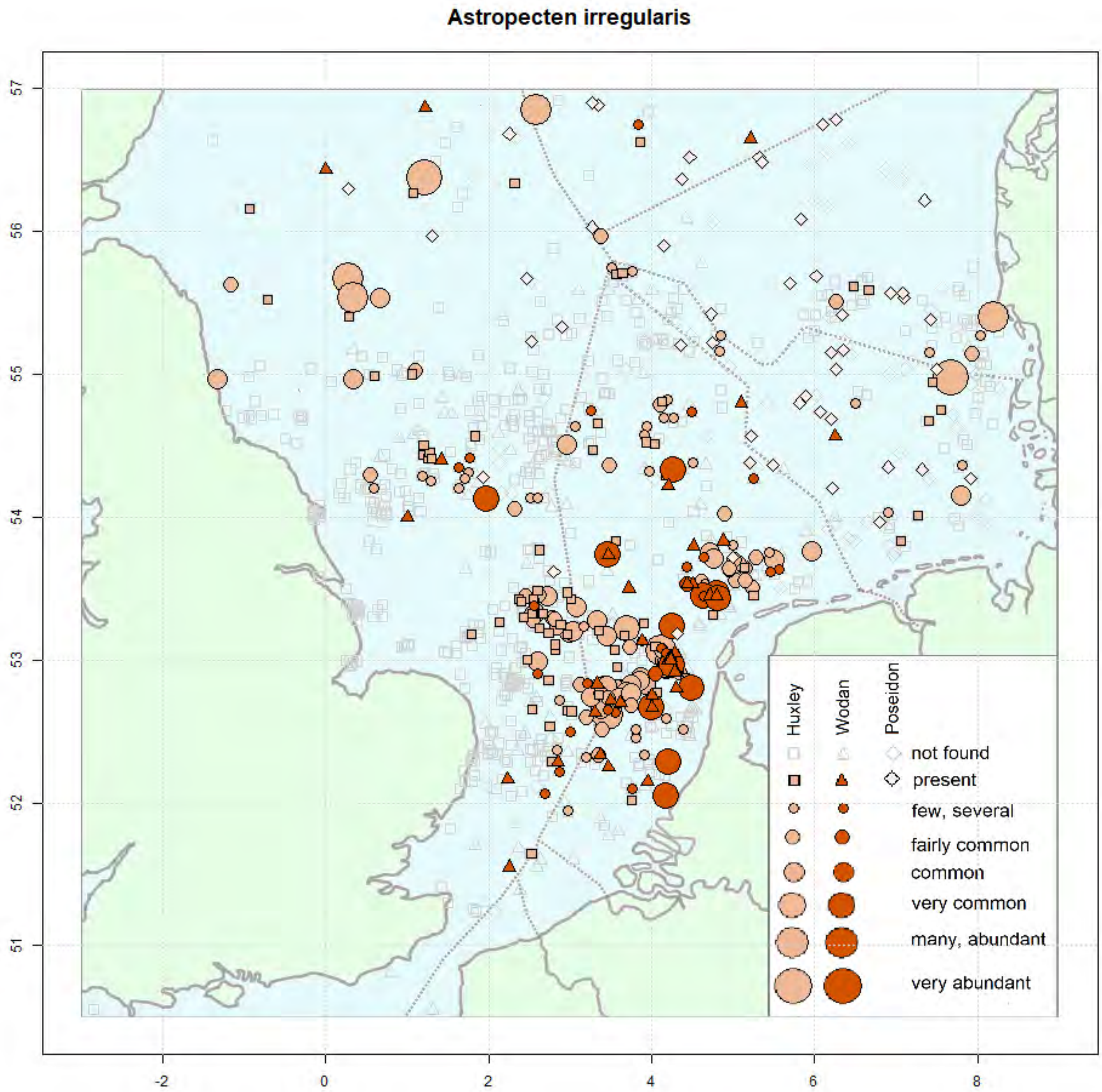


Asterias rubens Common starfish

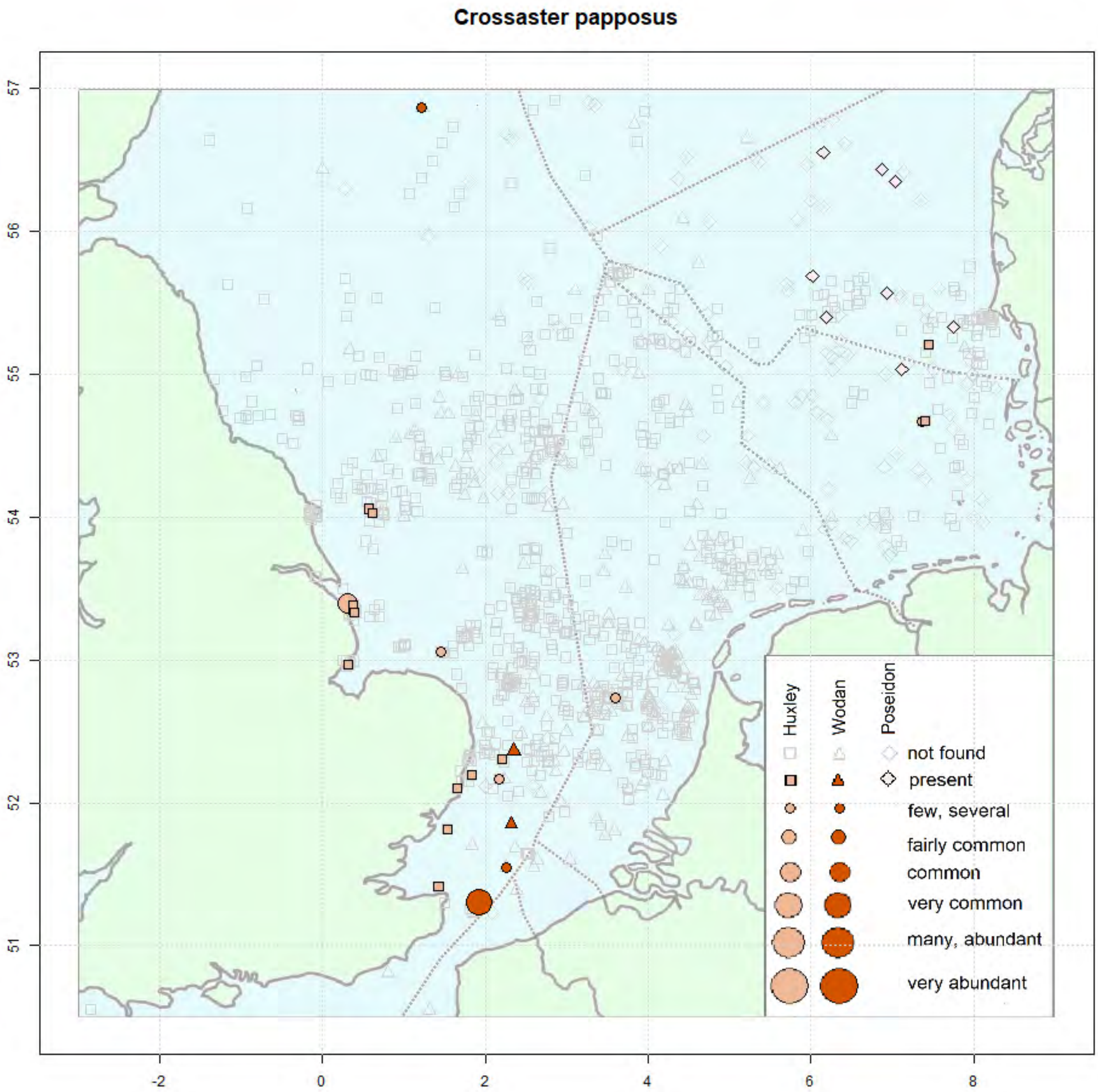


(b) *Asterias rubens*

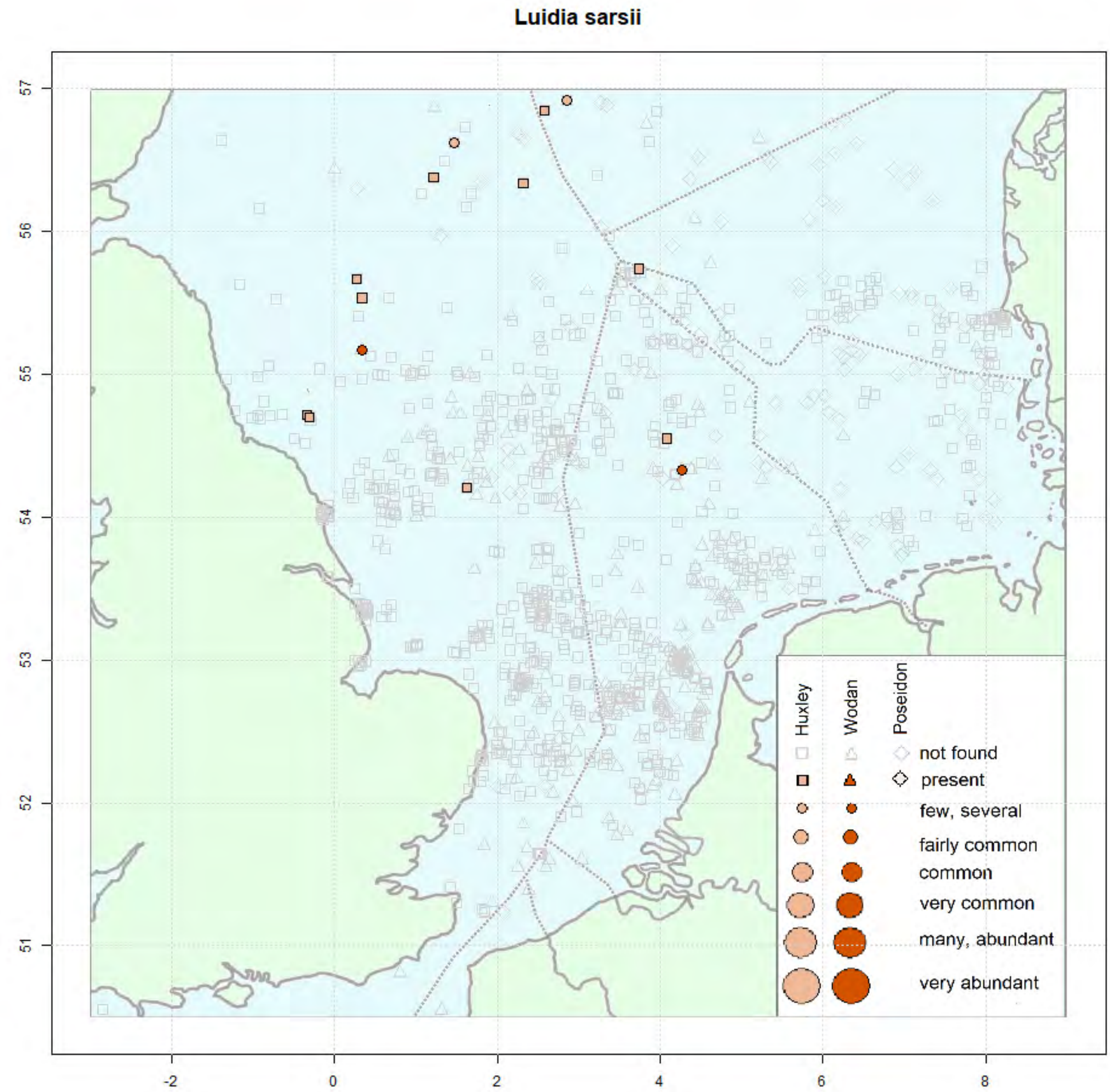
2000 distribution map (Callaway *et al.*, 2002).



