Astrid Winnberg Skoge

Richness, abundance, and spatial distribution of coastal fish around Hitra and Frøya

Master's thesis in MS Ocean Resources
Supervisor: Torkild Bakken
Co-supervisor: Alf Ring Kleiven, Carla Freitas
May 2023

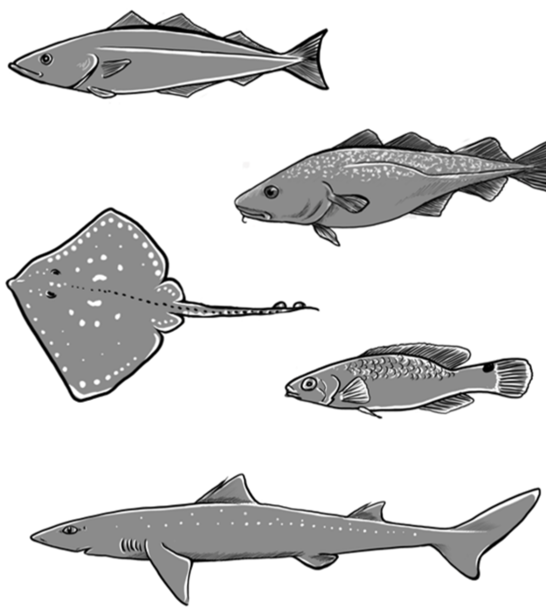

Illustration: Astrid Winnberg Skoge

NTNU
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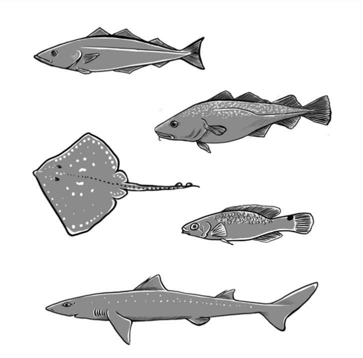

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ABSTRACT

In this master thesis, 228 hours of stereo-BRUV data collected over two years in the coastal areas surrounding Hitra and Frøya were analysed to observe the effects of wave exposure, current speed, temperature and depth on species richness as well as abundance, length and spatial distribution of Atlantic cod (*Gadus morhua*), goldsinny wrasse (*Ctenolabrus rupestris*), cuckoo wrasse (*Labrus mixtus*), spiny dogfish (*Squalus acanthias*), Atlantic halibut (*Hippoglossus hippoglossus*), thornback ray (*Raja clavate*), pollock (*Pollachius pollachius*) and saithe (*Pollachius virens*). The eight fish species examined in this study all had different associations with the environmental variables, indicating different habitat use within the small spatial scale of the study area. Spatial distribution of these species was affected by the species preferred environmental ranges. The associations uncovered in this study has implications for ecosystem-based management in general, and specifically for the planned implementation of a marine protected area (MPA) in one part of the study area. Management strategies that aspire to protect the whole ecosystem will need to consider all species within the fish community and their biotic and abiotic associations. Biodiversity and species richness is not only protected through the protection of the one species alone, but through protection of the whole fish community, their environmental and spatial range, and a diverse habitat covering niches on a community level.

SAMMENDRAG

I denne masteroppgaven har jeg brukt 228 timer med stereo-BRUV-data samlet over to år langs kysten av Hitra og Frøya til å observere effekten av bølgeeksponering, strømhastighet, temperatur og dybde på artsrikhet og artstetthet, lengde og romlig fordeling av torsk (*Gadus morhua*), bergnebb (*Ctenolabrus rupestris*), blåstål/rødnebb (*labrus mixtus*), pigghå (*Squalus acanthias*), kveite (*Hippoglossus hippoglossus*), piggskate (*Raja clavata*), lyr (*Pollachius pollachius*) og sei (*Pollachius virens*). Disse åtte fiskeartene assosierte på ulik måte med miljøvariablene jeg undersøkte, noe som indikerer ulik habitatbruk mellom artene på en liten romlig skala innenfor studieområdet. Romlig fordeling av arter i studeområdet var påvirket av artenes miljøbehov. Forholdene som avdekkes i denne studien har implikasjoner for økosystembasert forvaltning generelt, og er spesielt viktig i forhold til et planlagt marint bevaringsområde i en del av studieområdet. Forvaltningsstrategier som har som mål å bevare økosystemet er nødt til å ta hensyn til hele fiskesamfunnet og hver enkelt arts biotiske og abiotiske tilknytninger. Biodiversitet og artsrikhet beskyttes ikke kun gjennom vern av en enkelt art, men gjennom bevaring av hele fiskesamfunnet, deres foretrukne miljø- og romlige behov, og et mangfoldig habitat med nisjer som dekker hele samfunnets behov.

PREFACE

This thesis is written for the Department of Biology (IBI) at the Norwegian University of Science and Technology (NTNU) in cooperation with the Institute of Marine Research (IMR) and concludes a two-year master program in Ocean Resources with a specialisation in ecosystems, which I started in August of 2021.

I would like to extend thanks to my supervisors for guiding me through this project. Torkild Bakken, thank you for all your feedback on my writing, for always being reliable, answering messages on weekends, lending me books about marine protected areas, for all our interesting conversations, and for always encouraging my ideas and aspirations. Alf Ring Kleiven, thank you for giving me the opportunity to work on this project, for all your helpful feedback, for always being super enthusiastic about my project, and for inspiring me and challenging me to see a wider perspective. Carla Freitas, thank you for all your support, guidance, and patience during the analysis, for teaching me about statistics and R coding, and for explaining difficult concepts in a way that make them easy to understand.

I would also like to thank Marit Bull who did the initial 2019 analysis for introducing me to this project and for being so forthcoming and offering help and support if I ever needed it.

To everyone at Flødevigen field station, thank you for making me feel welcome everytime I visited. An extra thanks to Jon Albretsen, for providing me with the current and wave exposure data. And to Portia Joy Nillos Kleiven, thank you for teaching me video analysis, for good conversations and fun fieldwork times, and for constantly cheering me on.

To my friends and fellow students, thank you for all the coffee breaks and lunch conversations and moral support throughout the process. To my mom and dad, thank you for always encouraging my curiosity and allowing me to explore the world. Thank you for teaching me the names of animals and plants and always answering a million questions. Thank you for teaching me love and respect for the world and the sea and all the wonders of nature. And lastly, thank you, Hanne, for your endless patience and support, for all your good advice, and for always believing in me.

Without you, this project would not have been what it is today.

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LIST OF ABBREVIATIONS

BRUV – Baited Remote Underwater Video

MPA – Marine Protected Area

PPA – Partially Protected Area

TL – Total Length

FL – Fork Length

CPUE – Catch Per Unit Effort

WE – Wave Exposure at seafloor

BC – Bottom Current speed

IMR – Institute of Marine Research

MSFD – Marine Strategy Framework Directive

GES – Good Environmental Status

BACI – Before-After, Control-Impact

ICES – International Council for Exploration of the Sea

IUCN – International Union for Conservation of Nature

GLMM – Generalised Linear Mixed effects Model

MaxN – Maximum Number of individuals per frame (*In EventMeasure*)

CTD – sensor for Conductivity (salinity), Temperature and Depth

VU – Vulnerable (*IUCN red list of species*)

NT – Near Threatened (*IUCN red list of species*)

LC – Least Concern (*IUCN red list of species*)

1. INTRODUCTION

Marine ecosystems are a sum of biotic and abiotic factors in marine environments. In recent years, marine ecosystems all over the globe are facing changes in temperature, nutrient supply, water mixing, light availability, and salinity due to human-induced climate change. The severity of the effect of these changes will depend on the region and the vulnerability of individual species and communities to such changes. For fish communities this can look like geographic shifts, changes in phenology and phenological mismatch, and changes in recruitment, growth and survival rate on population and species level (Hollowed *et al.*, 2013).

Fisheries act as a strong selection pressure on fish populations globally, introducing non-natural mortality which often is size selective (Baskett *et al.*, 2005). While traditional fisheries have existed for hundreds of years, marine ecosystems are now faced with global warming and large scale industrial fisheries too (Baskett *et al.*, 2005; Hollowed *et al.*, 2013; Pita and Freire, 2014; Marshall *et al.*, 2021). In addition to removing a great fraction of the population, fisheries can act as an evolutionary force selecting for earlier sexual maturation in some species, because the fisheries typically target the bigger size fraction of fish populations (Baskett *et al.*, 2005). Smaller fish are typically less fecund and produce less offspring than bigger fish, and the effect of systemic removal of big, highly fecund individuals on reproductive yield is often underestimated (Marshall *et al.*, 2019, 2021). As many fisheries target fish with schooling behaviours, it has also been suggested that fisheries induced evolution could be selecting for smaller preferred group sizes and less schooling behaviour in some fish species. This has major ecological implications as schooling fish often play an important role in the food web. It also has implications for the schooling species as this behaviour is an anti-predator behaviour (Guerra *et al.*, 2020). Industrial fishing gear such as bottom trawls and dredges cause serious harm to marine habitats and reduce abundance of fish and benthic invertebrates in trawled areas (Olsgard *et al.*, 2008; Johnson *et al.*, 2015). Studies have also revealed effects of bottom trawling on nutrient cycling and primary production (Dounas *et al.*, 2007; Olsgard *et al.*, 2008). In the EU, abundance of vulnerable indicator species of sharks, skates and rays have decreased by 69% in heavily trawled areas compared to un-trawled areas (Dureil *et al.*, 2018).

In fisheries management, populations of fish in the same geographic area are placed in one unit, "stock" which is assumed to have the same reproductive rate, growth rate and maturation. However, within the stock, there can be many smaller populations with different life history traits (Wright et al., 2006; Sherwood and Grabowski, 2010; Kuparinen et al., 2016). In the case of the Newfoundland cod (*Gadus morhua*) in the North Atlantic, the once abundant cod population was drastically decreased in the 1970s-1990s, and has not been able to recover, even after 30 years (Cooke, 2022). The collapse of the cod population and, subsequently, the local fishery traditions have been attributed to failed management and wrongful estimates about population size and robustness. Criticism has been made of fisheries science practices for treating this cod population as a harvestable crop, failing to recognise the life history and ecology of the cod, and failing to listen to local fishers knowledge and experiences with cod fishery in the area (Bavington, 2010; Mather, 2013).

Coastal ecosystems are more vulnerable to human induced change compared to the high seas, as they are more affected by pollution, eutrophication, invasive species, fishing and shoreline development (Hollowed *et al.*, 2013). A collapse of an economically and ecologically important species, such as cod has negative effects on the ecosystem as a whole, and on people who live and work in coastal areas (Cooke, 2022). To have successful management of marine species and resources, management decisions should be based on evidence, transparency, and as integration of local knowledge and communication with stakeholders (Grorud-Colvert *et al.,* 2021).

As the worlds wild populations of fish slowly decline, some nations have tried to implement stock enhancement, rearing juvenile fish, and releasing them into their natural habitats. In Norway, cod stock enhancement was attempted in the 1980s and 1990s, with no significant increase in cod production or landings (Svåsand *et al.*, 2000).

As an alternative to catching wild fish, many nations look to fish aquaculture to secure a supply of seafood and economic growth. In Norway, finfish aquaculture is a well-established industry: 1031 marine fish farms produced 1.7 million tons of fish at a value of 80 billion NOK in 2021 alone. Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) are the most well-established species, although in recent years there has been an increasing investment in cod aquaculture (Directorate of fisheries, 2022, 2023). Fish aquaculture typically includes the rearing of fish in flow through net-pens in coastal areas, allowing significant interaction between the sea-cages and the marine ecosystem. In salmon aquaculture, dense populations of salmon lead to accumulation of pathogens such as sea lice, which can disperse and be transferred to wild salmonoid fish (Krkosek, *et al.,* 2005; Uglem *et al.*, 2014; Asplin *et al.*, 2020). Chemicals and medicines used for treating sea lice have bleaching effects on coralline algae (Legrand *et al.*, 2022) and are potentially harmful to crustaceans (Moe *et al.*, 2019). Faeces and organic waste released from fish farms may cover the benthic environment and have a strong negative impact on coralline algae (Legrand *et al.*, 2021). Fish farms located in shallow dispersive sites can have a significant biological effect on marine benthic environments up to 1000 meters away from the farm (Keeley *et al.*, 2019). Wild fish like cod and saithe (*Pollachius virens*) have been observed to aggregate around finfish farms and feed on surplus feed (Dempster *et al.*, 2009, 2011; Skjæraasen *et al.,* 2022), something that can affect metabolic composition (Maruhenda Egea *et al.*, 2015; Meier *et al.*, 2023) and possibly fish quality of wild fish (Uglem *et al.*, 2020). However, it has been suggested that these aggregations could act as a population source for wild fish populations if managed well (Dempster *et al.*, 2011). Escaped fish from fish farms compete and reproduce with wild fish, and caged cod sometimes spawn in the sea cages, causing genetic mixing even if there has not been an escape event. This can affect the genetic structure of the wild populations (Jensen *et al.*, 2010).

Species diversity, richness, abundance, and size distribution of fish

Biodiversity is linked to productivity and general ecosystem health in marine ecosystems, and monitoring this is important to achieve good management of marine areas (Narayanaswamy *et al.*, 2013). In the EUs Marine Strategy Framework Directive (MSFD), biodiversity, species abundance, size range, species range and habitat use are all criterions used to determine whether good environmental status (GES) is achieved (Vasilakopoulos *et al.*, 2022). Abundance is typically measured by catch per unit effort (CPUE) in fisheries or by trends in fish landings. Size distribution and habitat use is typically observed through scientific surveys according to this directive. Fish size is a useful indicator of the overall condition of a fish population as it can be affected by both fisheries pressure, changes in temperature and food web structure (Queiros *et al.*, 2018), and can act as an indicator of fecundity (Marshall *et al.*, 2019, 2021).

Fish diversity and abundance in Norwegian waters

The Institute of Marine Research in Norway (IMR) has several regular research cruises to monitor fish populations, mostly using extractive methods such as trawling, Danish seines and gillnets to sample fish communities, and plankton nets to map spatial abundance of early life stages of fish (Franze *et al.*, 2021; Institute of Marine Research, 2022). Abundance, age and size data on commercially important species, such as cod and saithe, are gathered yearly by the IMR by acoustic surveys and bottom trawl stations along the coast (Aglen *et al.*, 2021). Other studies of fish abundance and diversity have used traps (Moland *et al.*, 2012), telemetry (Freitas *et al.*, 2015, 2021; Skjæraasen *et al.*, 2022), and mark-recapture methods (Fernández-Chacón *et al.*, 2017).

Stereo-BRUVS

Stereo Baited Remote Underwater Video Systems (stereo-BRUVs) are a simple and cost-effective method of optical sampling underwater. Two cameras are positioned in an aluminium rig pointing at the same point at a known angle of overlap, creating a stereo video. Using software, the overlapping images can be translated into three-dimensional information, and an object's length and distance to the camera can be calculated. The rig is provided with a bait to attract fish that are in the area (Langlois *et al.*, 2020).

Stereo-BRUVs are non-destructive and non-intrusive ways to observe marine species in their natural environment and perform well when compared to other visual survey methods and extractive fisheries based survey methods (Bernard and Götz, 2012; Logan *et al.*, 2017; Bull, 2019; Davis *et al.*, 2019; Wong *et al.*, 2019; Di Blasi *et al.*, 2021), although other methods have worked better for observing herbivore fish communities (Goetze *et al.*, 2015). The non-invasive nature of the stereo-BRUV allows researchers to observe interactions and feeding behaviour of aquatic species outside of lab experiments (Di Blasi *et al.*, 2021; Ovegård *et al.*, 2022). The use of stereo-BRUVs to assess and monitor ecosystems and fish assemblages is a useful tool in both marine (Jones *et al.*, 2020; Torres, *et al.*, 2020; Davies *et al.*, 2021; Jackson-Bué *et al.*, 2023), estuarine (Lowry *et al.*, 2012) and freshwater environments (Schmid *et al.*, 2017; Schmid and Giarrizzo, 2019). Recently, a meta study of 6701 pelagic and 10710 benthic stereo-BRUV deployments from all over the world used size and abundance data from stereo-BRUVs to study fish communities, food webs, and effects of human interaction on fish communities (Letessier *et al.*, 2023).

Marine protected areas (MPAs) in relation to fish diversity, abundance, and size

Protecting whole areas from various fishing activities can lead to an increase in diversity and abundance of marine fauna inside the MPA as well as outside it due to spillover and recruitment effects (Fernández-Chacón *et al.*, 2015; Davies *et al.*, 2021). These effects make protection measures an economic investment as well as an ecological one. In fact, it has been predicted that long lived species like cod respond almost twice as well to spatial-temporal protection like MPAs, compared to quotas. This is because MPAs preserve larger, more fecund individuals and allows them to reproduce (Marshall *et al.*, 2021). In December 2022, the United Nations Convention on Biological Diversity adopted the Kunming-Montreal Global Biodiversity Framework (GBF), committing to managing 30 percent of nature through protected areas and other effective area-based conservation measures (CBD, 2022). This includes marine protected areas with both partial and full protection, as long as they are effective.

Since the term MPA incorporates a wide range of management strategies, from relatively weak protection to no-take zones, comparing effects of MPAs can be challenging. Here, "no-take MPAs" refer to areas with full protection, where no fishing activity is allowed. The term "partially protected MPA" or "PPA" will refer to areas where there is some protection, but fishing with some equipment or for some species is still allowed. Lastly, "MPA" will be used as an umbrella term to refer to both PPAs and no-take MPAs. A study of 91 no-take MPAs in Australia found that the age and size of a no-take MPA as well as connectivity to other no-take MPAs increased the effect of protection on abundance of fished species. Stricter regulations and a greater depth range within the protected area was connected to increased biomass of fished species within these no-take MPAs (Goetze *et al.*, 2021). A study of 74 European no-take MPAs, found a significant increase in density, biomass, body size and species richness inside no-take MPAs compared to unprotected areas (Fenberg *et al.*, 2012).

While it is mostly agreed upon that no-take MPAs have a positive effect on abundance and biodiversity, the effect of partially protected MPAs is not as clear in the literature. In 2018, trawling intensity was 1.4 times higher inside PPAs, compared to non-protected areas in the EU. Here, the abundance of threatened and vulnerable sharks and skates were up to five times higher outside PPAs (Dureil *et al.*, 2018). However, a Before-After Control-Impact (BACI) study of a PPA where traps and gillnets were prohibited on the Norwegian Skagerrak coast led to an increase in cod size and population density after just four years (Moland *et al.*, 2012). A study of 18 PPAs and 19 no-take MPAs in Southern Australia suggested PPAs were not ecologically effective and were more poorly understood by the public. No-take MPAs had more fish species and a higher fish biomass compared to open areas, and were to a greater degree supported and understood by the public (Turnbull, *et al.*, 2021).

The understanding and support from the public in management of MPAs are important if the implementation of an MPA is to have social benefits in the local community. Possible negative social and economic outcomes of establishing an MPA are conflicts between stakeholders and loss of income. Positive outcomes are increased ecosystem health and fisheries yield. The prior can be minimised and the latter maximised if the process of establishing an MPA is characterised by knowledge integration between parties, transparency, communication, public participation, and long term political will and commitment (Grorud-Colvert *et al.*, 2021). Di Franco *et al.*, (2016) reported that social and ecological success of marine protected areas were greater when local fishermen were involved in decision making and sustainable fishing was promoted.

In 2021, the Norwegian government issued a statement claiming (a) that Norway will be a leading country when it comes to ecosystem-based management of marine resources, taking care of nature, and developing knowledge about marine the environment, (b) that the goal of creating marine protected areas is to take care of important marine nature and ecosystem functions, (c) that Norway is committed to protecting 30% of marine areas either by MPA implementation or other effective area-based conservation efforts (OECMs) by 2030, and (d) that this conservation work is built on mapping, research and monitoring of natural resources (Klima- og miljødepartementet, 2021, p.5-7). In 2020, MPAs constituted less than 5% of Norwegian waters (Jørgensen *et al.*, 2021). Moreover, most of these are PPAs and are not considered protected to a high degree by international standards. In fact, in several Norwegian national parks and MPAs, industrial trawling is still happening on a regular basis. Although there are few no-take MPAs on the Norwegian coastline, there are examples that show marine protection has an effect here. In several small scale PPAs designed for lobster protection in Skagerrak, fishing with nets and pots were banned. Here, abundance and mean size of lobster have increased (Moland *et al.*, 2012; Nillos Kleiven *et al.*, 2019; Knutsen *et al.*, 2022). In some cases this has also resulted in an increase of coastal cod size and abundance, compared to surrounding areas (Moland *et al.*, 2012).

Fish communities

Fish are not randomly distributed in the coastal environment. Species richness, abundance, and total biomass may change with habitat type, topographical complexity, management strategy, and substrate evenness within a small spatial scale (Friedlander, *et al.*, 2007; Sørensen and Pedersen, 2021). Which individual species make up the total fish assemblages may depend on time of year, time of day, light conditions, and substrate type (Nickell and Sayer, 1998; Friedlander, *et al.*, 2007; Schlaff, *et al.*, 2014; Furness and Unsworth, 2020; Sørensen and Pedersen, 2021). The distribution of different species in the water column may be attributed to temperature (Heino *et al.*, 2012; Freitas *et al.*, 2021), water movement affected by wave exposure (Fulton, *et al.*, 2001) and current speed (Lecchini and Galzin, 2005; Schlaff, *et al.*, 2014). Juveniles often have different habitat requirements compared to adults (Lafrance *et al.*, 2005; Lecchini and Galzin, 2005), causing different distribution for different age groups of the same species. In addition to this, biotic factors like competition, predator avoidance, prey availability, spawning behaviour and human influence affect fish behaviour and habitat use (Nickell and Sayer, 1998; Dempster *et al.*, 2009; Armsworthy, *et al.*, 2014; Schlaff, *et al.*, 2014).

There is a lack of historic data and timeseries to describe the natural variability in marine ecosystems, including coastal fish communities globally, because most research has been done to gauge the effect of human stressors such as climate change, habitat loss and fisheries on marine species (Hollowed *et al.*, 2013). Designating marine reserves and no-take zones can give insight into population and ecosystem functions without the ongoing pressure from fisheries, and can help disentangle the effect of environmental drivers from the effect of active fisheries on marine ecosystems (Wilson *et al.*, 2020). A before-after-control-impact (BACI) study design is a commonly used and robust method of studying the effect of marine protection (Kerr, *et al.*, 2019).

Hitra and Frøya

The study area is situated in Trøndelag county, in the coastal waters surrounding the two islands Hitra and Frøya (Figure 2). Hitra and Frøya are located on the west coast of Norway where the Norwegian Sea meets the Norwegian coastline. This area is known for a productive marine ecosystem and both historically and in the present the area is characterised by active commercial and tourist fisheries and a strong aquaculture industry (*see Appendix 1, Figure A1, and Figure A2*). Located within the study area is the Froan nature reserve, which protects birds and mammals, but not fish (*Forskrift om Froan naturreservat, Frøya*, 1979). Fishing, especially with pots, is prevalent in parts of the nature reserve (*Appendix 1: Figure A2*).

Active Management (2018-2021)

During the timeframe 2018-2021, The Institute of Marine Research (IMR) did stakeholder surveys and biological and oceanographical data collection in Hitra and Frøya as part of the Active Management project. The goal was to include knowledge from local fishermen and other stakeholders to make recommendations for protecting and managing important local marine habitats and resources (Kleiven *et al.*, 2021). In 2018, 2019 and 2020, data were collected using stereo-BRUVs. Bull (2019) found that data collected using stereo-BRUVs showed a greater species richness and abundance compared to data collected with traps in the Hitra-Frøya marine area. The same study also found a wider range of size in Atlantic cod (*Gadus morhua*) using stereo-BRUVs compared to traps (Bull, 2019). One goal of the

Active Management project was to establish an MPA to study the effects of protection of local populations of cod (*Gadus morhua*), wrasse (family Labridae), scallops (*Pecten maximus*), and Norwegian lobster (*Nephrops norvegicus*). These species are all fished in substantial amounts in this area (Kleiven *et al.*, 2021). In a plan document released by Hitra municipality outlining plans for area use in 2022-2034, an area dubbed the "Grønnholmråsa nature area", which is marked with green in Figure 2, was suggested based on the findings and recommendations presented in the final project report for the Active Management project (Hitra kommune, 2023).

Atlantic cod (*Gadus morhua*)

Both coastal cod and migratory cod use coastal habitats for feeding, spawning and nursery grounds (Seitz *et al.*, 2014). Cod is a generalist species in terms of habitat use and diet. Along the Norwegian coast, cod diet varies according to the availability of different food items. A general trend is that smaller cod eat mainly benthic invertebrates, while larger cod have a more piscivorous diet (Svåsand *et al.*, 2000). Across ecosystems, cod experience a thermal range from -1.5 °C to almost 20 °C, with a mean peak at around 7 degrees. However, thermal habitat occupation differs between populations, and is narrower during the spawning season. Optimal growth rate for cod increased with mean thermal experience to around 16 °C, but authors note that growth rate could also be affected by food availability and the level of intraspecific competition (Righton *et al.*, 2010). Field studies of coastal cod in Skagerrak have shown a thermal range between 0 to 19.3°C, and a preference for colder water layers during summer and winter compared to ballan wrasse (*Labrus bergylta*) and pollack (*Pollachius pollachius*) (Freitas *et al.*, 2015, 2021). This preference for colder water layers were especially pronounced for larger cod, who would migrate less into warmer and shallower waters during summer compared to smaller cod (Freitas *et al.*, 2015). Similar predictions have been made based on laboratory experiments (Lafrance *et al.*, 2005; Björnsson, *et al., 2007)*. Cod larvae from populations with different thermal regimes react differently to changing temperatures (Oomen and Hutchings, 2016).

Cod is one of the most heavily fished species in the northeast Atlantic, where it is mostly fished by trawl (Seitz *et al.*, 2014). There are several different cod populations in this area, experiencing different environmental pressures and fishing intensity. According to The International Council for the Exploration of the Sea (ICES), cod populations are below the abundance limit which implies a risk of stock collapse in the Eastern Baltic Sea, North Sea, Eastern English Channel and Skagerrak. In Kattegat, cod landings have been less than a ton since 2006, and although there is no targeted cod fishery in this area anymore, the populations of cod have shown no sign of recovery (ICES, 2023). Coastal cod populations north of 62° N are stable, and above the limit of stock collapse. Our study area in Hitra and Frøya is in sub-area 6 for Southern Norwegian coastal cod. The stock assessment for this population is done by CPUE from reference fleets fishing with gillnets in this area (ICES, 2022a). Total catch in 2021 was 7735 tonnes, half of the total catch in 1977 (14550 tonnes). Commercial landings are caught by gillnet (49.8%), bottom trawls (5.3%) and other equipment, including Danish seine and longline (44.9%) (ICES, 2023).

Wrasse

In coastal Norway, five wrasse species, family Labridae, are relatively common: Ballan wrasse (*Labrus bergylta*), goldsinny wrasse (*Ctenolabrus rupestris*), cuckoo wrasse (*Labrus mixtus*), rock cook (*Centrolabrus exoletus*) and corkwing wrasse (*symphodus melops*). All these wrasse species have a southern distribution and are associated with warm, shallow coastal waters. Even though they are found in the same geographical areas, species and size composition of wrasse showed considerable variation over very small distances in a 2014 study of distribution and habitat preference. Corkwing were found in greater abundance in more sheltered areas, while Rock cook were found in greater abundances in more exposed areas. Goldsinny and ballan wrasse were associated with intermediate wave exposure. For all species, size was negatively associated with wave exposure (Skiftesvik *et al.*, 2014a). There seems to be a need for more data on wrasse ecology and habitat use. Especially for cuckoo wrasse, there is little in the literature. In one study, cuckoo wrasse along with rock cook were found in deeper water layers compared to ballan and corkwing wrasse (Halvorsen *et al.*, 2020). Skagerrak ballan wrasse have been observed to seek out warmer layers of water in both winter and summer (Freitas *et al.*, 2021). Corkwing wrasse and goldsinny wrasse both have high site fidelity and relatively small home ranges (Halvorsen *et al.*, 2021; Cresci *et al.*, 2022). Male goldsinny will swim in the direction of their home if translocated (Cresci *et al.*, 2022).

Wrasse are known to feed on ectoparasites on other fish (Skiftesvik *et al.*, 2014a). Because of this feeding behaviour, the goldsinny, ballan and corkwing wrasse are commonly used as cleaner-fish in aquaculture for salmonoids, which are frequently plagued by sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) (Skiftesvik *et al.*, 2013; Skiftesvik *et al.*, 2014a, 2014b; Gonzalez and de Boer, 2017, 2017; Halvorsen *et al.*, 2017). Targeted fisheries for wrasse increased drastically from 2005-2015 (Gonzalez and de Boer, 2017), and reached a top in 2017 of almost 30 million wrasses caught. From 2017 to 2022 landings have almost halved, and the quota for 2023 is set to 18 million (Fiskeridirektoratet, 2022). Ballan wrasse is the biggest, and therefore the most sought-after cleaning-fish. However, landings of this species are small compared to corkwing and goldsinny wrasse and wild caught ballan wrasse are not enough to cover market demand. There is an increasing interest in ballan wrasse aquaculture to produce cleaner-fish for salmonoid aquaculture, and lighten fishing pressure on wild ballan populations, but this is still in the development phase (Hamre *et al.*, 2013; Skiftesvik *et al.*, 2013; Cavrois-Rogacki *et al.*, 2021).

Most wrasse in salmon aquaculture come from the wild. Sometimes they are sourced locally, while other times they are translocated from their native habitat. Translocation especially happens in areas where there is low abundance of wrasse to begin with. Cleaner fish are introduced into the environment around the sea cages either by escaping from the sea cages or by being deliberately released when the salmon are harvested (Gonzalez and de Boer, 2017; Institute of Marine Research, 2023). There is proof of genetic mixing of southern and northern populations of both corkwing and goldsinny wrasse in Flatanger, which is an aquaculture site at the edge of the northern distribution range of corkwing wrasse and goldsinny wrasse (Jansson *et al.*, 2017; Faust *et al.*, 2018).

