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The importance of artificial coastal structures (tetrapods) as refuge and settlement area for fish and crustacea

by

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A thesis submitted in partial fulfilment
of the requirements for the degree of

Doctor of Philosophy

in Biology

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Date of Defence: June 21, 2012

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CONTENTS

INTRODUCTION

Artificial reefs and coastal defence structures

Millions of people benefit from the goods and services provided by well-functioning marine and coastal ecosystems. The tourism sector and the fishing industry are important sources of income for humans. Almost half of the EU's population lives less than 50 km from the sea, the majority concentrated in urban areas along the coast (EEA 2010).

Rapid changes in climate during the last decades will result in the destruction of coastal areas through flooding and erosion (IPCC 2007b, a, Hawkins et al. 2009, Wiltshire et al. 2010). About 40 million people are currently exposed to a one in 100 year coastal flood event (Hanson et al. 2011). The establishment of more coastal defences is currently pushed to save the livelihood of millions of people and to protect urban coastal areas (Tsai et al. 2006, Chapman & Underwood 2011, Zanuttigh 2011).

In parts of Japan, the U.S., Europe and Australia more than half of the coastline has been replaced by artificial structures (Browne & Chapman 2011). Regarding Germany, 85 % of the North Sea coast is artificially protected (Rupp-Armstrong & Nicholls 2007).

Artificial structures are used in many countries and regions across the world for coastal management purposes, including the enhancement or concentration of living marine resources, compensation for habitat loss, and coastal protection (OSPAR 1999).

Specifically constructed artificial reefs have been established, e.g. for rehabilitation actions for damaged natural reefs, to enhance fish populations (Fabi et al. 2002, Seaman 2007), for the aquaculture or even to establish ecotourism (Fukunaga & Bailey-Brock 2008). The majority of the artificial reefs in Europe play a role in protecting valuable Mediterranean sea grass beds from trawl damage or support fisheries function (Jensen 2002, Whitmarsh et al. 2008). Man-made reefs in Japan are primarily used by commercial fishermen and are designed by engineers (Bohnsack & Sutherland 1985). Furthermore, there is an increasing number of offshore artificial substrate in form of wind power plants or oil platforms (Bohnsack & Sutherland 1985, Whitmarsh et al. 2008).

Artificial reefs are often specifically designed to enhance the abundance in local biota, diversity and species richness and therefore are normally guided by a thorough

ecological assessment. Coastal defence structures, on the other hand, are mainly built to protect mankind and therefore have to follow primarily engineering guidelines. The ecological consequences of coastal defence structures for the ecosystem remain thereby mostly unclear (Bacchiocchi & Airoldi 2003, Airoldi et al. 2005a, Moschella et al. 2005).

An increasing research effort has to be made to gain a better understanding of the ecological impacts of such anthropogenic infrastructures to meet the engineering requirements on the one side but also to increase their value as habitat. This approach is today defined as ecological engineering (Browne & Chapman 2011, Chapman & Underwood 2011).

In order to assess the functioning and the relative value of artificial substrate, the investigation of such structures is essential to reveal potential ecological impacts on the natural environment (Airoldi et al. 2005a, Martin et al. 2005, Moschella et al. 2005) and to understand the temporal and spatial characteristics of the prevalent communities (Nickell & Sayer 1998). In general, the insertion of artificial structures introduces a source of variation into the natural habitat and can lead to changes of the natural community (Chapman & Underwood 2011). The effects of artificial introduced structures are often highly site specific and can vary over different spatial scales (Chapman & Bulleri 2003, Airoldi et al. 2005a, Martin et al. 2005, Clynick et al. 2008, Burt et al. 2009).

Community development on artificial substratum

The community development on substratum starts with the initial settlement of epibiotic organisms, such as algae and sessile invertebrates, and is followed by the colonization of mobile organisms such as fish and crustaceans (Moschella et al. 2005, Andersson et al. 2009). The epibiota attached on artificial substrate may provide an important source of food. Algal cover in particular can be utilized as shelter and protection from predation by small cryptobenthic species and juveniles (Coleman & Connell 2001, Wilhelmsson et al. 2006b, Clynick et al. 2007, Andersson et al. 2009). Depending on the complexity of artificial structures, they also increase the supply of refuges in form of microhabitats and can be important nursery grounds for fish and crustaceans (Rooker et al. 1997, Wilhelmsson et al. 2006a, Fischer et al. 2007).

Man-made structures can produce significant benthic biomass, which may be useful in supporting fish biomass recovery (Leitao et al. 2007). Wilhelmsson et al. (2006a) suggest that offshore windmills may function as combined artificial reefs and fish aggregation devices for demersal fish. Several other studies also suggest that artificial substrata can act as fish attractor and they can increase production. It is a common fact that artificial reefs attract fish from the surrounding (Bohnsack & Sutherland 1985, Fabi & Fiorentini 1994, Simon et al. 2011). However, it still has to be resolved whether if the artificial substratum only accumulates mobile species from the surrounding areas or if there is truly an additional net increase in biomass by the artificial structures as well as in the surrounding (Bohnsack & Sutherland 1985, Bohnsack 1989, Osenberg et al. 2002). Post-hoc studies, which are often performed years after the deployment of the artificial structures, offer only limited insights. Furthermore, many investigations have focused almost exclusively on the artificial structures rather than on how nearby natural reefs or the surrounding may have been affected (Osenberg et al. 2002).

Tetrapods

Tetrapods are four-footed coastal defence concrete structures, built to protect the coasts from wave action and erosion (Gürer et al. 2005). The weights of the tetrapods vary worldwide in dependence of the prevailing local weather conditions. On the coastline of the small rocky island of Helgoland in the German Bight, the weight of the tetrapods is six-tons each but on the north coast of Taiwan, where on average three to four typhoons affect the island every year, massive tetrapods weighing 20 – 30 t were introduced (Tsai et al. 2006). Even greater in size with a weight of 40 t are the tetrapods used for the breakwater of the Misurata Steel Factory Port in Libya (Gürer et al. 2005).

Tetrapods represent valuable protection measures mainly for hard-bottom substratum, but often fail in soft-bottom areas, for example on the East Frisian Islands like Sylt. There, tetrapods have been exposed as breakwaters in the 1980's. They have been almost completely buried into the sand over the years, however, caused by undercutting and therefore lost their function as a protection measure (source: Fa. HC Hagemann).

Despite the overall importance of tetrapods for coastal protection measures worldwide, only little information is available so far concerning the ecological influence of tetrapods and their biological significance on the surroundings. In 2003, an artificial reef area of 15,000 m^2 was established in the Baltic Sea, called the Nienhagener Riff.

A total of 107 six-ton tetrapods and an additional 820 two-ton tetrapods were established among other artificial structures in this area (Mohr 2006). Schygula (2007) found that the surface of tetrapods are highly suitable for fouling organisms and Mohr (2006) published data on the homepage of the project (http://www.riff-nienhagen.de/), which show that these elements are appropriate in providing shelter for endangered and over-fished species, like the cod (*Gadus morhua*).

The study site

The rocky island Helgoland is located in the German Bight (54°11' N, 07°52' E). The "Helgoländer Felssockel" covers an area of about 35-km². The next natural hard-bottom communities occur along the Norwegian and East English coastline about hundred kilometres away (Harms 1993). Therefore Helgoland is the only natural hard-bottom area in the otherwise soft-bottom dominated southern North Sea.

Hydrographical and biological data indicate a recent shift in the physical and biological parameters of the North Sea (Franke et al. 2004, Franke & Gutow 2004, Wiltshire et al. 2008, Wiltshire et al. 2010). Caused by climate change, westerly winds are increasing in frequency and strength especially during winter months leading in an influx of warmer and more saline waters from the Atlantic. The average water temperature at Helgoland has increased by 1.67 °C since 1962 (Wiltshire et al. 2010) and the salinity has risen by 1.0 practical salinity unit (PSU) since 1962 (Franke & Gutow 2004, Wiltshire & Manly 2004).

By now almost the entire coastline of Helgoland and its associated small island "Düne" is protected through coastal defence structures. Especially the establishment of breakwaters in form of tetrapods or boulders is becoming more and more important to save Helgoland's coast from high-wave exposure and flooding.

Around 10,000 tetrapods protect mainly the exposed west side of the island. In total, 16 % of the coast of the Düne and 6 % of Helgoland are protected through tetrapods and additionally 4 % through the so-called dolosse (tetrapod similar structures; introduced at the east side, Fig. 1). The rest of the coast is protected through seawalls, harbour moles and breakwaters in form of boulders (Fig. 1).
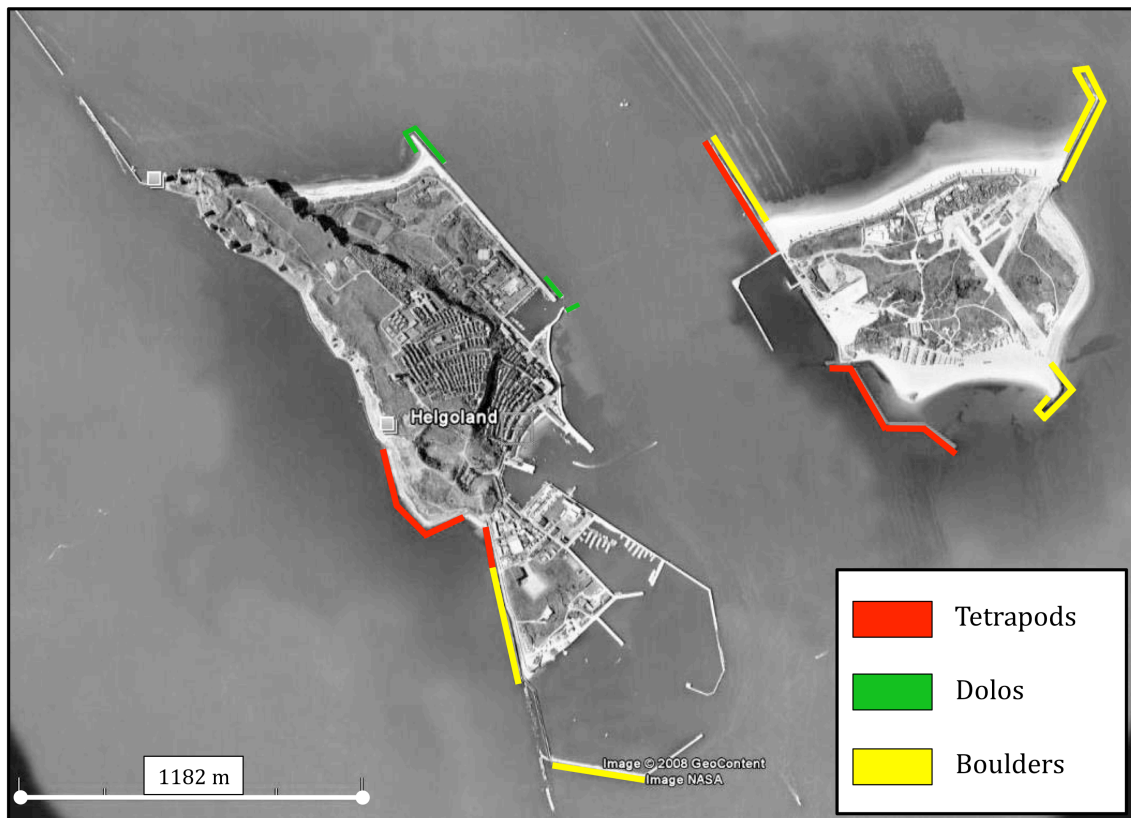
Fig 1 Coastal defence structures (only low-crested breakwaters are highlighted in colour) around the coast of the rocky island Helgoland and its corresponding small island Düne

Previous studies on Helgoland

Most studies on the temporal and spatial dynamics of the macro-biota of the "Helgoländer Felssockel" have focussed on the rocky intertidal zone (Reichert & Buchholz 2006, Reichert et al. 2008), where data can be sampled directly from land. Additionally, subtidal investigations focussing on epifaunal organisms were conducted by Anger (1978) to a water depth of about one meter using fixed stations. In 1988, Franke & Gutow (2004) started a long-term monitoring programme on species (particularly isopod- and amphipod species) associated with uprooted, surface-floating seaweed that accumulates around Helgoland. Nonetheless, information about the sublittoral communities - especially of the mobile macro benthos and fish - in greater depths and away from the direct coast of Helgoland is lacking.

Adequate *in situ* studies of the subtital community in deeper areas require the use of SCUBA technology. However, this is difficult especially in the southern North Sea, caused by the frequently harsh weather conditions (Harms 1993) and strong tidal currents. From October to April the weather is stormy most of the time; high waves and

strong tidal currents make the fieldwork difficult. However, even during summer months, good weather conditions, allowing easy access to sublittoral habitats by SCUBA, are rare. Good logistical support and an on-site presence are therefore required for a continuous data sampling through SCUBA diving. Because of these conditions, only a few studies (e.g. De Kluijver 1991) have dealt with the temporal and spatial patterns of the macrobiotic community around Helgoland. Concerning fish species, the only systematic study of the biology of the sublittoral fish community around Helgoland was completed by Krüß (1988) in his diploma thesis.

The MarGate field

In February 2010 the work group "*in situ* ecology and scientific diving" of the Alfred Wegener Institute for Polar and Marine Research, Biologische Anstalt Helgoland, Germany, established six experimental fields of tetrapods 400 m north of Helgoland in close cooperation with engineers of the company HC HAGEMANN GmbH & Co. KG (Hamburg, Germany) and the Waterways and Shipping Office (WSA) (outlying district Helgoland, Germany). The initiation of the project and the application procedure started in the end of 2008 by Prof. Dr. Philipp Fischer and Stephanie Wehkamp. The project was approved in late 2009 by the Federal Maritime and Hydrographic Agency (BSH) (Hamburg, Germany), the Waterways and Shipping Office (WSA) (Tönning, Germany), and the Ministry for agriculture, environment and rural areas (Kiel, Germany). Detailed information about the construction of the tetrapod fields is described in Chapter II and Chapter III.

The MarGate experimental field was mainly established to investigate the impact of breakwaters on the natural surrounding. Additionally, however, it is used by other scientists to test materials by fixing them on or nearby the tetrapods. The MarGate project is also associated to the large-scale infrastructure project "Coastal observations for Northern and Arctic Seas (COSYNA)" and hosts an underwater data node for long-term hydrographic and biological measurements (www.cosyna.de).

Field methods

Scientific diving

Since structure-associated living organisms can hardly be assessed by ship and/or net supported sampling methods (Fischer et al. 2007), "scientific diving" was used as the

main operation method for the *in situ* assessments. The "Center for Scientific Diving" of the Alfred Wegener Institute for Polar and Marine Research at the Biologische Anstalt Helgoland provides a safe and reliable framework for professional under water *in situ* studies, which made the diving supported studies in the above described experimental field "MarGate" possible.

Transect mapping

A widely adopted method for sampling nearshore habitats, such as artificial structures or rocky substratum, is underwater visual census (e.g., De Girolamo & Mazzoldi 2001, Wilhelmsson et al. 2006a, Brotto et al. 2007). This is, in contrast to using traps, nets or anesthetics, a non-invasive sampling technique. Especially cryptobenthic species over small areas can be recorded by visual census (Sayer & Poonian 2007).

Species identification and counting of fish and crustaceans were therefore performed by SCUBA-supported line-transect counting. Because of the often low visibility and cold water temperatures during a majority of the *in situ* assessment time the diver counted at fixed transect-lines instead of laying out new transects each dive – a method which is often used in warm tropical environments with good visibility and orientation under water. With this method, enough time for the sampling and data collection even under the often harsh and unfavourable weather conditions in the North Sea was given. In addition to the counting above the substrate hidden and highly cryptobenthic species were detected by turning stones up to a size of 10 cm (Beldade & Goncalves 2007).

Species identification

Mobile species under water are often difficult to identify because of limited visibility. Furthermore, colours and sizes appear different than on land. Therefore it is important to identify species based on distinct features like e.g. the positioning of fins in fish species and of chelipeds in crustacean species. Before starting the real data sampling, the first identifying of species was practiced four times in the aquarium and then six times directly in the field. To aid with proper identification, underwater tables with photos of the target species were used. Specific identification features were marked in the photographs with red arrows. For the identification of size classes, a ruler (unit: cm) was drawn on the edge of the table.

Statistical analyses

The most data collected were not normally distributed. Therefore, data were either transformed to a normal distribution with classical transformation procedures (Köhler et al. 1992) or rank transformed prior to the application of parametric statistical test procedures such as ANOVA (Conover & Iman 1981).

ANOVA's with subsequent post-hoc tests were applied to detect spatial and temporal effects on fish and crustacean abundances. Following factors were used as fixed factors: "month" (Chapter I, II, II), "year" (Chapter II, III), "distance" (Chapter II, III).

Additionally, analyses of co-variances (ANCOVA) were applied:

- Chapter I: to analyse the effects of algal density on fish and crustacean abundances with "month" as fixed factor and "algal density" as co-variable.

- Chapter II and III: to analyse the effects of "water temperature" on fish and crustacean abundances with "month" as fixed factor and "water temperature" as co-variable.

- Chapter II and III: to analyse the effects of "tidal cycle" on fish and crustacean abundances with "distance" as fixed factor.

Terminology used in this thesis

Artificial reef

The term "artificial reef" is excessively used in the literature. We did not define the tetrapod experimental fields as artificial reefs, referring to the OSPAR Guidelines on Artificial Reefs in relation to Living Marine Resources (1999). They define artificial reefs as follows: "An artificial reef is a submerged structure placed on the seabed deliberately, to mimic some characteristics of a natural reef. It could be partly exposed at some stages of the tide" (OSPAR 1999). The focus of this study is on the investigation of generally used coastal defence structures and not on the imitation of a natural reef.

Biodiversity

Biodiversity is a concept with multiple meanings and with attributes that can be measured in different ways. It is important to predetermine the meaning of this term and its contents for this study. The definitions of the following terms are congruent with those by Magurran (2004) and Buckland et al. (2005):

- Abundance: The number of all individuals of a specific species in a defined area.
- Overall (total) abundance: The number of all individuals of all species in a defined area.
- Species richness: Number of all species in a defined unit.
- Evenness: Variability in species abundances. High evenness exists when all species have approximately equal numbers of individuals.
- Dominance: The reverse of evenness is dominance, which is the extent to which one or a few species dominate the community.
- Biodiversity: The term biodiversity in this case is equal with the terms ecological diversity and biological diversity; no difference is made in this thesis between these terms. It contains the two components: species richness and evenness.
- Diversity index: A single statistic that incorporates information on richness and evenness.

Abbreviations used in this thesis

ANCOVA	Analysis of co-variance
ANOVA	Analysis of variance
HB	Brillouin diversity index
HB_{max}	Maximum value of Brillouin diversity
E	Brillouin evenness
YOY	Young-of-the-year

RESEARCH AIMS

The general research aim of this work was to provide detailed information on the effects of coastal defence structures (tetrapods) with respect to the temporal and spatial dynamics of a local fish and macro-crustacean community in a northern-boreal rocky shore habitat.

Spatial distribution

To understand why a certain species does or does not settle in a certain area at a certain time is crucial to unravel relationships between the individual species and the habitat parameters. However, too large sampling units represent a basic problem in the assessment of such functional relationships, when relying on ship-supported methods like dredging. Both, the characterisation of the fish community and the substratum types in an area are mostly done on a very broad range according to the sampling methodology. Fish and macro-crustaceans, however, are distributed also on substratum characteristics on a micro-scale unit. Only few studies dealing with this topic have been done in temperate or cold-water areas, especially in northern boreal hard-bottom systems.

Therefore this study aims to provide detailed information on the spatial distribution on the small-scale range for the main demersal fish and decapod crustacean species of a typical hard-bottom kelp site over different natural substratum types.

The introduction of additional hard substratum can result in changes of the local community. Particularly in northern Europe studies on the impact of coastal defence structures are rare – especially studies on fish and macro-crustaceans. Only a few studies have investigated the impact of freshly introduced coastal defence structures and even fewer studies sampled data before the introduction. A further lack of information concerns the range of the possible impact. This study aimed to gain knowledge about the spatial extends of the impact of introduced artificial structures in the surrounding habitat and its demersal fish and decapod crustaceans community.

Temporal distribution

It is well known that factors like seasons, light, temperatures, food supply, competition and life cycles influence the occurrence of almost all species. The establishment of

long-term studies is necessary to reveal temporal occurrences of species and is helpful to obtain more detailed information about life cycles, behaviour strategies and the biology of species over the seasons. Therefore field observations were carried out during the complete study time. This was done in an attempt to get information on the temporal dynamics of the fish and macro-crustacean community over the seasonal cycle. The sampling was implemented monthly year round even in the winter months as long as safety for the divers was guaranteed. An associated diploma study (Seidler 2012) offered the opportunity to extend the normal sampling procedure for additional samplings during twilight phases to reveal information about possible diurnal pattern of the main fish and crustacean species within the tetrapods. The analysis of the data is still in progress, but first results are presented in the general discussion.

OUTLINE

This thesis consists of a general introduction, three chapters (representing one manuscript each) and a general discussion.

CHAPTER I

Manuscript published in *Helgoland Marine Research*

Stephanie Wehkamp and Philipp Fischer (2012)

Impact of hard-bottom substrata on the small-scale distribution of fish and decapods in shallow subtidal temperate waters

This manuscript provides an insight into the small-scale distribution patterns of local fish and macro-crustaceans in a sublittoral hard-bottom environment in relation to substratum types (rock, cobbles and large pebbles) and the density of algae. Using counting stations along line-transects, the *in situ* fish and crustacean abundances were assessed. The effects of the different substratum types on the demersal fish and decapod crustacean assemblage is discussed in general and furthermore in a species-specific manner.

The planning, evaluation and manuscript writing was carried out by Stephanie Wehkamp under the guidance of Philipp Fischer. Stephanie Wehkamp performed the fieldwork with the assistance of the scientific diving group of the Center for Scientific Diving (mainly Antje Klawon and Matthias Wehkamp) AWI, BAH.

CHAPTER II

Manuscript submitted to *Marine Ecology Progress Series*

Stephanie Wehkamp and Philipp Fischer (2012)

Impact of coastal defence structures (tetrapods) on a demersal hard-bottom fish community in the southern North Sea

This manuscript reveals the impact of typically used breakwaters (tetrapods) on the demersal fish community in a hard-bottom area in the southern North Sea. Using experimentally introduced tetrapod fields, the changes in the demersal fish community before and after the introduction of the artificial structures were studied. Possible

reasons for findings in differences of the fish abundances and community structure between the natural substrate and the tetrapods are discussed in detail.

The planning, the analysis of the data and manuscript writing was carried out by Stephanie Wehkamp under the guidance of Philipp Fischer. Stephanie Wehkamp performed the fieldwork with the assistance of the scientific diving group of the Center for Scientific Diving (mainly Suse Homagk, Christoph Walcher and Matthias Wehkamp) AWI, BAH. The study was done in the frame of the project MarGate.

CHAPTER III

Manuscript will be submitted to *Marine Biology*

Stephanie Wehkamp and Philipp Fischer (2012)

Impact of introduced artificial structures (tetrapods) on decapod crustaceans in the southern North Sea

This manuscript reveals impacts on decapod crustaceans, which were possible caused by the establishment of artificially, introduced structures. Furthermore, this study highlights the importance of long-term studies to distinguish between short-term impacts caused by natural variability (e.g. life cycles for species) and long-term impacts caused by anthropogenic influence (e.g. through the establishment of artificial substratum) on the species community.

The planning, the analysis of the data and manuscript writing was carried out by Stephanie Wehkamp under the guidance of Philipp Fischer. Stephanie Wehkamp performed the fieldwork with the assistance of the scientific diving group of the Center for Scientific Diving (mainly Suse Homagk, Christoph Walcher and Matthias Wehkamp) AWI, BAH. The study was done in the frame of the project MarGate.

CHAPTER I

Impact of hard-bottom substrata on the small-scale distribution of fish and decapods in shallow subtidal temperate waters

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ABSTRACT

The micro-scale spatial distribution patterns of a demersal fish and decapod crustacean assemblage were assessed in a hard-bottom kelp environment in the southern North Sea. Using quadrats along line-transects, we assessed the *in situ* fish and crustacean abundance in relation to substratum types (rock, cobbles and large pebbles) and the density of algae. Six fish and four crustacean species were abundant, with *Ctenolabrus rupestris* clearly dominating the fish community and *Galathea squamifera* dominating the crustacean community. Differences in the substratum types had an even stronger effect on the micro-scale distribution than the density of the dominating algae species. Kelp had a negative effect on the fish abundances, with significantly lower average densities in kelp beds compared with adjacent open areas. Averaged over all of the substrata, the most attractive substratum for the fish was large pebbles. In contrast, crustaceans did not show a specific substratum affinity. The results clearly indicate that, similar to other complex systems, significant micro-scale species-habitat associations occur in northern hard-bottom environments. However, because of the frequently harsh environmental conditions, these habitats are mainly sampled from ships with sampling gear, and the resulting data cannot be used to resolve small-scale species-habitat associations. A detailed substratum classification and community assessment, often only possible using SCUBA diving, is therefore important to reach a better understanding of the functional relationships between species and their environment in northern temperate waters, knowledge that is very important with respect to the increasing environmental pressure caused by global climate change.

Keywords Micro-scale, Substratum, North Sea, Cryptobenthic, Sublittoral, SCUBA, Kelp

INTRODUCTION

It is well known that substratum characteristics play an important role in the temporal and spatial distribution of benthic and demersal fish (Gotceitas et al. 1995, Fischer & Eckmann 1997b, a, Anderson & Millar 2004, Stal et al. 2007, Damalas et al. 2010) and crustacean species (Simoes et al. 2001, Jackson et al. 2006, Pallas et al. 2006). Species-habitat interactions affect communities on a large-scale (among habitats including sandy flats, rocky shores or seagrass beds) but also within small-scale microhabitat ranges (e.g., within a specific reef structure or stone formation; Gotceitas et al. 1995, Fraser et al. 1996, Jackson et al. 2006, Pallas et al. 2006, Scharf et al. 2006) and some processes can only act at small scales and other only at large scales (Underwood & Chapman 1996). To understand why a certain species does or does not settle in a certain area at a certain time, it is crucial to unravel the associations between the individual species and the detailed habitat parameters to elucidate which habitat features are relevant for a positive settlement decision of the individual species (Robinson & Tully 2000b, Pardo et al. 2007, Moore et al. 2010). A basic problem in the assessment of such functional relationships on microhabitat scales, however, is the often overly large scale of the sampling units (Garcia-Charton & Ruzafa 1998, Fischer et al. 2007, Sayer & Poonian 2007), especially in studies using classical time- or space-integrative methods, such as dredges or fyke nets. Using these methods, a characterisation of substratum types is often completed only on a very broad range, such as *Posidonia* beds, rocky or sandy bottom or artificial habitats (Stal et al. 2007, Hunter & Sayer 2009, La Mesa et al. 2011).

