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Colonisation of wave power foundations by mobile mega- and macrofauna – a 12 year study

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ABSTRACT

Environmental impacts from wave energy generators on the local mobile mega- and macrofauna community have been investigated in the Lysekil project by Uppsala University. Offshore renewable energy installations provide hard, artificial substrates, and as such, they could act as artificial reefs. Foundations with manufactured holes served as complex habitats and foundations without served as non-complex. In this long-term study, SCUBA surveys of mobile fauna in the years 2007, 2008 and 2016–2019 were analyzed. The results show a distinct reef effect on the foundations with significant greater species richness, total number of individuals, greater values of the Shannon-Wiener biodiversity index, and greater abundance of specific reef fauna. Complex foundations accommodated a greater abundance of brown crabs than non-complex foundations, other taxa did not show differences between the two foundation types. A successional increase of species richness, numbers of individuals and Shannon-Wiener biodiversity could be revealed from the first to the second survey period. Inter-annual variation was visible throughout all taxa and years.

1. Introduction

The aim of a fossil free electricity generation will necessitate an increased development of renewable energy sources. Offshore renewable energy sources will further expand in the coming years such as offshore wind but also wave and tidal energy may establish commercialization. This means further introduction of manmade structures in an already heavily used marine environment (Hammar et al., 2017). The term “urban sprawl” comprehensively including all kind of intensifying development of urban shores, coastlines, but also offshore areas has been introduced in this context (Duarte et al., 2013; Heery et al., 2017). Nature conservation concerns focus on offshore energy deployments and operational impacts, such as electromagnetic fields from cables, noise emission, changes in hydrodynamics (Gill, 2005; Witt et al., 2012; Copping et al., 2016; Iglesiasa et al., 2018). An additional impact may be invasive species which have been found to a higher extend on artificial structures than on natural hard substrate (Herbert et al., 2017). Increased deployment activities of offshore renewable installations could facilitate the spread, expand the range (De Mesel et al., 2015) and help the establishment of invasive species (Glasby et al., 2007).

Offshore renewable energy installations can also lead to positive effects for the marine fauna. They can provide hard substrate and as such they act as artificial reefs. An artificial reef is a submerged structure placed on the substratum (seabed) deliberately, to mimic some characteristics of a natural reef as defined by the European Artificial Reef Research Network (Jensen et al., 2000). For centuries humans have taken advantage of the behavior of some aquatic organisms to be attracted to submerged objects. This knowledge was used to support artisanal fishing in coastal communities, particularly in tropical regions (Seaman and Lindberg, 2009). This phenomenon also called ‘reef effect’ will be used in terms of increased fishes and invertebrate abundance on introduced structures throughout the text. In the past 60 years, artificial reefs have been used by many countries to enhance the commercial and recreational fishing (Bohnsack and Sutherland, 1985). Nowadays, intentionally placed artificial reefs play an important role as management tools for stock enhancement of recreational fisheries, marine habitat restoration and prevention of illegal fishing activities (Seaman and Lindberg, 2009; Serrano et al., 2011; Komyakova and Swearer, 2019). Artificial hard substrates have been reported to attract and concentrate fishes and invertebrates and/or to enhance local stocks (Bohnsack, 1989; Leitão et al., 2009, 2008). Such aggregation behavior can be explained by reasons such as shelter against currents and predators (Bohnsack, 1989), additional food supply (Fabi et al., 2006; Leitão et al., 2007), increased feeding efficiency and provision of nursery and

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recruitment areas (Bull and Kendall, 1994). Initial colonisation by sessile species of such new deployed hard structures relies on larval availability. Thus, early succession is dependent on the deployment time in the year since larval dispersion is affected by seasons in temperate regions.

Habitat characteristics and structural complexity are well known to play an important role in community structure (Komyakova et al., 2018; Komyakova, Munday, and Jones, 2019). Those characteristics can be enhanced on offshore renewable energy foundations to provide shelter properties for mobile fauna to enhance the biological productivity (Langhamer and Wilhelmsson, 2009). Enhancement of structural complexity of offshore installations could increase biodiversity on artificial structures and thus be able to enhance the resilience of ecosystem functions (McCann, 2000). The gradual colonisation of the structures can have positive impacts on ecosystem services such as formation of biogenic habitat and thereby provide feeding and nursery grounds for other species (Fowler et al., 2018; Langhamer, 2012).

Offshore renewable energy installations can act as artificial reefs and evidence has been found already on deployed offshore installations such as oil and gas platforms (Claisse et al., 2014; Fowler et al., 2018; Fujii, 2015; Meyer-Gutbrod et al., 2019; Schutter et al., 2019), but also around wind power devices (Andersson and Öhman, 2010; De Mesel et al., 2015; Hammar et al., 2010; Krone et al., 2017; Langhamer et al., 2016; Lindeboom et al., 2011; Methratta and Dardick, 2019; Raoux et al., 2017; Reubens et al., 2013a, b; Van Hal et al., 2017) and wave power installations (Andersen et al., 2009; Bicknell et al., 2019; Langhamer, 2012; Langhamer et al., 2009; Langhamer and Wilhelmsson, 2009; Witt et al., 2012). A comparison of different wind turbine foundations indicated that increased complexity of artificial reefs has the potential to increase the abundances of commercial important reef species such as the brown crab (*Cancer pagurus*) but also cod (Krone et al., 2017). Brown crabs prefer more complex foundation s with manufactured holes compared to foundations without holes (Langhamer and Wilhelmsson, 2009). Other research on artificial reefs in the northern hemisphere indicates that offshore renewable energy structures such as wind and wave energy devices and development infrastructure will be densely populated by various sessile and mobile fauna (Herbert et al., 2017; Krone et al., 2017, 2013; Langhamer and Wilhelmsson, 2009; Sheehan et al., 2018). However, many questions of environmental effects around this relatively young technologies exist (Copping, 2018), and long-term observations are scarce. As climate change drives increases in temperature in many coastal regions (Pachauri and Meyer, 2014) and extreme weather events are more likely to occur, species responses to climate variations are expected. Colonisation processes are gradual and species response to inter-annual temperature variation can be high (Flanagan et al., 2019). Many studies only provide and use data from one year observations, so the risk of over- or underestimating results is high (Bicknell et al., 2019). A need for long-term studies is necessary to investigate successional changes over several years and to provide robust results.

At Uppsala University a wave power generator design of a linear type has been developed and practical research is conducted at the associated research site at the west coast of Sweden (Lejerskog et al., 2011; Parwal et al., 2015). Environmental studies from 2007 revealed that foundations act as artificial reefs and attract different fish and decapod species (Langhamer and Wilhelmsson, 2009). Typical reef associated species at the site were the economically important decapods, brown crab (*Cancer pagurus*), the European lobster (*Homarus gammarus*) and cod (*Gadus morhua*). Other decapod and invertebrate species occurred, but also fishes such as flatfish species (Pleuronectidae), dragonet species (Callionymus) and goby species (*Pomatoschistus* spp.). The purpose of our four year follow up study was to investigate the status, more than a decade after the first survey was conducted, shortly after the deployment in 2007. The study by Langhamer and Wilhelmsson (2009) functioned as a reference study. The current study uses the data from 2007, from year 2008 (O. Langhamer, unpublished data) and the survey data from the years 2016–2019.

Our study addresses the following questions: Are metrics such as species richness, total number of individuals, Shannon-Wiener index and evenness different on foundations compared to controls in all survey years? Does the species assemblage differ between the foundations and the controls or between the complex foundations and the non-complex foundations? How is it for single specific species such as *Cancer pagurus, Pagurus* spp. *Marthasterias glacialis* and *Astropecten irrgeularis*. Are brown crabs still greater in abundance on complex foundations after long-term establishment of the artificial habitat? Do other taxa occur to a greater extend on complex foundations compared to the non-complex foundations such as *Cancer pagurus, Pagurus* spp. *Marthasterias glacialis* and *Astropecten irrgeularis*. As part of a long-term investigation we hypothesized that the foundations would be colonized to a greater extend by mobile fauna in the latter years, 2016–2019, of the study compared to the first two years, 2007 and 2008.

2. Methods

2.1. *Study site, experimental setup and survey methods*

The Lysekil research site is located on the Swedish west coast ca. 100 km north of Gothenburg. Marker buoys highlight the northern (58° 11′850 N, 11° 22′460 E) and southern limit of the site (58° 11′630 N, 11° 22′460 E) (Fig. 1 a). The area is characterized by rocky shorelines covered in algae and soft bottom below rocky slopes (Cato and Kjellin, 2008), with a water depth of around 25 m. Water surface temperatures range between 15 and 20 °C during the summer and 0–2 °C during the winter, average salinity is 25‰ (Åberg, 1992) and the tidal range is ca. 0.3 m (Johannesson, 1989). In April 2004 the first deployment on the research site was a Datawell wave rider buoy (Leijon et al., 2008). The first linear generator including a power cable was deployed in 2006 followed by further generator deployments in the following years (Leijon et al., 2008; Lejerskog et al., 2011; Parwal et al., 2015).

A total of 21 ‘ecological foundations’ (foundations without generator for ecological studies in the Lysekil research site, hereafter referred to as ‘foundations’) were deployed in the Lysekil research site in 2007 to conduct studies on environmental impacts. Each foundation is of cylindrical shape, ca. 3 m diameter, 1 m height and with a weight of 10 tons. Eleven of the 21 foundations are perforated on the lateral side of the cylinder with rectangular holes measuring 12 cm in width, 15 cm in height and 30 cm in depth (complex foundations) (Fig. 2). Half of the holes are situated on the lower edge of the cylinder and the other half is in the upper third (Fig. 2). Holes on the lower edge were not visible anymore during the visual surveys 2016–2019, because of sediment accumulation around the foundations and settling of the foundations into the sediment. In 2007, 2008, 2016 and 2017 notations on occupied upper holes by brown crabs were made. The other 10 foundations were without modifications. The setup of the foundations was as follows, ten in the northern part of the Lysekil research site and eleven in the southern part: alternating with holes and without holes (Fig. 1 b). The distance between the foundations is 15–20 m.

The ecological foundations were sampled once a year during July and August in 2007, 2008 and 2016–2019, as observed differences are considered to be independent of seasonal effects when conducted in similar times of the year. Scientific SCUBA diving was used for visual surveys of mobile mega- and macrofauna on and around the ecological foundations and control areas. All mobile fauna associated with the foundations and within 1 m distance to the foundations were recorded during visual censuses as well as for a control area in 10 m distance to the foundation. Highly mobile species such as fishes were counted first while approaching the foundations. Secondly, the top of the cylindrical foundation was surveyed in a circular manner. Following the species on the sides of the foundations were registered, including the manufactured holes where they were present and the adjacent sand bottom within 1 m around the foundation. Thereafter, a measuring tape was connected to

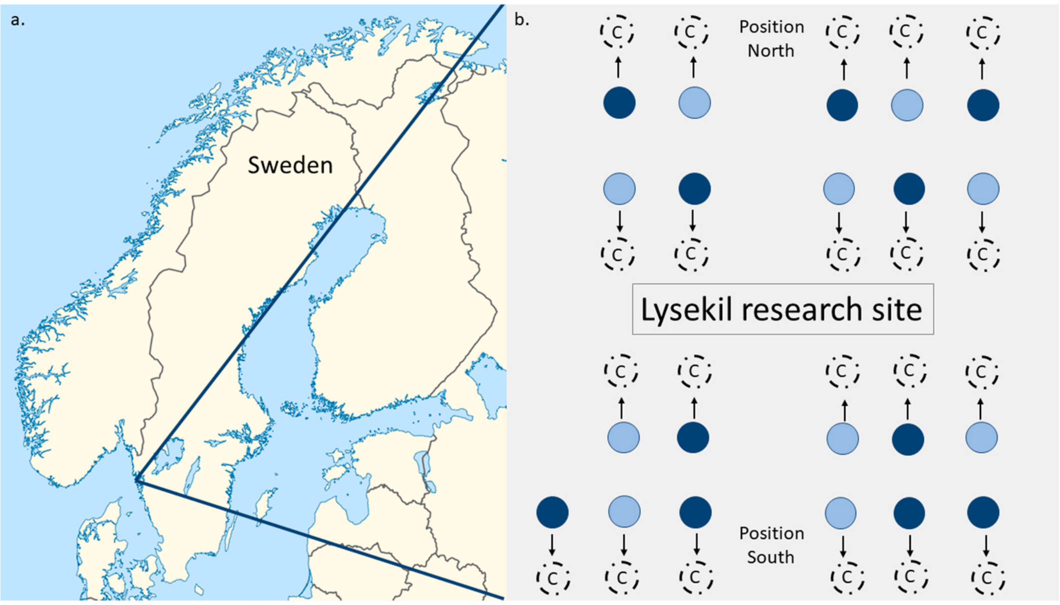

Fig. 1. a.) Location of the study area, Lysekil research site on the west coast of Sweden. b.) Configuration of complex foundations (dark blue circles) and non-complex foundations (light blue circles) within the site. Upper part "Position north" represents the foundations and controls of the geographical position north and lower part represents the southern geographical position. Black arrows indicate direction of associated control sites and black dashed circle with "C" indicates location of control in around 10 m distance to foundations (figure not in scale).

Fig. 2. Foundations surveyed during the study. Upper foundation represents complex version with manufactured holes and lower foundation represents non-complex version.

the center of the foundation and rolled out 10 m north or south, respectively, depending on the location of the foundation. The control areas of the upper row of the northern foundations and the upper row of the southern foundations were conducted northwards (Fig. 2 b). The control areas of the lower row of the northern foundations and the lower row of the southern foundations were conducted southwards (Fig. 2 b). This measure was applied in order to prevent approaching the adjacent foundation row. Visual surveys of control areas with similar size in bottom surface were conducted on predominantly flat bare substratum. During 2007, 2008 the ecological foundations also contained a surface buoy connected to the foundation via a line. In the survey period 2016–2019 no wave power buoys were connected to the foundations. All divers were experienced in marine ecology and had detailed knowledge about the local species.

During 2007 the surveys covered all 21 foundations with associated 21 controls. In 2008, 19 foundations and associated 19 controls were sampled. The surveys on ecological foundations during the years 2016–2019 could not be conducted on all foundations due to meteorological conditions and included 13–15 foundations with associated controls (Table 1).

2.2. Statistical data analyses

Shapiro-Wilk normality test (shapiro.test) and Q-Q plot (qqnorm) revealed non-normal distribution of the data and thus non-parametric analyses methods were applied. Species richness, total number of individuals, Shannon-Wiener diversity 'H' ($H = \sum[(pi) \times \ln (pi)]$ (pi = abundance of a species/total abundance; ln = natural log)) and Pielou's evenness 'E' ($E = H/H_{MAX}$ (H = Shannon-Wiener Diversity index; H_{MAX} = the highest possible diversity for that sample (calculated by ln (richness)) were calculated for the different sampling areas. The sampling areas included either all foundations (complex and non-complex foundations) and controls of each year or complex foundations and non-complex foundations of each year. Individual samples with no species

Table 1
List of surveyed foundations 2007, 2008, 2016–2019, split in complex foundations with holes and non-complex foundations without holes and split for their location north or south in the Lysekil research site.

