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## Epibenthic assemblages of hard-substrate habitats in the German Bight (south-eastern North Sea) described using drift videos



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## ABSTRACT

Globally, marine subtidal hard-substrate habitats provide important ecological functions to a variety of sessile and mobile taxa. The southern North Sea is a marine environment with relatively low amounts of hard-substrate areas. Surveys with high taxonomic resolution on the associated hard-substrate epifauna, e.g. by diving observations, are challenging in this region because of strong tidal currents and considerable water depths. Therefore, the characteristics and functions of hard-substrate habitats in the North Sea remain poorly understood.

The goal of this study was to extend the knowledge on sessile taxa assemblages in four hard-substrate areas within the German Bight (SE North Sea) using underwater video observations as a straight-forward and visual method to obtain and process detailed data on seafloor characteristics. Still images from drift videos were analyzed to determine the epifaunal assemblages attached to the stones on a presence/absence scale. A subsample of cobbles, boulders and large boulders was further investigated to derive quantitative data on the colonized area for each taxon and stone size. The four areas showed significant differences in sessile taxa richness, with higher numbers of sessile taxa in the deeper far-shore areas than in the shallower nearshore areas, despite a generally high similarity in the sessile animal taxa spectrum. Within the areas, cobbles were mainly dominated by short-lived taxa (< 5 years) like *Spirobranchus triqueter* and ascidians, while boulder-sized stones were largely colonized by long-lived taxa (> 5 years) like *Metridium dianthus*, *Flustra foliacea* and *Alcyonium digitatum*. Most of the stones were typically covered by epifauna by more than 50%. The differences in the sessile taxa spectrum between the areas were interpreted as a consequence of reduced abiotic stress and higher habitat complexity in the far-shore areas. The dominance of short-lived taxa on cobbles, in comparison to long-lived taxa on boulder-sized stones, possibly reflects the frequency of disturbance and the competitiveness of these taxa.

### 1. Introduction

Increasing anthropogenic usage of the marine environment, including oil and gas exploitation, sand extraction, stone extraction, fisheries, and the installation of offshore wind farms, generates pressure on marine habitats (Airoidi and Beck, 2007; Crowe et al., 2000; Gray, 1997). This is of particular importance for the scattered hard substrates located in the heavily anthropogenically-influenced southern North Sea as they provide important ecological habitat functions (Wiltshire, 2017). For example, subtidal reefs serve as a nursery and feeding ground for various fishes and as substrate for sessile taxa, in an otherwise mostly sandy environment (Wahl, 2009). For more than a decade,

legal directives such as the European Habitats Directive (92/43/EEC; European Commission, 1992) and the Marine Strategy Framework Directive (2008/56/EC; European Commission, 2008) have demanded the protection of reefs in the German Bight. However, technical difficulties restrain precise observation data and the standard monitoring strategies of these reefs are unsuitable when compared to monitoring of unconsolidated habitats (Hatcher, 1997). Non-destructive investigations are limited to video- and diving observations, and guidelines for the use of underwater videos have only recently become available (e.g. BS EN 16260:2012, 2012; Coggan et al., 2007; Turner et al., 2016). Both methods have considerable limitations with respect to both the taxonomic resolution and/or the frequent applicability under complex

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hydrographic conditions (Beisiegel et al., 2017). However, an effective monitoring of these natural habitats requires information on the associated taxa assemblages and the variations thereof, with regard to natural (e.g. sediment dynamics) and anthropogenic disturbance, to meet the demands of a sustainable management and conservation (Firth et al., 2016; Markert et al., 2013).

Previous investigations of epibenthic reef assemblages in the German Bight (SE North Sea) were primarily performed in the intertidal zone and in sites dominated by macroalgae around the island of Helgoland (e.g. Bartsch and Tittley, 2004; Franke and Gutow, 2004; Reichert et al., 2008; Schultz et al., 1990). In contrast, studies of subtidal hard-substrates are comparatively rare and only few are available in the scientific literature (e.g. De Kluijver, 1991; Kühne and Rachor, 1996 for Helgoland; Coolen et al., 2015 for the Dutch part of the Borkum Reef Ground). According to De Kluijver (1991), the availability of solar radiation for photosynthesis of macroalgae and the exposition to water currents are the major factors controlling the composition of the hard-substrate assemblages. The importance of different substrates and combinations thereof on the taxa diversity was highlighted by Kühne and Rachor (1996) and Coolen et al. (2015). However, even though most of the studies provided extensive species lists including e.g. anthozoans, bryozoans and polychaetes, none of them related the sessile epibenthic assemblages to the size of the colonized hard substrate. Moreover, the vulnerability of these assemblages to a variety of abiotic and biotic disturbances is only poorly understood. However, this knowledge forms an essential base for habitat modelling efforts, e.g. to support the implementation of international legal directives to protect the marine environment.

A recent study based on underwater videos revealed a positive correlation between the size of the rocky substrate and the presence and absence of attached epifauna in subtidal environments (Michaelis et al., 2019). This was especially the case in nearshore areas with strong bottom currents and a high sediment mobility. Accordingly, we expect that the size of the unconsolidated hard substrate might also have an effect on the composition of the associated epifaunal assemblages.

The aim of this study is firstly, to compare the species composition of sessile taxa assemblages on unconsolidated hard substrates in four discrete areas in the German Bight using underwater video observations, and secondly, to evaluate the effect of physical and biological

parameters (such as stone size or competition) on the local variability in the composition of the assemblages.

## 2. Materials and methods

### 2.1. Study site

All video-investigations were performed in the German Bight, SE North Sea (Fig. 1). The North Sea basin morphology was determined to a large degree by the Pleistocene glaciations (primarily: Saale and earlier glaciations). This resulted in the deposition of glacial tills and proglacial meltwater deposits (Graham et al., 2011; Zeiler et al., 2008). The current seafloor of the central and southern North Sea is largely characterized by a layer of relatively mobile sand and local outcrops of coarser glacial and proglacial deposits (Becker et al., 1992; Diesing and Schwarzer, 2006; Figge, 1981). These outcrops of cobble to boulder-sized stones form habitats for various sessile and mobile marine animals (including rare and protected taxa), which form typical reef assemblages. These are the basis for this study.

Four regions containing hard substrates were selected for this study. They provide an extensive coverage of the general presence of hard-substrate areas in the German Bight and comprise a set of different oceanographical conditions. The areas ‘Sylt Outer Reef’ (SOR) and ‘Helgoland’ are located far-shore, whereas the areas ‘Borkum Reef Ground’ (BRG) and ‘Sylt’ (SYL) are located nearshore. All areas provide unconsolidated hard substrates in the range of cobbles, boulders and large boulders. However, the stone-size distribution and the amount of intermixed smaller-sized sediments (i.e. gravel and sand) are different between the areas (Michaelis et al., 2019). The areas SYL and HEL are composed of relatively dense stonefields, whereas SOR and BRG show larger areas of sand between the stony patches. Individual stones in the areas SOR, HEL and SYL are more closely aggregated when compared to BRG. The seafloor west of HEL is characterized by bedrock built-up out of sand- and limestone. However, this bedrock and its colonization by sessile organisms were not considered in this study. Water depths in the areas range from 10 to 60 m (SYL: 12–15 m, BRG 20–30 m, HEL 20–60 m, SOR 30–45 m). A semidiurnal tidal regime leads to a strong mixing of the water masses and prevents a thermohaline stratification throughout the water column in the south-eastern North Sea (Quante

