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The importance of reef habitats for fish, harbor porpoise and fisheries management

Jon C. Svendsen, Bo M. Kruse, Tim Wilms, Karsten Dahl, Helle Buur, Ole G. N. Andersen, Jeannet L. Bertelsen and Lotte Kindt-Larsen

DTU Aqua Report no. 371-2020

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[1]DTU Aqua, Technical University of Denmark

[2]The organization Als Stenrev

[3]Danish Centre for Environment and Energy (DCE), Aarhus University

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Colophon

Title:	The importance of reef habitats for fish, harbor porpoise and fisheries management
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DTU Aqua Report no.:	371-2020
Year:	Scientific work finalized August 2019. Report published January 2022.
Reference:	Svendsen, J.C., Kruse, B.M., Wilms, T., Dahl, K., Buur, H., Andersen, O.G.N., Bertelsen, J.L., Kindt-Larsen, L. (2022). The importance of reef habitats for fish, harbor porpoise and fisheries management. DTU Aqua Report no. 397-2022. National Institute of Aquatic Resources, Technical University of Denmark, 79 pp.
Cover photo:	Cod at rocky reef in Sønderborg Bay. Photo: Jon C. Svendsen. (https://www.youtube.com/watch?v=4kKwXNNwYcE)
Published by:	National Institute of Aquatic Resources, Kemitorvet, 2800 Kgs. Lyngby, Denmark
Download:	www.aqua.dtu.dk/publikationer
ISSN:	1395-8216
ISBN:	978-87-7481-324-8

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Preface

This report is based on the collaborative project “Betydning af rev-habitater for fisk, marsvin og fiskeriforvaltning” (DTU Aqua no. 33113-B-19-057, Als Stenrev no. 33113-B-16-058 and DCE Aarhus University no. 33113-B-16-059) and funded by the European Maritime and Fisheries Fund and the Danish Fisheries Agency.

European Union
European Maritime and Fisheries Fund

HAV & FISK

This project examined the importance of reef habitats for fish, harbor porpoise and fisheries management. While previous reef studies in Denmark have been concerned with cavernous boulder reefs (large rocks), the present study targets reefs constructed using cobble and similar stones and rocks with an average diameter up to approximately 30 cm. The project covered four specific work packages, including 1) reef positioning and construction in Sønderborg Bay in southern Denmark, 2) the responses of fish to the established reefs, 3) flora and fauna in relation to benthic coverage of cobble and smaller stones, and 4) the responses of harbor porpoise to the established reefs. Data were collected to guide future reef restoration projects and support management of benthic substrate extractions and fisheries in Danish waters. In this report, the results of the four work packages are described. The reports covering the individual work packages were designed independently of the remaining reports. This implies a limited overlap in the information provided in each work package report. The project is the result of collaboration between DTU Aqua, DCE Aarhus University and the organization Als Stenrev in Sønderborg.

Copenhagen, January 2022

Jon C. Svendsen

Content

Summary

This project deployed cobble reefs in Flensburg Fjord (Sønderborg Bay) to study the reef effects in relation to fish abundance, benthic flora and fauna as well as harbour porpoise abundance. Extraction of boulders from the seabed has been prohibited in Denmark since 2010. In contrast, sand, stones and small rocks are still extracted from the seabed in dedicated marine areas. Extraction of relatively small stones and rocks (cobble) has the potential to influence marine life locally, but the topic has received limited attention in Denmark. This project examined the hypothesis that deployed reefs could provide substrate for macro algae and host various fish species as well as harbour porpoise. For example, it is well known that Atlantic herring is spawning near hard surfaces, where the eggs attach to rocky substrates or macro algae growing on the rocky substrates. Other fish species may accumulate in the area to feed on both the eggs and the adult herring. The herring and the predators may further attract harbor porpoises and thereby enable trophic interactions. Moreover, this project describes methodology to restore cobble reefs in Sønderborg Bay in Denmark. Collaborating closely with local stakeholders, and the organization Als Stenrev in particular, the project provides stepwise guidelines for 1) finding evidence of previous benthic extractions, 2) identifying sites for reef deployments, 3) getting permits for the reef deployments, and 4) collaborating with the contractor eventually deploying the reef. The study found no evidence of recent cobble extraction in the Sønderborg Bay. Reefs were successfully deployed at two sites in the bay. Likewise, the project identified marine sites with natural cobble reefs and sites without any reefs for comparisons across the timeframe of the project. Underwater cameras revealed that total fish abundance increased after reef deployment. For example, the abundance of Atlantic cod appeared to respond positively to the constructed reefs. Likewise, abundance of a number of prey fish species increased after reef deployments. As expected, the abundance of flatfish decreased after reef deployment. Baited underwater recordings revealed elevated abundances of herring in the natural reef sites, but spawning herring or herring eggs were not observed. Assessments of benthic flora and fauna on natural reef sites, and comparisons with sites without reefs, indicated that reef substrates favour high abundances of many invertebrates that are important food resources for fish. Specifically, the total epifauna abundance correlated positively with the seabed coverage of rocks (mainly cobble). Previous studies have revealed high abundance of harbour porpoise in Sønderborg Bay. The present project confirmed the presence of harbour porpoise in the area, but elevated abundance of harbour porpoise near the deployed reefs was not demonstrated, probably because of limited data availability and the short time frame of the project. The project indicated that distinct biological communities are associated with reefs consisting of cobble and similar small stones and rocks. The reefs provide foraging conditions that are favourable for many fish species. These benefits may diminish locally if cobble and similar small stones and rocks are extracted. Complete colonization of the deployed reefs takes several years, suggesting that comprehensive assessments of the reef effects require long-term investigations. The project was carried out independently of Horizon 2020 and EU LIFE projects.

Danish summary

Dette projekt udlagde småstenede ral-rev i Flensborg Fjord (Sønderborg Bugt) for at undersøge rev-effekterne i forhold til forekomster af fisk, bentisk flora og fauna såvel som den lille hval-art marsvin. Indvinding af kampesten fra havbunden i Danmark har været forbudt siden 2010. Det står i kontrast til, at der fortsat indvindes sand, grus og ral fra havbunden i dedikerede havområder. Indvinding af relativt små sten og ral har potentialet til at påvirke livet i havet lokalt, men emnet er dårligt belyst i Danmark. Dette projekt undersøgte muligheden for, at udlagte rev kan give grobund for tangskove, levesteder for fisk og øget fødeudbud for marsvin. Det er bl.a. velkendt, at sild ofte gyder over stenede bundtyper, hvor æggene klæber til stenene eller til tang, der vokser på stenene. Gydeaktiviteten kan ofte betyde, at andre fiskearter tiltrækkes og anvender æggene eller de gydende sild som fødegrundlag. De forskellige fiskearter, der således kan samles ved revet, kan ligeledes tiltrække marsvin, der bliver del af en større fødekæde. Projekt beskriver endvidere metoder til at udlægge småstenede ral-rev i Sønderborg Bugt i Danmark. I tæt samarbejde med lokale aktører og især foreningen Als Stenrev, leverer projektet trinvise retningslinjer i relation til 1) dokumentation af tidligere tiders indvinding fra havbunden, 2) identifikation af steder hvor rev kan udlægges, 3) indhentning af tilladelser til udlægning af rev og 4) samarbejde med entreprenøren om at udlægge revet. Projektet fandt ikke dokumentation for nylig indvinding af småstenet ral i Sønderborg Bugt. Projektet udlagde rev i to områder i bugten og identificerede ligeledes områder med naturlige rev samt områder uden revforekomster. Forekomster af dyr og vegetation i de forskellige områder blev sammenlignet i løbet af projektets varighed. Undervandskameraer viste, at de samlede forekomster af fisk steg efter udlægning de småstenede ral-rev. Eksempelvis tyder resultaterne på højere forekomst af torsk efter revudlægning. Tilsvarende var der højere forekomster af nogle mindre fiskearter, der bidrager til fødegrundlaget for større fiskearter. Som forventet faldt forekomsten af fladfisk på revene. Undervandsoptagelser med kameraer udstyret med agn viste høje forekomster af sild i områderne med naturlige rev, men projektet dokumenterede ikke gydende sild eller deres æg. Flora og fauna på havbunden blev sammenlignet i områder med og uden naturlige rev. Undersøgelserne viste, at der ofte var høje forekomster af smådyr i områderne med rev, hvilket indikerer et godt fødegrundlag for fisk. Der blev bl.a. fundet positive korrelationer mellem dækningsgraden af sten og ral på havbunden og forekomst af epifauna (smådyr der lever over eller på havbunden). Tidligere undersøgelser i Sønderborg Bug har indikeret høje forekomster af marsvin i området. Projektet dokumenterede ligeledes marsvin i området, men forhøjede forekomster ved de udlagte rev blev ikke observeret. Det skyldes sikkert de begrænsede mængder data, der var til rådighed samt projektets korte tidsramme. Projektets undersøgelser viste, at småstenede ral-rev rummer biologiske samfund, der ofte er forskellige fra de biologiske samfund på bundtyper med sand eller mudder. Revene giver fødemæssige fordele for en række fiskearter. Indvinding af ral og lignende stenstørrelser kan derfor betyde, at fødegrundlaget for en række fiskearter reduceres. Komplet kolonisering af de udlagte rev vil tage adskillige år. En mere fuldstændig evaluering af revenes biologiske betydning for området forudsætter derfor gentagne undersøgelser over mange år. Projektet blev udført uafhængigt af Horizon 2020 og EU LIFE-projekter.

Introduction

Anthropogenic pressures on marine ecosystems have been recorded globally; highly impacted areas range from the North Sea and coastal areas of the Baltic Sea, to eastern Caribbean and Japanese waters (Halpern et al., 2008; Korpinen, Meski, Andersen, & Laamanen, 2012). Impacts can be due to direct exploitation of coastal resources, including overfishing, sediment extractions and land reclamation of shallow-water habitats, but also indirect effects of rapid population growth on urbanisation and industry (Brown et al., 2018; Halpern et al., 2008; Korpinen et al., 2012; Lin & Yu, 2018; Pihl et al., 2006; Vasconcelos et al., 2007). Globally, directives have been put in place to protect marine habitats (European Parliament & Council of the European Union, 2008; Feng, Chen, Li, Zhou, & Yu, 2016; Fernandes et al., 2005; UK Parliament, 2009). In the European Union, protection includes the establishment of Natura 2000 areas. The Natura 2000 legislation covers one of the largest protected areas in the world (Kristensen et al., 2017). Management of Natura 2000 areas varies from minor interventions, such as reducing disruptive activities during breeding seasons, to major restoration works of degraded marine habitats to protect various species and habitats (Kristensen et al., 2017; Nature Agency, 2016). Surveys of these habitats allow for the assessment of changing habitat variables and associated marine community responses. These surveys generate important information, including abundance data, commonly used to investigate the impacts of restoration activities and anthropogenic pressures (Bellwood, Hoey, & Hughes, 2012; Hillebrand et al., 2018; Stallings, 2009).

Extraction of marine sediments, including boulders, cobble, gravel and sand, has been carried out for many decades in Danish waters. Boulder extraction, for the numerous harbor jetties constructed along the Danish coastline, took off in the late 1800s and degraded the local marine areas and the quality of many coastal reefs. Boulder extraction, involving extraction of individual boulders from the seabed, was managed in the 1990s with restrictions to specific marine extraction areas. No boulders have been extracted since 2002, and boulder extraction as a method was banned in 2010 (Anon, 2009).

Sand and gravel extraction from the Danish seabed is still ongoing using a suction aggregate. The extraction is typically carried out either as a point suction for deeper resources in the seabed or by surface dredging leaving long up to 40 cm deep tracks on the seabed while slowly moving the vessel forward. Sand and gravel extractions are managed with restrictions only to operate in specific areas where new areas substitute areas depleted for resources. Dedicated extraction areas include Køge Bay, Fakse Bay and Århus Bay. Sand and gravel extraction is generally not permitted in shallow water (< 6 m). New areas proposed for sand and gravel extraction need an environmental impact assessment, including a description of the surface sediment composition.

Though boulder extraction is prohibited, hard substrate is still extracted from the Danish seabed. Specifically, extractions include gravel, pebble and smaller stones (e.g. cobble) that are removed and processed by the suction aggregate. In 2012, the total exploitation was 1,231,804 m^3 stones (gravel, pebble and cobble) with individual stone diameters typically ranging between 6 – 30 cm (Anon 2013). A component of the extracted material is removed from the upper layer of the seabed, where the stones may form substrates for macro algae and fauna proliferation. In sheltered conditions, macro algae can grow on rocks and stones with a diameter smaller than 10 cm (Figure 1).

Macro algae form a vital part of the marine environment, including production of oxygen and habitat provisioning for many fish species. Macro algae host large numbers of invertebrates that supply food resources for numerous fish species, including Atlantic cod (*Gadus morhua*). Specifically, one kelp alga may support more than 80,000 individuals from a wide range of different invertebrates (Christie, Norderhaug, & Fredriksen, 2009). Based on stomach contents, many taxa associated with macro algae are important prey organisms for cod, indicating that macro algae areas provide good feeding opportunities (Norderhaug, Christie, Fosså, & Fredriksen, 2005; Wennhage & Pihl, 2002). After removal of a kelp forest, the abundance of juvenile cod may drop more than 90% (Lorentsen, Sjøtun, & Grémillet, 2010), indicating the important nursery function of macro algae areas. Thus, substrates (i.e. stones with a diameter larger than 5 - 6 cm), where macro algae can grow, are important for the marine environment and fisheries in particular.

Figure 1. Macro algae grow on small stones (down to 5 - 6 cm in diameter) in sheltered areas. The macro alga (*Saccharina latissima*) in the picture is about 90 cm long and is growing on a small stone. The small stone, and the macro alga, originate from water depths of 6 - 7 m in Sønderborg Bay.

Danish waters, boulder reefs have been restored for several years (Støttrup et al., 2017). Studies have revealed that many commercially important species respond favorably to the reef restoration. For example, a study on cod revealed a significant preference for a restored boulder reef near the island Læsø in northern Kattegat (Kristensen et al., 2017). To date, no study has examined the effects of restoration of reefs consisting of rocks smaller than boulders. The present project constructed cobble reefs in Sønderborg Bay in southern Denmark and examined the effects in terms of fish abundance and diversity, benthic flora and fauna as well as harbor porpoise (*Phocoena phocoena*).

1. Restoration of cobble reefs near Sønderborg in southern Denmark

1.1 Introduction

Reef restoration is an increasing activity in Denmark involving local stakeholders, communities and larger organizations. Reefs have been restored in many areas, including near the island Læsø in northern Kattegat and close to Århus; and restoration activities are presently scheduled in Roskilde Fjord and Vejle Fjord. While past reef restoration projects have mainly targeted boulder reefs, reef activities are increasingly diversifying towards various reef types, including reefs targeting certain animal species, habitats or coastal protection. The implication of the diversifying activities is that novel guidelines are required. The present report covers cobble reef restoration, using an example from the western Baltic Sea.

In southern Denmark, Flensburg Fjord, Bredgrund and the sea surrounding the island Als are included in Natura 2000 area number 197. For this specific Natura 2000 area, both reef habitats (1170) and harbor porpoise (1351) are listed and therefore protected. In the area, extensive removal of rocks from the seabed has occurred for at least a century to construct piers, jetties and other types of coastal constructions. The outcome is that rocky reefs are severely depleted in the area. For this reason, establishment of rocky reefs is considered reef restoration in the area. Harbor porpoises are also listed in the Natura 2000 area, because Flensborg Fjord is known as a key area for the species. Harbor porpoises are often associated with rocky reefs where they are presumably foraging successfully. Near the island Læsø, for example, reef restoration positively influenced the local abundance of harbor porpoise (Mikkelsen, Mouritsen, Dahl, Teilmann, & Tougaard, 2013).

Here, cobble reef restoration is described. Specifically, the report outlines how cobble reefs were restored near the city of Sønderborg in the winter 2017-2018. In the present context, cobble is defined as rocks with a diameter up to approximately 30 cm. This definition deviates slightly from the more common definition of cobble, which includes rocks with a diameter up to 25.6 cm. The reef restoration project was carried out as a collaboration between the organization Als Stenrev in Sønderborg and DTU Aqua in Lyngby. The project used the reef restoration guidelines published in 2013 and available here: https://dce2.au.dk/pub/TR91.pdf. Study locations, including sites for cobble reef restoration, control sites and sites with natural cobble reefs, were identified in close collaboration with the organization Als Stenrev.

1.2 Materials and methods

1.2.1 Study area

The study was carried out in Sønderborg Bay in the Flensburg Fjord. The area is relatively deep, with water depths exceeding 25 m in many locations. Numerous fish species are present in the area, including Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), European eel (*Anguilla anguilla*), brown trout (*Salmo trutta*), plaice (*Pleuronectes platessa*), European flounder (*Platichthys flesus*) and several species of gobies (*Gobidae*).

1.2.2 Identifying study sites

Study sites may be identified in a range of ways, depending on the objective of the sites. The present study identified 1) areas suitable for reef restoration (experimental sites), 2) areas with natural cobble reef (natural reef site) and 3) areas without any reefs for comparisons (control sites). To identify past alterations of benthic habitats, the project examined historic records of excavations, dredging and rock removal (i.e. stone fishing) from the area. This work involved contact to elderly fishermen and other local sources of information (e.g. historic newspaper articles) that indicated whether resources had been extracted from the sea bed. The records were from a time when GPS equipment was unavailable, and the exact locations therefore remained unknown. Therefore, information from historical bathymetric maps were examined, because such maps may indicate where reefs have been removed. Specifically, reef removal may be revealed by comparing water depths across time. For example, by comparing bathymetric maps between 1869, 1904, 1940 and today, increasing water depths would probably indicate that benthic material (i.e. rocks) were extracted (Figure 1.1).

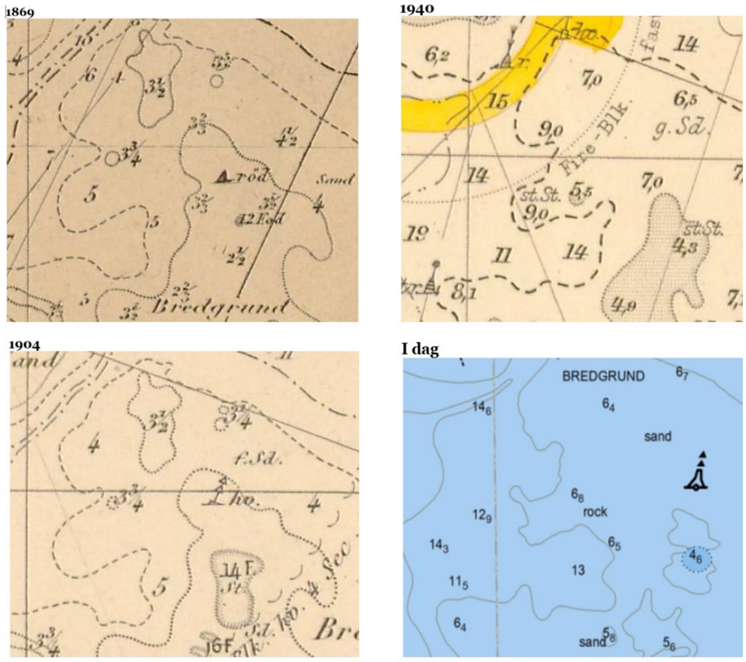


Figure 1.1. Four bathymetric maps from the Sønderborg Bay in southern Denmark. After 1940, water depths increased in the area, indicating extraction of benthic resources (i.e. boulders). Note that units differ between maps and numbers are therefore not directly comparable

In Denmark, extraction of boulders was prohibited in 2010, but other types of benthic material (e.g. sand, gravel and cobble) are still extracted in dedicated Danish marine areas. These areas include Fakse Bay, Køge Bay and Århus Bay. The extraction areas are carefully mapped and available online. Similar to Figure 1.1, the impact of these ongoing extractions may be estimated by comparing old bathymetric maps with updated bathymetric maps. Increasing water depths indicate the impact of the extractions.

Moreover, recent marine maps are available by consulting "Marin habitatkortlægning" and "Marin Råstofdatabase (MARTA)" at www.geus.dk. Both the habitat mapping, and the raw material database, contain a large collection of different maps, images and films that provide detailed information about the conditions in the marine areas (Figure 1.2). This information was further used to identify areas where it is most likely that reefs have been removed and where the project may be able to restore or establish reefs successfully.

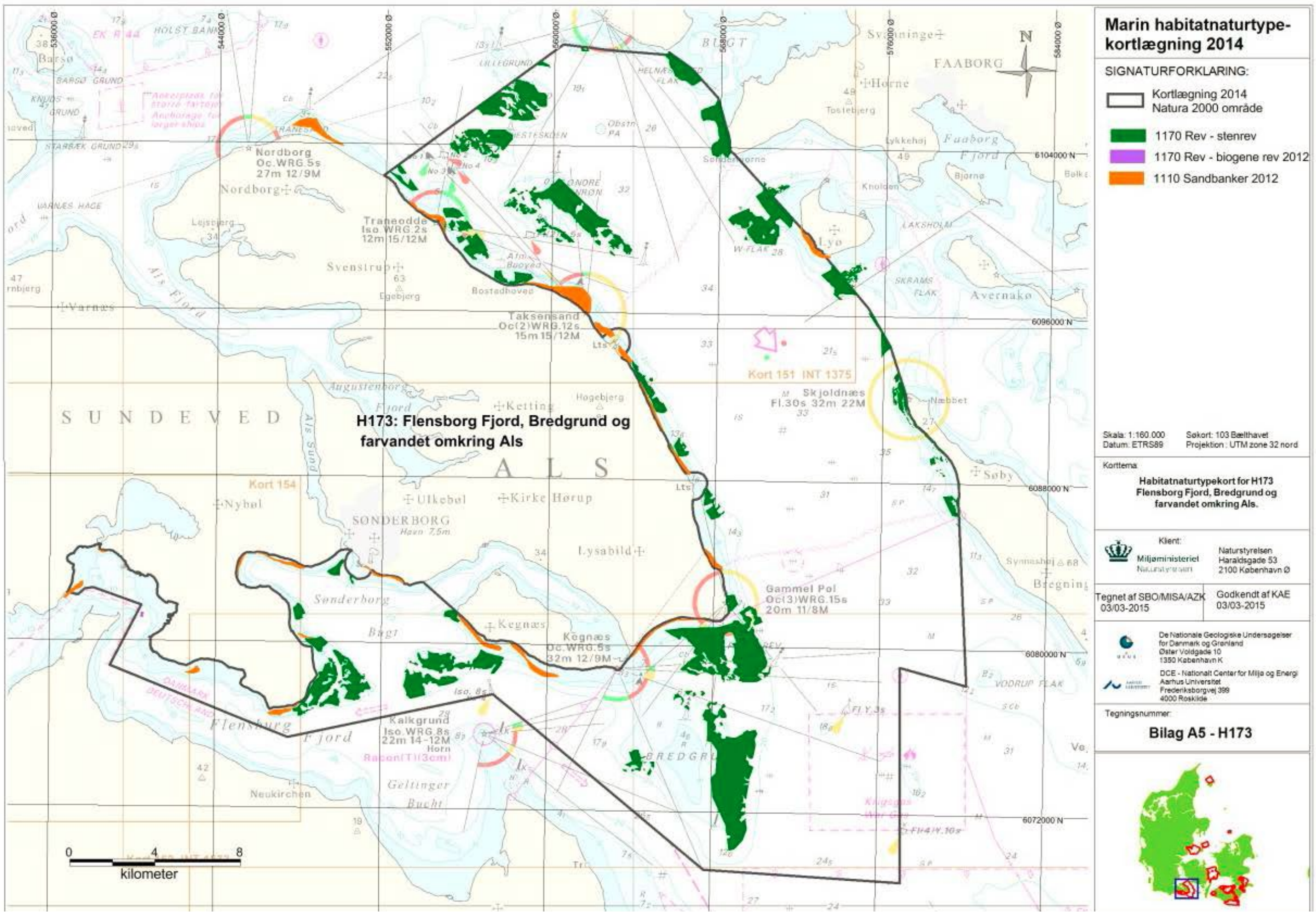


Figure 1.2. Marine habitats in Natura2000 area 197 covering Flensborg Fjord, Bredground and the sea surrounding most of the island Als.

The present study aimed at testing the effects of cobble reefs in terms of herring spawning. Specifically, it was hypothesized that herring would use restored cobble reefs for spawning, because it is well known that herring often spawn on hard surfaces, including rock surfaces and the surfaces of the vegetation growing on rocks (i.e. macro algae). Similar to elsewhere in the Western Baltic Sea (Scabell, 1988), most herring are spawning in the spring in Sønderborg Bay. To identify locations where herring were spawning historically, or may still be spawning, this project interviewed old fishermen about past fishing activities targeting spawning herring. Interviews provided detailed locations where fishermen previously caught spring spawning herring.

Any reef project needs acceptance locally. This was ensured by the local organization Als Stenrev situated in Sønderborg. Members of Als Stenrev represent a range of other organizations, including the Danish Nature Conservation Association (Danmarks Naturfredningsforening), the municipality of Sønderborg, a local agricultural association (LandboSyd), the Belt Sea Fishing Association (Allan Buch; Bælternes Fiskeriforening), a local dive club (Poseidon), a local rod and line anglers club (ANA) and recreational fishermen (fritidsfiskere).

Project plans were continuously approved by the members of Als Stenrev. This ensured local support, expertise and interest.