Astropecten irregularis Sand star

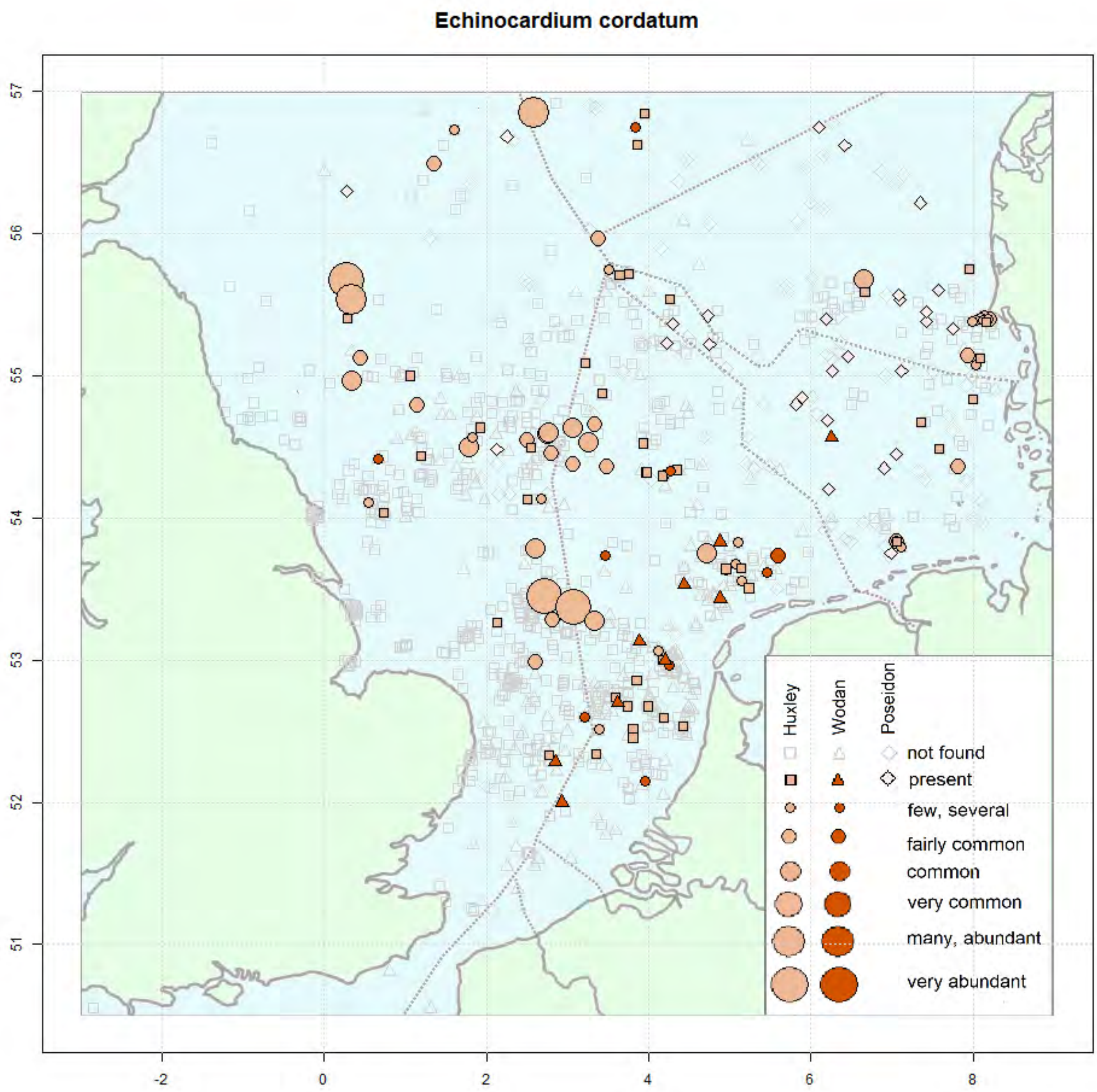


Crossaster papposus Common sunstar

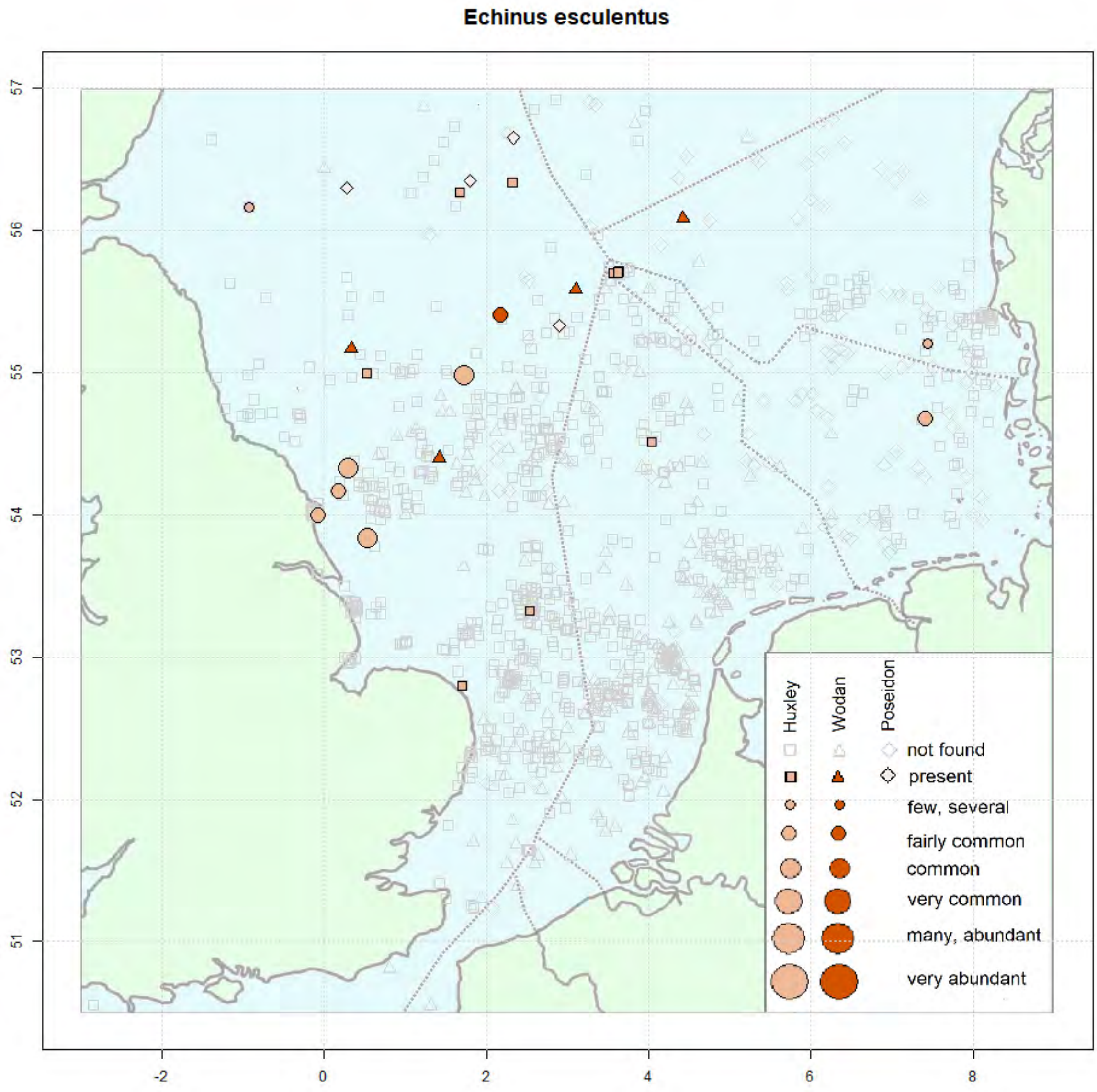