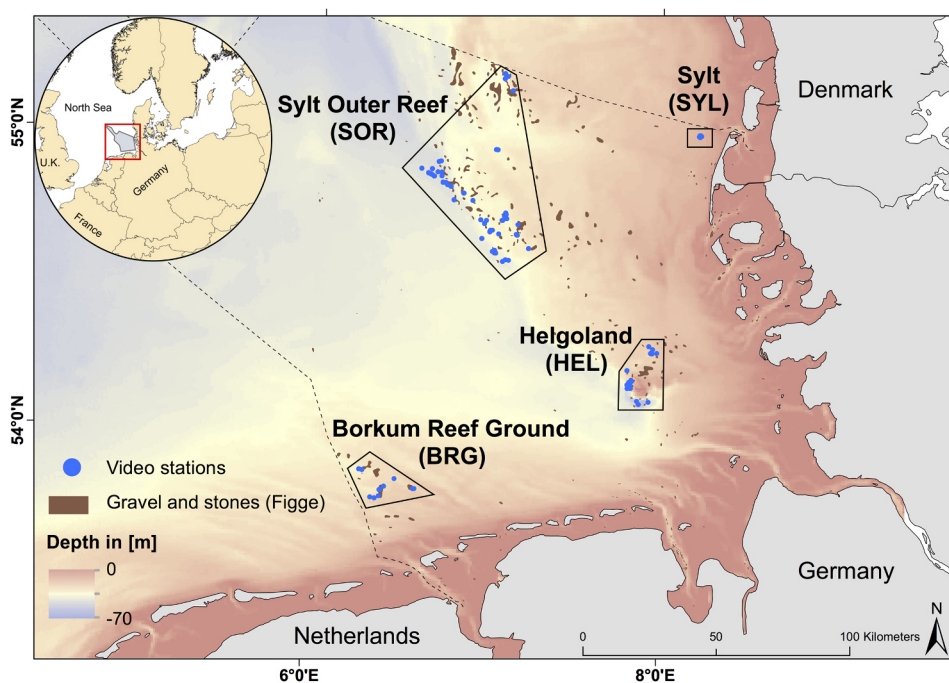


Fig. 1. Distribution of video stations (blue dots) and areas containing gravel and stones (brown areas) in the German Bight according to Figge (1981). Bathymetric data were derived from the General Bathymetric Chart of the Oceans (GEBCO, 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

et al., 2016). Long-term measurements of the German Bight at Helgoland Roads show an annual mean sea-surface temperature of 10 °C with a seasonal variability of  $\pm 8$  °C (Wiltshire and Manly, 2004). The surface waters of the German Bight are on average euhaline with salinity values of 34 in the central part and lower salinity values of 32 in the south-eastern areas, which are influenced by the rivers Weser and Elbe (Janssen et al., 1999). The average significant wave height is 1–1.5 m and mainly driven by winds from westerly and south-westerly directions (Quante et al., 2016). Maximum significant wave heights can reach 5–7 m, rarely up to 10 m (BSH, 2017; Korevaar, 1990). Such waves can have a fundamental impact on the seafloor, even in the deeper parts of the study sites (Armonies et al., 2014; Clukey et al., 1985; Otto et al., 1990). Most of the investigated hard substrates are located in a ‘high-energy’ regime, according to the European Marine Observation and Data Network (EMODnet, 2017). Only the deeper parts of the SOR (water depth > 36 m) and the area south of the island of Helgoland are described as ‘moderate-energy’ regimes. Bottom currents for the years 2013–2016 were modelled by the German Federal Maritime and Hydrographic Agency (BSH; models based on Dick et al., 2001, 2008) and show average bottom current velocities in the order of 0.2–0.3 m/s with maximum velocities of 0.4–0.7 m/s (SOR and HEL) and 0.6–0.9 m/s (BRG and SYL), respectively. Michaelis et al. (2019) have shown that boulders and large boulders were largely colonized by at least one sessile organisms (all working areas > 87%), irrespective of water depth and distance to coast. Cobbles, however, were clearly less colonized in the areas BRG (64%) and SYL (13%) compared to > 82% (SOR and HEL). The authors explained this pattern with the enhanced influence of sediment dynamics on cobbles as a consequence of the stronger bottom current velocities in the areas BRG and SYL (see also Table S1 in the Supplementary file for detailed information on the environmental parameters in the areas).

The terms ‘cobble’ (63–200 mm), ‘boulder’ (200–630 mm) and ‘large boulder’ (> 630 mm) are used to describe hard substrates of certain grain sizes, which is in accordance to the international standard ISO 14688-1:2017 (2017). In contrast, the terms ‘stone’ and ‘hard-substrate’ are used to address terrigenous clastic material with grain sizes larger than 63 mm. Here, the term ‘grain-size’ refers exclusively to the size of cobbles and boulders rather than their internal matrix. To describe hard-substrate habitats in combination with biological assemblages, the term ‘reef’ is applied as defined in the ‘Interpretation Manual of European Union Habitats’ (European Commission, 2007).

## 2.2. Data collection and video processing

Underwater video footage of hard-substrate habitats was acquired between 2012 and 2017 (Table 1, see also Table S2 in the Supplementary material for detailed cruise information). Most of the drift videos were obtained as ground-truth information during hydro-acoustic mapping surveys of the seafloor in the German Bight. Additional videos of hard-substrate areas were specifically generated to extend the database or to replace videos of bad quality. The camera systems were equipped with two ahead-oriented cameras, artificial

light sources and a laser scale reference. Recordings were taken from the drifting ship (max. speed: 1 knot) while the camera system was kept as close to the seafloor as possible. Positioning information during the recordings was received from the ship GPS. The videos used for this study were quality controlled (i.e. for the presence and visibility of hard substrates and their attached epifauna) and subsequently transformed into still images for further analyses of the benthic assemblages. The suitable still images were systematically analyzed for the presence of sessile and vagile taxa on cobbles, boulders and large boulders. More detailed information on the camera systems, the sampling design and period, and processing of the video data is given in Michaelis et al. (2019).

## 2.3. Classification of benthic taxa assemblages

The sessile and vagile taxa inventory of the study areas was derived from the investigation of the still images. The degree of coverage of hard substrates colonized by sessile organisms was evaluated for each study area from a set of at least thirty randomly selected images showing cobbles, boulders or large boulders. If too few images of a stone class (i.e. cobble, boulder or large boulder) were available for a specific area, all recognized stones displayed in adequate quality (i.e. distance to the camera to allow for proper identification of taxa) were analyzed. Taxa were identified to the lowest taxonomic level possible, based on the taxonomy of the World Register of Marine Species (WoRMS; Appeltans et al., 2012). Small sessile organisms manifesting as indistinguishable turf were classified as ‘bryozoan/hydrozoan turf’.

For each taxon, the percentage coverage was estimated by manually drawing polygons around the taxon and measuring the covered surface area of the visible projection area of the stone using the software ImageJ (National Institutes of Health, Bethesda, MD, Version 1.50i). The surface area of the stones was also estimated in this manner and used to calculate the resulting percentage of coverage for each taxon. The term ‘visible projection area’ describes the visible surface of a stone, whilst the back-side, especially of boulder-sized stones, might not be seen. This was caused by the drifting video system, which could not be directly operated to have an all-around perspective. Each investigated stone was assigned to a quantitative coverage class with steps of 10% according to its total degree of coverage. Here, 0% describes a completely barren surface whereas 100% relates to a fully colonized stone. Within each stone- and coverage class, the average percentage of covered area was calculated for each respective taxon.