	2007	2008	2016	2017	2018	2019
Total number of foundations (north/south)	21 (10/11)	19 (10/9)	14 (5/9)	15 (5/10)	13 (5/8)	15 (5/10)
Thereof complex foundations (north/south)	11 (5/6)	10 (5/5)	8 (3/5)	9 (3/6)	7 (3/4)	9 (3/6)
Thereof non-complex foundations (north/south)	10 (5/5)	9 (5/4)	6 (2/4)	6 (2/4)	6 (2/4)	6 (2/4)
Control areas (north/south)	21 (10/11)	19 (10/9)	14 (5/9)	15 (5/10)	13 (5/8)	15 (5/10)

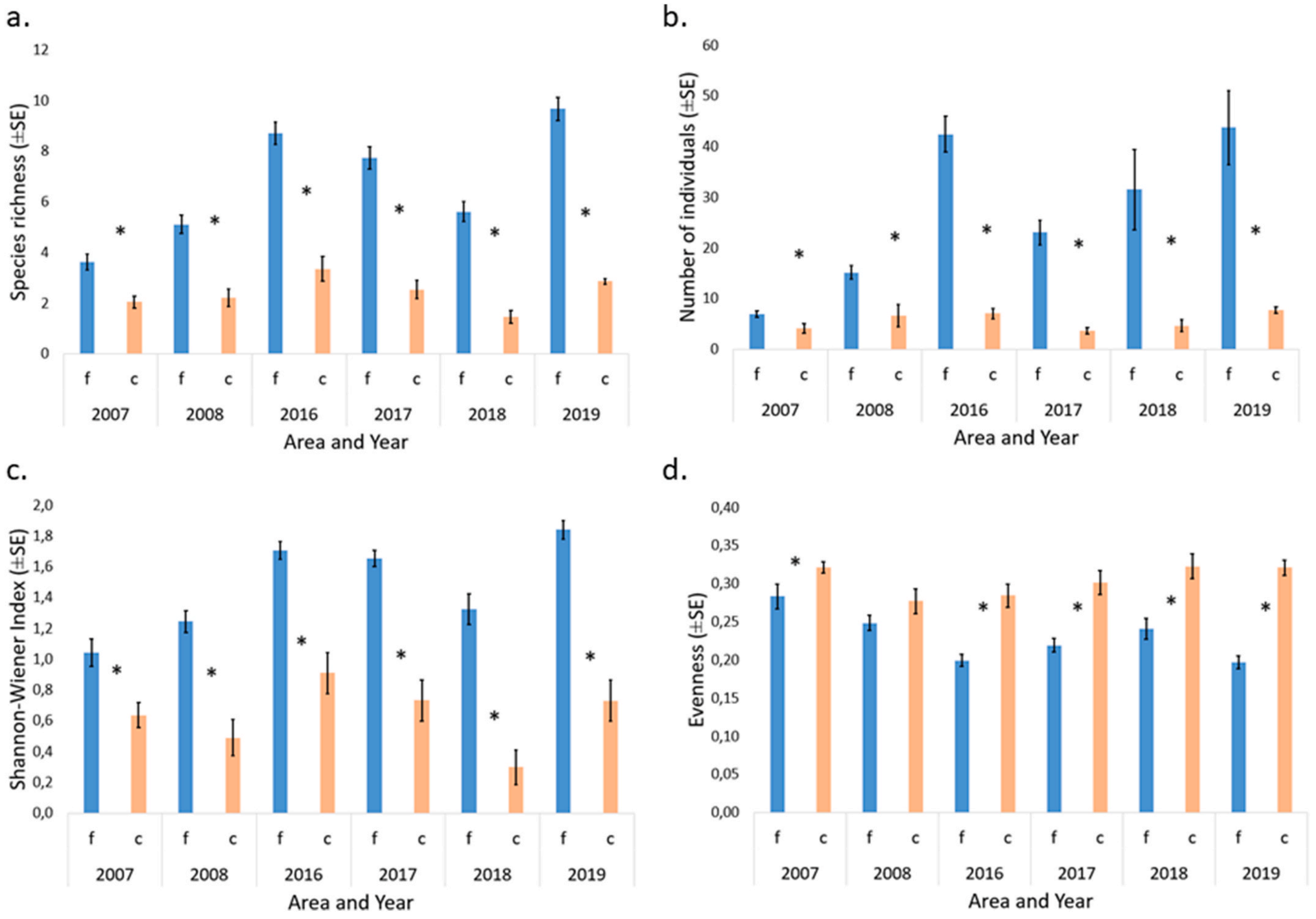

Fig. 3. Average a.) species richness (±SE), b.) total number of individuals (±SE), c.) Shannon-Wiener biodiversity index (±SE) and d.) evenness (±SE) on foundations (f complex and non-complex foundations combined) and controls (c) for all years. * indicates $p < 0.05$.

were excluded from the calculation for evenness, since a zero observation for evenness indicates a missing value. Comparison of species richness, total number of individuals, Shannon-Wiener diversity and evenness from different sampling areas was conducted with Wilcoxon's matched pair test (wilcox.test) for paired data or with Mann-Whitney U test (wilcox.test) for unpaired data. The successional change over time was analyzed for the matrices species richness, total number of individuals, Shannon-Wiener diversity and evenness. For that purpose the data of the years 2007 and 2008 and data of the years 2016–2019 were pooled into two time periods. Comparisons of pooled data between the two time periods were conducted with Mann-Whitney U tests. All values were given as average value (arithmetic mean) ± standard error (±SE).

Analyzation of the species assemblages between different factors were made using non-parametric multivariate analyses. Individual species were analyzed with non-parametric univariate analyses. The samples taken were divided a priori into groups (on the basis of their sampling area, year and geographical position). Grouping patterns of the species assemblages and sub-taxa such as fishes, crustaceans and echinoderms were assessed using non-metric multidimensional scaling ordination (nMDS) based on a similarity matrix using Bray–Curtis coefficients. Before the analysis, the Bray-Curtis similarity matrices were constructed based on the fourth-root transformed multivariate abundance data to reduce the influence of dominant species. Euclidean distance similarity matrices were constructed based on log (x+1) transformed data for reducing skewness of univariate data. A zero-adjusted resemblance matrix was calculated when samples with no species occurred. In case of no species in both levels of one factor (foundation and control, or complex foundation and non-complex foundation), single samples were removed (Clarke and Gorley, 2015). This was the case for the sampling area foundation and control for the taxa fishes, echinoderms, *Cancer pagurus*, *Marthasterias glacialis*, *Pagurus* spp. and *Astroprecten irregularis*. For the sampling area complex foundation and non-complex foundation this was the case for the taxa fishes, echinoderms, *Cancer pagurus*, *Marthasterias glacialis* and *Pagurus* spp.

Table 2

Wilcoxon's matched pair tests and Mann-Whitney U tests for comparison of species richness, total number of individuals, Shannon-Wiener biodiversity index and evenness between foundations and controls separate for each survey year 2007, 2008 and 2016–2019.

Wilcoxon's matched pair test	Foundations	Controls	p-value
Species richness	Mean ± SE	Mean ± SE	
2007	3.62 ± 0.32	2.05 ± 0.24	0.002
2008	5.11 ± 0.36	2.21 ± 0.35	<0.001
2016	8.71 ± 0.44	3.36 ± 0.48	<0.001
2017	7.73 ± 0.43	2.53 ± 0.36	0.001
2018	65.62 ± 0.4	1.46 ± 0.24	0.002
2019	9.67 ± 0.46	2.87 ± 0.12	0.001
Total number of individuals	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	6.95 ± 0.6	14 ± 0.96	0.005
2008	15.21 ± 1.38	68 ± 2.14	0.002
2016	42.5 ± 3.48	7.07 ± 0.98	<0.001
2017	23.07 ± 2.4	3.73 ± 0.63	<0.001
2018	31.54 ± 7.91	4.69 ± 1.2	0.004
2019	43.8 ± 7.28	7.73 ± 0.6	<0.001
Shannon-Wiener biodiversity	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	1.04 ± 0.09	0.64 ± 0.08	0.011
2008	1.25 ± 0.07	0.49 ± 0.12	<0.001
2016	1.71 ± 0.06	0.91 ± 0.13	<0.001
2017	1.65 ± 0.05	0.73 ± 0.13	<0.001
2018	1.32 ± 0.1	0.3 ± 0.11	<0.001
2019	1.84 ± 0.06	0.73 ± 0.13	<0.001
Mann-Whitney U test	**Foundations**	**Controls**	
Evenness	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	0.28 ± 0.02	0.32 ± 0.01	0.02
2008	0.25 ± 0.01	0.28 ± 0.02	0.149
2016	0.2 ± 0.01	0.28 ± 0.02	<0.001
2017	0.22 ± 0.01	0.3 ± 0.02	<0.001
2018	0.24 ± 0.01	0.32 ± 0.02	0.009
2019	0.2 ± 0.01	0.32 ± 0.01	<0.001

The species assemblages and individual species were analyzed using a 3-way crossed Analysis of Similarity ANOSIM for the factors sampling area, year and geographical position. Sampling area with either foundations and controls or complex foundations and non-complex foundations represented Factor A. Factor B represented the years with six levels 2007, 2008, 2016, 2017, 2018 and 2019. Geographical position specified the position of the foundations and controls and complex and non-complex foundation either north or south and represented Factor C.

In addition to a significance level, the ANOSIM test produces a global R-statistic that typically ranges from 0 (no separation of groups) to 1 (complete separation of groups), although negative values (indicating no separation) are possible. Statistical significance was assessed at a probability level of $p < 0.05$ and a global R value > 0.25.

Similarity percentage (SIMPER) with 80% cut-off level was performed on the transformed data when the ANOSIM global R value was >0.25 and p-value was significant. The SIMPER analyses was performed in order to identify the species that contributed mostly to the difference in species assemblages between the sampling areas, years and geographical positions.

Multivariate and univariate analyses were conducted in PRIMER v.7.0 (Clarke and Gorley, 2015) other analyses were performed with R (Version 3.5.1, R core team 2018).

3. Results

A total of 48 species were recorded around the foundations and controls during the sampling period 2007, 2008 and 2016–2019, with new species being recorded each year (appendix Table 18Table 18). No non-native species were found at any time.

3.1. Reef effects on foundations

A clear reef effect was found on the foundations throughout all study years (Fig. 3 and Table 2). The species richness was more than twice as high on foundations as in control areas in 2008, 2016–2018, and in 2019 even three times greater (Fig. 3 a). The total number of individuals increased more than 200% from the first to the second survey year (Fig. 3 b). In the last year the number of individuals were more than six times higher compared to the first year. In the years 2016–2018 the numbers of individuals fluctuated but never reached less than three times more individuals compared to year 2007. The Shannon-Wiener biodiversity index showed higher values on foundations compared to controls with more than double as high values in 2008 and 2017–2019 (Fig. 3 c). The evenness was always higher in the controls than on foundations (Fig. 3 d) and more similar between the sampling areas and years compared to the other metrics.

3.2. Single species

The clear reef effect found in the total numbers of individuals (Fig. 3 b) was also found throughout all tested single species of the survey: *Cancer pagurus*, *Pagurus* spp. and *Marthasterias glacialis* (Fig. 4 a-c). An opposite effect was found for the sand star (*Astropecten irregularis*). Densities of the sand star were greater in the control areas than on and around the foundations. However, inter-annual variations in numbers of individuals were high for all species.

A significant difference between the sampling area foundations and controls for the four species *Cancer pagurus, Pagurus* spp. *Marthasterias glacialis* and *Astropecten irrgeularis* was confirmed by a 3-way crossed ANOSIM analyses (Table 3). Differences between years and geographical positions did not show differences between the factor levels (Table 3). During all years almost all taxa had greater numbers of individuals on foundations than in controls. An opposite effect was found

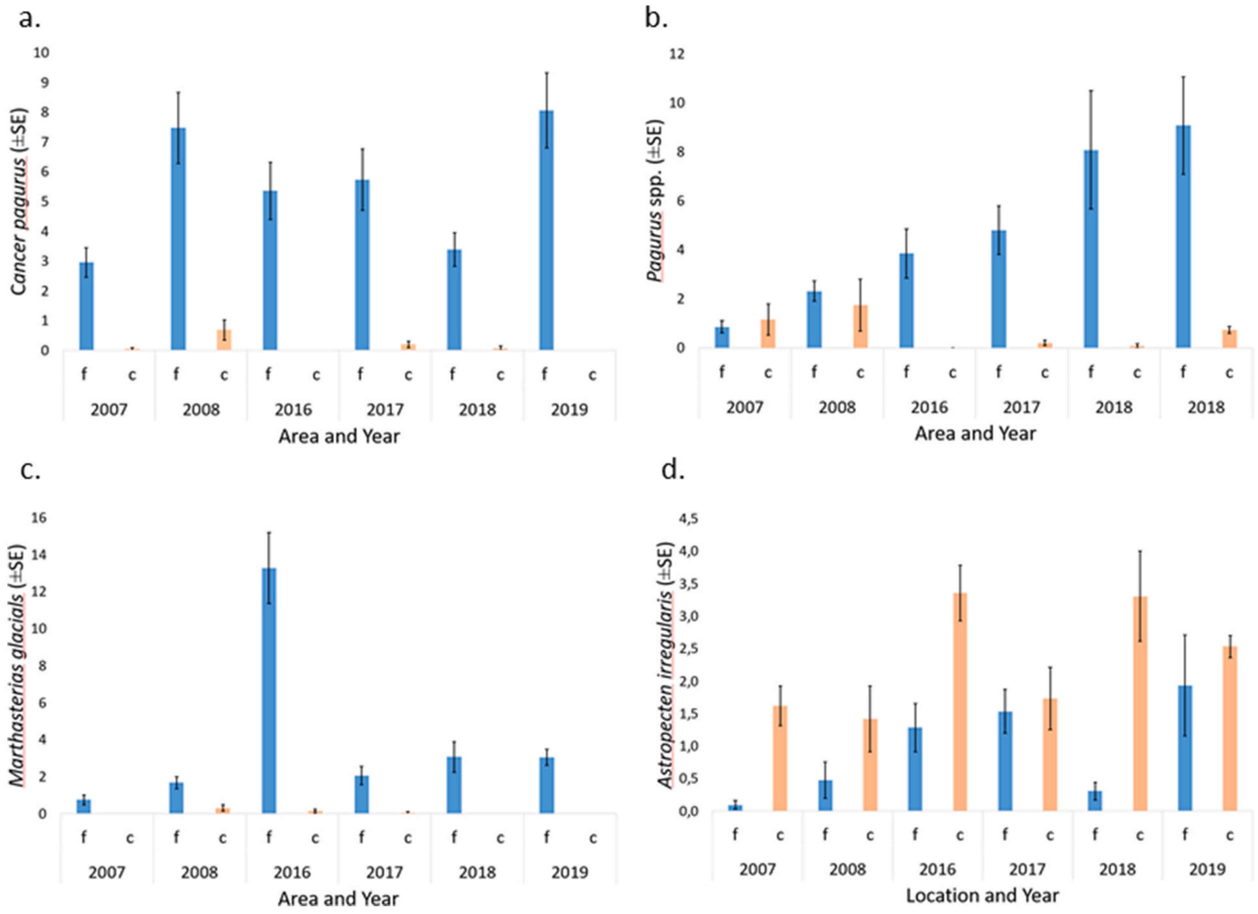

Fig. 4. Average number of a.) *Cancer pagurus* (±SE), b.) *Pagurus* spp. (±SE), c.) *Marthasterias glacialis* (±SE) and d.) *Astropecten irrgeularis* (±SE) on foundations (f complex and non-complex foundations combined) and controls (c) for all years.

Table 3
Results of the 3-way crossed ANOSIM analyses for the taxa *Cancer pagurus*, *Pagurus* spp., *Marthasterias glacialis* and *Astropecten irregularis*. Global tests on the effects of sampling area: foundations and controls, years and geographical positions.

Taxa	Sampling area		Year		Geographical position	
	Global R	P-value	Global R	P-value	Global R	P-value
Cancer pagurus	0.851	0.0001	0.003	0.052	−0.016	0.724
Pagurus spp.	0.585	0.0001	0.044	0.027	0.03	0.153
Marthasterias glacialis	0.872	0.0001	0.1	0.0001	−0.008	0.585
Astropecten irregularis	0.358	0.0001	0.186	0.0001	0.037	0.115

for the species *Astropecten irregularis*, where numbers of sand stars were always greater in controls than on foundations.