Luidia sarsii Seven-armed starfish

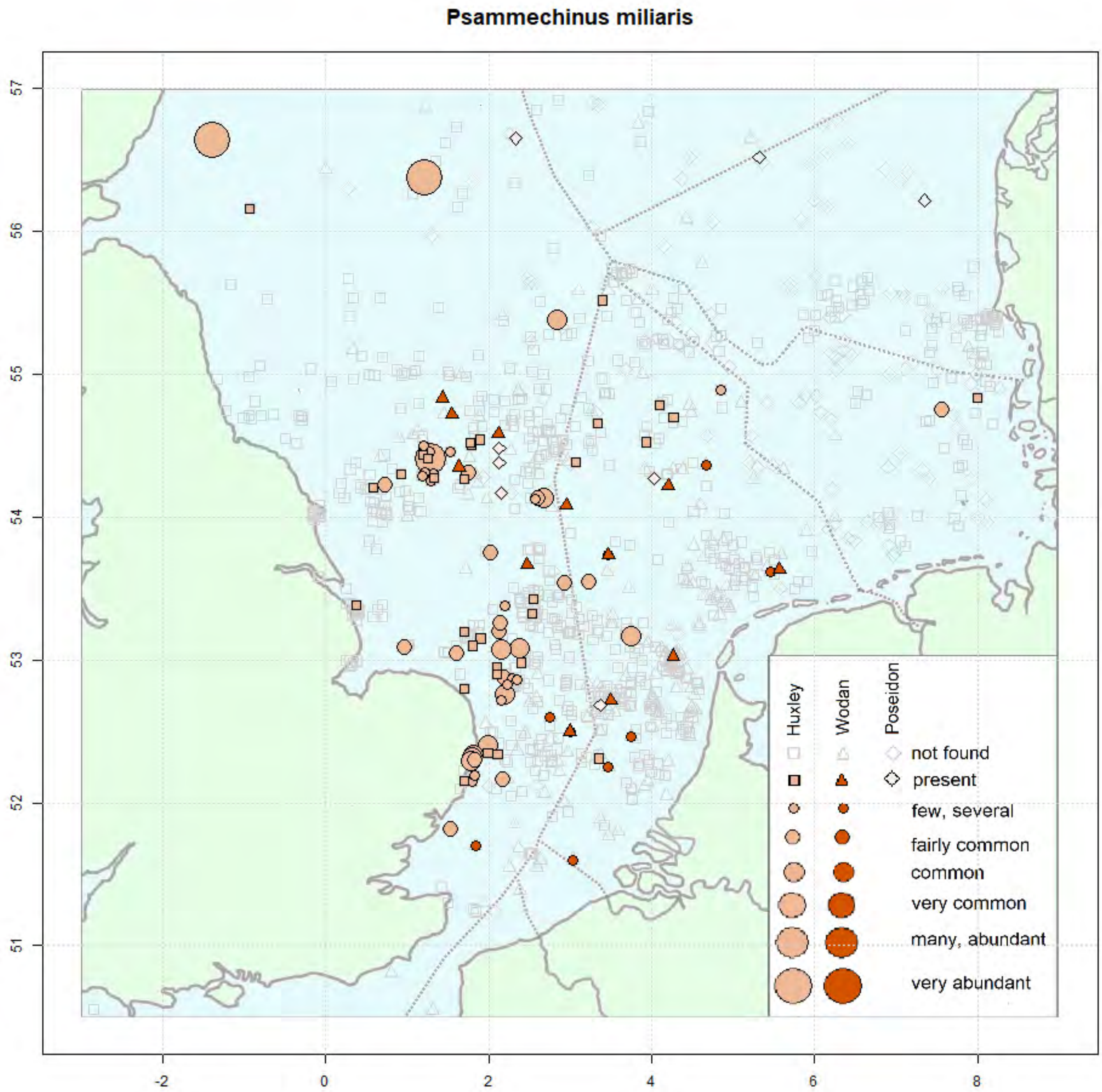
Echinodermata-Echinoidea



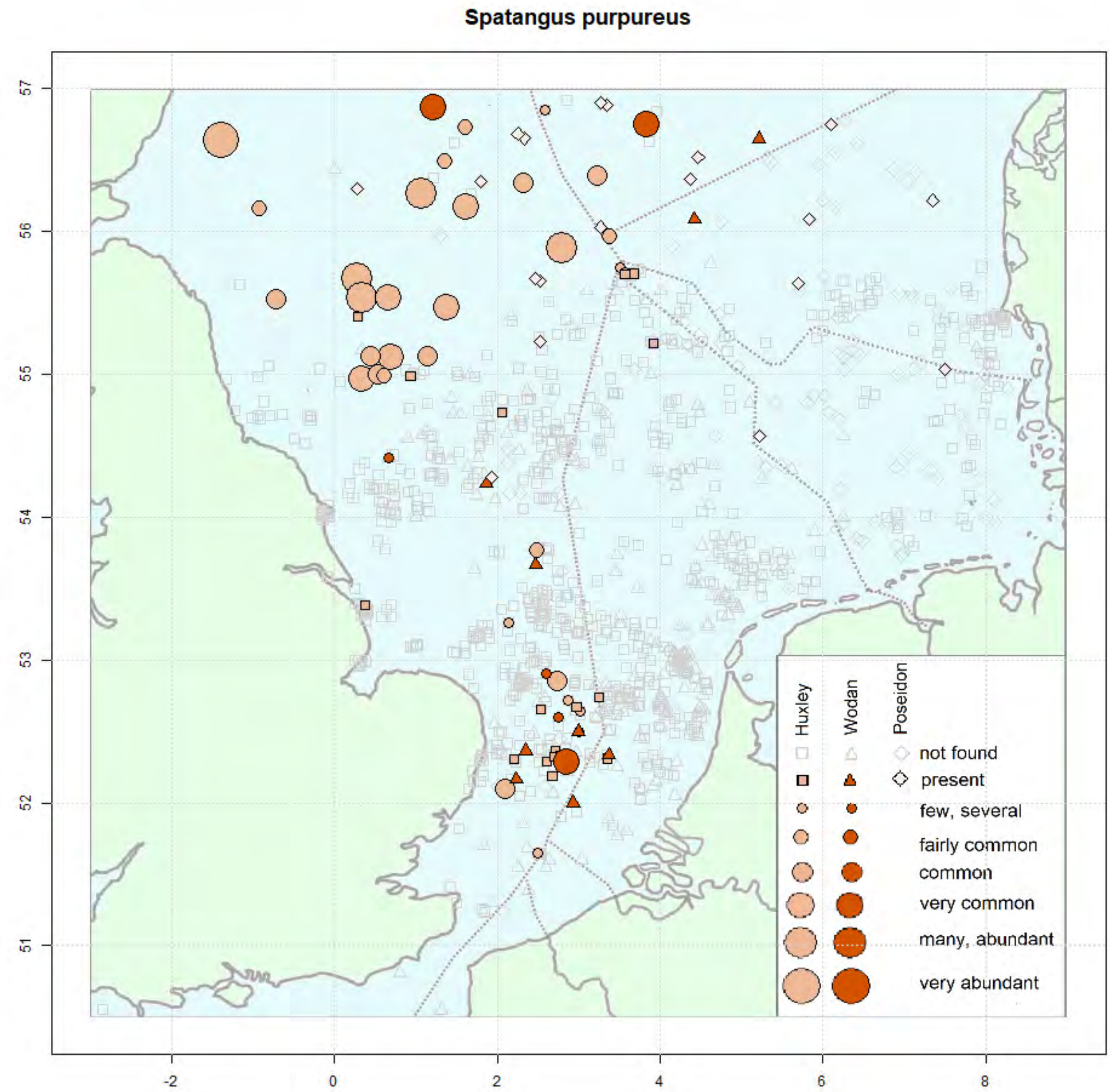
Echinocardium cordatum Common heart urchin