## 2.4. Statistical analyses

Multivariate comparisons of the epifaunal communities were computed using the software package PRIMER 6 (PRIMER-E, Ivybridge, U.K.). Similarities of epifaunal assemblages between the four areas were visualized by non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis-dissimilarities calculated from presence/absence data of the sessile epibiota. Analyses of similarities (ANOSIM) with 999 random permutations were used to test for differences in the assemblages

**Table 1**

Summarized information on the investigated videos. The approximated analyzed area is the product of the average estimated visible area of the investigated images per video, and the number of analyzed images. Videos from BRG were investigated in full length resulting in an analyzed area larger than in the other areas. The analyzed area in BRG is calculated by the product of the average width per video and the drifted distance of the video station. Abbreviations: SOR = Sylt Outer Reef, HEL = Helgoland, BRG = Borkum Reef Ground, SYL = Sylt.

Area	Date (MM/YY)	No. of video stations	Total length of videos [min]	No. of images analyzed	Approx. analyzed area [m <sup>2</sup> ]
SOR	05/13, 02/14, 11/14, 07/15, 04/16, 10/16, 03/17	49	532.6	930	552
HEL	10/13, 11/14, 06/17	18	161.7	276	143
BRG	07/12, 07/15	12	69.8	302	979
SYL	07/16	4	144.5	416	666

**Table 2**

Sessile and mobile taxa associated with subtidal terrigenous hard substrates in four areas of the German Bight. List of identified sessile and mobile taxa with further information on the sessile longevity, the larval season and the duration of the pelagic larval phase for the sessile taxa. Abbreviations: s = sessile, m = mobile, n.a. = not available, SOR = Sylt Outer Reef, HEL = Helgoland, BRG = Borkum Reef Ground, SYL = Sylt. \**Buccinum undatum* occurred only as attached egg masses.

	Taxa	Mobility	Sessile longevity [years]	Larval season [month]	Pelagic lifetime	SOR	HEL	BRG	SYL
Porifera	<i>Axinella polypoides</i>	s	n.a.	n.a.	n.a.		X		
	encrusting sponge	s	n.a.	n.a.	n.a.	X		X	
	<i>Halichondria (Halichondria) panicea</i>	s	> 40 <sup>a</sup>	IV–VI <sup>b</sup>	days <sup>c</sup>			X	
Anthozoa	Actiniaria	s	> 40 <sup>d</sup>	IV–VI <sup>e</sup>	weeks <sup>f</sup>	X	X	X	X
	<i>Alcyonium digitatum</i>	s	> 20 <sup>g</sup>	XII–I <sup>h</sup>	14 weeks <sup>h</sup>	X	X	X	X
	<i>Metridium dianthus</i>	s	> 11 <sup>i</sup>	IX–X <sup>j</sup>	months <sup>c</sup>	X	X	X	X
Hydrozoa	<i>Sertularia cupressina</i>	s	> 1 <sup>k</sup>	IV–VI <sup>l</sup>	n.a.	X	X		
	<i>Tubularia</i> sp.	s	> 1 <sup>m</sup>	III–VI <sup>m</sup>	minutes–days <sup>n</sup>	X			
Polychaeta	<i>Spirobranchus triqueter</i>	s	1.5–4 <sup>o,p</sup>	IV–IX <sup>q</sup>	2–8 weeks <sup>q</sup>	X	X	X	X
Bryozoa/Hydrozoa	Bryozoan/Hydrozoan turf	s	n.a.	n.a.	n.a.	X	X	X	X
Bryozoa	<i>Alcyonidium diaphanum</i>	s	> 6 <sup>r</sup>	n.a.	hours <sup>r</sup>		X		
	<i>Flustra foliacea</i>	s	7–12 <sup>s</sup>	II–IV <sup>t</sup>	hours <sup>u</sup>	X	X	X	X
	<i>Securiflustra securifrons</i>	s	n.a.	n.a.	n.a.	X			
Tunicata	Ascidacea	s	1–1.5 <sup>v</sup>	VII–VIII <sup>v</sup>	minutes–days <sup>w</sup>	X			
Mollusca	<i>Buccinum undatum</i> *	m				X			
Crustacea	<i>Cancer pagurus</i>	m				X	X	X	X
	<i>Homarus gammarus</i>	m				X	X		X
	<i>Hyas araneus</i>	m				X	X		
	<i>Pagurus bernhardus</i>	m				X	X		
	Portunidae	m				X	X	X	X
Echinodermata	<i>Asterias rubens</i>	m				X	X	X	X
	<i>Echinus esculentus</i>	m				X	X		
Pisces	<i>Agonus cataphractus</i>	m				X	X		
	<i>Callionymus lyra</i>	m				X		X	
	<i>Chelidonichthys cuculus</i>	m				X			
	Clupeidae	m							X
	<i>Ctenolabrus rupestris</i>	m				X	X		X
	<i>Gadus morhua</i>	m				X			
	<i>Merlangius merlangus</i>	m							X
	<i>Pholis gunnellus</i>	m				X	X		
	<i>Phrynorhombus norvegicus</i>	m				X			
<i>Trisopterus luscus</i>	m				X			X	

<sup>a</sup> Beuchel and Gulliksen (2008).

<sup>b</sup> Witte et al. (1994).

<sup>c</sup> Sebens (1986).

<sup>d</sup> Gulliksen and Svensen (2004).

<sup>e</sup> Chia and Spaulding (1972).

<sup>f</sup> Shaw et al. (1987).

<sup>g</sup> Hartnoll (1998).

<sup>h</sup> Hartnoll (1975).

<sup>i</sup> MarLIN (2006a).

<sup>j</sup> Bucklin (1982).

<sup>k</sup> Schmidt and Warner (1991).

<sup>l</sup> Reitzenstein (1913).

<sup>m</sup> Hughes (1983).

<sup>n</sup> Cornelius (1992).

<sup>o</sup> Klöckner (1976).

<sup>p</sup> Føyn and Gjølén (1954).

<sup>q</sup> Castric-Fey (1983).

<sup>r</sup> MarLIN (2006b).

<sup>s</sup> Stebbing (1971).

<sup>t</sup> Eggleston (1972).

<sup>u</sup> Hayward, Ryland (1998).

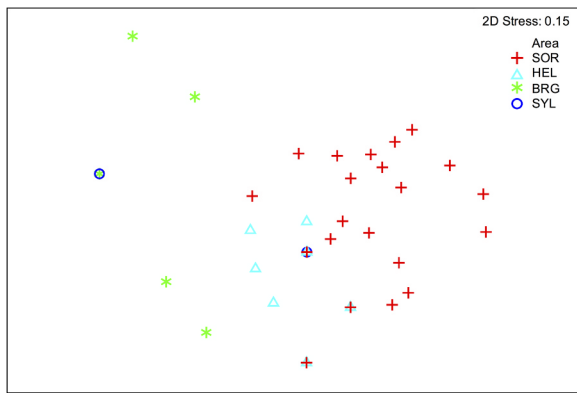
<sup>v</sup> Millar (1952).

<sup>w</sup> Osman and Whitlatch (2007).