3.3. Composition of species assemblage on foundations and controls

The species assemblage is split into two groups based on the factor sampling area including foundations (complex and non-complex) and controls. A fair representation of the species community into this groups is visualized in a two dimensional space with an nMDS ordination (stress value 0.22) (Fig. 5).

A significant difference in the species assemblage between the sampling area, foundations and controls was confirmed by a 3-way crossed ANOSIM analyses (global R = 0.678, $p < 0.0001$). The difference of the assemblage between the years was as well significant (global R = 0.279, $p < 0.0001$) but not between the geographical positions (global R = 0.125; $p < 0.0001$).

The dissimilarity between the two sampling areas (foundations and

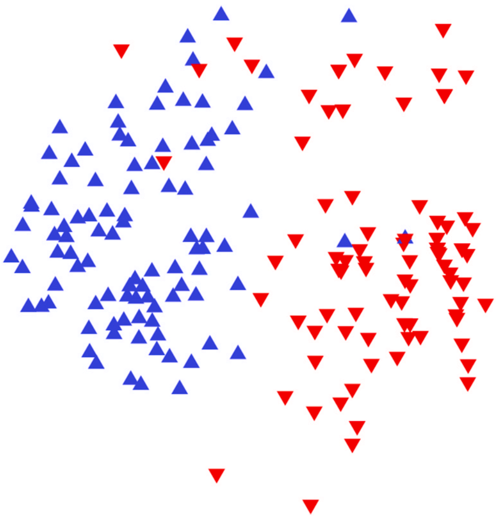

Fig. 5. NMDS ordination plot for the species assemblages on foundations (blue upward pointing triangles) and controls (red downward pointing triangles) constructed from Bray–Curtis similarity matrix (stress value 0.22). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4

Summary of the 2-way crossed SIMPER results for the comparison of the species assemblage between sampling areas. Average abundance of discriminating species in each sampling area, foundation and control, their contribution (%) to the dissimilarity between sampling areas, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the foundations and controls.

Species	Abundance		Contribution	Cumulative
	Foundations	Controls		
Cancer pagurus	1.39	0.11	16.71	16.71
Pagurus spp.	1.13	0.28	12.03	28.74
Marthasterias glacialis	1.04	0.08	10.61	39.35
Astropecten irregularis	0.48	0.94	9.42	48.77
Gadus morhua (juv.)	0.79	0.21	6.52	55.29
Liocarcinus depurator	0.54	0.28	6.35	61.64
Asterias rubens	0.47	0.03	4.93	66.57
Ctenolabrus rupestris	0.45	0	4.04	70.61
Hyas araneus	0.29	0.05	3.67	74.28
Ophiuroidea	0.45	0.01	3.41	77.69
Pomatoschistus spp.	0.13	0.2	2.72	80.4
Average dissimilarity				81.56

Table 5

Pairwise comparisons between the years of the species assemblages of foundations and controls. A 3-way crossed ANOSIM analyses of the species assemblages revealed significant differences between the years (global R = 0.279; p < 0.0001). Significant differences between years are italicized.

Pairwise Tests			Permutations		No. obs.
Years compared	R value	Significance Level %	Possible	Actual	
2007 vs. 2008	0.212	0.01	Very large	9999	0
2007 vs. 2016	*0.443*	*0.01*	*Very large*	*9999*	*0*
2007 vs. 2017	*0.298*	*0.01*	*Very large*	*9999*	*0*
2007 vs. 2018	0.169	0.1	Very large	9999	9
2007 vs. 2019	*0.317*	*0.01*	*Very large*	*9999*	*0*
2008 vs. 2016	*0.397*	*0.01*	*Very large*	*9999*	*0*
2008 vs. 2017	*0.255*	*0.01*	*Very large*	*9999*	*0*
2008 vs. 2018	*0.282*	*0.02*	*Very large*	*9999*	*1*
2008 vs. 2019	*0.383*	*0.01*	*Very large*	*9999*	*0*
2016 vs. 2017	0.101	1.9	Very large	9999	192
2016 vs. 2018	*0.445*	*0.01*	*Very large*	*9999*	*0*
2016 vs. 2019	*0.373*	*0.01*	*Very large*	*9999*	*0*
2017 vs. 2018	0.243	0.02	Very large	9999	1
2017 vs. 2019	*0.275*	*0.01*	*Very large*	*9999*	*0*
2018 vs. 2019	*0.314*	*0.01*	*Very large*	*9999*	*0*

controls) was driven by 11 species covering the taxa fishes, crustaceans and echinoderms, which collectively accounted for 82% of the dissimilarity as shown by a 2-way crossed SIMPER analyses (Table 4).

Pairwise comparisons between the years showed significant differences in the assemblage between all year combinations but for the combinations 2007 vs. 2008, 2007 vs. 2018, 2016 vs. 2017, and 2017 vs. 2018 (Table 5).

The dissimilarity of the species assemblages between years was driven by 10–15 species covering the taxa fishes, crustaceans, echinoderms and others as resulted in the SIMPER analyses. These 10 to 15 species collectively accounted for a dissimilarity of 57%–71% between the tested years (appendix Table 9). For detailed information on SIMPER analyses between years see appendix (Table 9). For information of species composition of other taxa see appendix.

3.4. *Habitat type effects – complex foundations and non-complex foundations*

The picture for the diversity metrics between the complex and the non-complex foundations did not reveal a clear trend as it has been found between the foundations and the controls. The species richness, total number of individuals, Shannon-Wiener biodiversity and evenness did not show differences between the complex foundation and the non-complex foundation within a year (Fig. 6). The only significant difference was found for the number of individuals between the complex and the non-complex foundation in year 2008 (Table 6) where greater numbers of individuals have been found on the complex foundations (Fig. 6 b).

3.5. *Cancer pagurus*

For specific species habitat complexity plays a key role in determining the community structure as exemplified by brown crabs. Brown crabs were more attracted by the complex foundations when compared to the non-complex foundations (Fig. 7). A 3-way crossed univariate ANOSIM analyses showed a significant difference between the complex foundations and the non-complex foundations for the species *Cancer pagurus* (global $R = 0.581$; $p < 0.0001$) but not between the years (global $R = 0.166$, $p < 0.0002$) nor between the geographical positions (global $R = -0.08$; $p < 0.927$). Number of brown crabs were always up to three times greater on complex foundations compared to the non-complex foundations but for the year 2018 where the numbers of brown crabs were still 1,5 times greater (Fig. 7).

In 2007, 2008 holes on the complex foundations were still visible. In 2007 on average three of the upper holes were occupied with at least one brown crab (23%) and on average 1.55 of the lower holes (12%). In 2008, on average 6.1 (47%) of the upper holes and 3.5 (27%) of the lower holes were occupied with a brown crabs, respectively. Occupation of upper holes in 2016 and 2017 were similar to the occupation of the upper holes in 2008. In 2016 on average 6.4 (49%) upper holes were occupied by a crab and in 2017 on average 5.8 (44%).

Other investigated taxa such as fishes, crustaceans and echinoderms and single species such as *Pagurus* spp. and *Marthasterias glacialis* did not reveal differences between the complex foundations and the non-complex foundations but showed differences between the years. For information on ANOSIM analyses of previous mentioned taxa see appendix.

Composition of species assemblages of complex and non-complex foundations.

The species assemblages revealed a low between-factor level (complex and non-complex foundations) difference between the complex foundations and the non-complex foundations (global $R = 0.115$; $p < 0.014$) as well as between the geographical positions (global R value $= 0.142$; $p < 0.011$). However, strong differences in the species assemblage between the years were found (global $R = 0.379$, $p < 0.0001$) with a 3-way crossed ANOSIM analyses. Pairwise tests between years showed significant differences between all years but year 2016 vs. 2017 (Table 7).

The SIMPER analyses revealed that the dissimilarity of the species assemblages between significant different years was driven by 10–16 main species covering the taxa fishes, crustaceans, echinoderms and others, which collectively accounted for between 48%–70% of the dissimilarity between the tested years (appendix Table 12). All pairwise comparisons between the years were significant but for the years 2016 vs. 2017 (Table 7). For detailed information on SIMPER analyses between years see appendix (Table 12).

3.6. *Successional change over time*

The first surveys were conducted, shortly after the deployment of the foundations, in 2007. Mobile species were attracted quickly and 18 species were recorded during the surveys on all foundations, three month after deployment (appendix Table 18).

A successional change over time was observed on the foundations but not on the controls for the following variables. Species richness, total

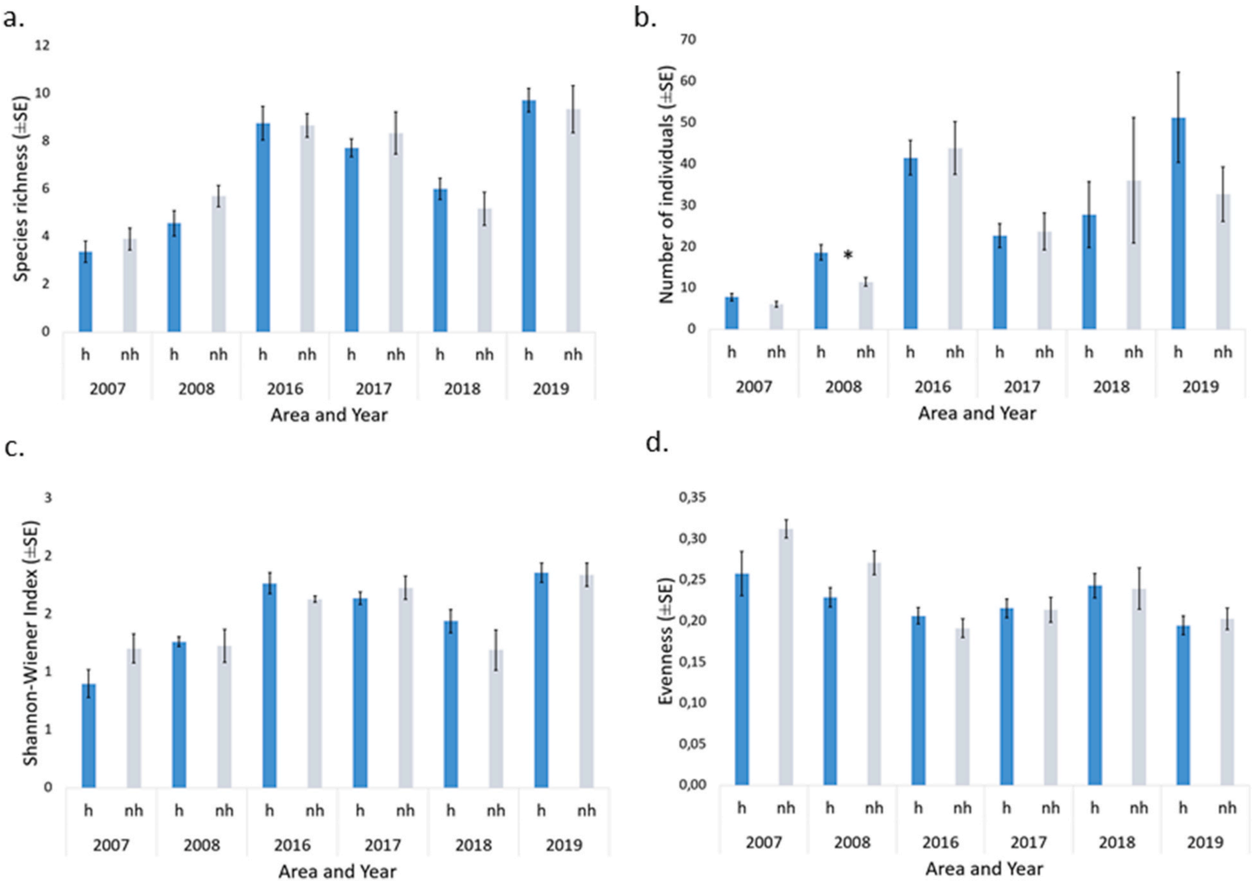

Fig. 6. Average a.) species richness (±SE), b.) total number of individuals (±SE), c.) Shannon-Wiener biodiversity index (±SE) and d.) evenness (±SE) on complex foundations with holes (h) and non-complex foundations with no holes (nh) for all years. * indicates $p < 0.05$.

number of individuals and Shannon-Wiener biodiversity index showed a clear increase when comparing the pooled data from 2007 to 2008 with the pooled data from 2016 to 2019 (Table 8 and Fig. 8 a-c). The total number of individuals increased more than three times from 2007 and 2008 to the second period 2016–2019 (Fig. 8 b). The species richness increased to 185% compared to the first period and the Shannon-Wiener biodiversity up to 144% in the second period. The evenness had significant higher values on the foundations for the first survey period 2007 and 2008 compared to the second survey period 2016–2019 (Table 8 and Fig. 8 d).

4. Discussion

In 2007, 2008 and 2016–2019, visual surveys of mobile fauna on foundations and control areas were conducted in the Lysekil research site at the west coast of Sweden. These long-term studies were made with an attempt to answer questions about changes in species richness, total number of individuals, evenness, Shannon-Wiener biodiversity index, species specific responses and changes in species assemblages on artificial habitats over several years.

4.1. Reef effect

More than 12 years after the initial study, foundations continued to function as artificial reefs and showed greater species richness, total number of individuals and greater Shannon-Wiener biodiversity compared to control areas, but also revealed taxa and species-specific responses. Almost all taxa showed differences between the sampling location foundation and control with greater numbers of individuals on foundations than in controls. Studies comparing artificial reef communities with communities on natural reefs or in randomly chosen control areas almost always show higher density and biomass e.g. in Bohnsack and Sutherland (1985); Stål et al. (2007); Wilhelmsson et al. (2006), which is in accordance with our findings where all taxa showed greater numbers of individuals on foundations than in controls. Foundations that alter the environment provide hard substrate, but can also change the hydrodynamics and accumulation of sediment and detritus. Colonisation of epifauna on foundations occurs and provides feeding and spawning ground, alteration in the local food web, providing of shelter or landmarks for orientation (Langhamer and Wilhelmsson, 2009). Such a process can create habitat with food sources which can reflect an attractive aggregation habitat for mobile fauna (Bohnsack, 1989; Bull and Kendall, 1994; Fabi et al., 2006; Leitão et al., 2007; Reubens et al., 2013b). This can explain a generally greater mega- and macrofauna community with higher species richness and total number of individuals on foundations compared to the nearby soft bottom controls. The results also show that artificial structures such as foundations placed on the bottom directly, and over a long-term, may enhance general species abundance and diversity.

The dwelling sand star, *Astropecten irrgeularis*, showed a reverse effect with greater abundances in controls compared to foundations during all years. *A. irregularis* occurs naturally on soft bottom and thus lower numbers of individuals on foundations are not surprising.

The difference between the foundations and controls was also reflected in the species assemblage. Not only the species richness and the total number of individuals differed between the foundations and control, but also the species assemblage showed a different composition. The two sampling areas reflected very different habitats with the foundation reflecting hard substrate and the control reflecting sand bottom. It is thus not surprising, that the areas also differ between the species

Table 6
Mann-Whitney U tests for comparison of species richness, total number of individuals, Shannon-Wiener biodiversity index and evenness between complex foundations and non-complex foundations for the years 2007, 2008 and 2016–2019.