It is highly interesting to keep an eye on wrasses in areas where both wrasse fishery and aquaculture are a part of the environment and can affect local populations. Our study area in Hitra and Frøya are located within aquaculture production area 6 (Nærings, og fiskeridepartementet, 2017). In 2021, 2.3 million goldsinny wrasse, 600 000 ballan wrasse and 70 000 corkwing wrasse were fished in area 6. (Grefsrud *et al.*, 2023).

In addition to the species presented above, some more species which were observed will be examined in this study. Elasmobranchs like spiny dogfish (*Squalus acanthias*) and thornback ray (*Raja clavata*) are vulnerable to overfishing because they are generally slow growing and have low fecundity (Dureil *et al.*, 2018). The spiny dogfish is classed as vulnerable (VU) by the IUCN Red List of Threatened Species, and the Norwegian red list (Hesthagen *et al.*, 2021a; IUCN, 2022). The thornback ray is not considered endangered or vulnerable on the Norwegian red list or the IUCN red list. Atlantic halibut (*Hippoglossus hippoglossus*) is another slow growing and late maturing species which is found in the study area. By the IUCN, this species is considered Near Threatened (NT), and by the Norwegian red list of species, it is considered Least Concern (LC) (Hesthagen *et al.*, 2021b; Munroe *et al.*, 2021).

Study aims and goals

This project has two main aims:

(1) Investigate small scale spatial distribution and species richness of fish in the marine ecosystems around Hitra and Frøya to further build the foundation of knowledge for ecosystem-based management strategies.

(2) Provide insight into size and abundance of fish species and how they relate to depth, temperature, wave exposure and current speed.

(3) Provide a point of comparison by which to compare future abundance, size, and distribution within fish communities in the study area, to determine possible effects of future environmental change or marine protection in the study area.

To achieve this, data collected by stereo-BRUVs in the Active Management project will be interpreted and analysed as generalised linear mixed effects models (GLMMs). This project can in future act as a baseline of the fish community before an MPA is implemented and can possibly be incorporated into a BACI- study of the effects of an MPA, or a time series of the area.

2. METHODS

2.1. Study site and sample design

The study area is situated in Trøndelag county in the coastal waters surrounding the islands Hitra and Frøya, including the Froan nature reserve. The area has a varied marine nature ranging from sheltered fjords and bays to the exposed open ocean of the Norwegian Sea. Habitats vary between kelp forests, rocky bottom, muddy flats, and areas of shell sand habitats. The study area also has a varied topography with both shallow and deep areas. A map of the study area can be viewed in Figure 2.

The stereo-BRUV data used in this master project were collected in 2019 and 2020. The study area was split into eight smaller areas (1-8) of varying size. In each area, between 3 and 13 clusters of 14-16 stations in each cluster were randomly placed at depths between 5-40 m (Figure 2). The stereo-BRUVs were not equipped with lights and all stations were plotted between 5-40 m depth to ensure cameras would have enough natural light for the video to be clear. Each station was given a unique code which points to the area and cluster the station is a part of, as explained by Figure 1. The sample design was given this nested structure so that any dependence in the measured data caused by the geographical closeness between stations in the same cluster could be accounted for in the statistical models.

Note that Figure 1 does not show all 8 areas and 228 stations, but gives an overview of the data structure, exemplified by 12 stations divided between four clusters and two areas.

In the survey, stations for each field day were selected by a randomised draw from a pool of pre-plotted sample points and sample areas were chosen within the limits given by the weather conditions (Bull, 2019). From a total of 1110 pre-plotted sample points, 275 stations were sampled within this two year period; 147 stations from areas 1, 2, 3, 4 and 6 were sampled from May 2nd – May 11th in 2019 (Bull, 2019), and 128 stations from areas 2, 5, 7 and 8 were sampled between May 19th – May 26th in 2020. Out of these, 12 stations, all within area 2, were sampled both years. A total list of stations, clusters, areas, and coordinates can be viewed in Appendix 2, Table A1. A map showing all stations can be viewed in Appendix 1: Figure A3.

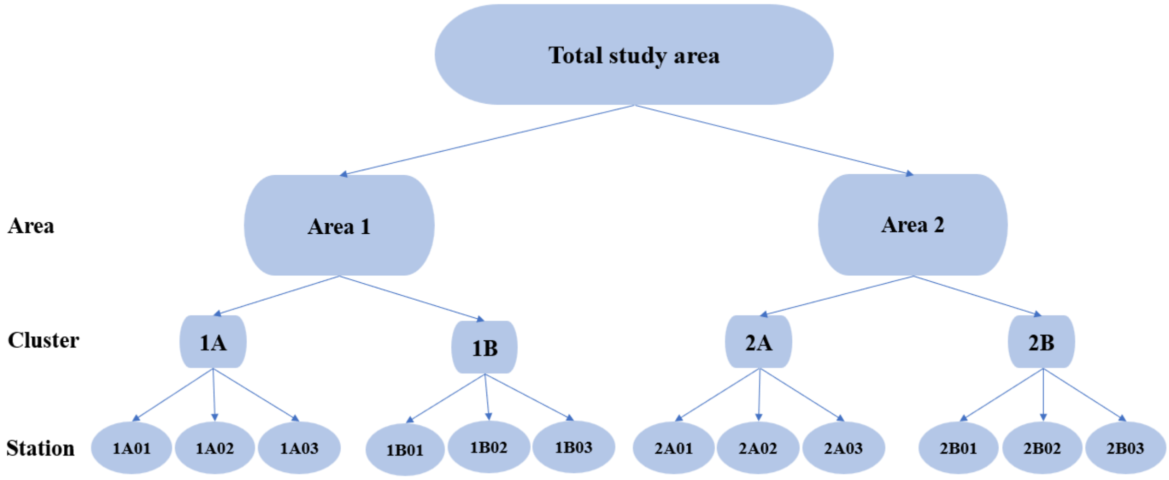


Figure 1: Schematic illustration with simplified structure showing sampling design by two of the eight areas. Each station is referred to with a unique combination of numbers and letters. First, a number which reflects the area the station is located in. Then, a letter which refers the cluster within this area where the station is located. And lastly, a number so the stations within clusters can be told apart. Stations within a cluster are close to each other geographically and cluster is counted as a random effect in the statistical models.

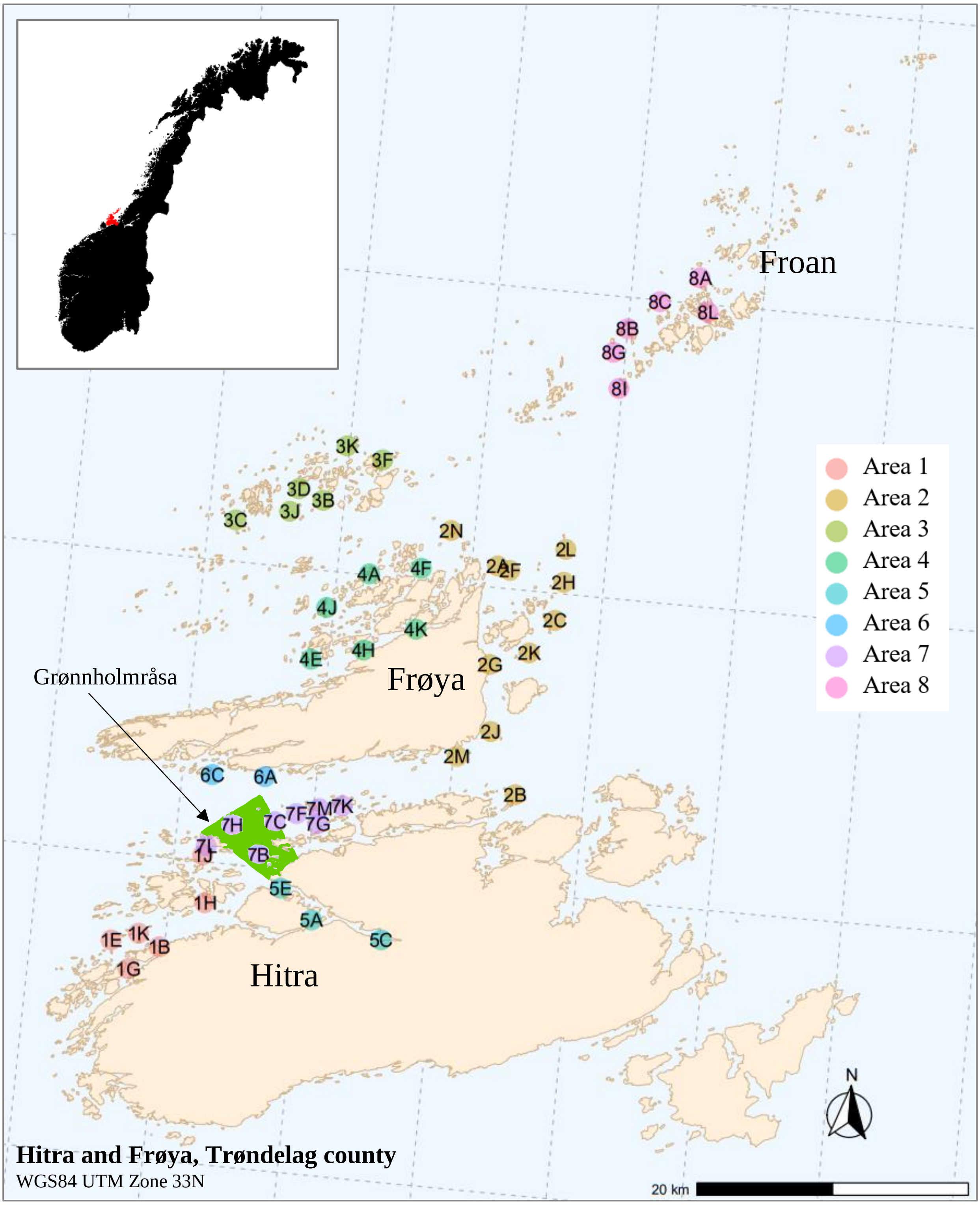


Figure 2: Map of the study area around Hitra and Frøya, including Froan nature reserve. Every cluster is marked with a circle, with the colour of the circle indicating the sub-areas (1-8) within the larger study area. Clusters consist of 1-10 stations in close proximity.

2.2. Data collection using stereo-BRUVs.

Video material was collected in 2019 and 2020 using stereo Baited Remote Underwater Video systems (stereo-BRUVs). A stereo-BRUV is a rig containing two water-tight camera houses and a bait which can be lowered onto the seafloor to capture marine life on video (Figure 3). The camera houses fit GoPro cameras and are spaced 0.7 m apart on the rig with an 8 degrees inward converging angle. This overlap is what allows three-dimensional information to be extracted in the analysis, making it a stereo-video system. The camera rig is also equipped with a bag of bait at the end of a 1.5 m rod which is in the field of view of both cameras to motivate fish in the nearby area to approach the bait and get caught on camera. In this study, chopped up frozen herring (*Clupea harengus*) was used as bait (Bull, 2019). In addition to this, a CTD-logger was attached to each of the stereo-BRUVs to measure temperature and depth at each station.

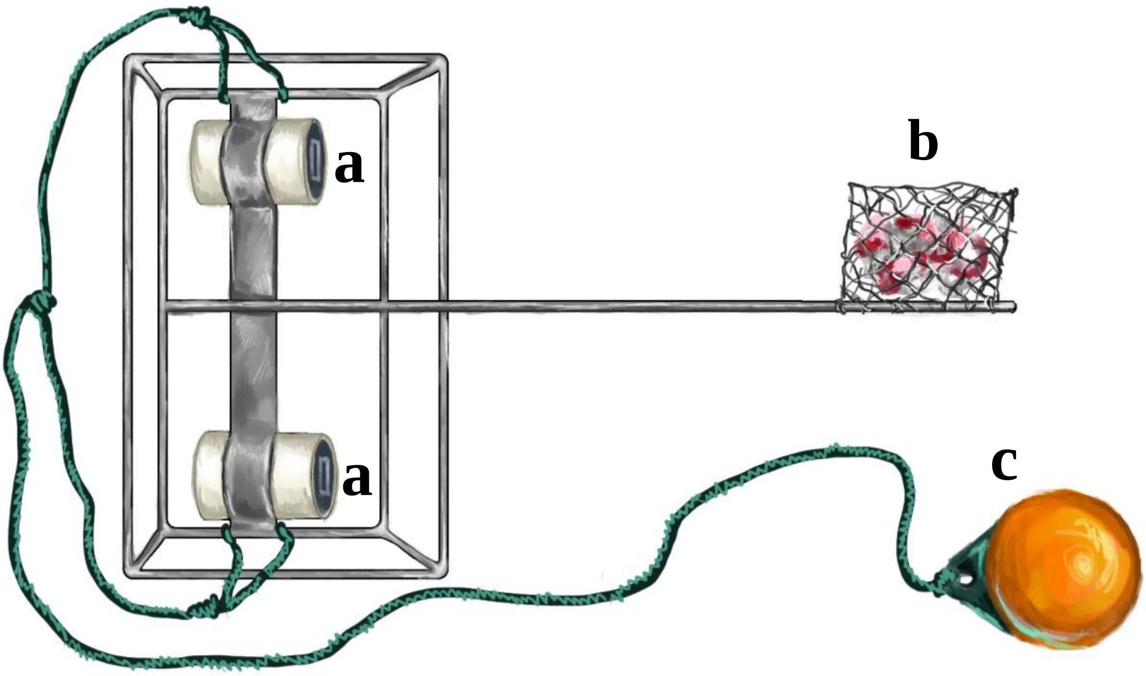


Figure 3: Illustrated stereo-BRUV setup, viewed from above. Steel rig with **(a)** cameras in waterproof housing, **(b)** bait in bag in front of the cameras **(c)** buoy connected to the rig by a rope. The rope would normally be longer than indicated in the figure. *Illustration: Astrid Winnberg Skoge.*

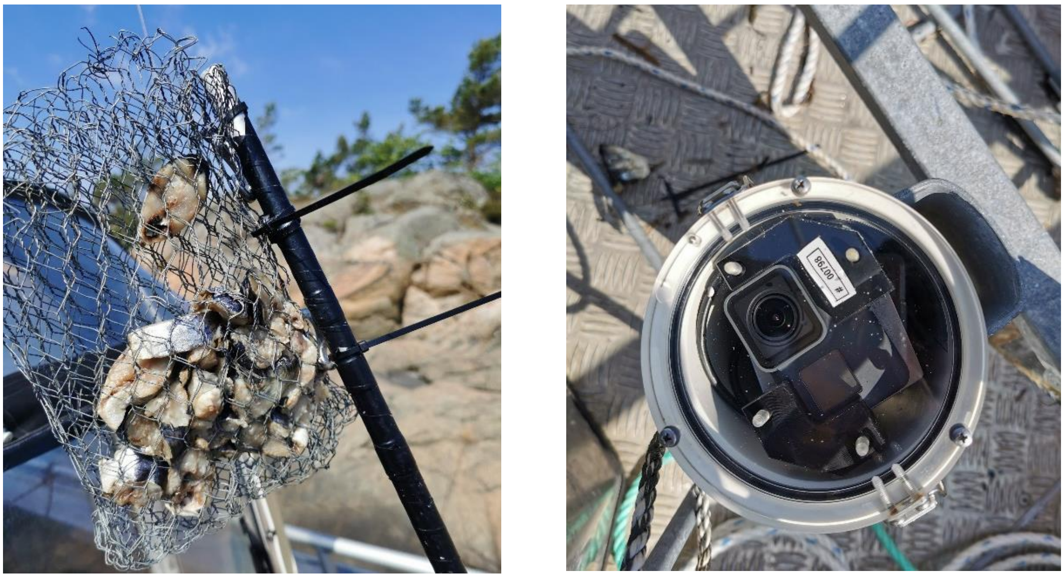


Figure 4: Stereo-BRUV details. **(a)** Chopped up herring was used as bait. **(b)** Go-pro cameras were used in this stereo-BRUV setup. *Photo: Astrid Winnberg Skoge.*

To record videos, the ship travelled to the pre-determined destination, fresh bait was placed in the bait bag and the two GoPro cameras connected to power banks for extended battery time were placed in the watertight housing and started recording. A sheet of paper showing the details of the location, date and weather was shown in front of each of the cameras while they were filming to make sure the video could be traced back to the original position and station. The researcher clapped once in the view of both cameras to ensure synchronisation. The rig was then carefully lowered onto the seafloor by a rope, lifted 1-2 meters, and slowly lowered onto the seafloor again to make sure the rig was standing upright and stable on the surface. The rig was then marked with a buoy and left to record for at least 60 minutes. Six stereo-BRUVs were lowered consecutively, and then retrieved after an hour of each individual deployment between 3-5 times each field day. At the end of the field day, video material was collected from the GoPro cameras and downloaded to a hard drive.

2.3. Video analysis

Stereo-videos from stereo-BRUVs were analysed using the EventMeasure software by SeaGis (SeaGIS, 2020), which allows for viewing both the right and left camera at the same time. Initial analysis and synchronisation of most videos from the 2019 dataset were done by Bull (2019) according to the methods described by Bull (2019). Re-analysis of those videos and full analysis of the rest of the 2019 videos were done by me for this master thesis using the following method, based on Bull (2019) and Langlois *et al.*, (2020).

Videos and camera files were imported into EventMeasure and both were stopped at the frame when the researcher is clapping. They were then synchronised, and as the left video frame was opened and fast forward until the rig hit the seafloor, the other video would follow so they were always showing the same moment in time. Analysis started when the rig had landed on the seafloor and any sand or mud disturbed by the landing of the stereo-BRUV had settled so the view was clear. Analysis was done in the left camera when possible. In cases where the left camera was covered in algae or for some reason had not recorded, analysis was done in the right camera. Videos were excluded if analysis was not possible due to technical problems, camera malfunction, mislabelling of videos, severe macroalgae coverage of both cameras, and the rig landing upside down. In 2019 and 2020 respectively, 20 out of 148 stations, and 29 out of 129 stations were excluded from analysis for these reasons.

All fish that appeared were identified to species based on physical characteristics like colour patterns, silhouettes, the shape of the sideline and the bite. In the case of Gadidae, a family in which several species have similar silhouettes, behavioural characteristics such as movement patterns and swimming style were used to help with the identification. When species identification was not possible, the observed animal would be determined to either genus or family.

Abundance of each observed species per video was recorded in EventMeasure as MaxN per video. EventMeasure defines MaxN by the maximum number of individuals of the same species that are visible within a single video frame at any point of a video (Langlois *et al.*, 2020). Any frame containing the highest number of individuals of a species within the video will automatically overwrite previous abundances that were registered for this species in this video, and only this MaxN is included when the MaxN data is downloaded. This way of measuring abundance ensures abundances are not over-estimated by individual fish appearing in front of the camera several times.

Length measurements were done only on individuals present at the MaxN frame. Although MaxN was registered when all individuals were in frame at the same time, this frame was not always ideal for measurement. Ideally, fish were measured when close to the middle of the frame, showing their lateral side so both the tip of the snout and the tip of the tail was visible in both cameras. This did not always happen at the exact frame MaxN was registered. A fish could be measured at any time from its appearance in the field of view to its disappearance out of the field of view as long as the MaxN measurement was done between these two time points.

Bony fish were measured from the tip of the snout to the shortest part of the caudal fin, this is known as the fork length (FL). Sharks and rays were measured from the tip of the snout to the tip of the longest part of the caudal fin, also known as total length (TL). Figure 5 shows length measurements for different groups of fish.

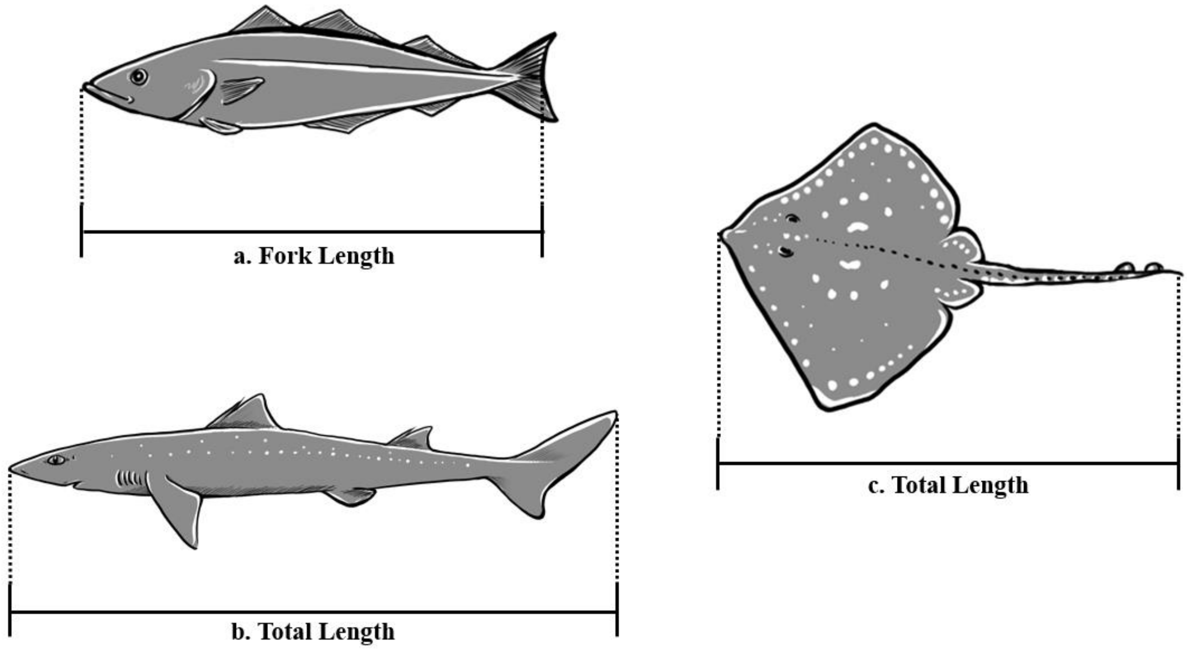


Figure 5: Length measurements for **(a)** bony fish (fork length), **(b)** sharks (total length), and **(c)** rays (total length). *Illustration: Astrid Winnberg Skoge.*

2.4. Environmental variables

Temperature and depth readings were recorded at the seafloor level by the sensors of the CTD attached to the stereo-BRUV rig. The environmental variables wave exposure at the sea floor (WE), and bottom current speed (BC) were provided by the Institute of Marine Research. Wave exposure at seafloor were calculated based on wave height given by the state-of-the-art, open-source wave model SWAN, which is developed at Delft University of Technology (http://swanmodel.sourceforge.net), using a grid model for the Smøla and Frøya area with 200m x 200m horizontal resolution. Calculations were similar to what was demonstrated by (van Son *et al.*, 2020). Ocean current speed were given by long-term median values from the main hydrodynamical model system for the Norwegian coastal zone run at the IMR (Asplin *et al.*, 2020). Bottom current speed was calculated from hourly values to resolve the semi-diurnal tidal motion which can be important in straits and fjords along the Norwegian coast.

2.5. Statistical analysis

Data were downloaded as CSV-file from EventMeasure, formatted in Excel and then imported to R. Analyses were done in RStudio using R version 4.2.1 (R Core Team, 2022). Before models were fitted, the data were thoroughly explored to avoid collinearity, overdispersion due to outliers and other statistical errors (Zuur and Ieno, 2016). The collinearity between variables was explored using scatterplots and correlation coefficients. No correlation was found (*Appendix 1: Figure A4*). Outliers were detected using boxplots and Cleveland dotplots, as suggested by (Zuur, *et al.*, 2010). The data were visualised using mainly the *ggplot2* package in R (Wickham, 2016).

Using the *lme4* package in R (Bates *et al.*, 2015), generalised linear mixed effects models (GLMM) for species richness and abundance were fitted with a Poisson distribution, cluster as a random effect and WE, BC, Temperature and Depth as fixed effects. Because different stations and areas were explored in the different years, Year was not used as an explanatory variable as any effect of year could cloak the effect of current, temperature, depth, exposure that may occur due to differences between the locations being surveyed in the different years.

$$Abundance = WE + BC + Depth + Temperature + (1|cluster), family = poisson$$

$$Richness = WE + BC + Depth + Temperature + (1|cluster), family = poisson$$

Poisson models were validated by checking for overdispersion and by observing the structure of the simulated residuals provided by the *DHARMa* package in R (Hartig, 2022). In the cases where a Poisson model was overdispersed, a negative binomial model was fitted instead and validated the same way. In the case of the Species richness model, the *DHARMa* test indicated slight underdispersion in the residuals, which is something that can happen if the model is too complex or the data is zero-inflated (Hartig, 2022). Underdispersion can cause p-values to be too high, and under-estimate the significance of the effects in the model. In this case, there were no zeroes in the data and model structure was based on the sampling structure, so the model was not changed.

Lengths were modelled using a linear nested mixed effects model with a normal distribution and station nested within cluster as a random effect and WE, BC, Temperature and Depth as fixed effects. These models were done using the *nlme* package in R (Pinheiro, Bates and R Core Team, 2023).

$$Length = WE + BC + Depth + Temperature + (1|cluster/station)$$

In some cases, there were less data than required by the nested model. In these cases, the model was simplified, either dropping the nested structure and keeping the random effect or dropping the random effect altogether if there were few stations with length measurement per cluster for certain species. These models were made using the *nlme* package, or base R for the simple linear model.

$$Length = WE + BC + Depth + Temperature + (1|cluster)$$

$$Length = WE + BC + Depth + Temperature$$

Length models were validated by checking normality of the residuals by plotting the theoretical quantiles against the sample quantiles (QQ-plot) and plotting the residuals against the values fitted by the model (residuals vs fitted plot), as outlined by Zuur and Ieno (2016).

3. RESULTS

A total of 277 stations were sampled from 2019 to 2020. Out of these, 49 stations were excluded due to technical problems, camera malfunctioning, rig landing upside down, or obscured vision by either darkness or kelp covering the camera. A total of 228 hours of stereo-BRUV videos have been analysed and included in the final dataset. A table of all stations including coordinates, depth, temperature, WE and BC can be found in Appendix 2, Table A1.

3.1. Variation in environmental factors

In the stations sampled in this study, depth ranged between 5 m and 37 m. A similar range of depths were represented in all areas of the larger study area, with mean values around 20 m for each area (Figure 6). Temperature ranged between 4.5 °C and 10.0 °C, with a peak in the normal distribution at around 7 °C. Most stations had temperatures between 6.5°C and 8 °C. There was little variation within areas except for area 1, 3 and 4. In area 1, there seemed to be more stations with higher temperatures. This is the area which is closest to the mainland, and it is quite sheltered (Figure 6). The high temperature measurement in area 3 and the low temperature measurement in area 4 might be due to sampling errors, but I chose to keep them because they may also be caused by natural variation in the environment. According to the exposure model, Wave Exposure at the seafloor (WE) in the study area ranged from 0.000 m s^{-1} to 0.687 m s^{-1} with the highest exposure in areas 8 and 3, which are the outermost island groups including Froan nature reserve (Figure 6). WE was lowest in area 5 which was in a narrow fjord, and area 4 which was quite sheltered by the topography of the area. According to the hydrodynamical ocean current model, bottom current speed (BC) ranged between 0.007 m s^{-1} to 0.225 m s^{-1} throughout the study, with most values landing between 0.03 m s^{-1} and 0.8 m s^{-1}. The strongest bottom currents are found in areas 2, 3, 8 and 7 (Figure 6).

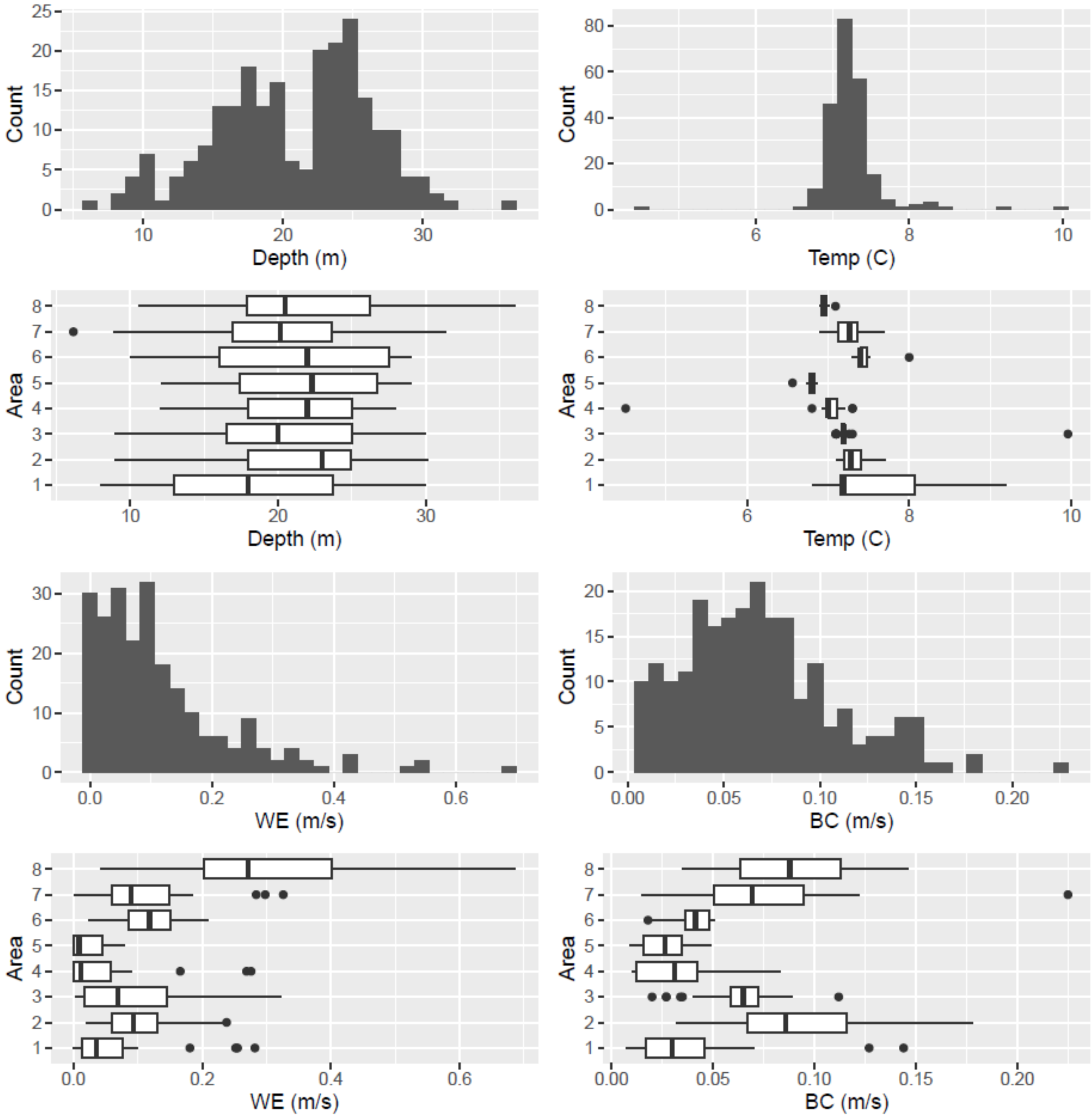


Figure 6: Distribution of environmental variables depth, temperature, wave exposure (WE) at seafloor and current speed (BC) at the bottom. The histograms show the general distribution of these environmental variables throughout the survey. The boxplots show how the variables are distributed across the smaller sub-areas 1-8 of the study area.