(presence/absence and percentage coverage) from the four study areas and between the different stone sizes (Clarke, 1993). The significance level of  $p = 0.05$  was adjusted using Bonferroni-corrected  $p$ -values to account for multiple pairwise comparisons. Taxa that contributed most to the observed dissimilarities were identified with a similarity percentage routine (SIMPER). The multivariate comparisons for the test of

the sessile-taxa inventory between the areas were based on data from videos of which at least ten images were analyzed.

To estimate the species richness of the different areas we generated species accumulation curves (species observed curve – Sobs) from 999 random permutations each. For each curve the maximum number of species was estimated using non-linear regression analysis. We fitted a



**Fig. 2.** Two-dimensional nMDS plot based on the Bray-Curtis-similarities calculated from presence/absence data of sessile taxa in the four areas. Three points of SYL overlap in the center of the plot. Abbreviations (number of replicates per area): SOR = Sylt Outer Reef (34), HEL = Helgoland (9), BRG = Borkum Reef Ground (5), SYL = Sylt (4).

generalized ‘Weibull’ cumulative distribution function (Flather, 1996) to the curves with the least sum of the squared residuals as criterion for best fit. Maximum numbers of taxa were accepted as significantly different if the 95% confidence intervals of the upper asymptotes of the functions did not overlap.

### 2.5. Additional data

Data on local bottom trawling intensities were obtained from the NOAH data portal (North Sea – Observation and Assessment of Habitats; Diekmann, 2015a, 2015b, 2015c, 2015d) to assess the influence of fisheries on the investigated areas. Monthly minimum, average and maximum data on bottom current velocities, bottom salinity and bottom temperature for the years 2013–2017 were provided by the BSH according to models of Dick et al. (2001) and Dick et al. (2008). Monthly average and maximum data of the significant wave height are based on the EWAM model operated by The Deutscher Wetterdienst (DWD; Germany’s National Meteorological Service).

## 3. Results

Michaelis et al. (2019) have shown that the areas SOR, HEL and SYL are dominated by cobbles (at least 75% of the hard substrates) with lesser proportions of boulders and large boulders. In BRG boulders were more dominant (~55% of the hard substrates) followed by cobbles and large boulders. They further showed that boulders and large boulders were largely colonized, whereas cobbles were clearly less colonized in the areas BRG and SYL. Please see Section 2.1 for further information and also Table S1 in the Supplementary file for detailed information on the environmental parameters).

### 3.1. Taxa inventory of the four areas

A total of fourteen sessile and eighteen mobile taxa were found in the four areas (Table 2). The highest number of taxa was found in SOR (27 taxa) followed by HEL (19 taxa). Taxa richness was lowest in SYL (14 taxa) and BRG (12 taxa). Only nine out of 32 taxa were encountered in all areas.

The majority of the sessile taxa were bryozoans and anthozoans, which were identified in all survey areas. Sessile taxa restricted to specific areas, were Ascidiacea, *Securiflustra securifrons* and *Tubularia* sp. in SOR, *A. diaphanum* and *Axinella polypoides* in HEL, and *Halichondria (Halichondria) panicea* in BRG.

**Table 3**

ANOSIM global test and pairwise comparisons of the assemblages of sessile taxa (presence/absence) in the four areas. Sample statistic (Global R): 0.354. Significance level of sample statistic:  $p = 0.001$ . Number of permutations: 999. Number of permuted statistics greater than or equal to Global R: 0. Asterisk (\*) indicates significant difference between the areas at a significance level of  $p < 0.008$ . Abbreviations (number of replicates per area): SOR = Sylt Outer Reef (34), HEL = Helgoland (9), BRG = Borkum Reef Ground (5), SYL = Sylt (4).

Areas compared	R-statistics	p-Value
BRG-SYL	-0.078	0.61
BRG-HEL	0.607	< 0.008*
BRG-SOR	0.852	< 0.008*
SYL-HEL	-0.138	0.75
SYL-SOR	0.119	0.18
HEL-SOR	0.218	< 0.008*

The mobile taxa were dominated by crustaceans and fishes. The edible crab *Cancer pagurus* was abundant in all areas. Fishes occurred mainly in SOR, HEL and SYL. Large schools of *Merlangius merlangus* and Clupeidae were observed especially in SYL, whereas fish species occurred primarily as single individuals in the other areas. The echinoderm *Asterias rubens* was found in all areas, whereas *Echinus esculentus* was only observed in SOR and HEL, often on stones, which were colonized by *S. triqueter*.

The two-dimensional nMDS plot showed clustering of the four study areas according to the qualitative composition of the assemblages of sessile taxa (Fig. 2). Samples from the areas HEL, SYL and from parts of SOR were closely aggregated indicating structurally similar sessile taxa assemblages, whereas samples from BRG and another part of SOR were more separated when compared to samples from the other areas.

The ANOSIM revealed significant structural differences (global  $R = 0.354$ ,  $p = 0.001$ ) between the composition of the sessile assemblages of three areas (Table 3). The subsequent pairwise comparisons confirmed differences between the assemblages at BRG, HEL and SOR with average dissimilarities ranging from 23% to 42% (Table 4). The assemblage in SYL was not different from the assemblages of the other areas. When compared to BRG, *F. foliacea*, Actiniaria, *A. digitatum* and *P. triqueter* were more frequent around HEL. This was also true for the comparison between BRG and SOR, but the presence of Ascidiacea in SOR also contributed to the dissimilarity. The dissimilarities between HEL and SOR were mainly driven by the more frequent presence of Ascidiacea and Actiniaria in SOR and *M. dianthus* in HEL.

### 3.2. Structure of assemblages on different stone sizes

In the areas SOR, BRG and HEL, most stones were colonized by epifauna by at least 50% (Fig. 3). In SOR, *Spirobranchus triqueter*, *Metridium dianthus* and an upright bryozoan/hydrozoan turf colonized the majority of the stone classes. In BRG, the stones were colonized by *M. dianthus*, bryozoan/hydrozoan turf and *F. foliacea*. An encrusting orange sponge occurred on some stones. In HEL, *F. foliacea*, *M. dianthus*, bryozoan/hydrozoan turf and *S. triqueter* were dominant, whereas *A. digitatum* and *Alcyonidium diaphanum* occurred less frequently. In the area SYL, cobbles were colonized by 10–50%. Most of the boulders were colonized by 40–50%, whereas the majority of large boulders were colonized by 40–50% and 60–70%. *M. dianthus*, bryozoan/hydrozoan turf and *A. digitatum* dominated the taxa assemblage in the SYL area, with lower contributions of *S. triqueter*, *F. foliacea* and taxa of the order Actiniaria.

A few large boulders were seen from all sides due to a coincidental rotation of the camera system. These stones were found being colonized by the same structure of the sessile assemblage all over.

**Table 4**

SIMPER routine identifying the sessile taxa that contributed most to the differences between the assemblages at HEL, BRG and SOR. The analysis was based on Bray-Curtis dissimilarities calculated from presence/absence data of sessile taxa. Abbreviations (number of replicates per area): SOR = Sylt Outer Reef (34), BRG = Borkum Reef Ground (5), HEL = Helgoland (9).