To examine effects of restored reefs, this study applied an approach that involves sampling before and after restoration in control and impacted locations. Thus, both control sites and reef restoration sites were required. In addition, natural reef sites were included in the sampling scheme. In total, this project identified two restoration sites, two control sites and two natural reef sites.

Boat based mapping was carried out to identify the exact locations of control sites, restoration sites and natural reef sites. The field mapping involved surveying several sites using a boat (Joker 515, RIB type) equipped with a Lowrance Elite 7Ti instrument, including map plotter, digital log and side scanner. The equipment was used for mapping and documenting the seabed in several locations in Sønderborg Bay (Figure 1.3).

Figure 1.3. Screen pictures of the Lowrance Elite 7Ti instrument used for surveying the seabed in Sønderborg Bay. To the left is a contour plot including waypoints. To the right is a scan of the seabed revealing a scatted cobble reef in Sønderborg Bay.

After completing the surveying, SCUBA divers visited the area to further examine the selected sites. Diving included an underwater camera (SONY Cyber-shot RX100 IV) to document conditions in the individual sites. Video recordings were used for comparing different sites as part of the selection process aimed at finding ideal control sites, natural reef sites and restoration sites (i.e. experimental sites) (Figure 1.4). Underwater video recordings were also used for documenting the colonization of the reefs after restoration.

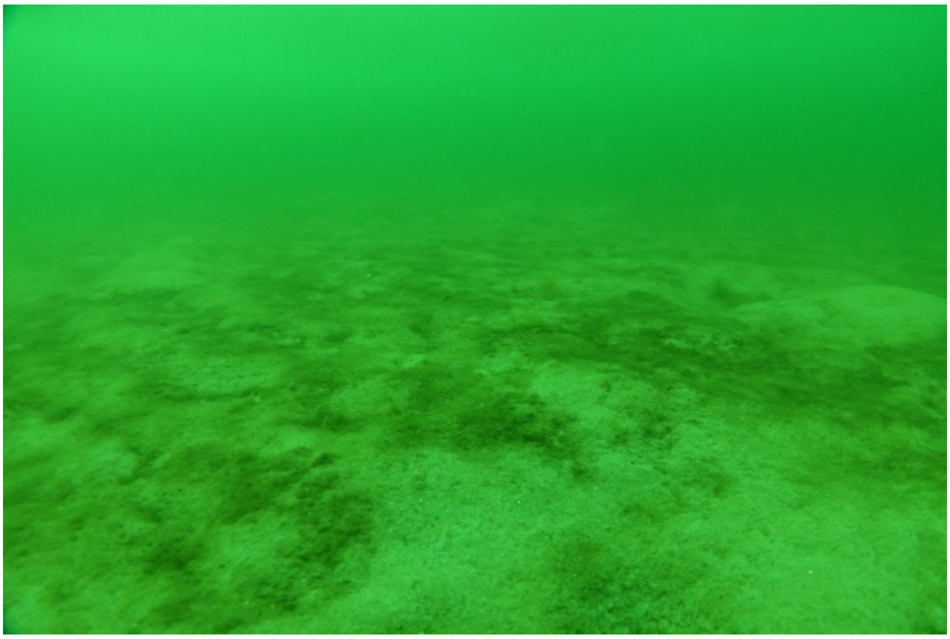


Figure 1.4. Restoration site (experimental site) revealing a sand bottom before reef restoration. The site was surveyed using SCUBA diving.

Combining knowledge from existing maps, local resources (e.g. Als Stenrev), new bottom surveys, SCUBA diving (Figure 1.4.) and comparisons of underwater video ensured that the seabed was suitable for reef construction and likely had the carrying capacity to sustain the rocks after construction. Moreover, the knowledge also ensured that establishing reefs was feasible without destroying existing important habitats (e.g., eel grass beds or biogenic reefs). Finally, the selection process also secured that well-functioning stone reef habitats were available near the restoration sites and control sites. This supported colonization of the reefs after construction. The selected sites were Stenholt and Hvide Mur as reef restoration sites (i.e. experimental sites), Viemose and Kegnæs Ende as control sites, and Vesterhage and Spar Es as natural reef sites. All sites are located in the Sønderborg Bay and are 6-7 m deep.

1.2.3 Getting permits and finding a contractor for the reef construction

When the exact sites had been identified, permits and a contractor were required. All installations on the Danish seabed require a permit from the Danish Coastal Directorate. The permit was obtained by submitting an application according to the guidelines of the directorate. The directorate considers the application based on local shipping traffic, professional fishing interests, archaeological interests etc. In the present study, reef tops had to be at least 4 m below the water surface to allow boating activities above the reefs.

Contractors were contacted to get quotes on the construction job. In reef projects with a fixed economy, the construction work may be tendered in a fashion where there is no competition on price. Instead, the contractors were competing on volumes of reef material (cobble in the present case), they could deliver and use for reef construction at a fixed price. This approach ensured that the total budget for reef construction was spent while maximizing the sizes of the reefs. In the present case, all plans were approved by the local organization Als Stenrev.

1.2.4 Reef composition and designs

Reefs were constructed using cobble imported from Lyngdal in Norway (Figure 1.5). Rock diameters ranged between 6 cm and 30 cm, approximately.

Figure 1.5. Examination of cobble available in Lyngdal Norway.

To plan the reefs, individual reefs units were designed. The individual reef units were shaped as truncated square pyramids (Figure 1.6). The foot (*a*) of each reef unit was 11 m x 11 m, covering an area of 121 m^2, whereas the top (*b*) of each reef unit was 5 m x 5 m. The reef unit heights (*h*) were either 0.6 m or 1.3 m (i.e. low and high reef units, respectively). Low reef units used 40.2 m^3 of cobble, whereas high reef units used 87.1 m^3 of cobble. In each experimental site (Stenholt and Hvide Mur), the reef units were positioned in two lines parallel to the coastline situated at water depths of 6 m and 7 m. In each experimental site, a total of 20 reef units were deployed. The 20 reef units were divided into 10 reef units placed on the 6 m line and 10 reef units placed on the 7 m line. The reef units alternated between low (0.6 m) and high (1.3 m) reef units with an individual distance of approximately 20 - 30 m.

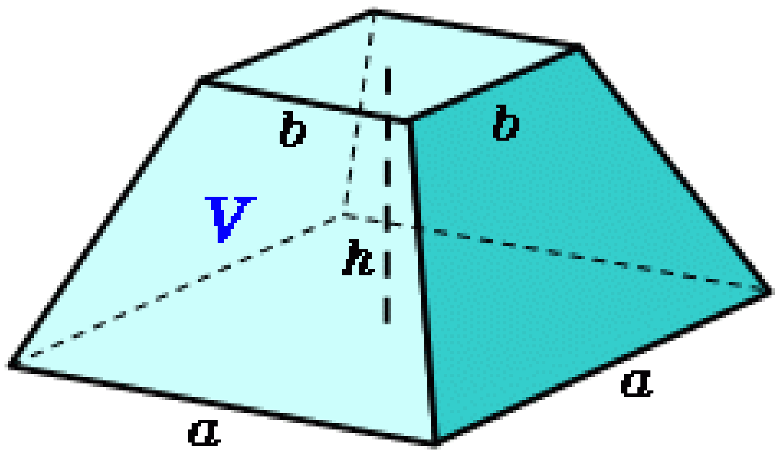


Figure 1.6. A truncated square pyramid revealing the shape of each reef unit.

1.2.5 Reef deployments

Reefs were deployed by the contractor Rederiet Høj A/S (http://eh-dk.com/). The work included mapping of the planned reefs (Figure 1.7 and 1.8).

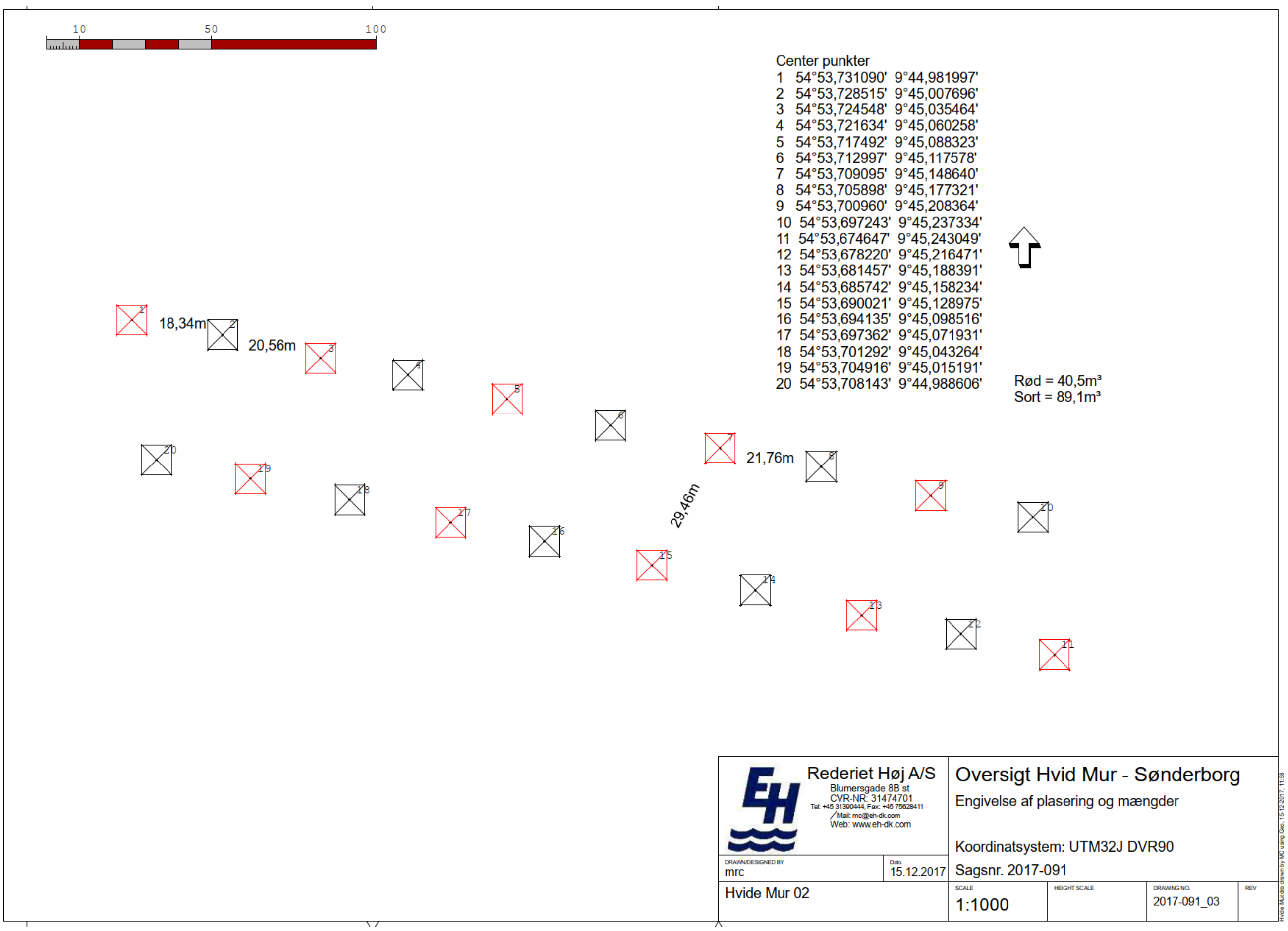


Figure 1.7. Planned reef units at Hvide Mur. Red squares are low reef units, and black squares are high reef units.

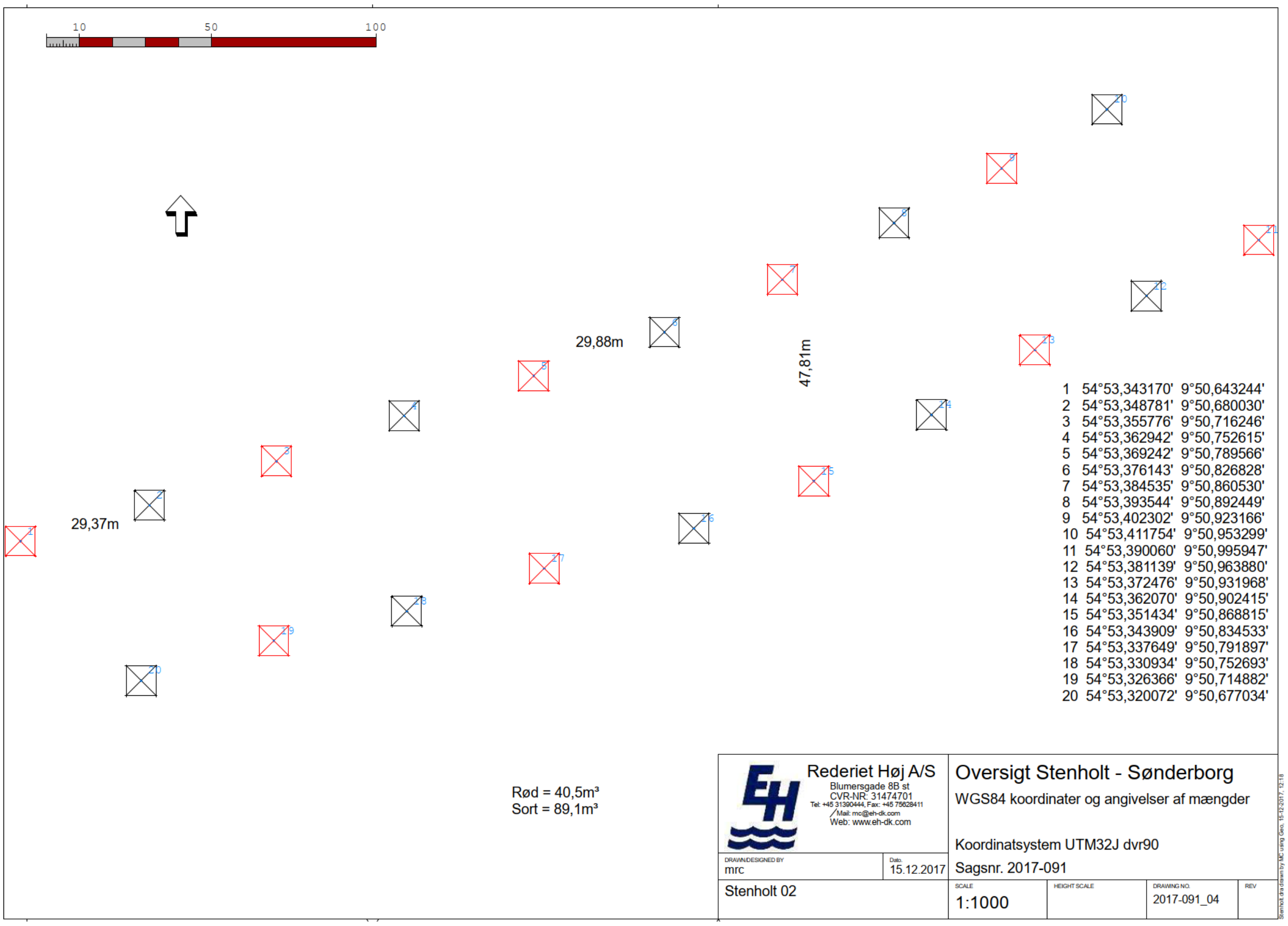


Figure 1.8. Planned reef units at Hvide Mur. Red squares are low reef units, and black squares are high reef units.

1.2.6 After reef deployments

After the reef construction, reefs were surveyed by SCUBA diving to confirm correct construction. Furthermore, the contractor surveyed the area and submitted the updated bathymetry data to the Danish Coastal Directorate and the Danish Maritime Authority. The information was used by the Danish Maritime Authority to update the bathymetry maps of the area.

1.3 Results

While historic boulder extraction is well documented in Flensburg Fjord, Bredgrund and the sea surrounding the island Als (i.e. in Natura 2000 area number 197), the present study found no evidence of recent cobble extractions in Sønderborg Bay.

The six study sites are depicted in Figure 1.9. A total of 900,000 kr. was spent on the cobble, reef construction and subsequent bathymetric mapping.

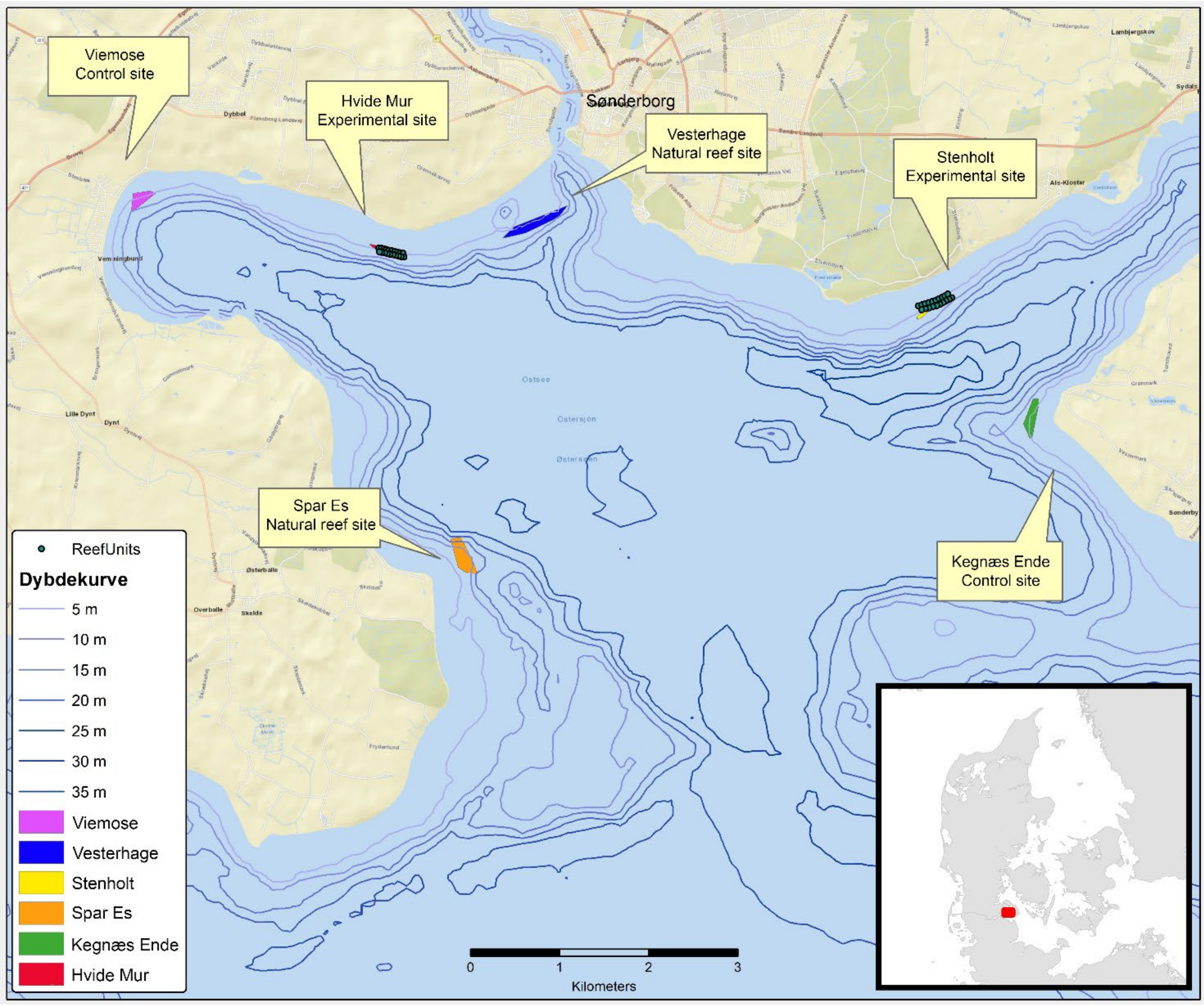


Figure 1.9. Map showing reef construction sites (experimental sites), control sites and natural reef sites.

Bathymetric surveys confirmed that reef units were successfully deployed at the two experimental sites Hvide Mur and Stenholt (Figure 1.10 and Figure 1.11). Likewise, SCUBA diving confirmed the positioning and shapes of the individual reef units (Figure 1.12).

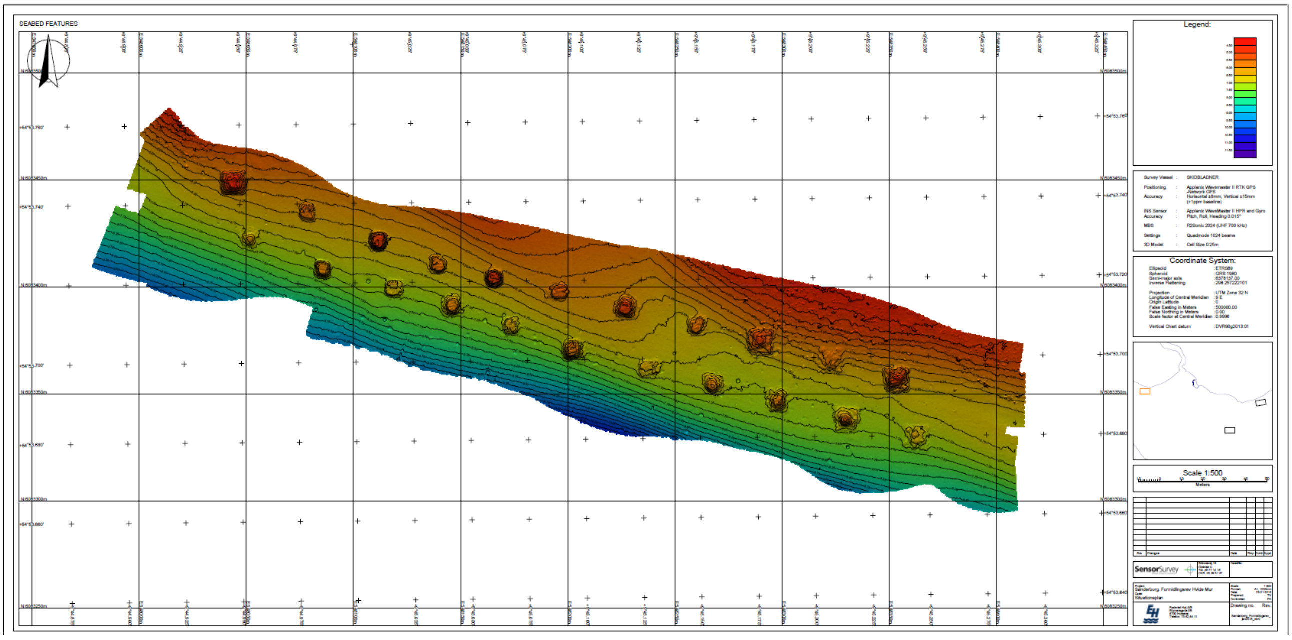


Figure 1.10. Map showing individual reef units deployed at Hvide Mur.

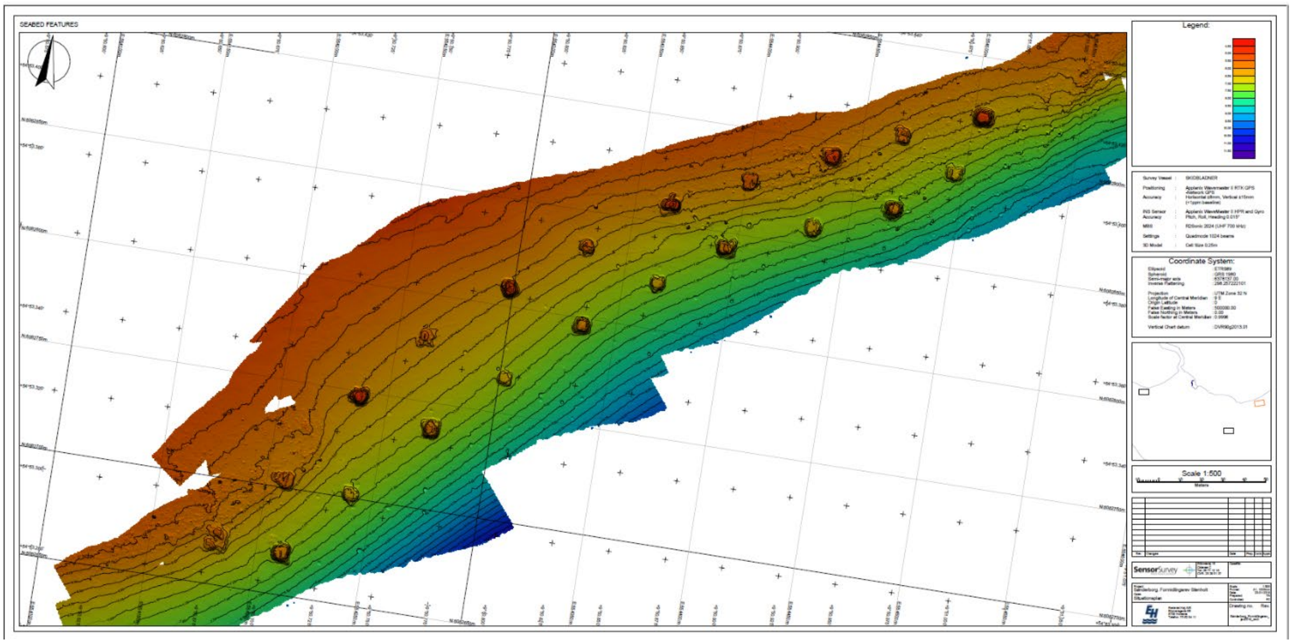


Figure 1.11. Map showing individual reef units deployed at Stenholt.