Echinus esculentus	Common sea urchin

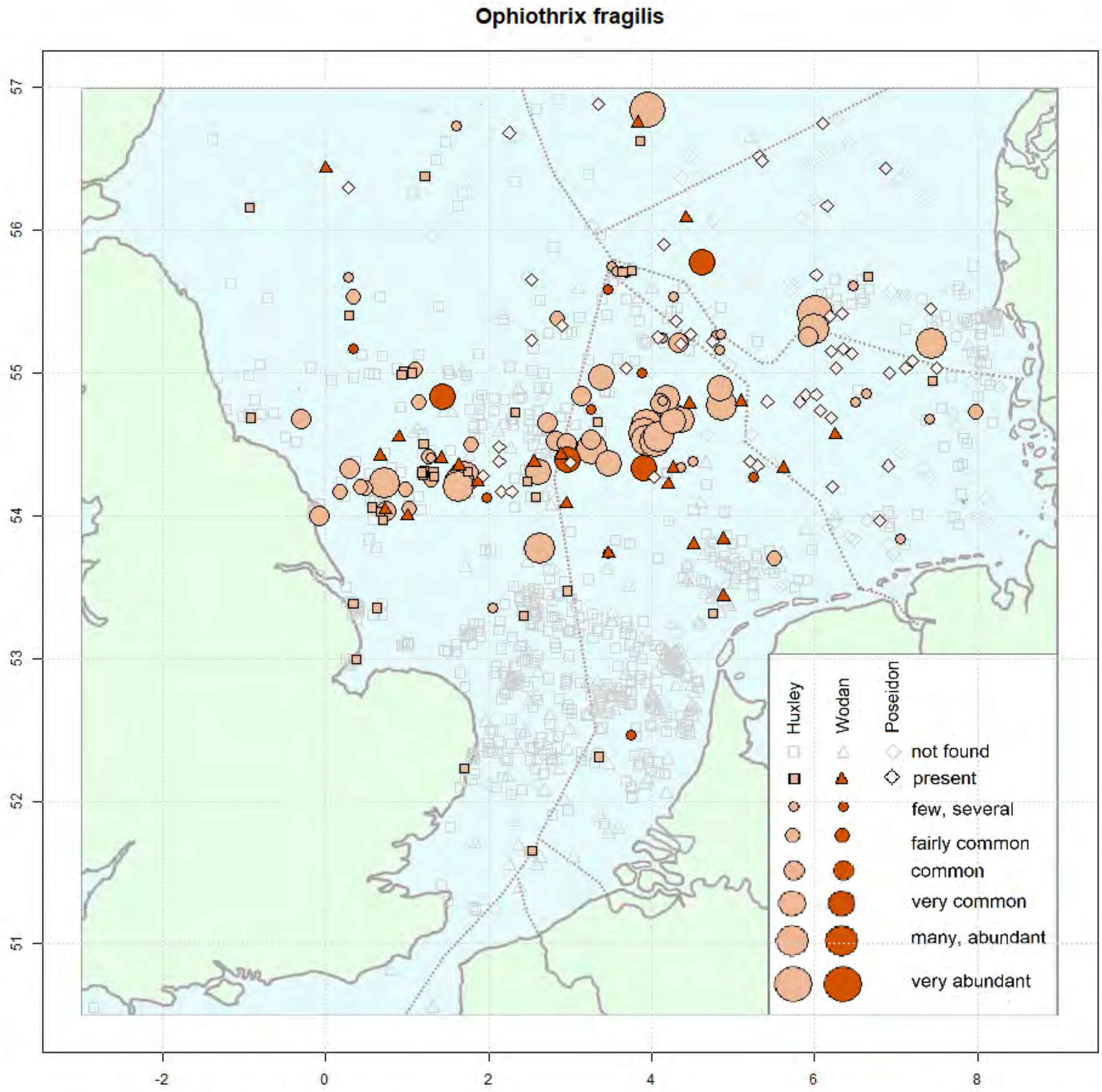


Psammechinus miliaris Shore sea urchin

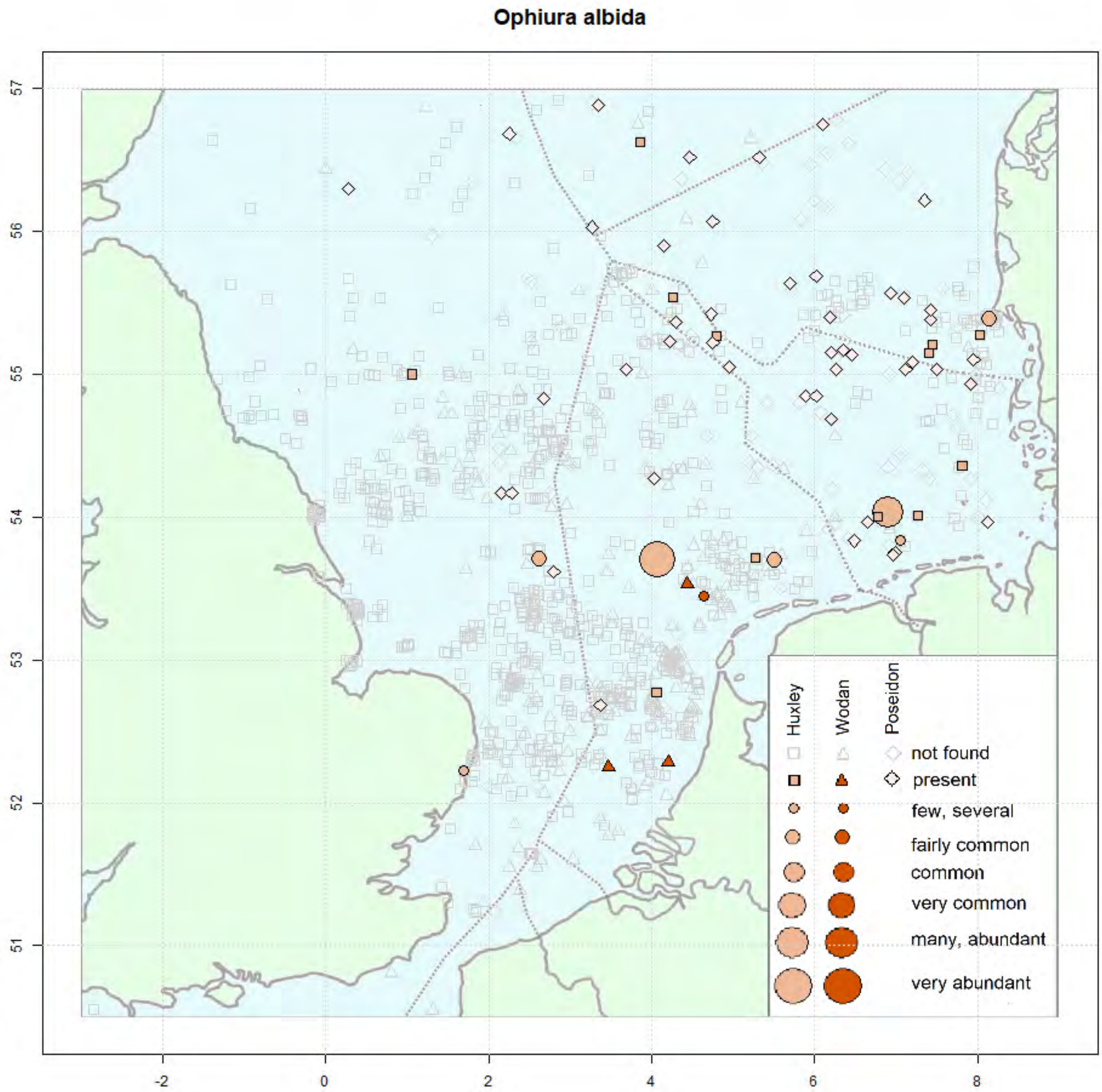


Spatangus purpureus Purple heart urchin

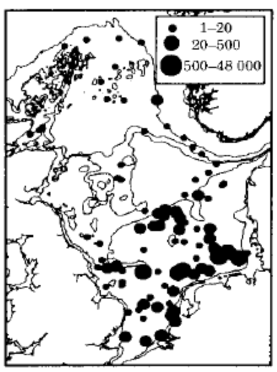
Echinoderma-Ophiuroidea



Ophiothrix fragilis Common brittle star

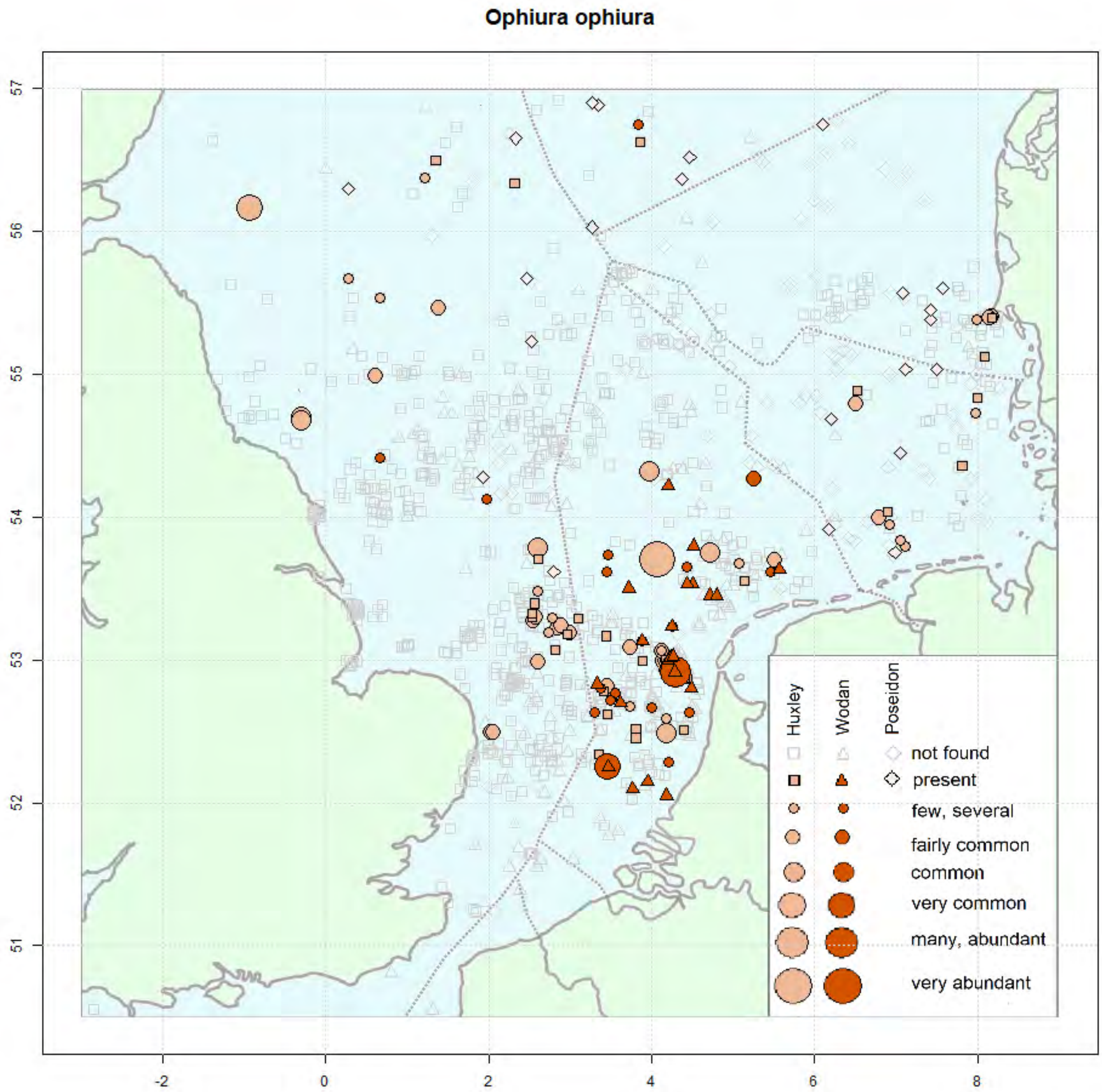


Ophiura albida Serpent's table brittle star



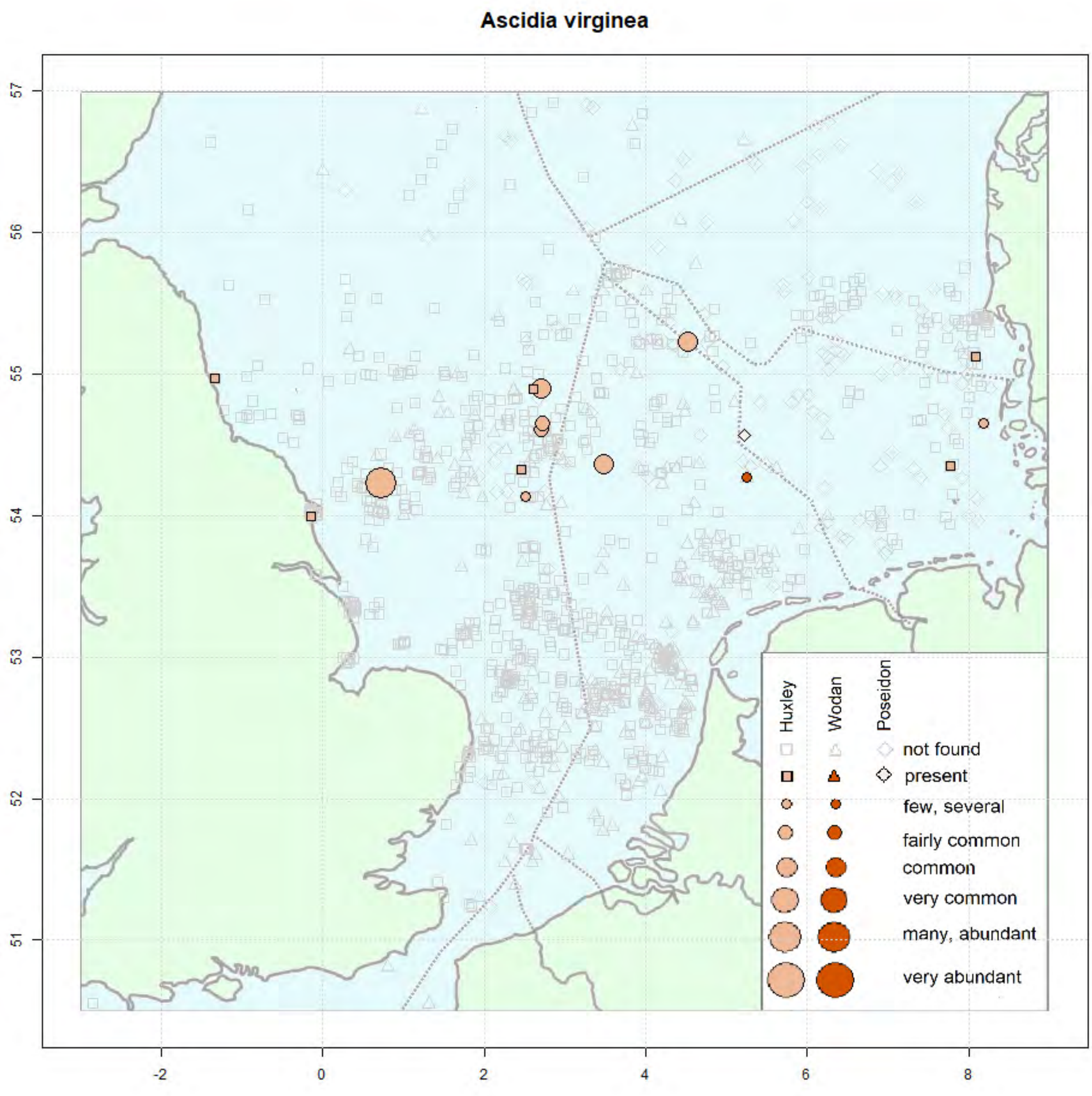
(d) *Ophiura albida*

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



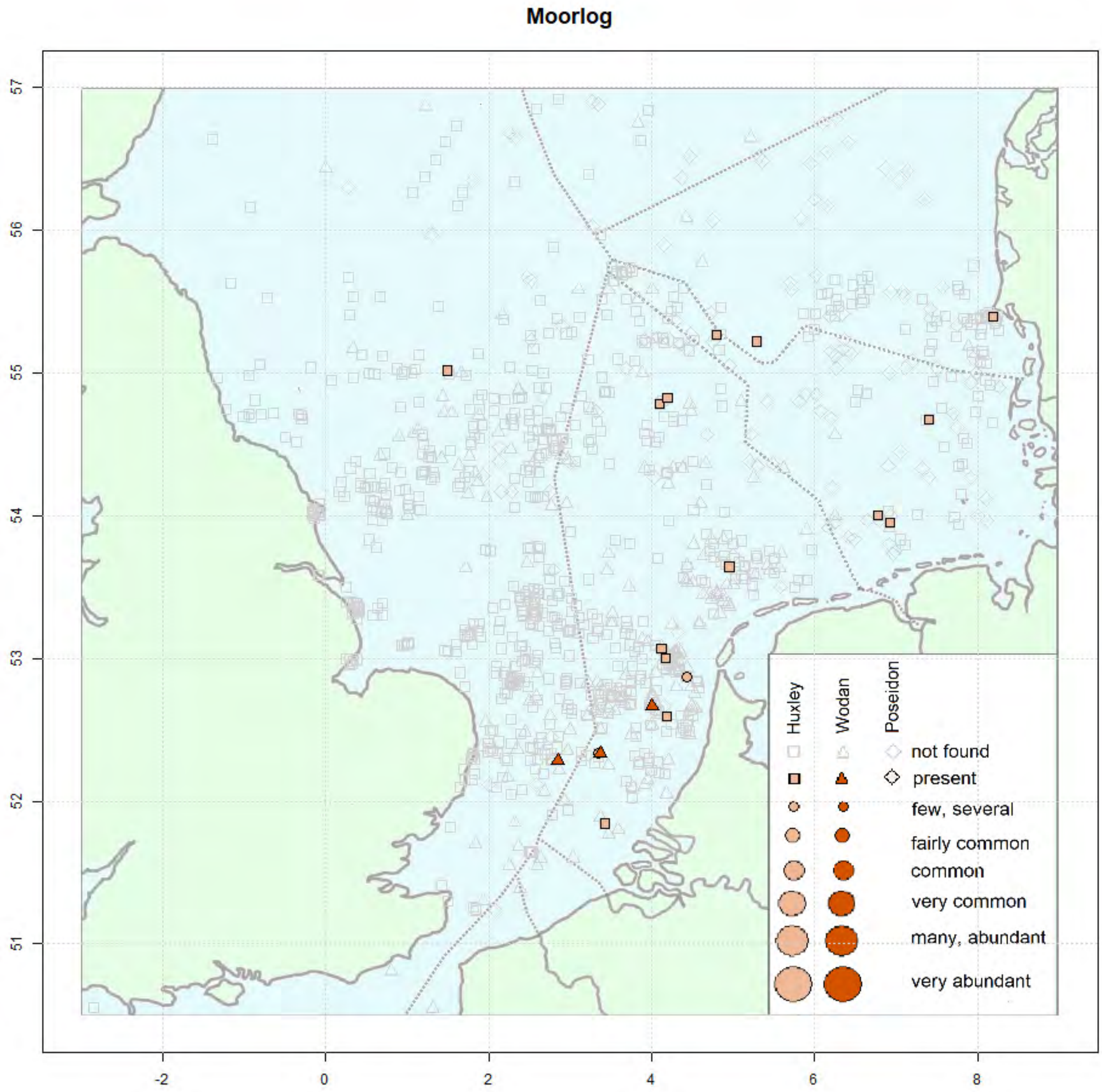
Ophiura ophiura Sand brittle star

Chordata-Ascidiacea



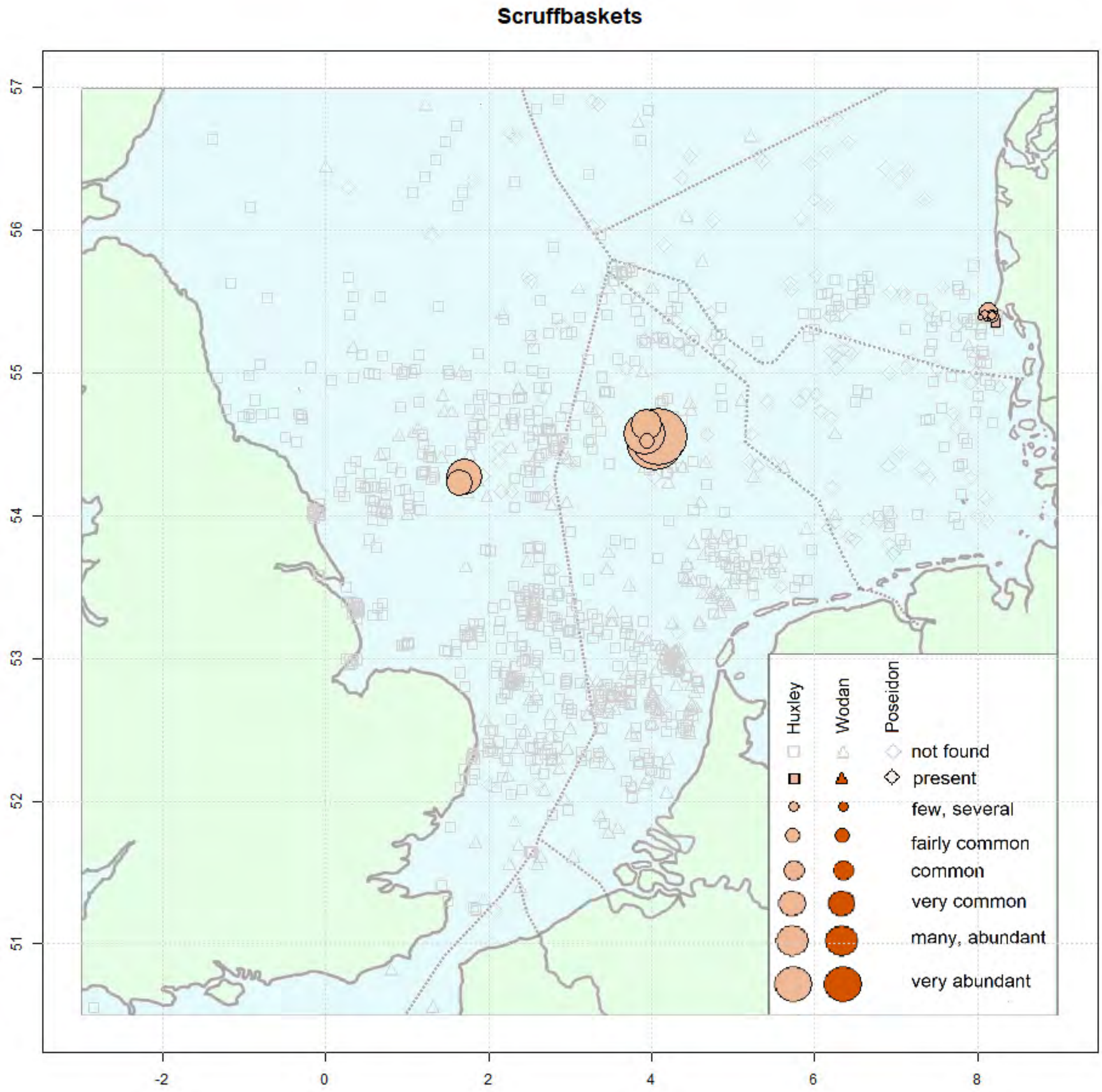