Several studies, however, have proven that even within areas commonly characterised as uniform habitats, fish and macro-crustaceans are not distributed at random but rather strictly following the micro-scale occurrences of specific habitat patterns that occur at scales sometimes even smaller than the organisms themselves (Gotceitas et al. 1995, Fraser et al. 1996, La Mesa et al. 2006, Chatfield et al. 2010). Chatfield et al. (2010) recently hypothesised that for a thorough explanation of fish distributions and a deeper functional understanding of why certain fish species are found where they are, a much finer substratum classification is necessary than that normally produced in field studies. Most of the studies with a sufficient spatial resolution have been conducted on species associations in warm or temperate areas and on suprabenthic fish species (Anderson & Millar 2004, Morton & Gladstone 2011). In contrast, only few researchers have studied

the fish-habitat relationships of sublittoral cryptobenthic fish assemblages in northern boreal rocky, hard-bottom systems (La Mesa et al. 2006), although this type of substratum forms a main part of the substratum of many northern coasts. Most of the fish communities of these habitats contain a large fraction of cryptobenthic fish, which are small and spend most of their time closely associated with the bottom substrate. Because these small fish are often highly vulnerable to predation by larger fish, the cryptobenthic species are typically heavily camouflaged and often dwell in complex, hard-bottom structures that are proportional to their own body size. For these species, the depth and bottom slope, for example, can be considered as macro-scale habitat features, while relevant micro-scale substratum characteristics may include the proportion of the substratum with larger stones or the complexity and heterogeneity of a rocky substratum itself (La Mesa et al. 2006). Robinson and Tully (2000) stated the same finding for macro-crustacean species. These authors found that variations in the physical complexity of the substratum and other habitat characteristics significantly affect the small-scale spatial distribution of decapod species and the decapod age structure in a certain area. Pallas et al. (2006) even suggest that the variability in spatial patterns of decapod crustaceans on rocky bottoms is primarily related to substratum type and geographical location. However, most of these studies have considered invertebrate communities in the more-accessible intertidal area or have investigated sessile and less-mobile organisms (Fraschetti et al. 2005, Reichert et al. 2008), and only few studies have dealt with the subtidal community in northern areas to date.

In this study, we therefore focussed on the temporal and spatial distribution patterns of the sublittoral demersal fish and decapod macro-crustacean community in a northern hard-bottom system of Helgoland in the southern North Sea (54°11' N, 07°52' E). The island Helgoland is well known for its complex hard-bottom substratum characteristics and extensive sublittoral kelp forests (De Kluijver 1991). A systematic study of the sublittoral fish community around Helgoland was completed by Krüß (1988), who investigated the biology of the common benthic fish species at different sampling stations. He discussed the spatial distribution of different fish species with respect to substratum types and proposed that some of the species showed significant preferences for specific habitat characteristics. De Kluijver (1991) and Reichert et al. (2008) investigated the spatial patterns of the sublittoral and intertidal benthic community around Helgoland but focussed on sessile organisms. Unfortunately, only a few of these studies (De Kluijver 1991, Harms 1993) included the mobile macro-fauna, and none of

the researchers analysed the species-substratum associations of vagile organisms on a quantitative level.

To address this lack of knowledge regarding the mobile macro-fauna of one of the most important nature reserve areas in the southern North Sea, we examined the micro-spatial distribution patterns of fish and crustacean species with respect to substratum characteristics.

The study was conducted at a typical sublittoral kelp site in approximately 5-m of water depth. The species were counted along line-transects and the substratum was classified into three different types (rock, cobbles and large pebbles). Using these data, we tested the null hypothesis that the fish and macro-crustacean species in the area are distributed independently on a particular hard-bottom substratum type.

MATERIALS AND METHODS

Study site

Helgoland island is located in the southern North Sea (German Bight) at 54°11'N and 7°55'E, approximately 50 km off the German coastline. The island is the tip of a 35-km^2 subtidal rock formation located in the southern part of the soft-bottom-dominated North Sea. This sedimentological particularity has led to a geologically and ecologically isolation from similar hard-bottom areas, the closest of which occur in Norway and Britain (Franke & Gutow 2004). Since 1981, about 5.138 ha of the rocky area around Helgoland, the "Helgoländer Felssockel" has been classified as a nature reserve through the federal state Schleswig-Holstein. The influence through fishing activity is limited because fishing is allowed only for professional Helgoland fishermen with standing gear like weirs or pots but no trawling or gill-netting is allowed. Fisheries activity in general is limited to catches of lobster and edible crabs for the gastronomy whereas catch rates for the endangered lobster (*Homarus gammarus*) are given.

The dominating types of substrata around Helgoland are red sandstone and limestone (De Kluijver 1991). Additionally – especially in the deeper northeasterly direction – fields of pebbles (debris of red sandstone, chalkstone and rock) exist. During the summer, a considerable portion of the sublittoral region to approximately 4-m of depth is dominated by dense growth of brown algae (*Laminaria hyperborea*), with single individuals reaching depths down to 8-m (Lüning 1970). The study site was located to the north of the island, approximately 400 m away from the coastline. In about 5-m water depth by mean low-water spring (MLWS) after hydrographic chart, three experimental sites were established parallel to the shoreline (Fig. 1). The seabed of the study area is almost flat with a slight increase of the depth in the northeasterly direction and a slight decrease in the southwesterly direction towards the coastline. The average local tidal range is about 2.5 m. During the study time the lowest tidal range was 2.18 m in June and the highest tidal range was reached with 3.01 m in September.
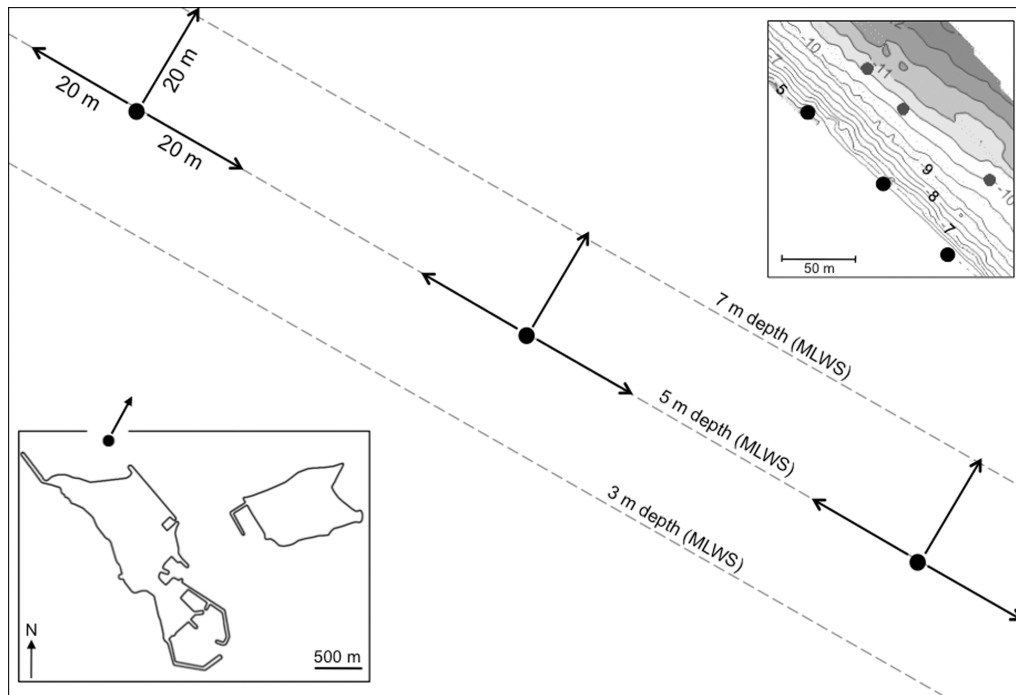
Fig. 1 The study area, approximately 400 m north of Helgoland's coastline. At each of the three sites, in 5-m water depth by mean low-water spring (MLWS), the sampling was performed through SCUBA diving on a monthly basis using quadrats (1 x 1 m) along three 20-m-long transect-lines. Depth data provided by Klaus Ricklefs (FTZ, Kiel)

Survey methods

Fish and crustaceans

This study was set within the frame of a major project with specific guidelines for the experimental design. To ensure high safety for the divers and enough time under water for a solid data sampling we decided to fix the line-transects. The positions of the counting stations were marked on the transect-lines. Possible risks for divers can exist through strong tide currents or bad visibility especially after storm events.

At each site, three 20-m-long line-transects were sampled from June to September 2009 on a monthly basis using SCUBA-supported line-transect counting (Fig. 1). Sampling was conducted at 0 m, 5 m, 10 m, 15 m and 20 m along each line-transect. At each of the station two square-metres were sampled within a virtual square-metre quadrat to the left and another square-metre quadrat to the right of the transect-line.

Unfortunately, the diver could not finish the counting at some occasions because of extremely bad visibility or swell induced seasickness under water and we missed a total of 32 m^2 so that a total of only 328 m^2 were available at the end of the study instead of possible 360 m^2.

To determine the quadrat size under water, the diver used a 1-m-long PVC pipe. Approaching the counting station, the diver began by counting the fish above the substrate up to eye level and then, when positioned in front of the counting area, counting the benthic species. In a last step, the stones measuring up to 10 cm were turned carefully to look for hidden organisms (Beldade & Goncalves 2007). Because the area is subject to severe and frequent storm events with significant substratum disturbance also of larger stones and cobbles on a regular basis, this procedure can be assumed as a comparatively minor impact and disturbance to the species compared to normal disturbances because of weather conditions.

To standardise the counting and to eliminate differences in the sampling technique, the same diver made the observations throughout the survey period (Sayer et al. 1993, Magill & Sayer 2002). All of the samplings were conducted between 10 a.m. and 2 p.m. to reduce the possible effects of diel activity. The field campaigns were conducted between the 14th and 30th of June, the 15th and 21st of July, the 3rd and 8th of August and the 8th and 18th of September 2009.

Substratum classification

Following the dieback of *L. hyperborea* in October, we assessed the natural bare substratum in the counting quadrats along the line-transects. A photo frame of 50 x 50 cm was placed at each counting station randomly and 16 photos (12.5 x 12.5 cm) of the substratum were taken with a digital camera (Olympus µ 1030 SW waterproof). Based on the Udden-Wentworth grain-size scale (Wentworth 1922), the substratum of each photo was classified by four independent observers into one of the three substratum categories – rock (smooth rock with few irregularities, sometimes covered with sand or fine gravel), cobbles (rock with cobbles of approximately 65 - 250 mm) and large pebbles (pebbles between approximately 15 - 65 mm in between fine gravel) (Fig. 2) – depending on the dominant substratum category found in the 12.5 x 12.5 cm square. The predominant substratum type of each station was defined by using the modal value of the 16 substrata determinations within the photo frame.
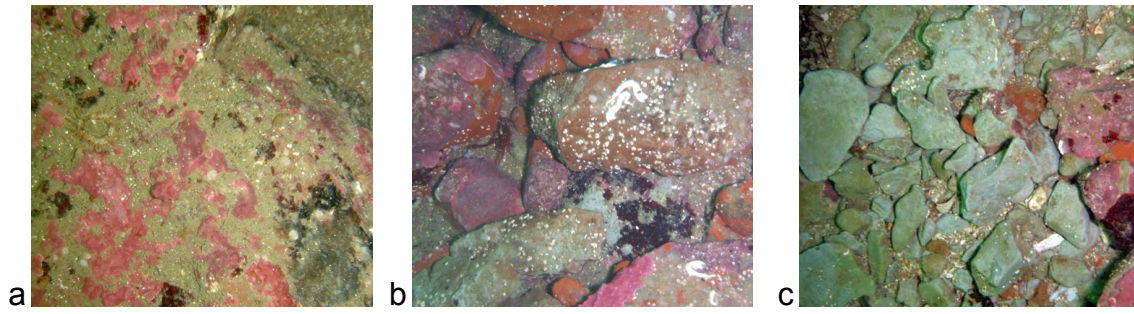
Fig. 2 The three substratum categories in the study area. **a** Rock (smooth rock with few irregularities, sometimes covered with sand or fine gravel), **b** cobbles (rock with cobbles between approximately 65 - 250 mm), **c** large pebbles (pebbles between approximately 15 - 65 mm, in between fine gravel). The viewed photo frame originally measured 12.5 x 12.5 cm

Algae

In addition to the substratum types we analysed the algal growth along the line-transects for each counting station and the corresponding substrata characteristics. The density of *Laminaria* and red algae was calculated for every month. For the brown algae *L. hyperborea*, the stipe density was determined on an ordinal level. We classified a density of 20 - 50 *Laminaria* m^{-2} as "dense", 5 - 20 *Laminaria* m^{-2} as "present" and <5 *Laminaria* m^{-2} as "sparse". Additionally, the coverage by bushy or branched red algae, such as *Delesseria sanguinea*, *Membranoptera alata*, *Cystoclonium purpureum*, *Plocamium cartilagineum* and species of the genus *Polysiphonia*, was classified as "present" (dense growth, covering over 50 % of a counting station) or "absent" (no or only sparse algal growth). No further discrimination among different species was made. For the different substratum types we calculated which algal density occurred mainly at each sampling station (Table 1).

Abiotic factors

The water temperature was measured continuously at the "Kabeltonne" site (54°11.3′ N, 7°54.0′ E) within the frame of the Helgoland Roads time series (Wiltshire et al. 2008, Wiltshire et al. 2010) nearby the study side. We calculated the average temperatures for the sampling period for each month using the mean value of all sampling days in the specific month. To quantify the transparency of the water in metres during the transect counting, a Secchi disc was fixed at the starting position of the southern-most transect in the horizontal direction, and the horizontal Secchi distance was measured by the

diver. The observations were completed only when the horizontal Secchi distance was at least 1 m. Furthermore, the dive time, tides and special observations were recorded during each sampling.

Data analysis

All of the visible benthic and suprabenthic fish and decapod crustaceans were identified to the species level if possible. We determined benthic gobies as *Pomatoschistus minutus*. This classification was made because catch data of benthic gobies around Helgoland (Hielscher 2012, pers. comm.) indicate that the majority of the gobies in this area belong to this species. Because the species identification of gobies in the field is almost impossible, we accepted the risk that some *Pomatoschistus microps*, especially smaller individuals, were included accidentally.

Statistical analyses

To first discriminate the seasonal and substratum effects on the overall abundances of the fish and crustaceans, a two-way ANOVA mixed model for repeated measures (month) based on the number of fish m^{-2} was applied, with a subsequent Bonferroni-corrected post-hoc test. The homogeneity of variance of the data was tested using the Bartlett test.

To detect a possible impact of the algal density on the fish and crustacean abundances over the months and as well over the substratum types an ANCOVA was applied whereas the algal density was used as co-variable.

For a detailed analysis of the effects of the different substratum types on the fish and crustacean abundances, the absolute abundance data – individual number per square metre (ind. m^{-2}) – were converted into a percentage of occurrences per substratum type. For this calculation, all of the fish that were counted in a single month (e.g., July) were summed up and were taken as 100 %. Then, the percentage of the occurrence of each species in each of the types of substratum was calculated for each month separately. The effects of the different substrata on the fish and crustacean occurrence were then tested using the non-parametric Friedman test procedure, with a subsequent non-parametric Nemenyi post-hoc test. All of the statistical analyses were performed using a significance level of $\alpha = 0.05$.

The effects of the different substratum types on the individual species were analysed in detail. For this calculation, we also used the distribution (as a percentage) of the

individual fish and crustacean species among the three substratum categories separately for each month. This analysis was conducted for the six most abundant fish species (the species with a total count of more than 20 over the season) and for the four most abundant crustacean species (the species with a total count of more than 100 over the season).

RESULTS

Water temperature

The average on-site water temperature during the sampling period showed a typical bell-shaped curve, with a mean value of 14.03 °C (SD 1.4) over the sampling days in June, 16.70 °C (SD 0.2) in July, a maximal value of 18.05 °C (SD 0.4) in August and slightly lower values of 17.43 °C (SD 0.4) in September (Fig. 3).

Substratum types and algae

Substratum type

Of the 41 sampling stations eight were classified as substratum type rock, 13 stations as cobbles and 20 stations as large pebbles. All substratum types were found at each site and every transect direction whereas the category large pebbles was predominant in the northeasterly direction.

Laminaria hyperborea

A dense (20 - 50 m^{-2}) substratum coverage of large kelp (mainly *L. hyperborea*) was observed in June, July and August in the categories cobbles and rock (Table 1). The growth of kelp in the area was generally closely associated to these two substratum categories, and no or only few kelp plants were found on the substratum category large pebbles at any time (Table 1). In September, the kelp died back in the entire area, dropping quickly to a level of only few to no plants m^{-2}.

In terms of structural complexity, *L. hyperborea* reached its maximum stipe length (>50 cm) in June to August, with an overall height of the entire plant of approximately 2 – 3 m. In June and July, the leaves were broad and without fouling, and the stipes had a diameter up to 3 cm with complex and broad holdfasts. In September, the older plants began to collapse, and only the multiannual holdfasts, sometimes with the stipes, remained; thus, the structural complexity of the kelp habitat significantly decreased.

Over the months the *Laminaria* density showed no significant effect on the fish (ANCOVA, $F = 2.669$, $df = 2$, $p = 0.0725$) or crustacean abundances (ANCOVA, $F = 0.73$, $df = 2$, $p = 0.484$). Because the substratum types influenced the fish abundances significantly (see below) we analysed a possible impact of the *Laminaria* density over the different substratum types. The density of *Laminaria* is negatively

correlated to the fish abundances (ANCOVA, $F = 4.898$, $df = 2$, $p = 0.0086$) and the substratum large pebbles with the lowest density of *Laminaria* contained the most fish.

Red algae

Following the same pattern as the kelp, a dense growth of bushy or branched red algae was observed on the rocky and cobble substratum in June to August, while no or sparse growth was found in the substratum large pebbles (Table 1). In contrast to the kelp pattern, red algae plants remained present in September on the category rock, whereas in the areas with cobbles and large pebbles, only sparse or no red algae were found.

The density of red algae had no significant effect on the fish (ANCOVA, $F = 0.287$, $df = 1$, $p = 0.593$) and crustacean (ANCOVA, $F = 0.294$, $df = 1$, $p = 0.589$) abundances over the months. Furthermore no effect of red algae was observed over the substratum types on fish abundances (ANCOVA, $F = 0.577$, $df = 1$, $p = 0.4487$).

Table 1 Density of *Laminaria hyperborea* (left side of the table) over the study time: ++ stands for *dense*, with $20 - 50$ *Laminaria* m^{-2}; + stands for *present*, with $5 - 20$ *Laminaria* m^{-2} and 0 stands for *sparse*, with only $0 - 5$ *Laminaria* m^{-2}. The growth of bushy or branched red algae (right side of the table) over the study time was reported as + for present (dense growth, covering a main part of the substratum) and 0 for absent (no or only sparse algal growth)

Laminaria hyperborea	Rock	Cobbles	Large pebbles	Red algae	Rock	Cobbles	Large pebbles
June	++	++	0	June	+	+	0
July	++	++	0	July	+	+	0
Aug	++	++	0	Aug	+	+	0
Sept	0	0	0	Sept	+	0	0

Fish and crustacean abundances

A total of 510 fish and 2708 macro-crustaceans were counted over the entire sampling period. With a total of 328 quadrats (1 x 1 m) analysed, a mean fish density of 1.55 ind. m^{-2} (SD 1.0) and a mean crab density of 8.26 ind. m^{-2} (SD 3.6) was calculated, averaged throughout the entire study.

When analysing the temporal (month) and spatial (substratum categories) effects in detail, a significant increase in the fish and crustacean abundances was observed over the months, with the highest average values of 2.79 (SD 1.9) fish m^{-2} (ANOVA, $F = 19.83$, $df = 3$, $p < 0.0001$) and 12.84 (SD 5.5) crustaceans m^{-2} (ANOVA, $F = 42.57$, $df = 3$, $p < 0.0001$) in September, over all of the substrate categories.

The fish were significantly more abundant in the large pebbles substratum to cobbles and rock (Fig. 3a, ANOVA, $F = 5.41$, $df = 2$, $p = 0.008$), and this effect was most prominent in September (Bonferroni post-hoc test: $p < 0.01$, Fig. 3a). Summarised over all of the months, the large pebbles region contained 42.3 % (SD 2.2) of the total fish abundances and therefore significantly more fish (Nemenyi post-hoc test, $k = 2$, $p = 0.05$) than the cobble substratum (27.2 %, SD 3.0). In terms of the fish abundances, the rocky substratum (30.5 %, SD 1.8) contained intermediate values and did not significantly differ from either of the other substratum types (Fig. 4a).

In contrast, for the overall crustacean abundances, no significant substratum effect could be found (Fig. 3b, ANOVA, $F = 0.93$, $df = 2$, $p = 0.4015$). The highest percentages of crustaceans were counted in the category cobbles (36.64 %, SD 2.3), followed by large pebbles (34.82 %, SD 4.6) and rock (28.54 %, SD 3.9; Fig. 4b).
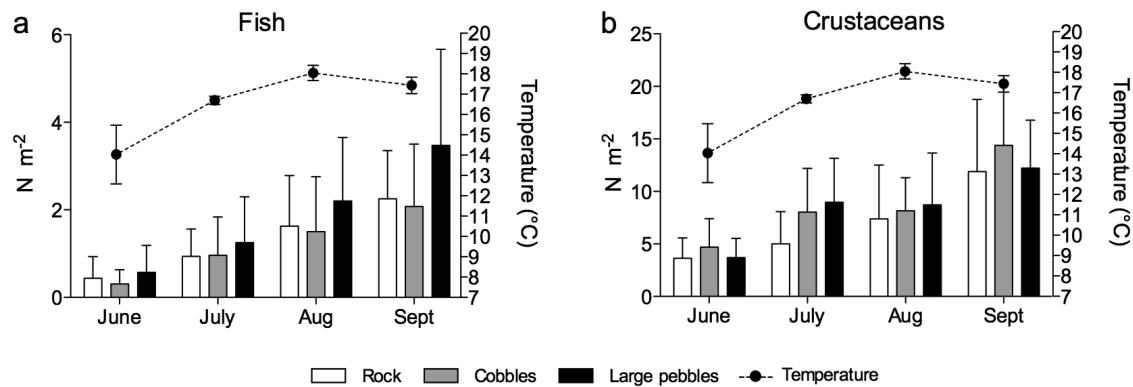

Fig. 3 The average temperature in °C (right y-axis) over the sampled days in the studied months and the fish (**a**) and crustacean (**b**) abundances m^{-2} (mean and SD) over the sampling period in the three substrate categories, rock, cobbles and large pebbles
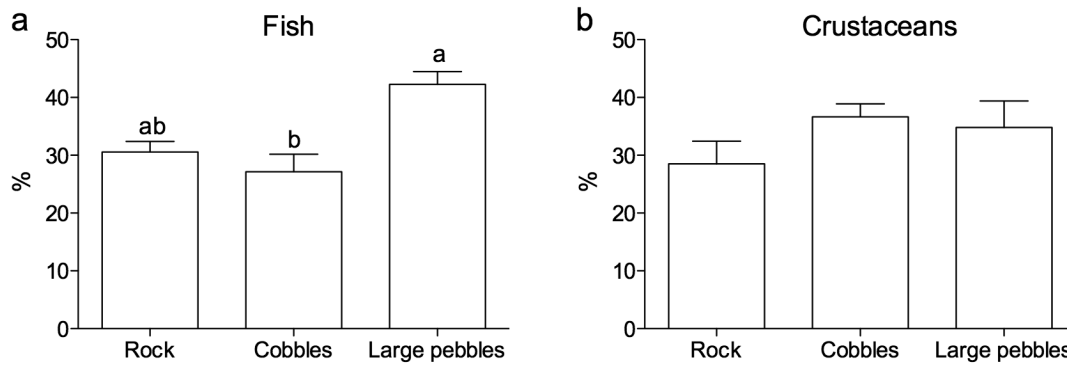
Fig. 4 The distribution of the fish (**a**) and crustaceans (**b**) over all months among the three substratum categories. The presence of different letters above the bars indicates significant differences among the substratum categories

Species-specific distribution

Ctenolabrus rupestris

The goldsinny (*C. rupestris*) was the most abundant fish species in the area, with an average abundance of 0.5 ind. m^{-2} (SD 0.2). The goldsinnies were almost equally distributed throughout all of the three substratum categories, with 37 %, 33 % and 30 % of their occurrence in the categories rock, cobbles and large pebbles, respectively (Fig. 5a). Most of the goldsinnies were counted in August and September, followed by July and June (Fig. 6a).

Pholis gunnellus

With an average abundance of only 0.24 ind. m^{-2} (0.1 SD), benthic gunnels (*P. gunnellus*) were clearly less abundant than goldsinnies, even though gunnels were the second most abundant species in the sampling area. Contrary to the suprabenthic goldsinny, *P. gunnellus* showed a distinct substratum affinity, with 50 % of the total number of sightings in large pebbles and only 31 % and 22 % of the gunnels found in the substratum categories cobbles and rock (Fig. 5a). The high appearance in large pebbles was present in all of the months except June (Fig. 6a).

Taurulus bubalis

The long-spined sea scorpion (*T. bubalis*) was found in all of the substratum categories (Fig. 6a), with an average density of 0.19 ind. m^{-2} (SD 0.1), but was mostly found in the substratum large pebbles (44 % of the total number of sightings). Only 29 % of the fish were observed on the rocky substratum, and 27 % were found on the cobble substratum

(Fig. 5a). However, both the substratum associations as well as the abundances of *T. bubalis* strongly varied among the months (Fig. 6a).

Pomatoschistus minutus

The sand goby (*P. minutus*) (0.19 ind. m^{-2}, SD 0.2) was almost as abundant as the long-spined sea scorpion and *P. minutus* was observed mainly in the substratum large pebbles (Fig. 5a). A total of 72 % of the sand gobies was observed in this substratum type, while only 17 % of the total number of this species was found in rocky habitats, and 11 % was found in cobbles (Fig. 5a). *P. minutus* revealed a distinct seasonality, with no or only rare specimen observations in June and July and significantly higher mean abundances in August and September (Fig. 6a).