Figure 1.12. Pictures showing a newly deployed reef (December 2017) to the left, and the same reef surveyed in July 2019 to the right. About 1.5 years after reef construction, fish and macro algae increasingly occur on the reefs.

The presence of the reef units is also partly visible from the air when the water is sufficiently clear. Specifically, aerial photos revealed many individual reef units at both Hvide Mur and Stenholt (Figure 1.13 and Figure 1.14).

Figure 1.13. Aerial photo of constructed reefs at Hvide Mur photographed in 2019.

Figure 1.14. Aerial photo of constructed reefs at Stenholt photographed in 2019.

1.4 Discussion

In this work package, a series of cobble reefs were constructed at two sites in Sønderborg Bay, more specifically at Hvide Mur and Stenholt. The work package also located areas used as control sites and sites where natural reefs occur. Water depths at all sites varied between 6-7 m. At all sites, historic evidence revealed that herring had been spawning in the springtime and were possibly still using the sites as spawning grounds. This information was gathered by consulting elderly fishermen who knew about past fishing activities and captures. The presence of spawning herring was important, because the project hypothesized that the cobble reefs could be used as spawning areas, because herring have benthic eggs that attach to hard surfaces, including rock surfaces and the surfaces of macro algae growing on rocks. The spawning herring are likely to attract various other fish species eating the eggs or targeting the spawning herring. Moreover, spawning herring and other fish species could serve as food for harbor porpoise attracted to the reef areas. Identification of control sites and natural reef sites was important for the work packages investigating abundance of fish (WP2) and harbor porpoise (WP4) on the constructed reefs and on natural reefs. Likewise, the work package investigating sessile fauna and vegetation (WP3) also relied on the availability of the different marine sites.

Throughout the project, local support was ensured through many meetings and other ways of communicating with local experts. Local knowledge facilitated the identification of the six project sites. Moreover, local ownership of the project also resulted in a great deal of awareness about the project and its purpose. The project was carried out in an area where various marine reefs have been restored at a large scale since 2012. The projects have been carried out by the local organization Als Stenrev. The fact that the organization has been carrying out reef projects for several years means that a lot of local acceptance, experience and knowledge is available. Some previous reef projects have faced opposition by local stakeholders (Støttrup et al., 2017). This was never the case in the present project, probably owing to the fact that reefs have been restored in the area for several years combined with the strong involvement of numerous individual stakeholders and organizations throughout the entire process. The enormous value of local support, experience and knowledge is also reflected in many restoration projects internationally (Flávio, Ferreira, Formigo, & Svendsen, 2017). There are cases where ships have hit restored reefs (Støttrup et al., 2017). No such problems were encountered in the present project, probably because of the close collaboration with local stakeholders as well as the collaboration with the Danish Coastal Directorate. For example, constructed reef tops were always more than 4 m below the water surface to ensure adequate space for boats passing over the reefs.

In this project, we selected the best contractor by comparing reef volumes (m^3) offered by the different bidding contractors. The contractor delivering the largest reef volume at a fixed price (900,000 kr.) was requested to carry out the reef construction. Comparing the different contractors, this approach more than doubled the reef volume available for reef deployment in Sønderborg Bay. Thus, there were substantial differences between the reef volumes that the different companies offered to deploy for the fixed amount of funding. In the present project, the contractor provided 2.600 m^3 of cobble for reef deployment in Sønderborg Bay. The price was 900.000 kr. (excluding VAT), which also covered mapping and surveys after the reef deployment. The price corresponds to 350 kr. per m^3 cobble. In future reef construction projects, it is recommended that a price of 500 kr. per m^3 is expected during the early planning phases of the project (i.e. before the different reef volume estimates are received from the contractors). This estimated price seems to reflect the economic costs associated with previous and ongoing reef construction projects relying on rocks delivered from Norway.

Few contractors have experience in terms of constructing reefs, and reefs with certain shapes in particular. The present project aimed at creating low and high reefs with certain dimensions. It required substantial communication between the contractor and the project managers to reach an agreement in terms of what would be feasible for the contractor to construct on the seabed. Reef deployment was delayed in the present study, because the contractor's ships needed for the deployment were unavailable. Even after the reef deployment had started, completing the reef deployment got further delayed, because spare parts were lacking for a ship. This meant that the reef completion was delayed by several months. Delayed reef deployment meant that fish, sessile fauna, vegetation and harbor porpoises had less time to colonize the reefs within the time frame of the project.

Although many resources were allocated towards mapping of the different marine sites, further detailed mapping of the seabed would have been beneficial. A complete bathymetric map, including boulder coverage, cobble coverage, sand bottoms etc., covering the study areas, as well as the neighboring marine areas, would have been useful for the reef designs and deployments. Given the growing availability of tools for mapping different types of seabed, future studies should allocate resources towards accurate benthic mapping before reef deployment. The mapping information should be available before applying for a permit at the Danish Coastal Directorate and before inviting contractors to estimate the reef volumes that they can deliver.

2. Abundance and diversity of marine fish species associated with restored cobble reefs in coastal areas

2.1 Introduction

Coastal marine ecosystems worldwide are facing a multitude of human-induced stressors including pollution, habitat degradation, overexploitation and climate change (Andersson et al., 2015; Lin & Yu, 2018; Lotze et al., 2006; McDermott, Meng, McDonald, & Costello, 2019; Vince & Hardesty, 2016). Coastal habitat degradation is often a relatively slow process, e.g. the transformation of shorelines by coastal development projects over multiple human generations (Sundblad & Bergström, 2014), or the gradual (although accelerating) loss of seagrass meadows due to various anthropogenic stressors (Waycott et al., 2009). However, degradation of habitats may also take place on much shorter time scales, for example when mass bleaching events transform the topography of coral reefs (Hughes et al., 2018), or when destructive overexploitation removes large areas of biogenic (e.g. oyster) reefs and geogenic (i.e. rocky) reefs (Støttrup et al., 2017; Beck et al., 2011). The extraction of marine substrates, i.e. ranging from gravel to boulders, has been ongoing for decades in many countries, with deleterious effects on species that depend on hard-bottom substrates (Støttrup et al., 2014; Boyd et al., 2005; Desprez, 2000; Groot, 1980). Cessation of such extractive activities may induce recolonization of benthic communities, although likely characterized by a composition that differs substantially from the pre-disturbance community (Desprez, 2000). Active restoration efforts may enhance the potential to recover the associated marine community (Boyd et al.; 2005), in particular since the extraction of hard substrates constitutes a fundamental shift in habitat structure and availability that is unlikely to be reversed without human intervention (i.e. habitat restoration; Støttrup et al.; 2017).

Century-long extraction of large boulders from Danish coastal waters has severely degraded (or in some places completely removed) large temperate reef areas in the Baltic Sea (Dahl et al., 2003; Støttrup et al., 2014). The removal of boulders from the seabed was prohibited in 2010 by Danish law (Kristensen et al., 2017), yet it remains legal to extract other substrates, including gravel, pebbles and small cobbles, from dedicated marine areas. Such areas covered by smaller marine rocks may, however, support a diverse assemblage of marine fauna including commercially important taxa such as Atlantic cod (*Gadus morhua*) and European Eel (*Anguilla Anguilla*) (Christoffersen et al., 2018; Lough et al., 1989; Tupper & Boutilier, 1995b). Similarly, for other temperate juvenile fish species, cobble areas may also provide elevated post settlement survival and recruitment success compared to sand bottom areas (Tupper & Boutilier, 1997). In addition to juvenile nursery habitat, reef areas with small rocks may also support spawning of commercially valuable fish species. For example, Atlantic herring (*Clupea harengus*) often utilizes hard substrate for spawning in the North Sea and Baltic Sea, by depositing eggs either directly onto marine rocks or on various species of macroalgae that grow on the rocks (Kanstinger et al., 2018; Geffen, 2009; Aneer et al., 1983; Groot, 1980). Removal of hard substrate may therefore negatively impact local herring populations by restricting the availability of their spawning habitat (Wolff, 2000; Groot, 1980). In the Baltic Sea, herring mainly spawn in coastal waters of shallow depth (< 10 m; Aneer, 1989) and the deposition of eggs may attract a range of predators that feed on the eggs or directly on the herring (Kotterba et al., 2014). One example of such a predator includes the threespine stickleback (*Gasterosteus aculeatus*), which is known to occasionally feed on large quantities of herring eggs (Kotterba et al., 2017). The presence of sticklebacks may in turn attract larger predatory species (e.g. cod), exemplifying how herring spawning can ultimately induce various trophic interactions.

Ecological restoration, i.e. the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed (Clewell, Aronson & Winterhalder, 2004), is an increasingly popular tool to counteract the loss of habitats worldwide. Restoration efforts within the marine environment are scarce and have thus far mainly focused on re-establishing marine vegetation (Hale et al., 2019). One of the few examples to date of hard-bottom reef restoration includes the 'Blue Reef' project (Støttrup et al., 2017), in which 100,000 tons of marine boulders were restored in the Kattegat Sea between Denmark and Sweden. The re-establishment of cavernous boulder reefs resulted in a higher abundance and longer residence time of commercially important species and apex predators in the area, relative to pre-restoration conditions (Kristensen et al., 2017; Støttrup et al., 2014; Mikkelsen et al., 2013). However, given the relative infancy of the field of marine habitat restoration, knowledge on effective restoration methods is limited (Støttrup et al., 2017) and empirical assessments of restoration success are often inadequate or entirely absent. In particular, studies assessing community responses following an impact event (e.g. construction of an artificial structure in the marine environment) rarely employ a sampling design that includes multiple sampling years with adequate control sites (Mills, Hamer, & Quinn, 2017; Hale et al., 2019).

In the present study, cobble reefs were constructed at degraded coastal sites in southern Denmark. The efficacy of the restoration effort was evaluated by a before-after control-impact (BACI) sampling design, which allows for disentangling of restoration effects from natural occurring variations in the system (Underwood, 1991). To this purpose, field monitoring took place 7-8 months before and subsequently 4-5 months after the restoration of the reefs. Fish abundance, richness and species composition were compared between restoration sites (termed "experimental sites" in section 1.2.2; WP1) and control sites, which consisted of an empty sand or mud bottom. In addition, nearby natural reefs were monitored to allow for comparison with established hard-bottom reference sites. Specifically, we hypothesized that the reef restoration would result in higher fish abundance and richness compared to soft-bottom control sites, with a distinct community assemblage developing at restoration sites. We further hypothesized that the reef restoration would benefit a number of commercial species, in particular Atlantic herring (*Clupea harengus*), cod (*Gadus morhua*) and European eel (*Anguilla anguilla*), by providing a hard substrate for herring to spawn on while facilitating juvenile cod and eel survival by offering increased structural complexity and shelter availability.

2.2 Materials and methods

2.2.1 Study location

This study took place in Sønderborg Bay, a coastal area located in the Flensborg Fjord between Denmark and Germany (Figure 1.9; WP1). The bay is characterized by large areas of soft sediment and mud, locally forming small patchy mosaics with natural cobble reefs. Rocks have historically been extracted from the bay, as revealed by interviews with elderly fishermen with local knowledge. We monitored six field sites as part of this study (Fig. 1.9; WP1), which included two soft-bottom sites that served as control sites ('Kegnæs Ende' and

‘Viemose’), two natural reef sites serving as reference sites (‘Spar Es’ and ‘Vesterhage’) and two experimental sites at which cobble reefs were restored (‘Hvide Mur’ and ‘Stenholt’). Experimental sites were characterized by soft-bottom habitat prior to the restoration efforts, similar to control sites, yet hosted multiple reef units after the restoration was complete. Field monitoring was performed at water depths between 6 m and 7 m at designated sampling areas along the coastline (polygons in Fig. 1.9; WP1), with a maximum size of 500 m in length and 200 m in width.

2.2.2 Reef designs

Reefs were made out of granite, shipped to Denmark from Norway. Rock diameters varied, but were mainly characterized as cobble. All rocks were larger than 6 cm in diameter, and the mean rock sizes were aimed at matching the larger fractions of cobble (> 20 cm in diameter). As revealed by previous studies, such cobble reefs provide a complex habitat that contributes to replenishing fish populations (Tupper & Boutilier, 1995a, 1997). Reefs were restored in the locations ‘Hvide Mur’ and ‘Stenholt’ situated in Sønderborg Bay (Figure 1.9; WP1). In each location, a total of 20 individual reef units were constructed. The distance between each reef unit was approximately 20 - 30 m. Individual reefs units were shaped as truncated square pyramids. The foot of each reef unit was 11 m x 11 m, whereas the top of each reef unit was 5 m x 5 m. The height of each reef unit was either 0.6 m or 1.3 m high (i.e. low and high reef units). Further details are provided elsewhere in the report (WP1; Figure 1.6).

2.2.3 Reef deployments

Cobble reefs were deployed over two months during the winter 2017-2018 (Figure 2.1A). Deployments were carried out from an anchored ship using machinery that extended from the ship to the seabed to ensure that the individual reef units were created in agreement with the planned designs. Reef units were deployed in two lines situated at water depths of 6 m and 7 m (i.e. one line of reef units at each water depth). At each experimental site (‘Hvide Mur’ and ‘Stenholt’), we divided a total of 20 reef units along a 6 m and 7 m depth line, with each depth line hosting 10 reef units. The reef units alternated in height between 0.6 m (i.e. low reef units) and 1.3 m (i.e. high reef units) along both depth lines. SCUBA divers confirmed the shape and locations of the individual units shortly after the reef deployment. These diving activities revealed that the reef units occasionally included rocks with a diameter up to 40 cm, implying that the average rock size used for constructing the reef units may have slightly exceeded the general classification of cobble used in this study (diameter up to 30 cm). Further details are provided elsewhere in the report (WP1; Figure 1.5 and 1.12).

2.2.4 Data collection

Field sites were monitored using baited and unbaited remote underwater video systems (BRUVS and UBRUVS, respectively). These non-invasive video sampling techniques are particularly useful to sample vulnerable areas (e.g. protected or restored habitats), as the impact to the benthic environment is minimized (Cappo et al., 2003). Video cameras in underwater housings were attached with horizontal orientation to a metal pole (3 cm in diameter; 100 cm in height) at a height of 20 cm above the seabed. For the BRUVS setup, a bait arm (80 cm in length) extended in front of the camera’s field of view (FOV), holding a mesh bait bag that contained

500 g of fresh chopped herring (*Clupea harengus*; chops of 1-2 cm diameter). Tape markers at 10 cm increments along the bait arm were used as a reference for visibility estimates (Fig. 2.1B). The setup of UBRUVS resembled that of BRUVS, with the exception of the bait arm being replaced with a marked rope extending horizontally in the FOV of the camera (Figure 2.1C). All camera units were mounted on a concrete base (dimensions: 45 cm x 45 cm x 5 cm length, width and height, respectively) to ensure stable positioning on the seabed. Kitchen sponges were used as markers on the ropes at 1 and 3 m distances from the camera (Figure 2.1E), again to allow for visibility estimates. Temperature loggers (HOBO; www.onsetcomp.com) were attached to one of the RUVS at each site for temperature measurements.

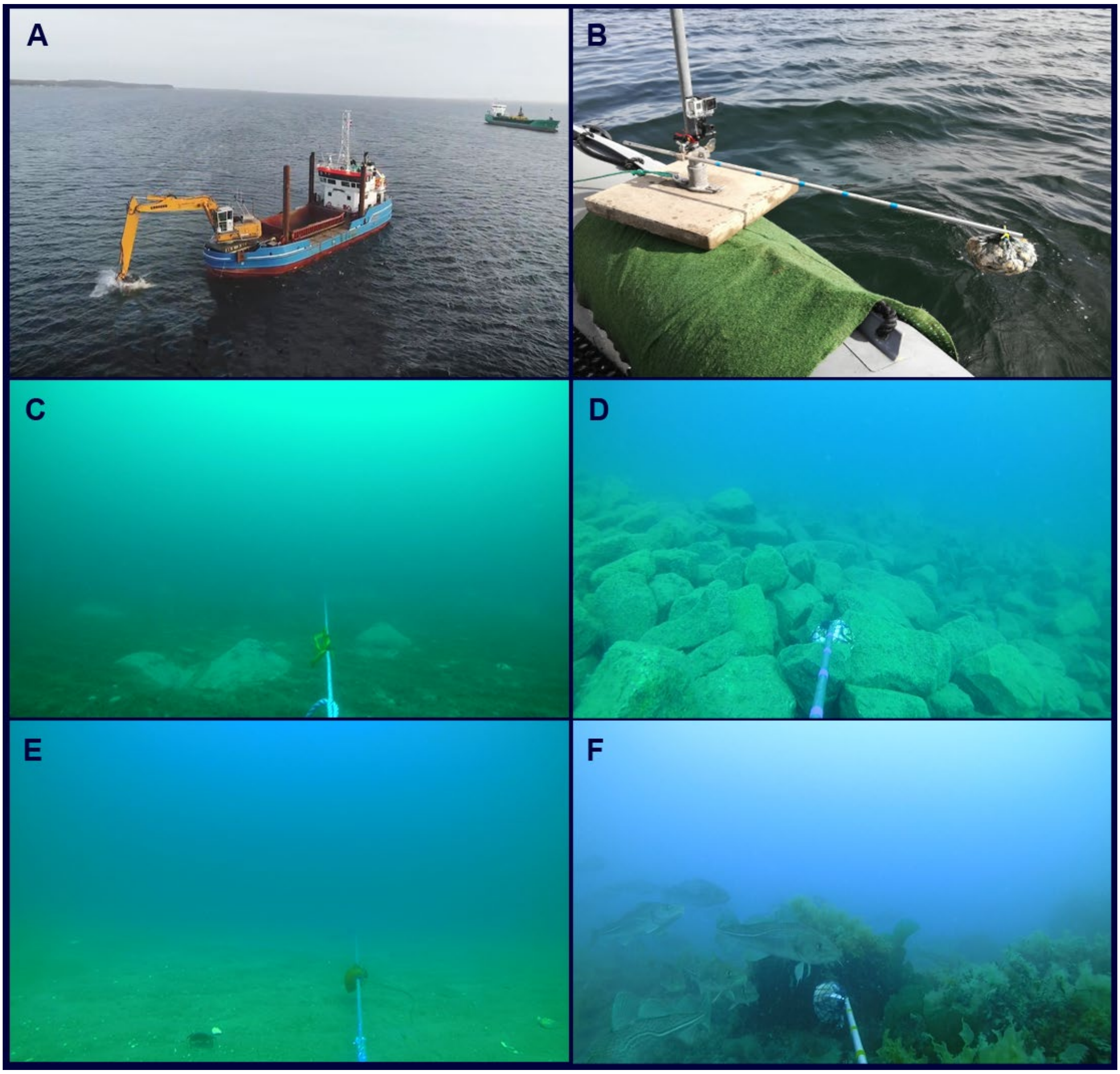


Figure 2.1. Multi-pane overview of the survey method and sampling sites, with A) construction of the reefs using a large crane on top of a vessel; B) BRUVS setup with a bait arm extended within the field of view, marked with tape at 10 cm increments for visibility estimates; C) experimental site before the reef restoration as recorded by UBRUVS; D) experimental site after the reef restoration as recorded by BRUVS; E) control site consisting of sandy bottom with a passing shore crab recorded by UBRUVS, and F) natural reef site recorded by BRUVS with a passing shoal of Atlantic cod.

We used GoPro cameras (Hero 3, 3+ & 4, www.gopro.com) at 720p video resolution and 30 frames per second (NTSC) for recording. UBRUVS were equipped with intervalometers (model: Time Lapse Intervalometer or BlinkX, CamDo Solutions; www.cam-do.com), which acted as a timer turning on the camera every hour for two minutes and turning it off again. Accordingly, UBRUVS were able to capture at least one diurnal cycle from early dawn to late dusk, with a large proportion of cameras recording two-minute sampling units for 40 hours or more. In contrast, BRUVS setups did not include a timer and the cameras instead ran continuously to effectively capture the effect of bait plume dispersal within the water column. BRUVS were equipped with an additional battery pack (BacPac; www.go-pro.com), which ensured soak times between 1 h and 2.5 h in line with recommendations for adequately capturing patterns in community compositions (Harasti et al., 2015). We did not include artificial light sources within the camera setup and therefore had to discard footage recorded at night, with BRUVS deployed 2 h before sunset at a minimum to ensure adequate light conditions. Day light hours varied between 13 h and 17 h during the study period.

We followed camera deployment procedures described in Langlois et al. (2018). A side scanner (Lowrance Elite-7 Ti; www.lowrance.com) was used to locate the field sites, detect the restored reef units and to verify suitable soft- and hard-bottom habitats for control and natural reef sites, respectively. A maximum of two RUVS units, either both baited or unbaited, were run simultaneously at each field site. BRUVS and UBRUVS were allowed to run concurrently at different sites (Figure 1.9; WP1), but never within the same site as UBRUVS recordings could be affected by the use of bait in the vicinity. In case either two BRUVS or two UBRUVS were recording simultaneously at a specific site, we actively maximized camera distance within the confines of each site to minimize potential spatial auto-correlation between deployments.

2.2.5 Video analyses

Recordings were analysed in VLC media player (VideoLan; www.videolan.org) by multiple observers. We expressed the relative abundance of observed individuals as the 'MaxN' metric, i.e. the maximum number of individuals of a particular species that is observed in a single video frame (Cappo et al., 2003; Willis & Babcock, 2000; Ellis & DeMartini, 1995). MaxN is widely regarded as a conservative estimate of species abundance, as only individuals that enter the FOV are recorded and duplicate counts of the same individual within a sample are avoided. Individuals were identified to the lowest attainable taxonomic category with aid of compiled reference images. Where species-level identification was unattainable, we instead grouped individuals based on higher taxonomic levels, e.g. by genus or family. For example, flatfish species (order: *Pleuronectiformes*) are often particularly challenging to identify due to their cryptic coloration and sedentary lifestyle, while sand gobies (genus: *Pomatoschistus*) were often too small or positioned at substantial distance from the camera, making species identification impossible. In such cases, unidentified flatfishes were denoted as *Pleuronectiformes sp.* and sand gobies as *Pomatoschistus sp.*, the latter in order to still enable a distinction with the often conspicuously larger black goby (*Gobius niger*). Besides describing total fish abundance and richness at the different sites, we aimed at studying the effects of the reef restoration on prominent taxonomic groups with either a high sand or reef affinity. As such, we ran separate analyses on the abundance of Atlantic cod (*Ga-*

dus morhua), Atlantic herring (*Clupea harengus*), flatfish (*Pleuronectiformes sp.*), goldsinny wrasse (*Ctenolabrus rupestris*), two-spotted goby (*Gobiusculus flavescens*), sand gobies (*Pomatoschistus sp.*), shore crab (*Carcinus maenas*) and starfish (*Asterias rubens*).

Ultimately, we denoted taxonomic species identification, MaxN count for each observed species, estimated body size category (in increments of 5 cm), cobble coverage and vegetation coverage on the seabed (%), functional visibility (m) and the camera field of view obstruction (mainly by rocks) (proportion between 0 and 1). In cases where individuals belonging to the same species but of conspicuously different body sizes were observed on different video frames, we included these individuals in the total MaxN count for that species within the sample (similar to Watson et al., 2010). We defined cobble and vegetation coverage as the percentage of visible seabed within the frame that was covered by cobbles and macroalgae, respectively. Functional visibility was estimated as the furthest distance at which species were still identifiable, with aid of the tape markers on the bait arm (BRUVS) or rope (UBRUVS) in front of the camera. Finally, we estimated the proportion (proportion between 0 and 1) of the video screen obstructed by seabed structures (mainly rocks) or macro algae within the functional visibility and subtracted these proportions from 1 to obtain a measure of the FOV obstruction for each sampling unit.

2.2.6 Statistical analyses

We used generalized linear mixed models (GLMMs) to analyze both the effect of the reef restoration efforts and reef height on the marine community. Similar to previous studies using a before-after control-impact (BACI) design (Stenberg et al., 2015; Streich et al., 2017), we investigated the significance of the Year x Treatment interaction to highlight the reef restoration effect using an alpha value of 0.05. In particular, a significant interaction would imply a difference between the two treatments over the sampling years (i.e. pre- and post-restoration), whereas significance in either of the two individual terms would merely constitute the within and between year variability in the community metrics. There are a number of different scenarios in which a positive effect of an impact event (here reef restoration) can be obtained in a BACI setup (Figure 2.2). The most evident scenario involves equal measures of the response variable of interest (e.g. fish abundance) at control and impact sites before the restoration, with an increase only for impact sites after the restoration (Figure 2.2A). However, a positive effect would also arise in case the response variable decreases for control sites only, without an actual change in values at impact sites (Figure 2.2B). An example of such a scenario could be a yearly fluctuation decreasing the species abundance at control sites, but improved environmental conditions caused by the impact event, preventing a similar decrease at impact sites. Finally, the response variable could change in the same direction for both control and impact sites following an event, in which case either a sharper increase at impact sites (Figure 2.2C) or a sharper decrease at control sites (Figure 2.2D) would also lead to a positive effect of the impact event (i.e. restoration).

