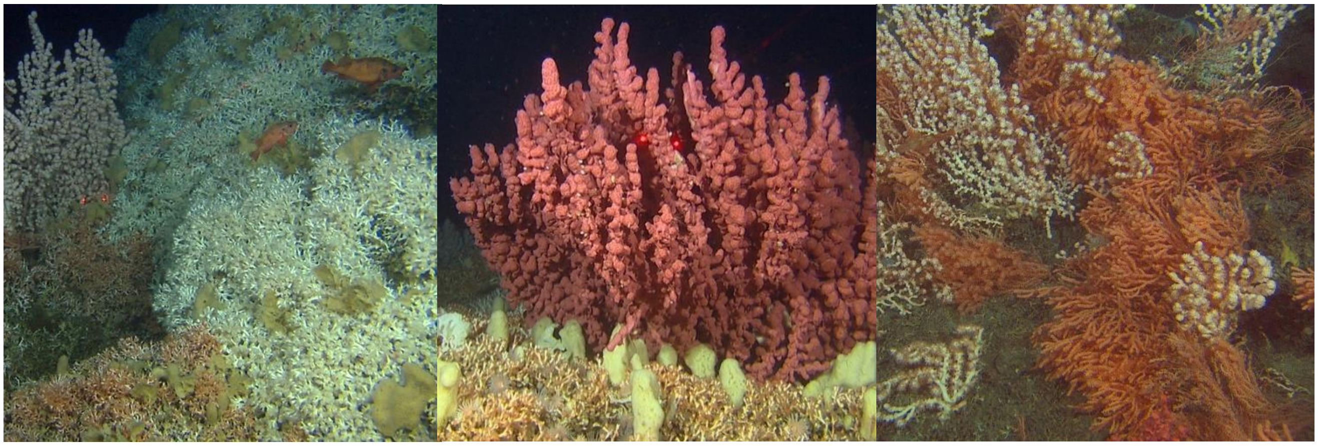
Driving forces in the distributions of the three most common deep-water coral species in Norway: *Lophelia pertusa*, *Paragorgia arborea*, and *Primnoa resedaeformis*



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Pictured on title page: video observations of a white *Lophelia pertusa* reef, a red *Paragorgia arborea* ("bubblegum coral"), and an orange *Primnoa resedaeformis* ("risengrynkorall").

Source: Pål Buhl-Mortensen (IMR)

ABSTRACT

This thesis explores a set of environmental variables may be used to predict the spatial distribution of the three most common cold-water coral (CWC) species in Norway: *Lophelia pertusa*, *Paragorgia arborea*, and *Primnoa resedaeformis*. CWCs are important biogenic habitats that provide substrate and living space for a variety of deep-sea sessile organisms and commercially important fish, but are threatened by various anthropogenic impacts (e.g. bottom trawling, petroleum exploration and mineral mining), leading to increased efforts to appraise and protect them. Deep-sea exploration is difficult due to cost, time and access constraints, so in order to target protection efforts, species distribution models (SDM) can be created to find areas with the highest probability of species presence.

The Maximum Entropy (Maxent) 3.4.1 program was used on CWC presence data and several environmental variable layers covering the Norwegian continental shelf from the southern end of Norway to Svalbard. Data on CWC presence positions from MAREANO video records for all three species together with the IMR *Lophelia* Reef Database with additional *Lophelia* presence points were used. The environmental variables were: depth and terrain proxies from a bathymetry layer (processed to 176 x 176m resolution) from EMODnet, oceanographic variables from the Norkyst-800 model, surface chlorophyll *a* concentration from the Ocean Biology Processing Group in NASA, and sediment and marine landscape type as defined by NGU. Data was prepared and visualized in ArcMap 10.5.1 and environmental characteristics at CWC presence points were summarized in Excel prior to modeling.

Maxent produced SDMs that indicated high probability of presence especially on the continental margin and along the Norwegian coast and near fjords. Jackknife tests showed that sediment was particularly important for the gorgonian corals, while chlorophyll *a* uniquely predicted well for *Lophelia*. Depth, mean current speed, marine landscape, and slope were important individual indicators of presence for all. The hope is that information gained from the modeled distributions and predictor variables used will help conservation efforts for *Lophelia*, *Paragorgia*, and *Primnoa*.

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1. INTRODUCTION

1.1 Cold-Water Corals

Lophelia pertusa (Linnaeus, 1758), *Paragorgia arborea* (Linnaeus, 1758) and *Primnoa resedaeformis* (Gunnerus, 1763) are the most abundant cold-water corals (CWCs) on the Norwegian shelf according to records so far (Buhl-Mortensen et al. 2015) and are important habitat providers for many commercially-important fish and other species (Costello et al. 2005). *Lophelia pertusa* is a reef-forming scleractinian (Subclass Hexacorallia) that has received most focus within research and management due to its extent, accessibility, and its status as a flagship species for deep-sea conservation (Davies et al. 2007; Davies et al. 2011). The gorgonian corals *Paragorgia arborea* and *Primnoa resedaeformis* are sea fans (subclass Octocorallia), which are solitary but may grow in dense "coral gardens" (Buhl-Mortensen et al. 2016). The CWC reefs at these high latitudes established after ice sheets receded after the last glaciation about 11,000 years ago (Mortensen et al. 2001; Roberts et al. 2009).