Taxa	Frequency of occurrence	Frequency of occurrence	Contribution [%]	Cumulative [%]
Areas BRG & HEL				
Average dissimilarity: 34.45				
	BRG	HEL		
<i>Flustra foliacea</i>	0.20	1.00	23.70	23.70
Actiniaria	0.20	0.56	15.30	39.00
<i>Alcyonium digitatum</i>	0.60	0.89	13.03	52.03
<i>Spirobranchus triqueter</i>	0.60	1.00	12.32	64.35
<i>Halichondria (H.) panicea</i>	0.40	0.00	10.63	74.98
<i>Metridium dianthus</i>	1.00	0.78	7.37	82.35
<i>Sertularia cupressina</i>	0.20	0.11	7.34	89.69
encrusting sponge	0.20	0.00	5.07	94.76
Areas BRG & SOR				
Average dissimilarity: 42.24				
	BRG	SOR		
<i>Flustra foliacea</i>	0.20	0.94	15.91	15.91
Actiniaria	0.20	0.88	14.83	30.73
Asciacea	0.00	0.65	12.56	43.29
<i>Alcyonium digitatum</i>	0.60	0.97	8.84	52.13
encrusting sponge	0.20	0.41	8.66	60.79
<i>Spirobranchus triqueter</i>	0.60	1.00	8.65	69.44
<i>Metridium dianthus</i>	1.00	0.68	7.92	77.37
<i>Halichondria (H.) panicea</i>	0.40	0.00	7.60	84.97
<i>Securiflustra securifrons</i>	0.00	0.38	7.14	92.10
Areas HEL & SOR				
Average dissimilarity: 23.69				
	HEL	SOR		
Asciacea	0.00	0.65	20.44	20.44
Actiniaria	0.56	0.88	16.25	36.69
<i>Metridium dianthus</i>	0.78	0.68	14.65	51.34
encrusting sponge	0.00	0.41	12.63	63.98
<i>Securiflustra securifrons</i>	0.00	0.38	11.66	75.63
<i>Sertularia cupressina</i>	0.11	0.26	9.53	85.16
<i>Alcyonium digitatum</i>	0.89	0.97	4.75	89.91
<i>Axinella polypoides</i>	0.11	0.00	3.12	93.03

A two-factorial ANOSIM based on the percentage coverage of the sessile taxa revealed significant differences between the areas (global  $R = 0.34$ ,  $p = 0.001$ ) and for the size of the stones (global  $R = 0.15$ ,  $p = 0.001$ ) (Table 5). No statistical differences were found between the assemblages of the areas BRG and SYL and for the comparison of the assemblages of boulders and large boulders. A subsequent ANOSIM revealed significant structural differences (global  $R = 0.33$ ,  $p = 0.001$ ) between the sessile assemblages of cobbles as compared to boulders and large boulders within the areas (Table 6). The assemblages did not differ between stone sizes in BRG. The subsequent pairwise comparisons confirmed differences between the assemblages of cobbles in comparison to boulders and large boulders in SOR, HEL and SYL with average dissimilarities ranging from 68% to 89% (Table 7). In SOR, *S. triqueter* and Asciacea were more abundant on cobbles as compared to boulders and large boulders, where *M. dianthus* and an upright bryozoan/hydrozoan turf contributed for most to the observed dissimilarities. In HEL, *S. triqueter* had a higher percentage coverage on cobbles, whereas *F. foliacea* and *M. dianthus* were more common on boulders and large boulders. The dissimilarities between cobbles and boulder-sized stones in SYL were mainly driven by high percentage coverages of *M. dianthus* and an upright bryozoan/hydrozoan turf on boulders and large boulders.

The taxa richness, estimated from the asymptote of the species accumulation curves by non-linear regression analysis on cobbles, boulders and large boulders (Fig. 4) was highest in SOR (8 taxa) followed by HEL (6 taxa). The 95% confidence intervals of the estimates of

the taxa richness did not overlap between the areas indicating significant differences in taxa richness between all areas (Table 8). In HEL and SOR, the taxa richness was higher on large boulders and cobbles than on boulders. In BRG boulders hosted more taxa than large boulders and cobbles whereas in SYL the cobbles hosted more taxa than boulders and large boulders. The differences in taxa richness between cobbles, boulders and large boulders were significant for all areas, except for the area HEL, where cobbles, boulders and large boulders hosted similar numbers of taxa. For each area and for all size classes of the stones 66–100% of the estimated taxa richness was encountered after the analysis of 20 stones (Fig. 4).

#### 4. Discussion

This study revealed significant differences in the structure of the epifaunal assemblages, the taxa richness on specific stone sizes, and the dominance of certain taxa in four investigated areas of the German Bight (cf. Fig. 1). An earlier study revealed significant differences in the physical characteristics of the hard-substrate habitats in the study areas (Michaelis et al., 2019). These results are shortly revisited in the discussion as they also influence the outcomes of this study.

##### 4.1. Effects of physical factors on the epibenthic assemblages

The differences in taxa richness between the investigated areas indicate regional differences, with higher numbers in the far-shore areas

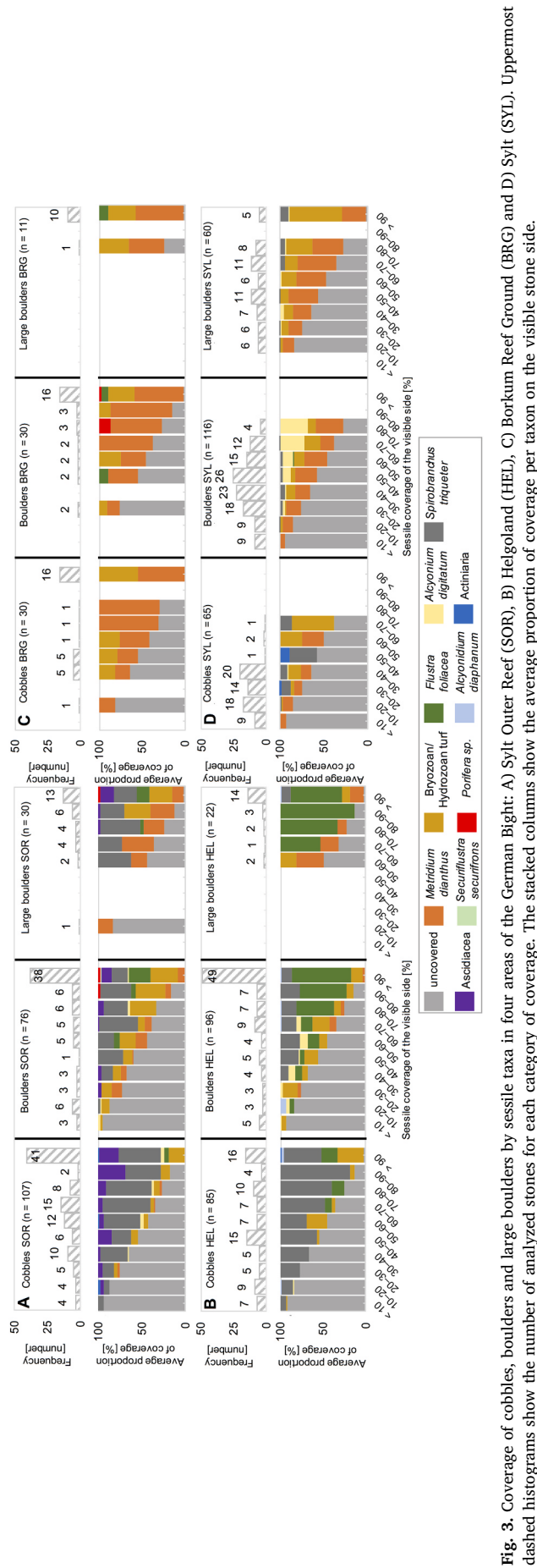


Fig. 3. Coverage of cobbles, boulders and large boulders by sessile taxa in four areas of the German Bight: A) Sylt Outer Reef (SOR), B) Helgoland (HEL), C) Borkum Reef Ground (BRG) and D) Sylt (SYL). Uppermost dashed histograms show the number of analyzed stones for each category of coverage. The stacked columns show the average proportion of coverage per taxon on the visible stone side.