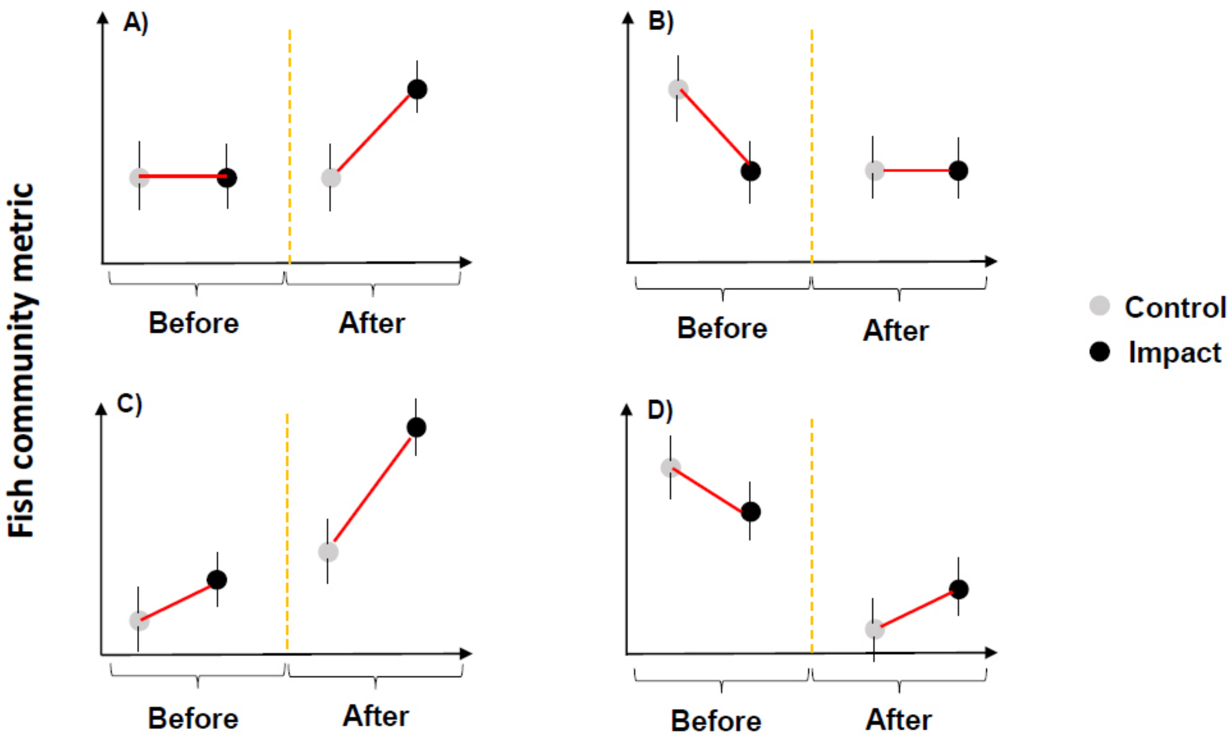


Figure 2.2. Conceptual plots showing four different scenarios in which a positive impact effect would be detected under a before-after control-impact (BACI) design. The orange dashed lines represent the impact event (i.e. reef restoration), while the solid red lines show the differences (i.e. slopes) between control and impact, which are compared before and after the impact event. A) Equal values of the response variable (i.e. the fish community metric) before the event, and higher values at impact sites only after the event. This scenario clearly indicates a positive effect of the impact event. B) Higher value of the response variable (i.e. the fish community metric) at control sites before the event, and equal values after the event (no net change in values at impact sites). This also indicate a positive effect of the impact event, because the impacted site remained unchanged while the control site declined. C) Increase in the response variable at both control and impact sites following the impact event, but with a sharper increase at impact sites. The positive effect is indicated by a steeper slope after the impact event. D) Decrease in the response variable at both control and impact sites following the impact event, but with a sharper decrease at control sites. The positive effect is indicated by a positive slope after the impact event, compared to a negative slope before the impact event

Since the main response variables of interest were integers (i.e. MaxN and species counts), these variables were initially modelled using a Poisson distribution with a log-link function. In case of overdispersion, we used either the negative binomial family with quadratically increasing variance or a generalized Poisson distribution based on Akaike's Information Criteria (AIC) values. However, a substantial number of models showed underdispersion, which was addressed by fitting a Conway-Maxwell Poisson (CMP) instead. The CMP distribution is effective at dealing with underdispersed count data and has become particularly useful in ecological studies after being parametrized via the mean (Huang, 2017).

Our exploratory analysis revealed a high correlation of cobble coverage with both vegetation coverage and treatment. This was expected, since cobble was only present at certain treatments (i.e. natural reefs and post-restoration experimental sites) and macro algae require a hard substrate for settlement, implying that vegetation growth at sites low in cobble coverage was minimal. We therefore excluded cobble coverage as a predictor from all models, assuming the effect of cobble was adequately covered by including the treatment predictor in all models. For UBRUVS, we defined a nested random effects structure, with 'Deployment ID' being nested in 'Site ID'. This was done to account for correlations in fish counts between samples (i.e. two-minute recordings) from the same deployment, as well as for correlations between deployments from the same field site. For BRUVS, a single random effect of 'Site ID' was sufficient since sampling units consisted of a single 1-3h deployment instead of multiple shorter recordings. Apart from vegetation coverage, we included temperature (standardized) as an additional predictor to account for large fluctuations in water temperature (2-20 degrees Celsius) throughout the sampling period. To analyze the effects documented by BRUVS, we set a minimum recording length requirement of 1 hour (section 2.2.4) and defined a soak time variable to account for differences in recording time between deployments. Specifically, this was done by adding the natural logarithm of soak time to the models and thereby defining soak time as an exposure term (Zuur & Ieno, 2016). Similarly, we defined the field of view (FOV) as an exposure term (i.e. modelling the fish count per visible field of view) by including the natural logarithm of FOV as a predictor in all BRUVS and UBRUVS models. Specifically, this allowed the models to assign additional weight to fish counts from highly obstructed videos (as we were potentially missing obscured individuals), while attributing less weight to counts from unobstructed recordings. Finally, functional visibility was defined as an offset (i.e. parameter value set to 1) for MaxN models, since the number of sampled individuals is likely to increase linearly with visibility within the limits of the field of view. However, this may not be the case for species richness, since individuals are generally more difficult to identify at greater distance from the camera. We therefore included visibility as a third exposure term (i.e. by adding a 'logVis' predictor) in the species richness models.

Effects of the reef restoration on the community composition at the field sites was assessed using multivariate methods described by Anderson & Willis (2003). Specifically, non-metric multidimensional scaling (nMDS) was performed to identify clustering of field sites in terms of species composition. We used Bray-Curtis dissimilarity as the distance measure and a Wisconsin double-standardization was applied on the data prior to running the ordination. As a second step, we followed the canonical axis of principal coordinates (CAP) approach to constrain the ordination on the Year and Treatment variables (Anderson & Willis, 2003). Individual species were fitted as vectors onto the constrained ordination and the significance of their contribution was assessed by running 999 permutations. To improve graphical presentation, we only plotted those species showing a significant correlation ($p < 0.05$) with one of the two CAP axes.

Statistical analyses were conducted in R version 3.6.0 (R Core Team, 2013). We used the 'glmm' package to fit the linear models (Brooks et al., 2017), after which post-hoc analyses were carried out using the pairs() and contrast() functions of the 'emmeans' package (Lenth, 2016). Species accumulation curves were created with the iNEXT (iNterpolation and EXTrapolation) package (Hsieh, Ma, Chao, & Hsieh, 2019), while constrained and unconstrained ordinations were performed using the capscale() and metaMDS() functions of the 'vegan' package (Oksanen et al., 2018), respectively.

2.3 Results

2.3.1 Sampling effort

We deployed a total of 743 RUVS across the two sampling years, comprised of 379 baited and 364 unbaited deployments (overview of number of samples per site provided in Table 1). We recorded a total of 47 different marine species belonging to 35 families, of which 41 species were recorded by BRUVS and 35 species by UBRUVS. Atlantic herring (*Clupea harengus*) was the most abundant species recorded by both methods, closely followed in UBRUVS by two-spotted goby (*Gobiusculus flavescens*). However, herring ranked only 6th and 8th in terms of encounter frequency for BRUVS and UBRUVS, respectively, reflecting the sporadic nature of large herring school encounters. Atlantic cod (*Gadus morhua*) was the most frequently encountered species for BRUVS, whereas starfish (*Asterias rubens*) was recorded most often in UBRUVS. The sampling effort, i.e. number of baited deployments and 2-minute unbaited sequences, was found to be adequate to capture the marine community as species accumulation curves of both methods plateaued at all treatment levels (Figure 2.3).

Table 2.1. Successful BRUV and UBRUVS deployments across the two sampling years. The six sampling sites are listed with their respective treatments. Cobble reefs were constructed at the end of 2017, implying that experimental (restoration) sites sampled in 2017 still consisted of empty sand and mud bottom. Two-minute hourly recordings were used as sampling units for UBRUVS, which are included in parentheses. For BRUVS, each deployment counted as a single sampling unit.

		2017		2018	
Site	**Treatment**	**BRUVS**	**UBRUVS**	**BRUVS**	**UBRUVS**
Hvide Mur	Experimental reef	23	27 (632)	54	46 (1117)
Kegnæs Ende	Control	23	24 (550)	35	30 (818)
Spar Es	Natural reef	24	24 (660)	33	32 (733)
Stenholt	Experimental reef	20	28 (560)	58	42 (1201)
Vesterhage	Natural reef	23	22 (461)	34	30 (738)
Viemose	Control	21	28 (606)	31	31 (764)

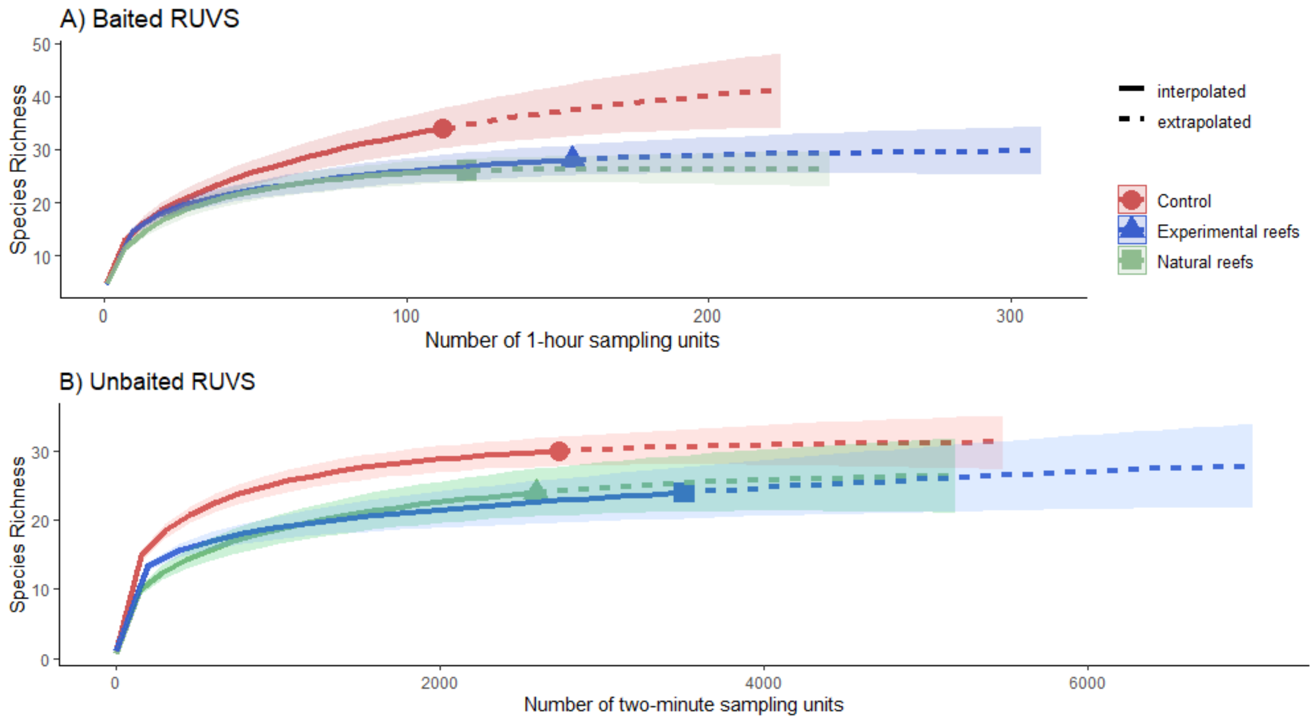


Figure 2.3. Species accumulation curves for A) BRUVS and B) UBRUVS. Solid lines represent the actual sample size obtained for each sampling method, while the dashed line shows the extrapolation of expected species richness under an increased sampling effort. The figures show that our sampling protocol was adequate, since additional sampling would have resulted in few additional species detected by the cameras.

2.3.2 Pooled community responses

Results from our BACI comparison of the pooled fish community before and after the restoration differed slightly for the two sampling methods. BRUVS recorded a significantly higher fish abundance at experimental reefs compared to control sites across the two sampling years (Figure 2.4A; $p < 0.01$; Table 2.2), whereas no differences were found in species richness (Figure 2.4B; $p > 0.05$; Table 2.2). Post-hoc analysis indicated similar regression slopes between natural and experimental reefs over time ($p > 0.05$), implying that the reef restoration did not significantly affect abundance and richness relative to natural reefs. Notably, UBRUVS recorded a strong reef restoration effect on both fish community metrics (i.e. fish abundance and richness; Figure 2.5). Relative fish abundance was found to show a strong increase at restored reef sites compared to control sites between the two years (Figure 2.5A; $p < 0.001$; Table 2.2). Similarly, a strong increase in the number of fish species recorded by UBRUVS was ob-served at the restoration sites (Figure 2.5B; $p < 0.001$; Table 2.2). Post-hoc analyses indicated that the experi-mental reefs even surpassed natural reefs in terms of fish abundance (Figure 2.5A; $p < 0.001$), but not signifi-cantly for species richness (Figure 2.5B; $p > 0.05$).

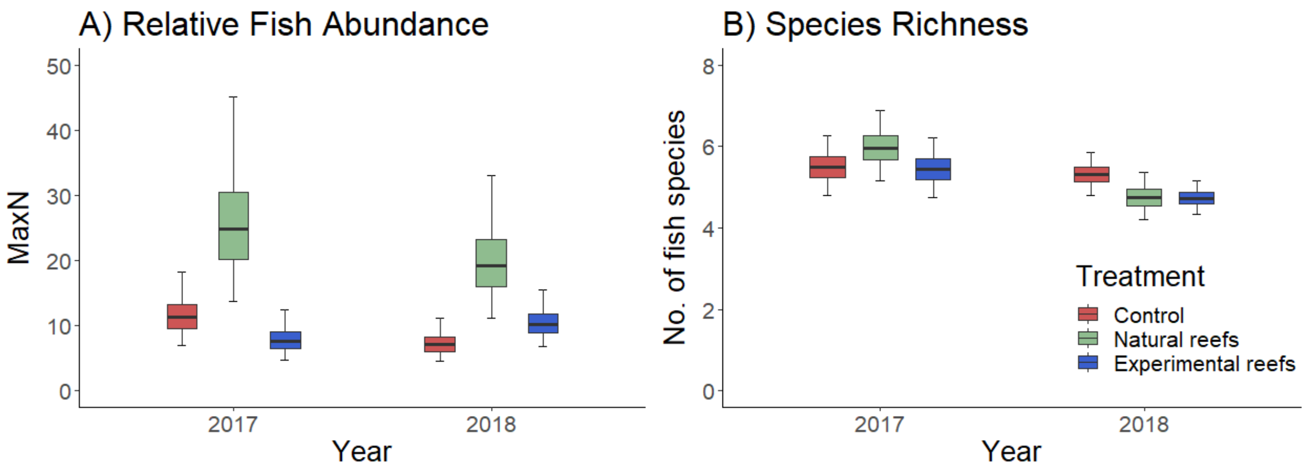


Figure 2.4. Fish community metrics (with 95% confidence intervals) before and after the reef restoration as documented by BRUVS. A) Relative fish abundance (in MaxN counts per deployment) and B) species richness (in number of fish species per deployment) between the two sampling years.

Table 2.2. GLMM parameter estimates (on log-scale) for all the BACI models and both sampling methods. The table only shows the variables related to the BACI comparison (exposure terms, temperature and vegetation coverage are not included). Models were fitted using either a Poisson (P), negative binomial (NB), generalized Poisson (GP) or Conway-Maxwell Poisson (CMP). The intercept column represents the parameter estimate for control sites sampled in year 2017. All other parameter estimates are expressed in relation to the intercept. The last column shows the variable of interest in the BACI comparison (control vs experimental reefs across the two years) for which significant effects are marked in bold (positive values indicate a positive reef restoration effect); [(*) = *p* < .1; * = *p* < .05; ** = *p* < .01, * = *p* < .001]. MaxN indicates relative abundance, whereas SR indicates species richness.**

Response variable	Sampling method	Distribution	Intercept	Year18	Treat_Nat	Treat_Exp	Year18 x Treat_Nat	Year18 x Treat_Exp
Total	BRUVS	NB	2.38	-0.46*	0.79(*)	-0.39	0.21	**0.76****
MaxN	UBRUVS	GP	-0.60	-0.52***	0.01	-0.52**	-0.46*	**1.13*****
Total	BRUVS	CMP	1.38	-0.03	0.08	-0.01	-0.20	-0.11
SR	UBRUVS	P	-1.33	-0.07	0.28	-0.53(*)	-0.28	**1.07*****
Cod	BRUVS	NB	2.23	-1.54***	0.76	-0.84	0.86(*)	0.95(*)
MaxN	UBRUVS	NB	-2.17	-2.49***	1.01(*)	-1.07*	1.99***	**2.44*****
Herring	BRUVS	NB	2.49	-0.50	2.37*	-0.50	1.52*	0.01
MaxN	UBRUVS	NB	-2.28	-0.17	-0.69	0.24	0.74	0.11
Flatfish	BRUVS	NB	0.32	-0.05	-0.37	0.59	0.26	**-1.09*****
MaxN	UBRUVS	NB	-5.58	1.51**	0.08	-0.41	-0.99	**-1.83***
Wrasse	BRUVS	NB	-2.05	-1.07*	1.14*	-0.97	-0.67	**2.22****
MaxN	UBRUVS	CMP	-6.25	-4.77***	3.35***	0.44	3.36*	**7.07*****
Two spot	BRUVS	GP	-2.36	1.36(*)	1.84*	0.20	-2.18**	0.38
goby MaxN	UBRUVS	NB	-6.87	-0.20	2.99*	0.32	-0.13	**4.72*****
Sand goby	BRUVS	NB	-1.65	1.24**	0.95	-0.01	-1.85*	-0.54
MaxN	UBRUVS	P	-4.92	2.36***	1.88	0.45	-3.04**	**-2.65*****
Crab	BRUVS	NB	2.40	-2.16***	-0.96**	-0.47	0.76***	**0.38***
MaxN	UBRUVS	CMP	-3.24	-0.20	-1.11(*)	-0.32	-0.41	-0.25
Starfish	BRUVS	NB	0.92	-1.61***	0.72	-0.06	-0.33	0.11
MaxN	UBRUVS	CMP	-0.86	-1.88	0.09	0.21	0.17	**-1.72*****

These findings suggest that our newly deployed reefs were colonized by reef species within four months of the reef construction, often resulting in higher total fish abundance at experimental reefs compared to natural cobble reefs.

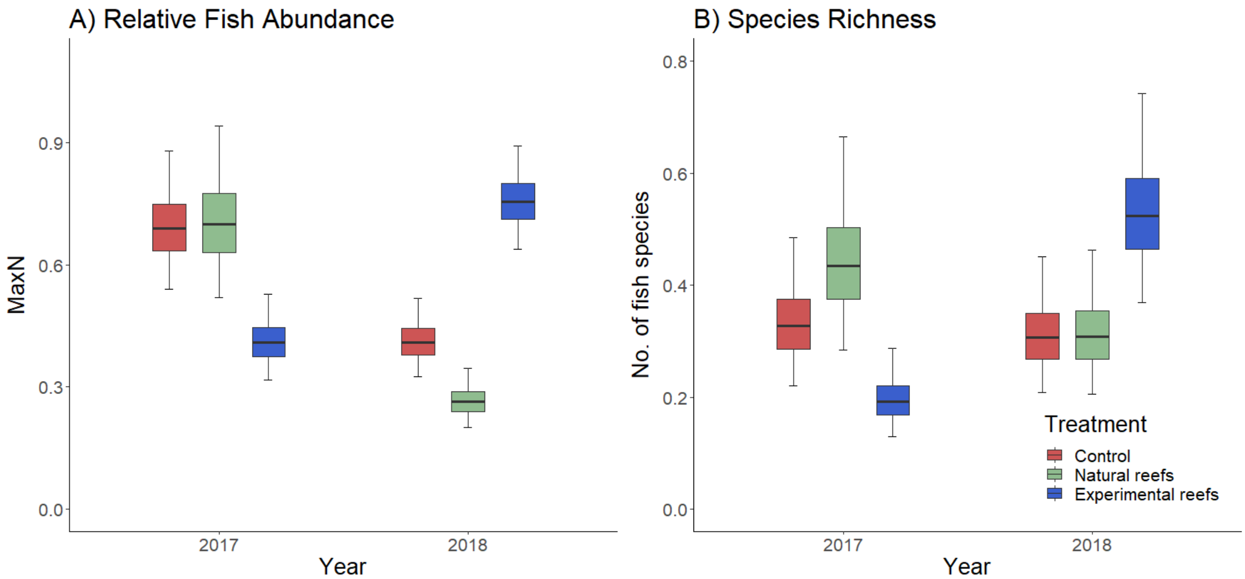


Figure 2.5. Fish community metrics (with 95% confidence intervals) before and after the reef restoration as documented by UBRUVS. A) Relative fish abundance (in MaxN counts per two-minute recording) and B) species richness (in number of fish species per two-minute recording) between the two sampling years for the three treatments.

2.3.3 Focal species responses

A number of different trends were observed when examining the response of the focal species to the reef restoration as recorded by the two sampling methods (UBRUVS and BRUVS). UBRUVS documented a significant positive reef restoration effect for three out of nine focal species, being Atlantic cod (*Gadus morhua;* $p < 0.001$; Figure 2.7A), goldsinny wrasse (*Ctenolabrus rupestris*; $p < 0.001$; Figure 2.7D) and two-spotted goby (*Gobiusculus flavescens*; $p < 0.001$; Figure 2.7E). Thus, these species increased in abundance as a consequence of reef restoration. A negative effect was found on the abundance of flatfish (*Pleuronectiformes sp.*; $p < 0.05$; Figure 2.7C), sand goby (*Pomatoschistus sp.*; $p < 0.001$; Figure 2.7F) and starfish (*Asterias rubens*; $p < 0.001$; Figure. 2.7H), while shore crab (*Carcinus maenas*) and herring (*Clupea harengus*) showed no response to the restoration efforts recorded by UBRUVS ($p > 0.05$). This implies that herring were not attracted to the restored reefs as expected. Results from BRUVS recordings were less pronounced, with only three out of nine focal species responding to the reef restoration. A positive restoration effect was found for goldsinny wrasse (Figure 2.6D; $p < 0.001$) and shore crab (Figure 2.6G; $p < 0.05$), while flatfish again decreased in abundance at restored reef sites (Figure 2.6C; $p < 0.001$). Atlantic cod did appear to be more abundant post-restoration compared to control sites, but the effect was not statistically significant at the 95% level (Figure 2.6A; $p < 0.1$). The remaining five focal species did not differ in relative abundance on BRUVS recordings following the reef restoration. Observations of European eel (*Anguilla anguilla*) were too limited for statistical comparison.

Our post-hoc comparison between natural and experimental reefs after the reef construction revealed few differences in terms of abundance of the focal species. Atlantic herring was clearly recorded in higher abundances at natural reefs after the reef restoration (Figure 2.6B; $p < 0.001$), but this trend was not evident in UB-RUVS. Atlantic cod was similarly more prevalent at natural reefs following the restoration efforts, this time only statistically significant in UBRUVS (Figure 2.7A; $p < 0.01$). The remaining six focal species did not exhibit a preference for either of the two reef types ($p > 0.05$ for both sampling methods). These results suggest that, although herring and cod preferred the well-established and rich cobble habitat of natural reefs, the newly restored reefs already showed a close resemblance to natural reefs in terms of relative abundance of the most prominent marine species in this study.