CWC colonies, whether individual sea pen stands, gorgonian coral gardens, or coral reefs, support numerous associated species, with species richness and biomass often orders of magnitude higher than in the surrounding seabed (Buhl-Mortensen et al. 2016). Corals are complex structures providing microhabitats for other organisms, such as substrate for sessile epifauna, and the coral skeleton and tissue may be inhabited by cryptofauna and endoparasites (e.g. crustaceans, nematodes, fungi, and sponges) (Buhl-Mortensen et al. 2016). Fish may use the coral habitats as a feeding place or shelter (Costello et al. 2005; Buhl-Mortensen 2017). There are no examples of obligate relationships between fish and CWC in the Northeast Atlantic, but they may still be defined as essential to parts of the fish lifecycle locally (Kutti et al. 2014; Buhl-Mortensen 2017). A number of studies (e.g. Husebø et al. 2002; Costello et al. 2005) have observed the presence of gravid females of redfish (*Sebastes*) at the Sula Reef, and ray eggs are often found attached to gorgonians, where they are supplied a high flow of oxygenated water (Buhl-Mortensen et al. 2016). Husebø et al. 2002 also reported that *Sebastes marinus*, tusk (*Brosme brosme*) and ling (*Molva molva*) at *Lophelia* reefs tend to be larger.

Cold-water corals are long-lived sessile organisms, and there are examples from radiocarbon dating of live corals of a four-meter-tall *Paragorgia* colony from New Zealand showing it is around 400 years old (Mortensen & Buhl-Mortensen 2005) and *Gerardia* from Little Bahama Bank being 200 years old (Druffel et al. 1995). Studies on *Primnoa* indicate that this coral may reach an age of >300 years (Risk et al. 2002), but most colonies are younger than 100 years (Andrews et al. 2002; Mortensen & Buhl-Mortensen 2005). These corals are true colonial corals, whereas *Lophelia* is a so-called pseudo-colonial coral, where the polyps do not have a common internal digestive system, and it also lose the surface tissue connections as it grows (Shelton, 1980; Mortensen 2001). Even though each individual *Lophelia* polyp has a relatively short life span (<20 years) (Mortensen & Lepland 2007), the structures they are building together can be of considerable age, with the oldest dating in Norway ranging back to 8600 years before present (Mortensen et al. 2001).

Like for all species, the distribution of CWCs is controlled by the physical environment. Substrate type, temperature, salinity, currents and food availability are recognized as some of the most important factors in this respect (Mortensen et al. 2001; Davies & Guinotte 2011), but surface productivity is also thought to be important factor in the distribution of *Lophelia*, providing food from the surface that is brought down by currents (Davies et al. 2008; Roberts et al. 2009). *Lophelia* is most abundant at a salinity of 35 PSU (Järnegren & Kutti, 2014). *Lophelia's* temperature tolerance window is 4-14 °C (Mortensen et al. 2001), and temperature measurements over a year at a *Lophelia* reef on Rockall Trough in the northeast Atlantic showed maximum daily fluctuations of 2.6 °C (which were correlated with tidal patterns) (Mienis, et al., 2007). *Paragorgia* and *Primnoa* show tolerance for a wider range of temperatures, 1-11 °C for *Paragorgia* and up to 12 °C for *Primnoa*, but are very stenothermal (unable to tolerate great variations in temperature) (Buhl-Mortensen et al. 2015). In terms of substrate, the gorgonians *Paragorgia* and *Primnoa* are often seen growing on *Lophelia* reefs (Järnegren & Kutti 2014; Buhl-Mortensen et al. 2016). The original substrate of an established *Lophelia* reef is harder to estimate, as it creates its own substrate, but hard substrates are more appropriate to settle and grow on. It may grow in a variety of landscapes, from fjords, to seamounts, on continental shelves and slopes, but observations of *Lophelia* growing on vertical substrates such as oil platforms have also been found (Brooke & Järnegren, 2013; Buhl-Mortensen et al. 2015). Finally, currents are important in that they supply food to these benthic feeders, disperse larvae, and prevents the CWCs from being smothered by sediment deposition (Davies et al. 2009). The part of *Lophelia* reefs facing prevailing current, where there is a fresh supply of nutrients, has the highest amount of coral polyps, (Buhl-Mortensen et al. 2016). CWCs are also very abundant on elevated topography, where there is stronger continuous or periodic flow (Mohn, et al., 2013).