Mann Whitney U test	Complex foundations	Non-complex foundations	p-value
Species richness	**Mean ± SE**	**Mean ± SE**	
2007	3.36 ± 0.45	3.9 ± 0.46	0.429
2008	5.6 ± 0.45	4.56 ± 0.53	0.2574
2016	8.75 ± 0.7	8.67 ± 0.49	1
2017	7.33 ± 0.41	8.33 ± 0.88	0.396
2018	6 ± 0.44	5.17 ± 0.7	0.3751
2019	9.89 ± 0.45	9.33 ± 0.99	0.2249
Total number of individuals	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	7.82 ± 0.89	6 ± 0.7	0.1854
2008	18.6 ± 1.92	11.44 ± 1.04	0.008
2016	41.5 ± 4.15	43.83 ± 6.39	0.7461
2017	22.67 ± 2.9	23.67 ± 4.45	0.9529
2018	27.71 ± 7.94	36 ± 15.16	0.943
2019	51.22 ± 10.92	32.67 ± 6.62	0.1569
Shannon-Wiener biodiversity	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	0.9 ± 0.12	1.2 ± 0.13	0.113
2008	1.26 ± 0.04	1.23 ± 0.14	0.549
2016	1.77 ± 0.09	1.63 ± 0.03	0.08125
2017	1.64 ± 0.05	1.73 ± 0.1	0.181
2018	1.44 ± 0.1	1.19 ± 0.17	0.2343
2019	1.86 ± 0.09	1.84 ± 0.1	1
Evenness	**Mean ± SE**	**Mean ± SE**	**p-value**
2007	0.26 ± 0.03	0.31 ± 0.01	0.07814
2008	0.23 ± 0.01	0.27 ± 0.01	0.04347
2016	0.21 ± 0.01	0.19 ± 0.01	0.4908
2017	0.22 ± 0.01	0.21 ± 0.02	0.607
2018	0.24 ± 0.01	0.24 ± 0.03	0.8357
2019	0.19 ± 0.01	0.2 ± 0.01	0.6797

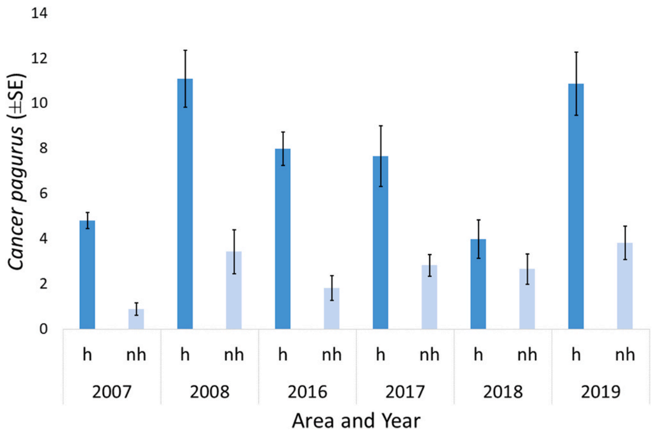

Fig. 7. Average number of *Cancer pagurus* (±SE) comparing complex foundations with holes (h) and non-complex foundations with no holes (nh) for all years.

assemblage (Bohnsack and Sutherland, 1985; Stål et al., 2007; Wilhelmsson et al., 2006). The assemblage of the particular habitats are colonised by species characteristic to the respective area, such as *Astropecten irregularis* and *Liocarcinus depurator* on the soft bottom and *Cancer pagurus* and *Pagurus* spp. on the foundations. A prospective approach is to compare the species assemblage of nearby natural hard bottom with the foundations. Natural hard bottom of the neighboring areas would be in a different successional stage, but most likely resemble a community more similar to the foundation. Comparisons with natural reefs are therefore useful for separating temporal changes due to succession at the artificial reef from regional changes which also affect nearby natural reefs (Becker et al., 2017).

Table 7
Pairwise comparisons between the years of the species assemblages of complex foundations and the non-complex foundations. A 3-way crossed ANOSIM analyses of the species assemblages revealed significant differences between the years (global R = 0.274; p < 0.001). Significant differences between years are italicized.

Pairwise Tests			Permutations		No. obs.
Years compared	R value	Significance Level %	Possible	Actual	
2007 vs. 2008	*0.298*	*0.08*	*924173712*	*9999*	*7*
2007 vs. 2016	*0.572*	*0.01*	*68457312*	*9999*	*0*
2007 vs. 2017	*0.478*	*0.01*	*68457312*	*9999*	*0*
2007 vs. 2018	*0.318*	*0.1*	*31116960*	*9999*	*12*
2007 vs. 2019	*0.471*	*0.01*	*68457312*	*9999*	*0*
2008 vs. 2016	*0.468*	*0.01*	*5186160*	*9999*	*0*
2008 vs. 2017	*0.459*	*0.01*	*19015920*	*9999*	*0*
2008 vs. 2018	*0.402*	*0.05*	*5186160*	*9999*	*4*
2008 vs. 2019	*0.526*	*0.02*	*19015920*	*9999*	*1*
2016 vs. 2017	0.108	12.2	485100	9999	1220
2016 vs. 2018	*0.548*	*0.02*	*132300*	*9999*	*1*
2016 vs. 2019	*0.612*	*0.01*	*485100*	*9999*	*0*
2017 vs. 2018	*0.313*	*0.3*	*220500*	*9999*	*24*
2017 vs. 2019	*0.279*	*0.06*	*485100*	*9999*	*5*
2018 vs. 2019	*0.482*	*0.02*	*220500*	*9999*	*1*

Table 8
Mann-Whitney U tests for comparison of pooled abundance of species richness, total number of individuals, Shannon-Wiener biodiversity index and evenness between foundations 2007 and 2008 and foundations 2016–2019 and controls 2007 and 2008 and controls 2016–2019.

Mann-Whitney U test	2007 and 2008	2016–2019	p-value
Species richness	**Mean ± SE**	**Mean ± SE**	
Foundations	4.33 ± 0.26	8 ± 0.29	<0.001
Controls	2.13 ± 0.21	2.58 ± 0.2	0.117
Total number of individuals	**Mean ± SE**	**Mean ± SE**	**p-value**
Foundations	10.88 ± 0.97	35.23 ± 2.99	<0.001
Controls	5.35 ± 1.14	5.82 ± 0.68	0.224
Shannon-Wiener biodiversity	**Mean ± SE**	**Mean ± SE**	**p-value**
Foundations	1.14 ± 0.06	1.64 ± 0.04	<0.001
Controls	0.57 ± 0.07	0.68 ± 0.07	0.285
Evenness	**Mean ± SE**	**Mean ± SE**	**p-value**
Foundations	0.27 ± 0.01	0.21 ± 0.01	<0.001
Controls	0.3 ± 0.01	0.3 ± 0.01	0.851

4.2. Habitat type effects

The aggregation by species is related to specific habitat characteristics (e.g. bottom type, maturity of the system and prey availability), while the seasonal patterns are related to life-history characteristics (e.g. feeding times, spawning period) (Reubens et al., 2013a, b). In our study, brown crabs (*Cancer pagurus*) were especially attracted to the complex foundations during all years. Similar results were found in a study on offshore wind farms where attraction of brown crabs and cod was clearest (Van Hal et al., 2017). Higher degree of complexity attracts greater abundance of brown crabs as it was also found on wind farm foundations with scour protection compared to other foundation types (Krone et al., 2017). It could be shown that scour protection around monopiles resemble a more complex habitat and thus attract more brown crabs than jacket foundations. The foundations in our study could be compared to a simplified scour protection of monopiles. Number of brown crabs more than twice as high have been found on complex

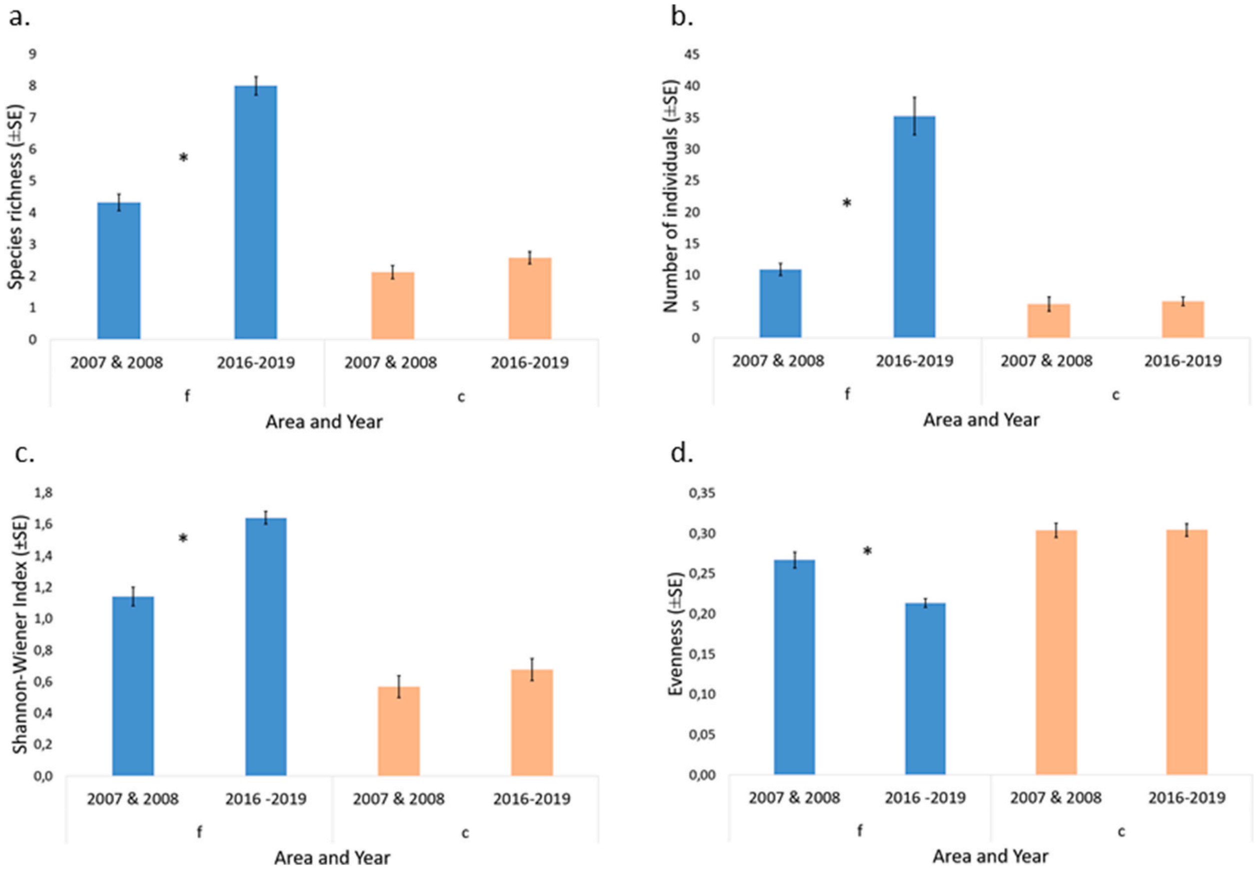

Fig. 8. Average a.) species richness (±SE), b.) total number of individuals (±SE), c.) Shannon-Wiener biodiversity index (±SE), d.) evenness (±SE) of pooled data from 2007 to 2008 and 2016–2019 comparing wave power foundations, blue bars, (complex and non-complex foundations combined) and controls, orange bars, of both survey periods. * indicates $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)j

foundations compared to non-complex foundations for both survey periods 2007 and 2008 and 2016–2019 in our study. However, the manufactured holes provide complexity on a relatively low level. This may explain why *C. pagurus* was the only species which was more abundant of the complex foundations compared to the non-complex foundations. Artificial structures are often not successfully mimicking the natural habitat and lack small refuges for newly settled fishes (Komyakova and Swearer, 2019). The manufactured holes of the foundations in our study added structural complexity to the foundations, but did not provide small scale refuges, thus lacking escape options and less water exchange may explain the low abundance of fishes on the complex foundations during all survey years (Langhamer and Wilhelmsson, 2009). Instead scour protection of wind turbine monopiles offer various hiding places for different species and sizes (Krone et al., 2017). For offshore renewable installations, the main purpose of the foundations is to provide anchoring for the installation. The function as an artificial reef is of secondary importance for foundations of renewable offshore devices. Furthermore, the complexity of those structures are limited compared to “intentionally” placed artificial reefs. However, both simple and cheap modifications of structures, such as the manufactured holes on the foundations, can provide enhancement of specific species, such as for the economic interesting brown crab as it was the case with the manufactured holes in our complex foundations, without affecting the performance of the device.

The species assemblage was not different between the complex and the non-complex foundation. Both foundations resemble quite similar habitats. All foundations were deployed in the same year and the stage of succession can be thereby comparable and no difference in terms of succession stages are expected (Andersson and Öhman, 2010). The different degrees in complexity of the foundations seemed to be exclusively an advantage for the brown crab and did not affect other species or the general species assemblage. Future renewable device foundations of similar types could be enhances by holes of various sizes and passages to increase the attraction for different species.

4.3. *Successional change over time*

A successional change from the first to the second survey period could be revealed. Foundations were populated to a higher extent in the second survey period 2016–2019 as compared to the first survey period 2007 and 2008, shorter after the deployment. Increased species richness, total number of individuals and greater values of the Shannon-Wiener biodiversity index were observed. Colonisation on newly induced hard substrate occurs gradually but is also depending on installation season (Causon and Gill, 2018).

Highly mobile species such as fishes can occur on the structure rather quickly after the deployment. Fishes of several different species are known to appear fast on and around artificial reefs, often within hours after deployment (Leitão et al., 2009; Reubens et al., 2013a, b). They are also highly mobile and can be very dynamic (Lindeboom et al., 2011) and thus can disappear quickly or use the structure as a transient (Van Hal et al., 2017).

Establishment of less mobile species such as brown crabs and the spiny sea star *Martastherias glacialis* are dependent on sufficient food sources, cover of epibenthic communities and appropriate habitat with shelter opportunities to hide from predators (Bohnsack, 1989; Bull and Kendall, 1994; Langhamer and Wilhelmsson, 2009; Leitão et al., 2007) which take time to establish. For the brown crab, *C. pagurus*, the percentage of occupation of the manufactured holes increased from 23% in the first year to almost 50% in second year 2008. In the years 2016 and 2017 occupation stayed around 50% indicating that the brown crabs reached a number representing a stable size of community after already two years. This finding is in accordance with a study on successional processes of macrobenthic fouling community in deeper water of cold temperate regions. These communities were stable after one and a half years and further only seasonal changes occurred (De Mesel et al., 2015). Growth of a fouling community on foundations is the basis for mobile mega- and macrofauna species to provide food sources and to provide attractive colonisation habitat (Leitão et al., 2007).

Despite inter-annual changes in species assemblages, species richness at the end of the study 2019 was similar to the beginning of the second survey period 2016. Given that annual changes in the community were observed, a relatively similar diversity between these years occurred. We suggest that successional changes in the assemblage composition on the foundations did not necessarily lead to an overall increase in diversity during the last survey years 2016–2019. Essentially, one group of species may be replacing another, and such patterns are well documented in successional studies (Becker et al., 2017; Connell and Slatyer, 1977).

4.4. *Inter-annual variation and natural variation*

Species assemblages differed between years comparing the foundations and controls and comparing the complex with the non-complex foundations. Inter-annual variation seems to have a higher influence on species assemblage than the difference between the complexity levels of the foundation. Inter-annual variation was high for both the single species *Cancer pagurus*, *Pagurus* spp., *Marthasterias glacialis*, *Astropecten irregularis* and for the total number of individuals. In other studies, the abiotic factor temperature has been identified as the dominating factor to regulate mobile fauna in shallow areas (Magill and Sayer, 2002; Pihl and Rosenberg, 1982). Samples in our study were taken one time per year. All samples were taken between July and August when similar seasonal conditions are present in order to avoid seasonal effects. In cold temperate environments, such as the Swedish west coast, species are highly influenced by seasons (Pihl and Wennhage, 2002). In earlier studies observed differences were considered to be independent of seasonal effects when conducted in similar times of the year (Krone et al., 2017; Reubens et al., 2014). However, storm or other weather events can have an influence on inter-annual variation between abundances of species and individuals besides seasonal and natural variations (Komyakova et al., 2019a, b).