Callionymus lyra

We found only females or immature males of *C. lyra* (Wheeler 1978), with an average size of approximately 8 – 10 cm and a density of 0.17 ind. m^{-2} (SD 0.2) (Fig. 5a). The dragonet was equally found in the substrata large pebbles (48 %) and rock (41 %) but only 11 % occurred in the substratum type cobbles (Fig. 5a). The dragonets showed the strongest seasonality during the sampling period; virtually the only times dragonets were observed was in August and September (Fig. 6a).

Gobiusculus flavescens

The two-spotted goby (*G. flavescens*) was mainly present in September (Fig. 6a). During September, the gobies occurred with an average abundance of 0.15 ind. m^{-2} (SD 0.2) and were mainly distributed in the substrata cobbles (49 %) and large pebbles (47 %) but were only sparse in rocky areas (4 %; Fig. 5a).

Additional fish species

Besides the species described above, six other species that were less abundant were observed in the area. These species were *Spinachia spinachia* (n = 2 over the entire sampling period), *Ciliata mustela* (n = 1), *Entelurus aequoreus* (n = 1), *Myoxocephalus scorpius* (n = 4), *Liparis* spp. (n = 13) and *Zoarces viviparus* (n = 14). Because these species were only sighted occasionally, it was not possible to establish a reliable species-substratum association.

Galathea squamifera

The squat lobster (*G. squamifera*) was by far the most abundant crustacean species, with an average of 5.2 ind. m^{-2} (SD 2.3), and was more or less equally distributed over all of the substrata, with 30 % of the sightings in rock, 39 % in cobbles and 31 % in large pebbles (Fig. 5b). *G. squamifera* was observed in all of the months but showed a slight seasonality, with the highest occurrence in September (Fig. 6b).

Pisidia longicornis

With an average abundance of 1.9 ind. m^{-2} (SD 1.1), the long-clawed porcelain crab (*P. longicornis*) was the second most abundant crustacean species (Fig. 5b) and 49 % of the members of this species were observed in the category large pebbles. This species was also sighted in the category rock (23 % of the sightings) and in cobbles (28 %) (Fig. 5b). Like the squat lobster, this species was most abundant in September, followed by August and July. In June, only a few members of this species were found (Fig. 6b).

Cancer pagurus

The edible crab (*C. pagurus*) was the third most abundant crustacean species, with an average abundance of 0.6 ind. m^{-2} (SD 0.1). Similar to the squat lobster (*G. squamifera*), the edible crab was found equally distributed in the substrata of cobbles (39 %), rock (29 %) and large pebbles (32 %) (Fig. 5b). *C. pagurus* was observed in all of the months, with slightly higher abundances in August and September compared with June and July (Fig. 6b).

Pilumnus hirtellus

The hairy crab (*P. hirtellus*) was found in an average abundance of 0.4 ind. m^{-2} (SD 0.1) and showed the strongest substratum affinity, with 51 % of the individuals found in the cobble substratum followed by the rock category (31 %) (Fig. 5b). The substrate large pebbles contained only 18 % of the observed members of this comparatively small species. The presence in the category cobbles was obvious in all of the months, except for September, when the hairy crab was mostly seen in the substratum rock (Fig. 6b). *P. hirtellus* showed no clear seasonality but was mainly seen in September, followed by July.

Additional crustacean species

In addition to the four decapod species described above, the following crustaceans were observed in lower numbers over the sampling period: *Necora puber* (n = 17), *Liocarcinus* spp. (n = 12), *Pagurus* spp. (n = 8), *Carcinus maenas* (n = 4) and *Homarus gammarus* (n = 2). Because these species were sighted only occasionally, it was not possible to establish a reliable species - substratum association.
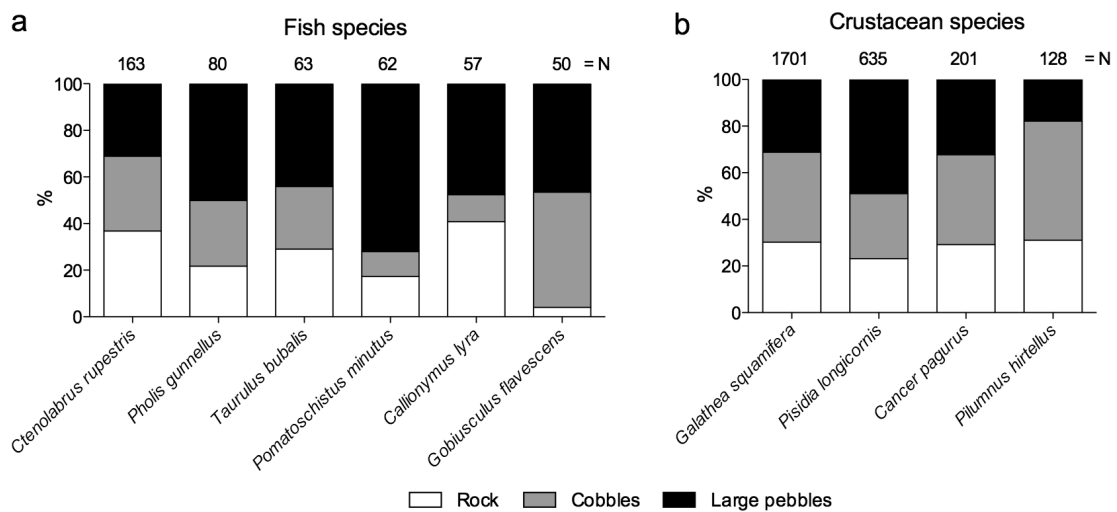

Fig. 5 Relative distributions of the six most abundant fish species (**a**) and the four most abundant crustacean species (**b**) with respect to the three substratum categories, rock, cobbles and large pebbles. The numbers above the bars represent the absolute counts of the different species over the sampling period
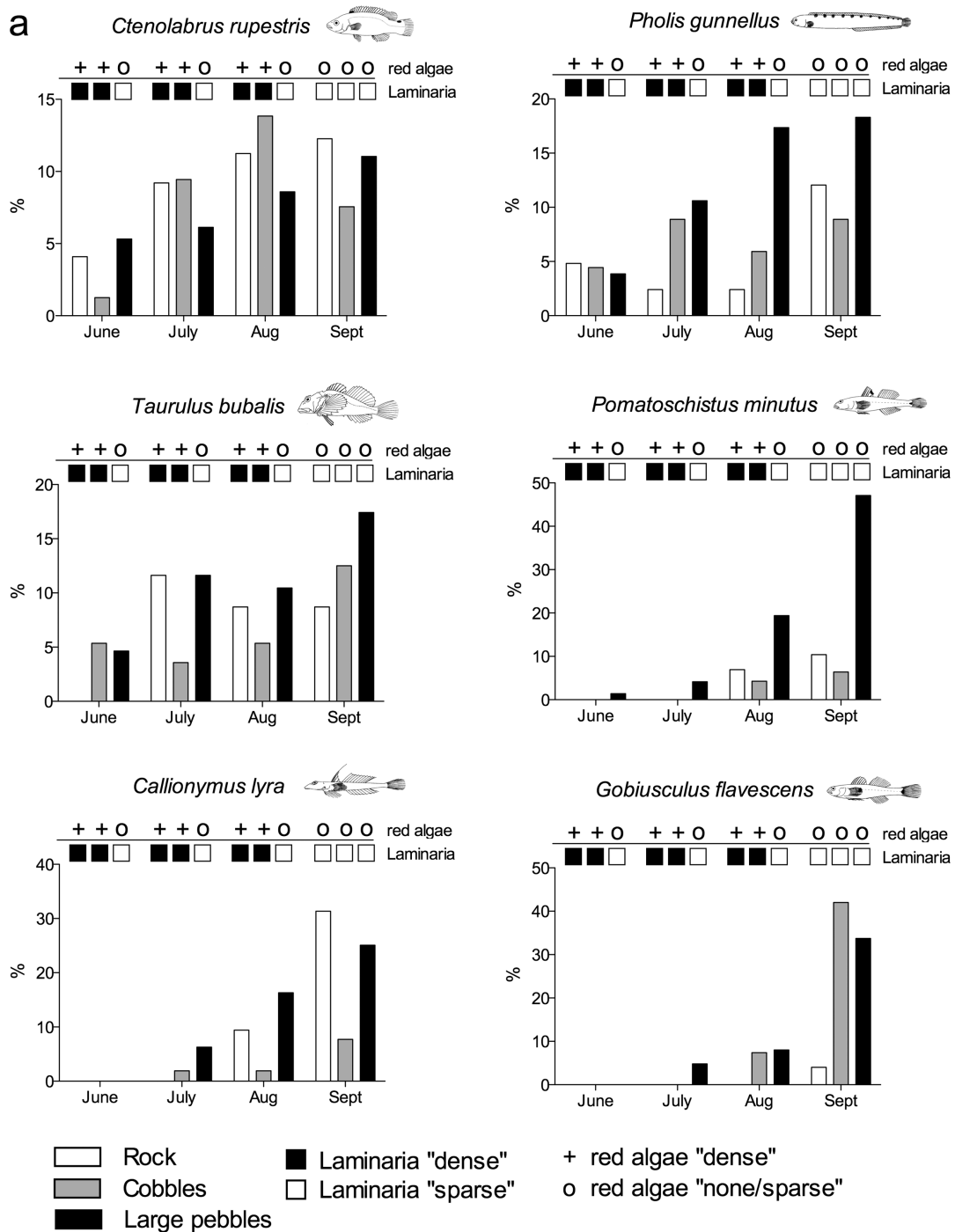
Fig. 6a Relative abundances for the six most abundant fish species in the three substrate categories over the whole sampling time. Additionally, the ordinal-scaled densities of the brown and red algae are given as present (+) or absent (o) for red algae and the density of *Laminaria* for every month in the substrate categories as "dense" (20 – 50 *Laminaria* m^{-2}) or "sparse" (0 – 5 *Laminaria* m^{-2}). The category "present" (5 – 20 *Laminaria* m^{-2}) was not found over the entire sampling period and was therefore excluded in the legend of the graph
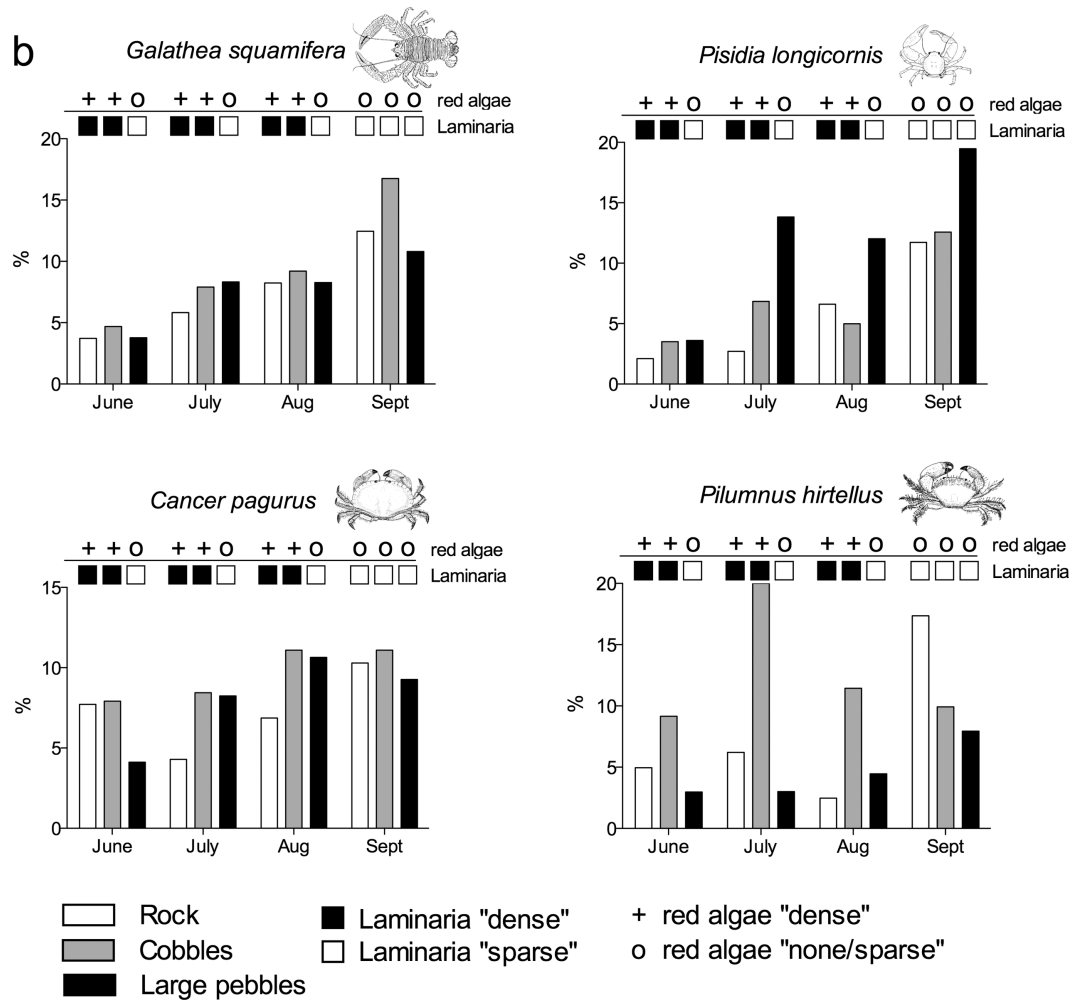
Fig. 6b Relative abundances for the four most abundant crustacean species (**b**) in the three substrate categories over the whole sampling time. Additionally, the ordinal-scaled densities of the brown and red algae are given as present (+) or absent (o) for red algae and the density of *Laminaria* for every month in the substrate categories as "dense" (20 – 50 *Laminaria* m^{-2}) or "sparse" (0 – 5 *Laminaria* m^{-2}). The category "present" (5 - 20 *Laminaria* m^{-2}) was not found over the entire sampling period and was therefore excluded in the legend of the graph

DISCUSSION

Different authors have stressed that standard visual sampling is not adequate to identify and accurately census cryptobenthic fish and crustaceans because this method frequently leads to an underestimation of the number of individuals and species (Willis 2001, La Mesa et al. 2006). We agree with this hypothesis when visual sampling only includes swimming above the substrate over transects. Similar to Beldade & Goncalves (2007), we therefore strongly recommend to invest in dive time and to carefully turn individual stones, especially for micro-scale assessments of small-scale substratum characteristics with regard to the associated cryptobenthic well-camouflaged assemblage. Using this method, hidden species between and under stones can be often identified, generating a precision in species – habitat assessments that are often not achievable even with retrospective underwater photography or video documentation of a certain area (Ehrenberg & Ejdung 2008). Another method to increase the efficiency of fish counting is the use of anaesthetics (Sayer et al. 1994). Because the application of anaesthetics to relatively flat areas with some stone coverage is technically problematic, has an unknown impact on the community and does not provide significantly better results than a thorough line-transect count that includes turning stones (Beldade & Goncalves 2007), we selected the latter method as most suitable for our repetitive fish and decapod crustacean assessment.

However, it has to be noted that this method still provides an underestimation, especially of smaller crustaceans, such as *P. hirtellus* and *P. longicornis*, because they are highly camouflaged under stones and in niches and do vanish quickly when disturbed by the observer. Furthermore, other species, such as hermit crabs, are difficult to detect, and highly mobile swimming crabs could escape before being detected by the observer. Therefore, we assume that these species were probably more abundant than represented in our study area. The species may form an unknown part of a hidden community that is only detectable using additional destructive sampling methods, such as the random use of suction samplers (Robinson & Tully 2000b, Pallas et al. 2006).

Letourneur et al. (2003) and Moore et al. (2010) stated that individual environmental and biological factors on a fine-scale are most important for driving the distribution and abundance of a fish assemblage and that broad-scale habitat definitions are often not able to give precise information about the assemblage structure and occurrence of species. Our study clearly supports these findings and provides evidence that the

composition of the fish assemblage in the sublittoral hard-bottom kelp forests of Helgoland depends on much finer classifications than "hard-bottom" or "kelp forest". Only three out of a total of 12 species occurred in high abundances in the area over the entire sampling period (*C. rupestris, P. gunnellus* and *T. bubalis*), whereas the other species either occurred as temporally restricted (*C. lyra, G. flavescens* and *P. minutes*) or in very low numbers. However, all of the strictly benthic fish species, which occurred in high abundances so that an association to a certain habitat type was possible, revealed a distinct association to one of the three substratum categories. A similar dominance feature is common to many inshore and shallow rocky shore communities, with few species forming the largest part of the community (Magill & Sayer 2002, La Mesa et al. 2006, Wilhelmsson et al. 2006b). For the crustaceans, the spatial distribution was not as distinct as for the fish. However, four species still dominated the crustacean community, and one of the species (*G. squamifera*) was significantly more abundant than the other three species (*P. longicornis, C. pagurus* and *P. hirtellus*).

When analysing the functional relationships between species and their habitats, a distinct knowledge about the specific habitat requirements of a species is necessary (Gotceitas et al. 1995, Fraser et al. 1996, Letourneur et al. 2003, Chatfield et al. 2010). Our study indicates that the strength of the association of a certain fish species to a certain kind of substratum and therefore also the probability of the occurrence of a certain fish species or age class in a certain area is basically structured hierarchically with three levels: the general lifestyle of the fish species (e.g., benthic or semi-pelagic), the availability of a adequately sized shelter with respect to the size of the fish in a very narrow size scale and finally the colouration of the substrate, which must suit the camouflage colour of the fish.

Therefore, we follow La Mesa et al. (2006) who stated that, especially for cryptobenthic fish assemblages, habitat use can only be investigated on small mosaic-like scales. In addition to this, we suggest that the size of the target fish species should be used as a reference in order to determine the dimensions of the optimal sampling scale.

Interestingly, the most abundant species in our study, the suprabenthic goldsinny (*C. rupestris*), did not show a distinct substratum association. Sayer et al. (1993) suggest that the availability of the preferred refuge type is essential to determining goldsinny presence and report that water depths, macro algal cover and high current speeds did not affect adult goldsinny distribution when suitable refuges were present. In their study, refuges consisted predominantly of spaces between or under rocks and

boulders with multiple narrow entrances. This refuge type was often found in our study area, mainly in the natural categories rock and sometimes cobbles. In contrast, in our study, the goldsinnies were similarly abundant throughout all of the three natural categories, including the category large pebbles, a substratum type that is not typically associated with goldsinnies because hiding places are rare in this category. Hillden (1981) reported that *C. rupestris,* although strongly territorial, leaves its refuge for short excursions normally of less than a minute if, for example, an attractive food source is available outside. This behaviour possibly biased our results for the goldsinnies by attracting them to less suitable substratum types because the diver had turned a stone and therefore uncovered small crustaceans serving as an unexpected additional food source.

Another remarkable finding was that the young-of-the-year (age class 0+) goldsinnies did not show a distinct substratum association. The spawning season of *C. rupestris* in the study area is in May and June (Hillden 1981, Krüß 1988). This result is consistent with the sightings of pregnant goldsinnies between June and July and the occurrence of 0+ individuals in July and August, reaching a size (total length) of 2 - 3 cm (sometimes up to 5 cm) in September. These juveniles showed no clear association for any of the three natural substrata (pers. observation) but were mostly detected after turning stones and sometimes in combination with bushy red algae. Sayer et al. (1993) found no significant combination between algal cover and 0+ goldsinnies but also observed some individuals in or around macro-algae.

For the crustaceans, we found the smaller species *P. longicornis* and *P. hirtellus* mainly between and under stones in the categories large pebbles or cobbles. The larger species *C. pagurus* and *G. squamifera*, in contrast, were observed in similar distributions over all of the substratum categories and in all of the size classes. Therefore, we assume that the use of a certain substratum may depend on the size of the individual itself and its mobility. For example, *C. pagurus* is a highly mobile species, and larger individuals were counted when they were moving above the substrate, whereas smaller individuals were generally hidden under stones or buried in the sediment. Silva et al. (2010) found that larger individuals of *C. pagurus*, for example, migrate during high water to the intertidal zone to feed. It is possible that the abundance of prey organisms is more important than the availability of refuges for this robust and dominant species.

Larger *G. squamifera* were mostly found between niches and cavities of larger stones, whereas smaller individuals were hidden under pebbles or in small holes. These results

are in accord with the study of Pallas et al. (2006), who found that some larger decapod invertebrates modified their habitat preference during their life cycle to minimise the trade-off among different stress factors. For other species, like *P. longicornis* and *Pilumnus* spp., the authors found no spatial segregation between juvenile and adult phases.

In addition to the substratum characteristics, the macro-algal coverage in the area was also assessed. We postulate that we did not miss a significant number of individuals, except perhaps some juveniles when counting between the *Laminaria*, because most benthic fish do not flee, and the suprabenthic goldsinny (*C. rupestris*) showed a distinct inquisitive behaviour and even came nearby when the diver started to turn stones. Some decapod crustacean species were detected in other studies between the holdfasts of *L. hyperborea*, such as *P. hirtellus, P. longicornis, G. squamifera* and juvenile *C. pagurus*, but only in lower numbers, and these species do not form a large part of the associated *Laminaria* community (Schultze et al. 1990, Christie et al. 2003).

In general, many fish species seem to be associated with macro-algal vegetation (Schultze et al. 1990, Anderson & Underwood 1994, Pihl et al. 1994, Norderhaug et al. 2007, Chatfield et al. 2010). Pihl et al. (1994) found positive correlations between the fish biomass and total vegetation biomass in rocky-bottom habitats on the Swedish west coast but also found a negative impact on the fish diversity when the proportion of filamentous algae (mainly green algae) was high. The authors suggest that the change in the physical complexity of the vegetation cover is not ideal for some foraging species. La Mesa et al. (2006) found significant species-substratum (rock, stones or plateau) relationships on a small and intermediate scale (2 x 5 m), but at the level of microhabitat (a 30 x 30 cm area centred on the fish), the authors suggest that the investigated species were almost completely dependent on whether the substrate was either vegetated or composed of bare rock. Similarly, Chatfield et al. (2010) also found that although the substrate type was the most influential variable for species distribution, the depth and macro-algal type also influenced the occurrence of species over the correlating substrate types. Epiphytes can provide refuge for fish and crustaceans against predation and can also offer a variety of prey organisms for fish and crabs (Christie et al. 2003, Norderhaug et al. 2005). For example, kelp forests serve as heterogeneous habitat for a variety of species (Schultze et al. 1990, Christie et al. 2003, Norderhaug et al. 2005). However, in our study, both the fish and decapod crustaceans were negatively correlated with the kelp coverage, and most of the fish were counted in the substratum

large pebbles, where no or only sparse growth of *Laminaria hyperborea* as well as bushy red algae was observed. A similar finding was also reported by Wilhelmsson et al. (2006b), who found no correlation between main cold-water fish species, such as the goldsinny, and algae cover but did find a positive correlation between fish occurrence and the availability of suitable habitat features in the form of hiding places. Furthermore, some studies also suggest that some species do not prefer dense stands of submerged aquatic vegetation *per se* because of a reduced detection distance of approaching predators or a reduced foraging ability (Gorman et al. 2009, Thistle et al. 2010, Smith et al. 2011). Submerged aquatic vegetation areas may therefore serve more as a temporal refuge in case of a real predation risk or to temporally exploit the invertebrate food source (Norderhaug et al. 2005) that is often found between structurally complex holdfasts, e.g., those of kelp.

In addition to substratum type and macro-algal coverage, the temperature and life cycles also had an impact on the fish and crustacean abundances over the study time, with a peak in September in the overall abundance and species richness. Similar to other factors, including periodic changes in salinity or nutrients over time, temperature is assumed to have a temporally intermediate or longer-scale influence on the overall abundance but less influence on the small-scale distribution within substratum types. However, an interesting factor is the time of the day and the tides, which act within smaller temporal scales instead of spatial scales. Because tides may significantly affect the habitat quality because of the energetic cost to an organism to maintain its position, and the time of the day and illumination may significantly affect the availability of prey and the presence of potential predators (Magill & Sayer 2002, Bell & Turner 2003, Silva et al. 2010), these variables may significantly affect the results. However, because these variables interact strongly and may confound each other, separate studies with a carefully planned experimental design are necessary to discriminate among these variables.

This study was done in the only existing natural hard-bottom area of the southern North Sea where fishing activity in general is just a minor influence. Towed fishing is forbidden and furthermore not practicable because of the existing kelp density and stony substratum. Therefore the results of this study can be transferred for similar hard-bottom areas which occurs e.g. in Britain or Norway but not for the southern North Sea in general which is dominated by soft and sandy substratum and highly disturbed by fishing activity.

Conclusion

Our study revealed strong species – substratum relationships in the subtidal benthic fish community off Helgoland, in the southern North Sea, on a micro-scale level. In contrast, no distinct relationships were found for the decapod crustaceans. In both of the assemblages, a single species dominated the community in terms of abundance, whereas the other species occurred in lower abundances, were temporarily restricted or were only occasionally seen over the entire sampling period. Especially for the benthic fish, we hypothesised, that habitat selection is based on a three-level hierarchical system, with the general lifestyle of the species (benthic or semi-pelagic) forming the first level, the availability of an adequately sized shelter with respect to the size of the fish in a very narrow size scale forming the second level and the colouration of the substratum with respect to the camouflage colour of the fish as the third level.

Based on the results of this study, we postulate that diver-supported assessment methods are adequate for micro-scale fish-habitat studies in shallow-water areas. Because of the distinct size dependency of the fish and crustaceans, however, we recommend for future studies to discriminate among different age- or size-classes within the species. This specificity would facilitate an even more accurate analysis, allowing deeper insight into the functional relationship between species and their habitat and leading to a better understanding of why fish settle during a certain time at a certain place.

CHAPTER II

**Impact of coastal defence structures (tetrapods) on a demersal hard-bottom
fish community in the southern North Sea**

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ABSTRACT

In coming decades, artificial defence structures will increase in importance for the protection of coasts worldwide against the impacts of global warming. However, the ecological effects of such structures on the natural surroundings remain unclear. We investigated the impact of typically used breakwaters (tetrapods) on the demersal fish community in a hard-bottom area in the southern North Sea. Using experimentally introduced tetrapod fields, we studied the changes in the demersal fish community before and after the introduction of the artificial structures. The results clearly demonstrated a significant decrease in fish abundances in the surrounding area caused by migration effects towards the artificial structures. Additionally, a significant increase in young-of-the-year (YOY) fish was observed near the structures within the second year after their introduction. Diversity (HB) and evenness (E) values exhibited a larger variation after the introduction of the tetrapods. We suggest that the availability of additional refuges in combination with the additional food resources provided by the artificial structures has a highly species-specific attraction effect. However, our findings also demonstrate that our knowledge of the impact of artificial structures on sublittoral fish communities of boreal temperate coastal habitats is still too limited truly to understand the ecological processes that are initiated by the introduction of artificial structures. Long-term investigations are indispensable, and more experimental *in situ* work is necessary worldwide to understand the mechanisms by which coastal defence structures interact with the coastal environment.