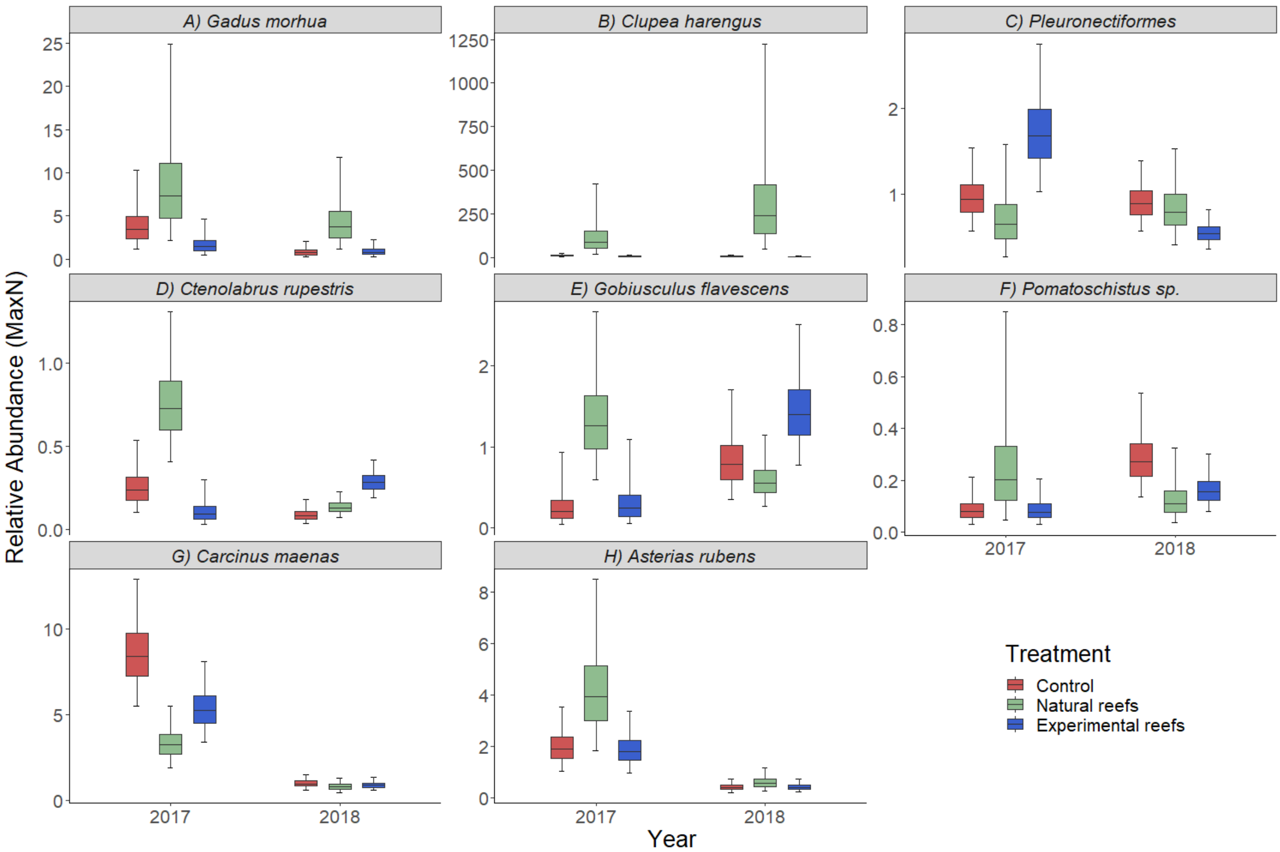


Figure 2.6. BACI comparison of relative abundance for eight focal species as recorded by BRUVS between the two sampling years. A) Atlantic cod (*Gadus morhua*), B) Atlantic herring (*Clupea harengus*), C) flatfish (*Pleuronectiformes sp.*), D) goldsinny wrasse (*Ctenolabrus rupestris*), E) two-spotted goby (*Gobiusculus flavescens*), F) sand goby (*Pomatoschistus sp.*), G) shore crab (*Carcinus maenas*) and H) starfish (*Asterias rubens*).

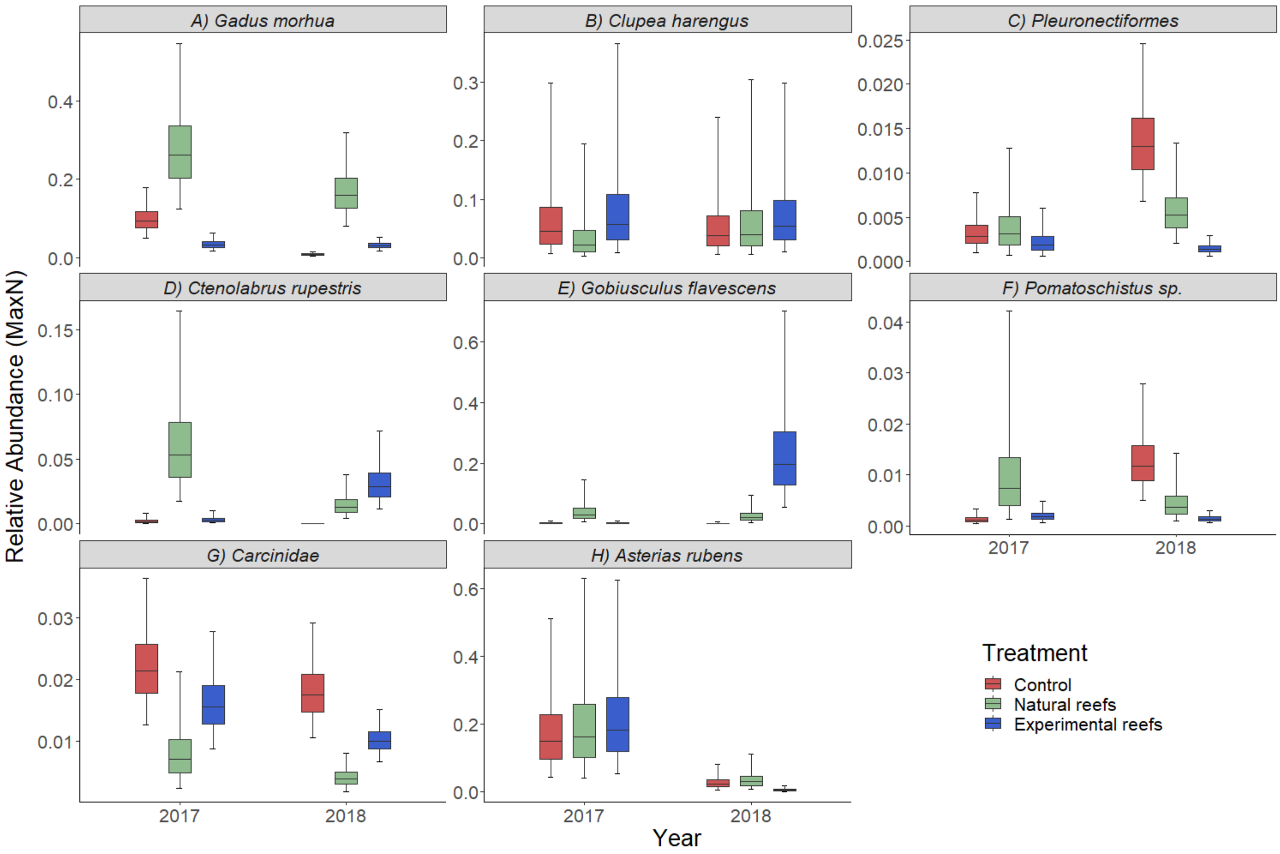


Figure 2.7. BACI comparison of relative abundance for eight focal species as recorded by UBRUVS between the two sampling years. A) Atlantic cod (*Gadus morhua*), B) Atlantic herring (*Clupea harengus*), C) flatfish (*Pleuronectiformes sp.*), D) goldsinny wrasse (*Ctenolabrus rupestris*), E) two-spotted goby (*Gobiusculus flavescens*), F) sand goby (*Pomatoschistus sp.*), G) shore crab (*Carcinus maenas*) and H) starfish (*Asterias rubens*).

2.3.4 Reef height effect

The construction of reef units at two different heights (i.e. 0.6 m and 1.3 m high) had minimal effects on the abundances of associated species (Figure 2.8). When pooling all fish species, no differences were found in relative fish abundance on low and high reefs for either sampling method (Figure 2.8A, E; $p > 0.05$). When focusing on Atlantic cod, UBRUVS recorded a significant preference for low reefs as opposed to high reefs (Figure 2.8F; $p < 0.05$). The remaining two focal reef species, goldsinny wrasse and two-spotted goby, did not seem to respond to the different reef heights used in this study (Figure 2.8C, D, G & H; $p > 0.05$). Atlantic herring could not be included in the reef height analysis, due to sporadic yet highly inflated counts (i.e. large schools) resulting in model convergence issues, even when using the Conway-Maxwell distribution, which generally has a better tendency to converge (Brooks et al., 2019).

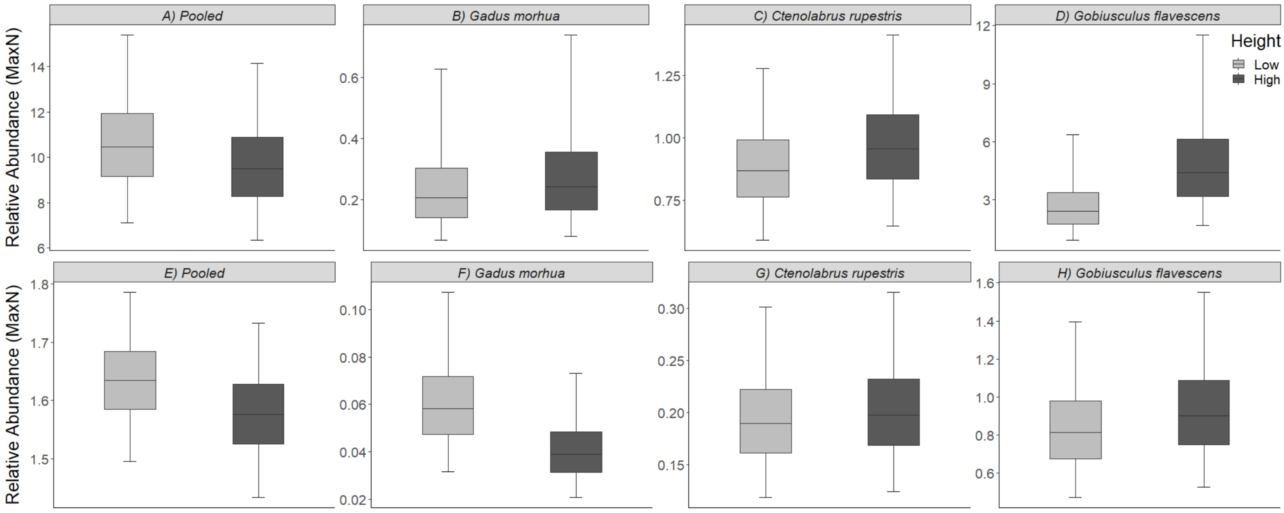


Figure 2.8. The effect of two different reef heights on relative fish abundance as recorded by BRUVS (A-D) and UBRUVS (E-H). Showing A,E) the pooled fish community responses; B,F) Atlantic cod (*Gadus morhua*); C,G) goldsinny wrasse (*Ctenolabrus rupestris*) and D,H) two-spotted goby (*Gobiusculus flavescens*).

2.3.5 Community composition

The unconstrained ordination of the species assemblage documented by UBRUVS revealed distinct community compositions for each of the different treatments (Figure 2.9A). Generally, an unconstrained ordination allows for the detection of patterns in the data (e.g. clustering of species compositions from different sites), before constraining the ordination on variables of interest (e.g. Year and Treatment; Anderson & Willis, 2003). Pre-restoration sites (i.e. blue circles in Figure 2.9A) were found to cluster together with control sites from 2017 (red circles), whereas the species composition of natural reefs (green circles) was already clearly distinct from the two sandy-bottom treatments. After the reef restoration, the species composition of restored sites diverged from the control sites to form their own unique assemblage (blue triangles in Figure 2.9A). The natural reef composition remained similar to the previous sampling year, while control sites seemed to diverge away from the composition of the previous year (red triangles). Assemblage clusters derived from BRUVS recordings were less pronounced. Apart from natural reefs hosting a distinct species community before and after our restoration efforts, the remaining control and restoration sites seemed to be similar in composition for the two sampling years (Figure 2.10A).

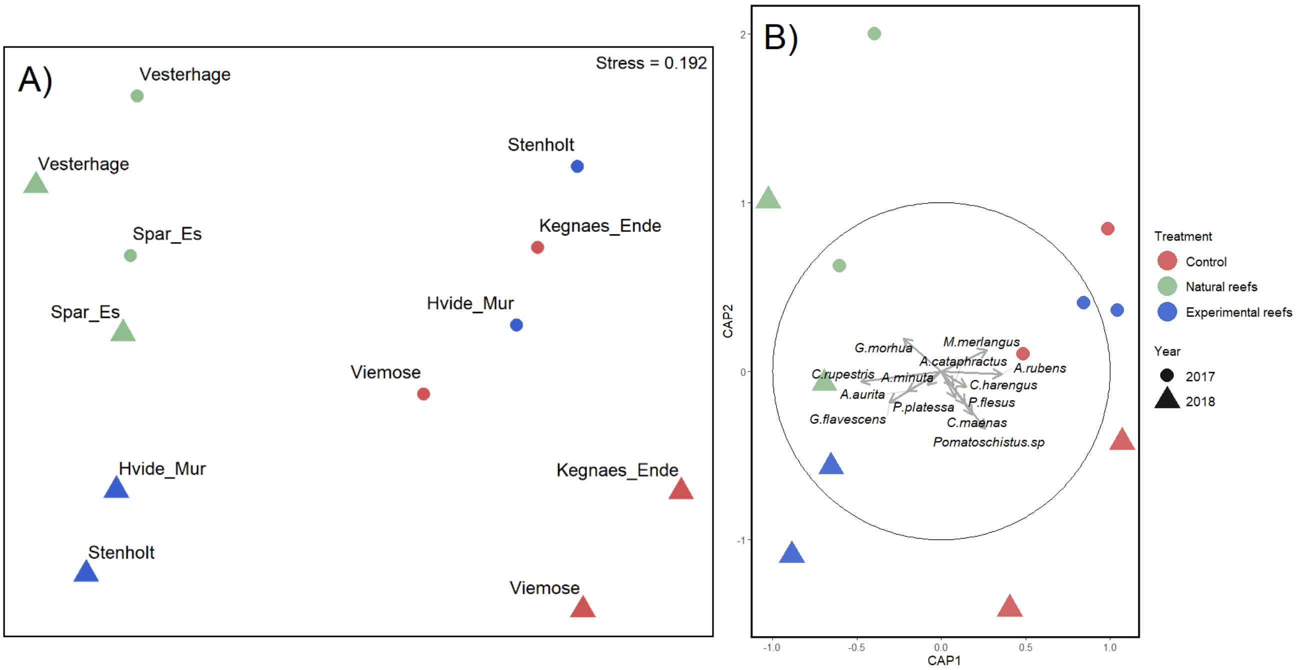


Figure 2.9. Community composition as recorded by UBRUVS, with A) the unconstrained ordination using non-metric multidimensional scaling (nMDS) and B) the constrained ordination using a canonical analysis of principal coordinates (CAP). Circles and triangles represent pre- and post-restoration sites respectively, while the colors indicate the different treatments. The length of the arrows are proportional to the contribution of each individual species, with the enclosed unit circle representing maximum contribution. For example, sand gobies (*Pomatoschistus sp.*) contributed more strongly toward 2018 control sites (red triangles) than herring (*C. harengus*)

Constraining the ordination on the Year and Treatment variables revealed the contribution of individual species to the unique assemblages for both sampling methods. Transparent goby (*Aphia minuta*), two-spotted goby (*Gobiusculus flavescens*) and moon jellyfish (*Aurelia aurita*) were identified by UBRUVS as the most important species driving the distinct composition at experimental reefs (Figure 2.9B). The latter two species were also identified by BRUVS (Figure 2.10B), in addition to greater sand eel (*Hyperoplus lanceolatus*) and black goby (*Gobius niger*). Species driving the natural reef assemblage included Atlantic cod (*Gadus morhua*) and goldsinny wrasse (*Ctenolabrus rupestris*) for both UBRUVS and BRUVS, in addition to eelpout (*Zoarces viviparus*) and corkwing wrasse (*Symphodus melops*) for BRUVS only (Figure 2.10B). Sand sites in 2017 (i.e. red and blue circles in Figure 2.9 & 2.10) were characterized by whiting (*Merlangius merlangus*) and starfish (*Asterias rubens*) for both sampling methods, in addition to shore crab (*Carcinus maenas*) and brill (*Scophthalmus rhombus*) for BRUVS only. The composition of sand sites in 2018 (i.e. red triangles in Figure 2.9 & 2.10) deviated from the 2017 sand sites, which was mainly due to the presence of sand gobies (*Pomatoschistus sp.*) and various species of right-eyed flatfish, e.g. dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*).

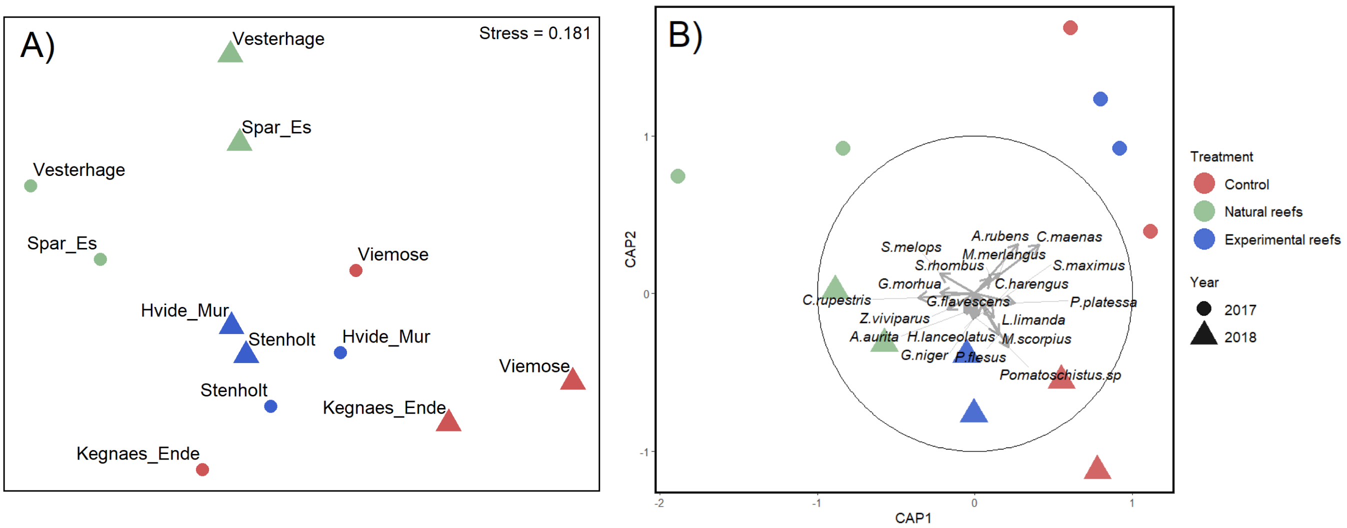


Figure 2.10. Community composition as recorded by BRUVS, with A) the unconstrained ordination using non-metric multidimensional scaling (nMDS) and B) the constrained ordination using a canonical analysis of principal coordinates (CAP). Circles and triangles represent pre- and post-restoration sites respectively, while the colors indicate the different treatments. The length of the arrows are proportional to the contribution of each individual species, with the enclosed unit circle representing maximum contribution.

2.4 Discussion

This study highlights the importance of cobble reefs in providing essential habitat for a variety of marine species, as evidenced by increases in total fish abundance and richness following the restoration of coastal cobble reefs, as well as by the positive effects on a number of focal species. Despite some occasions of strong yearly fluctuations in recorded fish abundances at the study site (e.g. Figure 2.5A & 2.6G), the implemented BACI sampling design enabled us to effectively differentiate between these natural variations and effects caused by the restoration of the reefs. Furthermore, including natural reefs as reference sites in the BACI comparison allowed us to compare our newly deployed reefs with well-established natural cobble habitat in terms of species abundance, richness and composition. Our results have direct implications for management strategies, as they show that conservation and active restoration of cobble reef habitat is warranted to preserve heterogeneous, structurally complex coastal habitats. Whereas marine boulder extraction is now prohibited in Danish waters, extraction of finer material, e.g. gravel, pebble and cobble is still feasible in a number of dedicated marine areas. Ultimately, this could lead to further degradation of coastal areas and increase the pressure on vulnerable commercial stocks that depend on these diverse habitat types.

The current study aimed at assessing the effects of restoring cobble reef habitat on the associated marine community, with a particular focus on the commercially important Atlantic cod, herring and European eel. In general, cod was documented by both sampling methods (i.e. BRUVS and UBRUVS) to have a high reef affinity, as evidenced by high abundance estimates on natural reefs in the BACI comparison and a substantial relative contribution to the species assemblage observed on reefs. In addition, both methods recorded a positive effect on cod abundance following the reef restoration, though not significant on the 95% level for BRUVS. Previous studies investigating demersal habitat use of Atlantic cod have found similar results. For example, large individuals of cod were recently found to utilize boulder reefs for shelter in a heavily fished area of the Baltic Sea (Beisiegel, Tauber, Gogina, Zettler, & Darr, 2019). Similarly, an otolith study from two artificial reefs in the Western Baltic revealed an overlap in presence of two different stocks of Atlantic cod, the Eastern and Western Baltic stocks (McQueen et al., 2019). These findings suggest that both these heavily exploited stocks may be resident at the reefs and utilize the hard and structurally complex substrate for shelter and access to prey species. In addition, juvenile cod exhibit feeding behavior on sand patches during the day, while resting nocturnally within rocky reefs (Clark & Green, 1990), highlighting the importance of reefs, even if juvenile cod are not always observed on reefs during the day. Our results corroborate these findings and highlight the importance of actively restoring degraded cobble reefs for the conservation of relatively slow-growing, yet highly exploited Western Baltic cod (McQueen et al., 2019).

Atlantic herring was similarly found to be highly abundant at natural reefs in the present study, although this trend was only documented by BRUVS. The relatively short recording times for UBRUVS, in combination with herring encounters consisting mainly of large schools rather than a few individuals, resulted in underdispersed counts, which may have masked any potential habitat effects (Brooks et al., 2019). We did not observe herring spawning at any of the three habitat types, and thus were unable to confirm our initial hypothesis based on previous observations of herring utilizing hard substrate for spawning (e.g. Aneer et al., 1983). However, we argue that our sampling methods, i.e. BRUVS and UBRUVS, are nonetheless suitable for observing herring spawning. If we had used other sampling methods, including snorkelling and SCUBA diving, spawning herring could have been disturbed by the physical presence of the snorkeler or air bubbles of the diver. Future monitoring studies using underwater video systems within the habitat range of herring should take note of unusual behavior, e.g. individuals darting vertically towards the bottom (Aneer et al., 1983), as knowledge on the occurrence of herring spawning events and associated habitat types is important to inform management strategies. Finally, we only observed one European eel (*Anguilla anguilla*) individual in the current study and were therefore unable to draw any conclusions on habitat selection or reef restoration effects for this species. A recent study has demonstrated a preference for hard substrate for the elver life stage of European eel through a tank experiment (Christoffersen et al., 2018), which underlines the importance to conserving and restoring gravel and cobble habitats for this critically endangered species. The nocturnal lifestyle of European eel, combined with low activity during winter months (i.e. water temperature < 4 ˚C; Nyman, 1972; van Veen, Hartwig & Müller, 1976), may however imply that individuals present in the study area remained largely unobserved, as our video sampling included only daytime observations during late winter – early spring. Therefore, we suggest that future studies aiming to assess habitat use by European eel in the field consider using underwater video systems equipped with infrared light sources, to record the nocturnal behaviour of eel while minimizing potential side effects on light-dependent motor activity (Bassett & Montgomery, 2011; van Veen et al., 1976).

The restored reefs in the present study were found to be rapidly colonized by two fish species in particular, goldsinny wrasse (*Ctenolabrus rupestris*) and two-spotted goby (*Gobiusculus flavescens*). Both sampling methods identified strong positive restoration effects for these species compared to control sites, with the post-hoc pairwise comparison revealing significantly higher increases in abundance compared to natural reefs. In addition, two-spotted goby was found to be one of the main species shaping the unique species assemblage at restored reef sites by both sampling methods. Previous studies also identified the two-spotted goby as a prominent species on reefs (Herbert et al., 2017; Perry, Staveley, & Gullström, 2018). Males are known to utilize hard substrates for nesting (Utne-Palm, Eduard, Jensen, Mayer, & Jakobsen, 2015) and several individuals were observed caring and guarding eggs laid on and near cameras monitoring the restored reefs, hinting at early reproductive behavior at these sites. In contrast, this behavior was not observed at the same sites prior to the restoration of the reefs. Wrasses are small-bodied sedentary reef fishes with a limited home range (Villegas-Ríos et al., 2013), indicating these species are likely beneficiaries of the reef units deployed in the present study. Commercial interest in goldsinny wrasse has seen a rapid increase over the past decade, mainly due to their use as cleaner fish to control sea lice infestations in the salmon aquaculture industry (Blanco Gonzalez & de Boer, 2017). However, wrasses play a vital role in structuring rocky reef systems by preying on small algae-eating amphipods (Olsen, Halvorsen, Larsen, & Kuparinen, 2019) while serving as prey species for large predators such as cod (Enoksen & Reiss, 2018). Wrasse abundance may thus be an indicator for reef system health (Støttrup et al., 2014). The early prevalence of both goldsinny wrasse and two-spotted goby on the restored reefs indicates suitable habitat availability for these important reef fishes and potential elevated food levels for higher trophic species.