Table 5

Two-factorial ANOSIM of the sessile assemblages (based on the percentage coverage) between the four areas (sample statistic (Global R): 0.34. Significance level of sample statistic:  $p = 0.001$ ) and the stone sizes (sample statistic (Global R): 0.15. Significance level of sample statistic:  $p = 0.001$ ). Number of permutations: 999. Number of permuted statistics greater than or equal to Global R: 0. Number of replicates (i.e. analyzed stones) per area: SOR = 213, HEL = 203, BRG = 71, SYL = 241. Number of replicates per stone class: cobbles = 287, boulders = 318, large boulders = 123. Asterisk (\*) indicates significant differences between the areas at a significance level of  $p < 0.005$ .

Pairwise tests	R-statistics	p-Value
area		
Sylt Outer Reef (SOR)-Helgoland (HEL)	0.095	< 0.005*
Sylt Outer Reef (SOR)-Sylt (SYL)	0.370	< 0.005*
Sylt Outer Reef (SOR)-Borkum Reef Ground (BRG)	0.408	< 0.005*
Helgoland (HEL)-Sylt (SYL)	0.524	< 0.005*
Helgoland (HEL)-Borkum Reef Ground (BRG)	0.543	< 0.005*
Borkum Reef Ground (BRG)-Sylt (SYL)	0.106	0.006
stone-size		
cobbles-boulders	0.177	< 0.005*
cobbles-large boulders	0.251	< 0.005*
boulders-large boulders	-0.022	0.84

Table 6

ANOSIM global test and pairwise comparisons of the assemblages of sessile taxa (percentage coverage) in the four areas. Sample statistic (Global R): 0.329. Significance level of sample statistic:  $p = 0.001$ . Number of permutations: 999. Number of permuted statistics greater than or equal to Global R: 0. Number of replicates (i.e. analyzed stones) per area and stone class (cobbles/boulders/large boulders): SOR = 107/76/30, HEL = 85/96/22, BRG = 30/30/11, SYL = 65/116/60. Asterisk (\*) indicates significant differences between the areas at a significance level of  $p < 0.004$ .

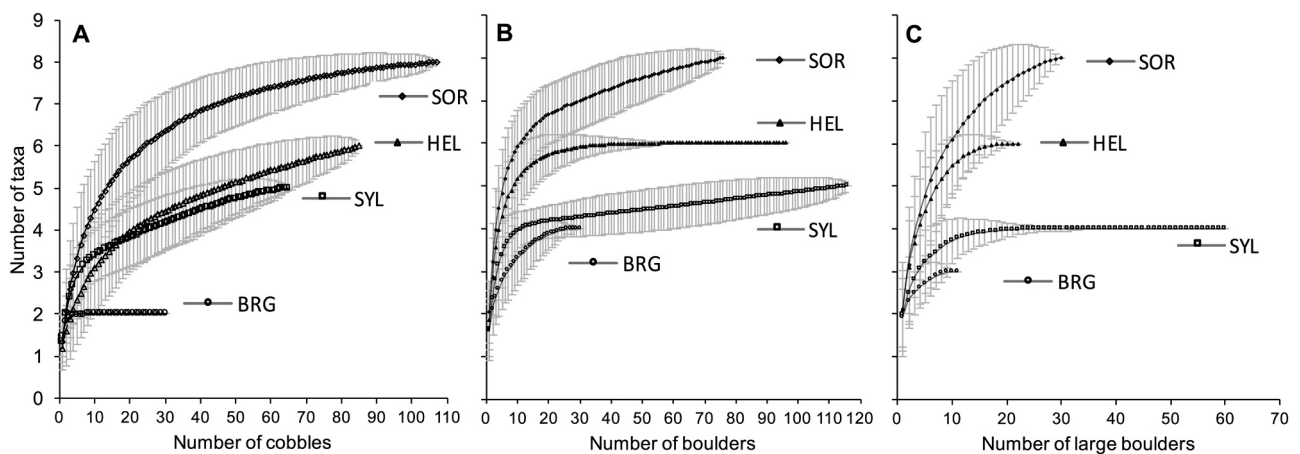
Stone sizes compared	R-statistics	p-Value
Sylt Outer Reef (SOR): cobbles-boulders	0.164	< 0.004*
Sylt Outer Reef (SOR): cobbles-large boulders	0.123	< 0.004*
Sylt Outer Reef (SOR): boulders-large boulders	0.026	0.23
Helgoland (HEL): cobbles-boulders	0.319	< 0.004*
Helgoland (HEL): cobbles-large boulders	0.549	< 0.004*
Helgoland (HEL): boulders-large boulders	-0.061	0.87
Borkum Reef Ground (BRG): cobbles-boulders	0.033	0.08
Borkum Reef Ground (BRG): cobbles-large boulders	-0.035	0.74
Borkum Reef Ground (BRG): boulders-large boulders	-0.024	0.55
Sylt (SYL): cobbles-boulders	0.078	< 0.004*
Sylt (SYL): cobbles-large boulders	0.203	< 0.004*
Sylt (SYL): boulders-large boulders	-0.014	0.71

SOR and HEL than in the nearshore areas BRG and SYL. Water depths and the bottom current velocities also vary between the areas. With increasing water depth and turbidity, the amount of sunlight available for photosynthesis is reduced and restricts the presence of seaweeds to shallow and sheltered hard substrates (e.g. Anthony and Fabricius, 2000). Furthermore, the influences of waves on the seafloor in deeper areas is lower and limited to storm-induced waves (Otto et al., 1990). A typical depth-zonation can be excluded, as no seaweeds were observed in this study and the sessile taxa inventory was mostly similar throughout the areas. Michaelis et al. (2019) showed that sediment transport, induced by different bottom current velocities and wave action seems to be the most relevant abiotic influence on the hard substrates and their associated fauna in the study areas. Higher current velocities generate stronger sediment transport and an improved food-supply, which promotes the dominance of more resistant taxa and passive filter-feeders like *M. dianthus* and *A. digitatum* (Sebens, 1986). In contrast, weaker bottom currents combined with reduced abrasion and erosion potential led to the settlement of active filter feeders, like tunicates, and of taxa less resistant to abrasion, which increases the taxa richness (Sousa, 1979). Furthermore, small-scale variations in grain

**Table 7**

SIMPER routine identifying the sessile taxa that contributed most to the differences between the assemblages of cobbles when compared to boulders and large boulders in SOR, HEL and SYL. The analyses were based on Bray-Curtis dissimilarities calculated from the percentage coverage of sessile taxa. Number of replicates (i.e. analyzed stones) per area and stone class (cobbles/boulders/large boulders): SOR = 107/76/30, HEL = 85/96/22, SYL = 65/116/60.