4.5. *Evenness*

The sandy seabed areas of the controls reflect a well establish and old habitat compared to the foundations where high evenness is likely to expect. Evenness shows higher values for the control sites compared to the foundations, both for the pooled data and individual years. One likely explanation why this is the case is the general low species richness and low number of individuals in the control sites. On the foundation species richness was higher as was total number of individuals. However, on almost all foundations there were some species observed with only one individual and, on the other hand, on all foundations there were some species observed in almost always high numbers. The calculation for evenness with low species richness and low numbers of individuals would result in more even distribution of species with higher values for evenness compared to an area with relatively higher species richness but with a much higher range of total number of individuals. This may explain the general lower evenness on the foundations compared to controls.

4.6. *No non-invasive species*

A concern exists that offshore renewable energy foundations can function as stepping stones (Adams et al., 2014), contribute to a faster spread of invasive species or promote range expansion of their previous natural existing range (De Mesel et al., 2015) and various examples of non-native species found on offshore renewable energy devices exist (Herbert et al., 2017; Nall et al., 2017; Sheehan et al., 2018). This is especially the case, when solid foundations are deployed on soft bottom dominated areas. The foundations in our study have been deployed since

2007 and no non-native species have been found during the surveys 2007, 2008 and 2016–2019 (see appendix Table 18).

4.7. SCUBA survey method

Many fish species are quickly attracted to artificial reefs (Reubens et al., 2013a) (Leitão et al., 2009, 2007) but fishes are also highly dynamic and mobile (Lindeboom et al., 2011). The method of SCUBA surveys is a widely used method for visual species observations (Krone et al., 2017; Langhamer and Wilhelmsson, 2009; Leitão et al., 2007; Love et al., 2017; Magill and Sayer, 2002; Reubens et al., 2014). However, species can either be disturbed or attracted by the presence of the diver and might thus impact and bias observations. Highly mobile species such as fishes were counted first while approaching the foundations. In the second instance less mobile species were assessed. The use of standardized measurement techniques was applied throughout all years and the impact by the chosen method can thus be negligible.

5. Conclusion

This quantitative long-term study provides information on successional colonisation of foundations by mobile mega- and macrofauna community over a period of more than 12 years. We conclude, that offshore renewable energy foundations in cold temperate regions can locally enhance the biodiversity, abundance of specific reef species and total number of individuals with a successional increase over time compared to surrounding sand bottom. Hereby, the provision of ecosystem services could be positively affected. A focus should be given to the improvement of complexity of the different renewable offshore foundations to widen the spectrum of species colonisation. Different sizes and depth of holes in the foundations but also passages for individuals to pass through, possibilities for escape could be implemented to increase the attraction for various species and sizes of individuals.

CRediT authorship contribution statement

Anke Bender: Methodology, Investigation, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Olivia Langhamer:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision. **Jan Sundberg:** Conceptualization, Funding acquisition, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.105053.

Appendix

SIMPER results of the species assemblage between years of the sample area foundations and controls

The species assemblages revealed significant difference between the foundation and the controls (global $R = 0.678$; $p < 0.0001$) and between the years (global $R = 0.279$; $p < 0.0001$) but not differences between the geographical positions (global $R = 0.125$, $p < 0.0003$) in a 3-way crossed ANOSIM analyses. Pairwise tests between years showed several significant differences (Table 5). Results of the SIMPER analyses are listed in the following table (Table 9Table 9).

Table 9

Summary of the 2-way crossed SIMPER results for the comparison of the species assemblage between years. Average abundance of discriminating species in each year and their contribution (%) to the dissimilarity between years, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the sampling years.

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Pagurus spp.	0.48	0.7	13.82	13.82
Astropecten irregularis	0.48	0.4	13.82	27.64
Liocarcinus depurator	0.53	0.2	10.63	38.27
Marthasterias glacialis	0.24	0.6	9.34	47.6
Cancer pagurus	0.57	0.9	8.7	56.3
Pomatoschistus spp.	0.05	0.2	5.83	62.13
Gadus morhua (juv.)	0.06	0.4	5.75	67.88
Hyas araneus	0.1	0.3	4.63	72.51
Asterias rubens	0.1	0.2	4.5	77.01
Callionymus maculatus	0.15	0.1	3.49	80.5
Average dissimilarity				71.01
Abundance				
Species	**Year 2007**	**Year 2016**	**Contribution**	**Cumulative**

(*continued on next page*)

Table 9 (*continued*)

Abundance

Species	Year 2007	Year 2008	Contribution	Cumulative
Gadus morhua (juv.)	0.06	1.3	14.18	14.18
Astropecten irregularis	0.48	1	12.23	26.41
Liocarcinus depurator	0.53	0.5	9.42	35.82
Pagurus spp.	0.48	0.6	8.43	44.25
Pomatoschistus spp.	0.05	0.4	7.94	52.2
Marthasterias glacialis	0.24	1	7.83	60.03
Asterias rubens	0.1	0.6	6.31	66.34
Ctenolabrus rupestris	0.05	0.5	4.08	70.41
Merlangius merlangius	0	0.4	3.86	74.28
Callionymus maculatus	0.15	0.1	3.66	77.93
Ophiuroidea	0	0.4	3.58	81.51
Average dissimilarity				69.96

Abundance

Species	**Year 2008**	**Year 2016**	**Contribution**	**Cumulative**
Astropecten irregularis	0.4	1	14.49	14.49
Gadus morhua (juv.)	0.44	1.3	12.15	26.63
Pomatoschistus spp.	0.17	0.4	8.88	35.51
Marthasterias glacialis	0.56	1	8.61	44.12
Liocarcinus depurator	0.17	0.5	7.33	51.45
Pagurus spp.	0.72	0.6	7	58.45
Cancer pagurus	0.92	0.7	5.14	63.58
Merlangius merlangius	0	0.4	3.74	67.32
Asterias rubens	0.22	0.6	3.72	71.04
Ophiuroidea	0	0.4	3.32	74.36
Hyas araneus	0.26	0.1	3.26	77.62
Ctenolabrus rupestris	0.15	0.5	3.24	80.87
Average dissimilarity				65.31

Abundance

Species	**Year 2007**	**Year 2017**	**Contribution**	**Cumulative**
Astropecten irregularis	0.48	0.8	15.08	15.08
Gadus morhua (juv.)	0.06	0.9	12.16	27.24
Pagurus spp.	0.48	0.8	11.35	38.6
Liocarcinus depurator	0.53	0.2	9.33	47.93
Pleuronectes platessa	0.08	0.2	5.8	53.73
Cancer pagurus	0.57	0.8	5.41	59.14
Marthasterias glacialis	0.24	0.5	4.32	63.46
Asterias rubens	0.1	0.2	3.97	67.42
Pomatoschistus spp.	0.05	0.2	3.96	71.38
Carcinus maenas	0	0.3	3.12	74.5
Ctenolabrus rupestris	0.05	0.3	2.96	77.46
Ophiuroidea	0	0.3	2.47	79.93
Callionymus maculatus	0.15	0	2.45	82.39
Average dissimilarity				71.73

Abundance

Species	**Year 2008**	**Year 2017**	**Contribution**	**Cumulative**
Astropecten irregularis	0.4	0.8	15.39	15.39
Gadus morhua (juv.)	0.44	0.9	11.28	26.68
Pagurus spp.	0.72	0.8	9.48	36.15
Marthasterias glacialis	0.56	0.5	7.23	43.39
Cancer pagurus	0.92	0.8	7.08	50.46
Pomatoschistus spp.	0.17	0.2	6.56	57.02
Pleuronectes platessa	0.03	0.2	4.65	61.67
Liocarcinus depurator	0.17	0.2	3.69	65.36
Hyas araneus	0.26	0.2	3.62	68.99
Asterias rubens	0.22	0.2	3.12	72.11
Carcinus maenas	0	0.3	2.75	74.86
Ctenolabrus rupestris	0.15	0.3	2.71	77.56
Ophiuroidea	0	0.3	2.24	79.8
Pleuronectidae	0.17	0	2.07	81.87
Average dissimilarity				67.35

Abundance

Species	**Year 2016**	**Year 2017**	**Contribution**	**Cumulative**
Astropecten irregularis	1	0.8	13.16	13.16
Gadus morhua (juv.)	1.25	0.9	13.11	26.26
Pomatoschistus spp.	0.43	0.2	9.08	35.34
Liocarcinus depurator	0.47	0.2	7.88	43.22
Marthasterias glacialis	1	0.5	5.98	49.21
Pleuronectes platessa	0.04	0.2	4.72	53.92
Asterias rubens	0.59	0.2	4.66	58.58
Pagurus spp.	0.62	0.8	4.51	63.09

(*continued on next page*)

Table 9 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Merlangius merlangius	0.38	0	3.98	67.06
Ophiuroidea	0.42	0.3	3.62	70.68
Cancer pagurus	0.72	0.8	3.62	74.3
Ctenolabrus rupestris	0.49	0.3	2.5	76.8
Carcinus maenas	0.11	0.3	2.34	79.14
Callionymus maculatus	0.11	0	2.3	81.44
Average dissimilarity				57.32

Abundance				
Species	**Year 2007**	**Year 2018**	**Contribution**	**Cumulative**
Astropecten irregularis	0.48	0.8	18.98	18.98
Pagurus spp.	0.48	0.8	14.74	33.72
Liocarcinus depurator	0.53	0.1	11.76	45.48
Ophiuroidea	0	0.6	7.94	53.42
Asterias rubens	0.1	0.3	6.34	59.77
Upogebia holes	0	0.2	5.54	65.31
Cancer pagurus	0.57	0.7	5.53	70.84
Marthasterias glacialis	0.24	0.6	5.52	76.36
Callionymus maculatus	0.15	0	3.12	79.48
Hyas araneus	0.1	0.1	2.51	81.99
Average dissimilarity				65.88

Abundance				
Species	**Year 2008**	**Year 2018**	**Contribution**	**Cumulative**
Astropecten irregularis	0.4	0.8	19.68	19.68
Pagurus spp.	0.72	0.8	10.94	30.62
Marthasterias glacialis	0.56	0.6	8.7	39.32
Cancer pagurus	0.92	0.7	8.3	47.62
Ophiuroidea	0	0.6	6.76	54.38
Upogebia holes	0.09	0.2	6.38	60.76
Pomatoschistus spp.	0.17	0	5.69	66.45
Gadus morhua (juv.)	0.44	0.1	5.16	71.61
Hyas araneus	0.26	0.1	3.98	75.59
Asterias rubens	0.22	0.3	3.89	79.47
Liocarcinus depurator	0.17	0.1	3.09	82.57
Average dissimilarity				65.37

Abundance				
Species	**Year 2016**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.25	0.1	15.85	15.85
Astropecten irregularis	1	0.8	12.43	28.28
Pomatoschistus spp.	0.43	0	9.52	37.8
Liocarcinus depurator	0.47	0.1	8.37	46.16
Ophiuroidea	0.42	0.6	5.9	52.06
Marthasterias glacialis	1	0.6	5.79	57.85
Upogebia holes	0	0.2	4.81	62.66
Merlangius merlangius	0.38	0	4.3	66.96
Ctenolabrus rupestris	0.49	0.1	3.94	70.9
Asterias rubens	0.59	0.3	3.92	74.82
Pagurus spp.	0.62	0.8	3.76	78.58
Mycocephalus scorpius	0.12	0.2	3.16	81.74
Average dissimilarity				57.62

Abundance				
Species	**Year 2017**	**Year 2018**	**Contribution**	**Cumulative**
Astropecten irregularis	0.84	0.8	18.87	18.87
Gadus morhua (juv.)	0.88	0.1	13.33	32.2
Pagurus spp.	0.76	0.8	7.01	39.22
Ophiuroidea	0.27	0.6	6.04	45.26
Cancer pagurus	0.84	0.7	5.64	50.9
Pleuronectes platessa	0.17	0	5.59	56.49
Upogebia holes	0	0.2	5.37	61.86
Asterias rubens	0.19	0.3	4.25	66.11
Pomatoschistus spp.	0.17	0	3.9	70.01
Marthasterias glacialis	0.52	0.6	3.51	73.51
Carcinus maenas	0.28	0	2.91	76.42
Ctenolabrus rupestris	0.31	0.1	2.82	79.25
Liocarcinus depurator	0.22	0.1	2.66	81.91
Average dissimilarity				60.85

Abundance				
Species	**Year 2007**	**Year 2019**	**Contribution**	**Cumulative**
Astropecten irregularis	0.48	1	14.06	14.06
Liocarcinus depurator	0.53	1	13.41	27.47

(*continued on next page*)

Table 9 (*continued*)

Abundance

Species	Year 2007	Year 2008	Contribution	Cumulative
Pagurus spp.	0.48	1	12.69	40.16
Upogebia holes	0	0.4	6.63	46.78
Gadus morhua (juv.)	0.06	0.5	5.25	52.03
Arenicola marina cast	0	0.3	4.4	56.44
Hyas araneus	0.1	0.4	3.9	60.34
Marthasterias glacialis	0.24	0.6	3.9	64.24
Cancer pagurus	0.57	0.8	3.38	67.62
Ctenolabrus rupestris	0.05	0.4	3.36	70.98
Asterias rubens	0.1	0.2	3.19	74.18
Pomatoschistus spp.	0.05	0.2	3.07	77.25
Mya arenaria	0	0.2	2.99	80.23
Average dissimilarity				66.08

Abundance

Species	**Year 2008**	**Year 2019**	**Contribution**	**Cumulative**
Astropecten irregularis	0.4	1	14.67	14.67
Liocarcinus depurator	0.17	1	12.39	27.06
Pagurus spp.	0.72	1	10.01	37.07
Upogebia holes	0.09	0.4	6.97	44.04
Marthasterias glacialis	0.56	0.6	6.03	50.07
Gadus morhua (juv.)	0.44	0.5	5.74	55.81
Pomatoschistus spp.	0.17	0.2	5.65	61.46
Cancer pagurus	0.92	0.8	5.17	66.63
Hyas araneus	0.26	0.4	4.11	70.74
Arenicola marina cast	0	0.3	4.05	74.79
Ctenolabrus rupestris	0.15	0.4	2.74	77.54
Mya arenaria	0	0.2	2.7	80.24
Average dissimilarity				67.07

Abundance

Species	**Year 2016**	**Year 2019**	**Contribution**	**Cumulative**
Liocarcinus depurator	0.47	1	11.65	11.65
Gadus morhua (juv.)	1.25	0.5	11.51	23.16
Astropecten irregularis	1	1	9.87	33.03
Pomatoschistus spp.	0.43	0.2	8.68	41.72
Pagurus spp.	0.62	1	6.26	47.98
Upogebia holes	0	0.4	6.13	54.11
Marthasterias glacialis	1	0.6	4.12	58.23
Arenicola marina cast	0	0.3	4.01	62.25
Mycocephalus scorpius	0.12	0.3	3.6	65.84
Merlangius merlangius	0.38	0	3.59	69.43
Ophiuroidea	0.42	0.3	3.52	72.95
Asterias rubens	0.59	0.2	3.51	76.46
Hyas araneus	0.07	0.4	3.16	79.62
Mya arenaria	0	0.2	2.61	82.23
Average dissimilarity				57.04

Abundance

Species	**Year 2017**	**Year 2019**	**Contribution**	**Cumulative**
Astropecten irregularis	0.84	1	12.63	12.63
Liocarcinus depurator	0.22	1	12.1	24.73
Gadus morhua (juv.)	0.88	0.5	10.17	34.9
Pagurus spp.	0.76	1	7.74	42.64
Upogebia holes	0	0.4	6.45	49.09
Pomatoschistus spp.	0.17	0.2	4.72	53.82
Arenicola marina cast	0.03	0.3	4.42	58.24
Pleuronectes platessa	0.17	0	4.19	62.43
Cancer pagurus	0.84	0.8	3.5	65.93
Ophiuroidea	0.27	0.3	2.96	68.89
Mya arenaria	0	0.2	2.82	71.72
Hyas araneus	0.16	0.4	2.54	74.25
Asterias rubens	0.19	0.2	2.47	76.72
Callionymus lyra	0.03	0.1	2.44	79.16
Marthasterias glacialis	0.52	0.6	2.39	81.55
Average dissimilarity				61.81

Abundance

Species	**Year 2018**	**Year 2019**	**Contribution**	**Cumulative**
Liocarcinus depurator	0.08	1	15.81	15.81
Astropecten irregularis	0.76	1	15.2	31.01
Upogebia holes	0.21	0.4	10.6	41.61
Pagurus spp.	0.77	1	8.75	50.36
Ophiuroidea	0.6	0.3	5.99	56.36
Gadus morhua (juv.)	0.08	0.5	5.37	61.73

(*continued on next page*)

Table 9 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Arenicola marina cast	0	0.3	5.16	66.89
Mya arenaria	0	0.2	3.5	70.39
Cancer pagurus	0.66	0.8	3.24	73.63
Ctenolabrus rupestris	0.08	0.4	3.18	76.81
Hyas araneus	0.08	0.4	3.17	79.97
Asterias rubens	0.34	0.2	3.05	83.03
Average dissimilarity				57.28

Composition of the species assemblage of other taxa on foundations and controls

Two groups for the fishes assemblage, crustacean assemblage and echinoderm assemblage based on the two sampling areas (foundations and controls) can be seen in the two dimensional nMDS ordinations, as for the whole species assemblage (Figure 9Fig. 9a–c.).