Ascidia virginea A sea squirt

Moorlog



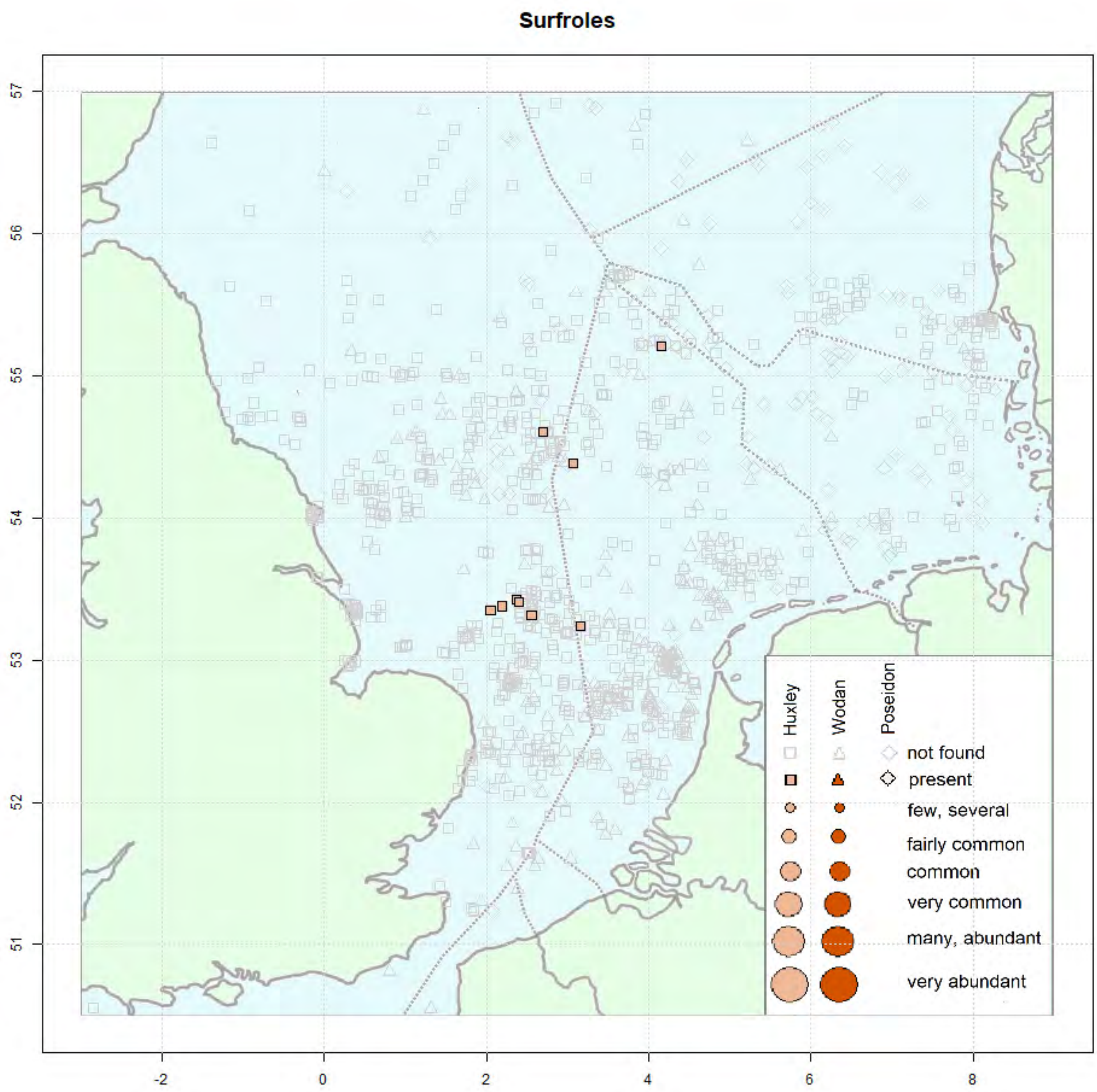
Peat layer fragments

Scruff



Scruff, size representation of ‘baskets full’.

Surfroles



Surfroles (hydroids)

7 Supplement: species names

7.1 Huxley species

Huxley	**Modern name**
Acanthodoris pilosa	*Acanthodoris pilosa*
Actiniloba senile	*Metridium senile*
Actinozoa	Cnidaria_or_Ctenophora
Acquorea sp.	Scyphozoa
Acteon tornatilis	*Acteon tornatilis*
Aeolidia papillosa	*Aeolidia papillosa*
Aeolidella alderi	*Aeolidiella alderi*
Aeolis sp.	Aeolidiidae
Alcyonidium gelatinosum	*Alcyonidium diaphanum* or (less) *A. condylocinereum*
Alcyonidium hirsutum	*Alcyonidium diaphanum* or (less) *A. condylocinereum*