3.2. Species richness and distribution of abundance

A total of 22 fish species were observed in the survey. Atlantic cod (*Gadus morhua*) was observed most of all, at 174 stations, or 76% of all stations (Figure 7C). Species were defined as common if they were observed at 25 or more stations. Common species were pollack (*Pollachius pollachius*), saithe (*Pollachius virens*), poor cod (*Trispoterus minutus*), haddock (*Melanogrammus aeglefinus*), two-spotted goby (*Pomatoschistus flavescens*), common ling (*Molva molva*), goldsinny wrasse (*Ctenolabrus rupestris*), Atlantic halibut (H*ippoglossus. Hippoglossus*) and cuckoo wrasse (*Labrus mixtus*). Species richness ranged from one to seven observed species at each station. Species richness of three species per station was the most common observation in areas 1,2 and 3, while two species per station was most common in stations 7 and 8. In area 4, four species was the most common and in area 6, five species was most common. Note in Figure 7A that areas 8, 3 and 2 were the only ones with observations of seven species in one station. The modal value for species richness throughout the dataset was 2 species in 2020 and 3 species in 2019 (Figure 7B). Bars representing 2020 data are generally lower than bars representing 2019-data, reflecting the smaller total number of stations in 2020 (n=98) compared to 2019 (n=147). Stations 2N14, 2N90, 2M08, 2K08, 2B05, 2A15 and 2A12 were sampled in both 2019 and 2020. Cluster 2N was the cluster which had the most total fish abundance across stations and species (Figure 8). A linear mixed effects model with a Poisson distribution suggested there was no significant effect of wave exposure at sea floor (WE), bottom current speed (BC), temperature, depth, or year on the number of fish species observed at each station, using a significance threshold of $p < 0.05$ (*Appendix 2: Table A2*). Some invertebrate species were also recorded in the survey, but they will not be discussed here as fish were the focus of this project.

Some species were consistently present in most clusters (Figure 8). Pollack was observed at every cluster, except 5A. Cod were observed at 46 out of 48 clusters and were absent only at clusters 5C and 7M, both which had only one station (Appendix 2: Table A1). The poor cod (*Trispoterus minutus*) was observed at 31 clusters, representing every area. The common ling (*Molva molva*) was also observed throughout most of the study area (27 clusters), only missing from area 5. Goldsinny and cuckoo wrasses were observed at respectively 25 and 31 clusters and were both absent in all of area 5. Ballan wrasse was observed in area 2, 3, 4 and 7, while corkwing wrasse was only seen in 7K and 8C. Two less common wrasses, the rock cook (*Centrolabrus exoletus*) scale-reyed wrasse (*Acantholabrus palloni*) were both seen in cluster 2M. In fact, in cluster 2M all wrasses were observed, making it the most diverse cluster in terms of Labridae. The two-spotted goby (*Pomatoschistus flavescens*) was seen in most clusters but was absent from areas 5 and 6.

Some species which were observed rarely in the study were herring (*Clupea harengis*) which was only seen once at 8G, spiny dogfish (*Squalus acanthias*), which was seen in 5 % of stations but mainly in area 8, and cusk (B*rosme brosme*) observed in 7H and 8C.

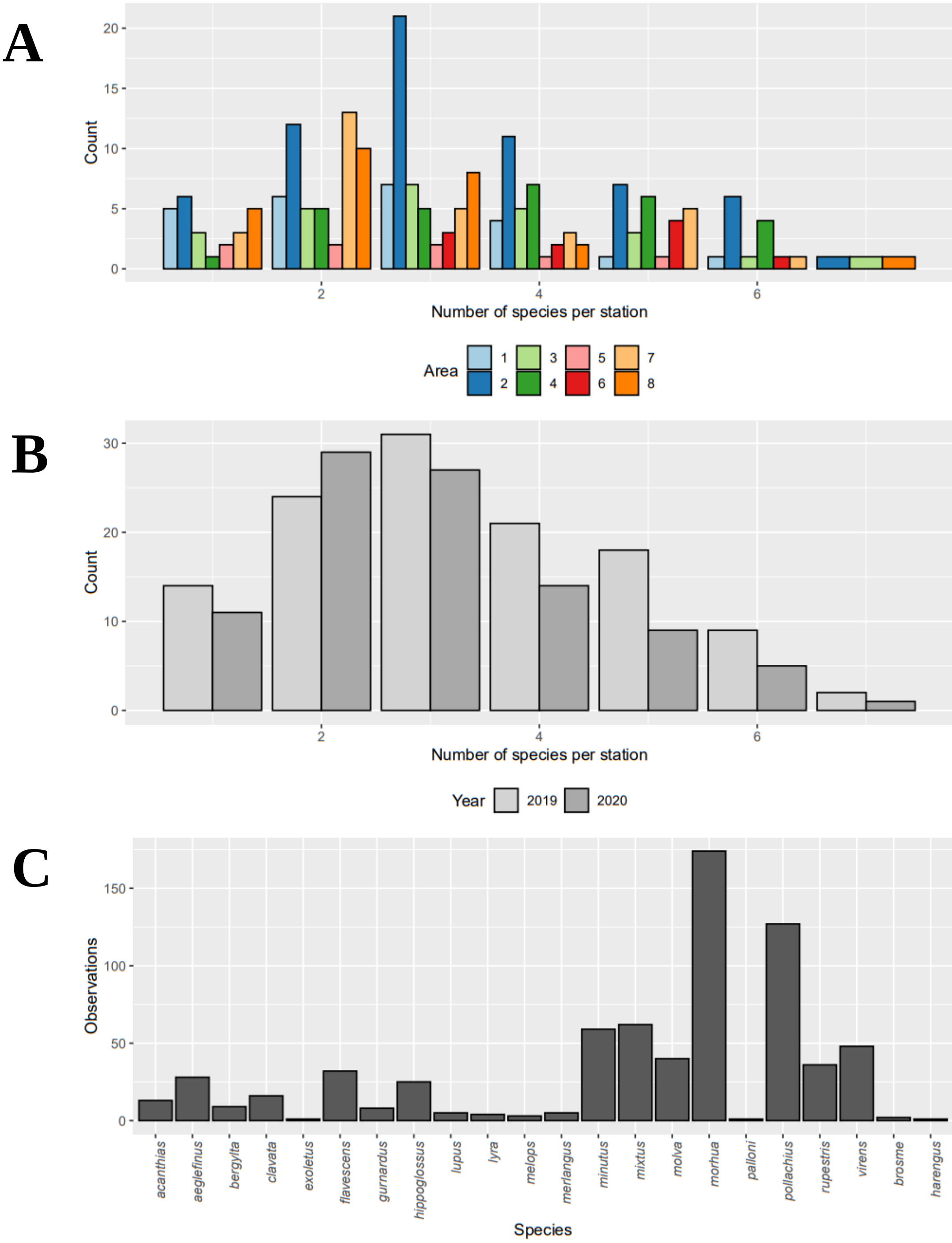


Figure 7: A) Distribution of fish diversity, defined as number of fish species observed per station, for the different areas within the study area. Bar height represents the number of stations (count) within an area in which a given number of species, defined by the x axis, was observed. Areas are represented by different colours. **B)** Distribution of fish diversity defined as number of fish species observed per station in 2019 and 2020. Bar height represents the number of stations in either 2020 (dark grey) or 2019 (light grey) in which a given number of species, defined by the x axis, were observed. **C)** Total number of observations of all fish species observed in this survey. This barplot does not reflect the abundance of the different species within a station, but the number of individual stations where one or more individuals of the species were observed. All plots are made in R using the ggplot2 package.

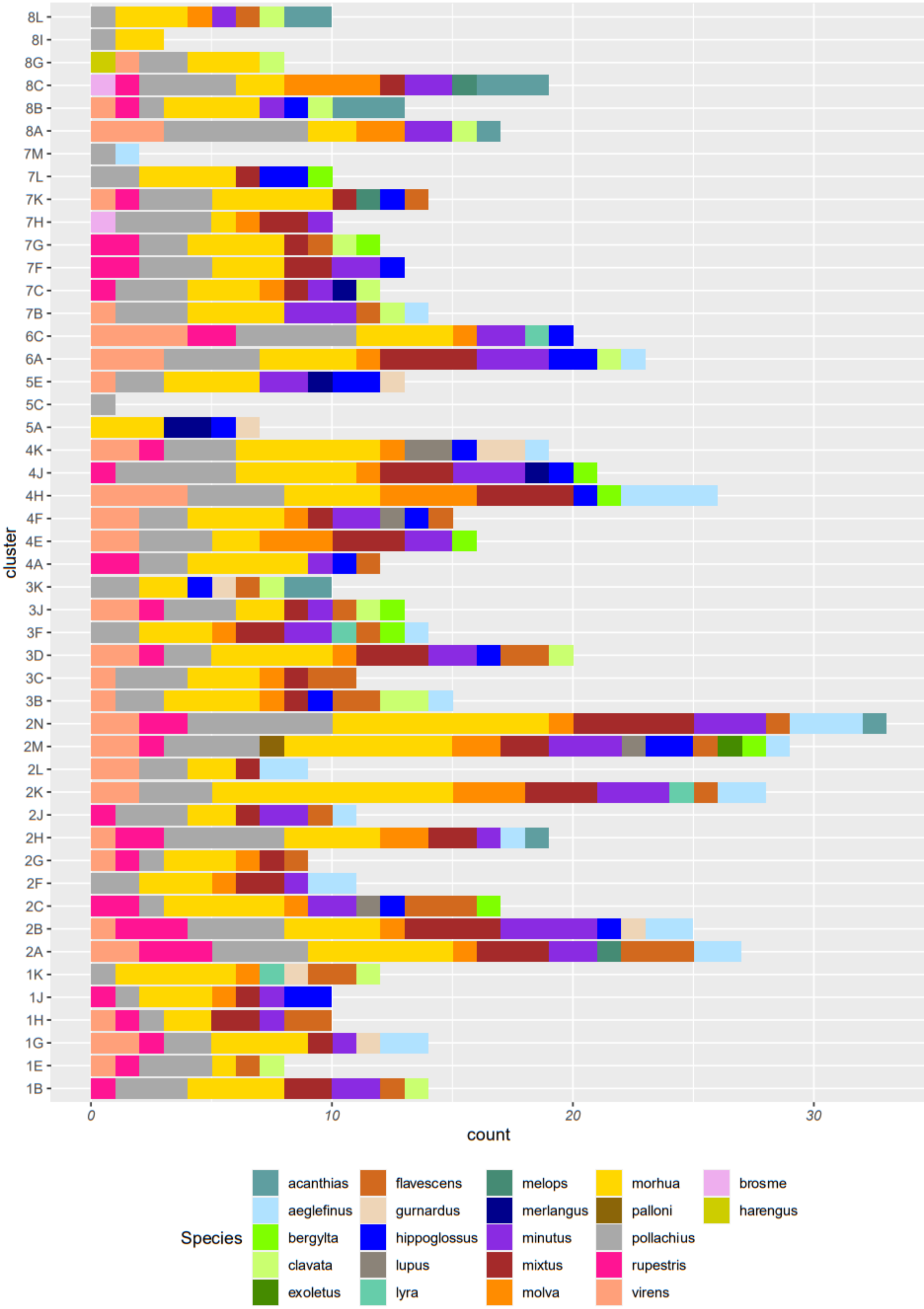


Figure 8: Fish species distribution in the different clusters of this survey. The colour represents the species observed. Length of the coloured field represents the number of stations within the cluster at which this species was observed.

3.3. Effect of environmental factors on fish abundance

For the sake of statistical weight, abundance models were only made for species represented in at least ten separate stations. The survey target species, Atlantic cod (*Gadus morhua*), goldsinny (*Ctenolabrus rupestris*), ballan (*Labrus bergylta*) and corkwing (*Symphodus melops*), thornback ray (*Raja clavata*), Atlantic halibut (*Hippoglossus hippoglossus*) and spiny dogfish (*Squalus acanthias*) were observed at 174, 36, 9, 3, 16, 25, and 13 stations, respectively. Six wrasse species were registered in this survey: goldsinny, cuckoo, ballan (*Labrus bergylta*), corkwing (*Labrus melops*), rock cook (*Centrolabrus exoletus*), and scale rayed wrasse (*Acantholabrus palloni*). Out of these, only goldsinny and cuckoo wrasse were observed at more than 10 different stations, and models were fitted for these two only. Cuckoo was included even if it is not targeted by fisheries because it was the most abundant wrasse.

Another aim of this study was to look at species distribution in general. Two commonly observed fish species, pollack (*Pollachius pollachius*) and saithe (*Pollachius virens*) were included in the analysis. They were observed at respectively 127 and 48 stations. The commonly observed species poor cod (*Trispoterus minutus*), haddock (*Melanogrammus aeglefinus*), two-spotted goby (*Pomatoschistus flavescens*) and ling (*Molva molva*) were not included in the analysis due to time constraints.

Table 1: Results of the statistical models fitted to the abundance data for Atlantic cod (*Gadus morhua*), goldsinny (*Ctenolabrus rupestris*), cuckoo (*Labrus mixtus*) spiny dogfish (*Squalus acanthias*) Atlantic halibut (*Hippoglossus hippoglossus*), thornback ray (*Raja clavate*), pollock (*Pollachius pollachius*) and saithe (*Pollachius virens*). Presence is defined as the percentage of all stations (228 stations) where the species was observed. Observations is the exact number of stations in which the species was observed. In the case of saithe and pollack, the Poisson models were overdispersed and negative binomial models were fitted instead. Effect sizes are not transformed, meaning an effect of 1 predicts and increase of 1 individual to the station abundance for an increase of 1 unit of the environmental variable. Significant associations (p<0.05) are highlighted with bold numbers.

Abundance																
Species	***Gadus morhua***				***Ctenolabrus rupestris***				***Labrus mixtus***				***Squalus acanthias***			
Presence (%)	76.3				15.8				27.2				5.7			
Observations	174				36				62				13			
	Effect	SE	Z	*p*	Effect	SE	Z	*p*	Effect	SE	Z	*p*	Effect	SE	Z	*p*
WE (ms^{1})	**-2.988**	**0.867**	**-3.324**	**<0.001**	-3.521	2.092	-1.669	0.092	-1.165	1.773	-0.657	0.511	**7.865**	**2.316**	**3.389**	**0.001**
BC (ms^{1})	-0.742	1.711	0.059	0.709	-1.636	4.184	-0.417	0.695	1.154	3.784	0.305	0.760	**18.56**	**9.063**	**2.048**	**0.039**
Depth (m)	**-0.027**	**0.012**	**-2.227**	**0.035**	**-0.075**	**0.028**	**-2.655**	**0.008**	0.040	0.025	1.603	0.109	0.106	0.060	1.748	0.080
Temp (°C)	0.074	0.169	0.570	0.667	**0.721**	**0.296**	**2.418**	**0.015**	0.392	0.302	1.298	0.194	-1.239	1.050	-1.180	0.239
Distribution	*Poisson*				*Poisson*				*Poisson*				*Poisson*			
Species	***Hippoglossus hippoglossus***				***Raja clavata***				***Pollachius pollachius***				***Pollachius virens***			
Presence (%)	10.96				7.02				55.70				21.05			
Observations	25				16				127				48			
	Effect	SE	Z	*p*	Effect	SE	Z	*p*	Effect	SE	Z	*p*	Effect	SE	Z	*p*
WE (ms^{1})	**-6.497**	**3.271**	**-1.985**	**0.046**	-0.709	3.174	-0.223	0.823	0.944	0.708	1.333	0.183	4.276	2.910	1.469	0.142
BC (ms^{1})	-0.852	5.547	-0.164	0.878	-10.09	9.414	-1.071	0.284	-2.154	2.109	-1.021	0.307	3.769	5.808	0.649	0.516
Depth (m)	0.002	0.038	0.057	0.968	0.079	0.055	1.424	0.155	0.013	0.015	0.857	0.392	**-0.100**	**0.040**	**-2.484**	**0.013**
Temp (°C)	0.036	0.516	0.066	0.944	-0.058	0.756	-0.077	0.939	0.259	0.205	1.264	0.206	-0.428	0.850	-0.503	0.615
Distribution	*Poisson*				*Poisson*				*Negative Binomial*				*Negative Binomial*			

Cod abundance was significantly associated with lower wave exposure at the seafloor (WE) (p<0.001) and at shallower depths (p=0.035). Abundance of goldsinny were significantly associated with shallower stations (p=008) and higher temperatures (p=0.015). Cuckoo abundance was not significantly associated with the environmental variables included in the survey. The Atlantic halibut (*H. hippoglossus*) was significantly associated with lower wave exposure (p=0.046). Abundance of the spiny dogfish (*Squalus acanthias)* was significantly associated with high wave exposure (p=0.001) and strong bottom currents (p=0.039). Both saithe and pollock sometimes occurred in great schools of >50 individuals, and these high abundance numbers caused overdispersion in the Poisson models, so negative binomial models were fitted instead to avoid type I errors. Saithe (*Pollachius virens*) was significantly associated with shallower depths (p=0.013). Pollack was not significantly associated with any environmental variable.

The models predict some trends for these fish species in the Hitra Frøya area:

(1) Higher abundances of cod, goldsinny and saithe can be found in shallower stations.
(2) Higher abundances of cod and halibut can be found in more sheltered locations with low wave exposure.
(3) Higher abundances of spiny dogfish can be found in stations with high wave exposure and high bottom current speed.
(4) Higher abundance of goldsinny will be found in higher temperatures.

3.4. Effect of environmental factors on fish length

Table 2: Results of the statistical models fitted to the length measurements of cod (*Gadus morhua*), goldsinny (*Ctenolabrus rupestris*), cuckoo (*Labrus mixtus*), pollock (*Pollachius pollachius*), saithe (*Pollachius virens*), and spiny dogfish (*Ctenolabrus rupestris*). Presence is defined as the percentage of all stations (228 stations) where the species was observed. Measurements indicate how many individual fish of the species were measured. Random effect show which random effects were considered in the mixed effects model. For species which had few instances of more than one measurement at the same station, station as a nested factor within was making the model unnecessarily complex and was removed. This is the case for the goldsinny wrasse (*Ctenolabrus rupestris*) and the Cuckoo wrasse (*Labrus mixtus*). Significant associations (p<0.05) are highlighted with bold numbers.

Lengths															
Species	***Gadus Morhua***					***Ctenolabrus rupestris***					***Labrus mixtus***				
Presence (%)	76.3					15.8					27.2				
Measurements (n)	238					20					61				
	Effect	SE	Df	*t*	*p*	Effect	SE	Df	*t*	*p*	Effect	SE	Df	*t*	*p*
WE (ms^1)	129.3	152.1	100	0.850	0.307	58.83	166.9	2	0.353	0.758	88.15	1.853	19	1.143	0.468
BC (ms^1)	-248.8	366.4	100	-0.679	0.470	13.18	281.9	2	0.047	0.967	**551.9**	**18.01**	**19**	**0.283**	**0.039**
Depth (m)	1.146	2.615	100	0.438	0.687	-1.090	2.668	2	-0.408	0.723	2.118	119.0	19	0.741	0.267
Temp (°C)	**77.81**	**38.56**	**100**	**2.018**	**0.049**	2.210	30.04	2	0.074	0.948	5.098	248.4	19	2.222	0.780
Random effect	*cluster/Station*					*cluster*					*cluster*				
Species	***Pollachius pollachius***					***Pollachius virens***					***S. acanthias***				
Presence (%)	**55.7**					**21.1**					5.7				
Measurements (n)	142					138					11				
	Effect	SE	Df	*t*	*p*	Effect	SE	Df	*t*	*p*	Effect	SE		*t*	*p*
WE (ms^1)	-4.168	154.4	44	-0.027	0.934	-196.6	200.6	9	-0.980	0.429	**22.33**	**7.681**		**2.906**	**0.034**
BC (ms^1)	372.8	330.4	44	1.128	0.261	-971.2	631.9	9	-1.537	0.118	-241.8	122.6		-1.972	0.106
Depth (m)	0.482	2.432	44	0.198	0.778	4.238	2.939	9	1.442	0.231	176.5	213.0		0.829	0.445
Temp (°C)	-9.009	45.21	44	-0.199	0.918	228.9	128.8	9	1.777	0.113	127.3	491.4		0.259	0.806
Random effect	*cluster/Station*					*cluster/Station*					*none* R^2=0.78, adjusted R^2=0.60				

Atlantic cod length was positively associated with temperature (p=0.049). Cuckoo wrasse length was positively associated with current speed (p=0.039). No significant associations were found between the environmental variables and length for goldsinny wrasse, saithe, and pollock.

There were not enough length measurements of Atlantic halibut, thornback ray or spiny dogfish for the mixed effects model to yield p-values, and for spiny dogfish, a simple linear model was fitted instead. For spiny dogfish, R^2>0.7 and adjusted R^2>0, which indicated an ok model fit, although residuals deviated slightly from normal distribution. Wave exposure had a significant positive association with length of spiny dogfish in this model (p=0.034).

For thornback ray and Atlantic halibut, the simpler linear models did not perform well in terms of explaining the variation (R^2=0.51, adjusted R^2<0.13 for thornback ray and R^2=0.092, adjusted R^2<0 for halibut) and fulfilling the model requirements for normally distributed residuals.

The models predict some trends for these fish size species in the Hitra Frøya area:

(1) Bigger cod can be found in warmer water.
(2) Bigger cuckoo wrasse can be found in locations with less current.
(3) Bigger spiny dogfish can be found in locations with higher wave exposure.

3.5. Spatial distribution of species

Atlantic cod (*Gadus morhua*)

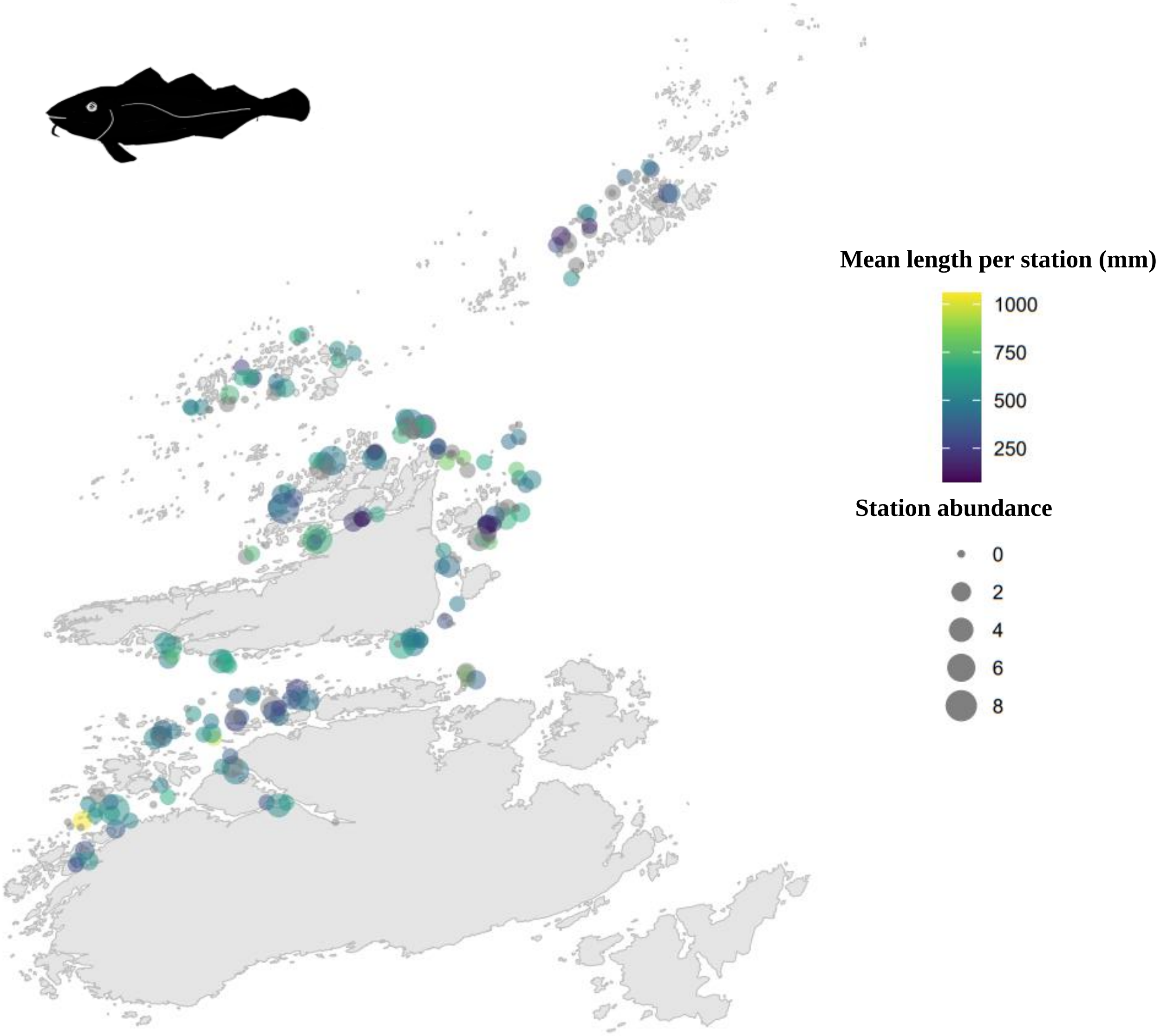


Figure 9: Map showing the abundance and mean length of cod (*Gadus morhua*) per station in the sample area. The abundance of cod is lower in the most exposed areas, 3 and 8, as predicted by the model. Grey dots with 0 abundance mark stations where cod was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Goldsinny wrasse (*Ctenolabrus rupestris*)

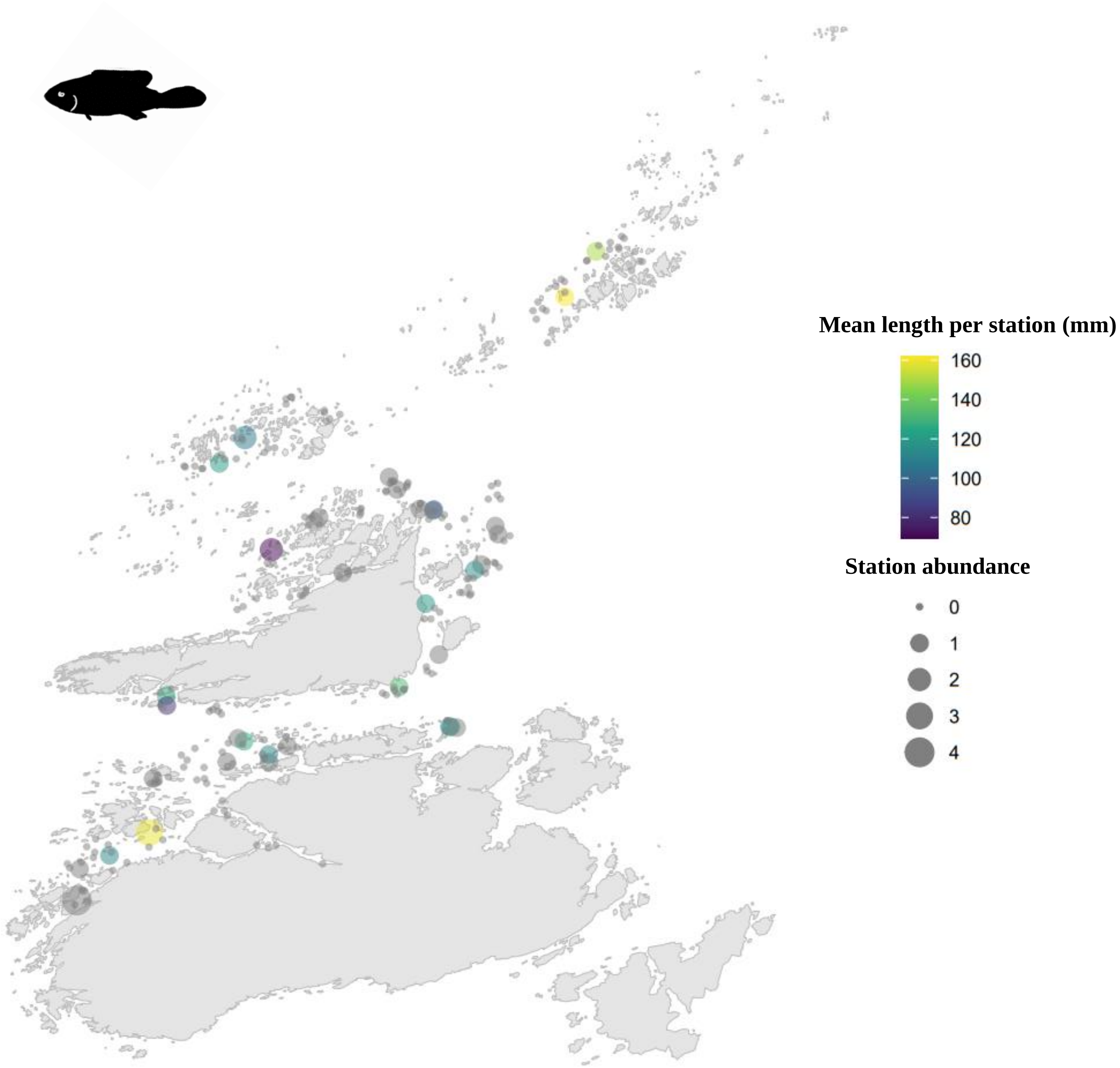


Figure 10: Map showing the abundance and mean length of goldsinny wrasse (*Ctenolabrus rupestris*) per station in the study area. Goldsinny wrasse was observed in all areas. The greatest goldsinny abundance was found in area 1. The model predicted higher abundance in shallow, warm water, and area 1 had the lowest median depth and highest temperatures (see figure 6). All observations from area 8 were in the high end of the size range recorded in this study. Grey dots with 0 abundance mark stations where the thornback ray was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Cuckoo wrasse (*Labrus mixtus*)