A number of focal species showed a decrease in relative abundance following our reef restoration efforts. As expected, fewer individuals of flatfish (order: *Pleuronectiformes*) were recorded on the reefs by both sampling methods than on sand control sites. Flatfish are ambush predators, predominantly found on featureless sandy bottoms where they feed on polychaetes and small crustaceans (Shucksmith, Hinz, Bergmann, & Kaiser, 2006; Vinagre, França, Costa, & Cabral, 2005). Similarly, UBRUVS showed a decrease in abundance of sand gobies (*Pomatoschistus sp.*) and starfish (*Asterias rubens*) on newly restored reef sites, although these trends were not supported by BRUVS. However, considering the small spatial scale of our samples obtained from the underwater video systems (e.g. cameras recording on top of reefs) and the relatively small area (11x11 m) taken up by the individual reef units, these findings might underestimate the true impacts of the new reefs on benthic species in the study area. For example, small reefs could have substantial edge effects on the surrounding sand habitats, if food sources for flatfish (e.g. benthic invertebrates) are exported from the reefs onto the neighboring sand areas. By this mechanism, reefs could indirectly support an elevated abundance of flatfish in the sand habitats surrounding the reefs. This hypothesis was not investigated in the present study, but should be included as a research aim in a follow-up examination of the reefs.

Our results revealed a noteworthy discrepancy between fish community metrics as sampled by BRUVS and UBRUVS. While both methods documented a significant increase in total fish abundance following the reef restoration, BRUVS did not detect a difference in species richness. Studies examining the species community on newly deployed artificial reefs generally report sharp increases in the number of species detected within the first year (Leitão, Santos, Erzini, & Monteiro, 2008; Mills et al., 2017), in some cases surpassing richness of natural reefs (Folpp, Lowry, Gregson, & Suthers, 2013; Rilov & Benayahu, 2000), which is in agreement with results from UBRUVS in this study. We provide two possible explanations for BRUVS failing to detect a similar pattern. Firstly, we observed species with a high reef affinity, e.g. cod, eelpout and sculpin, to occasionally be attracted to BRUVS at sandy control sites, making them highly conspicuous and easily observed. Conversely, sand associated species were either not crossing the barrier of swimming up against the sloping reef units to reach the bait, or were less conspicuous if they did due to high coverage of ephemeral algae on the experimental reefs (i.e. the restored reefs). Second, while UBRUVS recorded short sequences across the entire diurnal period, including early dusk and late dawn, BRUVS ran continuously for about two hours outside twilight hours to ensure sufficient bait plume dispersal under adequate light conditions. This may imply that UBRUVS were capable of capturing cryptic species mostly active during twilight hours, which potentially remained hidden in BRUVS recording despite the attractive effect of bait. Studies comparing the number of species detected by BRUVS with e.g. underwater visual census often find higher richness detected by the visual census technique (Colton & Swearer, 2010; Lowry, Folpp, Gregson, & Suthers, 2012), as divers are able to scan holes and crevasses for cryptic species. Whereas the current study benefitted from using two comparable, yet different sampling methods, this implies that future RUV studies aiming to accurately describe species compositions of various habitats would benefit from covering the entire diel cycle using artificial light sources, as well as a multitude of sampling techniques.

The effect of reef height on the relative abundance of fish species was found to be minimal. Total fish abundance was similar between low and high reefs and no differences were found in goldsinny wrasse and two-spotted goby abundance using either of the two sampling methods. UBRUVS did record more Atlantic cod on low reefs compared to high reefs, but this trend was not found in BRUVS recordings. The importance of reef height in shaping fish communities has received much attention (e.g. Granneman & Steele, 2015; Paxton et al., 2017; Komyakova et al., 2019), although experiments actively manipulating the height of structures within reef systems remain scarce. One field experiment carried out by Wilhelmsson et al. (2006) in Sweden investigated the effect of presence and height of vertical PVC pipes on temperate fish communities. Their PVC pipes varied in height between 1 m and 3 m (comparable to the 0.6 m and 1.3 m height in our study), and similarly the authors found no effect of height on the associated fish communities. Cobble reefs protruding higher up into the water column could potentially influence macroalgae and filter-feeding invertebrates through enhanced light intensities and current velocity at reef tops, while increasing the detection rates of the reefs by roaming pelagic species (Granneman & Steele, 2015; Wilhelmsson et al., 2006). However, it would be realistic to assume that detecting such effects requires adequate time for the development of macroalgal communities within the reef system, which due to the relative young age of the restored reefs in this study (i.e. < 6 months) were still underdeveloped. Therefore, if reef height plays an important role in shaping the community assemblage of reef species, long-term monitoring of restored reefs is warranted for the evaluation of such effects.

Collectively, this study provides evidence that fish abundance and communities differ between cobble reefs and bottoms covered by sand. We emphasize that our conclusions are based on the upper size range for cobbles (diameter > 20 cm) and that we did not assess the effect of smaller rock sizes (diameter < 15 cm). Our findings suggest that removal of large cobbles from the seabed may impact fish communities and fish abundance. Restoration of cobble reef habitats was found to be feasible, yet the associated reef community was clearly distinct from the community observed at natural reef systems within the time frame tested here. Specifically, Atlantic cod and herring were more abundant on established natural cobble habitat compared to our newly deployed reefs, whereas other species (e.g. goldsinny wrasse, two-spotted goby and shore crab) were equally abundant on both reef types. We tested the hypothesis that the restored cobble reefs would provide suitable habitat for herring spawning, as elevated herring abundance and the presence of herring eggs could potentially attract larger predators (e.g. harbour porpoise) to the newly restored reefs. We were, however, unable to detect any evidence of herring spawning at the restored reefs. Still, anecdotal evidence provided by local fishermen during the sampling period did confirm the presence of spawning herring in close vicinity to the field sites that were monitored. We therefore hypothesize that herring may have been spawning at the natural reefs, where BRUVS monitoring revealed significantly higher herring abundance relative to restored reefs, or that spawning events instead occurred at night or at different water depths than examined here; and were thus not recorded by our cameras. Re-examination of the restored reefs is warranted and should allow for adequate time for colonization and development of macroalgal and sessile communities. Finally, additional studies are needed to assess the importance of the small cobble fraction (diameter < 15 cm), pebble and gravel, which are at present still removed from the Danish seabed in dedicated areas.

3. Benthic flora and fauna associated with cobble reefs in Sønderborg Bay

3.1 Introduction

The objective of this work package was to document and compare abundance and diversity of benthic flora and fauna associated with different bottom types in the Sønderborg Bay in 2017 (before reef construction) and 2018 (after reef construction). Erect benthic algal vegetation adds to the physical complexity of reef structures, and the associated fauna makes up a direct or indirect food supply for the fish communities on or near reefs. Specifically, the physical complexity established by the algal vegetation provides shelter for fish, which may enhance fish survival and recruitment. Moreover, benthic fauna provides diverse food resources for a diversity of fish species.

3.2 Materials and methods

3.2.1 Sampling time, locations and replicates

In the project-planning phase, sampling was restricted to the experimental sites (Hvide Mur and Stenholt) and soft sediment sites (Kegnes Ende and Viemose) as control sites due to financial restrictions. However, the sampling was extended during the sampling campaign to include the two natural reef sites Spar Es and Vesterhage. A map showing experimental sites, control sites and the natural reef sites is included in WP1 (Figure 1.9).

Sampling on the seabed for biomasses of macro algae and bentic fauna as well as abundance of benthic fauna was conducted between 27-31 March 2017 and then repeated again the following year between 19-21 March 2018 and finalized on 16 April 2018. The time of sampling was planned in accordance with the expected time of herring spawning in the area, as eggs would then likely be collected. In the western Baltic Sea, spring spawning herring typically spawn in several waves between early March to early June (Scabell 1988).

We sampled six replicates on each of the two experimental sites (Stenholt and Hvide Mur) and the two control sites (Viemose and Kegnæs Ende) each year. In addition, although not part of the planned sampling scheme, we sampled three replicates on each of the two natural reef sites (Vesterhage and Spar Es) in 2017 and five and six replicates on the same reef sites in 2018. Table 3.1 and Table 3.2 provide sampling locations, water depth and hard bottom cover (i.e. coverage by rocks, mainly cobble) on each sampling station on the six sampling sites (experimental sites, control sites and natural reef sites).

Table 3.1. Sampling locations, station numbers, position, water depth and cover of hard bottom coverage within the sampling frame in 2017. Hard bottom coverage mainly consisted of cobble.

Sampling Year 2017						
	Location	**Station code**	**position**	**position**	**Hardbottom cover (%)**	**Depth (m)**
Reef site	Spar ES	1	54° 51.828	9° 45.853	20	7,0
	Spar ES	2	54° 51.820	9° 45.901	40	8,2
	Spar ES	3	54° 51.809	9° 45.950	70	8,0
Reef site	Vesterhage	1	54° 53.894	9° 46.668	5	5,4
	Vesterhage	2	54° 53.892	9° 46.739	45	7,6
	Vesterhage	3	54° 53.907	9° 46.802	50	6,9
Control sites	Kegnæs Ende	1 (208)	54° 52.477	9° 51.840	5	8,2
	Kegnæs Ende	2	54° 52.542	9° 51.818	0	6,2
	Kegnæs Ende	3 (213)	54° 52.809	9° 51.809	0	6,2
	Kegnæs Ende	4 (216)	54° 52.581	9° 51.800	0	5,9
	Kegnæs Ende	5 (217)	54° 52.621	9° 51.742	0	7,0
	Kegnæs Ende	6 (215)	54° 52.581	9° 51.741	0	7,2
Control site	Viemose	1	54° 54.028	9° 42.473	0	6,5
	Viemose	2	54° 54.053	9° 42.523	0	7,5
	Viemose	3	54° 54.078	9° 42.559	0	6,7
	Viemose	4	54° 54.075	9° 42,614	0	7,5
	Viemose	5	54° 54.077	9° 42.697	0	7,1
	Viemose	6	54° 54.076	9° 42.735	0	7,1
Exp. Site	Hvide Mur	1	54° 53.729	9° 45.068	0	6,6
	Hvide Mur	2	54° 53.722	9° 45.035	0	7,0
	Hvide Mur	3	54° 53.713	9° 44.988	0	7,9
	Hvide Mur	4	54° 53.708	9° 45.106	0	6,1
	Hvide Mur	5	54° 53.704	9° 45.164	0	7,0
	Hvide Mur	6	54° 53.692	9° 45.237	0	6,3
Exp. Site	Stenholt	1	54° 53.371	9° 50.823	0	6,7
	Stenholt	2	54° 53.394	9° 50.860	0	6,6
	Stenholt	3	54° 53.401	9° 50.898	0	6,4
	Stenholt	4	54° 53.371	9° 50.789	0	6,7
	Stenholt	5	54° 53.358	9° 50.767	0	6,6
	Stenholt	6	54° 53.340	9° 50.733	0	6,6

Table 3.2. Sampling locations, station numbers, position, water depth and cover of hard bottom coverage within the sampling frame in 2018. Hard bottom coverage mainly consisted of cobble.

Sampling Year 2018						
	Lokalitet	**Station code**	**Position**	**position**	**Hardbottom cover (%)**	**Depth (m)**
Reef site	Spar Es	1				
	Spar Es	2	54.518.236	9° 45.9219	40	6,7
	Spar Es	3	54.518.233	9° 45.9667	35	7,5
	Spar Es	4	5.451.954	9° 45.719	Sampling failed	
	Spar Es	5	5.451.793	9° 45.931	50	8
	Spar Es	6	54.517.741	9° 45.9686	50	6,8
	Spar Es	7	54.518.264	9° 45.9653	30	7,5
Reef site	Vesterhage	1	54° 53.8958	9° 46.6721	60	5,4
	Vesterhage	2	54° 53.8803	9° 46.739	40	7,7
	Vesterhage	3	54° 53.9086	9° 46.7954	45	6,8
	Vesterhage	4	54° 53.8801	9° 46.78	70	7,5
	Vesterhage	5	54° 53.7896	9° 46.299	50	7
	Vesterhage	6	54° 53.807	9° 46.3895	90	7
Control site	Kegnæs	1	54.524.721	9° 51.8248	0	8,4
	Kegnæs	2	54.525.404	9° 51.8096	5	6,2
	Kegnæs	3	54° 52.7363	9° 51.9082	0	5,1
	Kegnæs	4	54° 52.577	9° 51.81092	0	6,4
	Kegnæs	5	54° 52.6192	9° 51.7584	30	6,9
	Kegnæs	6	54° 52.5748	9° 51.7601	5	7,2
Control site	Viemose	1	54° 54.0294	9° 42.4616	0	6,5
	Viemose	2	54° 54.0466	9° 42.5029	0	8
	Viemose	3	54° 54.0845	9° 42.5402	0	6,8
	Viemose	4	54° 54.0751	9° 42.6123	0	8
	Viemose	5	54° 54.0822	9° 42.6951	0	7
	Viemose	6	54° 54.0788	9° 42.7381	0	7
Exp. Site	Hvide mur	12 (1.3m)	54° 53.6865	9° 45.211	100	5,1
	Hvide mur	13 (0.6 m)	54° 53.689	9° 45.186	100	5,4
	Hvide mur	14 (1.3 m)	54° 53.692	9° 45.151	100	5,5
	Hvide mur	17 (0.6 m)	54° 53.712	9° 45.067	100	6
	Hvide mur	18 (1.3 m)	54° 53.715	9° 45.044	100	5,5
	Hvide mur	19 (0.6 m)	54° 53.721	9° 45.017	100	6,2
Exp. Site	Stenholdt	12 (1.3 m)	54° 53.372	9° 50.932	100	5,7
	Stenholdt	13 (0.6 m)	54° 53.391	9° 50.909	100	5,9
	Stenholdt	14 (1.3 m)	54° 53.381	9° 50.877	100	5,6
	Stenholdt	17 (0.6 m)	54° 53.341	9° 50.793	100	6,1
	Stenholdt	18 (1.3 m)	54° 53.328	9° 50.763	100	5,2
	Stenholdt	19 (0.6 m)	54° 53.306	9° 50.73	100	6,1

3.2.2 Sampling macro algae and benthic fauna

Sampling in both years was carried out using a suction sampler mounted with a 1 mm filter system operated by divers (Figure 3.1). This sampling system is efficient in terms of collecting benthic fauna as well as sea-weed vegetation (e.g. macro algae).

Sampling took place within 1/6 m^2 metal frames dropped arbitrarily on the seabed on instructions by the dive operator while the diver was swimming over the seabed (figure 3.2). Before sampling, the diver estimated the percentage hard stable substrate within the frame. The sampling was planned to focus on the surface of the expected cobble dominated seabed, but at some sampling stations cobble was largely missing and the sea-bed was dominated by rough sandy sediment or muddy-sandy sediment. Suction sampling included the upper 13 cm of the seabed. At some stations, large boulders buried in the sediment hindered the planned suction to 13 cm depth, and at the control site Viemose, a hard clay layer under the silty-muddy sediment obstructed the sampling. Boulders form a natural boundary for burrowing species. Likewise, divers operating the suction sampler observed that the clay layer also formed a natural boundary for burrowing species, as no holes were penetrating deep into the clay layer. Stones too big for the suction pipe (diameter ≥10 cm. were collected by hand and stored in the filter box when suction was completed.

Figure 3.1. Suction sampling. The filter is either a box with 1 mm stainless mesh size used for sam-pling sand, gravel and stones or a net made of plastic with the same mesh size used for sampling macro algae vegetation and fauna scraped from larger stones and boulders. From Dahl et al. (2005).

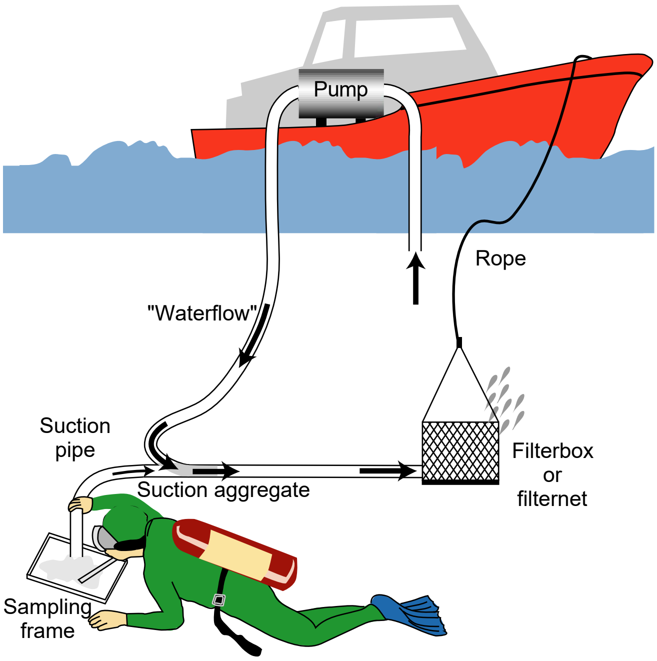
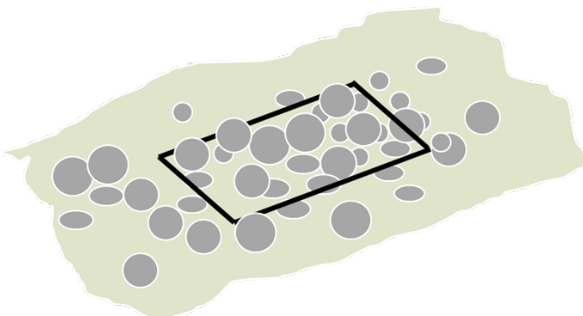


Figure 3.2. Frame sample on a sand cobble cov-ered seabed. Area covered is 1/6 m2 and sam-pling depth is at least 13 cm into the sediment if possible.



3.2.3 Laboratory procedures

In the laboratory, samples were sorted in three fractions for further analysis and quantification: 1) algal vegetation, 2) smaller animals from sediment and algae 1 - 5 mm using a sieve, and 3) larger animals > 5 mm. The algal vegetation was separated into species level for larger algae species, but threat forming algae were kept in one common group. A subsample of 20 % of the total weight of the 1 - 5 mm fraction was taken due to financial constraints. Fauna species were sorted and identified to nearest taxonomic level and abundance estimated. To estimate the ash-free dry weight, each species, higher taxonomic group or algae group was first dried in an oven at 105 degree C for 24 hours, and then the weight was measured. Afterwards, the sample was burned at 550 degree C for 2 hours and the ash free dry weight calculated by subtracting the ash weight from the dry weight.

3.2.4 Data handling and analysis

Biomass and abundance data from subsamples were adjusted according to sample size and all samples adjusted by a factor six for expression as biomass and abundance per m^2. All identified species or higher taxonomic groups were characterized according to the following functional groups: Epifauna (animals living on top of the seabed or sitting/crawling on vegetation), infauna (animals living in the sediment), algae, higher plants (eelgrass), pelagic fauna species (fish and other fauna living in the water column). There are species that might be grouped as both pelagic and epifauna, as they can move up from the seabed and into the water column. In those cases, they are grouped based on expert judgement on the most common “location”. Finally, a group is termed “unknown”.

The planned BACI design with control sites and experimental sites turned out to be somewhat unsuccessful for the benthic sampling. First of all, the colonisation time on the new reef structures was too short for almost any benthic organism to settle. The two chosen control sites also differed in sediment composition. One control site (Viemose) was composed of mud and sand, whereas the other control site (Kegnæs Ende) was composed of rough sand with some gravel or boulders in between, especially in 2018 (Table 3.2). Finally, the percentage of gravel and boulders varied considerably between samples in the frames on the reef sites. For these reasons, another statistical approach was chosen. Differences between sites and samples regarding biomasses and abundances are described in details. Furthermore, the effects on macro algal vegetation, epifauna and infauna of hard bottom coverage (i.e. mainly cobble) are statistically tested using the following linear model:

Algae/infauna/epifauna biomass or abundance = B + A * hard bottom coverage (%) where B represents the value (e.g. biomass) associated with 0% hard bottom coverage. Geometric mean regression is used, and the independent variable (hard bottom cover (%)) is based on diver estimates.

3.3 Results

3.3.1 Biomasses on the three types of locations

The biomasses (converted to an area of 1 m^2) are given per sample for both years at the two reef sites, the two control sites and the two experimental sites (figure 3.3). The variation in biomasses between the single samples is substantial on most natural sites, even though the sampling area was as large as 1/6m^2.

Concerning the average ash free biomasses, there were large differences between the different sampling locations (Figure 3.4). By far, the highest biomasses were found on the natural reef locations Spar Es and Vesterhage (range: 129 – 165 g) where macro algae vegetation, bivalves, echinodermata and crustacean made up the majority of the fauna biomasses with macro algal vegetation being the most dominating.

The control sites Kegnæs and Viemose had considerably smaller biomasses compared to the reef sites (range: 4 – 11 g) (figure 3.4). Here, polychaeta, crustacean and echinodermata made up the majority of the fauna biomasses. The overall average biomasses were considerably higher in 2018 compared to 2017 on both locations. Although Kegnæs Ende was classified as soft sediment, algae vegetation occurred with 3 - 4 g ash free biomasses in both years. Minor eelgrass biomasses were sampled in Kegnes Ende in 2018.

The biomasses at the experimental sites Hvide Mur and Stenholt were the lowest of all sites (range: 0.1 – 0.8 g) (figure 3.4). The biomass was higher in 2017 when it was a soft sediment site compared to 2018, where the constructed cobble reef completely covered the seabed within the sampling area. Especially polychaetes were dominant in 2017, making up more than 2/3 of the biomasses on both locations. In 2018, a few brown thread forming algae had colonized the recently established reef structures and a sea star (*Asterias rubens*) was present on the constructed reef at Stenholt.

Figure 3.3. Variation in ash free biomasses across samples collected at the natural reef sites Spar Es and Vesterhage in 2017 and 2018 (top figure), at the control sites Kegnæs and Viemose (middle figure), and at the experimental sites Hvide Mur and Stenholt (lower figure). Note the different scales on the y-axes.

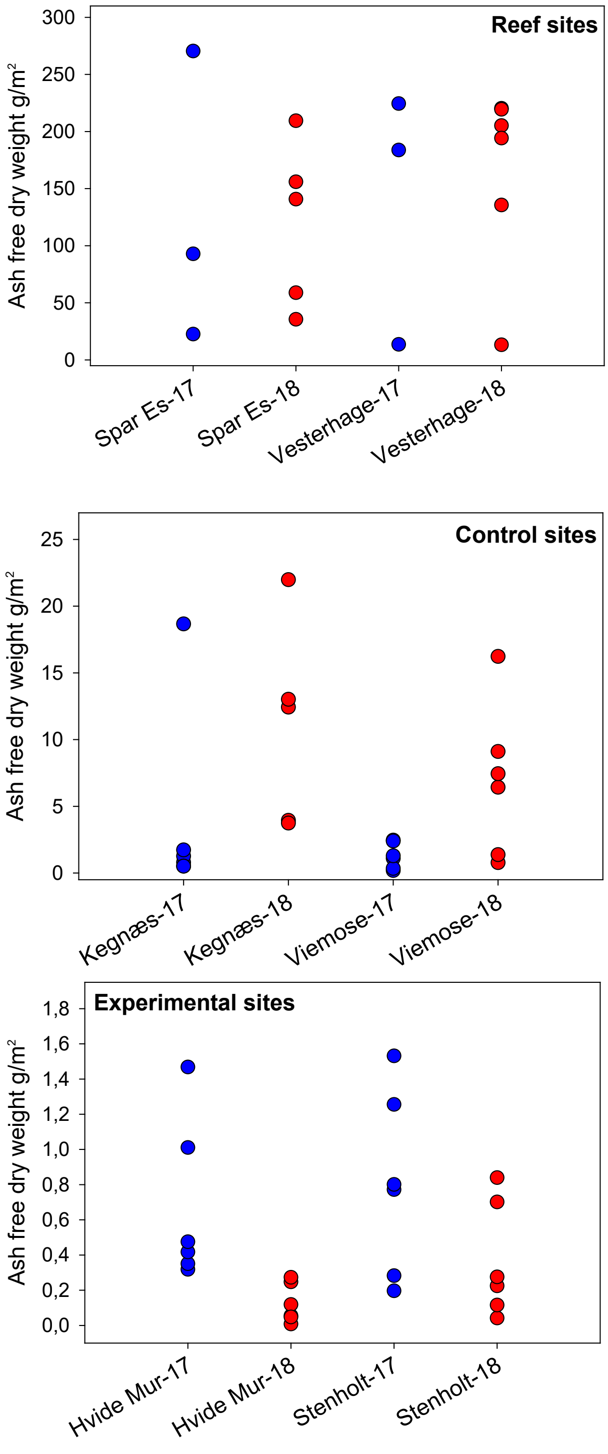
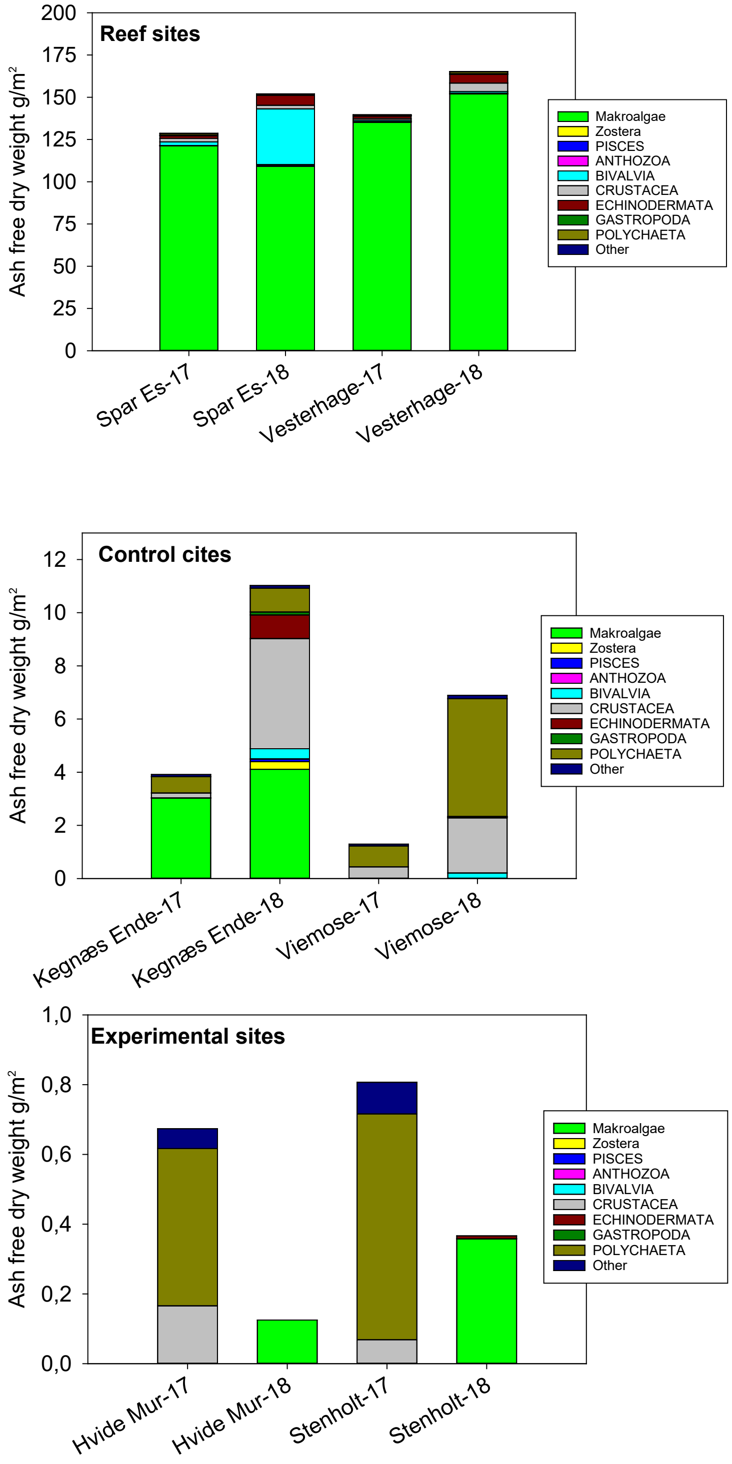


Figure 3.4. Average ash free biomasses in 2017 and 2018 at the two natural reef sites (Spar ES and Vesterhage), at the two control sites (Kegnæs Ende and Viemose) and at the experimental sites (Hvide Mur and Stenholt). Note the different scales on the y-axes.