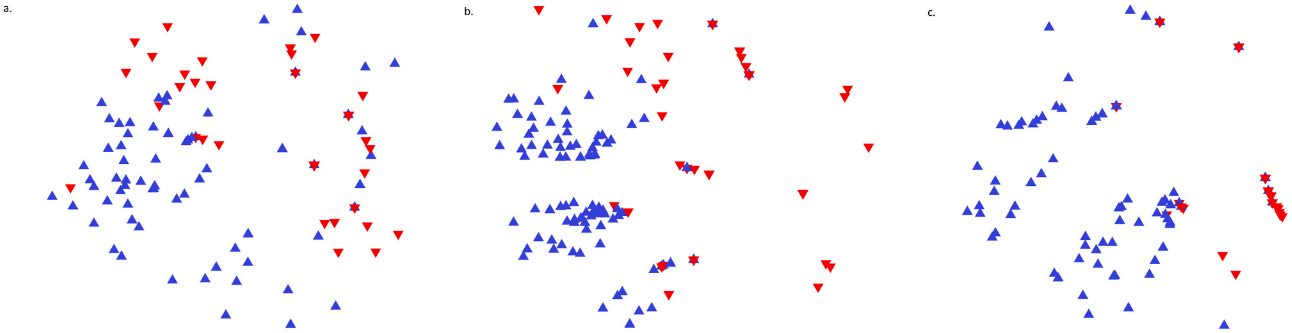

Fig. 9. NMDS ordination plot for a.) fishes assemblage (stress value 0.19), b.) crustaceans assemblage (stress value 0.18) and c.) echinoderms assemblage (stress value 0.13) on foundations (blue upward pointing triangles) and controls (red downward pointing triangles) constructed from Bray–Curtis similarity matrix.

A significant difference between sampling area foundations and control areas of the fishes, crustaceans and echinoderms assemblage were all confirmed by a 3-way crossed ANOSIM analyses (Table 10).

Table 10
Results of the 3-way crossed ANOSIM analyses for the taxa fishes, crustaceans and echinoderms. Global tests on the effects of sampling area foundations and controls, years and geographical positions.

	Sampling area		Year		Geographical position	
Taxa	Global R	P-value	Global R	P-value	Global R	P-value
Fishes	0.494	0.0001	0.19	0.0001	0.078	0.012
Crustaceans	0.68	0.0001	0.161	0.0001	0.034	0.122
Echinoderms	0.552	0.0001	0.152	0.0001	0.055	0.056

For the three taxa fishes, crustaceans and echinoderms a SIMPER analyses was performed in order to identify the species that contributed mostly to the difference between the sampling areas. The dissimilarity of the fishes assemblage between the two sampling areas (foundations and controls) was driven by seven species which collectively accounted for 94% of dissimilarity as shown by the SIMPER analyses (Table 11Table 11). Hereof juvenile cod (*Gadus morhua*), as the main species contributed up to 31% to the dissimilarity between the sampling areas. The dissimilarity of the crustaceans assemblage between the two sampling areas (foundations and the controls) was driven by three main crustacean species. *Cancer pagurus* contributed up to 38% to the dissimilarity, followed by *Pagurus* spp. and *Liocarcinus depurator* which all collectively accounted for 84% of dissimilarity (Table 11Table 11) as shown by the SIMPER analyses. The SIMPER analyses revealed 79% the dissimilarity of the echinoderms assemblage between the two sampling locations foundations and the controls (Table 11Table 11). It was driven by three main species, *Marthasterias glacialis*, *Astropecten irregularis* and *Asterias rubens*.

Table 11
Summary of SIMPER results for the comparison of the fishes assemblage, crustaceans assemblage and the echinoderms assemblage between sampling areas. Average abundance of discriminating species in each sampling area, foundation and control, their contribution (%) to the dissimilarity between sampling areas, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the foundations and controls.

Abundance				
Fishes	Foundation	Control	Contribution	Cumulative
Gadus morhua (juv.)	1.01	0.21	31.34	31.34
Ctenolabrus rupestris	0.58	0	18.32	49.66
Mycocephalus scorpius	0.28	0.02	10.04	59.7
Pomatoschistus spp.	0.16	0.2	9.43	69.13
Pleuronectes platessa	0.04	0.07	4.51	73,65

(*continued on next page*)

Table 11 (*continued*)

Abundance				
Fishes	Foundation	Control	Contribution	Cumulative
Callionymus maculatus	0.04	0.08	4.14	77.79
Pholis gunnelus	0.09	0	3.98	81.78
Average dissimilarity				94
Abundance				
Crustaceans	**Foundation**	**Control**	**Contribution**	**Cumulative**
Cancer pagurus	1.39	0.11	38.41	38.41
Pagurus spp.	1.13	0.28	27.78	66.19
Liocarcinus depurator	0.54	0.28	15	81.2
Average dissimilarity				84.37
Abundance				
Echinoderms	**Foundation**	**Control**	**Contribution**	**Cumulative**
Marthasterias glacialis	1.17	0.08	39.95	39.95
Astropecten irregularis	0.55	0.94	28.44	68.39
Asterias rubens	0.53	0.03	16.28	84.67
Average dissimilarity				78.56

SIMPER results of the species assemblage for differences between the years of the sample area complex and non-complex foundations

Species assemblage

The species assemblages revealed non-significant difference between the complex foundations and the non-complex foundations (global $R = 0.115$; $p < 0.015$) nor between the geographical positions (global R value $= 0.142$; $p < 0.013$) but significant differences between the years (global $R = 0.274$, $p < 0.0001$) in a 3-way crossed ANOSIM analyses. Pairwise tests between years showed several significant differences (Table 7). Results of the SIMPER analyses are listed in Table 12Table 12.

Table 12

Summary of SIMPER results for the comparison of the species assemblage between years. Average abundance of discriminating species in each year and their contribution (%) to the dissimilarity between years, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the sampling years.

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Pagurus spp.	0.54	1.01	11.69	11.69
Gadus morhua (juv.)	0.11	0.78	11.34	23.03
Marthasterias glacialis	0.48	0.88	10.92	33.96
Cancer pagurus	1.08	1.52	9.99	43.95
Liocarcinus depurator	0.58	0.23	9.08	53.03
Asterias rubens	0.1	0.44	6.64	59.67
Hyas araneus	0.14	0.34	6.07	65.74
Ctenolabrus rupestris	0.1	0.29	5.39	71.12
Astropecten irregularis	0.1	0.25	4.25	75.37
Gadus morhua	0.2	0.05	3.46	78.84
Pleuronectidae	0.05	0.21	3.41	82.24
Average dissimilarity				61.90
Abundance				
Species	**Year 2007**	**Year 2016**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.11	1.82	15.1	15.1
Marthasterias glacialis	0.48	1.86	12.13	27.23
Asterias rubens	0.1	1.19	9.9	37.13
Ctenolabrus rupestris	0.1	0.99	8.1	45.23
Pagurus spp.	0.54	1.24	7.12	52.35
Ophiuroidea	0	0.85	7.11	59.46
Astropecten irregularis	0.1	0.74	6	65.46
Liocarcinus depurator	0.58	0.47	5.12	70.57
Merlangius merlangius	0	0.6	4.84	75.41
Cancer pagurus	1.08	1.44	4.66	80.07
Average dissimilarity				70
Abundance				
Species	**Year 2008**	**Year 2016**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	1.82	12.77	12.77
Marthasterias glacialis	0.88	1.86	10	22.77
Asterias rubens	0.44	1.19	9.22	31.99
Ophiuroidea	0	0.85	8.22	40.21
Ctenolabrus rupestris	0.29	0.99	8.04	48.24
Astropecten irregularis	0.25	0.74	6.88	55.12

(*continued on next page*)

Table 12 (*continued*)

Abundance

Species	Year 2007	Year 2008	Contribution	Cumulative
Merlangius merlangius	0	0.6	5.62	60.74
Pagurus spp.	1.01	1.24	5.41	66.16
Liocarcinus depurator	0.23	0.47	5.01	71.17
Cancer pagurus	1.52	1.44	4.19	75.36
Hyas araneus	0.34	0.07	3.6	78.96
Pomatoschistus spp.	0.11	0.26	3.18	82.14
Average dissimilarity				52.72

Abundance

Species	**Year 2007**	**Year 2017**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.11	1.32	12.91	12.91
Pagurus spp.	0.54	1.33	9.78	22.69
Astropecten irregularis	0.1	0.86	8.98	31.67
Marthasterias glacialis	0.48	0.98	7.88	39.55
Carcinus maenas	0	0.57	6.62	46.18
Ctenolabrus rupestris	0.1	0.61	6.3	52.48
Liocarcinus depurator	0.58	0.37	6.26	58.74
Cancer pagurus	1.08	1.49	5.67	64.41
Ophiuroidea	0	0.53	5.25	69.66
Hyas araneus	0.14	0.31	3.93	73.59
Asterias rubens	0.1	0.31	3.73	77.32
Aeolidia papilosa	0	0.27	3.04	80.36
Average dissimilarity				67.15

Abundance

Species	**Year 2008**	**Year 2017**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	1.32	12.33	12.33
Astropecten irregularis	0.25	0.86	9.18	21.51
Carcinus maenas	0	0.57	6.97	28.48
Ctenolabrus rupestris	0.29	0.61	6.85	35.33
Pagurus spp.	1.01	1.33	6.81	42.14
Marthasterias glacialis	0.88	0.98	6.6	48.74
Asterias rubens	0.44	0.31	5.91	54.65
Ophiuroidea	0	0.53	5.67	60.32
Hyas araneus	0.34	0.31	5.36	65.68
Liocarcinus depurator	0.23	0.37	4.99	70.67
Cancer pagurus	1.52	1.49	4.46	75.13
Aeolidia papilosa	0	0.27	3.2	78.33
Mycocephalus scorpius	0.11	0.15	2.49	80.83
Average dissimilarity				53.18

Abundance

Species	**Year 2016**	**Year 2017**	**Contribution**	**Cumulative**
Asterias rubens	1.19	0.31	9.81	9.81
Ophiuroidea	0.85	0.53	9.17	18.98
Marthasterias glacialis	1.86	0.98	8.96	27.94
Gadus morhua (juv.)	1.82	1.32	8.9	36.84
Ctenolabrus rupestris	0.99	0.61	6.33	43.17
Astropecten irregularis	0.74	0.86	5.95	49.12
Carcinus maenas	0.21	0.57	5.94	55.06
Merlangius merlangius	0.6	0.09	5.86	60.92
Liocarcinus depurator	0.47	0.37	5.26	66.18
Pagurus spp.	1.24	1.33	4.9	71.09
Fjordia lineata	0.33	0.07	3.32	74.41
Hyas araneus	0.07	0.31	3.27	77.68
Cancer pagurus	1.44	1.49	3.2	80.88
Average dissimilarity				45.12

Abundance

Species	**Year 2007**	**Year 2018**	**Contribution**	**Cumulative**
Pagurus spp.	0.54	1.46	13.9	13.9
Ophiuroidea	0	1.12	13.47	27.37
Marthasterias glacialis	0.48	1.11	11.02	38.38
Asterias rubens	0.1	0.68	8.59	46.97
Liocarcinus depurator	0.58	0.15	7.81	54.78
Cancer pagurus	1.08	1.25	7.39	62.17
Astropecten irregularis	0.1	0.31	5.93	68.1
Aeolidia papilosa	0	0.41	4.47	72.57
Mycocephalus scorpius	0.1	0.32	4.44	77.01
Hyas araneus	0.14	0.17	3.55	80.56
Average dissimilarity				65.68

Abundance

Species	**Year 2008**	**Year 2018**	**Contribution**	**Cumulative**

(*continued on next page*)

Table 12 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Ophiuroidea	0	1.12	13.37	13.37
Gadus morhua (juv.)	0.78	0.17	10.06	23.44
Asterias rubens	0.44	0.68	9.22	32.65
Pagurus spp.	1.01	1.46	8.93	41.58
Marthasterias glacialis	0.88	1.11	8.13	49.71
Cancer pagurus	1.52	1.25	7.13	56.84
Astropecten irregularis	0.25	0.31	6.23	63.07
Hyas araneus	0.34	0.17	5.39	68.46
Ctenolabrus rupestris	0.29	0.15	4.87	73.33
Mycocephalus scorpius	0.11	0.32	4.56	77.89
Aeolidia papilosa	0	0.41	4.51	82.4
Average dissimilarity				55.12

Abundance				
Species	**Year 2016**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.82	0.17	16.2	16.2
Ophiuroidea	0.85	1.12	10.54	26.74
Ctenolabrus rupestris	0.99	0.15	8.58	35.32
Asterias rubens	1.19	0.68	8.55	43.87
Marthasterias glacialis	1.86	1.11	7.76	51.63
Astropecten irregularis	0.74	0.31	6.1	57.73
Pagurus spp.	1.24	1.46	5.55	63.28
Merlangius merlangius	0.6	0	5.41	68.69
Liocarcinus depurator	0.47	0.15	4.55	73.23
Cancer pagurus	1.44	1.25	4.02	77.26
Aeolidia papilosa	0.07	0.41	3.76	81.02
Average dissimilarity				52.74

Abundance				
Species	**Year 2017**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.32	0.17	13.05	13.05
Ophiuroidea	0.53	1.12	11.06	24.11
Astropecten irregularis	0.86	0.31	7.71	31.81
Asterias rubens	0.31	0.68	7.48	39.3
Carcinus maenas	0.57	0	6.64	45.93
Ctenolabrus rupestris	0.61	0.15	6.44	52.37
Pagurus spp.	1.33	1.46	6.38	58.76
Marthasterias glacialis	0.98	1.11	6.26	65.02
Aeolidia papilosa	0.27	0.41	5.33	70.35
Liocarcinus depurator	0.37	0.15	4.34	74.68
Cancer pagurus	1.49	1.25	4.32	79
Hyas araneus	0.31	0.17	4.18	83.19
Average dissimilarity				53.24