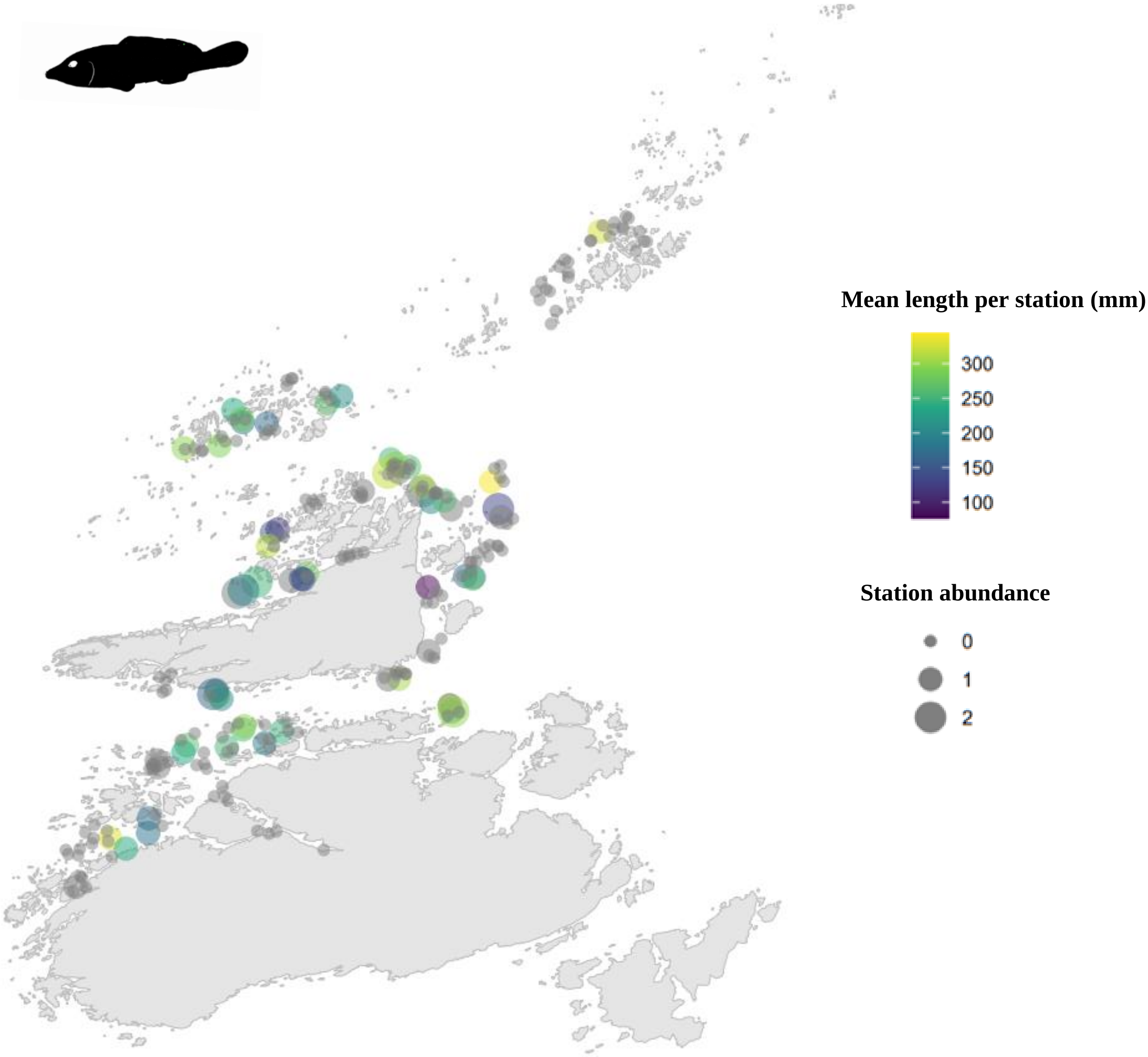


Figure 11: Map showing the abundance and mean length of cuckoo wrasse (*Labrus mixtus*) per station in the study area. Cuckoo wrasse was observed in all areas, but less in area 8. The abundance of cuckoo was highest in area 4, 6 and 2 and lengths were quite evenly spread out. Grey dots with 0 abundance mark stations where the thornback ray was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Spiny dogfish (*Squalus acanthias*)

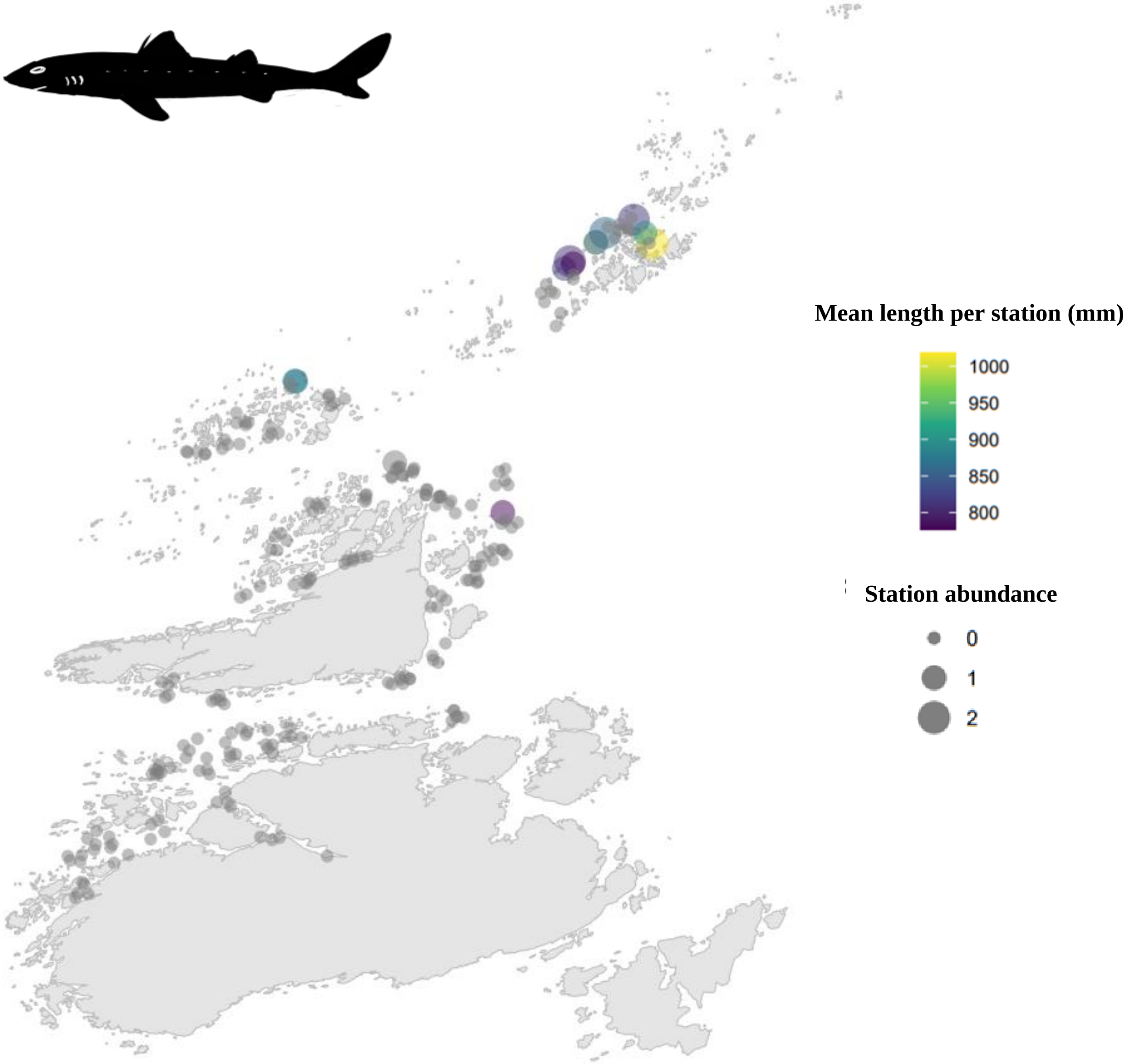


Figure 12: Map showing the abundance and mean length of spiny dogfish (*Squalus acanthias*) per station in the study area. The greatest observed abundance (2 individuals per frame) and mean length of spiny dogfish were in area 8, Froan nature reserve, which is the most exposed areas, as predicted by the models for length and abundance. Grey dots with 0 abundance mark stations where spiny dogfish was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Thornback ray (*Raja clavata*)

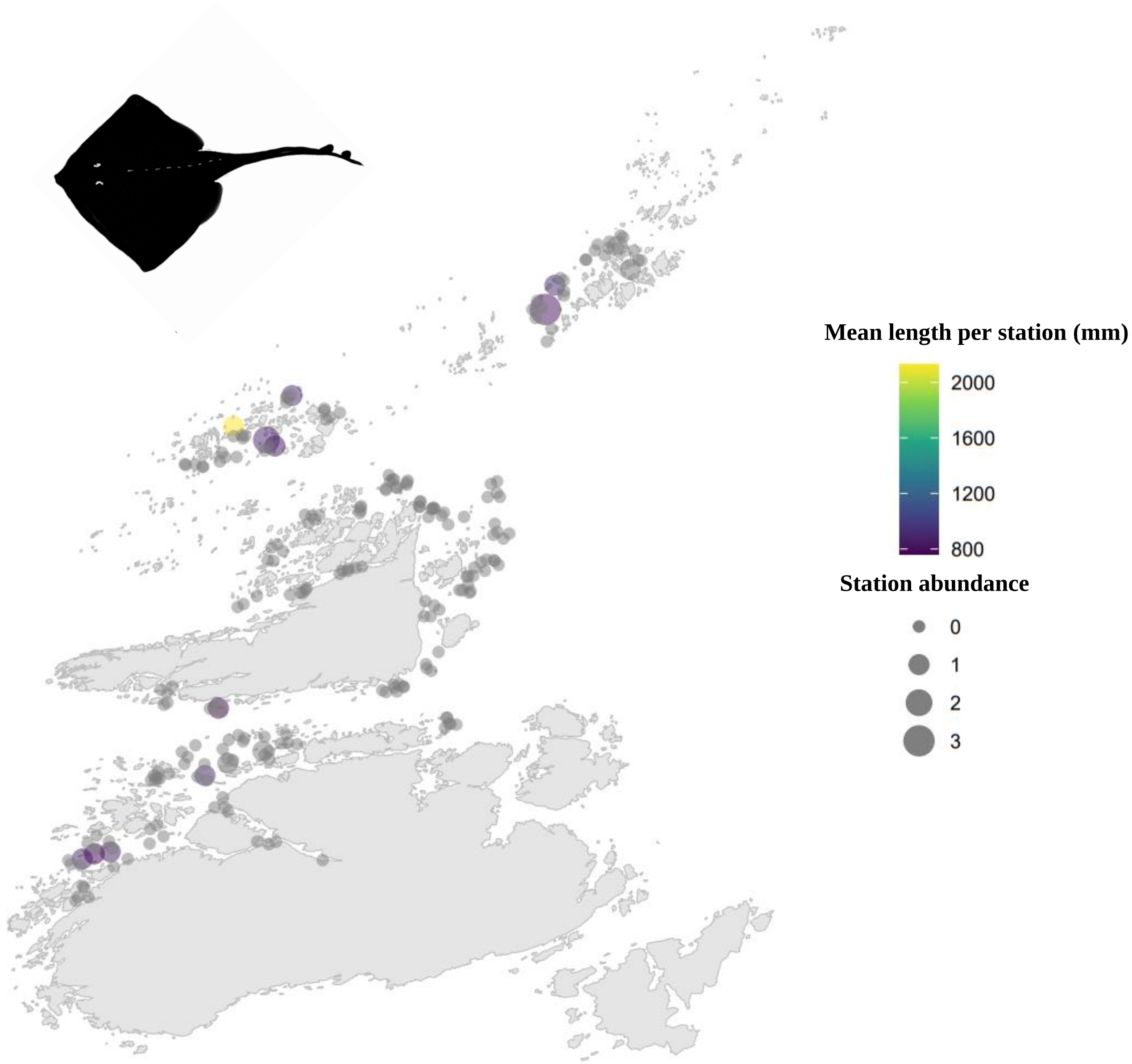


Figure 13: Map showing the abundance and average length of thornback ray (*Raja clavata*) per station in the study area. Thornback ray was observed in areas 1, 3, 6, 7 and 8. It was absent from areas 2, 4, 5 and 5. The abundance of thornback ray is highest in area 8 and the longest mean length individual was observed in area 3. Grey dots with 0 abundance mark stations where the thornback ray was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Atlantic halibut (*Hippoglossus hippoglossus*)

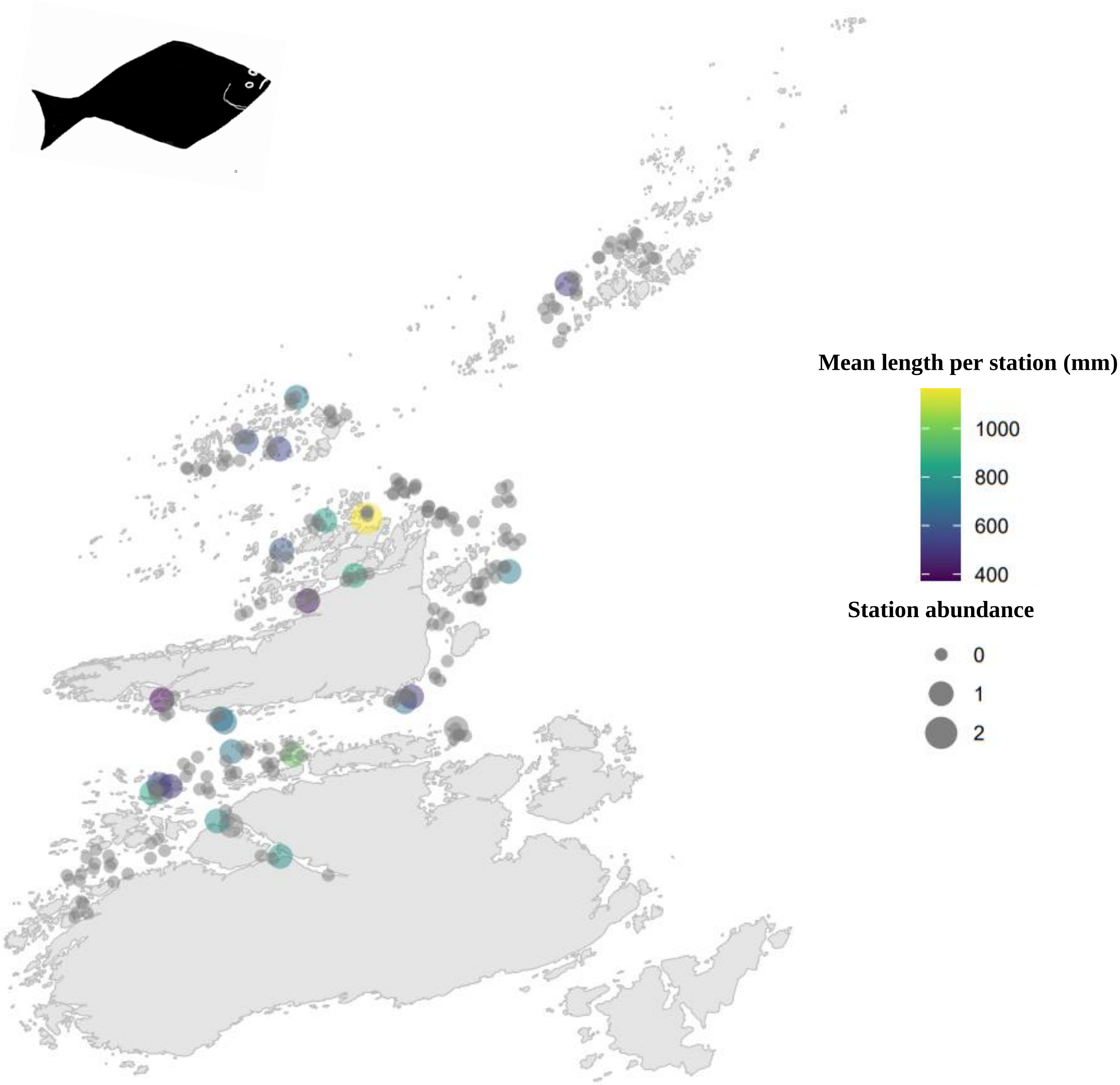


Figure 14: Map showing abundance and average length of Atlantic halibut (*Hippoglossus hippoglossus*) per station in the study area. Atlantic halibut was observed in areas 2, 3, 4, 5, 6, 7 and 8, but not in area 1. The greatest abundance (2 individuals) and longest individual (around 1178 mm) were recorded in area 4, at cluster 4F. Grey dots with 0 abundance mark stations where pollock was not observed. Grey dots with abundance above 0 are individuals that were not measured.'

Pollack (*Pollachius pollachius*)

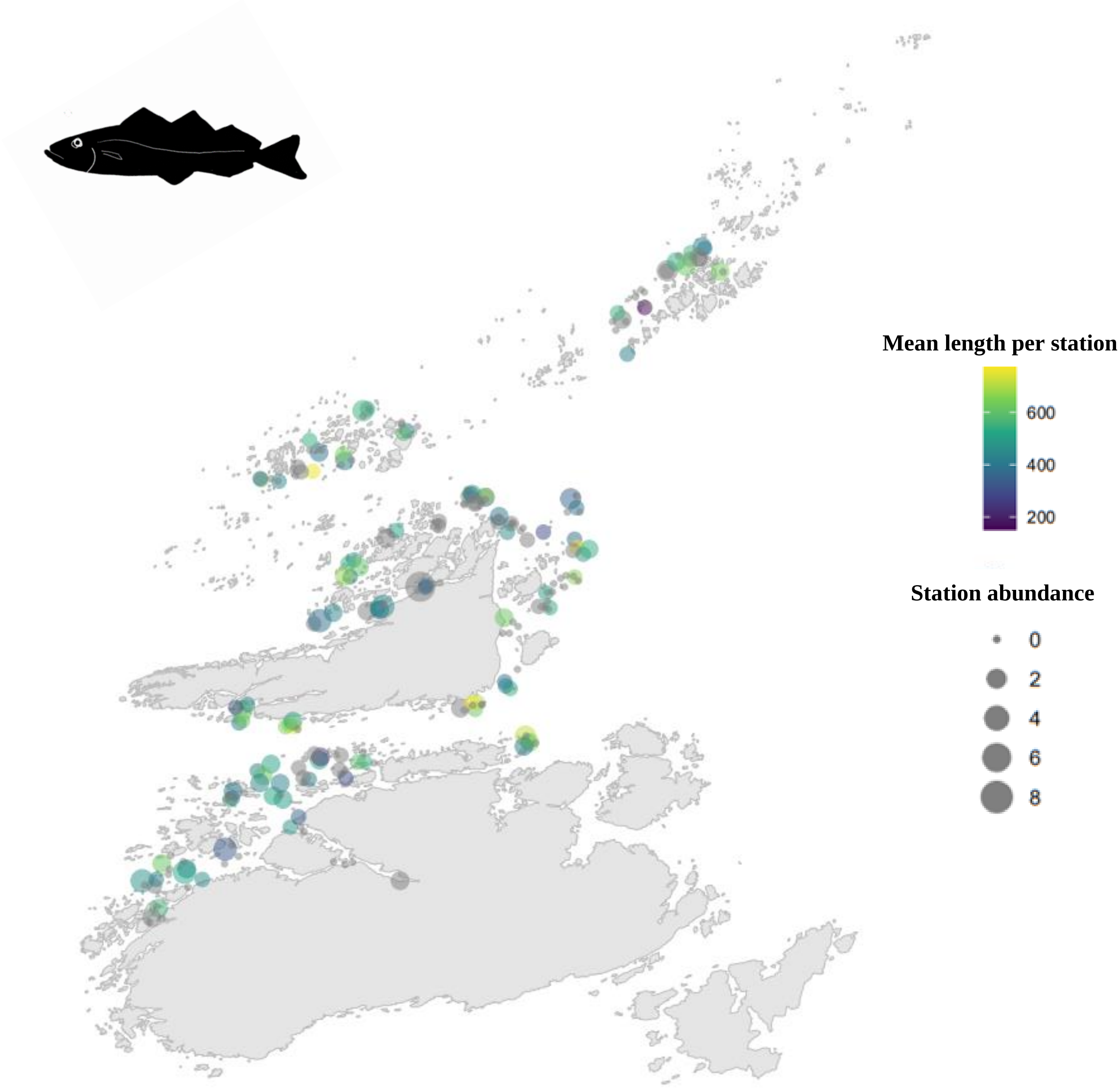


Figure 15: Map showing abundance and average length of pollack (*Pollachius pollachius*) per station in the study area. Pollack was observed all over the study area, and both size and abundance are quite evenly spread out. The greatest abundance (8 individuals) was observed at a sheltered location in area 4. Grey dots with 0 abundance mark stations where pollock was not observed. Grey dots with abundance above 0 are individuals that were not measured.

Saithe (*Pollachius virens*)

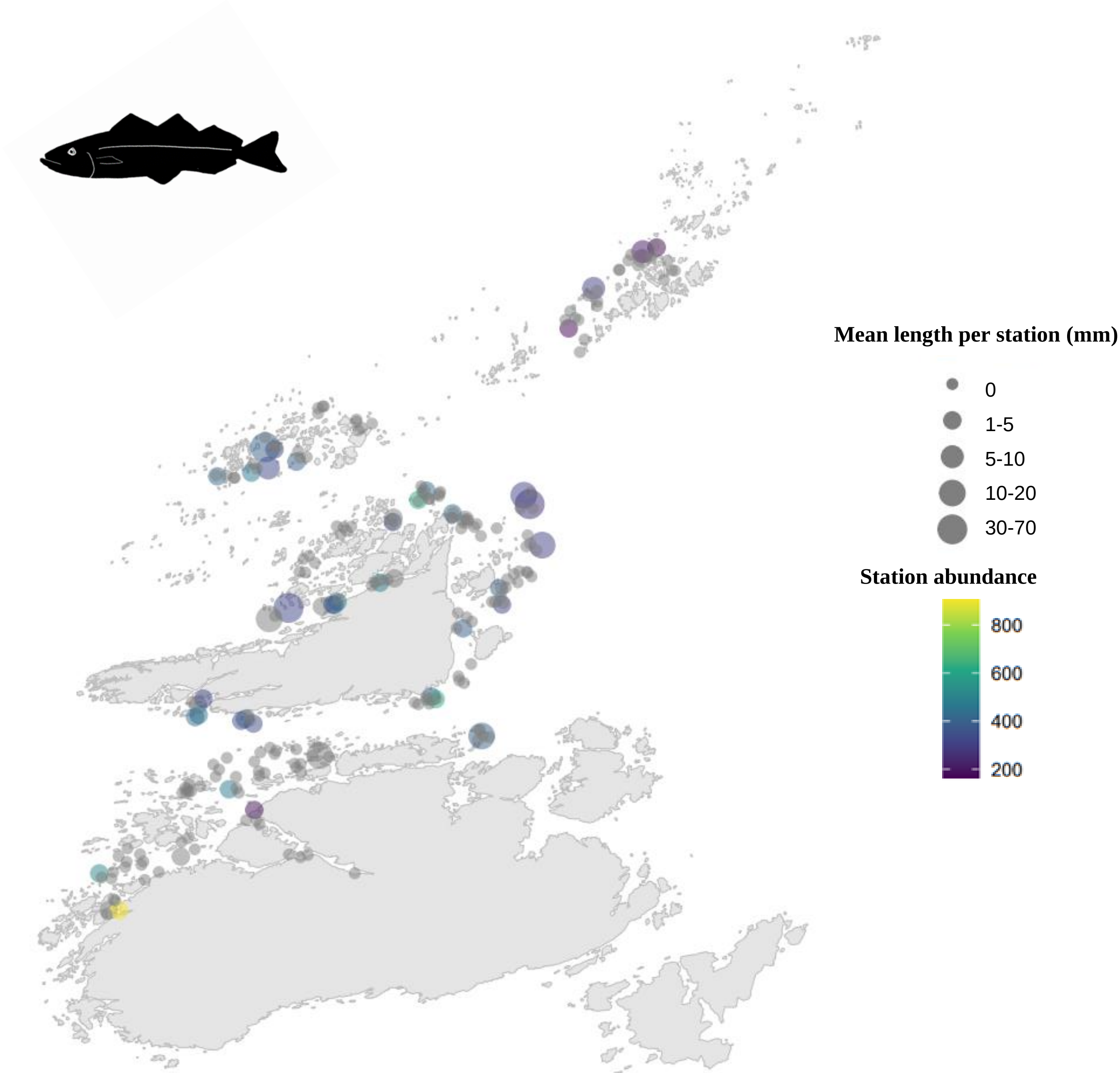


Figure 16: Map showing abundance and average length of saithe (*Pollachius virens*) per station in the study area. Saithe was observed in great abundances (10-20 and 30-70 individuals) in areas 2, 3 and 4, and in lower abundances (less than 10) in areas 1, 2, 3, 4, 5, 6, 7, and 8. The biggest saithe individual was measured at >90 cm, and was observed in area 1, signified by a yellow dot in the map. Grey dots with 0 abundance mark stations where the thornback ray was not observed. Grey dots with abundance above 0 are individuals that were not measured.

4. DISCUSSION

In this study we found that different fish species in the coastal areas surrounding Hitra and Frøya have different requirements for their environment in terms of Wave Exposure (WE), Bottom Current speed (BC), temperature, and depth. This affects their abundance, size, and spatial distribution within the study area. WE had a significant negative association with Atlantic cod (*Gadus morhua*) abundance and Atlantic halibut (*Hippoglossus hippoglossus*) abundance, and a significant positive association with spiny dogfish (*Squalus acanthias*) abundance. BC had a significant positive association with spiny dogfish abundance and cuckoo wrasse (*Labrus mixtus*) length. Depth had a significant negative association with Atlantic cod abundance, goldsinny wrasse (*Ctenolabrus rupestris*) abundance, and saithe (*Pollachius virens*) abundance, while temperature had a significant positive association with goldsinny wrasse abundance and Atlantic cod length. Species richness varied between stations but was not significantly affected by the environmental variables recorded here. However, the fish assemblages which make up species richness were not the same in all stations nor clusters.

Communities of marine fish species were investigated using stereo-BRUVs at 228 sample stations in the ecologically and economically important coastal marine ecosystems surrounding Hitra and Frøya. Species richness is presented at the spatial resolution of stations within clusters within areas. Distribution, abundance, and size of ecologically and economically important fish species are presented in relation to the four environmental variables. The data were collected as a part of the Active Management project by the IMR in 2019 and 2020 (Kleiven *et al.*, 2021). Data from 2019 were previously analysed by Bull (2019) and compared to results from traps at the same stations in areas 1, 2, 3, 4 and 6. In our study, a spatially and temporally expanded stereo-BRUV dataset was analysed, providing an opportunity to look at fish communities in a more comprehensive way. This study adds to the previous analyses and provides a more fine-scaled image of fish communities in the study area. The results provide insights which are helpful when designing effective ecosystem-based management strategies for local populations of coastal cod and wrasse.

In the former study, three species in the Pleuronectidae family were identified to species. However, it was later decided by the Active Management project that Pleuronectidae apart from the Atlantic halibut (*Hippoglossus hippoglossus*) would not be identified to species level as they present a great risk of misidentification, something that was commented on by Bull (2019). As a result, no records of other Pleuronectidae species were presented here, although common dab (*Limanda limanda*), lemon sole (*Microstomus kitt*) and European plaice (*Pleuronectes platessa*) were undoubtedly part of the fish community here, as they were caught in fish traps in 2019 (Bull, 2019).

4.1. Variation in environmental variables

There was little difference in the range of temperature and depth between the eight areas. There were, however, differences between clusters within the same area (*Appendix 1: Figure A5(a-b)*). Temperatures were around 7 °C for all clusters, except for cluster 1H with a median of around 8 °C and 1B which had a much wider temperature range than the other stations. Mean BC was highest in areas 2 and 8 followed by 7 and 3 (Figure 6). When looking at the clusters individually (*Appendix 1: Figure A5(c)*), area 2 stands out with some very high BC clusters (2H: median BC > 0.15 ms^{-1}) and others with comparatively low BC, (2K: median BC <0.05 ms^{-1}). Looking at the positions of the clusters (Figure 2), 2K is sheltered between two small islands, while 2H is situated further out. Area 2 is the biggest area spatially and was the only area to be sampled both years. In this area there are both sheltered, close to land stations and stations further from the main island of Frøya which explains the wide range of BC observed within this area. Cluster 7K stood out as having both one of the lowest (<0.025 ms^{-1}) and the highest (~0.25 ms^{-1}) measurements for BC.

Area 8 has by far the widest range in terms of WE (Figure 6), as well as the highest WE median value, setting it apart from all the other areas. Looking at clusters individually (*Appendix 1: Figure A5(d)*), we can see 8A, 8C and 8G all have median WE > = 0.3 ms^{-1}, which is higher than all other cluster median WE in the dataset. These three stations along with 8G are on the side of the Froan island group that faces the open ocean 8L is situated between islands and is more sheltered, and it has lower WE. Clusters 1G, 4K, 5A, and 5C all have the lowest recorded WE median value of 0.0 ms^{-1}. All these stations have a very sheltered geography. Area 5 is a narrow fjord, and here only 5E, which is at the mouth of the fjord, have a median BC > 0.0 ms^{-1}.

4.2. Species richness and distribution of abundance

The Poisson GLMM with cluster as a random effect did not indicate any significant ($p<0.05$) effect of environmental variables on species richness (*Appendix 2: Table A1*). The implications of the model, although the effects are non-significant, can be viewed as a basis for discussion and further investigations of factors affecting species richness outside Hitra and Frøya.