3.3.2 Effects of hard bottom coverage on biomass and abundance of functional groups

The correlation analyses involving the hard bottom cover (%; mainly cobble) within the sampling frame described by the diver and biomasses of different functional groups are shown in Fig. 3.5. All sampling sites are included, except those samples taken on the newly constructed reef structures (i.e. Stenholt and Hvide Mur in 2018).

The percentage of hard bottom coverage described by the divers within each sampling frame had a significant ($p < 0.001$, $R^2 = 0.78$) effect of the macro algae cover, whereas year had no significant effect. The overall algae vegetation cover was described as:

*Ash free algae biomass (g) = 2.8 + 3.3 * % hard bottom coverage.*

There were no clear correlation between hard bottom cover and biomasses of infauna and epifauna. However, one single very large mussel was responsible for the extraordinary high biomass approaching 200 g ash free biomass calculated for one m^2. Omitting this single large mussel resulted in significant relationship between hard bottom coverage and epifauna (Figure 3.6) ($p = 0.0016$), although the amount of explained variation was limited ($R^2 = 0.18$).

Figure 3.5. Distribution of ash free biomasses of macro algae, epifauna and infauna as a function of estimated hard bottom coverage (%; mainly cobble).

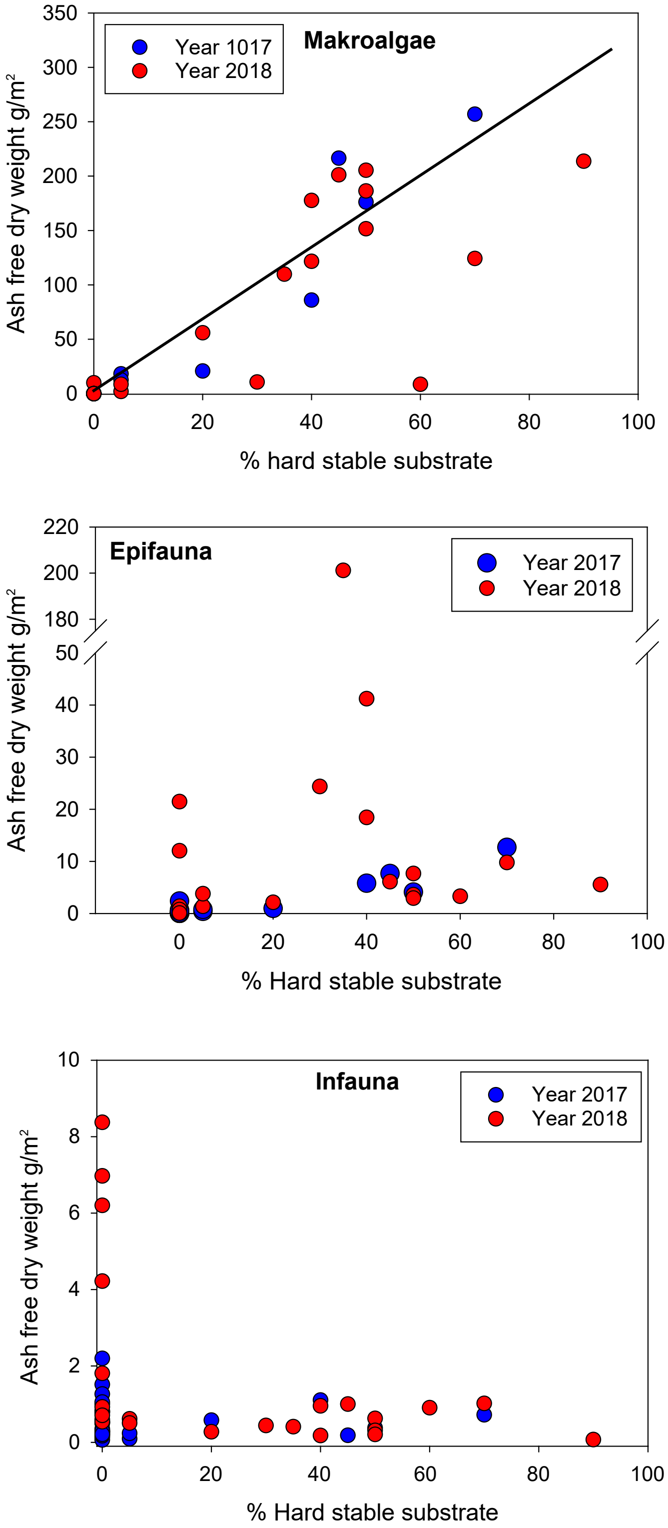
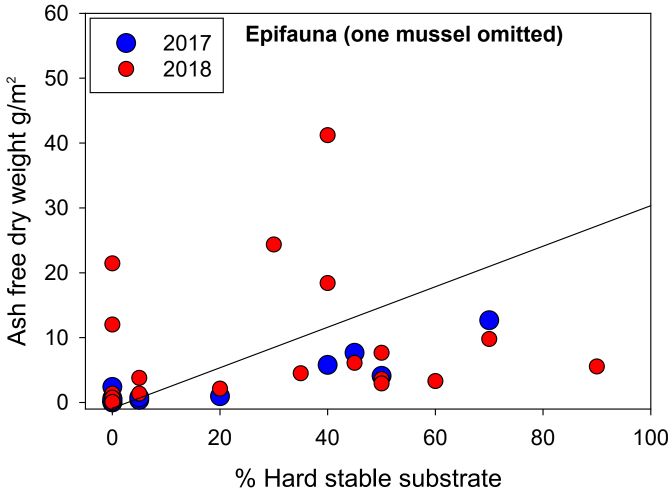


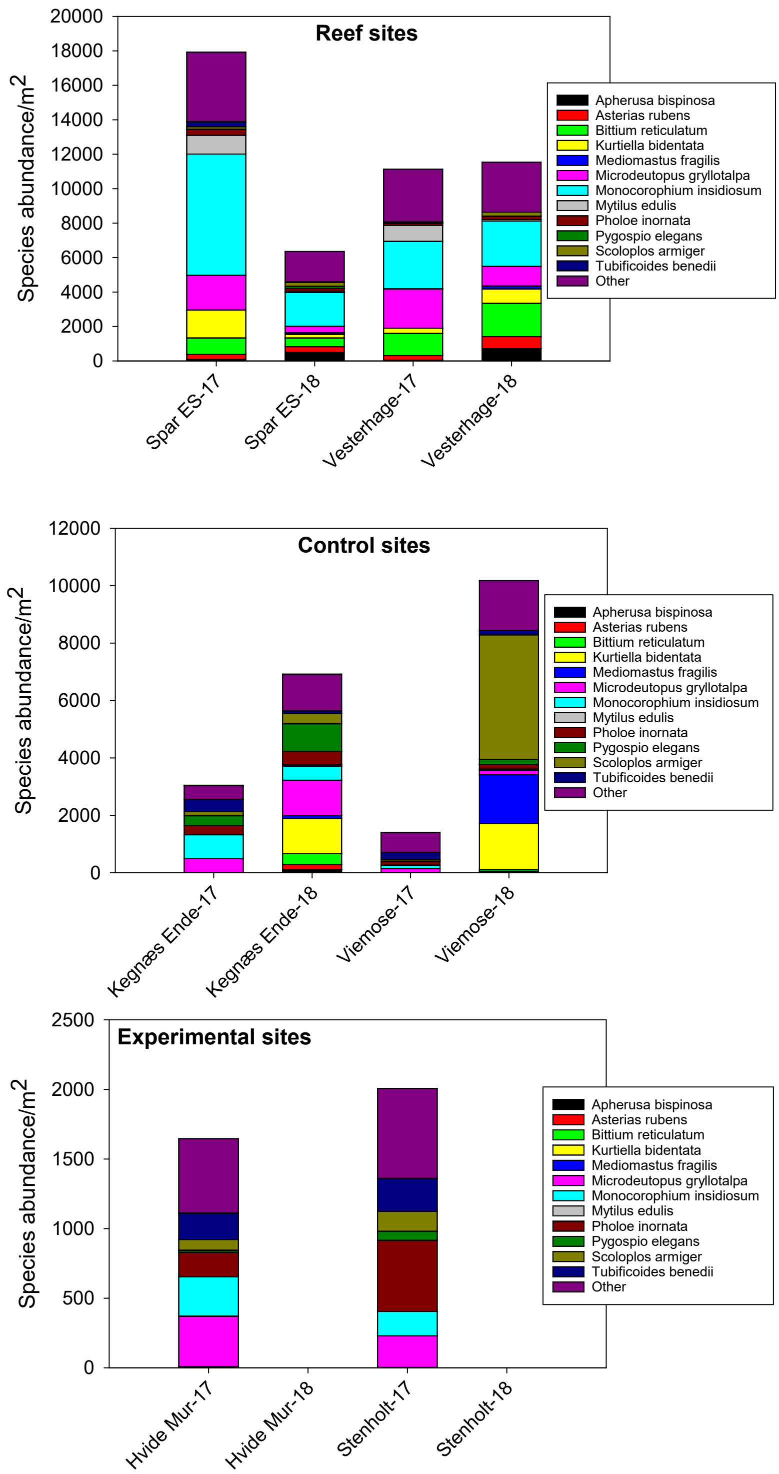
Figure 3.6. Distribution of ash free biomasses of epifauna as a function of hard bottom coverage (%; mainly cobble). One large mussel is omitted compared to the data in figure 3.5.



3.3.3 Abundance of the 12 most common species

The average fauna abundance of the 12 most common species overall and a group containing the rest (other) on the different sampling sites and years are given in Fig. 3.7. In general, abundance was considerably lower at the experimental sites compared with reef and control sites, with reef sites overall having the highest fauna abundance. The crustacean *Monocorophium insidiosum* was particularly dominant on the two natural reef habitats. The polychaetes *Scoloplos armiger* and *Pholoe inornata* were found in larger numbers on the control sites and the experimental sites before the cobble reefs were established. Other species like the crustacean *Microdeutopus gryllotalpa* were found more or less in the same relative fraction on all sites, although the absolute numbers in general were higher on the natural reef sites.

Figure 3.7. Abundance of the 12 most common species and the sum of all the other in all six sampling locations distributed on natural reef, control and experimental sites. Note the different scales on the y-axes.



The effects of hard bottom coverage (%; mainly cobble) on abundance of total epifauna and the most numerous classes of epifauna groups are shown in Fig. 3.8. There were significant and increasing relationships between the abundance of all epifauna species and the hard bottom coverage (%) ($p<0.001$), explaining the majority of the variation ($r^2=0.643$). Also, the number of the most dominating epifauna taxonomic class, crustaceans, as well as the group *gastropoda*, were likewise numerous in the samples, revealing highly significant correlations with % hard bottom cover ($P < 0.001$ and $R^2 = 0.585$ for crustacean species; $P < 0.001$ and $R^2 = 0.521$ for *gastropoda*). The epifauna group consisting of the taxonomic class polychaetes had a weak, but still significant positive correlation with the hard bottom coverage (P=0.0039 and R^2=0.1521). Importantly, the modeled increases in epifauna groups as a function of hard bottom coverages (%) were dramatic. For example, the modeled total abundance of epifauna increased from about 1.000 organisms per m^2 at 0% hard bottom coverage (i.e. sand bottom) to more than 20.000 organisms per m^2 at 100% hard bottom coverage. Thus, a sand seabed provides much less epifauna for fish to consume compared to a hard bottom seabed (i.e. mainly cobble reef).

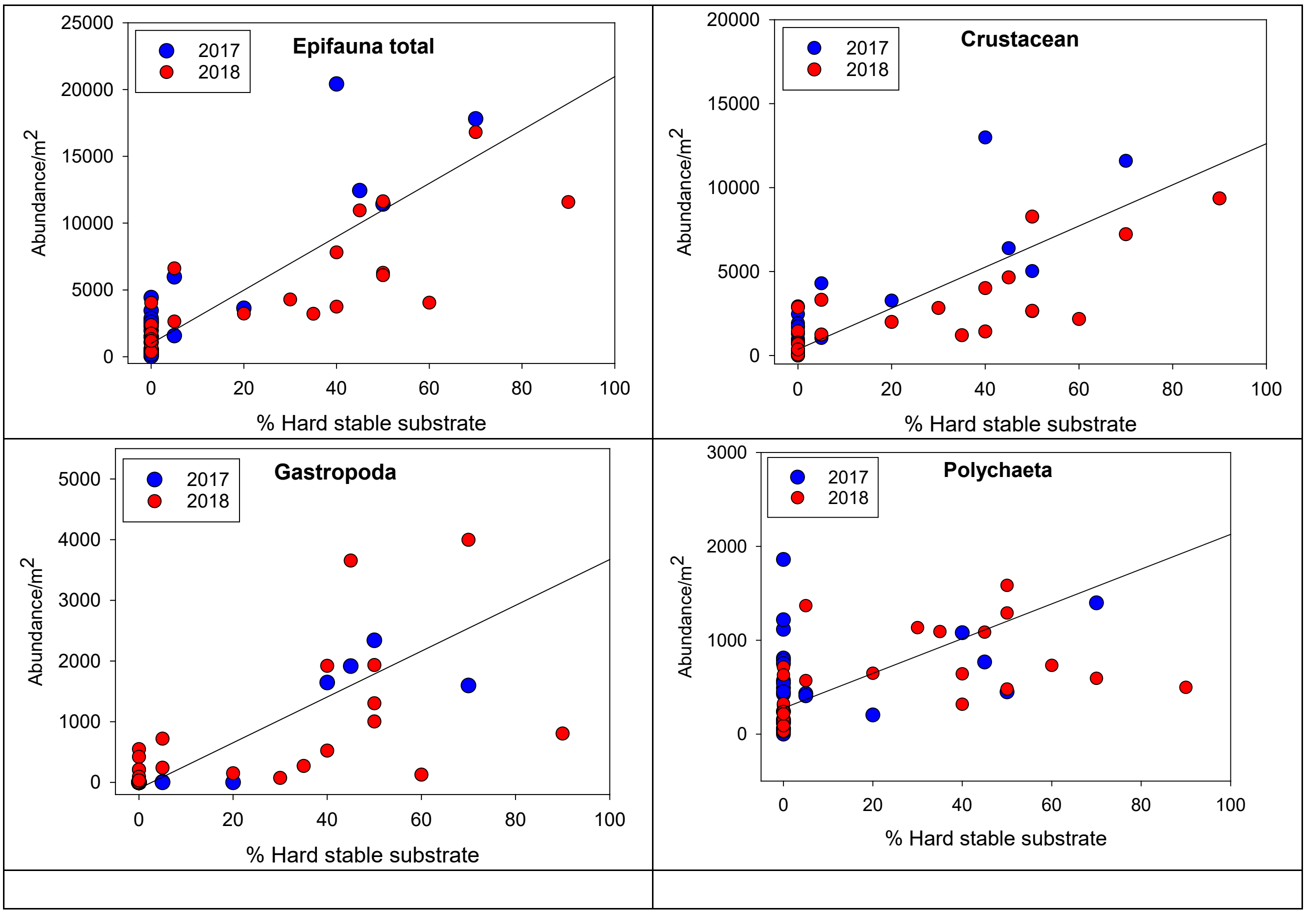


Figure 3.8. Linear correlations between hard bottom coverage (i.e. mainly cobble) and abundances of the total epifauna, Crustacean species and species belonging to Gastropoda and Polychaeta.

3.4 Discussion

Benthic extraction of rocks and stones with a diameter of 6 - 30 cm is an ongoing activity in Danish marine waters, mainly at water depths exceeding 6 m. The objective of work package 3 was to document the importance of cobble and minor boulder reefs as feeding habitats for fish.

Although part of the project design was to describe the colonization of the constructed cobble reefs almost one year after reef deployment, the time between the actual reef deployment happening between November 2017 and January 2018 and the second investigation in the spring 2018 was too short for almost any settlement of benthic fauna and algae species. The additional sampling on natural reef sites, on the other hand, clearly demonstrated that biomasses and abundances in general are closely linked and are often increasing dramatically with the cover of hard bottom (i.e. mainly cobble).

High algal biomasses in general improve the physical complexity of reef habitats, and algal production is the first important step in the food chain on a reef in the photic zone. Reef habitats not only provide shelter for fish, but also supply large quantities of food for many reef living fish species (Christie et al. 2009; Wennhage & Pihl 2002; Norderhaug et al. 2005).

The experimental sites (i.e. restoration sites) were selected as suitable sites for measuring the effects of restored cobble reefs, and the control sites were assumed to have a similar sandy or muddy sediment composition. It turned out that the locations at Viemose, but also at Hvide Mur were more sandy-muddy and overlaying a clay layer, whereas the sediment composition at Kegnæs Ende and Stenholt were dominated by more coarse sand and even with a few scattered stones at Kegnæs Ende.

We uncovered highly significant correlations between the percentage coverage of hard substrate within the sampling frames and abundance of epibenthic fauna organisms as an overall group, but also for the taxonomic classes with the highest abundance, crustaceans, gastropoda and to a less extent polychaets. These taxonomic groups constitute important parts of the diet of many reef living fish species. Excluding a single very large mussel in one sample (much too big for being a prey item for fish), we also found a significant relationship between epifauna biomass and cover of hard substrate. The variation both in abundance and biomasses between samples was high, even though we used a large sampling area of 1/6 m^2 (i.e. 1,666 cm^2). The normal soft bottom sampling in Danish waters is conducted with a HAPS sampler with a sampling area of 145 cm^2, more than 11 times smaller. This high variation stresses the importance of having sufficient replicates, and the three samples taken at the two natural reef sites in 2017 may be considered too few to give a solid description of the biomasses.

However, despite the considerable variation, it is possible give a rough estimate of biomasses and abundances of a seabed completely covered by small stones (mainly cobble) in the outer part of Flensborg Fjord using data from both sampling years. Algal biomasses around 350 g ash free dry weight/m^2 and epibenthic fauna higher than 30 g ash free dry weight/m^2 may be expected. Infauna will be of minor importance because space and food supply between boulders are limited. Similar investigations on large natural boulders on Lille Grund and Mejl Flak north of Samsø in Danish waters found considerably higher total biomasses at the same water depth with 1123 and 1641 g ash free dry weight/m^2 at 4 and 6 m depth (Dahl et al, 2005). Next to the reef sites at Lillegrund and Mejl Flak, on a seabed with sand and gravel, average biomasses of 24 – 81 g ash free dry weight/m^2 were recorded. The findings on the seabed with sand and gravel resemble findings at Læsø Trindel (ca. 86 g ash free dry weight/m^2) in northern Kattegat on a gravel seabed before reef restoration was started on this site (Dahl et al., 2009).

A projected estimate of epifauna abundance on the constructed cobble reefs (Hvide Mur and Stenholt), when colonization and time have resulted in a climax community, is around 20.000 individuals/m^2. The corresponding numbers on Lillegrund and Mejl flak were higher, but sampling at those locations was done in the summer season and included a very high number of newly settled *Mytilus edulis* individuals.

The observed differences in biomasses on hard substrate between the outer Flensborg Fjord and the northern, more open area of Samsø Belt and northern Kattegat is expected for two main reasons, the lower salinity as well as the coastal location with higher levels of eutrophication in Flensborg Fjord. Salinity plays a major role for biodiversity of both algae as well as bottom fauna (Nielsen et al., 1995). Decreasing biodiversity is reflected in lover biomasses as algae species become more scattered and eventually disappear when the salinity is too low (Nielsen et al., 1995). Eutrophication on the other hand reduce the light penetration to the seabed due to high levels of phytoplankton (Carstensen et al., 2008). Eutrophication limiting light results in reduced benthic algae vegetation in deeper waters, where light availability is severely limiting vegetation growth (Dahl & Carstensen, 2008). Eutrophication also increases the risk of oxygen deficiency, often occurring in Flensborg Fjord (Figure 3.9).

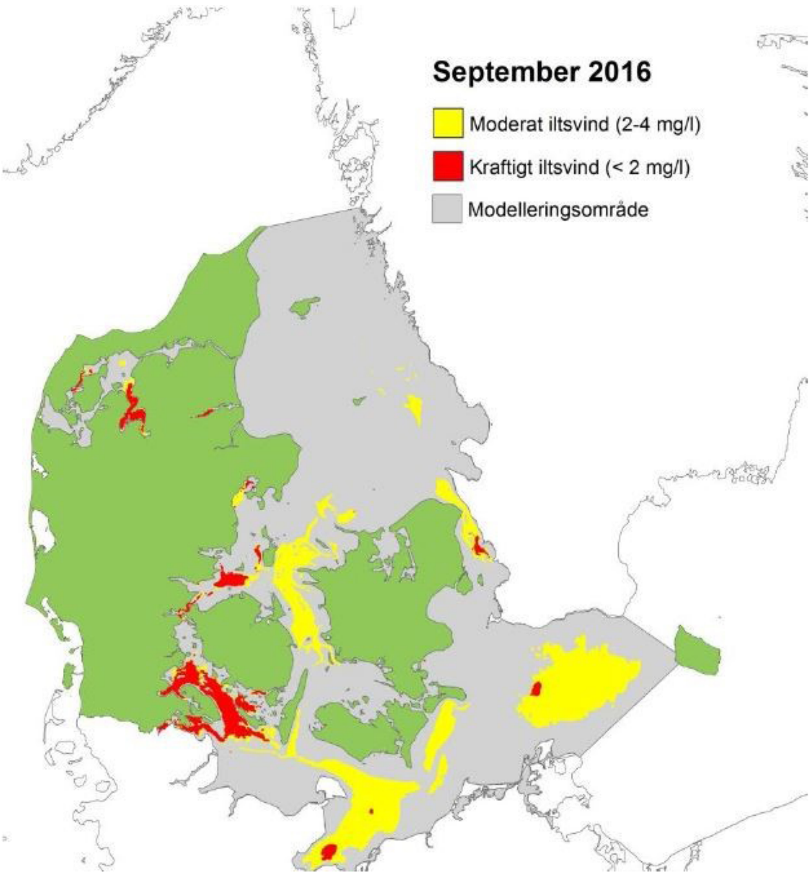


Figure 3.9. Areal distribution of oxygen depletion modelled for 12-21 September 2016 and based on measured oxygen contents in the bottom water (deeper than 6-7 m). The model is not detailed enough to show small oxygen depleted areas. Red color represents areas with severe oxygen depletion < 2 mg/l, whereas the yellow color represents areas with moderate oxygen depletion (2 – 4 mg/l) (Hansen et al, 2016). In the deep waters (> 10 m), Flensborg Fjord is severely affected by oxygen depletion.

3.4.1 Conclusion

This study in Sønderborg Bay in Flensborg Fjord corroborates the outcome of previous studies in open water areas that hard bottom in general increase biomasses and abundances of species on the seabed in shallow waters. Oxygen depletion caused by eutrophication is a severe problem in Flensborg Fjord and Sønderborg Bay. In deeper waters, severe oxygen depletion occurs annually in Flensborg Fjord (Fig. 3.9), and we cannot exclude the possibility that oxygen depletion periodically influences our study sites (Fig. 1.9; WP1). Over time, oxygen depletion may hamper positive effects of reef restoration.