Abundance				
Species	**Year 2007**	**Year 2019**	**Contribution**	**Cumulative**
Pagurus spp.	0.54	1.55	10.28	10.28
Liocarcinus depurator	0.58	1.45	8.39	18.67
Marthasterias glacialis	0.48	1.23	7.9	26.57
Astropecten irregularis	0.1	0.86	7.6	34.17
Gadus morhua (juv.)	0.11	0.82	7.37	41.54
Ctenolabrus rupestris	0.1	0.75	6.81	48.35
Hyas araneus	0.14	0.74	6.71	55.06
Cancer pagurus	1.08	1.63	5.65	60.7
Mycocephalus scorpius	0.1	0.63	5.53	66.23
Ophiuroidea	0	0.64	5.51	71.74
Asterias rubens	0.1	0.32	3.29	75.03
Pomatoschistus spp.	0.06	0.31	2.82	77.85
Upogebia holes	0	0.27	2.35	80.2
Average dissimilarity				64.95

Abundance				
Species	**Year 2008**	**Year 2019**	**Contribution**	**Cumulative**
Liocarcinus depurator	0.23	1.45	12.01	12.01
Gadus morhua (juv.)	0.78	0.82	8.78	20.79
Astropecten irregularis	0.25	0.86	7.6	28.4
Pagurus spp.	1.01	1.55	7.02	35.41
Ctenolabrus rupestris	0.29	0.75	6.76	42.17
Hyas araneus	0.34	0.74	6.6	48.78
Ophiuroidea	0	0.64	5.75	54.53
Mycocephalus scorpius	0.11	0.63	5.7	60.23
Marthasterias glacialis	0.88	1.23	5.25	65.47
Asterias rubens	0.44	0.32	5.06	70.53
Cancer pagurus	1.52	1.63	3.74	74.27

(*continued on next page*)

Table 12 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Pomatoschistus spp.	0.11	0.31	3.19	77.46
Upogebia holes	0	0.27	2.44	79.9
Gobius niger	0.11	0.2	2.41	82.31
Average dissimilarity				54.46

Abundance				
Species	**Year 2016**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.82	0.82	9.52	9.52
Liocarcinus depurator	0.47	1.45	8.42	17.94
Ophiuroidea	0.85	0.64	8.35	26.29
Asterias rubens	1.19	0.32	8.31	34.59
Hyas araneus	0.07	0.74	6.04	40.64
Marthasterias glacialis	1.86	1.23	5.38	46.02
Ctenolabrus rupestris	0.99	0.75	5.19	51.21
Astropecten irregularis	0.74	0.86	5.07	56.27
Mycocephalus scorpius	0.08	0.63	5.05	61.33
Pagurus spp.	1.24	1.55	4.98	66.31
Merlangius merlangius	0.6	0	4.75	71.06
Pomatoschistus spp.	0.26	0.31	3.55	74.61
Cancer pagurus	1.44	1.63	2.91	77.52
Fjordia lineata	0.33	0.07	2.78	80.29
Average dissimilarity				48.03

Abundance				
Species	**Year 2017**	**Year 2019**	**Contribution**	**Cumulative**
Liocarcinus depurator	0.37	1.45	10.19	10.19
Gadus morhua (juv.)	1.32	0.82	8.82	19.01
Ophiuroidea	0.53	0.64	7.5	26.51
Hyas araneus	0.31	0.74	6.42	32.93
Ctenolabrus rupestris	0.61	0.75	6.06	38.99
Mycocephalus scorpius	0.15	0.63	5.47	44.45
Carcinus maenas	0.57	0	5.43	49.88
Astropecten irregularis	0.86	0.86	5.24	55.12
Pagurus spp.	1.33	1.55	5.22	60.34
Marthasterias glacialis	0.98	1.23	4.44	64.78
Asterias rubens	0.31	0.32	4.26	69.04
Cancer pagurus	1.49	1.63	2.87	71.91
Pomatoschistus spp.	0.07	0.31	2.86	74.78
Aeolidia papilosa	0.27	0.07	2.8	77.57
Upogebia holes	0	0.27	2.33	79.91
Arenicola marina cast	0.07	0.21	2.19	82.09
Average dissimilarity				48.71

Abundance				
Species	**Year 2018**	**Year 2019**	**Contribution**	**Cumulative**
Liocarcinus depurator	0.15	1.45	12.36	12.36
Ophiuroidea	1.12	0.64	10.28	22.64
Gadus morhua (juv.)	0.17	0.82	7.27	29.9
Ctenolabrus rupestris	0.15	0.75	6.77	36.67
Hyas araneus	0.17	0.74	6.75	43.42
Asterias rubens	0.68	0.32	6.51	49.93
Astropecten irregularis	0.31	0.86	6.5	56.42
Pagurus spp.	1.46	1.55	5.73	62.15
Mycocephalus scorpius	0.32	0.63	5.38	67.53
Marthasterias glacialis	1.11	1.23	4.47	72
Cancer pagurus	1.25	1.63	4.41	76.41
Aeolidia papilosa	0.41	0.07	3.7	80.11
Average dissimilarity				53.63

Composition of the species assemblage of other taxa on complex foundations and non-complex foundations

Fishes

The fishes assemblage showed significant differences between the years (global $R = 0.263$; $p < 0.0001$), but not between the complex foundations and the non-complex foundations (global $R = 0.126$; $p < 0.026$), nor the geographical positions (global $R = 0.093$; $p < 0.075$) in a 3-way crossed ANOSIM analyses. Pairwise tests between years showed several significant differences (Table 13Table 13).

Table 13

Pairwise comparisons between the years of the fishes assemblage of complex foundations and the non-complex foundations. A 3-way crossed ANOSIM analyses of the species assemblages revealed significant differences between the years (global R = 0.263, p < 0.001). Significant differences between years are italicized.

Pairwise Tests			Permutations		
Years compared	R value	Significance Level %	Possible	Actual	No. obs.
2007 vs. 2008	0.163	3.6	49787136	9999	356
2007 vs. 2016	*0.634*	*0.01*	*1481760*	*9999*	*0*
2007 vs. 2017	*0.411*	*0.1*	*2222640*	*9999*	*12*
2007 vs. 2018	−0.05	64.6	105840	9999	6459
2007 vs. 2019	*0.433*	*0.07*	*2222640*	*9999*	*6*
2008 vs. 2016	0.211	2	5186160	9999	198
2008 vs. 2017	0.208	2	19015920	9999	203
2008 vs. 2018	0.188	7.5	246960	9999	750
2008 vs. 2019	0.168	3.6	19015920	9999	363
2016 vs. 2017	0.109	12.3	485100	9999	1229
2016 vs. 2018	*0.717*	*0.01*	*23520*	*9999*	*0*
2016 vs. 2019	*0.325*	*0.4*	*485100*	*9999*	*36*
2017 vs. 2018	*0.39*	*0.5*	*35280*	*9999*	*50*
2017 vs. 2019	*0.26*	*1.4*	*485100*	*9999*	*143*
2018 vs. 2019	0.141	12.5	35280	9999	1250

The SIMPER analyses showed that the dissimilarity of the fishes assemblage between significant different years was driven by three to seven species which collectively accounted for between 50%–94% of dissimilarity between the tested years (Table appendix). For detailed information on SIMPER analyses between years see (Table 14Table 14).

Table 14

Summary of SIMPER results for the comparison of the fishes assemblage between years. Average abundance of discriminating species in each year and their contribution (%) to the dissimilarity between years, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the sampling years.

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Gadus morhua (juv.)	0.14	0.78	26.55	26.55
Ctenolabrus rupestris	0.13	0.29	13.59	40.14
Gadus morhua	0.26	0.05	10.21	50.35
Pholis gunnelus	0.19	0.11	9.55	59.9
Pleuronectidae	0.06	0.21	8.83	68.73
Mycocephalus scorpius	0.13	0.11	7.7	76.43
Callionymus maculatus	0.19	0	7.34	83.77
Average dissimilarity				92.12
Abundance				
Species	**Year 2007**	**Year 2016**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.14	1.82	39.08	39.08
Ctenolabrus rupestris	0.13	0.99	19.98	59.06
Merlangius merlangius	0	0.6	13.38	72.44
Pomatoschistus spp.	0.07	0.26	6.3	78.74
Gadus morhua	0.26	0	5.17	83.9
Average dissimilarity				90.65
Abundance				
Species	**Year 2008**	**Year 2016**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	1.82	37.43	37.43
Ctenolabrus rupestris	0.29	0.99	22.07	59.5
Merlangius merlangius	0	0.6	15.97	75.47
Pomatoschistus spp.	0.11	0.26	8.39	83.86
Average dissimilarity				69.97
Abundance				
Species	**Year 2007**	**Year 2017**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.14	1.32	37.48	37.48
Ctenolabrus rupestris	0.13	0.61	19.93	57.41
Gadus morhua	0.26	0	7.56	64.98
Pleuronectes platessa	0.06	0.13	7.41	72.38
Callionymus maculatus	0.19	0	5.96	78.34
Mycocephalus scorpius	0.13	0.15	5.73	84.07
Average dissimilarity				90.92
Abundance				
Species	**Year 2008**	**Year 2017**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	1.32	39.93	39.93
Ctenolabrus rupestris	0.29	0.61	22.7	62.63

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Table 14 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Pleuronectidae	0.21	0	6.98	69.61
Mycocephalus scorpius	0.11	0.15	6.98	76.59
Pleuronectes platessa	0	0.13	5.89	82.48
Average dissimilarity				74.25

Abundance				
Species	**Year 2016**	**Year 2017**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.82	1.32	34.05	34.05
Ctenolabrus rupestris	0.99	0.61	22.43	56.49
Merlangius merlangius	0.6	0.09	20.38	76.86
Pomatoschistus spp.	0.26	0.07	9.21	86.07
Average dissimilarity				50.42

Abundance				
Species	**Year 2007**	**Year 2018**	**Contribution**	**Cumulative**
Mycocephalus scorpius	0.13	0.42	21.11	21.11
Gadus morhua (juv.)	0.14	0.22	15.07	36.19
Gadus morhua	0.26	0	13.06	49.24
Ctenolabrus rupestris	0.13	0.2	12.09	61.33
Callionymus maculatus	0.19	0	10.71	72.04
Pholis gunnelus	0.19	0	8.66	80.71
Average dissimilarity				94.25

Abundance				
Species	**Year 2008**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	0.22	31.72	31.72
Mycocephalus scorpius	0.11	0.42	19.79	51.51
Ctenolabrus rupestris	0.29	0.2	18.01	69.52
Pleuronectidae	0.21	0	9.75	79.27
Pomatoschistus spp.	0.11	0	6.7	85.98
Average dissimilarity				90.38

Abundance				
Species	**Year 2016**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.82	0.22	43.8	43.8
Ctenolabrus rupestris	0.99	0.2	21.88	65.69
Merlangius merlangius	0.6	0	15.42	81.11
Average dissimilarity				86.67

Abundance				
Species	**Year 2017**	**Year 2018**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.32	0.22	44.51	44.51
Ctenolabrus rupestris	0.61	0.2	24.89	69.4
Mycocephalus scorpius	0.15	0.42	15.17	84.56
Average dissimilarity				86.44

Abundance				
Species	**Year 2007**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.14	0.82	20.69	20.69
Ctenolabrus rupestris	0.13	0.75	17.58	38.27
Mycocephalus scorpius	0.13	0.63	16.55	54.82
Pomatoschistus spp.	0.07	0.31	8.89	63.71
Pholis gunnelus	0.19	0.15	7.65	71.36
Gadus morhua	0.26	0	6.57	77.93
Callionymus maculatus	0.19	0	5.12	83.06
Average dissimilarity				89.36

Abundance				
Species	**Year 2008**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.78	0.82	26.18	26.18
Ctenolabrus rupestris	0.29	0.75	19.1	45.28
Mycocephalus scorpius	0.11	0.63	17.45	62.73
Pomatoschistus spp.	0.11	0.31	10.28	73.01
Gobius niger	0.11	0.2	6.67	79.67
Pholis gunnelus	0.11	0.15	6.62	86.29
Average dissimilarity				78.06

Abundance				
Species	**Year 2016**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.82	0.82	29.95	29.95
Ctenolabrus rupestris	0.99	0.75	16.48	46.43
Mycocephalus scorpius	0.08	0.63	14.54	60.98
Merlangius merlangius	0.6	0	14.17	75.15
Pomatoschistus spp.	0.26	0.31	10.31	85.46

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Table 14 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Average dissimilarity				62.43
Abundance				
Species	**Year 2017**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	1.32	0.82	29.66	29.66
Ctenolabrus rupestris	0.61	0.75	19.94	49.6
Mycocephalus scorpius	0.15	0.63	17.45	67.05
Pomatoschistus spp.	0.07	0.31	9.12	76.17
Symphodus melops	0.09	0.15	5.49	81.67
Average dissimilarity				67.69
Abundance				
Species	**Year 2018**	**Year 2019**	**Contribution**	**Cumulative**
Gadus morhua (juv.)	0.22	0.82	25.36	25.36
Ctenolabrus rupestris	0.2	0.75	21.82	47.19
Mycocephalus scorpius	0.42	0.63	21.12	68.31
Pomatoschistus spp.	0	0.31	9.86	78.17
Symphodus melops	0.1	0.15	6.97	85.13
Average dissimilarity				79.68

Echinoderms

Similar to the species assemblage and the fishes, the taxa echinoderms revealed non-significant difference between the complex foundations and the non-complex foundations (global R = 0.108; $p < 0.042$) nor between the geographical positions (global R value = 0.018; $p < 0.367$) but also between the years (global R = 0.378, $p < 0.0001$) in a 3-way crossed ANOSIM analyses. Pairwise tests between years showed several significant differences (Table 15Table 15).

Table 15

Pairwise comparisons between the years of the echinoderm assemblages of complex foundations and the non-complex foundations. A 3-way crossed ANOSIM analyses of the species assemblages revealed significant differences between the years (global R = 0.378, $p < 0.0001$). Significant differences between years are italicized.

Pairwise Tests			Permutations		
Years compared	R value	Significance Level %	Possible	Actual	No. obs.
2007 vs. 2008	*0.309*	*0.5*	*68457312*	*9999*	*53*
2007 vs. 2016	*0.81*	*0.01*	*32598720*	*9999*	*0*
2007 vs. 2017	*0.604*	*0.01*	*32598720*	*9999*	*0*
2007 vs. 2018	*0.635*	*0.01*	*14817600*	*9999*	*0*
2007 vs. 2019	*0.634*	*0.01*	*32598720*	*9999*	*0*
2008 vs. 2016	*0.497*	*0.01*	*2222640*	*9999*	*0*
2008 vs. 2017	0.244	2.4	8149680	9999	236
2008 vs. 2018	*0.395*	*0.4*	*2222640*	*9999*	*37*
2008 vs. 2019	*0.341*	*0.4*	*8149680*	*9999*	*39*
2016 vs. 2017	0.205	4	485100	9999	401
2016 vs. 2018	0.24	2.6	132300	9999	262
2016 vs. 2019	*0.345*	*0.3*	*485100*	*9999*	*27*
2017 vs. 2018	−0.033	57	220500	9999	5694
2017 vs. 2019	−0.061	76.4	485100	9999	7641
2018 vs. 2019	0.075	22.5	220500	9999	2251

The SIMPER analyses showed that the dissimilarity of the echinoderm assemblages between significant different years was driven by two to four species which collectively accounted for between 44%–78% of dissimilarity between the tested years (Table appendix). For detailed information on SIMPER analyses between years see appendix (Table 16Table 16).

Table 16

Summary of SIMPER results for the comparison of the echinoderm assemblage between years. Average abundance of discriminating species in each year and their contribution (%) to the dissimilarity between years, and cumulative total (%) of contributions. Listed taxa contributed to at least 80% of the dissimilarity between the sampling years.