Taxa	Average percentage coverage	Average percentage coverage	Contribution [%]	Cumulative [%]
<b>Area Sylt Outer Reef (SOR)</b>				
Average dissimilarity: 79.36				
	Cobbles	Boulders		
<i>Spirobranchus triqueter</i>	40.93	19.03	36.55	36.55
Bryozoan/hydrozoan turf	9.21	23.93	25.02	61.57
Ascidacea	12.25	6.89	14.84	76.41
<i>Flustra foliacea</i>	1.98	13.04	11.44	87.84
<i>Metridium dianthus</i>	0.92	6.67	6.75	94.60
<b>Area Sylt Outer Reef (SOR)</b>				
Average dissimilarity: 74.41				
	Cobbles	Large boulders		
<i>Spirobranchus triqueter</i>	40.93	29.13	34.84	34.83
<i>Metridium dianthus</i>	0.92	20.73	20.38	55.23
Bryozoan/hydrozoan turf	9.21	17.13	19.51	74.73
Ascidacea	12.25	7.07	14.56	89.29
<i>Flustra foliacea</i>	1.98	6.80	7.11	96.39
<b>Area Helgoland (HEL)</b>				
Average dissimilarity: 81.46				
	Cobbles	Boulders		
<i>Flustra foliacea</i>	6.02	45.23	40.88	40.88
<i>Spirobranchus triqueter</i>	38.92	13.00	35.91	76.80
Bryozoan/hydrozoan turf	8.82	12.10	17.53	94.33
<b>Area Helgoland (HEL)</b>				
Average dissimilarity: 88.88				
	Cobbles	Large boulders		
<i>Flustra foliacea</i>	6.02	59.45	45.76	45.76
<i>Spirobranchus triqueter</i>	38.92	7.77	27.20	72.96
<i>Metridium dianthus</i>	0.00	15.45	12.88	85.84
Bryozoan/hydrozoan turf	8.82	7.95	9.80	95.64
<b>Area Sylt (SYL)</b>				
Average dissimilarity: 69.98				
	Cobbles	Boulders		
<i>Metridium dianthus</i>	10.25	18.93	39.60	39.60
Bryozoan/hydrozoan turf	7.00	7.56	24.87	64.47
<i>Spirobranchus triqueter</i>	6.09	3.09	18.53	83.00
<i>Alcyonium digitatum</i>	0.58	7.79	15.69	98.69
<b>Area Sylt (SYL)</b>				
Average dissimilarity: 68.01				
	Cobbles	Large boulders		
<i>Metridium dianthus</i>	10.25	29.83	44.69	44.69
Bryozoan/hydrozoan turf	7.00	22.08	36.87	81.57
<i>Spirobranchus triqueter</i>	6.09	2.47	14.14	95.71



**Fig. 4.** Taxa accumulation curves (999 permutations) for estimating the maximum number of sessile taxa on A) cobbles, B) boulders and C) large boulders per study area. Error bars indicate the standard deviations. Abbreviations: SOR = Sylt Outer Reef, HEL = Helgoland, BRG = Borkum Reef Ground, SYL = Sylt.

**Table 8**

Equations and goodness of fit ( $R^2$ ) of the Weibull cumulative distribution functions describing the species accumulation curves for the sessile epifauna on cobbles, boulders and large boulders in the four areas. The 95% confidence intervals for the estimates of the maximum number of taxa are given. Abbreviations: SOR = Silt Outer Reef, BRG = Borkum Reef Ground, HEL = Helgoland, SYL = Sylt.

Substrate size	Area	Weibull function	95%-CI	$R^2$	n
Cobbles	SOR	$Y = 7.851 * (1 - \exp(-0.0473 * (x + 6.224)))^1$	7.80–7.91	0.98	107
	HEL	$Y = 6.027 * (1 - \exp(-0.0349 * (x + 8.915)))^1$	5.92–6.13	0.98	85
	BRG	$Y = 2.000 * (1 - \exp(-1.041 * (x + 0.295)))^1$	1.99–2.00	0.99	30
	SYL	$Y = 5.034 * (1 - \exp(-0.0453 * (x + 11.77)))^1$	4.88–5.19	0.95	65
Boulders	SOR	$Y = 7.652 * (1 - \exp(-0.086 * (x + 5.246)))^1$	7.56–7.75	0.95	76
	HEL	$Y = 5.973 * (1 - \exp(-0.1749 * (x + 1.666)))^1$	5.96–5.99	0.99	96
	BRG	$Y = 4.059 * (1 - \exp(-0.1275 * (x + 3.524)))^1$	4.01–4.11	0.99	30
	SYL	$Y = 4.683 * (1 - \exp(-0.06691 * (x + 11.71)))^1$	4.63–4.74	0.83	116
Large boulders	SOR	$Y = 8.087 * (1 - \exp(-0.1169 * (x + 2.157)))^1$	7.95–8.23	0.99	30
	HEL	$Y = 6.058 * (1 - \exp(-0.2134 * (x + 1.172)))^1$	6.01–6.11	0.99	22
	BRG	$Y = 3.046 * (1 - \exp(-0.332 * (x + 2.058)))^1$	2.99–3.11	0.99	11
	SYL	$Y = 3.999 * (1 - \exp(-0.1169 * (x + 2.157)))^1$	3.99–4.00	0.99	60

sizes in SOR and the proximity to the intertidal rock platform of Helgoland in the area HEL lead to a higher habitat heterogeneity, which is known to increase the taxa richness in various marine and terrestrial environments (Tews et al., 2004).

The differences in the number of taxa between stone sizes within a certain area are too marginal to clearly confirm a dependency on the stone size. These differences need to be confirmed by data generated by methods with a higher taxa resolution, e.g. by divers (Beisiegel et al., 2017).

#### 4.2. Structure of assemblages on different stone sizes and biotic interactions

The great majority of the stones were intensively colonized by sessile taxa. This pattern was driven by the dominance of few sessile taxa with different live strategies (e.g. short-lived (< 5 years) vs. long-lived (> 5 years)) and competitive abilities. Especially boulder-sized stones were largely colonized by long-lived taxa. In relation to the main direction of tidal currents, no structural differences in the sessile assemblages were observed between the differently exposed sides of the stones. Hence, biotic interactions between different taxa seem to be as important for the structure of the taxa assemblages as abiotic effects like e.g. the coverage or abrasion by mobile sediments, the strength of current velocities and physicochemical properties of the marine environment. The most important biotic controls are competition, larval supply, seasonality and predation (Wahl, 2009). The effects of biotic interactions are more easily detectable under conditions of reduced abiotic disturbances, i.e. in areas of greater water depths (Armonies et al., 2014).

The long-lived anemone *M. dianthus* can be locally very abundant because the asexual reproductive mode of this taxon often results in dense local recruitment on single stones (Chia, 1976). Abundant *M. dianthus* can have a strong influence on the local assemblage of sessile taxa as the anemones capture pelagic larvae from the water column, thereby limiting the colonization of barren hard substrates (e.g. Nelson and Craig, 2011). Furthermore, *M. dianthus* is a hemi-sessile taxon effectively colonizing by attacking associated organisms with catch-tentacles (Purcell, 1977), mechanically or by compromising oxygen supply and reducing the pH when creeping slowly over the hard substrate (Woolmington and Davenport, 1983). Coolen et al. (2015) suggest that abundant *M. dianthus* are responsible for the low epifaunal diversity on the Dutch side of the BRG. Similarly, the relatively low diversity of the sessile assemblages in BRG and SYL and high amounts of *M. dianthus* especially on boulder-sized stones seem to confirm the colonization success of this taxon. However, *M. dianthus* is sensitive to elevated temperatures of > 20 °C and periods of oxygen depletion (Sebens, 1986; Wahl, 1985). Whilst higher temperatures can become more important in the shallower areas SYL and BRG, oxygen depletion is more likely to occur in deeper and less mixed areas (Greenwood et al., 2010).