The model indicates non-significant negative association of species richness with WE and BC, and positive non-significant associations with depth and temperature. Most of the analysed species (cod, goldsinny, cuckoo, halibut and pollack) have positive association with temperature, although most of these are non-significant except in the case of goldsinny wrasse. Spiny dogfish, thornback ray and saithe abundance have a negative association with temperature. If our eight focus species are representative of the fish community in this area, higher temperatures are attracting most species at this time of year, in accordance with what is indicated in the species richness model.

The species richness model indicates a slight decrease of species richness from 2019 to 2020, and this could be attributed to several things. Firstly, the effect could be due to different areas and stations being sampled in the different years. Secondly, a few weeks difference in sampling times could affect species richness and abundance by unequal representation of species with seasonal migration. Thirdly, the change could reflect a general lower species richness within the study area in 2020 compared to 2019.

Looking at species richness observed at the cluster level, we need to keep in mind that clusters had an unequal number of stations. Several common species (observed at more than 25 stations) were not observed in area 5: goldsinny wrasse, cuckoo wrasse, common ling (*Molva molva*), haddock (*Melanogrammus aeglefinus*) and two-spotted goby (*Pomatoschistus flavescens*). This indicates that area 5 was an unfavourable environment to these species. Area 5 was topographically more like a narrow fjord than a coastal ecosystem and this could account for habitat and substrate differences enabling different fish communities. Cluster 5C was in the innermost part of this fjord, where there was probably less interaction with the coastal system of area 7 and 1 which were closest. On the other hand, sampling bias could be a part of the picture. There was only one station in 5C, and one species observed: the pollack, which was observed at every cluster but one. For comparison, in cluster 2N there were 10 stations and 10 species observed.

Although counting the number of species per cluster gives an interesting insight into where different species were found, we should not draw definitive conclusions of a species being completely absent in an area because it was not observed at the time. However, few or no observations of a species in all stations in a cluster gives strong indication that this species was not common in the area, especially if there are many stations.

4.3. Effect of environmental variables on fish abundance

Models of abundance for eight different species revealed significant relationships between abundance and environmental variables for cod, goldsinny wrasse, spiny dogfish, halibut, and saithe. Models of length for six species found significant relationships between length and environmental variables for Atlantic cod, spiny dogfish and cuckoo wrasse.

Atlantic cod (*Gadus morhua*)

Cod was observed all over the study area; at 76% of stations and in 44 out of 46 clusters, with significantly lower abundance in stations with high WE and greater depths. The model also indicated cod abundance had a non-significant negative association of increased BC, and a non-significant positive association with increased temperature. Cod length was significantly associated with higher temperatures. Cod length was positively associated with WE and depth, and negatively associated with BC, although these relationships were non-significant.

Cod is a generalist predator associated with a wide range of coastal habitats like eelgrass, kelp forests, macroalgae, and subtidal soft bottom (Seitz *et al.*, 2014), so it is not surprising to see it widely distributed in the study area (Figure 9). The length model for cod had a significant positive interaction with temperature, indicating that cod in this area prefer warmer temperatures. Previous studies have demonstrated that larger cod prefer colder water (Lafrance *et al.*, 2005; Freitas *et al.*, 2015, 2021). However, in Freitas *et al.* (2015) cod movements were monitored throughout the whole year, when water temperatures ranged from 2-20 °C, and in Lafrance *et al.* (2005), cod were subjected to temperatures between 1-15 in a lab experiment. In our study, temperatures ranged from 5-10 °C, with most measurements at around 6-8 °C.

Temperatures recorded within this study were all well within the thermal range of this species, and below the temperature of optimal growth presented by Righton *et al.*, (2010). All stereo-BRUV data were collected in late spring (May), providing a low variation in temperature for the model to work with apart from a few outliers. It is possible that this is a local cod population where large individuals do prefer warmer water, but it is also likely that this could occur due to a variable correlating with temperature that was not part of this study. Also, in contrast to these previous studies, this study was not designed to record cod moving between water masses, but rather abundance at a fixed time and location, so methodical differences could be part of why these results seemingly do not match.

Doing stereo-BRUV surveys in a wider range of temperatures, for instance once a month throughout the year, or once every season, could help illuminate the effect of temperature on the local cod population.

Wrasse (Labridae)

Goldsinny wrasse (*Ctenolabrus rupestris*) was found in 16% of stations, in 24 out of 46 clusters, and was represented in every area except area 5 (Figure 10). Goldsinny abundance was significantly higher in higher temperatures and at shallower depths. Goldsinny abundance was also negatively associated with WE and BC, although these associations were non-significant ($p > 0.05$). Goldsinny have previously been associated with intermediate wave exposure (Skiftesvik *et al.*, 2014a), which might explain why there is no significant association in neither negative nor positive direction. Cuckoo wrasse (*Labrus mixtus*) was found all over the study area, but less so in area 8 (Figure 11). Cuckoo wrasse abundance was also positively associated with higher temperatures. In contrast to the goldsinny, cuckoo abundance was positively associated with both BC and depth, although these relationships were not significant in the model. Although all wrasses have a shallow coastal distribution, cuckoo has been reported to migrate as far as to 100 m depth in the winter (Moen and Svensen, 2020).

Previous research have reported different depth distributions for the different wrasse species (Halvorsen *et al.*, 2020, 2021; Moen and Svensen, 2020). In southern Norway, goldsinny were found across all depths (0-20 m), while cuckoo and rock cook were found in greater abundance in deeper areas (10-20m) and ballan and corkwing were found in shallower areas (0-5m) (Halvorsen *et al.*, 2020). Goldsinny distribution was not associated with any particular depth range between 0-20 in this study. Others have described the depth distribution of goldsinny to be between 0-20m (Moen and Svensen, 2020). In our study, we have sampled from 5-37m and here, goldsinny had a negative association with depth. This could indicate that general depth range for goldsinny goes further than 20m, but not as far as 37m. However, knowing that wrasse have strong site fidelity and distinct populations along the coast, these observations could be due to a difference between populations.

Due to few observations of ballan, corkwing and rock cook, no models were developed for these wrasse species. Ballan was observed mostly in areas 2, 3, 4 and 7, all with relatively low WE. Corkwing was observed at clusters 2A, 8A and 7K (Figure 8). Median depths for these stations are all below 20m, but wave exposure in 8A is quite high. Skiftesvik *et al.*, (2014a) made observations that that corkwing prefer sheltered habitats, unlike what we observed here. However. There could be sheltered microhabitats within areas that are exposed. Rock cook was observed only at 2M, which has low WE, but high BC and was deeper than 20m, contrary to expectations made by Halvorsen et al (2020). A sixth species, scale-rayed wrasse (*Acantholabrus palloni*) was observed in cluster 2M. This species is considered relatively rare, although it has been suggested that it is not rare but rather likes to stay well hidden in algae and is not often caught by traditional means (Moen and Svensen, 2020).

Goldsinny is the most abundant wrasse species in this area, something that is reflected in this dataset. Ballan are less abundant than goldsinny in this area and, if fisheries landings are any indication (2,3 million goldsinny, 600 000 ballan, and 70 000 corkwing in 2021), corkwing is less abundant than ballan

(Grefsrud *et al.*, 2023). However, fisheries landings are also based on demand from the market, so it is not necessarily parallel to abundance. The lack of corkwing in this dataset supports the claim that they are less abundant, but they could be more abundant than our survey indicates. Importantly, we sampled in May, when it was still relatively cold in the water. Possibly, some wrasses were not very active yet, or had not migrated to the upper water layers from the deeper water layers where they spend the winter. Results might have been different had we sampled later in the season. It is also possible that we were not sampling at the places where they are most abundant, as wrasse community composition is known to change drastically over small spatial scales (Skiftesvik *et al.*, 2014a). Another possibility is that they were observed but were not identified to the species level. There were a lot of un-identified wrasse in the dataset, as they were often seen swimming among algae and too far from the camera to identify.

Length of goldsinny wrasse had no significant associations, but had non-significant positive associations with WE, BC and temperature, and a non-significant negative association with depth. Cuckoo length was positively associated with all four variables, but only BC was statistically significant (p=0.04). This result complements the findings of (Skiftesvik *et al.*, 2014a), who found that size was negatively associated with exposure for ballan, corkwing, rock cook and goldsinny. However, with cuckoo wrasse, length is also linked to the sex of the fish, as they are hermaphrodites where males and females different morphology and colouring. Females are smaller and once they grow past a certain length they become males and grow bigger. Models were made for the male and female subsample but did not yield any useful output because there were not enough data (*See Appendix 1: Figure A6*). As there is not a lot of data on cuckoo wrasse ecology, this is an interesting prospect for further study.

Spiny dogfish (*Squalus acanthias*)

Abundance of the spiny dogfish had a significant positive association with WE (p<0.001) and BC (p=0.04). Spiny dogfish abundance was also positively associated with depth and temperature, but these associations were not significant. WE had a significant positive association with spiny dogfish length.

Populations of the widely distributed and vulnerable elasmobranch spiny dogfish have been observed to have either migratory or residential behaviour, or a combination of both, which makes stock assessment complicated (Sulikowski *et al.*, 2010; Carlson *et al.*, 2014; Thorburn *et al.*, 2015). Spiny dogfish are known to aggregate in shoals of same sex and/or size (Williams, *et al.*, 2008; Carlson *et al.*, 2014; Finucci *et al.*, 2018; Jac *et al.*, 2022). Several studies found that female spiny dogfish aggregate in warmer, shallower water compared to males (Shepherd, Page and Macdonald, 2002; Dell'Apa, *et al.*, 2017). Mature and bigger individuals have also been associated with shallower and warmer water (Shepherd, *et al.*, 2002; Jac *et al.*, 2022), and mature females were more likely to stay inshore rather than migrate (Shepherd, *et al.*, 2002). Spiny dogfish use the Norwegian coastal waters year round and for their whole life cycle, indicating that the population has a residential component (Albert *et al.*, 2019). Higher densities of spiny dogfish and other elasmobranchs have been observed in the coastal areas around Hitra, Frøya, and Smøla compared to other coastal areas along the Norwegian coast (Jac *et al.*, 2022). This is supported by the results of this study: Spiny dogfish were mainly found in Froan nature reserve (area 8), as seen in Figure 12, indicating aggregation at a smaller spatial scale than reported by Jac *et al.* (2022).

Our model predicted wave exposure and current speed to be the main factors determining spiny dogfish abundance. Research on habitat selection of spiny dogfish including wave exposure and current speed was hard to come by, but some shark species have been observed to move with tidal currents as a way to save energy or avoid predators when foraging in the intertidal zone (Schlaff, *et al.*, 2014). Other studies are needed to determine whether spiny dogfish move in the direction of the current or against it in this area. Area 8, where most spiny dogfish were observed, is characterised by high WE and BC (Figure 6). Spiny dogfish were also observed at four stations outside area 8; two stations in each of the adjacent areas 2 and 3, which have a higher BC compared to areas 1, 4 and 6, where spiny dogfish were not observed. No spiny dogfish were observed in area 7, which has similar WE and BC characteristics to area 2 and 3. If distance to the aggregation site is a determining factor, these observations could be explained by individuals exploring outside the area 8 aggregation, in area 2 and 3, but not as far as to area 7 which is further away from area 8. However, due to the low number of observations of this species in general, this could also be a random effect. Jac *et al.*, (2022) determined temperature and depth as the two most important factors for predicting spiny dogfish abundance, but they did not test wave exposure or current speed in their study. Our model predicted a non-significant negative effect of temperature on spiny dogfish abundance, which is contrary to the literature cited above. We have also predicted a higher abundance in shallower water, an effect which is in line with the literature cited above, but which was non-significant in our model.

Our length model yielded a significant effect of wave exposure on spiny dogfish length. Bigger individuals were found in higher wave exposure, compared to smaller ones. This can potentially be explained by bigger individuals being stronger and having better swimming abilities to tolerate a high exposure environment. According to the literature, bigger spiny dogfish are found in warm shallow water compared to smaller individuals. Our model indicated no significant effect of temperature on spiny dogfish length, but a non-significant positive effect of temperature, complementing previous research on the temperature range of this species. We also found a non-significant positive association with depth, suggesting that bigger individuals are deeper in this coastal system compared to smaller ones, contrary to previous research. When discussing depth range for this species, keep in mind that our sample size is very small (n=11) and our observations are all from the shallower end of the distribution range of this species, which can be found down to 1500 m depth.

It is hypothesized the females seek warmer and shallower coastal waters to optimise foetal growth, as this species incubate their eggs in their bodies and give birth to live pups after around two years of pregnancy (Albert, *et al.,* 2019; Jones *et al.*, 2019). If this is true, protecting known aggregation sites of spiny dogfish in shallow coastal areas, like the Froan nature reserve, could be an important and effective way to help this vulnerable, long lived, and slowly reproducing species recover from human overexploitation. Performing similar surveys throughout the year to determine if this aggregation is seasonal or constant will further inform management decisions in the area.

Thornback ray (*Raja clavata*)

Thornback was observed in a total of 16 stations spread out in areas 1, 3, 6, 7 and 8, but not in area 2, 4 and 5 (Figure 6, Figure 13). Thornback ray abundance was positively associated with depth and negatively associated with WE, BC, and temperature. None of these associations were statistically significant (p>0.5).

Thornback ray is associated with sand, gravel and pebble substrates where it can partially bury itself in the sediment (Heessen *et al.*, 2006; Moen and Svensen, 2020). Strong currents and wave exposure could wash away this kind of substrate, and this habitat preference could provide a possible explanation to why the association with these variables were negative in the model. Thornback ray is not a commercially fished species in Norway but is landed as bycatch in some fisheries. This means there are less data available on habitat use and stock assessments in Norwegian coastal waters. Because rays and skates can be difficult to identify, there are uncertainties related to using historic bycatch data for stock assessment and historic distribution of this species (Williams *et al.,* 2008). However, thornback ray is known to be found all along the Norwegian coast, although in lesser abundance in the northern parts. Thornback rays can be found all the way from 300m depth to shallow beaches, but are most common below 20m depth (Moen and Svensen, 2020). This is supported by our model, which indicates a negative (albeit insignificant) association with depth. Skates are known to migrate from the ocean to coastal areas in spring to release their egg capsules in the summer (Hunter *et al.*, 2005; Moen and Svensen, 2020) and juveniles stay in the nursery grounds over the winter (Heessen *et al.*, 2006). Like the spiny dogfish, the thornback ray aggregates in groups of individuals with the same sex and size (Heessen *et al.*, 2006; Simpson *et al.*, 2021). In future it would be a good idea to include habitat analysis to this survey to confirm substrate preference for thornback ray in this area and identify or predict possible aggregation sites.

Only 10 individuals were measured, and there were not sufficient data to fit a length model for this species. Females are known to be bigger than males, something which was observed through the few data points we have (*see Appendix 1: Figure A7*).

Atlantic halibut (*Hippoglossus hippoglossus*)

Atlantic halibut was observed at 11 % of all stations and was represented in all areas of the study area (Figure 6, Figure 14). Abundance of Atlantic halibut had a significant negative association with WE and a non-significant negative association with BC as well as non-significant positive association with depth and temperature.

The Atlantic halibut is a large benthic flatfish which can be found from shallow coastal waters and down to 2000 m depth. It is classed as near threatened (NT) by the ICUN Red List of Species due to the slow growth and reproduction of this species and a history of over exploitation (Munroe *et al.*, 2021). There are records showing that growth rates and average age of first spawning of Atlantic halibut in northern Norway changed between the 1950s and 1980s as a consequence of over exploitation (Haug and Tjemsland, 1986). In Norway, stock is increasing North of 62 °N, but landings are still low south of 62 °N. In the Norwegian system, the Atlantic halibut is classified as least concern (LC) (Hesthagen *et al.*, 2021b). Previous studies have described seasonal movements from deepwater continental slopes in the fall and winter to shallower coastal waters in summer, presumably for feeding purposes (Armsworthy, *et al.*, 2014). There is a direct relationship between size of nursing area habitat in coastal areas and stock productivity in Atlantic halibut in the continental slope and shelf of Canada (French *et al.*, 2018). Nursing areas for Atlantic halibut have been observed in Norwegian coastal waters as well, and here, abundance of halibut was positively associated with substrate evenness, indicating that this species prefers to be able to move between substrate types, possibly because of higher prey availability (Sørensen and Pedersen, 2021). Due to the nature of the stereo-BRUV survey, small and camouflaging animals are harder to identify and more likely to be identified to a lower taxonomic level like family or genus. It is therefore not impossible that juvenile or small sized halibut are underreported in this survey. Preserving areas of great substrate evenness where halibut juveniles are known to occur could therefore be a good management strategy for this species in coastal areas like Hitra and Frøya.

Saithe (*Pollachius virens*)

Saithe was observed at 27/48 clusters, 21.1 % of stations and is represented in all areas of the study area (Figure 16). Abundance of saithe was significantly negatively associated with depth in this survey (p=0.01). The model also indicated a non-significant negative association with temperature, and non-significant positive associations with WE and BC on saithe abundance. Saithe length was positively associated with depth and temperature, and negatively associated with WE and BC, but none of these associations were significant.

Saithe is an economically important gadid with a northern distribution. The stock of Northeast Arctic saithe is currently sustainably fished according to the ICES (ICES, 2022b). Previous studies have found that saithe CPUE in fjords is higher in deeper parts of the fjord in the summer, and in shallower parts the rest of the year (Heino *et al.*, 2012). Juvenile Northeast Arctic saithe are known to inhabit coastal waters and are associated with kelp forests (Rangeley and Kramer, 1995, 1998). Few mature saithe were observed in a fjord in a study by Heino *et al.*, (2012), indicating that this migration to the sea takes place before saithe reaches maturity. In our study too, most saithe were between 20-60 cm, and one individual observed in 1G, was 91.4+-2.7 cm. Saithe are known to aggregate into shoals for protection (Smith *et al.*, 1993; Rangeley and Kramer, 1998), something that was observed in this study. Groups of more than 10 saithe in the same frame were observed in 4E, 3D, 2L, 4E, 2B, 2L, 7K, and 2H. Saithe aggregations have been observed beneath aquaculture facilities and feeding off excess salmon feed (Dempster *et al.*, 2009; Uglem *et al.*, 2020). In future, it would be interesting to include a distance to sea cage variable in the analysis of species abundance to see if this occurs here.

The results of the model presented here indicate that saithe prefers colder water and is more abundant in deeper stations in May/June. This is in agreement with previous research on saithe ecology which has documented saithe seeking out the colder water layers (Heino *et al.*, 2012).

Pollack (*Pollachius pollachius*)

Pollack was the most widely distributed species in this survey (Figure 15), found at all but one cluster, and at 55.7 % of all stations, and was the second most observed fish after cod. The abundance model indicated non-significant associations which were positive for WE, temperature, and depth and negative for BC. The length model indicates non-significant associations which were positive for BC and depth, and negative for WE and temperature. No significant associations with environmental variables were indicated with either abundance or length of pollack. As this species was found at every cluster, these non-significant associations could mean that this species has tolerates a wide range of the environmental conditions found in this study.

Knowledge of pollack ecology and distribution is deficient, and ICES has no data on stock size to make assessments (ICES, 2011). Some previous studies have found that pollack preferred warmer water compared to cod, and would migrate to warmer water layers in both winter and summer in Skagerrak (Freitas *et al.*, 2021). A similar observation was reported in Western Norway by Heino *et al.*, (2012). Our model based on data from spring/early summer indicates a positive association with temperature and depth which both are non-significant. This could indicate an “in between” situation between summer and spring depth and temperature preferences in pollack. Our model also indicated a positive association with wave exposure, and a negative association with current speed. Pollack has been associated with kelp habitat in the western coast of the UK (Furness and Unsworth, 2020), and shallow areas with high wave exposure are more likely to be kelp habitats compared to deeper areas and very sheltered areas (van Son *et al.*, 2020). It is possible what we see as an association with WE, is in fact an indirect association with a common habitat of this species.

Our results match those of Heino *et al*., (2012) who reported that pollack was found in the upper layer in summer and in the lower layers in all other seasons, presumably seeking out warmer water, while saithe was found in the lower layers in summer and upper layers in all other seasons, presumably seeking out colder water. Temperatures in May in the study area are quite cold, and so conditions would be more adjacent to that of spring than of summer, also indicated by the low abundance of most wrasse species which are known to seek out warmer water and are abundant in summer.

4.4. Grønnholmråsa nature area, a suitable MPA?

The planned marine protected area (MPA) Grønnholmråsa nature area is placed within area 7 of the study area, incorporating clusters 7H, 7B, and about half of 7C (Hitra kommune, 2023) and for the sake of this discussion the whole of these three clusters will represent species richness within this area. Within area 7, modal species richness was two species, which is less than the modal species richness in area 1, 2, 3, 4, and 6, and the same as area 8 (Figure 7). Cod is represented within the bounds of Grønnholmråsa nature area, and at every cluster in the surrounding area. Goldsinny wrasse were not observed in 7H or 7B but was observed once in 7C and in surrounding areas outside the boundaries of Grønnholmråsa. Cuckoo wrasse is represented in clusters 7H and 7C within Grønnholmråsa. Corkwing, ballan, and goldsinny were observed in the area surrounding Grønnholmråsa, but were not observed within the bounds during this survey. In terms of other commercially valuable fish, pollack is observed in Grønnholmråsa as well as in the rest of the study area. Saithe is observed at one station in Grønnholmråsa, and Atlantic halibut was observed close by, but not within the bounds of the MPA. Spiny dogfish were not observed here, but thornback ray was observed within Grønnholmråsa and in the surrounding area. A total of 11 fish species were observed within Grønnholmråsa: Cusk (*Brosme brosme*), pollack (*Pollachius pollachius*), Atlantic cod (*Gadus morhua*), common ling (*Molva molva*), cuckoo wrasse (*Labrus mixtus*), poor cod (*Trispoterus minutus*), goldsinny wrasse (*Ctenolabrus rupestris*), whiting (*Merlangius merlangus*), thornback ray (*Raja clavata*), saithe (*Pollachius virens*), and haddock (*Melanogrammus aeglefinus*). Haddock, whiting, cusk, and ling are all commercially valuable but were not included in this survey due to time constraints and few observations.

For a protective area targeting mainly Atlantic cod and wrasse this seems to be an okay area, although only two wrasse species were observed here, and one of them was the cuckoo wrasse which is not targeted by fisheries and thus might gain less from protection compared to ballan and corkwing. However, as mentioned in a previous section, we sampled early in the season while the water was still cold, and this was probably not the ideal time to collect data on wrasse abundance. Observing wrasse abundance later in the season in this area would undoubtedly give more insight into how wrasse species are distributed in this area. For the vulnerable species Spiny dogfish, the proposed MPA would likely not be ideal based on the findings of this study. As this species was mostly observed at Froan nature reserve, management strategies to protect spiny dogfish should be focused on this area.

Data collection at more localities and throughout the summer season within Grønnholmråsa is desired for a greater overview of wrasse abundance and distribution. Doing this before the MPA is implemented will be advantageous as it can provide a good background for comparison and monitoring in a Before-After, Control-Impact (BACI) design. A control area with comparable habitat should be chosen before implementation of the MPA. Based on median values for BC, WE, depth, and temperature presented in Figure 6, somewhere in area 3 or 2 could be fitting.

4.5. Comments on methods

Earlier studies have described the efficiency of stereo-BRUVs at gathering information about species richness and abundance of commonly fished species in temperate coastal ecosystems (Jones *et al.*, 2020; Davies *et al.*, 2021; Ovegård *et al.*, 2022; Jackson-Bué *et al.*, 2023). Stereo-BRUVs are dependent on good visibility to make observations and accurate species identification. Some of the video material collected was quite dark and turbid, making identification and measurements difficult. In some videos, light varied considerably throughout the hour the rig was deployed, presumably as clouds covered and uncovered the sun during the survey. The stereo-BRUV method was developed in Australia and have been used mainly in tropical waters, where the visibility is high, and water is clear. Adding a Clear Liquid Optical Chamber (CLOC) could mitigate the effect of turbidity in temperate coastal waters and improve visibility in stereo-BRUV surveys (Jones *et al.*, 2019).

The desired taxonomic resolution was species. When species identification was not possible, the observed animal would be identified to either genus or family. For example, for many species of the Pleuronectidae family, individuals from different species can have similar colour and pattern variations and size. True species identification relies on the shape of the lateral line, the roughness of the skin, and the bony protrusions on the head, lateral line and around the fins. These characteristics are not easily identifiable on video and therefore it was judged that attempting to identify these to the species level comes with a too great risk of misidentification (*see discussion in* Bull; 2019). The exception is the Atlantic halibut, which has a more easily distinguishable silhouette and behaviour compared to other species of the Pleuronectidae family. In the case of very small benthic fish, like many species in the Gobiidae family, species identification was not possible with the video quality of the stereo-BRUVs, as the species are very small (2-13 cm) and are separated by slight variations in their patterns and the number of scales. They are also well camouflaged, so can spotted while moving, but hard to distinguish from the background when they lay still on the seafloor or when the video is paused. Bigger fish which did not camouflage on the seafloor were the easiest to spot and identify. However, when doing visual species identification, cryptic species can be mislabelled and can therefore be missing from the dataset. As pointed out by Bull (2019), ground truthing is needed to get the full species diversity including species which are hard or impossible to identify visually from video alone.

The stereo-BRUVs were deployed with a bait of chopped up herring to attract nearby fish, in accordance with the guidelines provided by Langlois et al (2020). This introduces a bias towards predatory fish which are attracted to this specific bait. Previous studies have shown differences in species richness and abundance when using different bait types, most commonly baited rigs attract a higher abundance and species richness than un-baited rigs (Bernard and Götz, 2012; Schmid *et al.*, 2017; Jones *et al.*, 2020), fish based bait attract a higher abundance of predators and a higher species richness compared to plant based bait, and plant based baits attract more herbivorous fish (Ghazilou, *et al.*, 2016; Schmid *et al.*, 2017). However, Norwegian coastal waters do not have any herbivore fish species, and studies done in Northeast Atlantic waters with ecosystems more similar to the Norwegian coast than the tropical reefs, have recommended cheap, oily fish like mackerel or herring for these conditions (Jones *et al.*, 2020).

In EventMeasure it is possible to register behaviour of every observed fish, a function which was not used consequently in this project, but have proven insightful in other studies (Di Blasi *et al.*, 2021; Ovegård *et al.*, 2022). Although behaviour was not part of this study, I made some observations while working with this material. One such observation is that the different species behave differently towards the bait. Especially cod are very attracted and often try to eat the bait and stay close for longer periods of time, sometimes more than twenty minutes, an observation which was also made by Bull (2019). Ling would feed on the bait aggressively in a similar manner and exhibited territorial behaviour by chasing off conspecifics. Ling were not observed to chase off cod. Flatfish (Pleuronectidae) and haddock would display interest in the bait and often attempt to feed from it. Saithe and pollock would typically swim by either alone or in schools, and sometimes approach the bait more carefully. Sharks and skates would often investigate the bait and sometimes try to eat it. Wrasses would rarely, if ever try to eat from the bait and were mostly observed passing or sometimes investigating the bait. In further stereo-BRUV studies in temperate waters it would be useful to register behaviour towards the bait as a part of the study, and possibly deploy un-baited rigs as controls to investigate to which degree bait-attraction is affecting species composition.

4.6. Outlook

In this study I have looked at the associations between wave exposure, temperature, current speed and depth on fish abundance and length. The effects uncovered here are a result of both sample size and the chosen environmental variables. Species like pollack, thornback ray and cuckoo wrasse did not have any significant association with the environmental variables tested here. There are a number of other environmental variables which could potentially affect fish abundance and length in the study area, like season, time of day, light conditions, pH, oxygen, salinity and substrate type. Substrate classification of each stereo-BRUV deployment can give important context to the species observations and is a tool for understanding of fish-habitat relationships and interactions at the deployment site. Langlois *et al.*, (2020) recommends using the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme for substrate analysis with stereo-BRUVs (described in Althaus *et al.*, 2015). The CATAMI system was developed and have been used to analyse AUV-videos in Australian deep reef assemblages, (James *et al.*, 2017; Monk *et al.*, 2018), deep corals in the southwest pacific ocean (Untiedt *et al.*, 2021) and on ROV footage and drop-camera footage on the continental shelf of South Africa (Pillay, Cawthra and Lombard, 2021; Pillay *et al.*, 2021). The CATAMI classification scheme has not been used in the northern temporal coastal habitats to my knowledge. Developing an approach based on the CATAMI classification for visual substrate and habitat types in northern temporal habitats was discussed but decided to be outside the scope of this master project. A standardised method for habitat analysis of stereo-BRUV data in temporal coastal waters is needed to fully utilise the potential of the stereo-BRUV method in these areas. This represents an exciting and important next step in the process of implementing stereo-BRUV surveys as a tool for fish community and biodiversity research in coastal Norway.

Deployment depth was another limiting factor in this survey. As the stereo-BRUVs deployed by the Active Management project did not have lights attached, the survey was limited to depths with sufficient natural light (5-40 m). However, most of the species we observed are known to be found lower than 37 meters depth, so studying fish abundances from 5-40 m depth provides only part of the picture. Extending the study area to deeper waters would give a more comprehensive picture of fish communities and distribution within the study area. Deployment with artificial lights at greater depths than 37 m could give additional information about distribution beyond what was examined in this study.

This study looked at effect of environmental variables on individual in coastal waters around Hitra and Frøya. In reality, a population of fish does not exist alone in its environment but is a part of a larger marine ecosystem where all components affect each other through complex interactions. The presence, abundance, and absence of one species can affect other species through interactions like competition, predation, or territoriality. In future studies it would be useful to apply multivariate analyses to this dataset, as suggested by Zuur et al. (2010), to look at the ecological implications of the joined absence or presence of more than one species, and to identify possible patterns in fish assemblages caused by interaction or common habitat preferences. It would also be useful to extend the study to include all four seasons to uncover local seasonal distribution patterns. Many species have seasonal migration, and these dynamic components of the distribution are not captured in this study.

In future studies, it will be useful to include more species in the study, like the commonly observed species poor cod (*Trispoterus minutus*), haddock (*Melanogrammus aeglefinus*), two-spotted goby (*Pomatoschistus flavescens*) and ling (*Molva molva*) which were not included in the analysis due to time constraints.