Keywords Breakwaters, Coastal Protection, Artificial Structures, Climate Change, Sublittoral, Temperate Waters, North Sea, Demersal Fish

INTRODUCTION

In recent decades, global warming has resulted in changes in wind speed, wind direction and the frequency and intensity of strong storm events (Beaugrand 2004, Wiltshire et al. 2010). Additionally, glacier melting is predicted to cause a sea-level rise of approximately 70 cm by 2100 (IPCC 2007b, a, Hawkins et al. 2009). The consequences of these changes may involve the destruction of coastal areas, including existing natural barriers and the erosion of existing coastal protection measures through flooding and increasing high-wave action (Bacchiocchi & Airoldi 2003, Airoldi et al. 2005a, Moschella et al. 2005). Therefore, the establishment of additional coastal protection measures will be emphasised in coming decades to adapt to or minimise these effects (Bulleri & Chapman 2010, Chapman & Underwood 2011).

Until recently, most hard defence structures, such as concrete breakwaters and seawalls, have been placed directly in the intertidal area in front of the exposed coastline as a coastal stabilisation measure. However, such structures are now introduced more often also in the subtidal area at a distance from the coastline to absorb and dissipate wave energy (Charlier et al. 2005). This development in coastal protection strategy indicates that in future decades, increasing areas of not only the tidal zone but also of coastal subtidal habitats will be altered through the establishment of artificial material. Because of gaps in the research in this field, the ecological consequences for the coastal environment and biota habitats are mostly unclear (Bacchiocchi & Airoldi 2003, Bulleri & Chapman 2010, Chapman & Underwood 2011).

Because most artificial subtidal coastal protection measures will never be removed after exposure, increasing research attention must be directed to a thorough understanding of the ecological impacts of such anthropogenic infrastructures to meet the engineering requirements while also fulfilling their future value as habitat. This approach is defined as ecological engineering (Browne & Chapman 2011, Chapman & Underwood 2011) and addresses the commitments of the international community with respect to a resilient management of coastal habitats as defined, e.g., in the OSPAR guidelines (OSPAR 1999).

In terrestrial environments, habitat loss caused by anthropogenic alterations is one of the most important factors in species declines worldwide (Sih et al. 2000). In aquatic environments, however, limited research is available on the effects of habitat alteration on shorelines (Chapman & Underwood 2011).

44

In recent decades, studies have addressed the differences between natural substrata and coastal defence structures with respect to infaunal, epibiotic and invertebrate assemblages (Ambrose & Anderson 1990, Bacchiocchi & Airoldi 2003, Chapman & Bulleri 2003, Airoldi et al. 2005b, Martin et al. 2005, Wilding 2006, Browne & Chapman 2011), as well as for fish communities (Guidetti 2004, Martin et al. 2005, Clynick et al. 2007, Pizzolon et al. 2008, Wen et al. 2010, Cenci et al. 2011).

Often, it is unclear if the impact of artificial introduced structures is "positive" or "negative" (Airoldi et al. 2005a, Moschella et al. 2005). The effects of artificial introduced structures are often highly site-specific and can vary over different spatial scales (Chapman 2003, Martin et al. 2005, Clynick et al. 2008, Burt et al. 2009). The introduction of artificial hard substrata results in a change in the original habitat complexity (especially in soft-bottom areas) and consequently disturbs or changes the regional species community (see reviews: Bulleri & Chapman 2010, Chapman & Underwood 2011). Artificial substrata can also serve as "stepping stones" for invasive species (Bulleri & Airoldi 2005, Vaselli et al. 2008, Feary et al. 2011). A positive effect could be the enhancement of the value of a fish nursery ground and fisheries, particularly in overfished areas (Martin et al. 2005, Sayer et al. 2005, Cenci et al. 2011). Many studies have revealed significant differences between natural and artificial substrata with respect to fish abundance and richness (Duffy-Anderson et al. 2003, Guidetti 2004, Clynick 2006, Arena et al. 2007, Pizzolon et al. 2008) as well as for species composition (Wen et al. 2010). Studies suggest that artificial substrata can act as a fish attractor and/or fish producer (Guidetti 2004, Arena et al. 2007, Cenci et al. 2011, Simon et al. 2011). While many highly valuable studies have examined the effects of specifically designed artificial reefs on the enhancement of local fish communities (Bohnsack & Sutherland 1985, Jensen 2002, Wilding & Sayer 2002, Seaman 2007), only a few studies have been applied for studying effects of coastal defence structures (Guidetti 2004, Martin et al. 2005, Clynick et al. 2007, Pizzolon et al. 2008, Wen et al. 2010, Cenci et al. 2011). Most of the studied artificial reefs, however, were constructed completely or partially in coastal defence structure such as breakwaters (Bohnsack & Sutherland 1985, Bohnsack 1989, Pondella & Stephens 1994, Froeschke et al. 2005, Feary et al. 2011).

Particularly in northern Europe, ecological studies on coastal defence structures are rare (Martin et al. 2005, Moschella et al. 2005), and almost no studies of the impact on fish are available (but see Martin et al. 2005). Although 85 % of the 1155-km-long North

Sea coast of Germany is artificially protected (Rupp-Armstrong & Nicholls 2007), no published data about the impact of coastal defence structures on the local fish community are available for this area (to our knowledge).

Studies of the impact on fish are available for offshore wind turbines in the Baltic Sea (Wilhelmsson et al. 2006a) and North Sea (Reubens et al. 2011), wave power generators in Sweden (North Sea; Langhamer & Wilhelmsson 2009) and oil rigs in Norway (North Sea; Jorgensen et al. 2002, Soldal et al. 2002). Furthermore, few studies are available on artificial reefs in northern Europe (Jensen et al. 2000, Leewis & Halli 2000, Sayer et al. 2005). All of these studies have found high abundances of fish nearby or directly by the artificial substrata, and several have also revealed differences among the fish assemblage with respect to the natural surroundings.

In this study, we want to extend our knowledge of the impact of so-called "tetrapods" on northern subtidal communities. Tetrapods are artificial concrete structures that are used worldwide as breakwaters to absorb and dissipate wave energy, either in the tidal zone or in the sublittoral zone in front of exposed hard-bottom coastlines (Gürer et al. 2005).

In this study, experimental tetrapod fields in a boreal hard-bottom area, the sublittoral zone off Helgoland in the southern North Sea, were established to evaluate the impact of coastal defence structures on the demersal fish community. Using fixed counting stations along line-transects, we specifically analysed differences in total and species-specific fish abundances before and after the introduction of the tetrapods, spatial patterns in the demersal fish community with respect to the distance to the tetrapods and the impact of the artificial structures on the main fish species in more detail, including YOY ages.

The results are discussed with respect to the effects of tetrapods on the fish community directly associated with the structures and the fish community in the vicinity of the structures.

MATERIALS AND METHODS

Study site

Helgoland is located in the southern North Sea (German Bight) at 54°11'N and 7°55'E approximately 50 km off the German coastline. The island is the tip of a 35-km^2 subtidal rock formation surrounded by the soft-bottom-dominated North Sea. This sedimentological particularity has led to an ecological isolation from similar hard-bottom areas, the closest of which occur in Norway and Britain (Franke & Gutow 2004). Helgoland's coastline is highly exposed because of strong storm events and high-wave action, especially between September and March. Therefore, almost the entire coastline of Helgoland and its corresponding small island "Düne" is protected with artificial defence structures. The majority of these structures (approximately 10,000) are so-called "tetrapods", which are four-footed concrete breakwaters that weigh six-tons each (Fig. 1).

A total of six experimental tetrapod fields were established parallel to the shoreline in February 2010 north of Helgoland at an approximate 400-m distance to the coastline. Three of the fields were introduced in 5 – 7-m-depth by mean low-water spring (MLWS) according to hydrographic charts and another three fields in 10-m water depth (MLWS; Fig. 1). The three fields in each depth contour were placed at a distance of 80 m from each other to reduce reciprocal impacts while ensuring similar environmental conditions. One field consists of six tetrapods, which were arranged in two rows of three tetrapods. The size of one experimental field is approximately 7 x 4.5 m and approximately 2 m in height (Fig. 1).

This study focused on the three tetrapod fields in the 5 – 7-m-depth contour. The area surrounding the 5-m-depth tetrapod fields is dominated by rocky to pebbly substrate. A detailed study of the substratum typology of this area is given in Wehkamp & Fischer (2012b).
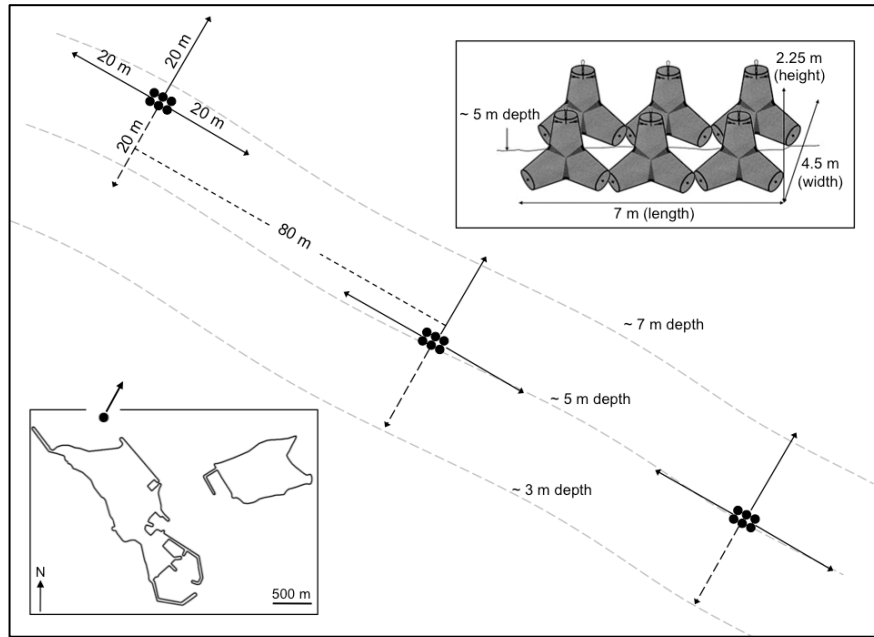
Fig. 1 The study areas in about 400 m northern of Helgoland. Three tetrapod fields were established in February 2010 along the 5 – 7 m depth contour. The fields are in a distance of 80 m to each other and are arranged as six tetrapods in two rows of three each. Fish counting was done by SCUBA along four 20 m long line-transects at each tetrapod field. Before the introduction of the tetrapods in 2010, a thorough assessment of the fish a macro-crustacean community was done in 2009 along three transects (continuous lines) at each experimental side

Survey methods

The assessment methodology in 2009 (without tetrapods) and 2010 and 2011 (with tetrapods) was identical. Transect-lines were laid out cross-like (Fig. 1) at the beginning of the tetrapod fields (in 2010 and 2011) or the proposed position of the tetrapod fields (in 2009), which was subsequently named the 0-m sampling site. Sampling was performed every 5 m (0, 5, 10, 15, 20 m) along the transect by counting and identifying all fish in a 1 x 1 m square left of the transect-line and a 1 x 1 m square right of the transect-line. The diver used a 1-m-long PVC rod to determine the size of the 2 x 1 m rectangle.

After approaching the appropriate counting station along the transect-line very carefully, the diver first identified and counted all fish above the substrate up to eye level and, when subsequently positioned in front of the counting area, the benthic species. In the final step, all stones measuring up to 10 cm were turned carefully to look for hidden organisms (Beldade & Goncalves 2007, Wehkamp & Fischer 2012b). To standardise the counting and to eliminate differences in the sampling technique, the same diver made the observations throughout the survey period (Sayer et al. 1993, Magill & Sayer 2002). At each transect-line, five 2 x 1 m counting stations were

analysed at distances of 0, 5, 10, 15 and 20 m from the tetrapods. Under good weather conditions, we were able to count all four (in 2010 and 2011) or three (in 2009) transect-lines (with five counting stations each) per tetrapod field for a total of 60 counting stations per month in 2010 and 2011 and 45 counting stations per month in 2009.

Sampling was performed monthly from June – September 2009 and March – November 2010 and 2011. Data assessment was not possible in September 2010 or September 2011, due to poor weather conditions with extremely poor visibility.

Abiotic factors

The water temperature (°C) was calculated for each month from the mean value of all sampling days in the specific month. In all years, the temperature was measured continuously at the "Kabeltonne" site (54°11.3′ N, 7°54.0′ E; Wiltshire et al. 2010) in the frame of the Helgoland Roads long-time data series near the study side. The transparency of the water (m) was quantified during each counting event with a Secchi disc fixed at the southernmost transect at each sampling site. Identical to a normal Secchi depth estimation procedure, water transparency was defined as the diver's distance from the Secchi disc at which the disk was no longer visible. Fish assessments were performed only when the horizontal Secchi distance was at least 1 m. Furthermore, the exact dive time, tide cycle (low tide, slack tide, high tide) and special observations were recorded during each sampling.

Data analysis

All benthic and suprabenthic fish were identified at the species level, if possible. Benthic gobies were identified as *Pomatoschistus minutus*. This classification was made because catch data of benthic gobies around Helgoland (Hielscher 2012, pers. comm.) indicate that the majority of the gobies in this area belong to this species. Because the species identification of gobies in the field is almost impossible, we accepted the risk that some *Pomatoschistus microps*, particularly smaller individuals, were included accidentally.

In 2010 and 2011, we discriminated, if possible, YOY individuals from older individuals for the following species: *Ctenolabrus rupestris*, *Gadus morhua*, *Pholis gunnellus*, *Taurulus bubalis* and *Callionymus lyra*. We used data from Krüß (1988),

who determined age-at-length relationships for some species off Helgoland by otolith analysis. Additional age-at-length information for some species was taken from the literature (Hillden 1978, King & Fives 1983, Sayer et al. 1995, Campana 1996, Vallis et al. 2007).

Statistical analysis

All statistical analyses were performed in R (version 2.14.1) at a significance level of p = 0.05 (unless otherwise stated). Most of the data collected were not normally distributed. Therefore, data were either transformed to a normal distribution with classical transformation procedures (Köhler et al. 1992) or, if not successful, rank-transformed prior to the application of parametric statistical test procedures such as ANOVA (Conover & Iman 1981).

Because large shoals of *Gobiusculus flavescens* were occasionally observed in the area in 2011, we performed the statistical analysis with and without *G. flavescens*. In a first statistical procedure, no significant differences in the average fish abundances were observed between the three experimental tetrapod fields when excluding *G. flavescens* (ANOVA, 2009: $df = 2$, $F = 0.286$, $p = 0.752$; 2010: df = 2, $F = 0.455$, $p = 0.635$; 2011: $df = 2$, $F = 0.455$, $p = 0.635$). When *G. flavescens* was included, significant differences among the three experimental fields occurred in 2011 (ANOVA, 2009: $df = 2$, $F = 1.119$, $p = 0.329$, 2010: $df = 2$, $F = 1.069$, $p = 0.346$; 2011: $df = 2$, $F = 6.624$, $p = 0.0017$).

However, a subsequent post-hoc test revealed that the significance was based only on a difference in the abundances of *G. flavescens* in the northern and central tetrapod fields in August 2011 (Fig. 2, Tukey HSD, p = 0.0010). Because this was a singular event, which can be dealt with by excluding *G. flavescens* from subsequent statistical analyses if occurring in high abundances at a single site, we accepted the three experimental fields as replicates. Analyses of co-variances (ANCOVA) were applied to analyse the effects of water temperature and tidal cycle on overall fish abundance and distribution.

Fish abundances over year, month and distance

To assess the temporal patterns of total fish abundance among the three years 2009, 2010 and 2011 and among months within the years, ANOVA's with "year" and "month" as fixed factors were applied.

To analyse spatial effects with respect to the distance to the tetrapods, we used the months of June, July, August and September in 2009 (without tetrapods) and the months of June, July, August and October in 2010 and 2011 (with tetrapods). This approach ensured that the samples in the three years covered identical numbers of counting stations and samplings each year.

In these analyses, the factors "month", "year" and "distance to the tetrapods" (0 m, 5 m, 10 m, 15 m and 20 m) were used as fixed factors with subsequent post-hoc tests (Tukey HSD).

Species diversity and evenness

To parameterise the diversity and evenness of the demersal fish community, the Brillouin index (Magurran 2004) was applied for the 0 m, 5 m, 10 m, 15 m and 20 m sampling stations during June – September (2009) and October (2010 and 2011) of each year. In these calculations, *G. flavescens* was excluded. Because we assessed a finite collection in the form of fixed sampling stations, we used the Brillouin diversity index (1) (Pielou 1969) in this study with N = the total number individuals in the sample, n = the abundances of the single species and S = the total number of different species in the sample.

$$HB = (\ln N! - S \ln n_i!) / N. \tag{1}$$

In association with the Brillouin diversity (HB), the Brillouin evenness (E) (2) represents the proportion between the observed diversity (HB) and its possible maximum value (HB_{max}: each species is represented in the sample with the same abundance). E can reach values between 0 and 1, with 1 representing a numerically equal distribution of all observed species in the sample.

$$E = HB/HB_{max} \tag{2}$$

HB_{max} is calculated as $HB_{max} = 1/N \ln(N!/\{[N/S]!\}^{s-r} * \{([N/S] + 1)!\}^r)$, in which [N/S] is the integer of N/S and r is calculated as N-S [N/S].

RESULTS

The average water temperature in all three years followed a typical bell-shaped curve over the months (Fig. 2). Minimum average temperatures were observed in March 2011 (3.45 °C, SD 0.48) and in March 2010 (3.8 °C, SD 0.70). The month of August always included the highest average temperatures, with 17.90 °C (SD 0.26) in 2009, 17.73 °C (SD 0.5) in 2010 and 17.10 °C (SD 0.40) in 2011. The average temperatures in October 2010 and 2011 were similar with 14.85 °C (SD 0.64) in 2010 and 14.20 °C (SD 0.14) in 2011 but were significantly lower than the average temperature of 17.10 °C (SD 0.40) in September 2009 (Fig. 2).

Analyses revealed that the "tidal cycle" (ANCOVA with "distance" as fixed factor; 2009: $df = 1$, $F = 1.134$, $p = 0.288$; 2010: $df = 1$, $F = 2.870$, $p = 0.092$; 2011: $df = 1$, $F = 0.619$, $p = 0.432$) as well as the "water temperature" (ANCOVA with "month" as fixed factor; 2009: $df = 1$, $F = 0.71$, $p = 0.401$; 2010: $df = 1$, $F = 1.407$, $p = 0.237$; 2011: $df = 1$, $F = 0.746$, $p = 0.389$) had no significant effect on the fish abundances m^{-2}, and thus these variables were excluded from further analysis.

Fish abundances

The three years differed significantly in their average fish abundances during the summer months (June to September 2009 and October 2010 and 2011; without gobies: ANOVA, $df = 2$, $F = 3.998$, $p = 0.0189$; with gobies: $df = 2$, $F = 11.719$, $p < 0.0001$).

The highest values of average fish abundances were observed in 2011 with 5.07 fish m^{-2}, intermediate values in 2010 with 1.56 fish m^{-2} and lowest values in 2009 with 1.48 fish m^{-2}. The high values in 2011, however, were primarily based on the swarm-forming swimming goby (*G. flavescens*), which was highly abundant in 2011 with 1257 individuals, primarily in the month of August (Fig. 2).

When excluding *G. flavescens* from the analysis, the average fish abundance in 2011 decreased to 1.58 fish m^{-2}, and the values in 2010, 1.30 fish m^{-2}, were similar to the values in 2009, 1.34 fish m^{-2}.

An increase in fish abundances over the months from March – November 2010 and 2011 and from June – September 2009 was obvious for all three years, but statistical analysis revealed significance only for 2009 (ANOVA, $df = 3$, $F = 22.22$, $p < 0.0001$) (Fig. 2).
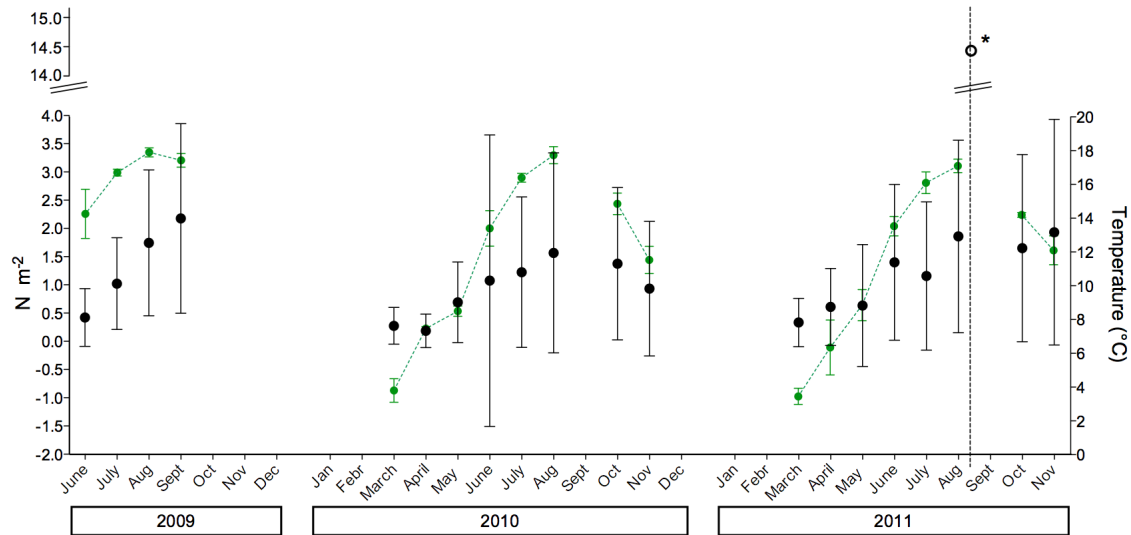
Fig. 2 Fish abundances m^{-2} (mean/SD; left y-axis, black symbols) and temperatures in °C (right y-axis, green symbols and dashed line) over all sampled months in the three years 2009, 2010 and 2011. The presented data was analyzed without the shoaling fish *Gobiusculus flavescens*. This species was counted in high numbers in August 2011 (* marked in the figure)

In addition to these temporal patterns, significant spatial patterns were observed with respect to the distance to the tetrapods (Fig. 3). In the years 2010 and 2011, we counted significantly more fish at the 0-m sampling station (in the immediate vicinity of the tetrapods; ANOVA; 2010: *df* = 4, *F* = 17.389, *p* = 0.0001; 2011: *df* = 4, *F* = 31.38, *p* = 0.0001) than in 2009, when no significant spatial effects were observed (ANOVA; *df* = 2, *F* = 1.241, *p* = 0.295).