Alcyonium digitatum	*Alcyonium digitatum*
Alcyonium parasiticum	*Alcyonidium parasiticum*
Anomia pattelliformis	*Pododesmus patelliformis*
Anomias, Anomia sp.	*Anomia* sp.
Antennularia antennina	*Nemertesia antennina*
Antennularia ramosa	*Nemertesia ramosa*
Aphrodite aculeata	*Aphrodita aculeata*
Artemis exoleta	*Dosinia exoleta*
Artemis lincta	*Dosinia lupines lincta*
Ascidians	Ascidiacea
Ascidiella virginea	*Ascidia virginea*
Astarte	Astartidae
Astarte borealis	*Astarte borealis*
Astarte compressa	*Astarte montagui*
Asteroids	Asteroidea
Asterias rubens	*Asterias rubens*
Astropecten irregularis	*Astropecten irregularis*
Aurelia aurita	*Aurelia aurita*
Balanus hameri	*Chirona hameri*
Beanii	Beania or Dendrobeania
Bolocera teudiae	*Bolocera tuediae*
Bolocera longicornis	*Bolocera tuediae*
Botryllus sp.	*Botryllus* sp.
Brittle-stars	Ophiuroidea
Brissopsis lyrifera	*Brissopsis lyrifera*
Buccinum undatum	*Buccinum undatum*
Bugula murrayana	*Dendrobeania murrayana*
Callisoma kroyeri	*Scopelocheirus hopei*
Calycella syringa	*Calycella syringa*
Campanularia verticillate	*Rhizocaulus verticillatus*
Caprella linearis	*Caprella linearis*
Cancer pagurus	*Cancer pagurus*
Carcinus maenas	*Carcinus maenas*
Cardium aculeatum	*Acanthocardia aculeata*
Cardium echinatum	*Acanthocardia echinata*