5. CONCLUSION

Species richness of fish in the shallow coastal areas surrounding Hitra and Frøya was not affected by temperature, depth, bottom current speed, or exposure in this study. Different fish species had different associations with the environmental variables, and this affected their spatial distribution.

We found that cod abundance decreased, while spiny dogfish abundance and size increased with higher wave exposure, causing these two species to have a different geographical distribution within the study area. Increased bottom current speed was associated with increase in spiny dogfish abundance, decrease in cod abundance, decrease in halibut abundance, and increased length of cuckoo wrasse. Higher temperatures were associated with higher abundance of goldsinny wrasse and increased size of Atlantic cod. Pollack is found all over the study area and had no significant association with environmental variables, perhaps indicating a tolerance for a wide range of environmental variables. Thornback ray was found in few stations but was not significantly associated with any environmental variables, reflecting either a wide habitat range or a distribution which is driven by environmental variables not included in this analysis. The findings within this study provide a good argument for designing MPAs that include microhabitats on a scale from shallow to deep, exposed to sheltered, and where areas of both cold and warm water are found, to ensure an ecosystem-based approach.

Three target species for the Grønnholmråsa MPA; cod (*Gadus morhua*), goldsinny (*Ctenolabrus rupestris*), and cuckoo wrasse (*Labrus mixtus*) were observed within the bounds of the proposed MPA. So were the slow lived elasmobranch thornback ray (*Raja clavata*) and seven other fish species, some of which are targeted by fisheries. Increased data sampling before an MPA is established will be advantageous as a good background for comparison and monitoring in a BACI design.

The vulnerable spiny dogfish was not observed within the suggested MPA area but appeared to be aggregating in the Froan nature reserve, an area where mammals and birds are protected, but fish are not. Our findings give strong indication that this site would be ideal as a marine protected area for this vulnerable shark species. It is my suggestion that protection from commercial fisheries is included in the management plan for Froan nature reserve either year-round or in certain parts of the year to protect local aggregations of spiny dogfish.

References:

Aglen, A. *et al.* (2021) *Abundance indices for norwegian coastal cod north of 62°N*. 6. Havforskningsinstituttet. Available at: https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-en-2021-6 (Accessed: 4 May 2023).

Albert, O.T., Junge, C. and Myrlund, M.K. (2019) 'Young mums are rebuilding the spurdog stock (Squalus acanthias L.) in Norwegian waters', *ICES Journal of Marine Science*, 76(7), pp. 2193–2204. Available at: https://doi.org/10.1093/icesjms/fsz156.

Althaus, F. *et al.* (2015) 'A Standardised Vocabulary for Identifying Benthic Biota and Substrata from Underwater Imagery: The CATAMI Classification Scheme', *PLOS ONE*, 10(10), p. e0141039. Available at: https://doi.org/10.1371/journal.pone.0141039.

Armsworthy, S.L., Trzcinski, M.K. and Campana, S.E. (2014) 'Movements, environmental associations, and presumed spawning locations of Atlantic halibut (Hippoglossus hippoglossus) in the northwest Atlantic determined using archival satellite pop-up tags', *Marine Biology*, 161(3), pp. 645–656. Available at: https://doi.org/10.1007/s00227-013-2367-5.

Asplin, L. *et al.* (2020) 'The hydrodynamic foundation for salmon lice dispersion modeling along the Norwegian coast', *Ocean Dynamics*, 70(8), pp. 1151–1167. Available at: https://doi.org/10.1007/s10236-020-01378-0.

Baskett, M.L. *et al.* (2005) 'Marine Reserve Design and the Evolution of Size at Maturation in Harvested Fish', *Ecological Applications*, 15(3), pp. 882–901. Available at: https://doi.org/10.1890/04-0723.

Bates, D. *et al.* (2015) 'Fitting Linear Mixed-Effects Models Using {lme4}', *Journal of Statistical Software*, 67(1), pp. 1–48. Available at: https://doi.org/10.18637/jss.v067.i01.

Bavington, D. (2010) 'From Hunting Fish to Managing Populations: Fisheries Science and the Destruction of Newfoundland Cod Fisheries', *Science as Culture*, 19(4), pp. 509–528. Available at: https://doi.org/10.1080/09505431.2010.519615.

Bernard, A.T.F. and Götz, A. (2012) 'Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion', *Marine Ecology Progress Series*, 471, pp. 235–252. Available at: https://doi.org/10.3354/meps10039.

Björnsson, B., Steinarsson, A. and Árnason, T. (2007) 'Growth model for Atlantic cod (Gadus morhua): Effects of temperature and body weight on growth rate', *Aquaculture*, 271(1), pp. 216–226. Available at: https://doi.org/10.1016/j.aquaculture.2007.06.026.

Bull, M. (2019) *Comparing Baited Remote Underwater Video Systems with Fish Traps Along the Coast of Frøya and Hitra*. Master Thesis. NTNU.

Carlson, A.E. *et al.* (2014) 'The Use of Satellite Tags to Redefine Movement Patterns of Spiny Dogfish (Squalus acanthias) along the US East Coast: Implications for Fisheries Management', *Plos One*, 9(7), p. e103384. Available at: https://doi.org/10.1371/journal.pone.0103384.

Cavrois-Rogacki, T. *et al.* (2021) 'Deformities prevalence in farmed ballan wrasse (Labrus bergylta) in relation to hatchery origin and life stage', *Aquaculture*, 533, p. 736212. Available at: https://doi.org/10.1016/j.aquaculture.2020.736212.

CBD (2022) 'Kunming-Montreal Global Biodiversity Framework', in *Kunming-Montreal Global Biodiversity Framework*. *COP15*, Montreal, Canada: Convention on Biological Diversity. Available at:

https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222 (Accessed: 30 April 2023).

Cooke, R. (2022) ‘Fish still missing, traditions extinct 30 years after N.L. cod moratorium’, *CBC*, 2 July. Available at: https://www.cbc.ca/news/canada/newfoundland-labrador/cod-moratorium-30th-anniversary-1.6506628 (Accessed: 2 May 2023).

Cresci, A. *et al.* (2022) ‘Goldsinny wrasse (Ctenolabrus rupestris) have a sex-dependent magnetic compass for maintaining site fidelity’, *Fisheries Oceanography*, 31(2), pp. 164–171. Available at: https://doi.org/10.1111/fog.12569.

Davies, B.F.R. *et al.* (2021) ‘Ecosystem Approach to Fisheries Management works—How switching from mobile to static fishing gear improves populations of fished and non-fished species inside a marine-protected area’, *Journal of Applied Ecology*, 58(11), pp. 2463–2478. Available at: https://doi.org/10.1111/1365-2664.13986.

Davis, J.P. *et al.* (2019) ‘Comparing video and visual survey techniques for Barred Sand Bass in rocky reef ecotone habitats-Web of Science Core Collection’, *California Fish and Game*, 105(4), pp. 233–253.

Dell’Apa, A., Pennino, M. and Bonzek, C. (2017) ‘Modeling The Habitat Distribution Of Spiny Dogfish (Squalus Acanthias), By Sex, In Coastal Waters Of The Northeastern United States’, *Fishery Bulletin*, 115(1), pp. 89–100. Available at: https://doi.org/<p>10.7755/FB.115.1.8</p>.

Dempster, T. *et al.* (2009) ‘Coastal salmon farms attract large and persistent aggregations of wild fish: an ecosystem effect’, *Marine Ecology Progress Series*, 385, pp. 1–14. Available at: https://doi.org/10.3354/meps08050.

Dempster, T. *et al.* (2011) ‘Proxy Measures of Fitness Suggest Coastal Fish Farms Can Act as Population Sources and Not Ecological Traps for Wild Gadoid Fish’, *PLOS ONE*, 6(1), p. e15646. Available at: https://doi.org/10.1371/journal.pone.0015646.

Di Blasi, D. *et al.* (2021) ‘The Challenge to Observe Antarctic Toothfish (Dissostichus mawsoni) under Fast Ice’, *Journal of Marine Science and Engineering*, 9(3), p. 255. Available at: https://doi.org/10.3390/jmse9030255.

Di Franco, A. *et al.* (2016) ‘Five key attributes can increase marine protected areas performance for small-scale fisheries management’, *Scientific Reports*, 6:38135. Available at: https://doi.org/10.1038/srep38135.

Directorate of fisheries (2022) ‘Salg 1998-2021’. fiskeridir.no. Available at: https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Akvakulturstatistikk-tidsserier/Totalt-hele-naeringen (Accessed: 9 May 2023).

Directorate of fisheries (2023) ‘Antall lokaliteter 2006-2022’. fiskeridir.no. Available at: https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Akvakulturstatistikk-tidsserier/Totalt-hele-naeringen (Accessed: 9 May 2023).

Dounas, C. *et al.* (2007) ‘Large-scale impacts of bottom trawling on shelf primary productivity’, *Continental Shelf Research*, 27(17), pp. 2198–2210. Available at: https://doi.org/10.1016/j.csr.2007.05.006.

Dureil, M. *et al.* (2018) ‘Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot’, *Science*, 362(6421), pp. 1403–1407. Available at: https://doi.org/10.1126/science.aau056.

Faust, E. *et al.* (2018) 'Cleaner fish escape salmon farms and hybridize with local wrasse populations', *Royal Society Open Science*, 5(3), p. 171752. Available at: https://doi.org/10.1098/rsos.171752.

Fenberg, P.B. *et al.* (2012) 'The science of European marine reserves: Status, efficacy, and future needs', *Marine Policy*, 36(5), pp. 1012–1021. Available at: https://doi.org/10.1016/j.marpol.2012.02.021.

Fernández-Chacón, A. *et al.* (2015) 'Demographic effects of full vs. partial protection from harvesting: inference from an empirical before–after control-impact study on Atlantic cod', *Journal of Applied Ecology*, 52(5), pp. 1206–1215. Available at: https://doi.org/10.1111/1365-2664.12477.

Fernández-Chacón, A. *et al.* (2017) 'Causes of mortality in depleted populations of Atlantic cod estimated from multi-event modelling of mark–recapture and recovery data', *Canadian Journal of Fisheries and Aquatic Sciences*, 74(1), pp. 116–126. Available at: https://doi.org/10.1139/cjfas-2015-0313.

Finucci, B. *et al.* (2018) 'Aggregations and associations in deep-sea chondrichthyans', *ICES Journal of Marine Science*, 75(5), pp. 1613–1626. Available at: https://doi.org/10.1093/icesjms/fsy034.

Fiskeridirektoratet (2022) *Regulering av fisket etter leppefisk i 2023*. Available at: https://www.fiskeridir.no/Yrkesfiske/Dokumenter/Reguleringsmoetet2/november-2022/saksdokumenter/Sak-14-2022-leppefisk.pdf (Accessed: 7 May 2023).

Forskrift om Froan naturreservat, Frøya (1979). Available at: https://lovdata.no/forskrift/1979-12-14-1 (Accessed: 9 May 2023).

Franze, G. *et al.* (2021) *North Sea Ecosystem Cruise*. 20. Havforskningsinstituttet. Available at: https://www.hi.no/hi/publikasjoner/toktrapporter/2021/north-sea-ecosystem-cruise-toktrapport-nr.-20-2021 (Accessed: 4 May 2023).

Freitas, C. *et al.* (2015) 'Behavioral responses of Atlantic cod to sea temperature changes', *Ecology and Evolution*, 5(10), pp. 2070–2083. Available at: https://doi.org/10.1002/ece3.1496.

Freitas, C. *et al.* (2021) 'Sea temperature effects on depth use and habitat selection in a marine fish community', *Journal of Animal Ecology*, 90(7), pp. 1787–1800. Available at: https://doi.org/10.1111/1365-2656.13497.

French, K.J., Shackell, N.L. and Heyer, C.E. den (2018) 'Strong relationship between commercial catch of adult Atlantic halibut (Hippoglossus hippoglossus) and availability of suitable habitat for juveniles in the Northwest Atlantic Ocean', *Fishery Bulletin*, 116(2), pp. 111–131.

Friedlander, A., Brown, E. and Monaco, M. (2007) 'Defining reef fish habitat utilization patterns in Hawaii: Comparisons between marine protected areas and areas open to fishing', *Marine Ecology-progress Series - MAR ECOL-PROGR SER*, 351, pp. 221–233. Available at: https://doi.org/10.3354/meps07112.

Fulton, C., Bellwood, D. and Wainwright, P. (2001) 'The relationship between swimming ability and habitat use in wrasses (Labridae)', *Marine Biology*, 139(1), pp. 25–33. Available at: https://doi.org/10.1007/s002270100565.

Furness, E. and Unsworth, R.K.F. (2020) 'Demersal Fish Assemblages in NE Atlantic Seagrass and Kelp', *Diversity*, 12(10), p. 366. Available at: https://doi.org/10.3390/d12100366.

Ghazilou, A., Shokri, M.R. and Gladstone, W. (2016) 'Animal v. plant-based bait: does the bait type affect census of fish assemblages and trophic groups by baited remote underwater video (BRUV) systems?', *Journal of Fish Biology*, 88(5), pp. 1731–1745. Available at: https://doi.org/10.1111/jfb.12935.

Goetze, J.S. *et al.* (2015) 'Diver operated video most accurately detects the impacts of fishing within periodically harvested closures', *Journal of Experimental Marine Biology and Ecology*, 462, pp. 74–82. Available at: https://doi.org/10.1016/j.jembe.2014.10.004.

Goetze, J.S. *et al.* (2021) 'Increased connectivity and depth improve the effectiveness of marine reserves', *Global Change Biology*, 27(15), pp. 3432–3447. Available at: https://doi.org/10.1111/gcb.15635.

Gonzalez, E. and de Boer, F. (2017) 'The development of the Norwegian wrassefishery and the use of wrasses as cleaner fish in the salmon aquacultureindustry', *Fisheries Science*, 83(5), pp. 661–670. Available at: https://doi.org/10.1007/s12562-017-1110-4.

Grefsrud, E.S. *et al.* (2023) *RISIKORAPPORT NORSK FISKEOPPDRETT 2023*. 6. Havforskningsinstituttet. Available at: https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-2023-6 (Accessed: 15 February 2023).

Grorud-Colvert, K. *et al.* (2021) 'The MPA Guide: A framework to achieve global goals for the ocean', *Science*, 373(6560). Available at: https://doi.org/DOI: 10.1126/science.abf0861.

Guerra, A. *et al.* (2020) 'Fisheries-induced selection against schooling behaviour in marine fishes', *Proceedings of the Royal Society B: Biological Sciences*, 287, p. 20201752. Available at: https://doi.org/10.1098/rspb.2020.1752.

Halvorsen, K. *et al.* (2020) *Kunnskapsbasert innovasjon for optimal ressursutnyttelse i leppefiskeriet*. 3. Havforskningsinstituttet. Available at: https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen-2020-3 (Accessed: 7 May 2023).

Halvorsen, K.T. *et al.* (2017) 'Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas', *Marine Biology Research*, 13(4), pp. 359–369. Available at: https://doi.org/10.1080/17451000.2016.1262042.

Halvorsen, K.T. *et al.* (2021) 'Movement patterns of temperate wrasses (Labridae) within a small marine protected area', *Journal of Fish Biology*, 99(4), pp. 1513–1518. Available at: https://doi.org/10.1111/jfb.14825.

Hamre, K. *et al.* (2013) 'A holistic approach to development of diets for Ballan wrasse (Labrus berggylta) - a new species in aquaculture', *Peerj*, 1, p. e99. Available at: https://doi.org/10.7717/peerj.99.

Hartig, F. (2022) 'DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models'. Available at: http://florianhartig.github.io/DHARMa/ (Accessed: 6 May 2023).

Haug, T. and Tjemsland, J. (1986) 'Changes in size- and age-distributions and age at sexual maturity in atlantic halibut, Hippoglossus hippoglossus, caught in North Norwegian waters', *Fisheries Research*, 4(2), pp. 145–155. Available at: https://doi.org/10.1016/0165-7836(86)90039-1.

Heessen, H. *et al.* (2006) 'ICES Fishmap - An electronic atlas of North Sea fish', in.

Heino, M. *et al.* (2012) 'Seasonal dynamics of growth and mortality suggest contrasting population structure and ecology for cod, pollack, and saithe in a Norwegian fjord', *ICES Journal of Marine Science*, 69(4), pp. 537–546. Available at: https://doi.org/10.1093/icesjms/fss043.

Hesthagen, T. *et al.* (2021a) ‘Fisker: Vurdering av pigghå Squalus acanthias for Norge’, *Rødlista for arter 2021*. Artsdatabanken. Available at: https://www.artsdatabanken.no/lister/rodlisteforarter/2021/12133.

Hesthagen, T. *et al.* (2021b) *Vurdering av kveite Hippoglossus hippoglossus for Norge*. Rødlista for arter 2021. Artsdatabanken. Available at: https://www.artsdatabanken.no/lister/rodlisteforarter/2021/17199.

Hitra kommune (2023) ‘Planbeskrivelse: Kommuneplanens arealdel 2022 – 2034’. Hitra Kommune. Available at: https://www.hitra.kommune.no/samfunnsutvikling/kommuneplan/kommuneplanens-arealdel-2022-2034/.

Hollowed, A.B. *et al.* (2013) ‘Projected impacts of climate change on marine fish and fisheries’, *ICES Journal of Marine Science*, 70(5), pp. 1023–1037. Available at: https://doi.org/10.1093/icesjms/fst081.

Hunter, E. *et al.* (2005) ‘repeated seasonal migration by a thornback ray in the southern north sea’, *Journal of the Marine Biological Association of the United Kingdom*, 85(5), pp. 1199–1200. Available at: https://doi.org/10.1017/S0025315405012300.

ICES (2011) *Pollack (Pollachius pollachius) in Subarea 4 (North Sea) and Division 3.a (North Sea, Skagerrak and Kattegat)*. report. ICES Advice: Recurrent Advice. Available at: https://doi.org/10.17895/ices.advice.18672539.v1.

ICES (2022a) *Cod (Gadus morhua) in Subarea 2 between 62°N and 67°N (Norwegian Sea), southern Norwegian coastal cod*. report. ICES Advice: Recurrent Advice. Available at: https://doi.org/10.17895/ices.advice.20072021.

ICES (2022b) *Saithe (Pollachius virens) in subareas 1 and 2 (Northeast Arctic)*. report. ICES Advice: Recurrent Advice. Available at: https://doi.org/10.17895/ices.advice.19453646.v1.

ICES (2023) ‘ICES Advice 2022’. Available at: https://doi.org/10.17895/ices.pub.c.5796935.v99.

Institute of Marine Research (2022) *Havforkningsinstituttets ulike tokt*, *Havforskningsinstituttet.no*. Available at: https://www.hi.no/hi/tokt/havforskningsinstituttets-ulike-tokt (Accessed: 20 May 2023).

Institute of Marine Research (2023) *Leppefisk*, *Havforskningsinstituttet*. Available at: https://www.hi.no/hi/temasider/arter/leppefisk (Accessed: 8 May 2023).

IUCN (2022) ‘The IUCN Red List of Threatened Species’. IUCN. Available at: https://www.iucnredlist.org (Accessed: 12 April 2023).

Jac, R. *et al.* (2022) ‘Of three sharks and one chimaera: varied habitat preferences across a latitudinal range revealed by coastal and offshore surveys’, *Journal of Fish Biology*, 100(3), pp. 660–674. Available at: https://doi.org/10.1111/jfb.14979.

Jackson-Bué, M. *et al.* (2023) ‘Spatial variability in the structure of fish assemblages associated with Laminaria hyperborea forests in the NE Atlantic’, *Journal of Experimental Marine Biology and Ecology*, 564, p. 151899. Available at: https://doi.org/10.1016/j.jembe.2023.151899.

James, L.C. *et al.* (2017) ‘Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia’, *Marine Ecology Progress Series*, 565, pp. 35–52. Available at: https://doi.org/10.3354/meps11989.

Jansson, E. *et al.* (2017) ‘Genetic analysis of goldsinny wrasse reveals evolutionary insights into population connectivity and potential evidence of inadvertent translocation via aquaculture’, *ICES Journal of Marine Science*, 74(8), pp. 2135–2147. Available at: https://doi.org/10.1093/icesjms/fsx046.

Jensen, Ø. *et al.* (2010) ‘Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention’, *Aquaculture Environment Interactions*, 1(1), pp. 71–83. Available at: https://doi.org/10.3354/aei00008.

Johnson, A.F. *et al.* (2015) ‘Effects of bottom trawling on fish foraging and feeding’, *Proceedings of the Royal Society B-Biological Sciences*, 282(1799), p. 20142336. Available at: https://doi.org/10.1098/rspb.2014.2336.

Jones, R.E. *et al.* (2019) ‘Improving visual biodiversity assessments of motile fauna in turbid aquatic environments’, *Limnology and Oceanography: Methods*, 17(10), pp. 544–554. Available at: https://doi.org/10.1002/lom3.10331.

Jones, R.E. *et al.* (2020) ‘The influence of bait on remote underwater video observations in shallow-water coastal environments associated with the North-Eastern Atlantic’, *PeerJ*, 8, p. e9744. Available at: https://doi.org/10.7717/peerj.9744.

Jørgensen, L. *et al.* (2021) *Marint vern. Havforskningsinstituttets ekspertvurdering av utfordringer og status for arbeid med marint vern i Norge.» Rapport fra havforskningen, 2021–9 Lis lindal Jørgensen, Even Moland, Vivian Husa, Tina Kutti, Alf Ring Kleiven og Gro van der Meeren*.

Keeley, N. *et al.* (2019) ‘Resilience of dynamic coastal benthic ecosystems in response to large-scale finfish farming’, *Aquaculture Environment Interactions*, 11, pp. 161–179. Available at: https://doi.org/10.3354/aei00301.

Kerr, L.A., Kritzer, J.P. and Cadrin, S.X. (2019) ‘Strengths and limitations of before-after-control-impact analysis for testing the effects of marine protected areas on managed populations’, *Ices Journal of Marine Science*, 76(4), pp. 1039–1051. Available at: https://doi.org/10.1093/icesjms/fsz014.

Kleiven, A.R. *et al.* (2021) *Aktiv Forvaltning av Marine Ressurser - Hitra og Frøya*. Sluttrapport 14. Havforskningsinstituttet.

Klima- og miljødepartementet (2021) *Heilskapleg nasjonal plan for bevaring av viktige område for marin natur*. Meld St. 29 (2020-2021). Available at: https://www.regjeringen.no/no/dokumenter/meld.-st.-29-20202021/id2843433/.

Knutsen, J.A. *et al.* (2022) ‘Lobster reserves as a management tool in coastal waters: Two decades of experience in Norway’, *Marine Policy*, 136, p. 104908. Available at: https://doi.org/10.1016/j.marpol.2021.104908.

Krkosek, M., Lewis, M.A. and Volpe, J.P. (2005) ‘Transmission dynamics of parasitic sea lice from farm to wild salmon’, *Proceedings of the Royal Society B-Biological Sciences*, 272(1564), pp. 689–696. Available at: https://doi.org/10.1098/rspb.2004.3027.

Kuparinen, A. *et al.* (2016) ‘Small-scale life history variability suggests potential for spatial mismatches in Atlantic cod management units’, *Ices Journal of Marine Science*, 73(2), pp. 286–292. Available at: https://doi.org/10.1093/icesjms/fsv181.

Lafrance, P. *et al.* (2005) ‘Ontogenetic changes in temperature preference of Atlantic cod’, *Journal of Fish Biology*, 66(2), pp. 553–567. Available at: https://doi.org/10.1111/j.0022-1112.2005.00623.x.

Langlois, T. *et al.* (2020) ‘A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages’, *Methods in Ecology and Evolution*, 11(11), pp. 1401–1409. Available at: https://doi.org/10.1111/2041-210X.13470.

Lecchini, D. and Galzin, R. (2005) ‘Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia)’, *Marine Biology*, 147(1), pp. 47–58. Available at: https://doi.org/10.1007/s00227-004-1543-z.

Legrand, E. *et al.* (2021) ‘Reduced physiological performance in a free-living coralline alga induced by salmon faeces deposition’, *Aquaculture Environment Interactions*, 13, pp. 225–236. Available at: https://doi.org/10.3354/aei00403.

Legrand, E. *et al.* (2022) ‘Effect of sea lice chemotherapeutant hydrogen peroxide on the photosynthetic characteristics and bleaching of the coralline alga Lithothamnion soriferum’, *Aquatic Toxicology*, 247, p. 106173. Available at: https://doi.org/10.1016/j.aquatox.2022.106173.

Letessier, T. *et al.* (2023) *Global human footprint on fish size-spectra across marine ecosystems*. preprint. In Review. Available at: https://doi.org/10.21203/rs.3.rs-2570676/v1.

Logan, J.M. *et al.* (2017) ‘Combining underwater video methods improves effectiveness of demersal fish assemblage surveys across habitats’, *Marine Ecology Progress Series*, 582, pp. 181–200. Available at: https://doi.org/10.3354/meps12326.

Lowry, M. *et al.* (2012) ‘Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries’, *Journal of Experimental Marine Biology and Ecology*, 416–417, pp. 243–253. Available at: https://doi.org/10.1016/j.jembe.2012.01.013.

Marshall, D. *et al.* (2021) ‘Reproductive hyperallometry and managing the world’s fisheries’, *Proceedings of the National Academy of Sciences*, 118, p. e2100695118. Available at: https://doi.org/10.1073/pnas.2100695118.

Marshall, D.J. *et al.* (2019) ‘Underestimating the benefits of marine protected areas for the replenishment of fished populations’, *Frontiers in Ecology and the Environment*, 17(7), pp. 407–413. Available at: https://doi.org/10.1002/fee.2075.

Maruhenda Egea, F.C. *et al.* (2015) ‘A Metabolomic Approach To Detect Effects of Salmon Farming on Wild Saithe (Pollachius virens) Populations’, *Journal of Agricultural and Food Chemistry*, 63(49), pp. 10717–10726. Available at: https://doi.org/10.1021/acs.jafc.5b04765.

Mather, C. (2013) ‘From cod to shellfish and back again? The new resource geography and Newfoundland’s fish economy’, *Applied Geography*, 45, pp. 402–409. Available at: https://doi.org/10.1016/j.apgeog.2013.06.009.

Meier, S. *et al.* (2023) ‘Terrestrial fatty acids from feed oil in feed for farmed salmonids are transferred to the liver, gonads, and muscle of wild Atlantic cod (Gadus morhua)’, *ICES Journal of Marine Science*, p. fsad051. Available at: https://doi.org/10.1093/icesjms/fsad051.

Moe, S.J. *et al.* (2019) ‘Effects of an aquaculture pesticide (diflubenzuron) on non-target shrimp populations: Extrapolation from laboratory experiments to the risk of population decline’, *Ecological Modelling*, 413, p. 108833. Available at: https://doi.org/10.1016/j.ecolmodel.2019.108833.

Moen, F.E. and Svensen, E. (2020) *Dyreliv i havet - norsk marin fauna*. 7th edn. Kolofon.

Moland, E. *et al.* (2012) ‘Lobster and cod benefit from small-scale northern marine protected areas: inference from an empirical before–after control-impact study’. Available at: https://doi.org/10.1098/rspb.2012.2679.

Monk, J. *et al.* (2018) ‘An evaluation of the error and uncertainty in epibenthos cover estimates from AUV images collected with an efficient, spatially-balanced design’, *Plos One*, 13(9), p. e0203827. Available at: https://doi.org/10.1371/journal.pone.0203827.

Munroe, T. *et al.* (2021) ‘IUCN Red List of Threatened Species: Hippoglossus hippoglossus’, *IUCN Red List of Threatened Species* [Preprint]. Available at: https://www.iucnredlist.org/en (Accessed: 14 May 2023).

Nærings, og fiskeridepartementet (2017) *Forskrift om produksjonsområder for akvakultur av matfisk i sjø av laks, ørret og regnbueørret*. Available at: https://lovdata.no/dokument/SF/forskrift/2017-01-16-61?q=produksjonsomr%C3%A5de (Accessed: 10 February 2023).

Narayanaswamy, B.E. *et al.* (2013) ‘Synthesis of Knowledge on Marine Biodiversity in European Seas: From Census to Sustainable Management’, *PLOS ONE*, 8(3), p. e58909. Available at: https://doi.org/10.1371/journal.pone.0058909.

Nickell, L.A. and Sayer, M. (1998) ‘Occurrence and Activity of Mobile Macrofauna on a Sublittoral Reef: Diel and Seasonal Variation’, *Journal of the Marine Biological Association of the United Kingdom*, 78, pp. 1061–1082. Available at: https://doi.org/10.1017/S0025315400044325.

Nillos Kleiven, P.J. *et al.* (2019) ‘Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area’, *Proceedings of the Royal Society B: Biological Sciences*, 286(1894), p. 20182455. Available at: https://doi.org/10.1098/rspb.2018.2455.

Olsgard, F. *et al.* (2008) ‘Effects of bottom trawling on ecosystem functioning’, *Journal of Experimental Marine Biology and Ecology*, 366(1–2), pp. 123–133. Available at: https://doi.org/10.1016/j.jembe.2008.07.036.

Oomen, R.A. and Hutchings, J.A. (2016) ‘Genetic variation in plasticity of life-history traits between Atlantic cod (Gadus morhua) populations exposed to contrasting thermal regimes’, *Canadian Journal of Zoology*, 94(4), pp. 257–264. Available at: https://doi.org/10.1139/cjz-2015-0186.

Ovegård, Mikael *et al.* (2022) ‘Previously undocumented relationship between spiny dogfish Squalus acanthias and juvenile Atlantic horse mackerel Trachurus trachurus revealed by stereo-BRUV’, *Environmental Biology of Fishes*, 105(3), pp. 453–458. Available at: https://doi.org/10.1007/s10641-022-01239-3.

Pillay, T. *et al.* (2021) ‘Benthic habitat mapping from a machine learning perspective on the Cape St Francis inner shelf, Eastern Cape, South Africa’, *Marine Geology*, 440, p. 106595. Available at: https://doi.org/10.1016/j.margeo.2021.106595.

Pillay, T., Cawthra, H.C. and Lombard, A.T. (2021) ‘Integration of machine learning using hydroacoustic techniques and sediment sampling to refine substrate description in the Western Cape, South Africa’, *Marine Geology*, 440, p. 106599. Available at: https://doi.org/10.1016/j.margeo.2021.106599.