A respective statistical analysis of the per cent distribution of fish along the transect-lines indicates that the observed significant increase in total fish abundances at the 0-m counting station can mainly be explained by a decrease in the fish abundances farther from the tetrapods (sampling stations 5 – 20 m). This analysis revealed a significant decrease in total fish abundances at the counting stations 5 – 20 m in the years 2010 and 2011 compared to 2009 (ANOVA; *df* = 2, *F* = 18.13, *p* < 0.0001, Tukey HSD; 2009: 2010, *p* < 0.0001; 2009: 2011, *p* < 0.0001, 2010: 2011, *p* = 0.6419).
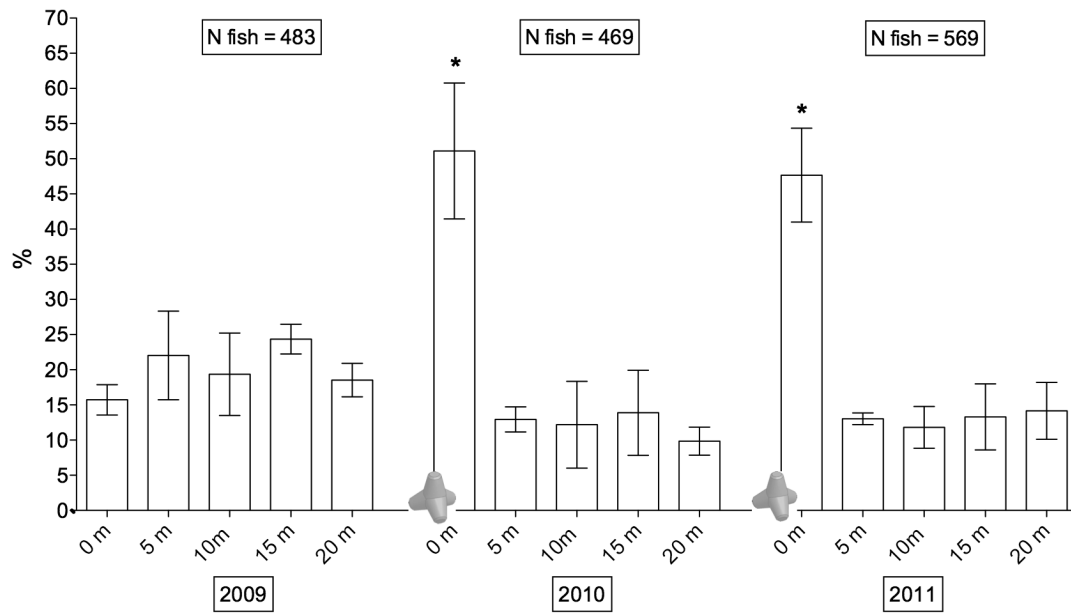
Fig. 3 Percentage distribution of all fish +/- SD; without the schooling fish *Gobiusculus flavescens* among the sampling stations (distance to the tetrapods) integrated over the months June – September in 2009 and June – August & October in 2010 and 2011. In 2009 483 fish, in 2010 469 fish and in 2011 569 fish (numbers without *G. flavescens*) were counted in total. The relative abundances differed significantly between the 0-m sampling stations to all other stations in 2010 as well as in 2011

Species distribution

A total of 18 species were observed over the three-year sampling time. However, only five species (*G. flavescens, C. rupestris, P. gunnellus, P. minutus* and *T. bubalis*) were counted in greater abundances over this time (>100 individuals per species - Fig. 4), six species were counted with intermediate abundances (between 10 and 100 specimen in total), and another seven species were observed only occasionally or even singularly (Fig. 4). Three of the higher abundant species (*C. rupestris, P. gunnellus* and *T. bubalis*) were observed throughout the year, while most other species occurred only temporarily during the summer and autumn months. Three species occurred in the area only after the introduction of the tetrapods but only as juveniles: the cod species *Gadus morhua, Pollachius pollachius* and *Trisopterus luscus* (Fig. 4). Juvenile pollacks were observed shoaling in the immediate vicinity of the tetrapods in June 2010. Juvenile cods were observed in June and July 2010 either close to the tetrapods or at a distance from them but then always associated with bigger stones or kelp. The third cod species that was observed in association with the tetrapods was the bib (*T. luscus*). While only one

individual was observed within one of the tetrapod fields from July to October of 2010, in 2011, each of the fields hosted one individual of this species.
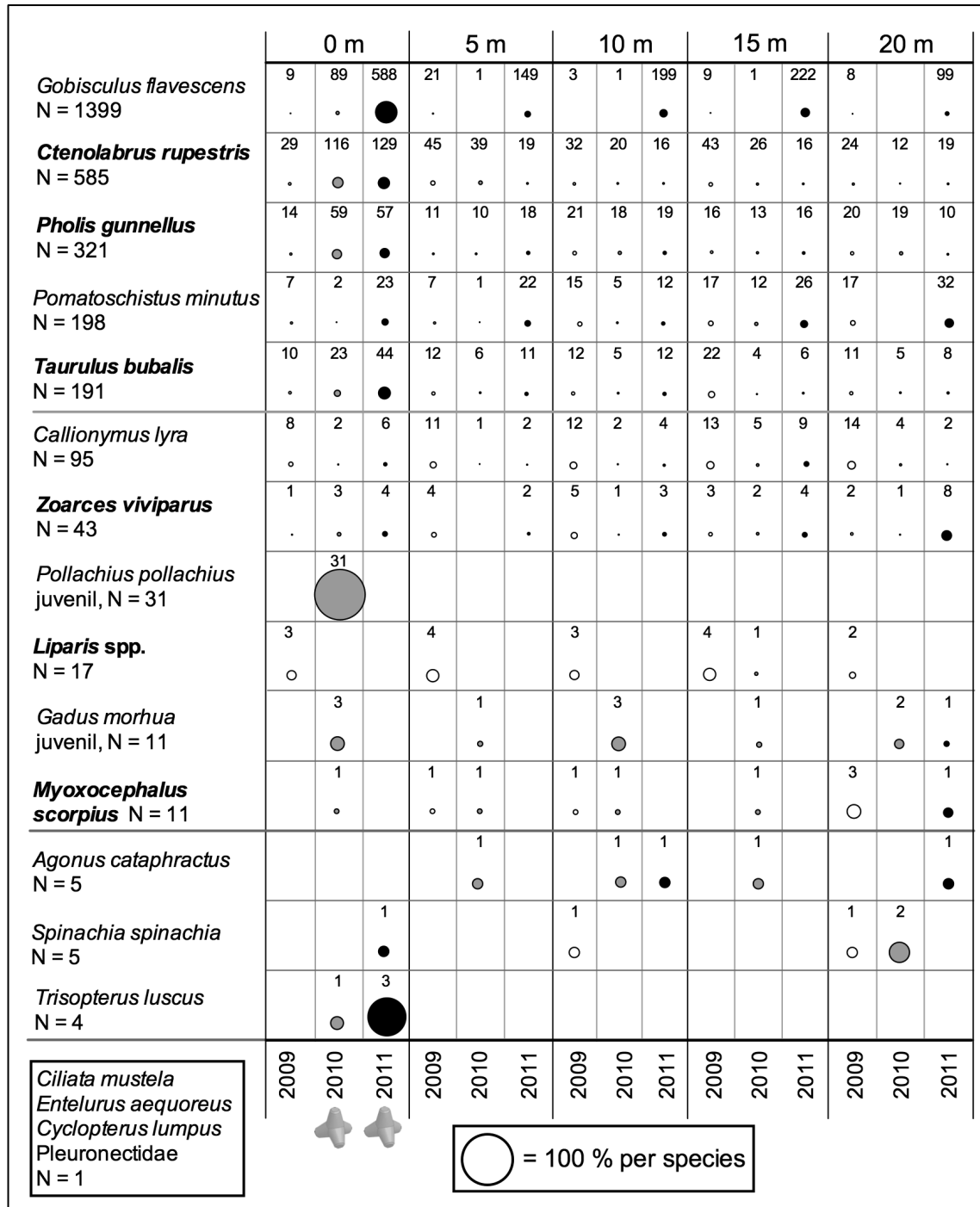

Fig. 4 Percentage distribution and numbers for all found species. The letters above the circles represent the individual number of the specific species found in each sampling station and in the corresponding year. The percentages were calculated for each species separately whereas the total found number of a species represents 100 %. The circle sizes constitute to the percentage distribution of the specific fish species for each sampling station in each year (integrated are the months June – September 2009, June – August & October 2010 and 2011)

In 2010 and 2011, we distinguished between YOY (age class 0+) and older individuals to evaluate a potential effect of the tetrapods as a nursery habitat. We observed for the three main species *T. bubalis*, *C. rupestris* and *P. gunnellus* more YOY individuals in 2011 (N = 225) than in 2010 (N = 132; Table 1). This pattern was particularly obvious for the 0-m station (2010, N = 37; 2011, N = 91; Table 1). However, the other stations also contained more 0+ fish in 2011, especially *T. bubalis* and *P. gunnellus*. The increase in *C. rupestris* was most clear at the 0-m station in 2011 with 23 more individuals than in 2010.

Table 1 Abundances of YOY-individuals for the fish species *Taurulus bubalis, Ctenolabrus rupestris* and *Pholis gunnellus* in the years 2010 and 2011 summarized over all months for each sampling station. The last column represents the total abundances of YOY fish for each counting station

YOY-fish	*T. bubalis*		*C. rupestris*		*P. gunnellus*		Fish in total	
Sampling station	**2010**	**2011**	**2010**	**2011**	**2010**	**2011**	**2010**	**2011**
0 m	9	23	21	44	7	24	37	91
5 m	4	11	20	13	5	8	29	32
10 m	6	8	11	12	7	15	24	35
15 m	2	9	15	12	10	14	27	35
20 m	4	4	6	15	5	13	15	32
Total	**25**	**55**	**73**	**96**	**34**	**74**	**132**	**225**

Species diversity and evenness

With an average HB value of 1.14 (SD 0.36), 0.92 (SD 0.23) and 1.08 (SD 0.20) in 2009, 2010 and 2011, the overall species diversity integrated over all sampling sites differed significantly between the years (df = 2, F = 3.427, p = 0.0393) with highest values in 2009 and significantly lower values in 2010 (Tukey HSD; p = 0.0381). This indicates that the HB values decreased after the introduction of the tetrapods and recovered in 2011 (Fig. 5). A more detailed analysis of these temporary changes can be derived from Fig. 6.

In 2009, a clear seasonality in species diversity was observed (ANOVA; df = 3, F = 19.17, p < 0.0001), with lower values in the months of June and July and higher values in August and September or October. After the introduction of the tetrapods, this

increase in diversity in the late summer and autumn months did not occur, and the overall diversity remained lower; thus, no significant differences among the months were found in 2010 (ANOVA; $df = 3$, $F = 1.163$, $p = 0.355$). In 2011, this month effect recovered (ANOVA; $df = 3$, $F = 3.806$, $p = 0.0311$) but only between August and October (Tukey HSD; $p = 0.0223$). Furthermore, both species diversity and evenness exhibited a significant increase in variation after the introduction of the tetrapods compared to 2009 (Fig. 5 + 6).
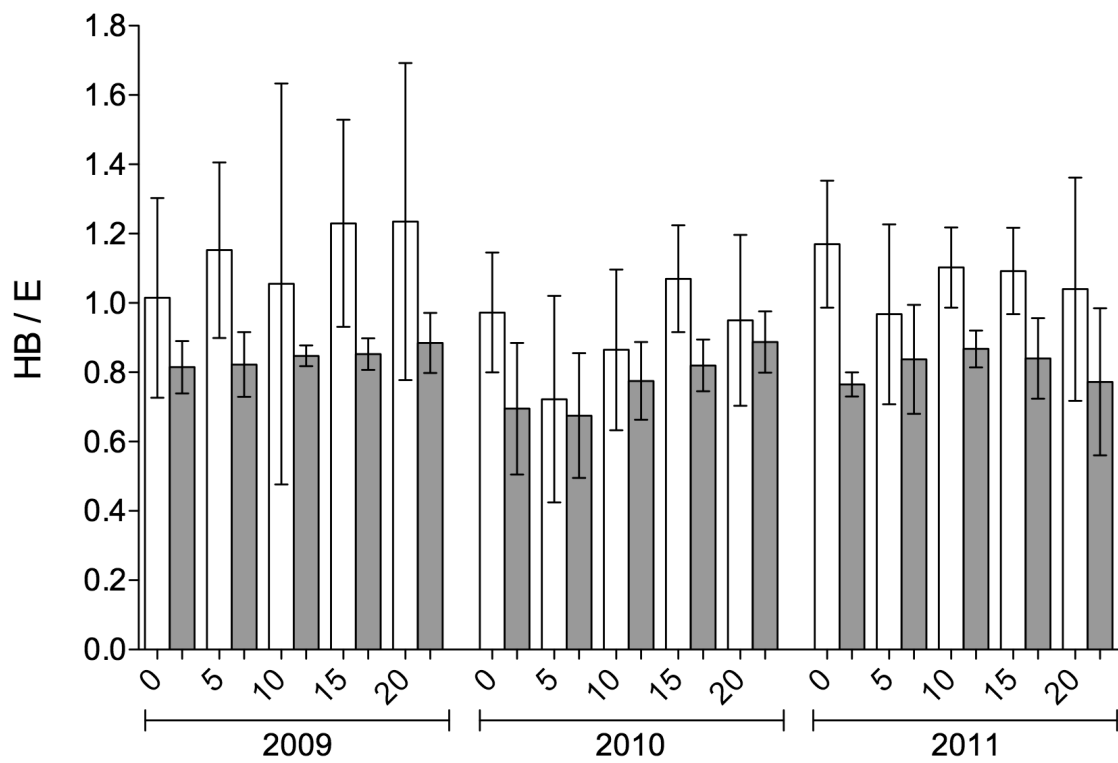

Fig. 5 The Brillouin species diversity values (HB; represented in the white bars) and the Brillouin evenness values (E; values, represented in the grey bars) for each counting station in the specific year (mean, SD; integrated in the calculations are the months June – September 2009, June – August & October 2010 and 2011)
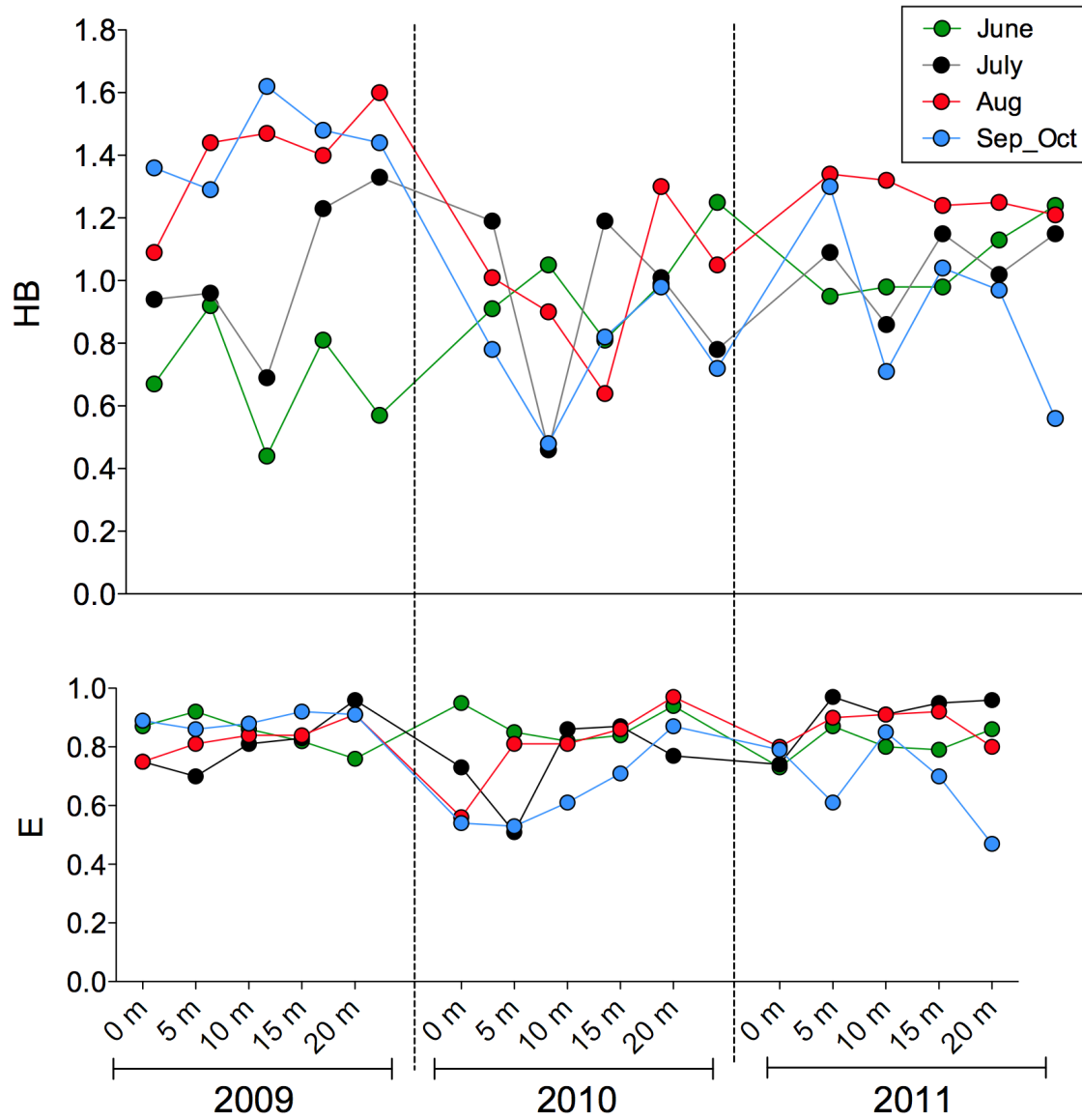
Fig. 6 The Brillouin species diversity values (HB; upper graph) and evenness values (E; lower graph) over the counting stations (0 – 20 m), over the years and over the same number of sampling months (integrated in the calculations are the months June – September 2009, June – August & October 2010 and 2011)

DISCUSSION

Different authors have stressed that standard visual sampling is not adequate to identify and accurately census cryptobenthic fish because this method frequently leads to an underestimation of the number of individuals and species (Willis 2001, La Mesa et al. 2006). In addition to the visual sampling above the substrate, we therefore invested additional dive time to carefully turn individual stones (Beldade & Goncalves 2007, Wehkamp & Fischer 2012b). Using this method, hidden species between and under stones can often be identified, which is not achievable even with retrospective underwater photography or video documentation of a specific area (Ehrenberg & Ejdung 2008). Other methods can be used to count these types of species, e.g., the application of anaesthetics (Sayer et al. 1994). This technique, however, is technically problematic in the mainly flat study area and furthermore has an unknown impact on the community.

We found distinct seasonal effects over the months during the study time, whereas the effects on the fish abundances were only significant in 2009. The fish species were most abundant over the late summer and the autumn months, which is a typical pattern for northern boreal communities (Hunter & Sayer 2009). Parameters such as temperature, migration, recruitment or the availability of food may responsible for the change in abundance of some species over a temporally intermediate or longer-scale period (Magill & Sayer 2002, Bell & Turner 2003, Clynick 2006). Another interesting influencing factor is the tidal cycle, which acts, however, within smaller temporal scales (Silva et al. 2010). We found no significant effects of the temperature or of the tidal cycle on fish abundances. However, because these variables interact strongly, may confound each other and behave differently depending on the type of species, separate studies with a carefully planned experimental design are necessary to discriminate more precisely among these variables.

Much of the literature focuses on differences in the fish community associated with artificial structures compared to the natural surrounding (e.g., Wilhelmsson et al. 2006a, Wen et al. 2010). However, only a few studies have been able to investigate the same area before and after the experimental introduction of the artificial material (but see Cenci et al. 2011).

In the here presented study, this experimental approach was quite promising because it permitted far greater insight into the effects of breakwaters on the natural benthic

community compared to a simple monitoring of an existing installation. Our study demonstrates that the fish abundances were significantly higher in close vicinity to the tetrapods in both years after the introduction. This was expected given the wide range of existing studies of artificial structures that have obtained similar results (Bohnsack & Sutherland 1985, Fabi & Fiorentini 1994, Simon et al. 2011). However, our study additionally demonstrated that overall fish abundance with distance from the tetrapods decreased by approximately the same amount as the fish abundances at the tetrapods increased. This result is most interesting because it clearly demonstrates that the artificial installations initiated a significant migration of fish from the surrounding area towards the structures. We performed our assessments up to a distance of 20 m from the tetrapods because we assumed that the effects would have levelled off at this distance. This assumption was clearly wrong, and the attraction effect apparently reached farther in the surrounding habitat with a range that remains unclear. However, assuming that this effect may be in some way correlated with the amount and size of artificial structures, it seems to be crucial to focus also on the effects of the spatial extension of artificial structures on the surrounding habitat to truly understand the ecological implications of such man-made structures for a coastal ecosystem (Airoldi et al. 2005a, Chapman & Underwood 2011).

After the introduction of the tetrapods, approximately 50 % of all fish were counted at the 0-m counting stations, while the other 50 % were equally distributed among the 5-, 10-, 15- and 20-m counting stations. To the best of our understanding, this observation provokes the most interesting ecological (or even physiological) question, specifically, why do the fish follow this distribution? This basic question remains unanswered in the most studies (Bohnsack & Sutherland 1985). More specifically, which behavioural or physiological advantage does a single fish have by shifting toward an artificial structure? In terrestrial ecology, it is well known that species often do migrate towards artificially changed (urban) areas. Cities, for example, are assumed to be hotspots of species diversity and sometimes harbour more species than rural landscapes (Yaukey 1996, Leveau & Leveau 2005, Knapp et al. 2008). Leveau & Leveau (2005) and Knapp et al. (2008) suggest an increase in spatial diversity in artificially changed environments compared to the rural surrounding habitat. Therefore, artificially modified habitats are often assumed to permit increased survival, increased reproduction, higher concentrated food availability and reduced predator risk (Yaukey 1996). By contrast, some taxa

appear sensitive to artificially urbanised habitats land-use, demonstrating a strong negative impact of urbanisation on species diversity (Knapp et al. 2008).

The rocky subtidal area off Helgoland is a highly diverse and structured natural habitat. The artificial tetrapods, however, appeared to be even more attractive for the majority of the fish compared to the natural surrounding habitat. This attraction may be due to the distinct vertical dimension of this type of artificial structure. This kind of structure provides different vertical layers of habitats throughout the water-column (Fabi et al. 2004, Clynick et al. 2008) as well as alternative microhabitat opportunities that are not provided by natural reefs or flat-bottom hard substrata (Clark & Edwards 1999, Wen et al. 2010). In particular, supra-benthic and territorial species may benefit from increased territory if a distinct vertical dimension is added to the natural habitat.

Previous studies have demonstrated the preferred association of the goldsinny (*C. rupestris*) and the two-spotted goby (*G. flavescens*) with three-dimensional structures (Hillden 1981, Sayer et al. 1993, Wilhelmsson et al. 2006a), as well as their attraction to hard-bottom substrata in shallow waters (Gjosaeter 2002, Wilhelmsson et al. 2006a, Andersson et al. 2009). The authors suggest that the complexity of the structures serves primarily as a shelter refuge (Wilhelmsson et al. 2006a, Andersson et al. 2009).

In addition to an increase in vertical shelter structures for certain fish species, artificial structures may also provide an increased biomass of algae and small invertebrates. This sessile community may be used as both a food source and a secondary shelter for smaller mobile organisms living among the structurally complex attached community (Coleman & Connell 2001, Wilhelmsson et al. 2006a, Andersson et al. 2009). The biota growing on subtidal hard substrata is thought to have a large effect on fish. Clynick et al. (2007) found a strong positive correlation between the amount of epibiota and the abundance and diversity of fish in marinas in Sydney Harbour. By contrast, Moreau et al. (2008) demonstrated that fish that consume epibiota on jetties do not depend on this food source. These researchers suggest that the availability of refuge and shelter are the main attractants for species. In addition, Coleman & Connell (2001) suggest that fish associated with pier pilings respond to the presence of the physical structure in the form of shelter or shade, rather than the epibiota growing on it. In our study, we did not focus on the role of the epibiota growing on the tetrapods and their use as a food source or microhabitat. However, we observed that the three most abundant fish species in our study (*C. rupestris*, *T. bubalis* and *P. gunnellus*) ate on the epibiota or the associated

small organisms and retreated quickly toward these biotic structures or between the tetrapods when a possible predator approached. Perhaps, the combination of an existing food source near shelter opportunities will determine the increase in some species. However, further studies are necessary to elucidate these complex interactions between fish and the epibiotic community on artificial structures in more detail.

Man-made structures can act as fish attractors and/or fish producers (Bohnsack & Sutherland 1985, Cenci et al. 2011, Feary et al. 2011, Simon et al. 2011), although which of the two processes occur is often unclear (Bohnsack & Sutherland 1985). There is little value in arguing about whether artificial reefs attract versus produce fish biomass – they probably do both (Bohnsack et al. 1994, Osenberg et al. 2002). Fish production will be limited not only by habitat limitations but also by larvae supply, post-settlement mortality as well as adult fish mortality (Wilson et al. 2001, Osenberg et al. 2002). Furthermore fish attraction can be limited by factors like food availability, space competition and/or predator pressure, which affect the density of species and individuals in a system (Wilson et al. 2001, Osenberg et al. 2002, Simon et al. 2011). Our study primarily supports the fish attractor hypothesis because we detected a significant shift of the fish from the surrounding habitat toward the artificial structures. However, we also observed an increase in the total number of fish with 1.34 fish m^{-2} in 2009, 1.3 fish m^{-2} in 2010 and 1.58 fish m^{-2} in 2011 (without the shoaling *G. flavescens)*. This increase was mainly due to the higher numbers of YOY fish at the artificial structures in 2011.

This increase in juvenile abundances and more shoaling fish such as *G. flavescens* may be an indicator of an increase in fish biomass production due to presence of the artificial structures.

Wilhelmsson et al. (2006a) observed great densities of *G. flavescens* near monopiles of wind turbines and suggest that the reason for their occurrence could be a combination of refuge and food availability, as well as enhanced recruitment to the vertical structures. Tetrapods also provide additional vertical structures and shelter, as well as additional food resources.

However, to study seriously the effects of biomass production as a function of artificial structures, longer time series and additional measurements, such as the individual somatic growth of the juveniles associated with the structures compared to others in the natural environment, are necessary.

The observed shift of the fish from the surrounding area towards the tetrapods consequently stimulated the question of the carrying capacity of certain complex structures. The abundances of fish in a specific area can be limited by such factors as food availability, space competition and predator pressure (Simon et al. 2011). We do not know when the carrying capacity of such artificial structures will be reached with respect to the associated fish community and if this is reached by continuous fish attraction from the surrounding area or by fish production because these artificial structures serve as additional spawning and nursery habitats. Nevertheless, understanding these mechanisms is crucial for a general understanding of the role of such structures in an ecosystem.

If an artificial structure continuously attracts fish from the surrounding habitat until the carrying capacity is reached, then both habitats and food in the surrounding area will be available and a surplus production of the natural fish community in the area can be stimulated. Under this assumption, the fish community in the surrounding area may be assumed to remain stable with respect to species composition and area diversity, and the artificial structure may be seen as a collector device that provides additional shelter and food for a structure-related additional fish stock.

By contrast, if an artificial structure itself serves as additional spawning habitat and therefore numerically increases the fish abundance in an area, this increase will occur until the carrying capacity of the structure is reached. At that point, fish may leave the structures and penetrate the surrounding habitats. If the species that reproduce at the artificial structures are the same as in the surrounding area, an increase in competition caused by a structure-related surplus production may occur. This increase may lead to a decrease in individual growth rates in the natural population, even though the growth rates at the structures remain high. When the artificial substrata support the abundance of specific species, e.g., predatory fishes, important ecological processes such as predation and competition would be altered. The loss of functional roles can lead to decreased ecological stability (Simon et al. 2011).

If the artificial structure provide spawning habitat for new or even alien species, the changes in the community become even more complex and possibly erratic, and the capacity for the enhancement of new species can require several years (Fabi & Fiorentini 1994).

Compared to the time before the installation of the structures, the species composition included increased numbers of native species (*C. rupestris, T. bubalis, P. gunnellus,*

G. flavescens, P. minutes) directly by the artificial structures. The increase in native species may result from the hard-bottom characteristic of the surrounding area (Froeschke et al. 2005, Clynick 2006, Perkol-Finkel et al. 2006). By contrast, the difference in the community structure may be the result of high abundances of dominant species (Feary et al. 2011) or structural differences (Perkol-Finkel et al. 2006, Wen et al. 2010).

In addition to the main species, juvenile cod species were detected by the artificial structures. Young-of-the-year cods (*G. morhua*) were detected in 2010 near the structures, as well as in the surrounding area in combination with stones or *Laminaria*.

An entirely new species that was associated with the tetrapod fields in 2011 was the bib (*T. luscus*). The bib was observed in 2010 with only one individual, but in 2011, each tetrapod field harboured one bib. The bib is a typical inhabitant of outer rocky reefs or offshore artificial hard substrata such as shipwrecks or wind turbines (Fowler et al. 1999, Zintzen et al. 2006, Reubens et al. 2011). Spawning occurs between March and April followed by an active inshore migration by YOY individuals to shallow nursery grounds in summer and autumn (Wheeler 1978, Hamerlynck & Hostens 1993, Fowler et al. 1999). Normally, *T. luscus* occur in large schools (Wheeler 1978, Fowler et al. 1999, Reubens et al. 2011). Our study cannot address why this species occurs only as single individual in each tetrapod field, and we found no published literature indicating a non-schooling behaviour.

In conclusion, our experimental study of artificial structures exposed to a boreal hard-bottom area in the southern North Sea demonstrated a significant attraction of native fish species from natural habitats, thereby leading to a decrease in the average fish abundance in the nearby surrounding areas. This indicates that the artificial structures used in this study act as fish collectors, at least during the first two-year period after the introduction. Besides changes in abundances, the diversity and evenness values exhibited a larger variation after the introduction of the tetrapods, supporting the need for long-term investigations to distinguish short-term variability from long-term trends, which are affected mainly by anthropogenic impact (Franke & Gutow 2004).