If critically high water temperatures are reached as a consequence of the current warming trend in the German Bight (Wiltshire et al., 2010), a significant change in the composition of assemblages dominated by *M. dianthus* can be expected in the future.

Another important colonizer was the serpulid polychaete *S. triqueter*. Barren space on hard substrates can be effectively occupied as a consequence of intense larval settlement after abrasion of the substrate surface during stormy winter- and spring season (Klößner, 1976). The tendency of the larvae to settle close to conspecifics and high juvenile growth rates during the first months further enhance the competitiveness of this taxon (Castric-Fey, 1983; Klößner, 1976) potentially explaining the dominance of this taxon on cobble-sized stones in HEL and SOR. The dominance by a single taxon may be enhanced on smaller sized substrates (Osman, 1977). However, due to the relatively short lifespan of *S. triqueter* of 1.5–4 years (Føyn and Gjøen, 1954; Klößner, 1976), dominance can be continuously shifted towards long-lived taxa (> 5 years) like the bryozoan *F. foliacea* (Rubin, 1985) or anthozoans. A shift towards dominance of long-lived species was repeatedly observed on more stable and less disturbed hard substrates like boulder-sized stones in HEL and SOR. However, just like for cobble-sized stones, boulders and large boulders can temporarily become fully colonized by this taxon, for example, following disturbance or abrasion of the sessile assemblage and a subsequent settlement of *S. triqueter* larvae.

Besides the dependency on the timing of recruitment after a disturbance event, the distance to larval sources and the duration of the pelagic larval phase (Botsford et al., 2001) are also important factors that can determine the presence or absence of taxa. The larvae of ascidians and of the bryozoan *F. foliacea* are known to be relatively short-lived (Osman and Whitlatch, 2007; Ryland, 1967). Decreasing larval densities at larger distance to dense aggregates of conspecifics (Ryland, 1976; Sebens, 1986) may explain why *F. foliacea* and ascidians dominated in HEL and SOR, respectively, but not in the other areas. Hence, the areas HEL and SOR might be important larval source sites for these taxa in the German Bight.

Several taxa show a clear seasonality with respect to growth, feeding and reproduction (Osman, 1977). Furthermore, they can also reduce their size or change to a dormant stage during the winter season (Coma et al., 2000; Osman, 1977). Seasonality was not considered in this study because not enough replicates were available from different seasons and years. Even though most of the presented taxa in this study were encountered throughout the year, differences in the assemblages between the areas might, however, also indicate seasonal differences as the areas were sampled at different seasons.

The number of images analyzed per area may affect the estimate of sessile taxa richness because a low sampling effort can compromise the ability to capture the full range of habitat complexity. However, the taxa richness was lowest in the areas with the highest image density

(BRG and SYL) and highest in the areas with the lowest image density (HEL and SOR). Therefore, we would expect that an equal sampling effort in all areas would support or even amplify the observed differences in taxon richness. Similarly, variable levels of taxonomic resolutions may have masked the real level of taxon richness and the variations thereof. Changes of diversity within aggregated taxa, such as bryozoan/hydrozoan turf, remain mostly undetected. However, the number of undetected taxa would be highest in taxon rich communities. Accordingly, we would expect that an improved methodological resolution would also support the observed differences in taxon richness among the areas.

Predators can efficiently suppress the development of an extensive layer of sessile animals or algae at various development stages (e.g. larval to adult stage) as indicated by a patchy epifaunal coverage of hard substrates (e.g. Sams and Keough, 2007). The starfish *A. rubens*, the sea urchin *E. esculentus* and the goldsinny wrasse *C. rupestris* were identified in this study and are known to forage intensively on bryozoans, polychaetes, crustaceans and gastropods (Konar and Iken, 2005; Paine et al., 1985; Scheibling, 1986). Similarly, nudibranchs are important predators of epibenthic taxa, especially of anthozoans and bryozoans (Sebens, 1986; Thompson, 1962). Nudibranchs were not discovered with this method, however, they are known to occur in the study area (Coolen et al., 2015; De Kluijver, 1991; Dederer et al., 2015). Hence, influences of predators on the sessile taxa assemblages can be expected, but methods with higher taxa resolutions are mandatory for detailed studies on the contribution of predators on the assemblage structure.

The most conspicuous pattern in the distribution of the mobile fauna was the absence of *E. esculentus* from the areas BRG and SYL. Higher current velocities in these areas may have negatively affected the moving and feeding behavior of sea urchins and their survival probability (Cohen-Rengifo et al., 2018). However, it was not possible to identify the actual reasons for the distribution of single species with the methods applied in this study.

#### 4.3. Anthropogenic disturbances

Bottom trawling is one of the most influential anthropogenic disturbance on subtidal reefs (e.g. Hinz et al., 2011). Heavy beam trawls and dredges are ploughing the seafloor thereby killing numerous sessile organisms on hard substrates and altering the habitat structure (Watling and Norse, 1998). However, no indications of intense trawling activities (e.g. presence of entangled nets, grinding marks or trawling traces) were evident on the videos. Apparently, fishermen seem to avoid the risk of destroying or losing equipment upon encounter with large boulders. Habitat maps of the NOAH project (Diekmann, 2015a, 2015b, 2015c, 2015d) have shown that fishing activity, with large and small bottom trawlers, is intense in the German Bight (in the years 2011 and 2012), but specified as absent to low in the investigated subtidal reef areas. Additionally, the absence of long-lived and sensitive taxa, such as *F. foliacea* and *E. esculentus*, have been suggested as indicators of the impact bottom trawling (MacDonald et al., 1996). At least one of these sensitive taxa was found in the reef areas of the German Bight indicating low fishery-induced disturbance.

#### 5. Conclusions

Data obtained by the analysis of underwater videos show significant differences in the sessile assemblages of four subtidal reef areas in the German Bight. While the general composition of taxa is similar for all areas, our analysis suggests that (1) regional variability can be explained by differences in the degree of physical disturbance induced by mobile sediment, and that (2) the dominance of specific sessile taxa is a function of their individual competitiveness and the stone size. We have shown that the majority of hard substrates is intensively colonized by a low-diversity assemblage (of up to eight taxa). Detailed knowledge of

the physical properties of natural hard-substrate areas and their associated taxa assemblages is crucial to support marine spatial planning and conservation initiatives. The identification of physical properties (e.g. sizes of hard substrates and bottom current velocities) using remote sensing techniques might assist in the demarcation and prioritization of particularly valuable areas. However, there is still a need for accurate spatial information on the occurrence, amount and size of hard-substrate dominated areas based on area-wide hydroacoustic mapping surveys as well as information about the ecology of epibenthic taxa. In general, an extensive protection and regular monitoring of these vulnerable reef systems is highly recommended to maintain their conditions and ecological functions.

#### CRedit authorship contribution statement

**Rune Michaelis:** Conceptualization, Methodology, Investigation, Writing - original draft, Visualization. **H. Christian Hass:** Conceptualization, Writing - review & editing. **Finn Mielck:** Writing - review & editing, Visualization. **Svenja Papenmeier:** Conceptualization, Writing - review & editing, Visualization. **Lasse Sander:** Writing - review & editing. **Lars Gutow:** Conceptualization, Writing - review & editing. **Karen H. Wiltshire:** Writing - review & editing.

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#### Conflict of interest

The authors declare no conflict of interest.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.csr.2019.01.011](https://doi.org/10.1016/j.csr.2019.01.011).

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