Pinheiro, J., Bates, D. and R Core Team (2023) ‘Linear and Nonlinear Mixed Effects Models’. Available at: https://CRAN.R-project.org/package=nlme.

Pita, P. and Freire, J. (2014) ‘The use of spearfishing competition data in fisheries management: evidence for a hidden near collapse of a coastal fish community of Galicia (NE Atlantic Ocean)’, *Fisheries Management and Ecology*, 21(6), pp. 454–469. Available at: https://doi.org/10.1111/fme.12095.

Queiros, A.M. *et al.* (2018) 'Climate change alters fish community size-structure, requiring adaptive policy targets', *Fish and Fisheries*, 19(4), pp. 613–621. Available at: https://doi.org/10.1111/faf.12278.

R Core Team (2022) 'R: A language and environment for statistical computing'. Vienna, Austria.: R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

Rangeley, R. and Kramer, D.L. (1995) 'Use of rocky intertidal habitats by juvenile pollock Pollachius virens', *Marine Ecology Progress Series*, 126, pp. 9–17. Available at: https://doi.org/10.3354/meps126009.

Rangeley, R.W. and Kramer, D.L. (1998) 'Density-Dependent Antipredator Tactics and Habitat Selection in Juvenile Pollock', *Ecology*, 79(3), pp. 943–952. Available at: https://doi.org/10.1890/0012-9658(1998)079[0943:DDATAH]2.0.CO;2.

Righton, D.A. *et al.* (2010) 'Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima', *Marine Ecology Progress Series*, 420, pp. 1-U344. Available at: https://doi.org/10.3354/meps08889.

Schlaff, A.M., Heupel, M.R. and Simpfendorfer, C.A. (2014) 'Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review', *Reviews in Fish Biology and Fisheries*, 24(4), pp. 1089–1103. Available at: https://doi.org/10.1007/s11160-014-9364-8.

Schmid, K. *et al.* (2017) 'Baited remote underwater video as a promising nondestructive tool to assess fish assemblages in clearwater Amazonian rivers: testing the effect of bait and habitat type', *Hydrobiologia*, 784(1), pp. 93–109. Available at: https://doi.org/10.1007/s10750-016-2860-1.

Schmid, K. and Giarrizzo, T. (2019) 'More than Fish – The Potential of Baited Remote Underwater Video to Assess Freshwater Herpetofauna and Dolphins', *Proceedings of the Academy of Natural Sciences of Philadelphia*, 166(1), pp. 1–7. Available at: https://doi.org/10.1635/053.166.0117.

SeaGIS (2020) 'EventMeasure'. Available at: https://www.seagis.com.au/event.html (Accessed: 9 February 2023).

Seitz, R.D. *et al.* (2014) 'Ecological value of coastal habitats for commercially and ecologically important species', *ICES Journal of Marine Science*, 71(3), pp. 648–665. Available at: https://doi.org/10.1093/icesjms/fst152.

Shepherd, T., Page, F. and Macdonald, B. (2002) 'Length and sex-specific associations between spiny dogfish (Squalus acanthias) and hydrographic variables in the Bay of Fundy and Scotian Shelf', *Fisheries Oceanography*, 11(2), pp. 78–89. Available at: https://doi.org/10.1046/j.1365-2419.2002.00191.x.

Sherwood, G.D. and Grabowski, J.H. (2010) 'Exploring the life-history implications of colour variation in offshore Gulf of Maine cod (Gadus morhua)', *ICES Journal of Marine Science*, 67(8), pp. 1640–1649. Available at: https://doi.org/10.1093/icesjms/fsq094.

Simpson, S.J., Humphries, N.E. and Sims, D.W. (2021) 'Habitat selection, fine-scale spatial partitioning and sexual segregation in Rajidae, determined using passive acoustic telemetry', *Marine Ecology Progress Series*, 666, pp. 115–134. Available at: https://doi.org/10.3354/meps13701.

Skiftesvik, A. *et al.* (2014) 'Distribution and habitat preferences of five species of wrasse (Family Labridae) in a Norwegian fjord', *ICES Journal of Marine Science*, 72. Available at: https://doi.org/10.1093/icesjms/fsu211.

Skiftesvik, A.B. *et al.* (2013) ‘Delousing of Atlantic salmon (Salmo salar) by cultured vs. wild ballan wrasse (Labrus bergylta)’, *Aquaculture*, 402, pp. 113–118. Available at: https://doi.org/10.1016/j.aquaculture.2013.03.032.

Skiftesvik, A.B. *et al.* (2014) ‘Wrasse (Labridae) as cleaner fish in salmonid aquaculture – The Hardangerfjord as a case study’, *Marine Biology Research*, 10(3), pp. 289–300. Available at: https://doi.org/10.1080/17451000.2013.810760.

Skjæraasen, J.E. *et al.* (2022) ‘Attraction of cod Gadus morhua from coastal spawning grounds to salmon farms’, *Aquaculture Environment Interactions*, 14, pp. 229–242. Available at: https://doi.org/10.3354/aei00440.

Smith, G.W. *et al.* (1993) ‘Diurnal patterns in the spatial relationships between saithe, Pollachius virens, schooling in the wild’, *Journal of Fish Biology*, 43(sA), pp. 315–325. Available at: https://doi.org/10.1111/j.1095-8649.1993.tb01195.x.

van Son, T.C. *et al.* (2020) ‘Achieving Reliable Estimates of the Spatial Distribution of Kelp Biomass’, *Frontiers in Marine Science*, 7. Available at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00107 (Accessed: 11 April 2023).

Sørensen, O.J.R. and Pedersen, T. (2021) ‘Effects of season, bottom substrate and population dynamics on fish communities in shallow subarctic northeast Atlantic waters’, *Journal of Sea Research*, 178, p. 102136. Available at: https://doi.org/10.1016/j.seares.2021.102136.

Sulikowski, J.A. *et al.* (2010) ‘Use of satellite tags to reveal the movements of spiny dogfish Squalus acanthias in the western North Atlantic Ocean’, *Marine Ecology Progress Series*, 418, pp. 249–254. Available at: https://doi.org/10.3354/meps08821.

Svåsand, T. *et al.* (2000) ‘The enhancement of cod stocks’, *Fish and Fisheries*, 1(2), pp. 173–205. Available at: https://doi.org/10.1046/j.1467-2979.2000.00017.x.

Thorburn, J. *et al.* (2015) ‘Winter residency and site association in the Critically Endangered North East Atlantic spurdog Squalus acanthias’, *Marine Ecology Progress Series*, 526, pp. 113–124. Available at: https://doi.org/10.3354/meps11210.

Torres, A., Abril, A.-M. and Clua, E.E.G. (2020) ‘A Time-Extended (24 h) Baited Remote Underwater Video (BRUV) for Monitoring Pelagic and Nocturnal Marine Species’, *Journal of Marine Science and Engineering*, 8(3), p. 208. Available at: https://doi.org/10.3390/jmse8030208.

Turnbull, J., Johnston, E. and Clark, G. (2021) ‘Evaluating the social and ecological effectiveness of partially protected marine areas’, *Conservation Biology*, 35. Available at: https://doi.org/10.1111/cobi.13677.

Uglem, I. *et al.* (2014) ‘Impacts of wild fishes attracted to open-cage salmonid farms in Norway’, *Aquaculture Environment Interactions*, 6(1), pp. 91–103. Available at: https://doi.org/10.3354/aei00112.

Uglem, I. *et al.* (2020) ‘Does waste feed from salmon farming affect the quality of saithe (Pollachius virens L.) attracted to fish farms?’, *Aquaculture Research*, 51(4), pp. 1720–1730. Available at: https://doi.org/10.1111/are.14519.

Untiedt, C.B. *et al.* (2021) ‘Identifying Black Corals and Octocorals From Deep-Sea Imagery for Ecological Assessments: Trade-Offs Between Morphology and Taxonomy’, *Frontiers in Marine Science*, 8, p. 722839. Available at: https://doi.org/10.3389/fmars.2021.722839.

Vasilakopoulos, P. *et al.* (2022) *Marine Strategy Framework Directive - Thresholds for MSFD criteria: state of play and next steps*, *JRC Publications Repository*. Available at: https://doi.org/10.2760/640026.

Wickham, H. (2016) *ggplot2:Elegant Graphics for Data Analysis*. Springer-Verlag New York. Available at: https://ggplot2.tidyverse.org.

Williams, T., Helle, K. and Aschan, M. (2008) 'The distribution of chondrichthyans along the northern coast of Norway', *ICES Journal of Marine Science*, 65(7), pp. 1161–1174. Available at: https://doi.org/10.1093/icesjms/fsn103.

Wilson, J.R. *et al.* (2020) 'Beyond protection: Fisheries co-benefits of no-take marine reserves', *Marine Policy*, 122, p. 104224. Available at: https://doi.org/10.1016/j.marpol.2020.104224.

Wong, M.Y.L. *et al.* (2019) 'Finding rockpool fishes: a quantitative comparison of non-invasive and invasive methods for assessing abundance, species richness and assemblage structure', *Environmental Biology of Fishes*, 102(1), pp. 81–94. Available at: https://doi.org/10.1007/s10641-019-0846-3.

Wright, P.J. *et al.* (2006) 'Evidence for metapopulation structuring in cod from the west of Scotland and North Sea', *Journal of Fish Biology*, 69(sc), pp. 181–199. Available at: https://doi.org/10.1111/j.1095-8649.2006.01262.x.

Zuur, A.F. and Ieno, E.N. (2016) 'A protocol for conducting and presenting results of regression-type analyses', *Methods in Ecology and Evolution*, 7(6), pp. 636–645. Available at: https://doi.org/10.1111/2041-210X.12577.

Zuur, A.F., Ieno, E.N. and Elphick, C.S. (2010) 'A protocol for data exploration to avoid common statistical problems', *Methods in Ecology and Evolution*, 1(1), pp. 3–14. Available at: https://doi.org/10.1111/j.2041-210X.2009.00001.x.

APPENDIX 1: FIGURES

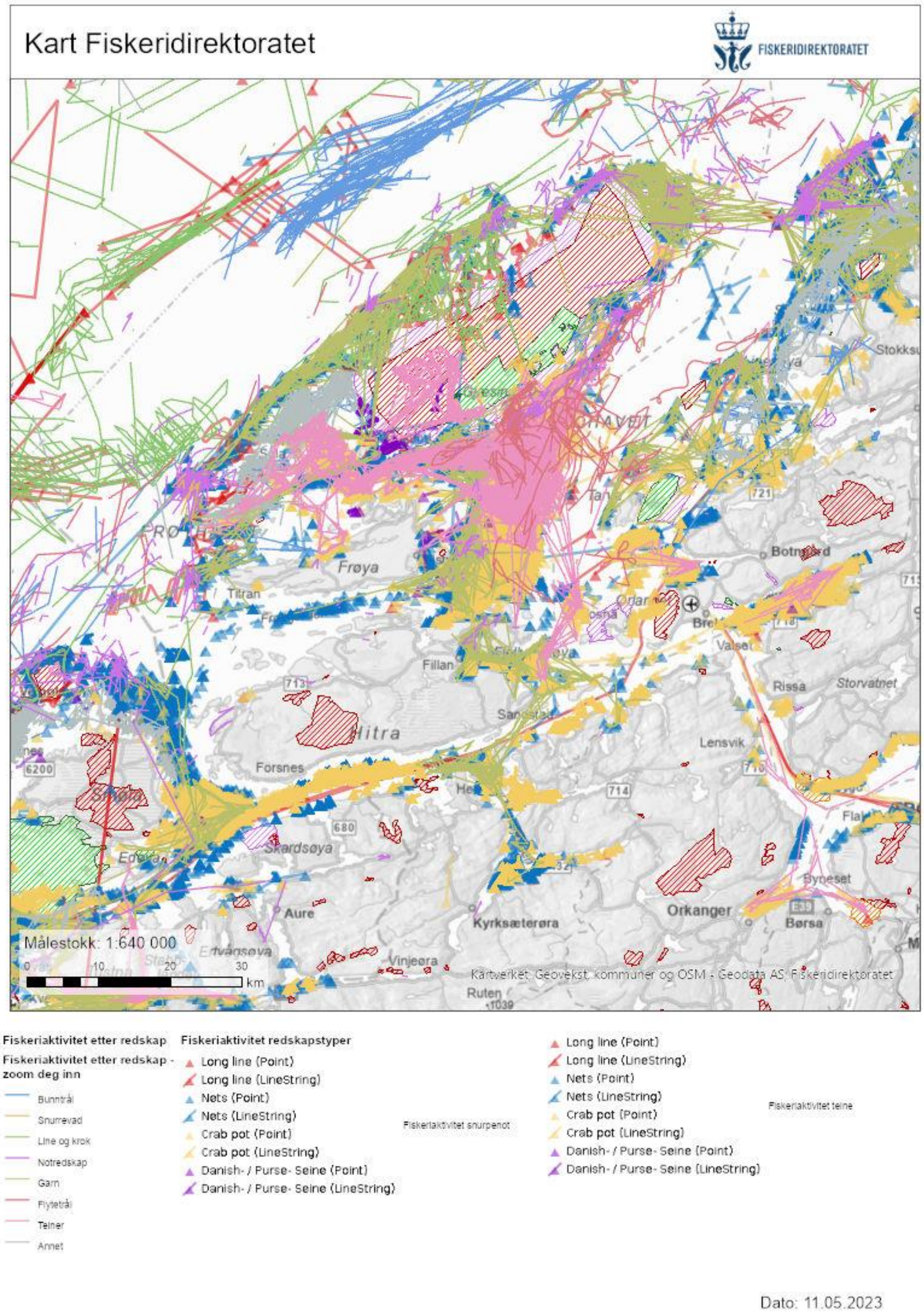


Figure A1: Subject map of fisheries in and around the study area, including Froan nature reserve. Made using Yggdrasil, a map service by the Norwegian directorate of fisheries.

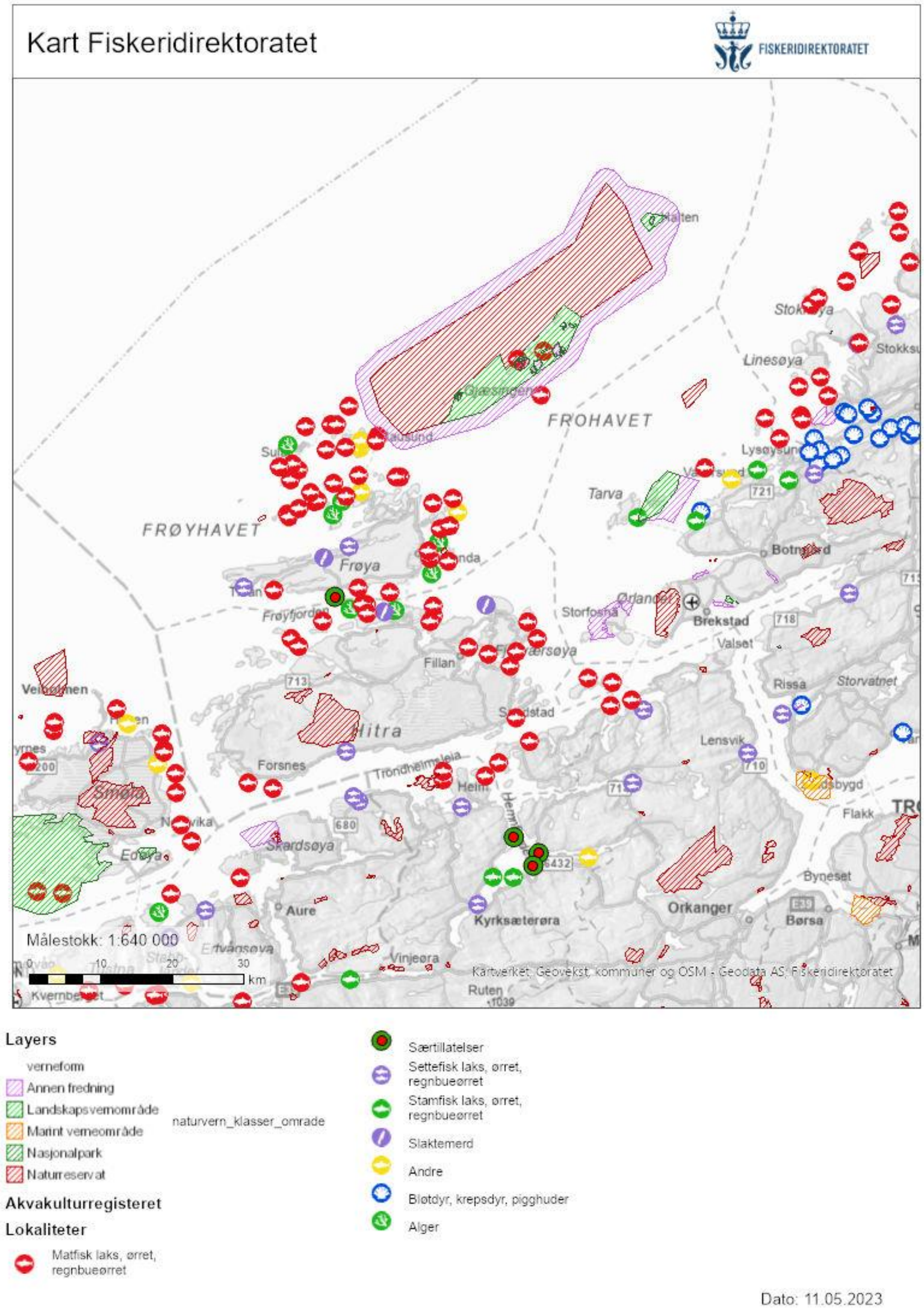


Figure A2: Subject map of aquaculture locations in and around the study area, including Froan nature reserve. Made using Yggdrasil, a map service by the Norwegian directorate of fisheries.

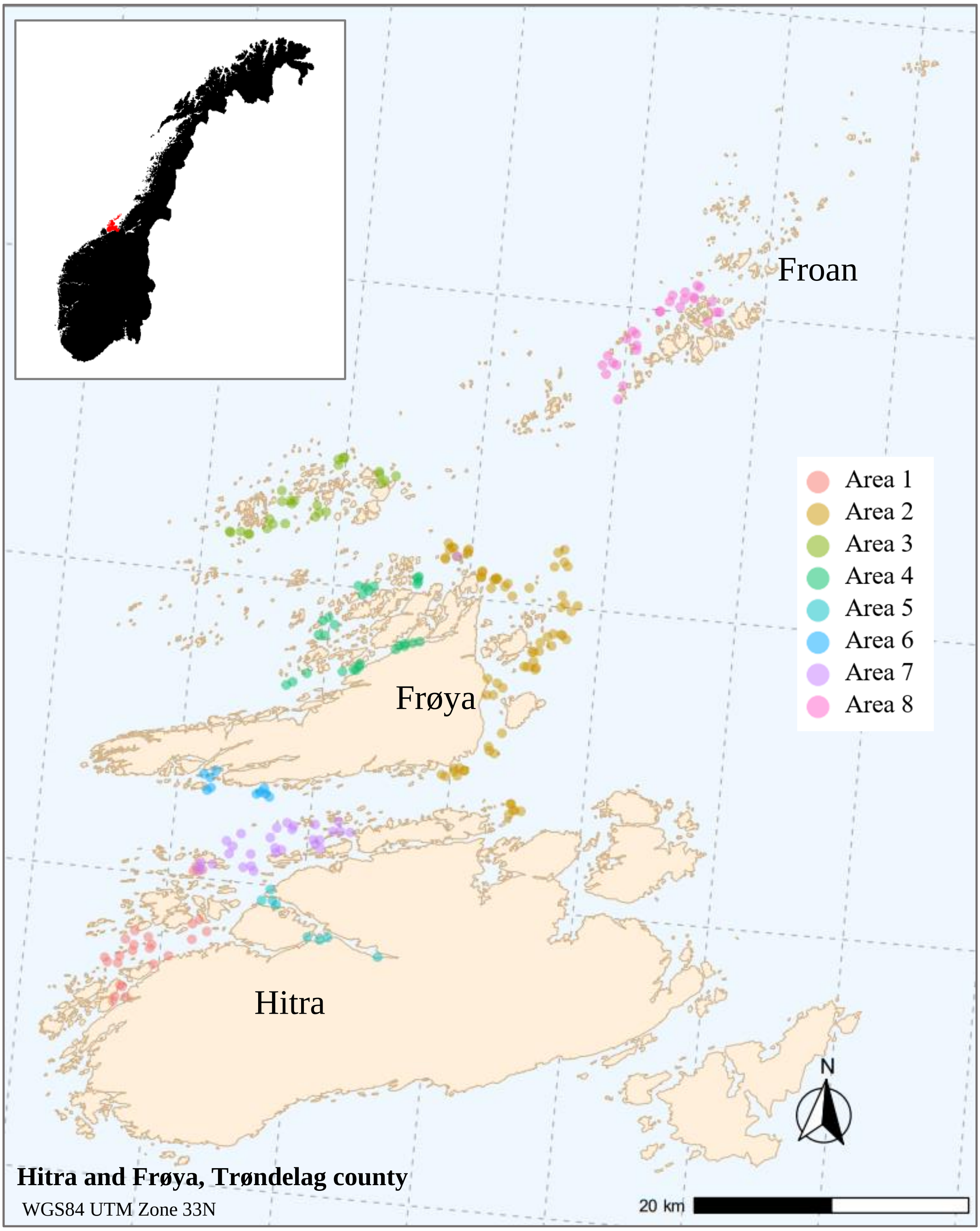


Figure A3: Map of the study area around Hitra and Frøya, including Froan nature reserve. Every station is marked with a point, in a colour which reflects a the sub-area (1-8) within the larger study area that the station is a part of.

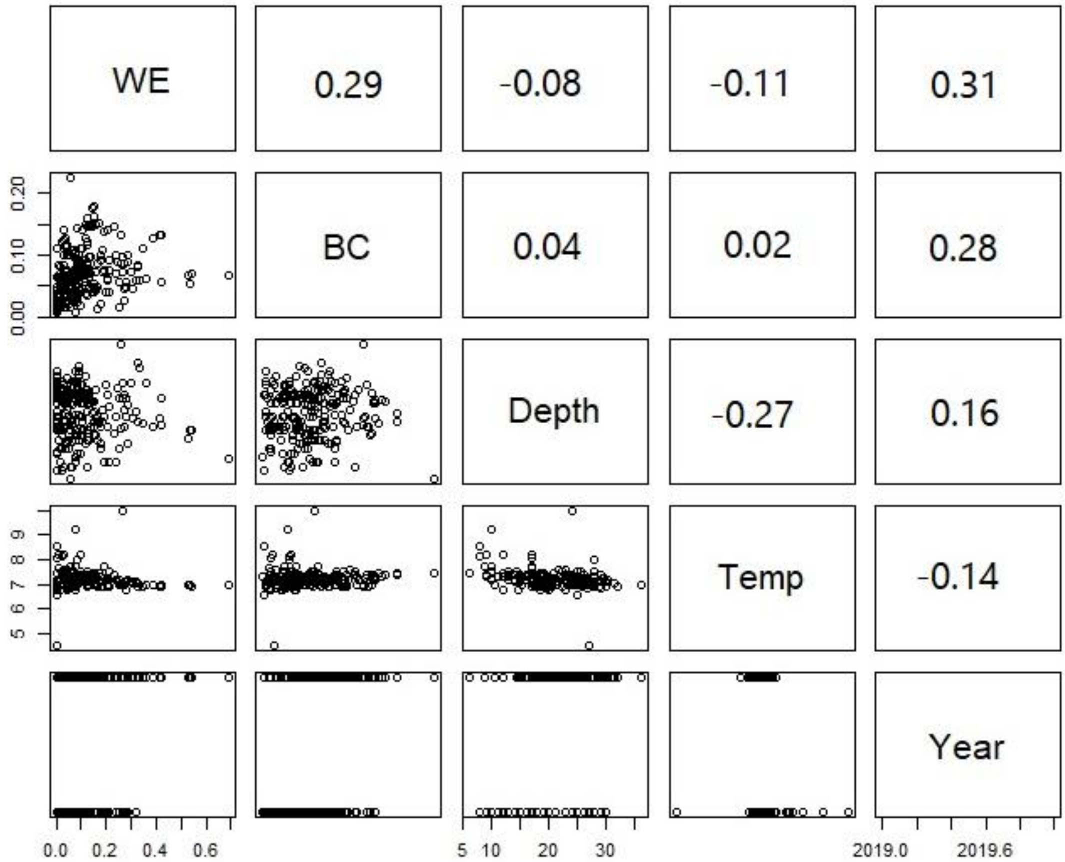
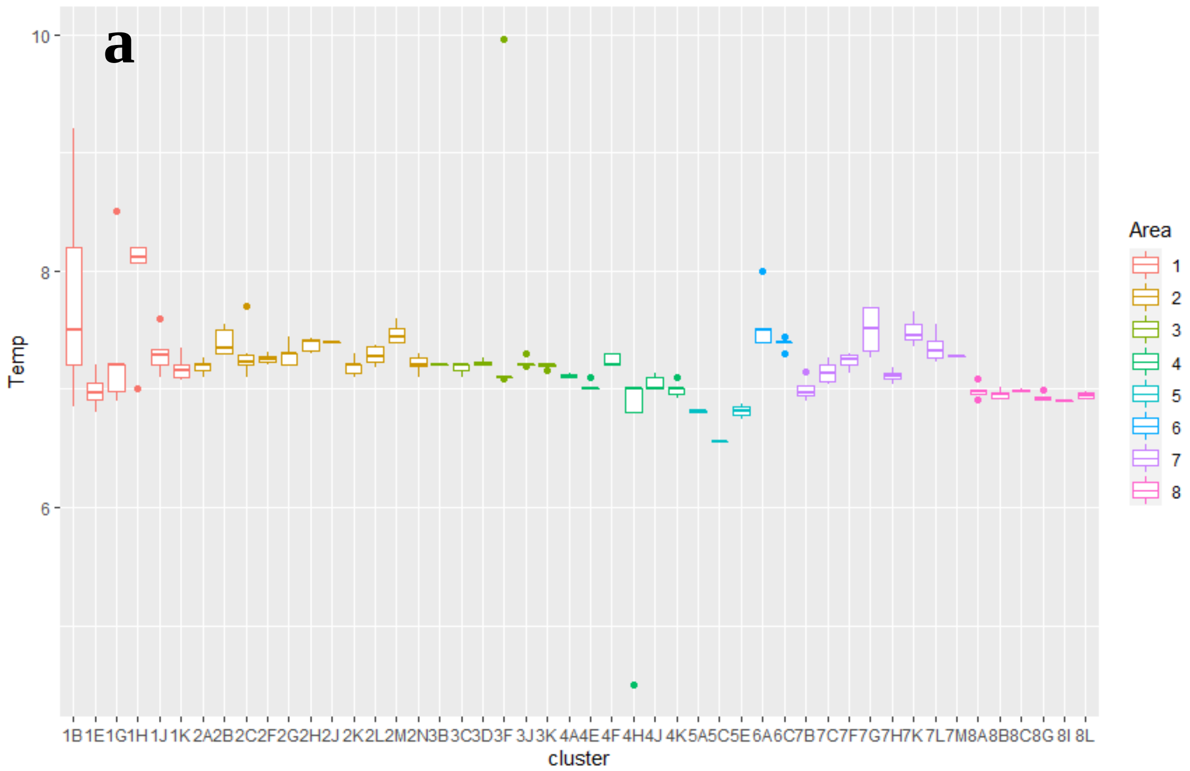


Figure A4: Correlation between explanatory variables were always below 0.32.


a
Temp
cluster
Area
1
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3
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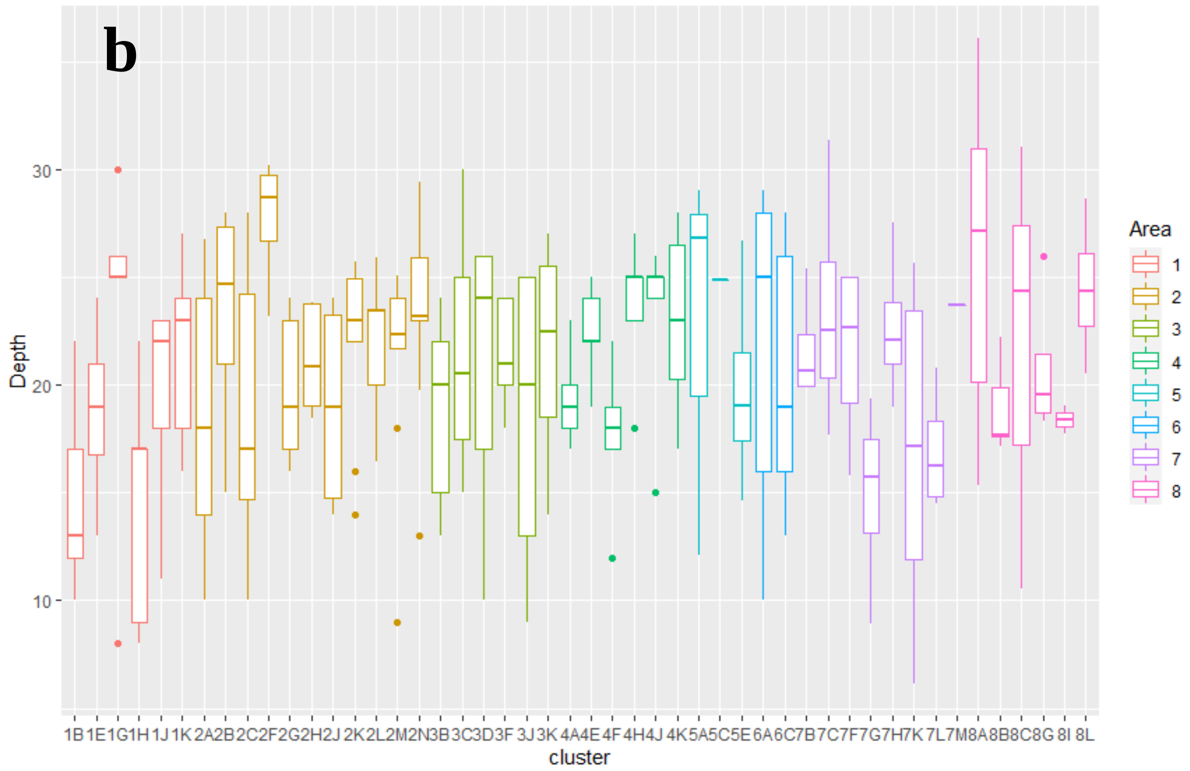
5
6
7
8


b
Depth
cluster
Area
1
2
3
4
5
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7
8

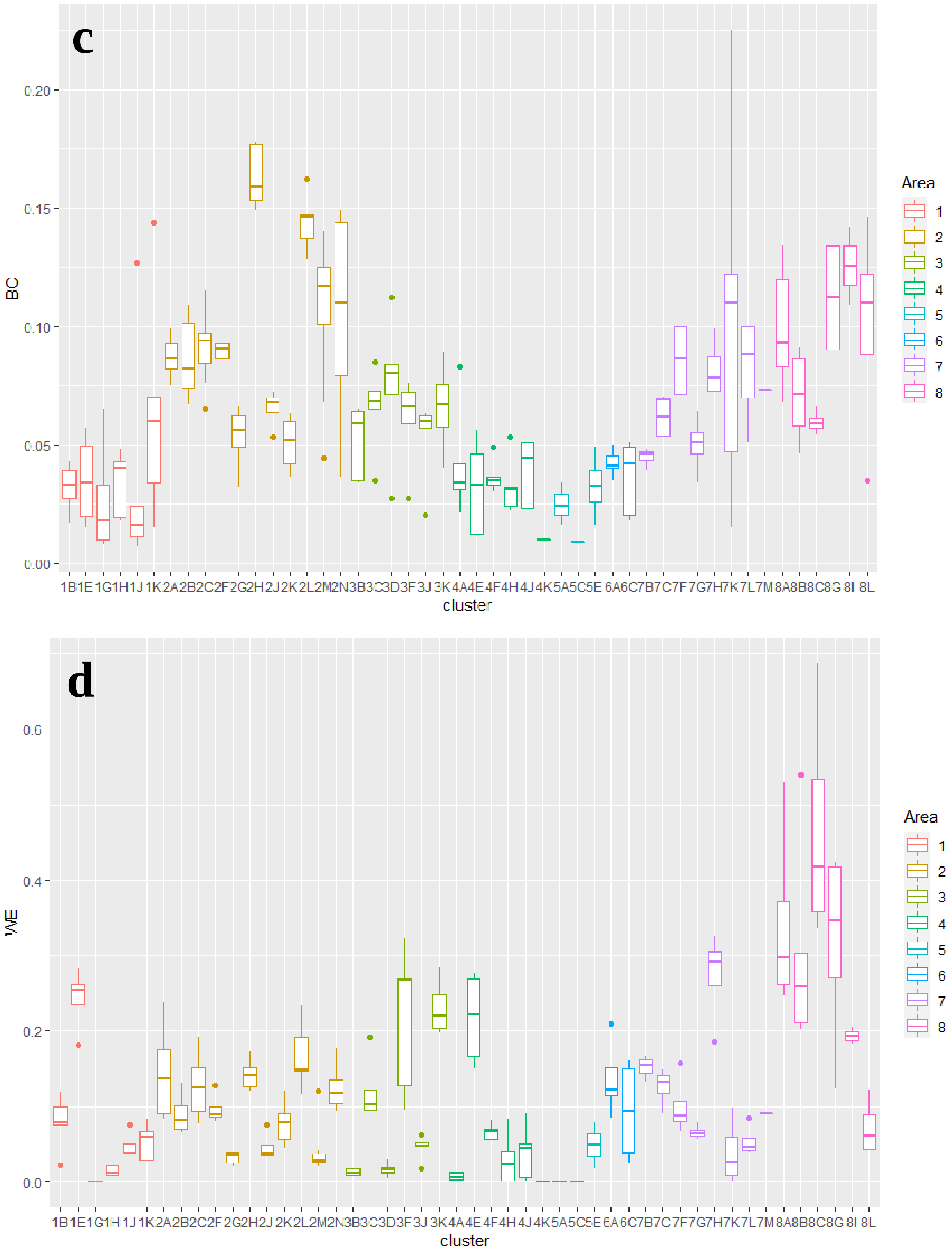

Figure A5: Variation of **(a)** temperature, **(b)** depth, **(c)** bottom current speed, and **(d)** wave exposure at the seafloor (WE), at different clusters in the study area.