We suggest that the availability of additional vertical refuges and shelters in combination with surplus food opportunities offered by the epibenthic fouling community on the tetrapods were the main factors that attracted certain fish species more than others. This finding raises the question of the consequences of the association of a highly specialised community that requires specific habitat features that are

probably unavailable in the natural substratum with large-scale construction of coastal-defence structures. Because coastal defence structures will be established over the coming centuries at even larger scales than those used today, due to global changes, more experimental *in situ* work is needed to understand the mechanisms by which these devices interact with the fish community and to develop a better understanding of the ecological impacts of such devices.

CHAPTER III

**Impact of artificial defence structures (tetrapods) on decapod crustaceans
in the southern North Sea**

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ABSTRACT

The establishment of coastal defence structures is becoming highly important to compensate predicted consequences of climate change processes.

We investigated the impact of commonly used breakwaters (tetrapods) on a decapod crustacean community since research in this field is still in the very early stages. We performed *in situ* studies on experimental tetrapod fields and in distance to them in a subtidal hard-bottom area in the southern North Sea. The species composition and abundances of macroscopic decapods were assessed before and after the introduction of the tetrapods.

We could detect a significant decrease of smaller, less vagile species (*Pisidia longicornis, Pilumnus hirtellus, Galathea squamifera)* after the establishment of the tetrapods in the complete study area.

For some species (*Hyas araneus, Homarus gammarus*) we can assume that the tetrapods were suitable as habitat and shelter refuge against predators.

On the other hand no attraction effects were revealed for highly mobile predatory crabs (*Cancer pagurus, Liocarcinus* spp.).

This study highlights the importance of long-term studies. Only using long-term studies we have the chance to distinguish between natural induced and anthropogenic induced factors, which can influence species distribution patterns over a long-term.

Our findings demonstrate that the impact of artificial structures on the temporal and spatial dynamics of macro-invertebrates in temperate hard-bottom areas is highly species-specific. The effects depend on the individually size, lifestyle and ecological claims.

INTRODUCTION

Coastal ecosystems are intensively affected by human influence with highly predicted cumulative impact scores especially for hard and soft continental shelves and rocky reefs (Halpern et al. 2008, Zanuttigh 2011). Among others, influencing activities are urban infrastructure to sustain commercial and tourist activities, recreational fishing, aquaculture, pollution and also coastal engineering (Halpern et al. 2008, Bulleri & Chapman 2010, Chapman & Underwood 2011).

As response to the forecasted climate change within the proposed rise of the sea level in the next decades (IPCC 2007b, a, Hawkins et al. 2009), the establishment of hard coastal defence structures will be intensified to save coastal areas of flooding and erosion (Airoldi et al. 2005a, Moschella et al. 2005, Bulleri & Chapman 2010, Chapman & Underwood 2011). The introduction of artificial hard substrata, however, is well known to affect the natural conditions. Changes in hydrodynamic and sediment-transport processes affect the conditions for sedentary organisms (Martin et al. 2005, Chapman & Underwood 2011). A variety of studies show that newly introduced artificial substratum facilitates the expansion of native or alien hard-bottoms species, especially when hard substrata are introduced in soft-bottom dominated areas (Bacchiocchi & Airoldi 2003, Bulleri & Airoldi 2005, Vaselli et al. 2008). The type and extend of the effects vary for different marine environments (shore types, rocky bottom vs. sandy bottom, slope, depth; Bulleri & Chapman 2010) and depend on the structure, material, size and direction of the artificial substrate (reviews: Bulleri & Chapman 2010, Chapman & Underwood 2011).

Because of these possible effects, a thorough understanding of the ecological functioning in dependence of the type of artificial substrata has to be achieved in the future. Coastal defence structures should be designed in ways, which optimize the maximum in technological functionality while simultaneously minimizing their ecological impact on the local biodiversity and ecosystem functioning (Bulleri & Chapman 2010, Airoldi & Bulleri 2011). In this context, Collins et al. (1994) stresses the importance to investigate the effects of artificial material on the natural surrounding over an ecological relevant timescale, which should compound rather years than months.

In Europe, 22,000 km^2 of the coastal zone (Airoldi & Bulleri 2011) are artificially protected, including 85 % of the North Sea coast of Germany (Rupp-Armstrong &

Nicholls 2007). Most often, hard defence structures serve as seawalls, groynes or breakwaters to reduce the intensity of wave forces in inshore waters and to protect ports, harbours, marinas or the coastline in general (Bulleri & Chapman 2010).

The differences between natural substrata and coastal defence structures as habitats have been addressed over the last decades with respect to infaunal, epibiotic and invertebrate assemblages as well as fish communities (Ambrose & Anderson 1990, Bacchiocchi & Airoldi 2003, Chapman & Bulleri 2003, Airoldi et al. 2005b, Martin et al. 2005, Wilding 2006, Browne & Chapman 2011).

Nevertheless, concerning the impact of artificial substratum on invertebrates only few studies have focussed on decapod crustacean communities. This group, however, plays a major ecological role in the dynamics of coastal benthic ecosystems (Pallas et al. 2006). Decapods are common members of rocky shore communities (DeGrave & Turner 1997, Pardo et al. 2007, Wehkamp & Fischer 2012b).

In contrast to fish, life cycles of benthic invertebrates are highly complex (Ingle & Christiansen 2004, Pallas et al. 2006). These species select their habitat in a trade off between minimising predation risk and physical disturbance. Especially larger decapods may modify their habitat preference during their different life cycles e.g. during moulting or breeding periods (Pallas et al. 2006, Pardo et al. 2007).

Studies revealed significant specific microhabitat preferences for some decapod crustaceans, whereas other species are more flexible in their habitat choice (Ingle 1983, Robinson & Tully 2000b, Pallas et al. 2006, Wehkamp & Fischer 2012b). For example, post-settlement movement is expected to be more important in active predators compared to less vagile detritivorous species with a lower overall foraging activity (Pardo et al. 2007).

Concerning studies on the impact of artificial structures on decapod communities, only superficial assumptions are available (Fabi & Fiorentini 1994, Martin et al. 2005, Zintzen et al. 2006, Mallefet et al. 2007). Most studies focus on different species and investigate the decapods only in passing. In general, it can be assumed that the alteration of natural habitat to a high extent leads to a deterioration of habitat quality for some species whereas other species can profit (Mallefet et al. 2007).

For commercial important species like *Homarus gammarus* and *Cancer pagurus,* studies revealed that these species could be highly attracted towards artificial structures (Jensen et al. 2000, Jensen 2002, Krone & Schröder 2011). Martin et al. (2005) assumes that low-crested defence structures, which were introduced in a soft-bottom habitat

provide additional habitat for new settlers and enhance the settlement of fish and crustaceans. Chou & Fang (2005), however, found no significant differences between the decapod community on a steel-slag disposal in Thailand and a rocky control site within a five-year long investigation.

The most studies which investigated the impact of artificial structures on invertebrates focus on microscopic epifaunal, small or less vagile crustaceans, molluscs or bivalves (Johannesson & Warmoes 1990, Bacchiocchi & Airoldi 2003, Chapman 2006, Andersson et al. 2009, Chapman & Underwood 2011). These species can be sampled easily through the application of suction samplers, (Robinson & Tully 2000b, Pallas et al. 2006, Zintzen et al. 2006) or through the removal of previously fixed panels (Antoniadou et al. 2010). In this study, we concentrated on macroscopic mobile decapod species inhabiting a rocky bottom system in the southern North Sea, which could be identified directly in the field through SCUBA diving.

Our objective was to reveal possible impacts of commonly used coastal defence structures (tetrapods) on decapod crustacean abundances and the associated community structure. Therefore, experimental fields, consisting of tetrapods, were introduced in the subtidal area in the north of the island Helgoland.

MATERIALS AND METHODS

Study site

The rocky island Helgoland is located in the German Bight (54°11' N, 07°52' E). Helgoland is the only natural hard-bottom area in the otherwise soft-bottom dominated southern North Sea and the "Helgoländer Felssockel" covers an area of about 35-km². The next natural hard-bottom communities occur along the Norwegian and East English coastline (Harms 1993) about hundred kilometres away. This sedimentological particularity has led to a geologically and ecologically isolation from similar hard-bottom areas, the closest of which occur in Norway and Britain (Franke & Gutow 2004).

Helgoland's coastline is highly exposed because of strong storm events and high-wave action. Therefore almost the entire coastline of Helgoland and its associated small island "Düne" is protected with coastal defence structures. The majority of these structures (approximately 10,000) are so-called "tetrapods", which are four-footed concrete breakwaters that weigh six-tons each.

A total of six experimental tetrapod fields were established parallel to the shoreline in February 2010 north of Helgoland in approximately 400 m distance to the coastline. The positions for the fields were determined previously. Three fields should be established in 5-m water depth by mean low-water spring (MLWS) in a typical kelp site and a further three in 10-m water depth (MLWS).

During the establishment procedure the working vessel drifted away from the original position because of bad weather conditions. Therefore one tetrapod field was established in about 7-m depth instead of planned 5-m. The other tetrapod fields were introduced as planned (Fig. 1).

The three fields in each depth contour were placed in a distance of 80 m to each other to, on one hand, reduce reciprocal impacts, and on the other hand, ensure similar environmental conditions. One field exists of six tetrapods, which are arranged in two rows of three tetrapods. The size of one experimental field is around 7 x 4.5 m and about 2 m in height (Fig. 1).

The data sampling took place by the tetrapod fields in the 5 – 7-m depth contour where the natural habitat was dominated by rocky to pebbly substrate. The surrounding of the field in 7-m depth was characterised by low density of the kelp *Laminaria hyperborea* and much finer pebbly substrate in contrast to the fields in 5-m depth.
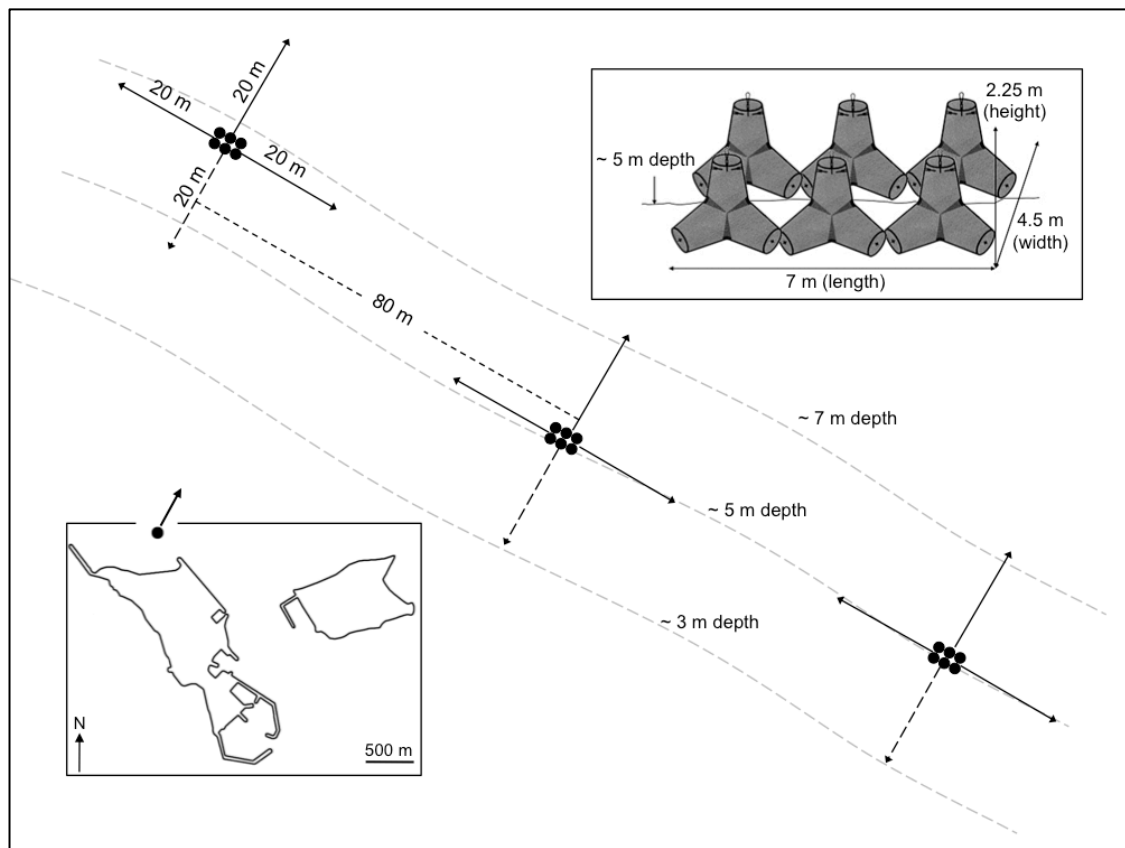
Fig. 1 The study area, 400 m north of Helgoland. Three tetrapod fields were introduced in February 2010 along the 5 – 7-m depth contour. The fields are in a distance of 80 m to each other and one field consists of six tetrapods arranged in two rows of three. Counting of crustaceans was done by SCUBA along four 20 m long transect-lines at each tetrapod field on fixed counting stations. Before the introduction of the fields in 2010, a thorough assessment of the fish and macro-crustacean community was done in 2009 along three transects (continuous lines) at each tetrapod field

Survey methods

The assessment methodology in 2009 (without tetrapods) and 2010 and 2011 (with tetrapods) was identical. Transect-lines were laid out cross-like (Fig. 1) at the beginning of the tetrapod fields (in 2010 and 2011) or the proposed position of the tetrapod fields (in 2009), which was subsequently named the 0-m counting station. Sampling was performed every 5 m (0, 5, 10, 15, 20 m) along the transect by counting and identifying all fish in a 1 x 1 m square left of the transect-line and a 1 x 1 m square right of the transect-line. The diver used a 1-m-long PVC rod to determine the size of the 2 x 1 m rectangle.

After approaching the appropriate counting station along the transect-line carefully the diver counted all crustacean species. In a final step, all stones measuring up to 10 cm were turned carefully to look for hidden organisms (Beldade & Goncalves 2007, Wehkamp & Fischer 2012b). To standardise the counting and to eliminate differences in the sampling technique, the same diver made the observations throughout the survey period (Sayer et al. 1993, Magill & Sayer 2002). At each transect-line, five 2 x 1 m counting stations were analysed at distances of 0, 5, 10, 15 and 20 m from the tetrapods. Under good weather conditions, we were able to count all four (in 2010 and 2011) or three (in 2009) transect-lines (with five counting stations each) per tetrapod field for a total of 60 counting stations per month in 2010 and 2011 and 45 counting stations per month in 2009.

Abiotic factors

The water temperature (°C) was calculated for each month from the mean value of all sampling days in the specific month. In all years, the water temperature was measured continuously at the "Kabeltonne" site (54°11.3′ N, 7°54.0′ E; Wiltshire et al. 2010) in the frame of the Helgoland Roads long-term series close to the study side. The transparency of the water (m) was quantified during each counting event with a Secchi disc fixed at the southernmost transect at each sampling site. Identical to a normal Secchi depth estimation procedure, water transparency was defined as the diver's distance from the Secchi disc at which the disk was no longer visible. Crustacean assessments were performed only when the horizontal Secchi distance was at least 1 m. Furthermore, the exact dive time, tide cycle (low tide, slack tide, high tide) and special observations were recorded during each sampling.

Data analysis

If possible, all visible macro-benthic crustaceans were identified to the species level. We concentrated on macroscopic species of the order Decapoda (largest natural grouping within the class Malacostraca), which were easily detectable and identifiable for the diver. Although sometimes detected, highly cryptic species such as *Macropodia rostrata* were excluded from analysis, because these occasional sights were only by chance. The following species were included in the analysis: *Homarus gammarus*, *Pagurus bernhardus*, *Galathea squamifera*, *Pisidia longicornis*, *Hyas araneus*, *Cancer pagurus*, *Necora puber*, *Liocarcinus* spp., *Carcinus maenas*, *Pilumnus hirtellus*.

74

Statistical analysis

All statistical analyses were performed in R (version 2.14.1) on a significance level of p = 0.05 (unless otherwise stated). Most of the data collected were not normally distributed. Therefore, data were either transformed to normal distribution using classical transformation procedures (Köhler et al. 1992) or, if not successful, data were rank-transformed prior to the application of parametric statistical test procedures like ANOVA (Conover & Iman 1981).

In this study, the three experimental fields were used as replicates. A statistical analysis revealed, however, that the fields differed in their average crustacean abundances over the three sampling years (ANOVA, *df* = 2, *F* = 21, p < 0.0001). A Tukey HSD test on species level displayed, that only two species, *G. squamifera* and *P. hirtellus* differed in their average abundances among the three fields (Table 3).

When excluding these two species, the experimental fields showed no significant difference in the average abundances over the three sampling years any more (ANOVA, *df* = 2, *F* = 0.51, *P* = 0.604). Because all other species were not affected through the position of the fields (Table 3), the tetrapod fields were used as replicates for analysis when focussing on impacts on the total abundances.

Analyses of co-variances (ANCOVA) were applied to analyse possible effects of water temperature and tidal cycle on overall crustacean abundances and distribution.

Crustacean abundances over year and month and distance

To assess the temporal patterns of total crustacean abundances among the three years, 2009, 2010 and 2011 and among the months within the years, ANOVA's with "year" and "month" as fixed factors were applied.

For a comparable detailed analysis of spatial effects of the tetrapods on the crustacean community, following months were used: June, July, August and September in 2009 (without tetrapods) and June, July, August and October in 2010 and 2011 (with tetrapods). This approach ensured that the samples in the three years covered identical numbers of counting stations and samplings each year.

The factors "month", "year" and "distance to the tetrapods" (0 m, 5 m, 10 m, 15 m and 20 m) were used as fixed factors to reveal possible impacts on the overall abundances with subsequent post-hoc tests (Tukey HSD).

Statistical analyses were additionally conducted to demonstrate species-specific impacts of the factors "field", "year", "month" and "distance" for the five most abundant species (*G. squamifera, C. pagurus, P. hirtellus, H. araneus, H. gammarus*) separately.

RESULTS

The average water temperature in all three sampling years followed a typical bell-shaped curve over the year (Fig. 2). Minimum temperatures were observed in March 2011 (3.45 °C, SD 0.48) followed by March 2010 (3.8 °C, SD 0.70). The months of August always included the highest temperatures, with 17.90 °C (SD 0.26) in 2009, 17.73 °C (SD 0.5) in 2010 and 17.10 °C (SD 0.40) in 2011. The average temperatures in October 2010 and 2011 were similar with 14.85 °C (SD 0.64) in 2010 and 14.20 °C (SD 0.14) in 2011, but were significantly lower than the average temperature of 17.10 °C (SD 0.40) in September 2009 (Fig. 2).

Analyses revealed that the "tidal cycle" (ANCOVA with "distance" as fixed factor; 2009: $df = 1$, $F = 0.005$, $p = 0.9460$; 2010: $df = 1$, $F = 0.470$, $p = 0.4931$; 2011: $df = 1$, $F = 1.967$, $p = 0.161$) as well as the "water temperature" (ANCOVA with "month" as fixed factor; 2009: $df = 1$, $F = 0.492$, $p = 0.484$; 2010: $df = 1$, $F = 0.515$, $p = 0.473$; 2011: $df = 1$, $F = 0.243$, $p = 0.622$) had no significant effect on the crustacean abundance m^{-2}, and thus these variables were excluded from further analysis.
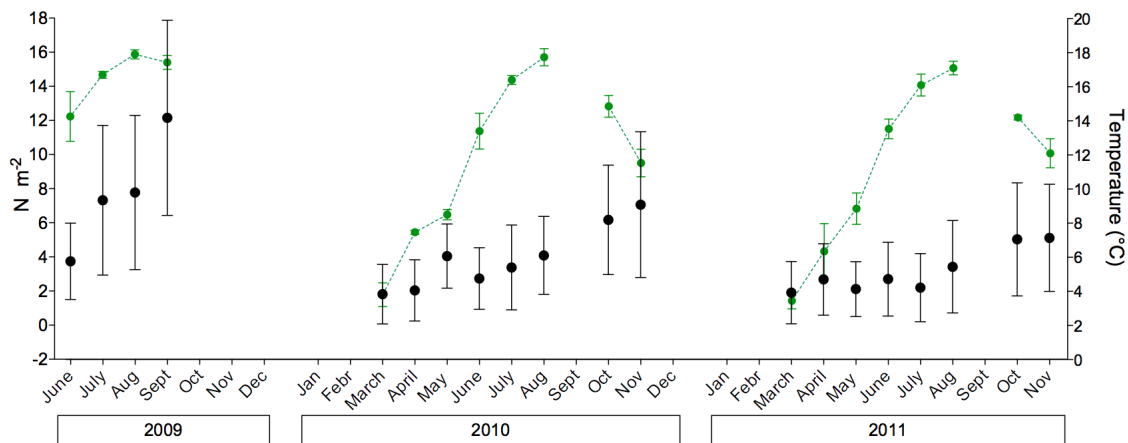

Fig. 2 Crustacean abundances m^{-2} (mean, SD; left y-axis, black symbols) and temperatures in °C (right y-axis, green symbols linked with dashed line). Shown are all sampled months for the three sampling years 2009, 2010, 2011

Crustacean abundances

The factor "year" had a significant impact on the average crustacean abundances m^{-2} (p < 0.0001, Table 1). A total of 2790 (7.75 ind. m^{-2}) crustacean individuals were counted in 2009, 1457 (4.05 ind. m^{-2}) in 2010 and only 1158 (3.22 ind. m^{-2}) in 2011. Fig. 4 shows, that this significant decrease (Table 1 + 4) in the years 2010 and 2011 was mainly caused by significant lower abundances of the species *G. squamifera, P. hirtellus* and *P. longicornis*.

Also the factor "month" (p < 0.0001, Table 1) as well as the factor "distance" (p < 0.0202, Table 1) showed a significant effect on the average crustacean abundances m^{-2}. Furthermore the factors "year" and "month" interacted significantly (p < 0.0013, Table 1). The crustacean abundances m^{-2} differed significantly over all months in every year (Table 2, Fig. 2).

The impact of the distance to the tetrapods on the average crustacean abundances was only significant in 2011 (p < 0.0117, Table 2). A Tukey HSD test showed that the 0-m station by the tetrapods in 2011 hosted significant more individuals compared to the counting stations in 15 m (*p* = 0.0135) and 20 m (*p* = 0.0244) distance (Fig. 3).

This pattern was also predominant, when the average abundances of the months were converted into percentages for each year. Although the second year after the introduction, 2011, showed less numbers of crustaceans in total, the 0-m station by the tetrapods contained more percentages of crustaceans than the other stations (Fig. 3).

This effect was caused by higher abundances of *H. araneus* and *H. gammarus* in 2011 at the 0-m counting station (Table 3, Fig. 4).

Table 1 Effects of the factors "month", "year" and "distance" on the crustacean abundances m^{-2} by the same number of sampled months within the same number of counting stations (June – September 2009, June – August and October for 2010 and 2011). Significance codes are given as followed: 0 $^{(***)}$ 0.001 $^{(**)}$ 0.01 $^{(*)}$ 0.05 $^{(.)}$ 0.1 $^{()}$ 1

Factor	df	F value	Pr (>F)
month	3	48.289	***
year	2	82.002	***
distance	4	2.939	*
month:year	6	3.694	**
month:distance	12	0.307	ns
year:distance	8	1.915	ns
year:month:distance	24	0.638	ns

Table 2 Effects of the factors "month" and "distance" (0 m, 5 m, 10 m, 15 m, 20 m) on the crustacean abundances m^{-2} for each sampling year including all sampling months (June – September 2009, March – August and October - November in 2010 and 2011). Significance codes are given as followed: 0 $^{(***)}$ 0.001 $^{(**)}$ 0.01 $^{(*)}$ 0.05 $^{(.)}$ 0.1 $^{()}$ 1

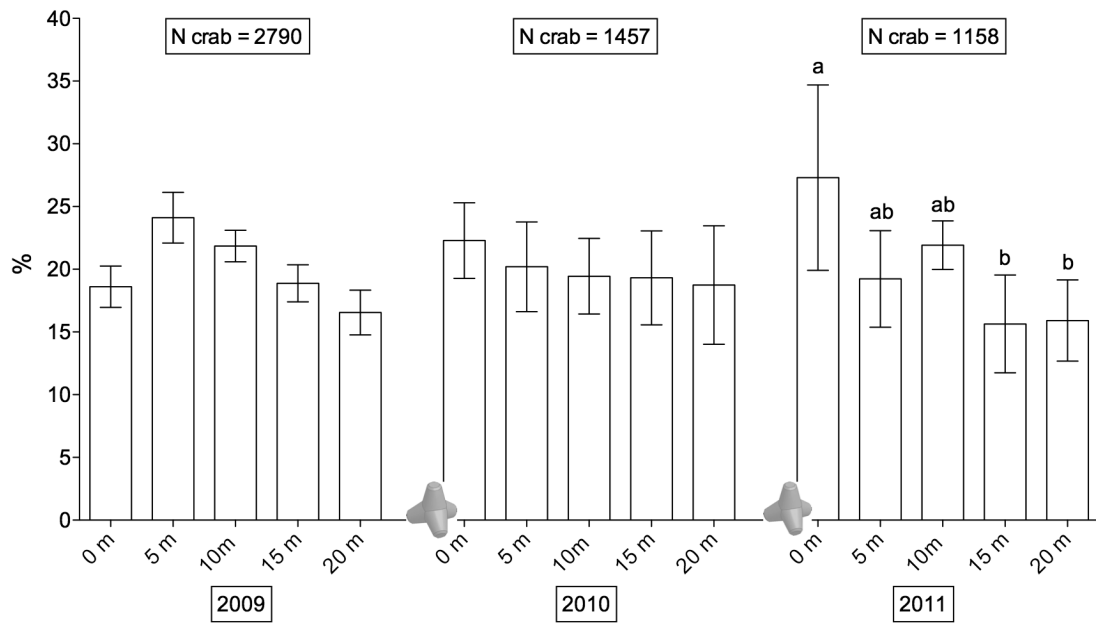| Factor	year	df	F value	Pr(>F)
month	2009	3	28.41	***
	2010	7	30.38	***
	2011	7	13.47	**
distance	2009	4	1.76	ns
	2010	4	0.508	ns
	2011	4	3.33	*

Fig. 3 Percentage distribution of all crustaceans (+/- SD) among the counting stations (distance to the tetrapods) integrated over the months June – September in 2009 and June – August & October in 2010 and 2011. In 2009 2790 crustaceans, in 2010 1457 crustaceans and in 2011 1158 crustaceans were counted in total. The letters above the bars represent significant differences between the average abundances m^{-2} in the year 2011

Species distribution

Besides the effects on the crustacean abundances in general, we observed also distinct species-specific effects (Table 3, Fig. 4).