Huxley species

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

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

Huxley species

Molluscs	*Mollusca*
Montacuta substriata	*Montacuta substriata*
Mya truncata	*Mya truncata*
Mytilus edulis	*Mytilus edulis*
Myxicola?	*Myxicola* sp.?
Natica sp.	*Euspira* sp.
Natica alderi	*Euspira nitida*
Natica catena	*Euspira catena*
Natica monifilera	*Euspira catena*
Nephrops norvegicus	*Nephrops norvegicus*
Nereis pelagica	*Nereis pelagica*
Nucula nucleus	*Nucula nucleus*
Nudibranchs	Nudibranchia
Nymphon	Nymphonidae
Obelia sp	*Obelia* sp.
Obelia geniculata	*Obelia geniculata*
Obelia longissima	*Obelia longissima*
Ophelia limacina	*Ophelia limacina*
Ophiurids	Ophiuroidea
Ophiopholis acuelata	*Ophiopholis aculeata*
Ophiothrix fragilis	*Ophiothrix fragilis*
Ophiura albida	*Ophiura albida*
Ophiura ciliaris	*Ophiura ophiura*
Ostrea edulis	*Ostrea edulis*
Pholas candida	*Barnea candida*
P. (Pholas) crispata	*Zirfaea crispata*
P. pinnata	*Kirchenpaueria pinnata*
P. pussilus	*Liocarcinus pusillus*
Pandalus sp.	*Pandalus* sp.
Pandalus annuliscornis	*Pandalus montagui*
Pandalus montagui	*Pandalus montagui*
Panopea norvegica	*Panomya norvegica*
Paratylus swammerdami	*Nototropis swammerdamei*
Pecten, Pecten purio	*Pecten* sp.
Pecten opercularis	*Aequipecten opercularis*
Pecten striatus	*Palliolum striatum*
Pecten varius	*Mimachlamys varia*
Philine aperta	*Philine quadripartita*
Pholas crispata	*Zirfaea crispata*
Pinnotheres pisum	*Pinnotheres pisum*
Pleurophillidia loveni	*Armina loveni*
Pleurotoma turricula	*Probela turricula*
Plumularia sp	Plumularia
Podocoryna carnea	*Podocoryna carnea*
Pomatocerus triqueter	*Spirobranchus triqueter*
Polynoids, Polynoe sp.	Polynoidae
Polyzoa	cf. Bryozoa
Porcellana longicornis	*Pisidia longicornis*
Portunus sp.	Polybiidae
Portunus depurator	*Liocarcinus depurator*
Portunus holsatus	*Liocarcinus holsatus*
Portunus puber	*Necora puber*

Psammobia feroensis	*Gari fervensis*
Pycnogonum littorale	*Pycnogonum littorale*
Rhizostoma sp.	*Rhizostoma octopus*
Rhodactinia crassicornis	*Urticina eques*
Sabella pavonina	*Sabella pavonina*
Sabellaria spinulosa	*Sabellaria spinulosa*
Sabellaria tubes	*Sabellaria* sp.
Sagartia minuata	*Cylista elegans*
Sagartia pallida	*Metridium senile*
Sagartia viduata	cf. *Cylista undatus*
Saxicava rugosa	*Hiatella rugosa*
Saxicava (Hiatella) arctica	*Hiatella arctica*
Scrupocellaria reptans	*Cradoscrupocellaria ellisii or C. reptans*
Schistomysis ornata	*Schistomysis ornata*
Sepia sp.	*Sepia* sp.
Serpula tubes	*Serpula* sp.
Sertularella polyzonias	*Sertularella polyzonias*
Sertularia abietina	*Abietinaria abietina*
Sertularia argentea	*Sertularia argentea*
Sertularia distans	*Amphisbetia distans*
Sertularia operculata	*Amphisbetia operculata*
Sertularia rosacea	*Diphasia rosacea*
Solen pellucidus	*Phaxas pellucidus*
Solen	cf. *Ensis* sp.
Solen ensis	*Ensis ensis*
Solaster endeca	*Solaster endeca*
Solaster operculata	Solaster or Crossaster
Solaster papposus	*Crossaster papposus*
Spatangus purpureus	*Spatangus purpureus*
Spirorbis	Spirorbidae
Sponge	Porifera
Starfish	Asteroidea
Stenorhynchus longirostris	*Macropodia longirostris*
Stenorhynchus phalangium	*Inachus phalangium*
Stenorhynchus tenuirostris	*Macropodia tenuirostris*
Stylifer	*Pelseneeria stylifera*
Suberites domuncula	*Suberites domuncula*
Syncoryne gravata	*Sarsia tubulosa*
Syndosmya	*Abra* sp.
Tealia coriacea	*Urticina felina*
Tealia crassocornis	*Urticina crassicornis*
Teredo sp.	Teredinidae
Thelepus cincinnatus	*Thelepus cincinnatus*
Thelepus sp.	*Thelepus* sp.
Thuiaria thuja	*Thuiaria thuja*
Triticella pedicellate	*Triticella pedicellata*
Tritonia hombergi	*Tritonia hombergii*
Tritonia plebeia	*Duvaucelia plebeia*
Tubularia coronata	*Ectopleura larynx*
Tubularia indivisa	*Tubularia indivisa*
Tubularia sp.	Tubulariidae
Tunicates	Tunicata

Huxley species

Turritella	Turritellidae
Velutina laevigata	*Velutina velutina*
Venus exoleta	*Dosinia exoleta*
Venus gallina	*Chamelea gallina*
Venus lincta	*Dosinia lupinus lincta*
Venus striatula	*Chamelea striatula*
Vesicularia spinosa	*Vesicularia spinosa*
Voluptosius norvegicus	

7.2 Wodan species

Wodan	**Modern name**
Acanthodoris sp.?	*Acanthodoris sp.*
Aeolis (papillosa?)	cf. *Aeolidia papillosa*
Aurelia aurita	*Aurelia aurita*
Alcyonidium albidum	*Alcyonidium albidum*
Alcyonidum gelatinosum	*Alcyonidium diaphanum* or (less) *A. condylocinereum*
Alcyonidium hirsitum	*Alcyonidium diaphanum* or (less) *A. condylocinereum*
Alcyonium digitatum	*Alcyonium digitatum*
Amathia lendigera	*Amathia lendigera*
Amphioxus lanceolatus	*Branchiostoma lanceolatum*
Amphiura filiformis	*Amphiura filiformis*
Anneliden	Annelida
Anomia ephippium	*Anomia ephippium*
Anomia patelliformis	*Pododesmus patelliformis*
Antennularia antennina	*Nemertesia antennina*
Antennularia ramosa	*Nemertesia ramosa*
Aphrodite acuelata	*Aphrodita aculeata*
Aplidiopsis pomum?	*Synoicum pulmonaria?*
Aporrhais pes pelicanae shell	*Aporrhais pespelecani shell*
Artemis exoleta	*Dosinia exoleta*
Artemis lincta	*Dosinia lupinus lincta*
Ascidien	Ascidiacea
Ascidiella virginea	*Ascidia virginea*
Ascidiella adspersa	*Ascidiella aspersa*
Ascidiella scabra	*Ascidiella scabra*
Ascidiella sp.*?*	*Ascidiella* sp.*?*
Astacilla longicornis	*Astacilla longicornis*
Astarte compressa	*Astarte montagui*
Asteriden, Zeesterren	Asteroidea
Asterias glacialis	*Marthasterias glacialis*
Asterias rubens	*Asterias rubens*
Asterias mulleri	*Leptasterias (Leptasterias) muelleri*
Astropecten irregularis	*Astropecten irregularis*
Atelecyclus heterodon	*Atelecyclus rotundatus*
Aurelia aurita	*Aurelia aurita*
Balanus porcatus	*Balanus balanus*
Balanus hameri	*Chirona hameri*
Bryssopsis lyrifera	*Brissopsis lyrifera*
Buccinum undatum	*Buccinum undatum*
Buccinum undatum shell	*Buccinum undatum shell*
Bugula murrayana	*Dendrobeania murrayana*
Campanularia johnstoni	*Clytia haemisphaerica*
Campanularia (Gonothyraea) gracilis	*Campanularia gracilis*
Campanularia sp.	Campanularia
Cancer pagurus	*Cancer pagurus*
Carcinus maenas	*Carcinus maenas*
Cardium echinatum	*Acanthocardia echinata*
Cardium edule	*Cerastoderma edule*
Cardium edule	*Cerastoderma edule*

Wodan species

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

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

Wodan species

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

Wodan species

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

Ascophyllum	*Ascophyllum nodosum*
Chorda filum	*Chorda filum*
Fucus	*Fucus* sp.
Zostera	*Zostera* sp.