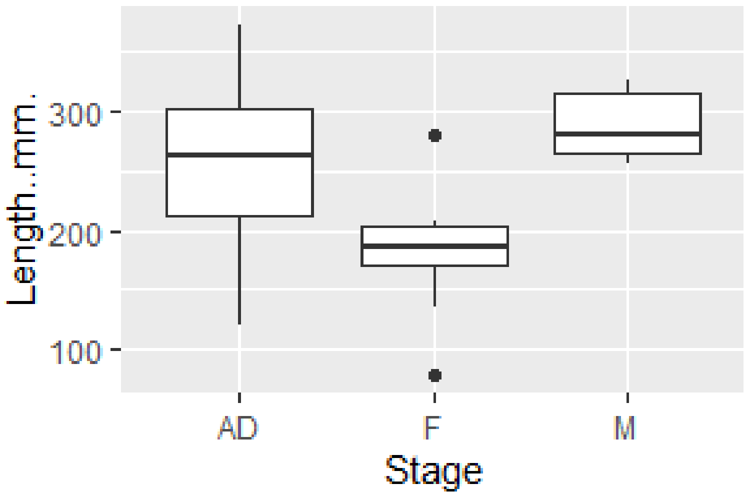

Figure A6: Cuckoo wrasse (*Labrus mixtus*) length distribution of individuals with undefined sex (AD), females (F) and males (M). Sexes are distinguished by colours. Females are red-orange with three black dots at the basis of the dorsal fin, and males are covered in an electric blue pattern, often with orange, red or yellow fins (Moen, 7.utg). Sex was not registered consistently in this study and therefore most individuals are classed as AD. In the cases where sex is defined, the males are longer than the females.

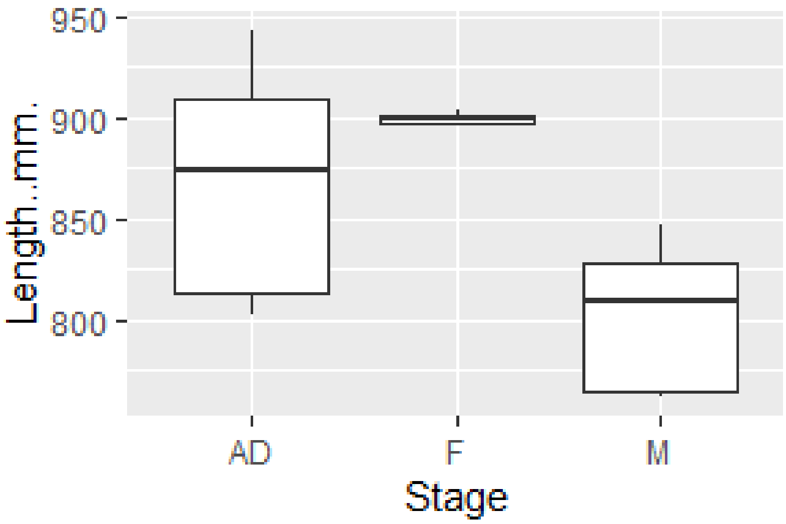

Figure A7: Thornback ray (*Raja clavata*) length distribution of individuals with undefined sex (AD), females (F) and males (M). Sexes are distinguished by the male having clasper organs and the female lacking it (Moen, 7.utg). Sex was not registered consistently in this study and therefore most indivudals are classed as AD. In the few cases where sex is defined, the males are shorter than the females.

APPENDIX 2: TABLES

Table A1: Sampling stations with coordinates and environmental variables.

Station-Year	cluster	Area	Lat	Long	WE	BC	Depth	Temp
1B01-2019	1B	1	63.5407914	8.3922673	0.078	0.027	17.0	7.2
1B02-2019	1B	1	63.5534485	8.3869455	0.076	0.039	10.0	9.2
1B08-2019	1B	1	63.5510097	8.3844151	0.100	0.043	12.0	8.2
1B11-2019	1B	1	63.5473351	8.4129844	0.022	0.017	13.0	7.5
1EE01-2019	1E	1	63.5420528	8.3200272	0.252	0.057	24.0	7.0
1EE02-2019	1E	1	63.5393248	8.3399082	0.255	0.015	13.0	7.2
1EE04-2019	1E	1	63.5393591	8.3245218	0.282	0.047	20.0	6.8
1EE08-2019	1E	1	63.5440370	8.3416400	0.181	0.021	18.0	NA
1G02-2019	1G	1	63.5242409	8.3497352	0.000	0.065	25.0	7.2
1G03-2019	1G	1	63.5172401	8.3407595	0.000	0.008	8.0	8.5
1G08-2019	1G	1	63.5176890	8.3571312	0.000	0.018	26.0	7.2
1G09-2019	1G	1	63.5141275	8.3384702	0.000	0.010	30.0	6.9
1G14-2019	1G	1	63.5251033	8.3466586	0.000	0.033	25.0	7.0
1H02-2019	1H	1	63.5729645	8.4529118	0.011	0.019	17.0	8.2
1H07-2019	1H	1	63.5698546	8.4434455	0.004	0.018	17.0	8.1
1H08-2019	1H	1	63.5657385	8.4655175	0.022	0.040	8.0	8.1
1H09-2019	1H	1	63.5596467	8.4448913	0.028	0.043	9.0	8.2
1J03-2019	1J	1	63.6043540	8.4428310	0.037	0.127	18.0	7.3
1J06-2019	1J	1	63.6076961	8.4403271	0.076	0.007	11.0	7.3
1J07-2019	1J	1	63.6043157	8.4369289	0.034	0.016	23.0	7.2
1J14-2019	1J	1	63.6058465	8.4501511	0.037	0.024	23.0	7.6
1K04-2019	1K	1	63.5483473	8.3595926	0.059	0.060	23.0	7.1
1K06-2019	1K	1	63.5554509	8.3474759	0.083	0.144	16.0	7.2
1K12-2019	1K	1	63.5521218	8.3609301	0.067	0.070	24.0	7.1
1K14-2019	1K	1	63.5583362	8.3807238	0.028	0.034	27.0	7.2
1K15-2019	1K	1	63.5614512	8.3601407	0.028	0.015	18.0	7.4
2A03-2020	2A	2	63.8143610	8.8387985	0.164	0.086	15.0	7.2
2A06-2019	2A	2	63.8137337	8.8370957	0.136	0.096	18.0	7.2
2A09-2019	2A	2	63.8143718	8.8421225	0.238	0.099	10.0	7.2
2A11-2019	2A	2	63.8151170	8.8401674	0.176	0.093	14.0	7.1
2A12-2019	2A	2	63.8148416	8.8173261	0.090	0.082	24.0	7.2
2A12-2020	2A	2	63.8145319	8.8179927	0.083	0.082	26.0	7.3
2A13-2019	2A	2	63.8080690	8.8337270	0.213	0.075	10.0	7.2
2A15-2019	2A	2	63.8180487	8.8179870	0.100	0.086	23.0	7.2
2A15-2020	2A	2	63.8185830	8.8185760	0.086	0.086	26.7	7.3
2B02-2019	2B	2	63.6646160	8.8976337	0.131	0.079	15.0	7.4
2B05-2019	2B	2	63.6685062	8.8927096	0.065	0.107	28.0	7.3
2B05-2020	2B	2	63.6687237	8.8937897	0.073	0.109	25.4	7.6
2B06-2019	2B	2	63.6645134	8.9001529	0.104	0.085	20.0	7.3
2B13-2020	2B	2	63.6644124	8.9092636	0.069	0.072	28.0	7.5
2B15-2019	2B	2	63.6613630	8.8918210	0.089	0.067	24.0	7.3
2C01-2019	2C	2	63.7821342	8.9320350	0.175	0.099	13.0	7.3

2C03-2019	2C	2	63.7742113	8.9313758	0.125	0.115	17.0	7.2
2C05-2019	2C	2	63.7798739	8.9239614	0.192	0.076	10.0	7.7
2C09-2020	2C	2	63.7757174	8.9139813	0.128	0.065	16.4	7.3
2C10-2019	2C	2	63.7821863	8.9435693	0.077	0.095	28.0	7.1
2C10-2020	2C	2	63.7817070	8.9457326	0.086	0.094	25.4	7.2
2C15-2019	2C	2	63.7792620	8.9520738	0.102	0.093	23.0	7.2
2F08-2020	2F	2	63.8121802	8.8577176	0.089	0.092	30.2	7.2
2F13-2020	2F	2	63.8106235	8.8900806	0.128	0.096	23.2	7.3
2F14-2020	2F	2	63.8041456	8.8661768	0.080	0.078	27.8	7.2
2F15-2020	2F	2	63.8099647	8.8541948	0.089	0.089	29.6	7.3
2G04-2019	2G	2	63.7488905	8.8416921	0.036	0.032	24.0	7.2
2G09-2019	2G	2	63.7464521	8.8562249	0.039	0.049	23.0	7.2
2G12-2019	2G	2	63.7385274	8.8521968	0.025	0.066	17.0	7.4
2G14-2019	2G	2	63.7381297	8.8419171	0.020	0.062	16.0	7.3
2G15-2019	2G	2	63.7438293	8.8650295	0.039	0.056	19.0	7.3
2H01-2020	2H	2	63.8077729	8.9399032	0.120	0.149	23.75	7.3
2H04-2020	2H	2	63.8022290	8.9453147	0.141	0.177	20.83	7.4
2H09-2020	2H	2	63.7980038	8.9557976	0.126	0.159	23.83	7.3
2H11-2020	2H	2	63.8018805	8.9642263	0.173	0.153	18.45	7.4
2H13-2020	2H	2	63.7999297	8.9394380	0.152	0.178	19.0	7.4
2J09-2019	2J	2	63.7047121	8.8522936	0.034	0.067	24.0	7.4
2J13-2019	2J	2	63.7141296	8.8702883	0.036	0.053	14.0	7.4
2J14-2019	2J	2	63.7004190	8.8617741	0.076	0.069	15.0	7.4
2J15-2019	2J	2	63.7018956	8.8540961	0.039	0.072	23.0	7.4
2K02-2019	2K	2	63.7590458	8.8983793	0.120	0.057	14.0	7.2
2K03-2019	2K	2	63.7588535	8.9117988	0.091	0.042	25.0	7.2
2K07-2019	2K	2	63.7693511	8.9056745	0.056	0.052	23.0	7.2
2K07-2020	2K	2	63.7689144	8.9031554	0.045	0.044	24.94	7.3
2K08-2019	2K	2	63.7699206	8.9134201	0.079	0.060	16.0	7.2
2K08-2020	2K	2	63.7577301	8.9098568	0.085	0.036	24.41	7.3
2K12-2020	2K	2	63.7630558	8.9068268	0.045	0.060	25.74	7.1
2K14-2020	2K	2	63.7589836	8.8937188	0.065	0.063	22.74	7.1
2L07-2020	2L	2	63.8296411	8.9384534	0.147	0.147	23.43	7.3
2L10-2020	2L	2	63.8260495	8.9246169	0.116	0.128	25.94	7.2
2L11-2020	2L	2	63.8377868	8.9371373	0.148	0.162	23.49	7.4
2L12-2020	2L	2	63.8269754	8.9440451	0.233	0.146	16.47	7.4
2L13-2020	2L	2	63.8354913	8.9278553	0.192	0.137	20.03	7.2
2M01-2019	2M	2	63.6862098	8.8058592	0.029	0.101	23.0	7.4
2M02-2020	2M	2	63.6836025	8.8104481	0.027	0.125	25.04	7.5
2M05-2019	2M	2	63.6888322	8.8126254	0.121	0.123	9.0	7.4
2M08-2019	2M	2	63.6872564	8.8197912	0.037	0.113	24.0	7.4
2M08-2020	2M	2	63.6875320	8.8204879	0.042	0.117	21.68	7.6
2M11-2020	2M	2	63.6834449	8.7872220	0.024	0.068	22.35	7.5
2M14-2019	2M	2	63.6824701	8.7933584	0.028	0.140	18.0	7.4
2M15-2020	2M	2	63.6882435	8.8045342	0.020	0.044	24.87	7.5
2N03-2020	2N	2	63.8347501	8.7642873	0.159	0.149	19.72	7.3
2N04-2020	2N	2	63.8307608	8.7939499	0.131	0.148	23.2	7.2
2N07-2020	2N	2	63.8304875	8.7670479	0.093	0.082	29.39	7.3

2N09-2019	2N	2	63.8320740	8.7731692	0.098	0.076	27.0	7.2
2N09-2020	2N	2	63.8322038	8.7704885	0.117	0.036	24.78	7.3
2N10-2019	2N	2	63.8292390	8.7940020	0.140	0.149	23.0	7.2
2N11-2019	2N	2	63.8321987	8.7951955	0.104	0.140	27.0	7.1
2N12-2019	2N	2	63.8250944	8.7616387	0.122	0.083	23.0	7.3
2N13-2019	2N	2	63.8241369	8.7619534	0.112	0.073	23.0	7.2
2N14-2020	2N	2	63.8265686	8.7786392	0.104	0.110	24.33	7.2
3B03-2019	3B	3	63.8462683	8.5681530	0.011	0.065	15.0	7.2
3B04-2019	3B	3	63.8432987	8.5631922	0.018	0.059	13.0	7.2
3B08-2019	3B	3	63.8472352	8.5788212	0.017	0.035	24.0	7.2
3B15-2019	3B	3	63.8509401	8.5642934	0.009	0.034	20.0	7.2
3C02-2019	3C	3	63.8274436	8.4405240	0.093	0.065	26.0	7.2
3C07-2019	3C	3	63.8287349	8.4553986	0.105	0.073	17.0	7.2
3C10-2019	3C	3	63.8280778	8.4384979	0.076	0.065	30.0	7.1
3C14-2019	3C	3	63.8276058	8.4684794	0.127	0.072	15.0	7.2
3C15-2019	3C	3	63.8275411	8.4667012	0.101	0.085	19.0	7.2
3D03-2019	3D	3	63.8522706	8.5300848	0.012	0.027	24.0	7.2
3D05-2019	3D	3	63.8580708	8.5098659	0.004	0.112	26.0	7.2
3D06-2019	3D	3	63.8502729	8.5265432	0.019	0.080	17.0	7.2
3D08-2019	3D	3	63.8510958	8.5116092	0.016	0.071	10.0	7.2
3D09-2019	3D	3	63.8523242	8.5246000	0.029	0.084	26.0	7.3
3F04-2019	3F	3	63.8768932	8.6513725	0.322	0.059	21.0	7.1
3F06-2019	3F	3	63.8714631	8.6609791	0.095	0.066	20.0	7.1
3F12-2019	3F	3	63.8753366	8.6518412	0.267	0.072	24.0	10.0
3F14-2019	3F	3	63.8693677	8.6561259	0.269	0.027	18.0	7.1
3F15-2019	3F	3	63.8751179	8.6767309	0.127	0.076	24.0	7.1
3J01-2019	3J	3	NA	NA	0.017	0.062	25.0	NA
3J03-2019	3J	3	63.8368197	8.5197282	0.063	0.057	9.0	7.3
3J10-2019	3J	3	63.8387951	8.4959841	0.052	0.020	20.0	7.2
3J14-2019	3J	3	63.8324276	8.4937817	0.047	0.060	25.0	7.2
3J15-2019	3J	3	63.8356814	8.5016234	0.047	0.063	13.0	7.2
3K04-2019	3K	3	63.8837700	8.5959235	0.205	0.063	25.0	7.2
3K06-2019	3K	3	63.8837711	8.5977975	0.197	0.040	27.0	7.2
3K12-2019	3K	3	63.8821936	8.5888854	0.236	0.071	20.0	7.2
3K15-2019	3K	3	63.8784808	8.5897901	0.284	0.089	14.0	7.2
4A11-2019	4A	4	63.8007889	8.6483457	0.012	0.031	20.0	7.1
4A12-2019	4A	4	63.7985768	8.6535192	0.003	0.042	23.0	7.1
4A13-2019	4A	4	63.8018036	8.6601530	0.002	0.021	19.0	7.1
4A14-2019	4A	4	63.7955228	8.6445416	0.006	0.034	17.0	7.1
4A15-2019	4A	4	63.8011298	8.6373383	0.011	0.083	18.0	7.1
4EE06-2019	4E	4	63.7407067	8.5740037	0.166	0.012	19.0	7.0
4EE07-2019	4E	4	63.7317135	8.5454114	0.276	0.056	24.0	7.1
4EE14-2019	4E	4	63.7342110	8.5542828	0.269	0.046	25.0	7.0
4F03-2019	4F	4	63.8079040	8.7250812	0.082	0.033	12.0	7.3
4F05-2019	4F	4	63.8110075	8.7252018	0.067	0.036	18.0	7.2
4F06-2019	4F	4	63.8100685	8.7233643	0.056	0.030	19.0	7.3
4F12-2019	4F	4	63.8060464	8.7239530	0.056	0.035	17.0	7.2
4H02-2019	4H	4	63.7501855	8.6509778	0.000	0.022	27.0	4.5

4H08-2019	4H	4	63.7441220	8.6263580	0.083	0.024	25.0	7.0
4H12-2019	4H	4	63.7484022	8.6504097	0.001	0.031	18.0	7.0
4H14-2019	4H	4	63.7461766	8.6425089	0.040	0.032	23.0	6.8
4H15-2019	4H	4	63.7459382	8.6460756	0.023	0.053	25.0	7.0
4J01-2019	4J	4	63.7758258	8.5896880	0.006	0.023	25.0	7.1
4J08-2019	4J	4	63.7785548	8.5982178	0.000	0.012	24.0	7.0
4J10-2019	4J	4	63.7741020	8.6081310	0.090	0.044	15.0	7.1
4J13-2019	4J	4	63.7665930	8.5949358	0.051	0.051	25.0	7.0
4J14-2019	4J	4	63.7665431	8.5856022	0.045	0.076	26.0	7.0
4K03-2019	4K	4	63.7673598	8.7259254	0.000	0.010	27.0	7.0
4K04-2019	4K	4	63.7663729	8.7145383	0.000	0.010	20.0	7.0
4K06-2019	4K	4	63.7620561	8.7017559	0.000	0.010	21.0	7.0
4K07-2019	4K	4	63.7646339	8.7059797	0.000	0.010	17.0	7.1
4K09-2019	4K	4	63.7646738	8.7142312	0.000	0.010	28.0	6.9
4K15-2019	4K	4	63.7687341	8.7361401	0.000	0.010	25.0	7.0
5A07-2020	5A	5	63.5687780	8.6137345	0.000	0.016	12.12	6.8
5A12-2020	5A	5	63.5698164	8.6432776	0.000	0.034	26.8	6.8
5A15-2020	5A	5	63.5676698	8.6321101	0.000	0.024	29.02	6.8
5C04-2020	5C	5	63.5602439	8.7195805	0.000	0.009	24.87	6.6
5EE01-2020	5E	5	63.5876656	8.5629832	0.018	0.049	18.37	6.7
5EE02-2020	5E	5	63.5903930	8.5570850	0.079	0.029	14.66	6.8
5EE06-2020	5E	5	63.5896473	8.5411138	0.040	0.036	26.67	6.9
5EE13-2020	5E	5	63.5973496	8.5523394	0.059	0.016	19.75	6.9
6A03-2019	6A	6	63.6601620	8.5233172	0.210	0.040	10.0	7.5
6A05-2019	6A	6	63.6586798	8.5179099	0.151	0.045	16.0	7.4
6A11-2019	6A	6	63.6594808	8.5314000	0.115	0.050	29.0	7.4
6A14-2019	6A	6	63.6630161	8.5284038	0.084	0.041	28.0	8.0
6A15-2019	6A	6	63.6575646	8.5372524	0.122	0.035	25.0	7.5
6C01-2019	6C	6	63.6579620	8.4447525	0.160	0.042	26.0	7.4
6C07-2019	6C	6	63.6664540	8.4474862	0.094	0.018	16.0	7.4
6C12-2019	6C	6	63.6713679	8.4550298	0.024	0.020	28.0	7.3
6C13-2019	6C	6	63.6683451	8.4373730	0.038	0.051	13.0	7.4
6C14-2019	6C	6	63.6597151	8.4500788	0.150	0.049	19.0	7.4
7B02-2020	7B	7	63.6082841	8.5252714	0.161	0.045	19.85	7.2
7B04-2020	7B	7	63.6100094	8.5092932	0.132	0.047	25.37	7.0
7B06-2020	7B	7	63.6113560	8.5209450	0.167	0.048	20.01	6.9
7B09-2020	7B	7	63.6191885	8.5184538	0.149	0.039	21.33	7.0
7C05-2020	7C	7	63.6311781	8.5447382	0.139	0.070	23.87	7.2
7C07-2020	7C	7	63.6239214	8.5628481	0.090	0.053	31.37	7.1
7C08-2020	7C	7	63.6215026	8.5549052	0.148	0.054	17.66	7.0
7C09-2020	7C	7	63.6246842	8.5532242	0.126	0.069	21.2	7.3
7F06-2020	7F	7	63.6379035	8.5754874	0.066	0.103	25.01	7.1
7F07-2020	7F	7	63.6379636	8.5528239	0.158	0.073	15.79	7.3
7F10-2020	7F	7	63.6402535	8.5771815	0.089	0.099	20.33	7.2
7F12-2020	7F	7	63.6419165	8.5672030	0.085	0.066	25.01	7.3
7G03-2020	7G	7	63.6325785	8.6081886	0.065	0.064	14.57	7.3
7G06-2020	7G	7	63.6273511	8.6197328	0.057	0.034	8.9	7.7
7G08-2020	7G	7	63.6299623	8.6114739	0.079	0.050	16.9	7.7

7G10-2020	7G	7	63.6328356	8.6179060	0.062	0.052	19.36	7.3
7H05-2020	7H	7	63.6261602	8.4809576	0.326	0.083	19.0	7.0
7H09-2020	7H	7	63.6318024	8.5011294	0.284	0.099	22.56	7.2
7H13-2020	7H	7	63.6230979	8.4907098	0.298	0.072	27.53	7.1
7H14-2020	7H	7	63.6179766	8.4865636	0.186	0.073	21.63	7.1
7K02-2020	7K	7	63.6460759	8.6425024	0.009	0.015	17.14	7.7
7K04-2020	7K	7	63.6399332	8.6462897	0.059	0.225	6.15	7.4
7K13-2020	7K	7	63.8265686	8.7786392	0.098	0.110	25.66	7.6
7K14-2020	7K	7	63.6391957	8.6356145	0.025	0.122	23.46	7.4
7K15-2020	7K	7	63.6397446	8.6612377	0.001	0.047	11.94	7.5
7L04-2020	7L	7	63.6104904	8.4466335	0.042	0.100	14.48	7.6
7L08-2020	7L	7	63.6071137	8.4442797	0.049	0.100	14.97	7.3
7L11-2020	7L	7	63.6100051	8.4638734	0.084	0.051	17.5	7.4
7L12-2020	7L	7	63.6055883	8.4465682	0.039	0.076	20.78	7.2
7M09-2020	7M	7	63.6426684	8.6086600	0.090	0.073	23.73	7.3
8A03-2020	8A	8	64.0171717	9.1015354	0.386	0.127	17.99	7.0
8A07-2020	8A	8	64.0093752	9.0949118	0.265	0.098	27.72	7.0
8A08-2020	8A	8	64.0086016	9.0798334	0.529	0.068	15.34	7.0
8A10-2020	8A	8	64.0183748	9.0971643	0.261	0.134	36.09	7.0
8A11-2020	8A	8	64.0133458	9.0801390	0.328	0.081	32.08	6.9
8A15-2020	8A	8	64.0106967	9.0934894	0.246	0.088	26.52	7.1
8B07-2020	8B	8	63.9791663	8.9997542	0.303	0.046	19.87	7.0
8B08-2020	8B	8	63.9724551	9.0156007	0.202	0.058	17.67	7.0
8B10-2020	8B	8	63.9844868	9.0073723	0.539	0.071	17.15	6.9
8B11-2020	8B	8	63.9830414	9.0128676	0.211	0.091	22.23	6.9
8B14-2020	8B	8	63.9755120	9.0152394	0.259	0.086	17.61	7.0
8C05-2020	8C	8	63.9989720	9.0448947	0.418	0.057	24.34	7.0
8C06-2020	8C	8	63.9992875	9.0457922	0.534	0.054	17.24	7.0
8C08-2020	8C	8	64.0061780	9.0584073	0.336	0.059	31.0	NA
8C13-2020	8C	8	64.0104752	9.0619426	0.687	0.066	10.57	7.0
8C14-2020	8C	8	64.0033910	9.0746857	0.358	0.061	27.38	7.0
8G05-2020	8G	8	63.9626855	8.9820033	0.271	0.086	21.44	7.0
8G07-2020	8G	8	63.9606003	8.9671958	0.417	0.134	19.55	6.9
8G08-2020	8G	8	63.9548985	8.9736961	0.347	0.112	18.73	6.9
8G13-2020	8G	8	63.9614940	8.9880608	0.123	0.090	25.96	6.9
8G14-2020	8G	8	63.9670213	8.9737030	0.424	0.134	18.35	6.9
8I04-2020	8I	8	63.9390934	8.9950893	0.205	0.142	17.77	6.9
8I05-2020	8I	8	63.9483083	9.0006396	0.182	0.109	19.02	6.9
8L06-2020	8L	8	63.9950406	9.1181051	0.042	0.035	23.49	7.0
8L10-2020	8L	8	64.0021459	9.1292163	0.079	0.106	20.5	6.9
8L11-2020	8L	8	64.0021512	9.1339396	0.044	0.114	28.63	6.9
8L12-2020	8L	8	64.0086415	9.1207815	0.122	0.146	25.23	7.0

Table A2: Species richness model output.

	Species richness			
	Effect	**SE**	**z**	***p***
WE	-0.025	0.390	-0.065	0.949
BC	-0.227	1.075	-0.211	0.833
Depth	0.006	0.008	0.769	0.442
Temp	0.156	0.121	1.292	0.196
Year (2020)	-0.092	0.088	-1.046	0.296

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