These species-specific distribution patterns were most prominent in the five species *C. pagurus, G. squamifera, P. hirtellus, H. araneus* and *H. gammarus* and the results of the statistical analysis are shown in Table 3.

Cancer pagurus

The factor "year" showed a significant effect on the average abundances of the edible crab (*C. pagurus*) with significant higher abundances in 2010 (0.86 ind. m^{-2}) compared to the years 2009 (0.59 ind. m^{-2}) and 2011 (0.61 ind. m^{-2}) (Table 3, Fig. 4). No significant patterns were found in average abundances of *C. pagurus* with respect to the three different tetrapod fields as well as to the distances to the fields (Table 3).
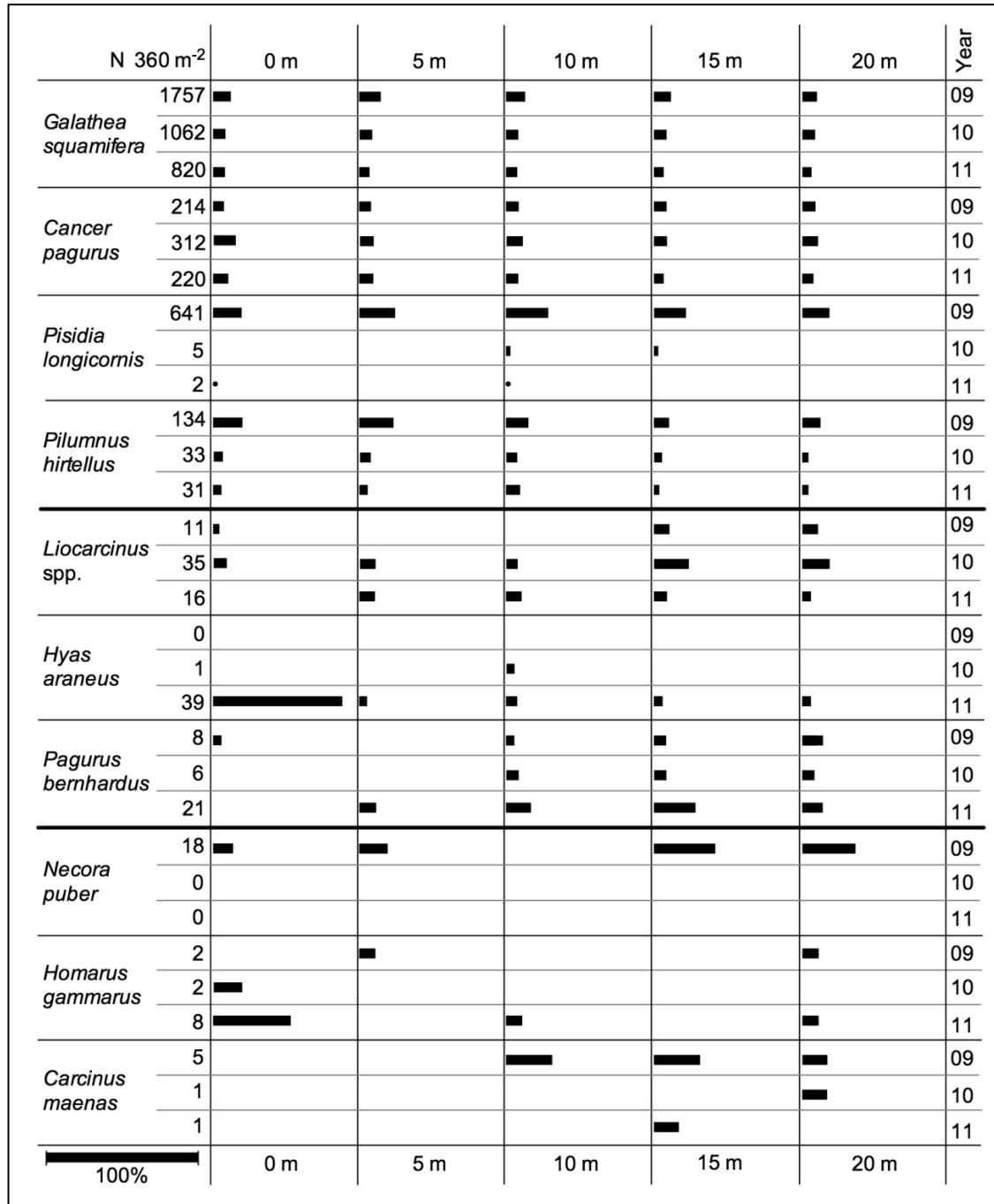
Fig. 4 Percentage distribution for all found species. Behind the species names the abundance for 360 m^2 is given for each year. The percentages were calculated for each species separately whereas the total found number over all three years (2009, 2010 and 2011) for a species represents 100 %. The size of the bars constitutes to the percentage distribution of the individual crustacean species over the counting station over the years (integrated are the months June – September 2009, June – August & October 2010 and 2011

81

Table 3 Effects of the factors "field" (1 = north, 2 = at centre, 3 = south), "year" (2009 = 09, 2010 = 10, 2011 = 11), "month" (June – Sept 09, June – Aug and Oct 10 and 11) and "distance" (0 m, 5 m, 10 m, 15 m, 20 m) on the average abundances m^{-2} of the five most abundant species. Letters in bold stand for the results of applied ANOVA's; regular letters for the results of Tukey HSD test procedures. Significance codes: 0 $^{(***)}$ 0.001 $^{(**)}$ 0.01 $^{(*)}$ 0.05 $^{(.)}$ 0.1 $^{()}$ 1

	field				**year**				**month**				**distance**			
		df	*F*	*p*		*df*	*F*	*p*		*df*	*F*	*p*		*df*	*F*	*p*
Galathea squamifera	**all**	**2**	**29.71**	*******	**all**	**2**	**41.43**	*******	**all**	**3**	**36.88**	*******	**all**			**ns**
	2-1			***	09-10			***	09	3	21.24	***				
	3-1			***	09-11			***	10	3	15.82	***				
	2-3			ns	10-11			**	11	3	15.44	***				
	09	**2**	**5.934**	******												
	2-1			ns												
	3-1			**												
	3-2			*												
	10	**2**	**12.21**	*******												
	2-1			**												
	3-1			***												
	3-2			ns												
	11	**2**	**23.49**	*******												
	2-1			**												
	3-1			***												
	3-2			ns												
Cancer pagurus				ns	**all**	**2**	**7.14**	*******	**all**	**3**	**5.36**	******	**all**			**ns**
					09-10			**	2009	3	3.53	*				
					09-11			ns	2010	3	15.48	***				
					10-11			**	2011			ns				
Pilumnus hirtellus	**all**	**2**	**2.56**	*******	**all**	**2**	**26.49**	*******	**all**			**ns**	**all**	**4**	**2.88**	*****
	2-1			ns	09-10			***					5-15			.
	3-1			***	09-11			***					15-10			.
	2-3			***	10-11			ns								
	09	**2**	**4.791**	******												
	2-1			ns												
	3-1			ns												
	3-2			**												
	10	**2**	**7.55**	*******												
	2-1			ns												
	3-1			***												
	3-2			.												
	11	**2**	**5.721**	******												
	2-1			ns												
	3-1			**												
	3-2			ns												
Hyas araneus				ns	**all**	**2**	**20.24**	*******	**all**			**ns**	**all**	**4**	**11.8**	*******
					09-10			ns					0-5			***
					09-11			***					0-10			***
					10-11			***					0-15			***
Homarus gammarus				ns	**all**			**ns**	**all**			**ns**	**all**	**4**	**4.50**	*****
													0-5			*
													0-10			*
													0-15			**
													0-20			*

Galathea squamifera

The squat lobster (*G. squamifera*) was differently distributed over the three tetrapod fields (Table 3). A Tukey HSD test demonstrated differences in their average abundances in 2009 between the field in the south (6.31 ind. m^{-2}) to both other fields (field north 4.02 ind. m^{-2}, field at centre 4.31 ind. m^{-2}). In 2010 and 2011, after the introduction of the tetrapods, the northern field contained significantly lower abundances (2010: 1.84 ind. m^{-2}, 2011: 0.98) compared to the two other fields (field at centre; 2010: 3.16 ind. m^{-2}, 2011: 2.7 ind. m^{-2} and field south; 2010: 3.85 ind. m^{-2}, 2011: 3.14 ind. m^{-2}).

The abundances of *G. squamifera* decreased after the introduction of the tetrapod fields from 4.88 ind. m^{-2} in 2009 to 2.95 ind. m^{-2} in 2010 and down to only 2.28 ind. m^{-2} in 2011 (Fig. 4). Statistical analyses showed significant differences in the abundances between 2009 to 2010 and 2011 (Table 3).

The months differed significantly in their abundances of *G. squamifera*, whereas the squat lobster was equally distributed among the counting stations in all three years (Table 3, Fig. 4).

Pilumnus hirtellus

Similar to the squat lobster, significant differences of abundances were found between the three tetrapod fields for *P. hirtellus*.

The hairy crab (*P. hirtellus*) was mostly abundant in all three years at the tetrapod field in the South (2009: 0.54 ind. m^{-2}, 2010: 0.18 ind. m^{-2}, 2011: 0.17 ind. m^{-2}). The field in the North contained in 2009 0.36 and in 2010 and 2011 only 0.03 ind. m^{-2} resp. 0.02 ind. m^{-2}. The field at the centre showed also lower numbers of *P. hirtellus* with 0.08 ind. m^{-2} in 2010 as well as in 2011.

Besides these spatial patterns, significant temporal effects were detected among the three years, but not among the months within each year (Table 3). Highest abundances were observed in 2009 prior to the tetrapod installation with 0.37 ind. m^{-2}. After the introduction of the tetrapods, the average abundances significantly dropped to only average values of 0.09 ind. m^{-2} in 2010 and 2011 (Table 3, Fig. 4).

Although an ANOVA revealed a significant impact of the factor distance on the average abundances m^{-2}, a Tukey HSD showed no distinct differences among the counting stations (Table 3).

Hyas araneus

The great spider crab (*H. araneus*) was almost absent in the years 2009 and 2010. In 2011, however, we observed a significant increase in average great spider crab densities with 0.11 ind. m^{-2}, especially in the immediate vicinity of the tetrapods at the 0-m counting station (Fig. 4, Table 3). In contrast, no significant effects were observed of the factor month.

Homarus gammarus

The common lobster (*H. gammarus*) was only counted two times in 2009 and in 2010 (Fig. 4). In 2011, however, we had a total of eight lobster sightings. All these sightings were made close by the tetrapods and the same lobsters were observed multiple times over the season at the same tetrapod fields.

Further species

All further species were observed only with very low abundances or only during a single year. The long-clawed porcelain crab (*Pilumnus hirtellus)* and the velvet swimming crab (*Necora puber)* for example were only spotted in the year 2009 (Fig. 4), before the tetrapods were established. The hermit crab *Pagurus bernhardus* was never counted at the 0-m station after the establishment of the tetrapods and only with low abundances in further distances to these structures. The swimming crabs (*Liocarcinus* spp.) and the shore crab (*Carcinus maenas*) were highly mobile species and were detected only by chance, when moving above the ground (pers. observation).

DISCUSSION

Many studies on the sublittoral crustacean community focus on small and only less vagile crustaceans. Those organisms can easily be sampled by scratch samplings or suction samplers (Robinson & Tully 2000b, Pallas et al. 2006) or through the removal of previously fixed panels (Antoniadou et al. 2010). These methods are highly effective to sample species which could not be identified *in situ* or which are hidden between algae. Larger species, however, which often form a considerable part of the decapod crustacean community, will be lost by these removal methods because of their mobility. Furthermore, the sampled area is relatively small in relation to the size of the species.

In this study, benthic decapod crustaceans were counted through visual censuses along transect-lines at fixed counting stations. The species, sampled in this study are difficult to detect due to their colouration and their characteristic to hide under stones. Therefore, we invested in dive time to carefully turn individual stones. Especially for micro-scale assessments with regard to cryptobenthic species this method is highly recommended (Beldade & Goncalves 2007, Wehkamp & Fischer 2012b). Hidden species between and under stones can be identified, which is not achievable even with retrospective underwater photography or video documentation of a certain area (Ehrenberg & Ejdung 2008).

However, we are sure that even with an intense visual sampling strategy, average abundances are still underestimated. Especially smaller species, such as *P. hirtellus* and *P. longicornis* are highly camouflaged and do vanish quickly when disturbed by the observer. These species may form an unknown part of a hidden community that is only detectable using additional destructive sampling methods, such as the use of suction samplers (Robinson & Tully 2000b, Pallas et al. 2006). Other species, such as hermit crabs are extremely difficult to detect because of their perfect camouflage. Additionally, highly mobile crabs such as *Liocarcinus* spp. or *Carcinus maenas* may escape before being detected by the observer.

A variety of studies postulate that the creation of artificial habitats destroys an existing natural habitat. It does not matter if the material is introduced for coastal protection or as artificial reef to enhance fisheries (Bulleri & Chapman 2010, Chapman & Underwood 2011)

We observed a significant decrease of the total crustacean abundances after the introduction of the tetrapods at the beginning of 2010. This finding can be explained by

the loss of smaller and less mobile decapod species like *G. squamifera*, *P. longicornis* and *P. hirtellus*. One possible reason for that decrease may by the "destruction" of about 100 m^2 of natural habitat through the introduction of the breakwaters. However, it has to be mentioned that the tetrapods do not only have a significant impact to the area where they were placed. We found the same decrease of abundances also in the surrounding area in a distance up to 20-m to the tetrapods. These areas have not been physically altered in any way.

Wehkamp & Fischer (2012a) showed, that in the same area, such outreach effects of the artificially introduced tetrapods to the surrounding environment do exist. The tetrapod fields contained half of the total abundances of the fish found in the complete study area. A migration effect towards the tetrapods was responsible for the high density of fish at the tetrapod fields.

The patterns of change in the crustacean community after the introduction of the tetrapods, however, seem to be much more complex. It could not be clarified, if the reason for the decrease in the crustacean abundances was caused only by the establishment of the tetrapods. Other studies have already shown, that individual decapod crustacean species have distinct microhabitat preferences (Samuelsen 1970, Wehkamp & Fischer 2012b), but have also distinct interannual abundance fluctuations depending on abiotic factors like water temperatures (Robinson & Tully 2000a).

The squat lobster (*G. squamifera*) was significantly less abundant at the northern tetrapod field after the introduction of the fields. This field was accidently introduced at 7-m depth instead of 5-m depth. The surrounding was characterised by finer pebbly substratum than the other both fields. Perhaps the decrease of the number of squat lobster resulted also on the lack of microhabitat in form of stones and cobbles by the northern field.

The minimal water temperatures in 2010 and 2011 in winter were exceptionally low (<2 °C) compared to 2009 and the years before. This low water temperatures may also caused the overall decrease in decapod abundances. In this study we found no significant effect of the water temperature on the crustacean abundances. However, we missed some winter months for sampling due to bad weather conditions. Furthermore, temperatures and other abiotic factors such as changes in salinity or nutrients interacted strongly and may confound each other. To detect possible effects of these factors on the species distribution we need separate studies with appropriate measuring tools.

Robinson & Tully (2000a) described temperature as the most influencing factor, affecting instar duration and moult increment, and therefore the period taken to reach maximum size. Variability in environmental parameters is the most likely determinant of the survival of juveniles and YOY groups. Natural mortality by age also influenced the abundance of crustacean species (Samuelsen 1970, Robinson & Tully 2000b, a). The porcelain crab (*P. longicornis*) reaches an age of only two years and reproduces in the first year (Samuelsen 1970). It is suggested that most females die after they released their larvae (Robinson & Tully 2000a). Therefore, a combination of adult mortality and larvae destruction caused by the strong winter seasons may be also responsible for the significant decrease in average abundances of these species in 2010 and 2011.

Another reason for the observed decrease of the crustacean abundances, especially of the smaller species, might be the higher abundances of predators like fish or larger decapods attracted by the tetrapods. It is suggested that fish and mobile crabs feed on the epibenthic organisms at artificial structures and on smaller invertebrates, which are associated within the fouling community (Clynick et al. 2007, Chapman & Underwood 2011). Furthermore, fish and larger crustaceans may migrate during specific times over the diurnal cycle to prey in the surrounding (DeGrave & Turner 1997, Nickell & Sayer 1998, Bell & Turner 2003). This may also be a factor putting extra pressure on the macro-invertebrate community, with respect to predation-induced mortality.

The findings of this study, supported by other studies on this topic, suggest that the temporal and spatial dynamics of macro-invertebrate communities in sublittoral boreal and cold-water environments are highly species-specific and are hardly regulated by a single abiotic or biotic factor such as temperature or predation pressure (Pallas et al. 2006, Hunter & Sayer 2009, Silva et al. 2010).

Complex artificial habitats are assumed to be attractive habitats also for some decapod crustaceans. Hunter & Sayer (2009) found higher abundances of crab species (*C. pagurus, N. puber*) at artificial complex structures than in less complex natural rocky habitats. Their findings, however, showed that the differences in abundances between the studied habitats were distinct only in specific seasons and depend furthermore on the individual species.

In this study, only two species were significantly more abundant at the tetrapod fields than in distance to them. Or rather, they were almost found only by the tetrapods. These species were the lobster (*H. gammarus*) and the great spider crab (*H. araneus*).

A strong positive attraction of artificial substrata on lobsters (*H. gammarus*) has been postulated also by other studies (Wollf & Sandee 1971, Jensen et al. 1994, Jensen et al. 2000, Krone & Schröder 2011). Clawed lobsters live solitarily within crevices between rocks or inside holes, which they shape between hard substrate and soft-bottom (Krone & Schröder 2011). Lobsters are nocturnal active predators and are hidden during daytime. Therefore, we assume that we may underestimate the number of lobster during the field observation, which were done only at day. However, our studies revealed that tetrapod fields offer an attractive habitat opportunity for lobsters within different openings and sufficient shelter possibilities – important for predator-prey interactions – for these large decapods (Spanier 1994).

For the squat lobster *H. aranues* no studies exist about the impact of artificial substrate on this species (to our knowledge) and only little information is present about their general habitat preferences. Wollf & Sandee (1971) investigated decapods in estuarine areas and suggested that *H. araneus* is confined to areas with a rough bottom formed either by stones used for the protection of the dikes or beds of mussels and oysters. Hartnoll (1963), however, found the species on rocky substrate within *Laminaria* beds as well as on inshore sandy bottoms. In the present study, *H. araneus* occurred mainly headfirst under the shady tetrapod feet in distance to the bottom. Sometimes up to five individuals were observed underneath one tetrapod foot where they remain motionless. The organisms were highly camouflaged within the surface of the structures. We assume, that the tetrapods were used mainly as shelter against predators like the benthic long-spined sea scorpion (*T. bubalis*).

No effect of the artificial habitat could be revealed for high mobile and active predators like the edible crab (*C. pagurus*). Hunter & Sayer (2009) found the edible crab mainly during winter at complex artificial structures. During the other seasons, no differences in densities between less complex habitats and the artificial substrate were found for the edible crab.

Other studies revealed also a positive effect on the abundance of *C. pagurus* in combination with artificial structures (Jensen et al. 2000, Langhamer & Wilhelmsson 2009). The artificial materials in these studies, however, were established on soft-bottom substrate where no other shelter opportunities are available in near distance. In contrast, the natural substratum of our study area consisted of hard substratum with most likely sufficient refuge possibilities. *C. pagurus* and other mobile crabs show daily, short- and long-term migration behaviour (Ingle 1983, Karlsson & Christiansen

1996, Ungfors et al. 2007, Silva et al. 2010), which occurs regarding the search for females, new habitats or prey and as response to seasonal temperature. Long-term migration of females seemed to be related to reproduction (Ungfors et al. 2007). Therefore, these factors seem to influence the distribution of *C. pagurus* additionally.

The tidal cycle was predicted by Silva et al. (2010) to influence especially the activity of mobile decapods. Significant relationships were found between the tidal cycle and the occurrence of decapods in intertidal areas. The authors suggest that the species migrate during specific tides and times over the diurnal cycle from subtidal into intertidal areas to feed on prey organisms. In our study we found no effect on the tidal cycle on the overall crustacean abundances. Since the investigation of the impact of the tides was not the main goal of this study, the results could be affected by the lack of suitable sampling strategies. Our sampling took place only on daytime. In following studies we have to sample at specific times over a 24-hour time period to detect differences in crustacean abundances over the diurnal rhythm in combination with the tidal cycle.

In general, knowledge of the temporal development and spatial patterns of artificial reef communities is still lacking and long-term monitoring of artificial communities is inevitable for the understanding of ecological processes and for evaluating their possible impact on the surrounding (Perkol-Finkel et al. 2006).

The initiations of decade-long monitoring programs are essential to distinguish between natural induced short-term (inter-annual to intra-decadal) variability from long-term changes - affected mainly by anthropogenic influence (Collins et al. 1994, Franke & Gutow 2004).

In conclusion, our study illustrate that the species reacted differently on the alteration of their surrounding and perhaps the occurrence of predators by the breakwaters. The results show that it is not possible to make clear statements about the impact of artificial structures on a decapod assemblage in general. This finding is important for further studies, which aim to investigate relationships between artificial structures and crustaceans. To reveal such effects on these kinds of species we have to differentiate between the individual species.

Nevertheless, we can state that for some species the tetrapods were attractive as refuge, e.g. for *H. araneus, H. gammarus* or for larger individuals of *G. squamifera*. For other, especially smaller species, this habitat form may not be optimal due to the lacking microhabitats and the occurrence of predators.

Furthermore this study highlighted the importance of the application of long-term studies. Only then we have the chance to distinguish between natural induced and anthropogenic induced factors which influencing species distribution patterns.

GENERAL DISCUSSION

The objective of this thesis was to reach a better understanding of the spatial and temporal distribution patterns of demersal fish and decapod crustaceans over different substratum types. The main goal was to gain knowledge about the response of species to the alteration of their natural surrounding caused by artificially introduced substrate in form of commonly used breakwaters (tetrapods).

To reveal possible impacts of artificial structures, however, a thorough understanding of the functional relationships between species and their natural habitats is necessary (Gotceitas et al. 1995, Fraser et al. 1996, Letourneur et al. 2003, Chatfield et al. 2010). Therefore, micro-scale distribution patterns over different natural habitat types within the study area for fish and crustacean species were investigated before the artificial structures were introduced.

Using SCUBA supported visual census along fixed line-transects as methodology, the species composition was analysed right by the artificial structures and in distance to them over a two-year sampling period after the introduction of the tetrapods.

In the following discussion, the before presented results (chapter I to III) and first results of an associated diploma thesis (Seidler 2012) will be discussed with respect to a general understanding of the spatial and temporal dynamics of fish and crustacean populations associated with subtidal coastal defence structures in the Southern North Sea.

Methodology

In general, the method used in this study proved to be highly suitable for such studies, dealing with the quantitative assessment of demersal fish and larger decapod species, abundances and size classes. The use of fixed transect-lines is recommended to ensure adequate diving time and safety in combination with a resilient data sampling. The additional turning over of stones after the visual counting above the substrate (Beldade & Goncalves 2007, Wehkamp & Fischer 2012b) was very effective to detect hidden and cryptobenthic species. Most of the species investigated in this study appeared to trust in their camouflage or showed an inquisitive behaviour towards the approaching diver. However, especially for small cryptic crustaceans like *P. hirtellus* and *P. longicornis* it has to be mentioned that this method most probably still provides an underestimation

because of the individuals' opportunity to vanish quickly before detected by a diver. These species may form an unknown part of a hidden community and are only detectable using additional but mainly destructive sampling methods, such as suction samplers (Robinson & Tully 2000b).

Spatial distribution patterns

Large-scale habitat definitions like "seagrass bed", "sandy flat" or "rocky shore" are often not able to give precise information about the assemblage structure and occurrence of species. Therefore, a number of authors (e.g., Letourneur et al. 2003, La Mesa et al. 2006, Moore et al. 2010) stated that individual environmental and biological factors on a small-scale level are most important for driving the distribution and abundance of fish assemblages.

This thesis strongly supports these statements. All benthic fish species, like *T. bubalis* and *P. gunnellus*, which occurred in high abundances in the study area, revealed a distinct association with a specific natural habitat type over a micro-scale dimension. Regarding the crustaceans, the findings were not as distinct as for fish and the study showed that the occurrence of decapods within a specific habitat is even more complex. Spatial patterns over habitats vary highly in dependence the decapod's mobility, their size and are additionally influenced by abiotic factors determining their life cycles. This was detected for larger species such as *C. pagurus* or *G. squamifera*, but also for smaller, less vagile species like *P. longicornis* and *P. hirtellus*.

The edible crab (*C. pagurus*) is a highly mobile predator and this species as well as the squat lobster (*G. squamifera*) were found in different sizes over all natural substratum types. The long-clawed porcelain crab (*P. longicornis*) and the hairy crab (*P. hirtellus*), however, were abundant mainly on habitat containing pebbly substrate.

The main findings of this thesis revealed that the association of species with a certain kind of microhabitat are related to three levels (examples see Fig. 1):

- The generally lifestyle of the species (e.g. benthic or semi-pelagic)
- The availability of an adequate shelter size with respect to the size of the species
- The colouration of the substrate, which must suit the camouflage colour of the species.