Extraction of pebble and gravel resources situated on top of the seabed targets similar types of stones that make up the hard substrates examined in this study. Depending on the physical environment, some stones are considered stable, and host large, important biomasses, whereas other stones are unstable and only support opportunistic species or young perennial species. In sheltered waters, even stones as small as 5 - 6 cm can host large types of vegetation, and numerous animals, whereas rocks (cobble) with a diameter of 30 cm function as stable substrates even on exposed reefs in the open part of Kattegat. Therefore, macro algae growth, and the associated fish habitats, are not only dependent on large boulders. Exploiting marine gravel, pebble and cobble directly from the seabed surface will have irreversible impacts on the marine productivity. After exploitation, new rocky surfaces might be exposed over time on a given location due to erosion of the fine grain sediment left by the extracting vessels. However, these new rocky surfaces will then be in deeper waters owing to the extraction. Therefore, less light will be available, resulting in less macro algal production and fewer complex habitats available for fish.

4. Occurrences of harbour porpoise (*Phocoena phocoena*) on restored cobble reefs in Sønderborg Bay

4.1 Introduction

Hard bottom marine habitats support diverse and abundant floral and faunal marine communities (Ojeda & Dearborn 1989, Andrulewicz et al. 2004). The stable surface of the reef is essential for fixation of many macro algae species and provides hide and protection for relatively small animals. Fish species are likewise attracted to reef habitats, as they offer both prey supply (Moreno & Jara 1984) and shelter (Demartini & Roberts 1990). The resulting aggregation of fish at the reef is also likely to attract top predators, such as the harbour porpoise (Mikkelsen et al 2013). The harbour porpoise is the only cetacean living permanently in the inner Danish waters, for example in the Sønderborg Bay (Hammond et al., 2002). The harbour porpoise has a small body size compared to larger whales and thus cannot built big fat depots in the body to cover their basal energy needs. The distribution of harbour porpoises is thus linked to prey abundance as they need to feed almost continuously (Koopman, 1998). Ross et al. (2016) investigated prey species for porpoises in the Western Baltic. Here, the most dominating prey species are Atlantic herring, Atlantic cod, European sprat and gobies. Sveegaard et al. (2012) furthermore revealed that the spatial distribution of harbour porpoises is correlated with the distribution of herring, supporting that porpoises are in the same areas as their prey. Porpoise abundance has also been linked to physical parameters, such as tidal phase, local hydrographic fronts and steep sea-bottom topography in combination with strong currents, as these features often lead to aggregation of prey (Johnston et al. 2005, Goodwin 2008). However, knowledge of specific foraging strategies and habitat selection of harbour porpoises is still limited.

During this project, we hypothesized that harbour porpoise abundance would increase in the time following cobble reef restoration, based on the presumption that the reef would increase the prey availability and thus attract the harbour porpoises.

4.2 Materials and methods

The study was carried out in the coastal waters of Sønderborg Bay. In relation to porpoises, Flensburg Fjord is a Natura 2000 area and therefore strongly connected to the Habitats Directive, listing the protection of harbour porpoises. The area was selected due to its high densities of harbour porpoises (Sveegaard et al., 2011). A total of 6 sites were sampled in the bay area: two natural reef sites (Vesterhage and Spar Es), two control sites (Kegnæs Ende and Viemose), and two experimental sites (Hvide Mur and Stenholt). The experimental sites are the sites where reef restoration occurred. Further details are available in Fig. 1.9 in WP1. Construction of the new cobble reefs began in late December 2017 (21+22/12-2017) and was finished in mid-January 2018 (16-18/01-2018). The method of the cobble reef construction is described in WP1.

Twelve acoustic data loggers, C-PODs (Chelonia Ltd.), were deployed at the six locations. The C-POD is a passive acoustic monitoring device (lyttepost in Danish language), used to detect echolocation signals made by Odontocetes. The CPODs were deployed over three periods. 1) “January-October 2017”, 2) “November 2017-February 2018” and 3) “March-June 2018”. However, due to lack of data from Hvide Mur (an experimental site) in the first two periods, one extra C-POD was deployed at this location in the third deployment period, resulting in a total of 37 C-POD deployments in all three periods. The C-PODs were placed in the bay area at water-depths ranging between 6-7 m, 1.5 m above the seafloor, 4-5 m below the surface, depending on depth. A diver deployed each of the C-PODs, to ensure the right position of the instrument. The C-PODs were deployed with an anchor at one end, connected via a rope to a buoy, which was placed below the water surface, to prevent possible theft of the devises. The GPS waypoints were carefully noted of each deployment, and used for the later retrieval.

4.2.1 C-POD data processing

The raw acoustic data files (CP1-files) were downloaded from the SD cards in each of the C-PODs after retrieval. All the CP1-files were then processed in the C-POD analysis software program CPOD.exe (Chelonia Ltd. V2.044), by applying filters to the KERNO classifier, which then identified NBHF echolocation click trains in the frequency range 125-145 kHz. Only click trains containing more than five clicks in each train were assessed as being harbour porpoise echolocation click trains. These detected click trains were then classified into different qualities (likelihood of cetacean/porpoise origins): “Hi” (High-probability cetacean trains) and “Mod” (Moderate-probability cetacean trains). Lower qualities were also found, but only “Hi” and “Mod” qualities were used (Nuuttila et al., 2013). The output was a CP3-file, containing harbour porpoise positive minutes registered per hour for each C-POD, which was then copied into an Excel spreadsheet for further analyses.

4.2.2 Statistical analysis

Two models were used to analyze the C-POD data. The purpose of the first model was to estimate the effect of the time of day for each of the seasons (spring, summer, autumn and winter) and used the original hourly data. The second model used daily averages rather than hourly values as the response. This was done to reduce the number of data points and reduce the number of estimated parameters in the model, because the time of day effect is not relevant for the daily averages. The purpose of the second model is to make inference about the mean proportion of porpoise positive minutes (PPM) in the periods April-May 2017 and 2018. While a model for the hourly data could be used for both questions, the separation allows a simpler model to be used for the hourly data, which can be estimated in the order of minutes.

(1) Model for hourly data:

$$\mathrm{logit}(E(p_i)) = \mu + \mathrm{logit}(p_{ti-1}) + \alpha(H_i) + f1(t_i) + f2(hour_i, Season_i) + U\mathrm{Location}(i) + UPod(i)$$

where p_i is the probability that a minute from the ith observation classified as a positive harbor porpoise minute. The parameter μ is the overall mean, $\mathrm{logit}(p_{ti-1})$ is a carry-over effect defined as the logit of the proportion positive minutes in the previous hour, α maps the ith observation to a categorical effect for each habitat type, $f1$ is the effect of time represented by a Duchon spline with first order derivative penalty, and $f2$ represents the effect of the time of day and is a cyclic cubic spline (one for each of the four seasons). Finally, *U*Location and *U*Pod are zero mean normal distributed random effects for the effect of Location and Pod. The response in this model is the number of porpoise positive minutes in an hour (0-60) and is assumed to be binomial distributed with success rate *p*.

(2) *Model for daily data:*

$$\text{logit}(E(p_i)) = \mu + \alpha\,(H_i) + f1(t_i) + f2(t_i, \text{Location}_i) + U\text{Location}(i) + U\text{Pod}(i)$$

where *pi* is the proportion of positive minutes per day for the *i*th observation. The function *f1* is the overall effect of time represented by a Duchon spline with first order derivative penalty, and *f2* represents location specific effects of time. The rest of the parameters are the same as in equation (1). The response in this model is the proportion of positive minutes per day and is assumed to be beta distributed. Since the beta likelihood is not defined for days with zero positive minutes, those zeroes are replaced with 1/1440 (one minute per day). Data were analyzed in R version 3.4.4 using package “mgcv” version 1.8-26.

4.3 Results

A total of 37 C-POD deployments were performed in three different periods: “Jan-Oct 2017”, “Nov 2017- Feb 2018” and “Mar-Jun 2018”, during the 1.5-year survey period from 17/1-2017 until 15/6-2018. Unfortunately, eight of these deployments were non-successful (four from first period and two from both second and third period). The 29 successful deployments and total hours of data collected by each of the 13 CPODs on the six different locations are listed in table 4.1. Not all C-PODs ran for the full periods. They ran from 34 to 261 days, with a mean number of 120 days. In total, 83,484 hours were collected. Data from the construction period (21-12-2017 to 18-01-2018) were discarded, leaving 76,737 hours for analysis.

Table 4.1. Total amount of recorded hours by each of the 13 C-PODS from the 6 locations.

Pod \ Location	Hvide Mur	Kegnæs	Spar Es	Stenholt	Vesterhage	Viemose
479	2256	0	0	0	0	0
786	0	0	1646	0	0	0
787	0	0	0	8382	0	0
788	0	0	0	0	0	5771
2177	0	0	0	0	8876	0
2180	3828	0	0	0	0	0
2181	0	10187	0	0	0	0
2390	3853	0	0	0	0	0
2394	0	0	0	4944	0	0
2395	0	10078	0	0	0	0
2396	0	0	0	0	0	6843
2471	0	0	0	0	3997	0
2472	0	0	6076	0	0	0

Overall, harbour porpoise echolocation activity in the sites is pictured in Fig. 4.1 (Jan 2017 – Jun 2018). The blue line is the level of porpoise presence; the grey areas indicate uncertainty levels from the model (95% confidence intervals) that are highly linked to periods when data are missing. The red vertical bars indicate the beginning and end of the cobble reef construction period, mainly influencing the two project sites “Hvide mur” and “Stenholt”.

Analysis of the harbour porpoise echolocation activity during the full period shows a significantly higher proportion of harbour porpoise echolocation activity at “Kegnæs” (control) compared to the remaining five locations. Spring and summer 2017 show a higher proportion of echolocation activity, compared to the autumn where a drop in the proportions of activity is seen in 2017. In early winter 2017, an increase in the activity was again detected until the time of construction period of the reefs. The construction period was followed by a low number of detections, especially Jan-Feb 2018, but followed by an increase in the spring and early summer period 2018.

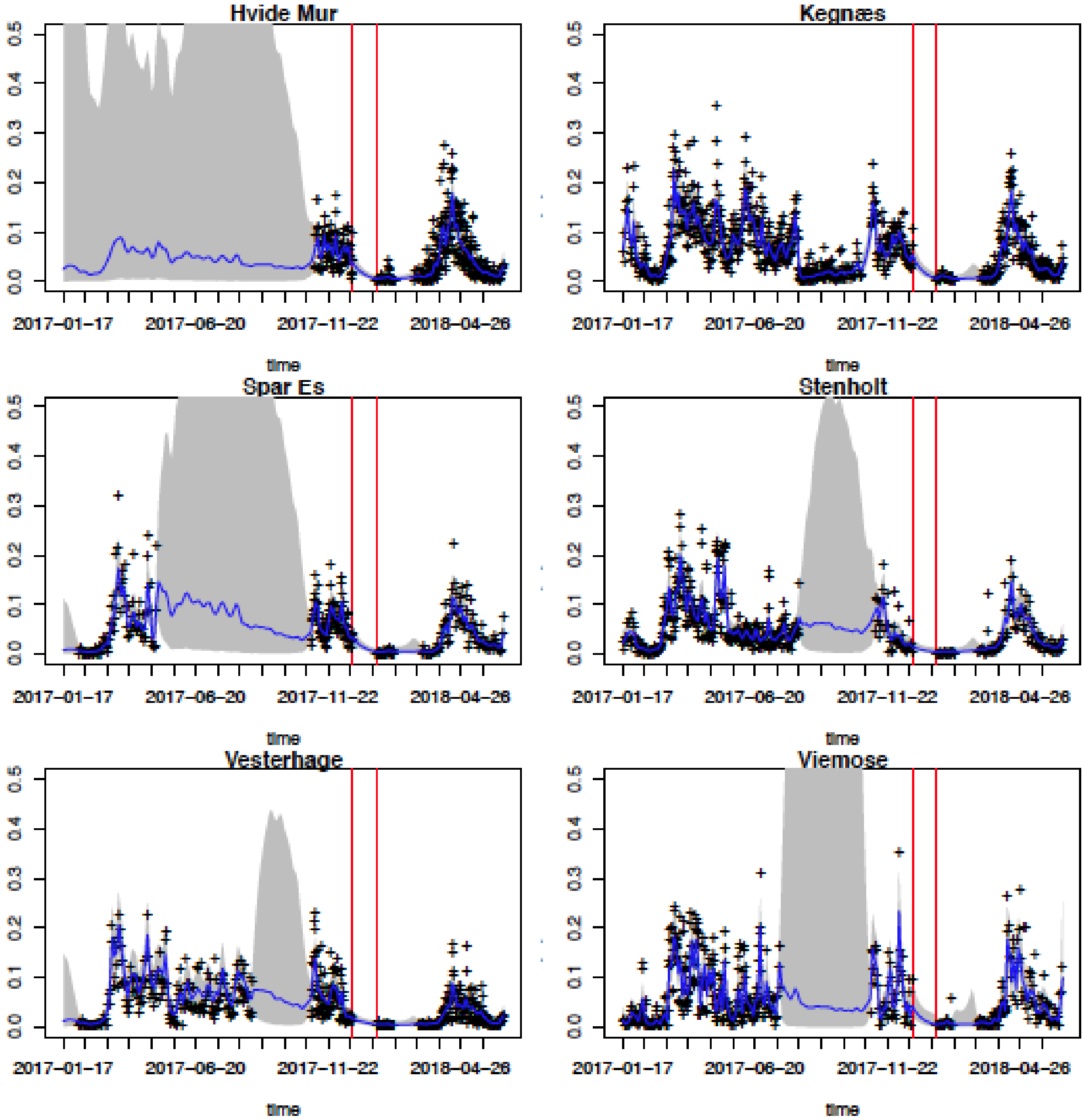


Figure 4.1. Model fit to the daily data by site. Shaded areas indicate 95% confidence intervals, blue line in shaded area arise from an estimate based on data from the remaining sites. Red vertical bars indicate the beginning and end of the cobble reef construction period, mainly impacting the two experimental sites "Hvide Mur" and "Stenholt". Further site specific details are available in Figure 1.9 in WP1.

In Fig. 4.2, harbour porpoise echolocation activity from April and May 2017 is plotted against the activity pattern observed in April and May 2018, 3 months after the construction of the cobble reefs at "Hvide mur" and "Stenholt". Lack of data from the project site "Hvide mur" in spring 2017, and from the natural reef site "Spar Es", in the summer period of 2017 is causing the large uncertainties. These data and data from the later periods have thus not been compared. Mean proportions of daily harbour porpoise activity on the three different habitats are almost equal in the 2017 spring period, indicating an equal use of the different areas in this period, possibly targeting different species of fish on the different benthic habitats. Data collected in the same period in 2018 show a slight decrease in activity in four of the six locations, only "Viemose" show the same mean level of daily activity between the two years. Since the acoustic data collection was unsuccessful at the “Hvide Mur” site (experimental site where cobble reef restoration was conducted) in spring 2017, no comparison can be made for that site. Table 4.2 shows the exact values of the mean number of porpoise positive minutes (PPM)/day (24hours) in April and May 2017 and in April and May 2018 detected on the six sites.

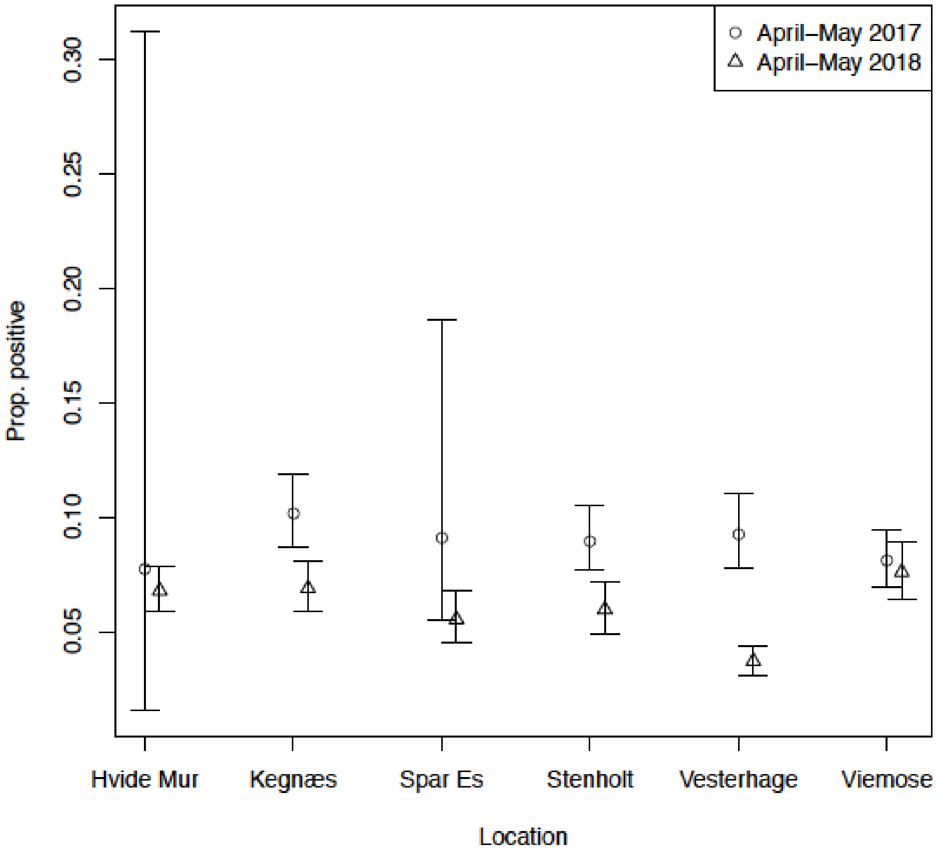


Figure 4.2. Estimated mean proportion of harbour porpoise positive minutes/hour from the six sites in April and May 2017 and 2018 with 95% confidence intervals (daily data model).

Table 4.2. Mean number of harbor porpoise positive minutes (PPM)/day (24hours) in April and May 2017 and 2018 detected on the six examined sites. * Spar Es 2017 only covers data until the 6th May, so daily estimates of PPM are made on the basis of the mean activity per day from 1st April until 6th May.

Location /Year	2017	2018
Viemose	115.97	117
Hvidemur	No data	101
Stenholt	125.18	76
Kegnæs	151	108.42
Vesterhage	107.48	51.05
Spar Es	108*	83.16

4.4 Discussion

This work package investigated if harbour porpoise abundance would increase in the time following reef construction, based on the presumption that the reef would increase prey availability and thus attract the harbour porpoises.

The work package examined the abundances by use of acoustic monitoring (C-PODs). Unfortunately, the C-PODs had severe data losses, despite full battery packages, correct commissioning and two C-PODs placed on each site (see Fig. 1.9 in WP1) (with 200 m spacing). C-PODs are, however, the main tool to collect data on porpoise presence and are used globally (Koblitz et al., 2014, Kindt-Larsen et al. 2018, Campbell et al., 2018), despite the high risk of data loss.

Seasonal variations were observed with substantially higher mean proportions of harbour porpoise echolocation activity during spring, summer and autumn, compared to winter. The observed increase in activity during the spring – autumn seasons support the existing knowledge of the Sønderborg Bay area being a hot spot of harbour porpoise (Sveegaard et al., 2011), likely utilizing the bay for foraging purposes. The high spring-autumn activity, covering the porpoise breeding season (Jun-Aug), could also indicate the area's importance as a breeding and mating area of the western Baltic population of harbour porpoise (Verfuß et al., 2007). During the early autumn season (September), there was a decrease in porpoise activity, until late autumn season (November) where there was an increase in the echolocation detected on five of the six sites, not including "Hvide mur" due to lacking data in this period. The decreased echolocation activity detected in the winter period, compared to summer – autumn season, could be linked to prey species migration into deeper waters during the winter season when the water temperatures decrease, which might then cause the porpoise to seek deeper waters during the winter period. A study analyzing the seasonal migration of Atlantic cod suggested that a large fraction migrates into deeper waters during the winter period, coinciding with the disappearance of the thermocline (Cote et al., 2004). Echolocation activity is low after the reef restoration period in January and February 2018, likely not connected to the actual construction event itself, but more likely due to the season of the year (i.e. winter), because all sites show low proportions of echolocation activity during the period, and the construction event would likely only impact the two experimental sites "Hvide Mur" and "Stenholt".

4.4.1 Short term effects of cobble reef construction

In this study, we expected an increase in harbour porpoise detections after the construction of the cobble reefs. This was, however, not the case because "Stenholt" (experimental site) revealed a fewer detections of porpoises in April and May 2018 after the reef construction, compared to 2017 before the reef construction. Unfortunately, no data for comparison were available from "Hvide mur" (experimental site) due to the described data loss. However, a slight decrease in the detections of harbour porpoise were found on almost all sites, which suggests that the observed decrease was not related to the construction event itself, but is more likely caused by natural fluctuations in the number of individuals visiting the Sønderborg Bay area between years. Fluctuations in harbour porpoise detections are common as observed elsewhere (Bailey et al., 2010;

Scheidat et al., 2011). Low water temperatures were observed in the spring 2018, possibly delaying the migration of herring into Sønderborg Bay in the spring period for spawning. If the porpoises follow the herring, as suggest by Sveegaard et al. (2012), the immigration of harbour porpoises would thus likewise be delayed. Another likely explanation why we did not find an increase in the porpoise detections after cobble reef construction at the "Stenholt" site is that the cobble reef was offered inadequate time for the colonization by prey species and thus attract porpoises. Few studies have investigated the short-term effects of reef construction. Liversage et al. (2017), however, found that the amount of floral and other sessile species colonizing an artificial boulder reef site within just seven weeks reflected the amount of species present on naturally occurring boulder reef sites. Much of the published literature on reef habitats and fish communities is, however, based on studies in tropical waters, differing significantly from the Sønderborg Bay. Mikkelsen et al. (2013) investigated if a restored boulder reef favored harbour porpoise. They found that the reef attracted porpoises, however, the study was done over a period of 7 years. Thus, it is possible that no reef effects are present in relation to harbor porpoises in the present study until after a long period (several years). We therefore recommend monitoring the porpoise abundance several years after reef establishment.

5. Conclusion

This project deployed cobble reefs in Flensburg Fjord and studied the reef effects in relation to fish abundance, benthic flora and fauna as well as harbour porpoise abundance. By collaborating closely with local stakeholders, the project demonstrated that cobble reef restoration is feasible to alleviate the impacts of previous extractions of seabed substrates. Future reef projects should expect that the economic costs of deploying reefs correspond to approximately 500 kr. per cubic meter of imported stones and rocks. Examinations of the deployed reefs revealed that they conform to the planned reef sizes and shapes, indicating that the construction of relatively complex reef structures is feasible. Fish appeared to respond quickly to the deployed reef. Sampling 3-5 months after reef deployment, underwater cameras revealed that total fish abundance had increased in the areas where the reefs were deployed and mimicked or occasionally exceeded abundances on natural reefs. For example, unbaited cameras (UBRUVs) indicated increased abundance of Atlantic cod after reef deployment. These data corroborate previous studies examining cod abundance in relation to rocky reefs and show that cod is often associated with reef habitats. Likewise, some smaller fish species were associated with the reef habitats and appeared to increase after reef deployments. As expected, the abundance of flatfish decreased after reef deployments. Baited cameras (BRUVs) revealed highly elevated abundances of herring in natural reef sites, but spawning herring, or herring eggs, were not observed by the underwater cameras throughout the field seasons. Fish communities were distinct and often differed between sites with and without reef habitats. Diver based assessments of benthic flora and fauna on natural reef sites, and comparisons with sites without reefs, indicated that reef substrates support both high biomasses of macro algae and elevated abundances of many invertebrates, thereby providing both shelter and food resources for fish. For example, the total epifauna abundance correlated positively with the seabed coverage of stones and rocks (mainly cobble). Similar trends were observed for specific invertebrate groups, including crustaceans, gastropods and polychaetes. Previous studies have revealed high abundance of harbour porpoise in Sønderborg Bay. The present project confirmed the presence of harbour porpoise in the area, but elevated abundance of harbour porpoise near the deployed reefs was not observed, probably because data availability was limited and the short time frame of the project. The project indicated that distinct biological communities are associated with reefs consisting of cobble and similar small stones and rocks. The reefs provide foraging and sheltering conditions that are favourable for many fish species. Thus, protection and restoration of cobble reefs have the potential to influence local fisheries positively. These benefits may diminish if cobble and similar small stones and rocks are extracted from the seabed. Colonization of the deployed reefs had only just started when they were sampled by the present project. Complete colonization of the reefs will take several years, suggesting that comprehensive assessments of the positive reef effects require long-term investigations (about 10 years).

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Acknowledgements

The authors are extremely grateful to a large group of people who supported the work completed by the project. The authors thank Dennis U. Andersen, Jeppe D. Balle, Mads O. Christoffersen, Lis V. Elmsted, Hanne M. Jacobsen, Berit L. Møller, Jeppe Olsen, Michael B. Rasmussen, Anna Rindorf and Josianne G. Støttrup for support, generous help and good advice throughout the project.

Technical
University of
Denmark

DTU Aqua
Kemitorvet
2800 Kgs. Lyngby

www.aqua.dtu.dk