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Marthasterias glacialis	0.53	0.99	52.35	52.35
Asterias rubens	0.11	0.49	31.25	83.6
Average dissimilarity				68.87
Abundance				
Species	**Year 2007**	**Year 2016**	**Contribution**	**Cumulative**

(*continued on next page*)

Table 16 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Marthasterias glacialis	0.53	1.86	33.59	33.59
Asterias rubens	0.11	1.19	26.96	60.55
Ophiuroidea	0	0.85	17.02	77.56
Astropecten irregularis	0.11	0.74	16.23	93.79
Average dissimilarity				77.62

Abundance				
Species	**Year 2008**	**Year 2016**	**Contribution**	**Cumulative**
Marthasterias glacialis	0.99	1.86	25.79	25.79
Asterias rubens	0.49	1.19	25.22	51.01
Ophiuroidea	0	0.85	20.96	71.97
Astropecten irregularis	0.28	0.74	19.46	91.43
Average dissimilarity				53.99

Abundance				
Species	**Year 2007**	**Year 2017**	**Contribution**	**Cumulative**
Astropecten irregularis	0.11	0.86	36.85	36.85
Marthasterias glacialis	0.53	0.98	30.19	67.04
Ophiuroidea	0	0.53	16.46	83.5
Average dissimilarity				75.56

Abundance				
Species	Year **2008**	Year **2017**	**Contribution**	**Cumulative**
Astropecten irregularis	0.28	0.86	33.31	33.31
Marthasterias glacialis	0.99	0.98	22.15	55.46
Asterias rubens	0.49	0.31	21.63	77.1
Ophiuroidea	0	0.53	17.15	94.25
Average dissimilarity				57.57

Abundance				
Species	**Year 2016**	**Year 2017**	**Contribution**	**Cumulative**
Asterias rubens	1.19	0.31	26.47	26.47
Marthasterias glacialis	1.86	0.98	24.57	51.04
Ophiuroidea	0.85	0.53	23.09	74.13
Astropecten irregularis	0.74	0.86	16.37	90.5
Average dissimilarity				50.27

Abundance				
Species	**Year 2007**	**Year 2018**	**Contribution**	**Cumulative**
Ophiuroidea	0	1.12	33.63	33.63
Marthasterias glacialis	0.53	1.11	28.01	61.63
Asterias rubens	0.11	0.68	20.23	81.86
Average dissimilarity				77.99

Abundance				
Species	**Year 2008**	**Year 2018**	**Contribution**	**Cumulative**
Ophiuroidea	0	1.12	34.81	34.81
Asterias rubens	0.49	0.68	24.53	59.34
Marthasterias glacialis	0.99	1.11	20.1	79.44
Astropecten irregularis	0.28	0.31	16.13	95.57
Average dissimilarity				59.67

Abundance				
Species	**Year 2016**	**Year 2018**	**Contribution**	**Cumulative**
Ophiuroidea	0.85	1.12	28.55	28.55
Asterias rubens	1.19	0.68	23.85	52.39
Marthasterias glacialis	1.86	1.11	21.77	74.17
Astropecten irregularis	0.74	0.31	16.99	91.16
Average dissimilarity				47.85

Abundance				
Species	**Year 2017**	**Year 2018**	**Contribution**	**Cumulative**
Ophiuroidea	0.53	1.12	31.56	31.56
Astropecten irregularis	0.86	0.31	22.89	54.45
Asterias rubens	0.31	0.68	20.88	75.33
Marthasterias glacialis	0.98	1.11	18.91	94.24
Average dissimilarity				54.55

Abundance				
Species	**Year 2007**	**Year 2019**	**Contribution**	**Cumulative**
Marthasterias glacialis	0.53	1.23	35.12	35.12
Astropecten irregularis	0.11	0.86	33.91	69.03
Ophiuroidea	0	0.64	16.84	85.87
Average dissimilarity				72.75

(*continued on next page*)

Table 16 (*continued*)

Abundance				
Species	Year 2007	Year 2008	Contribution	Cumulative
Abundance				
Species	**Year 2008**	**Year 2019**	**Contribution**	**Cumulative**
Astropecten irregularis	0.28	0.86	33.11	33.11
Asterias rubens	0.49	0.32	22.14	55.26
Marthasterias glacialis	0.99	1.23	20.27	75.53
Ophiuroidea	0	0.64	19.13	94.66
Average dissimilarity				53.17
Abundance				
Species	**Year 2016**	**Year 2019**	**Contribution**	**Cumulative**
Asterias rubens	1.19	0.32	28.54	28.54
Ophiuroidea	0.85	0.64	25.83	54.37
Marthasterias glacialis	1.86	1.23	18.98	73.35
Astropecten irregularis	0.74	0.86	17.4	90.74
Average dissimilarity				46.6
Abundance				
Species	**Year 2017**	**Year 2019**	**Contribution**	**Cumulative**
Ophiuroidea	0.53	0.64	29.69	29.69
Astropecten irregularis	0.86	0.86	23.94	53.64
Marthasterias glacialis	0.98	1.23	21.56	75.2
Asterias rubens	0.31	0.32	17.34	92.54
Average dissimilarity				43.79
Abundance				
Species	**Year 2018**	**Year 2019**	**Contribution**	**Cumulative**
Ophiuroidea	1.12	0.64	34.55	34.55
Astropecten irregularis	0.31	0.86	22.95	57.5
Asterias rubens	0.68	0.32	21.25	78.75
Marthasterias glacialis	1.11	1.23	16.62	95.37
Average dissimilarity				51.17

Crustaceans

The crustaceans revealed non-significant differences in a 3-way crossed ANOSIM analyses for none of the factors: complex foundations and non-complex foundations (global $R = 0.125$; $p < 0.014$), geographical positions (global $R = 0.003$, $p < 0.454$) and years (global R value $= 0.202$; $p < 0.0001$).

Single species

Marthasterias glacialis. The taxon *Marthasterias glacialis* revealed non-significant difference between the complex foundations and the non-complex foundations (global $R = 0.134$; $p < 0.035$) nor between the geographical positions (global R value $= 0.005$; $p < 0.445$) but significant differences between the years (global $R = 0.418$, $p < 0.0001$) in a 3-way crossed ANOSIM analyses. Pairwise tests between years showed several significant differences (Table 17Table 17).

Table 17
Pairwise comparisons between the years of the species *Marthasterias glacialis* of complex foundations and the non-complex foundations. A 3-way crossed ANOSIM analyses of the species Marthasterias glacialis revealed significant differences between the years (global $R = 0.388$, $p < 0.0001$). Significant differences between years are italicized.

Pairwise Tests			Permutations		
Years compared	R value	Significance Level %	Possible	Actual	No. obs.
2007 vs. 2008	*0.346*	*0.4*	*30561300*	*9999*	*37*
2007 vs. 2016	*0.891*	*0.01*	*9055200*	*9999*	*0*
2007 vs. 2017	*0.483*	*0.3*	*3622080*	*9999*	*28*
2007 vs. 2018	*0.516*	*0.06*	*4116000*	*9999*	*5*
2007 vs. 2019	*0.716*	*0.01*	*9055200*	*9999*	*0*
2008 vs. 2016	*0.683*	*0.01*	*1587600*	*9999*	*0*
2008 vs. 2017	0.211	2.8	1293600	9999	278
2008 vs. 2018	0.228	3.3	1058400	9999	332
2008 vs. 2019	0.245	2.2	3880800	9999	221
2016 vs. 2017	*0.502*	*0.1*	*485100*	*9999*	*12*
2016 vs. 2018	*0.362*	*0.6*	*132300*	*9999*	*59*
2016 vs. 2019	*0.51*	*0.01*	*485100*	*9999*	*0*
2017 vs. 2018	−0.087	70.3	63000	9999	7025
2017 vs. 2019	−0.013	45.2	138600	9999	4520
2018 vs. 2019	0.014	38.7	63000	9999	3870

Pagurus spp.. The taxa *Pagurus* spp. revealed non-significant differences in a 3-way crossed ANOSIM analyses for none of the factors: complex

Table 18
Mean abundance of species on the surveyed foundations total, complex foundations with holes, non-complex foundations without holes and controls during the years 2007, 2008 and 2016–2019.

Nr.	Taxa	Foundations all							Foundations complex (with holes)						Foundations non-complex (with no holes)						Controls					
		Latin name	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019
1	Fishes	*Merlangius merlangius*	0.00	0.00	3.71	0.20	0.00	0.00	0.00	0.00	5.25	0.00	0.00	0.00	0.00	0.00	1.67	0.50	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.00
2		*Gadus morhua*	0.24	0.05	0.00	0.00	0.00	0.00	0.18	0.10	0.00	0.00	0.00	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3		*Gadus morhua* (juv.)	0.19	5.32	15.79	10.67	0.23	2.07	0.09	6.60	16.63	8.67	0.43	2.00	0.30	3.89	14.67	10.33	0.00	2.17	0.00	0.50	2.43	1.33	0.00	0.20
4		*Ctenolabrus rupestris*	0.10	0.42	1.79	1.00	0.15	1.67	0.09	0.60	2.25	1.00	0.14	2.56	0.10	0.22	1.17	1.00	0.17	0.33	0.00	0.00	0.00	0.00	0.00	0.00
5		*Pomatoschistus* spp.	0.10	0.11	0.50	0.40	0.00	0.53	0.00	0.10	0.38	0.11	0.00	0.56	0.20	0.11	0.67	0.00	0.00	0.50	0.05	0.40	1.21	0.33	0.00	0.07
6		*Mycocephalus scorpius*	0.10	0.11	0.14	0.20	0.38	0.73	0.09	0.10	0.25	0.11	0.57	1.00	0.10	0.11	0.00	0.33	0.17	0.33	0.00	0.00	0.21	0.00	0.00	0.00
7		*Agonus cataphractus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
8		*Zoarces viviparus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
9		*Pleuronectidae* (other, undefined)	0.50	0.21	0.07	0.00	0.00	0.00	0.00	0.40	0.13	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.05	0.20	0.00	0.00	0.00	0.00
10		*Solea solea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
11		*Limanda limanda*	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.08	0.00
12		*Scophtalmus rhombus*	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
13		*Pleuronectes platessa*	0.05	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.10	0.00	0.00	0.17	0.00	0.00	0.14	0.10	0.07	0.20	0.00	0.00
14		*Callionymus lyra*	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.27
15		*Callionymus maculatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
16		*Callionymus* spp.	0.14	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.19	0.10	0.00	0.00	0.00	0.00
17		*Gobius niger*	0.00	0.11	0.00	0.00	0.00	0.20	0.00	0.20	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.10	0.00	0.00	0.00	0.00
18		*Syngnatus acus*	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00
19		*Pholis gunnelus*	0.14	0.11	0.00	0.00	0.00	0.20	0.18	0.10	0.00	0.00	0.00	0.11	0.10	0.11	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
20		*Symphodus melops*	0.00	0.00	0.00	0.20	0.08	0.20	0.00	0.00	0.00	0.00	0.14	0.22	0.00	0.00	0.00	0.50	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00
21		*Nerophis* spp.	0.05	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22	Crustaceans	*Cancer pagurus*	2.95	7.47	5.36	5.93	3.38	8.07	4.82	11.10	8.00	7.67	4.00	10.89	0.90	3.44	1.83	2.83	2.67	3.83	0.05	0.70	0.00	0.20	0.00	0.00
23		*Carcinus maenas*	0.00	0.00	0.21	1.27	0.00	0.00	0.00	0.00	0.25	1.56	0.00	0.00	0.00	0.00	0.17	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24		*Liocarcinus depurator*	0.86	0.37	0.71	0.60	0.15	5.13	0.82	0.20	0.38	0.33	0.29	6.00	0.90	0.56	1.17	0.83	0.00	3.83	0.71	0.10	0.64	0.07	0.00	0.87
25		*Homarus gammarus*	0.05	0.05	0.07	0.13	0.00	0.07	0.09	0.10	0.13	0.22	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26		*Pagurus* spp.	0.86	2.32	3.86	5.00	8.08	9.07	0.82	2.10	3.75	3.89	8.43	11.67	0.90	2.56	4.00	6.17	7.67	5.17	1.14	1.70	0.00	0.20	0.08	0.73
27		*Nephrops norvegius*	0.05	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
28		*Hyas araneus*	0.14	0.42	0.07	0.53	0.23	1.67	0.09	0.30	0.13	0.22	0.14	1.22	0.20	0.56	0.00	1.00	0.33	2.33	0.05	0.30	0.07	0.00	0.00	0.00
29		*Macropodia rostrata*	0.00	0.00	0.00	0.07	0.00	0.20	0.00	0.00	0.00	0.11	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30		*Galathea* spp.	0.00	0.00	0.00	0.07	0.00	0.07	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00
31		*Galathea strigosa*	0.00	0.00	0.00	0.07	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32		*Glathea squamifera*	0.00	0.00	0.00	0.07	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00
33		*Corystes cassivelaunus*	0.00	0.11	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.20	0.00	0.00
34		Upogebia holes	0.00	0.00	0.00	0.00	0.08	0.27	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.17	0.33	0.00	0.00	0.00	0.00	1.08	2.33
35	Echinoderms		0.76	1.68	13.29	2.13	3.08	3.07	0.18	1.30	11.88	2.22	2.86	2.89	1.40	2.11	15.17	1.83	3.33	3.33	0.00	0.30	0.14	0.07	0.00	0.00

(*continued on next page*)

Table 18 (*continued*)

Nr.	Taxa	Foundations all							Foundations complex (with holes)						Foundations non-complex (with no holes)						Controls					
		Latin name	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019	2007	2008	2016	2017	2018	2019
		Marthasterias glacialis																								
36		*Astropecten irregularis*	0.10	0.47	1.29	3.27	0.31	1.93	0.00	0.10	1.38	1.44	0.14	1.11	0.20	0.89	1.17	1.67	0.50	3.17	1.62	1.40	3.36	1.73	3.31	2.53
37		*Asterias rubens*	0.10	0.79	3.57	0.60	3.00	0.67	0.09	1.20	4.50	0.78	2.57	0.78	0.10	0.33	2.33	0.17	3.50	0.50	0.10	0.00	0.00	0.07	0.00	0.00
38		*Crossaster papposus*	0.00	0.11	0.21	0.07	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.22	0.33	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
39		*Solaster endeca*	0.00	0.00	0.07	0.00	0.08	0.07	0.00	0.00	0.13	0.00	0.14	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
40		Ophiuroidea	0.00	0.00	7.93	3.13	11.23	8.20	0.00	0.00	5.00	0.00	7.14	9.22	0.00	0.00	11.83	3.83	16.00	6.67	0.00	0.00	0.00	0.00	0.08	0.00
41		*Luidia sarsi*	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
42	Others	*Fjordia lineata*	0.00	0.00	1.29	0.07	0.00	0.07	0.00	0.00	0.38	0.11	0.00	0.00	0.00	0.00	2.50	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00
43		*Aeolidia papilosa*	0.00	0.00	0.07	0.27	1.08	0.07	0.00	0.00	0.00	0.11	0.71	0.00	0.00	0.00	0.17	0.50	1.50	0.17	0.00	0.00	0.00	0.00	0.00	0.00
44		*Oxydromus flexuosus*	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
45		*Polychaeta* unidentified	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
46		*Arctica islandia*	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47		*Arenicola marina* cast	0.00	0.00	0.00	0.07	0.00	0.27	0.00	0.00	0.00	0.11	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.47
48		*Mya arenaria*	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.27
Total number of species			18	19	20	32	15	27	15	17	19	20	14	22	16	14	15	17	11	23	11	13	13	14	5	9
Total number of surveyed foundations			21	19	14	15	13	15	11	10	8	9	7	9	10	9	6	6	6	6	21	19	14	15	13	15

foundations and non-complex foundations (global R = −0.032; p < 0.665), geographical positions (global R = 0.21; p < 0.0002) and years (global R value = 0.136; p < 0.029).

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