The results of an associated diploma thesis (Seidler 2012) support these findings and showed a distinct microhabitat selection of some species within the tetrapod fields (Fig. 2). The long-spined sea scorpion (*T. bubalis*) used different microhabitats depending on its stage of life (Fig. 1a+b, Fig. 2). Young-of-the-year individuals of this species seemed to prefer the algal covered substrate on the tetrapods as shelter. The individuals were perfectly camouflaged within the epifauna. Older individuals were mainly found between stones on the ground where they strongly adopt the colouration of the natural substrate. *G. squamifera* were found, in dependence of their individual size, both between and under stones of different sizes (Fig. 1c). The great spider crab (*H. araneus*) remained mainly underneath the tetrapod feet, away from the ground (Fig. 1d). It is suggested that this species used this microhabitat as shelter. A detailed analysis of the results is still in progress and will be published later on.
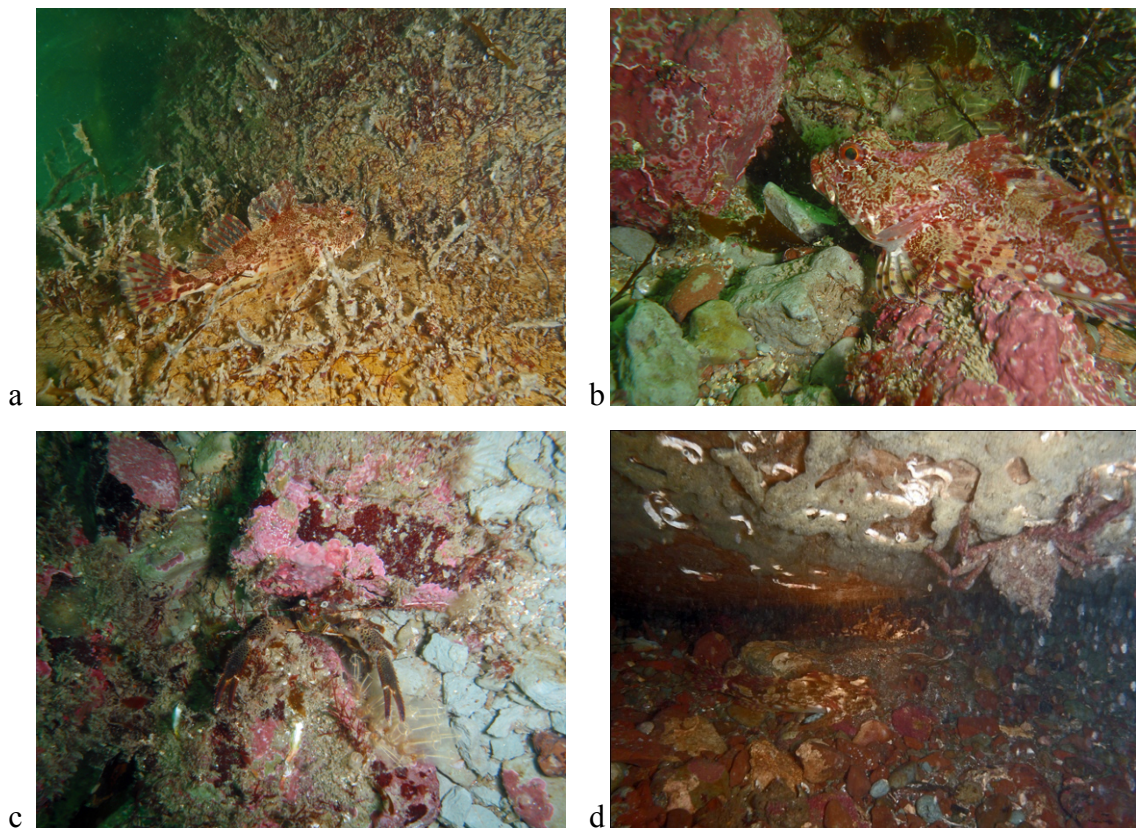

Fig. 1 The photographs show the camouflage of the species within specific habitat types. Young-of-the-year individuals of *T. bubalis* (a) preferred the algal covered tetrapod feet as microhabitat whereas older *T. bubalis* individuals were found mainly on the ground between stones (b). *G. squamifera* (c) was found in dependence of its individual size between and under stones and the species *H. araneus* (d) was almost always found under the tetrapod feet
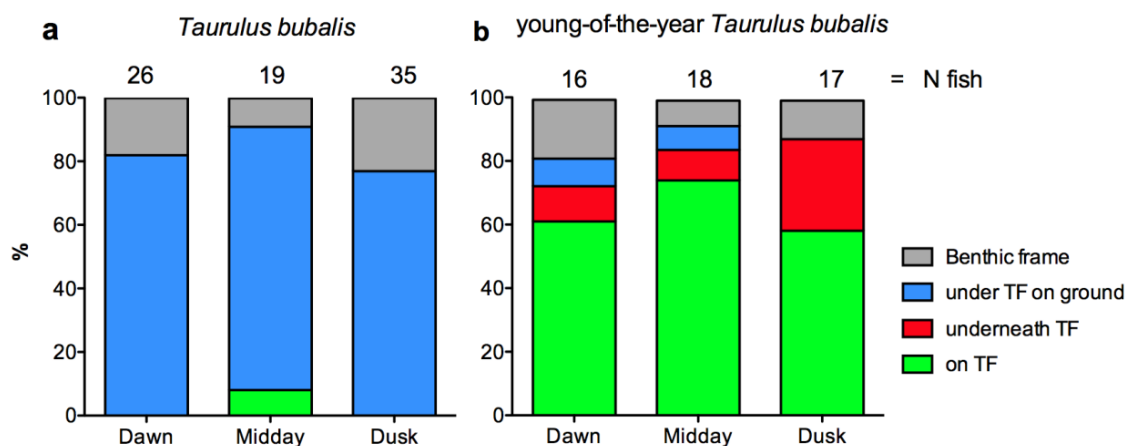
Fig. 2 Spatial distribution of *T. bubalis* in percentages over microhabitats offered by the tetrapods. Older individuals of *T. bubalis* (a) were mostly abundant under the tetrapod feet lying on the ground (under TF on ground). Young-of-the-year individuals of *T. bubalis* (b) in contrast were observed most often on the tetrapod feet (on TF). Graph: Anika Seidler

For the suprabenthic goldsinny (*C. rupestris*) the findings of this thesis showed no distinct substratum association within the natural habitat types. The goldsinny was similarly distributed over different habitat types (rock, cobbles, large pebbles) found in the study area. The three-dimensional tetrapod fields, however, seemed to provide the ideal habitat for this territorial species (Hillden 1981, Sayer et al. 1993).

The thesis highlights the attractiveness of artificial structures for fish. Especially the most abundant species, *T. bubalis, P. gunnellus, G. flavescens* and *C. rupestris*, occurred in disproportionally high numbers after the introduction of the tetrapods in close association with the artificial structures. This result was comparable to the findings of other studies dealing with the effects of artificial structures on the coastal environment (Bohnsack & Sutherland 1985, Fabi & Fiorentini 1994, Simon et al. 2011).

However, in this thesis, I had the possibility to sample also prior to the introduction of the tetrapods, which most of the other studies did not. This methodological difference proved to be of great importance for the interpretation of the results. The findings demonstrated that the high abundances at the tetrapods were caused by high migration of the fish towards the tetrapods. This finding is unique and was - to my knowledge - not reported to date to this extent.

This signifies that native species in the study area left their well-structured and diverse natural habitat to migrate towards the artificial substratum. This observation provokes the highly interesting question of which ecological or physiological reasons induced the species to do so.

Possible factors, which may explain this distinct habitat shift of the species, were the availability of adequate refuge and shelter possibilities in form of microhabitat provided by the artificial substrate and/or feeding opportunities provided by e.g. a developing fouling community (Coleman & Connell 2001, Wilhelmsson et al. 2006a, Clynick et al. 2007, Andersson et al. 2009). The results of this study indicated that a combination of both factors might have induced the species' shift.

The study revealed that the tetrapods acted as fish attractor inducing also an increase especially in more young-of-the-year and shoaling fish. This however, does not conclusively solve the question of whether the artificial structures lead to an increase of fish biomass. We were not able to clarify if there has been an increase in fish biomass net production over the complete study area.

Fish production will be limited not only by habitat limitations but also by larval supply and post-settlement mortality, as well as adult fish mortality (Wilson et al. 2001, Osenberg et al. 2002). Furthermore, fish attraction can be limited by factors such as food availability, space competition and/or predation pressure, which affect the density of species and individuals in a system (Wilson et al. 2001, Osenberg et al. 2002, Simon et al. 2011).

Thus, the most urgent question concerns the carrying capacity of certain complex structures. The carrying capacity of a structure can hypothetically be reached by a continuous migration of fish from the surrounding or by fish production based on resources (e.g. spawning habitat) provided by the artificial structures. If fish are continuously attracted towards the artificial habitats, the resources in the surrounding habitat will theoretically be underexploited. Native fish could use the free habitat resources in the surrounding and a surplus production of fish could be stimulated. The artificial structure can then be seen as collector device for an additional fish population while the surrounding area may be assumed to remain stable (Fig. 3).

In contrast, if an artificial structure does not act as collector but as a producer of native and possibly alien species (e.g. because the artificial structure provides spawning habitat

96

and food resources), these species may soon reach the carrying capacity of the artificial structure. Then, dominant fish species, which reproduce on the artificial structures, may migrate towards the surrounding habitats. They then intrude the surrounding habitat and perhaps eliminate other individuals of the same species or even of other species. This could result in a change of the community structure with changes in diversity and evenness in the entire area. The loss of functional roles caused by a loss of specific species and a change in the dominance hierarchies may lead to a decreased ecological stability (Simon et al. 2011; Fig. 3).
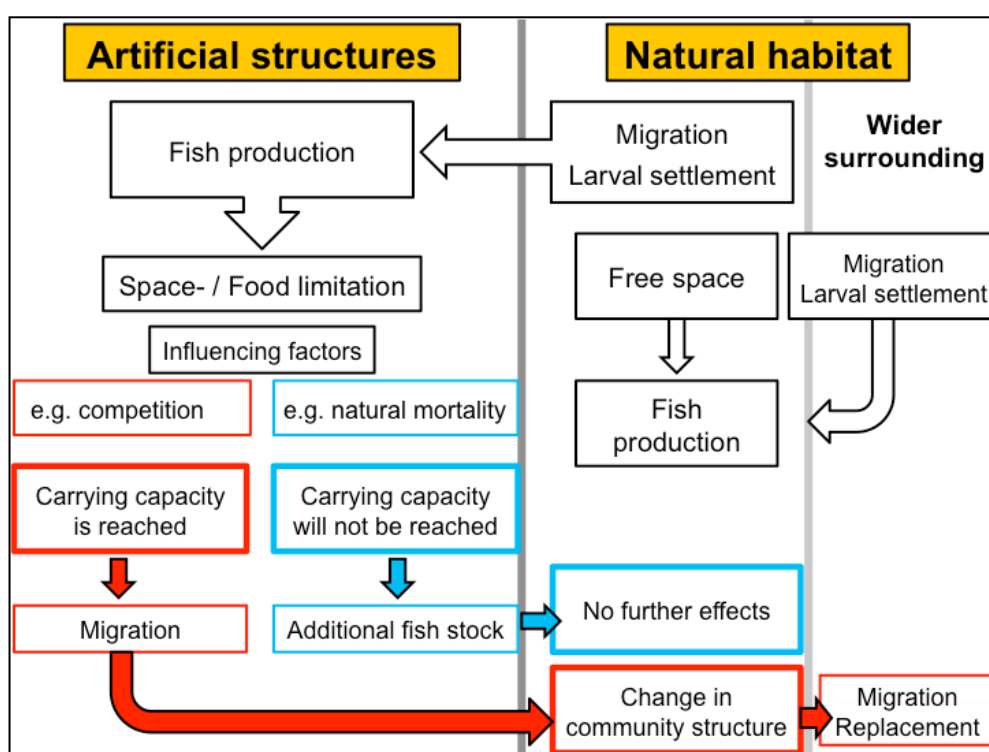

Fig. 3 Future scenarios of possible changes in the fish community structure by a starting fish production caused by the artificial structures

It is clear that these two scenarios are hypothetical and are subject to a variety of further influencing factors including the size of the artificial substrate, the locality, the rate of larval supply, competition, food occurrence and many others. Within a combination of the methodology used here and the introduction of additional methods (e.g. to measure individual somatic growth of the juvenile fish), however, effects of biomass production could be revealed in the long-term. Furthermore, observations of colonization processes

like larval settlement should also be embedded in the future. This is only possible through short (daily) sampling intervals to reveal processes such as larval mortality caused by predation pressure (Bohnsack et al. 1994).

Whereas this thesis showed distinct impacts caused by the artificial structures on the fish community, less clear results were achieved concerning the impact on the decapod crustacean community. Since invertebrates are characterised by highly variable life cycles with different juvenile stages as well as complex adult morphology, it is difficult to state what their ecological requirements on the ecosystem are (Ingle 1983, Ingle & Christiansen 2004). Crustaceans may alter their habitat preference during their different life cycles e.g. during moulting or breeding periods (Pallas et al. 2006, Pardo et al. 2007).

The only species, which showed a clear preference for the artificial habitat structures were *H. araneus* and *H. gammarus*. *H. araneus* appeared within the second year after the introduction of the tetrapods and was only observed underneath the tetrapod feet (Fig. 2d). At least one lobster (*H. gammarus*) was observed at each tetrapod field. Previous studies have also illustrated an attraction of lobster towards artificial substrates (Wollf & Sandee 1971, Jensen et al. 1994, Krone & Schröder 2011).

The significant decrease of the total crustacean abundances was noticeable (1750 ind. 360 m^{-2} in 2009, 1062 ind. 360 m^{-2} in 2010, 820 ind. 360 m^{-2} in 2011), mainly caused by reduced numbers of the smaller crustacean species (*G. squamifera, P. longicornis, P. hirtellus*) after the establishment of the experimental fields. An increased predation risk caused by high abundances of fish may be a factor responsible factor for the reduced number of crustaceans. However, it has to be considered that a distinct increase of total fish was observed only directly at the structures with a concurrent decrease in the surrounding caused by migration of fish towards the tetrapods. Furthermore, the decrease of crustaceans was obvious for the complete sampling area, both in the immediate vicinity of the tetrapods and in the wider surrounding. Perhaps some fish species migrated into the surrounding area to prey on crustacean species. First results of an associated diploma thesis, however, revealed no significant differences of the fish abundances over a diel cycle at the tetrapods (see detailed discussion below and Fig. 4). Therefore, I assume that other factors were more important for the depression of the crustacean abundances in this study, such as:

- The destruction of adequate natural habitat caused by the alteration through the establishment of the tetrapods (Samuelsen 1970)
- Mortality caused by extreme winter temperatures (Robinson & Tully 2000a)
- Natural mortality by age and larvae mortality (Samuelsen 1970, Robinson & Tully 2000a)
- Higher predation by larger decapod species (Spanier 1994)
- A combination of the listed factors

To discriminate between these possible reasons, high-frequency samplings over a long time scale would be necessary to distinguish between natural changes and long-term – mainly anthropogenic – changes. Furthermore, sampling needs to distinguish between different age groups and life stages for the crustaceans. This, however, may be difficult in the field and requires additional destructive methods, like the use of suction samplers or scratch samples.

Temporal distribution pattern

The abundances varied seasonally for both the fish and the crustacean species, with the highest numbers found in late summer and autumn. This pattern was observed for all three sampled years, although a statistically significant seasonal cycle was only detected for the fish abundances in 2009.

Some species were abundant only over a short time period whereas others occurred over the complete sampling period. Temporal peaks in abundances may be caused by behavioural or ontogenetic responses to seasonal variation in water temperature (Sayer & Reader 1996).

Many studies postulate distinct seasonal migration patterns for the most species towards less exposed and potentially warmer deeper waters during winter months (Fabi & Fiorentini 1994). Other authors assumed that some substratum-dependent species may remain motionless deeper within crevices in complex habitats to avoid predation risk (Sayer et al. 1994, Nickell & Sayer 1998). This study was not able to resolve which factors were responsible for the seasonal patterns in fish and crustacean abundances. Reasons for seasonal patterns are normally highly species-specific. Therefore separate species-specific studies are necessary to discriminate between possible variables influencing seasonal occurrences.

Although the tidal cycle may influence species on smaller temporal scales (Magill & Sayer 2002, Silva et al. 2010), no effect of the tidal phase on the abundances was detected in this study. Since the investigation on the impact of currents was not a main goal of this thesis, the results could be affected by the lack of suitable methods like the application of flow metres.

Diurnal changes in activity have been revealed for many species in temperate rocky habitats (DeGrave & Turner 1997, Nickell & Sayer 1998). Some species migrate between different habitat types in dependence of prey occurrence, whereas others remain passive within refuges to avoid predators (Nickell & Sayer 1998, Silva et al. 2010). Predator avoidance in certain species has been shown to lead to predominantly nocturnal activity of the prey when the predator is diurnally active, and vice versa (Nickell & Sayer 1998, Bell & Turner 2003, Silva et al. 2010).

First statistical analyses from an associated diploma thesis showed no significant differences concerning the abundances of fish ($p = 0.265$) and crustaceans ($p = 0.241$) during different daytimes (dawn, midday, dusk) at the tetrapods. Nevertheless, slightly lower abundances of fish were observed during midday (Fig. 4), while abundances of crustaceans were highest during this time (Fig. 4). This might be an indicator for a migration of fish away from the artificial structures to prey on e.g. crustaceans in the surrounding. Crustaceans on the other hand may remain in their refuges during midday (and therefore could be found by visual census) and migrate away from the tetrapods during twilight or night (DeGrave & Turner 1997, Bell & Turner 2003).

The experimental approach used in the diploma thesis is highly promising per se. However, only four complete data sets (each data set representing a complete sampling day with sampling times during dawn, midday and dusk) were collected within the diploma thesis. This was due to bad weather conditions.

In order to obtain meaningful data on patterns of diel distribution of fish and crustaceans at artificial structures an intense *in situ* sampling with SCUBA is necessary. This will need to be conducted over a short period of time (within a month) so as to exclude any possible seasonal effects, which may influence the patterns, while collecting enough data to corroborate the findings.
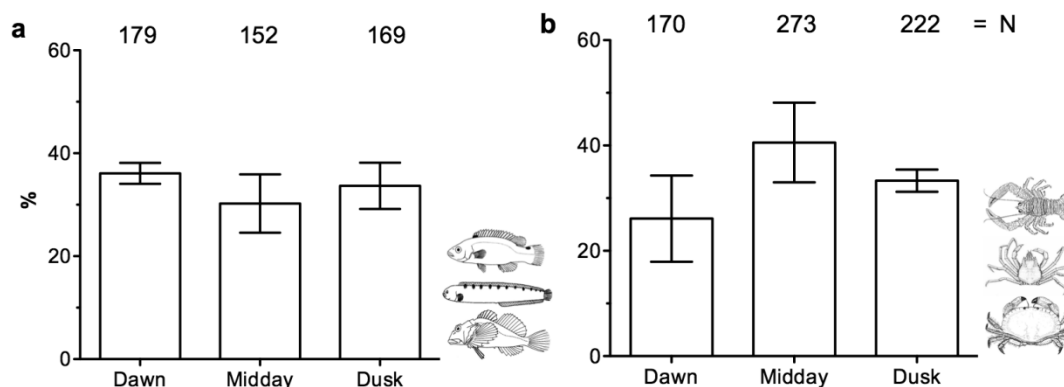
Fig. 4 Relative abundances (mean + SD) of the fish species (C. *rupestris, P. gunnellus, T. bubalis*) and crustacean species (*G. squamifera*, *H. araneus*, *C. pagurus*) averaged over all four data sets during the day. Additionally, the total abundances of fish found over all data sets (N) are given. Graph: Anika Seidler

Conclusion

The findings of this thesis revealed strong species-substratum relationships on a micro-scale level. This was observed for the use of microhabitat types within the natural substratum as well as for the use of microhabitats offered by the artificial substrate.

The thesis clearly demonstrated that habitat selection in demersal fish and macro-crustaceans in our coastal areas is highly species-specific and depends on the lifestyle, the size and the colouration of the species. Therefore, large-scale habitat definitions are not very elucidative to accurately predict assemblage structure or species occurrence, even for the most numerically dominant species in coastal shallow water habitats.

Furthermore, significant effects of coastal defence structures on the spatial and temporal distribution pattern of demersal fish and crustacean assemblages were demonstrated with this work.

Demersal fish and decapod crustaceans reacted differently to the alteration of their natural habitat. Whereas native fish species were highly attracted towards the tetrapods, most crustacean species showed no preference for this kind of artificial substrate.

The thesis highlighted that field studies are inevitable when studying the spatial and temporal distribution of cryptobenthic species. The findings showed that the used methodology can be strongly recommended for *in situ* studies in temperate- or cold-water areas. This is important knowledge for further studies and the development of sampling strategies.

The monthly sampling strategy illustrated spatial as well as temporal effects on the fish and crustacean abundances. Besides a seasonal pattern over the sampling months, migration patterns seemed to occur also over small time periods. The results, however, were not as distinct in crustaceans as in fish and revealed that other sampling procedures should be integrated in future to introduce clarity into this complex topic. This, however, will only be possible by working *in situ* on an experimental basis with continuous observation technologies and intense diver support.

We are just beginning to understand how communities respond to the alteration of their natural habitat by the establishment of artificial structures in coastal zones. The findings of this study contribute to the understanding of the effects of coastal defence structures on the natural fish and crustacean community in a boreal hard-bottom area. Moreover, this work provides a good basis for further studies investigating the impact of artificial structures on temperate hard-bottom communities.

The knowledge gained through this study is even more important when considering that the establishment of coastal protection measures will be intensified in the coming decades to adapt to possible consequences of climate change (IPCC 2007b, a, Bulleri & Chapman 2010, Chapman & Underwood 2011).

SUMMARY

Anthropogenic impacts and dramatic changes in climate result in the destruction of coastal areas through flooding and increasingly high-wave action. Therefore the establishment of coastal defence structures is gaining increasing importance in the protection of coastal areas worldwide.

The introduction of artificial substrate generally introduces a source of variation in the natural environment and can lead to changes of the natural community.

The ecological consequences for the coastal environment and biota, however, remain mostly unclear. Particularly in northern Europe studies on the impact of coastal defence structures on the associated biota are rare.

The aim of this thesis was to obtain detailed information on the effects of typically used coastal defence structures (tetrapods) with respect to temporal and spatial dynamics of a fish and macro-crustacean community in a boreal rocky shore habitat.

Experimental fields, consisting of tetrapods, were established in the subtidal area north of the coast of Helgoland, a small rocky island in the southern North Sea. In an *in situ* approach the abundances and community structure of demersal fish and decapod crustaceans were assessed before and after the introduction of the artificial structures.

Field studies were carried out at three tetrapod fields and in their surroundings. Visual sampling took place monthly by SCUBA on fixed counting stations along line-transects. The findings demonstrated that the tetrapods are significantly preferred by fish over the natural habitat. The high fish density by the artificial substrate was caused by migration of native species (*Ctenolabrus rupestris, Taurulus bubalis, Pholis gunnellus*) towards the tetrapods. An increasing number of young-of-the-year (YOY) was also detected at the artificial structures within the second year after the introduction of the tetrapods. This thesis revealed that the tetrapods acted as fish attractor and that the increase of more YOY individuals may be an indicator for an increase of fish biomass. The findings present a stable basis for further studies dealing with the question of the carrying capacity of such complex structures and the resulting consequences for the surrounding fish community, when the carrying capacity is reached.

Concerning the decapods, the impact of artificial structures was highly species-specific. After the placement of the tetrapod fields significantly lower numbers of small and less vagile species (e.g. *Pisidia longicornis, Pilumnus hirtellus*) were found in the complete

study area. The reason for this finding could be explained by the destruction of natural habitat but also by abiotic and biotic factors like temperature or life cycles.

Only two species (*Homarus gammarus, Hyas araneus*) were found in higher abundances at the tetrapods. The tetrapods offered ideal habitat and shelter opportunities for these species. For the highly mobile and predatory crab species (e.g. *Cancer pagurus*) no attraction of the artificial structures was demonstrated during the study time.

Further findings of this thesis revealed strong species-substratum relationships on a micro-scale level. Especially benthic fish species (*Taurulus bubalis, Pholis gunnellus*) but also smaller decapod species (*Pisidia longicornis, Pilumnus hirtellus*) showed a preference for specific microhabitat types offered within the natural as well as artificial substrate. The species were distributed in dependence of specific species features like size, life cycle and lifestyle and substratum features like the colouration and adequate shelter size.

The findings of this thesis contribute profoundly to the understanding of the effects of coastal defence structures on the natural fish and crustacean community. Furthermore, the findings and the methodology used provide a strong basis for further studies investigating the impact of artificial structures on boreal hard-bottom communities.

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ACKNOWLEDGEMENT

First of all I would like to thank my committee members for "scientific support":

I would like to thank my direct supervisor Prof. Dr. Philipp Fischer for helping me to find my way in the world of science and for believing in "Thinking Big" – you gave me the confidence to initiate the project "MarGate".

Special thanks to Prof. Dr. Karen Wiltshire for giving valuable critique. Especially, I would like to thank Prof. Heinz-Dieter Franke and Dr. Gerd Niedzwiedz for their helpful support and for their calmness during meetings, presentations and discussions.

Thanks a lot to Dr. Ingo Hadrych and Arne Weber from HC Hagemann for sponsoring the tetrapods and for the great collaboration, the WSA Helgoland - especially Carsten Keden – for all help and support, the crew of the "Lumme" and the company "Colcrete –von Essen" for the successful establishment of the tetrapods during harsh and cold conditions on two stormy winter days.

I would like to thank Thomas Mohr and Gerd Niedzwiedz for the warm collaboration between the team "Riff Nienhagen" and the team "MarGate".

Special thanks to all the divers, especially Suse Homagk, Antje Klawon, Anika Seidler, Christoph Walcher, Matthias Wehkamp and "the singing tetrapods" for their help in the field and a lot of fun on board with laughter, singing and whistling (or something like that).

Kat and Sonja: special thanks to both of you for language assistance and highly helpful comments and final corrections!

Martin, I want to thank you for answering all the "organizational" questions.

And I would like to thank our work group *in situ* ecology for the welcoming atmosphere and for being such a great team! Anika, I liked it a lot to work with you and I wish you a great travel time after your diploma-defence.

Now I come to the most difficult part because I'm sure that I forget some people….

I would like to thank my Helgoland friends, Sonja, Kat, Betti, Rebi, Martin, Tommy, Jan, Ced and Stöff for the great time we had together with laughing, cooking, drinking, dancing and all the other crazy stuff…

Especially I want to thank Kat, Betti, and Sonja for all the motivation, walks, the funny Skype conferences, food supply and Rebi for the nice coffee breaks at the right times.

For helping me during a really sad and difficult time I would like to thank Betti, Kat, Martin and Rebi for their great comfort and in particular Matthias and Sonja, who were always and absolutely with me (without you I would not be able to laugh again today).

But I will not forget to thank my oldest and best friends on the mainland, Birgit, Britta, Ilka, Imke, Matze and Tanja, who supported me as a matter of course during "good times and bad times" and who made me to the person I am!

Last but not least I would like to thank my parents-in-law, Monika and Werner, for their heartiness and my beloved mom, who believed in me and supported me during her lifetime and who is now always with me in my heart and in my thoughts!
But my biggest thanks go to my love Matthias for all his understanding and the strength he gave me!

STATUTORY DECLARATION

I, Stephanie Wehkamp, hereby declare that I have written this PhD thesis independently, unless where clearly stated otherwise. I have used only the sources, the data and the support that I have clearly mentioned. This PhD thesis has not been submitted for conferral of degree elsewhere.

Helgoland, June 30, 2012

Stephanie Wehkamp

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