1.2 Need for Protection

Cold-water coral ecosystems are vulnerable due to their susceptibility to anthropogenic impacts (e.g. bottom trawling, petroleum exploitation, seabed mining, and cable laying, and threat of ocean acidification) and slow rates of recovery from disturbance (Davies & Guinotte 2011; Buhl-Mortensen et al. 2015). The damage done by bottom trawling on the corals is well documented, leaving crushed *Lophelia* frameworks behind (Fosså et al. 2002). Many countries have therefore protected CWC habitats within their Exclusive Economic Zones, e.g. Norway in 1999 (Fosså, et al., 2005). In the Atlantic high seas, the presence of CWCs have been one of the criteria for the establishment of MPAs (O'Leary et al. 2012). In order to conserve a threatened species, we first need to know the requirements for the species so that we know where it prefers to live and under what conditions, i.e. its ecological niche (Phillips et al. 2004).

1.3 Habitat Distribution Modelling

Of the factors affecting cold-water coral distribution, some show little variation at broad horizontal spatial scales (>1km) (e.g. water-mass properties), and some show great variation (e.g. substrate type). At the vertical scale (depth), variation is greater mainly due to the stratification of water masses. Many factors influence each other and are correlated: currents are influenced by topography at all scales, water mass properties (temperature and salinity) vary with depth, food availability is controlled by current patterns, and substrate composition is influenced by topography. Therefore, environmental conditions at multiple scales influence the coral distribution (Mortensen et al. 2001; Dolan et al. 2008).

Understanding the characteristics of a species' habitat allows the identification of relevant environmental variables, or surrogates (here used for topographic indexes, which are not environmental variable per se, but serve as practical proxies) to be used for predicting the distribution of the species. Such information can help manage the conservation of the species. In the marine environment, a combination of bathymetric (depth) data, benthic terrain (geomorphological) variables, backscatter data (characteristics of the seafloor), and other environmental variables (e.g. currents, salinity, temperature) are examples of environmental variables that can be recorded and used as predictor variables for species presence (Buhl-Mortensen et al. 2015).

The distribution of cold-water corals is affected by environmental factors acting on all life stages (gametes, larva, and colony). The factors may have different importance for the different life stages, e.g. broad scale current patterns are important for the dispersal of long lived larva, whereas food supply and substrate are crucial factors for adult corals. How coral larva respond to temperature and salinity is not well known (Buhl-Mortensen et al 2015).

Many environmental variables are correlated. For instance, food supply is influenced by current patterns, where the velocity sets the transport rate of food particles, and turbulence may cause accumulation and higher food concentration. Both velocity and turbulence is influenced by the topography of the seabed. Furthermore, many variables are correlated with depth due to stratification of water masses and the indirect effects of decreasing light and increasing pressure (Buhl-Mortensen et al 2015).

Changes in global climate may change the suitability for coral reef growth spatially; changes in sea level and resulting changes in currents and food delivery may affect the growth and waning of corals, as proposed for coral in the Porcupine Seabright (Rüggeberg et al. 2007).

It is not possible to sample or observe all areas of the sea bed, and sampling is expensive due to the cost of operating ROVs, submersibles, and seabed sampling from ships, so a way to provide spatial information in the absence of full coverage real data is to create species distribution models (SDM). The predictive power of SDMs can help identify locations where vulnerable marine ecosystems may occur so that research can focus on these areas (Davies & Guinotte 2011).

SDMs are often distinguished by the type of species data they use; systematically collected data where a site is surveyed and the presence/absence or abundance of a species allows the use of standard regression methods such as generalized linear/additive models (GLMs or GAMs) or random trees (Elith et al. 2011). However, deep-sea research often lacks reliable absence data and the recording of environmental factors that may control deep-sea species are often limited in spatial resolution (Davies & Guinotte 2011). Presence-only records are more available, e.g. many herbarium and museum databases with data collected from well over a century (Phillips et al. 2006; Elith et al. 2011).

For this study, presence data of *Lophelia, Paragorgia,* and *Primnoa* recorded from the MAREANO (Marine Area database for Norwegian waters) program is used. The MAREANO program records presence data at sea while conducting surveys with the video rigs Campod and Chimaera (Buhl-Mortensen et al. 2015). Recorded material from the MAREANO cruises is analyzed in detail providing both absence data and quantitative abundance data. However, the absence data is not used in this study. To account for the lack of absence data, using a model that can work with just presence data is desired. A model that has often been used in the past is the ecological niche factor analysis (ENFA)

(Roberts et al. 2009). A newer software called Maxent, short for Maximum Entropy, (Phillips et al. 2004) has become popular among ecologists in recent years (see Table 1 in Elith et al. 2011 for an overview) due to its good performance compared to other SDM methods and being easy to use (Ghisla et al. 2012; Merow et al. 2013; Phillips et al. 2017).

1.4 Aims of this Study

The aim of this thesis is two-fold (similar to those of Yesson et al. 2012):

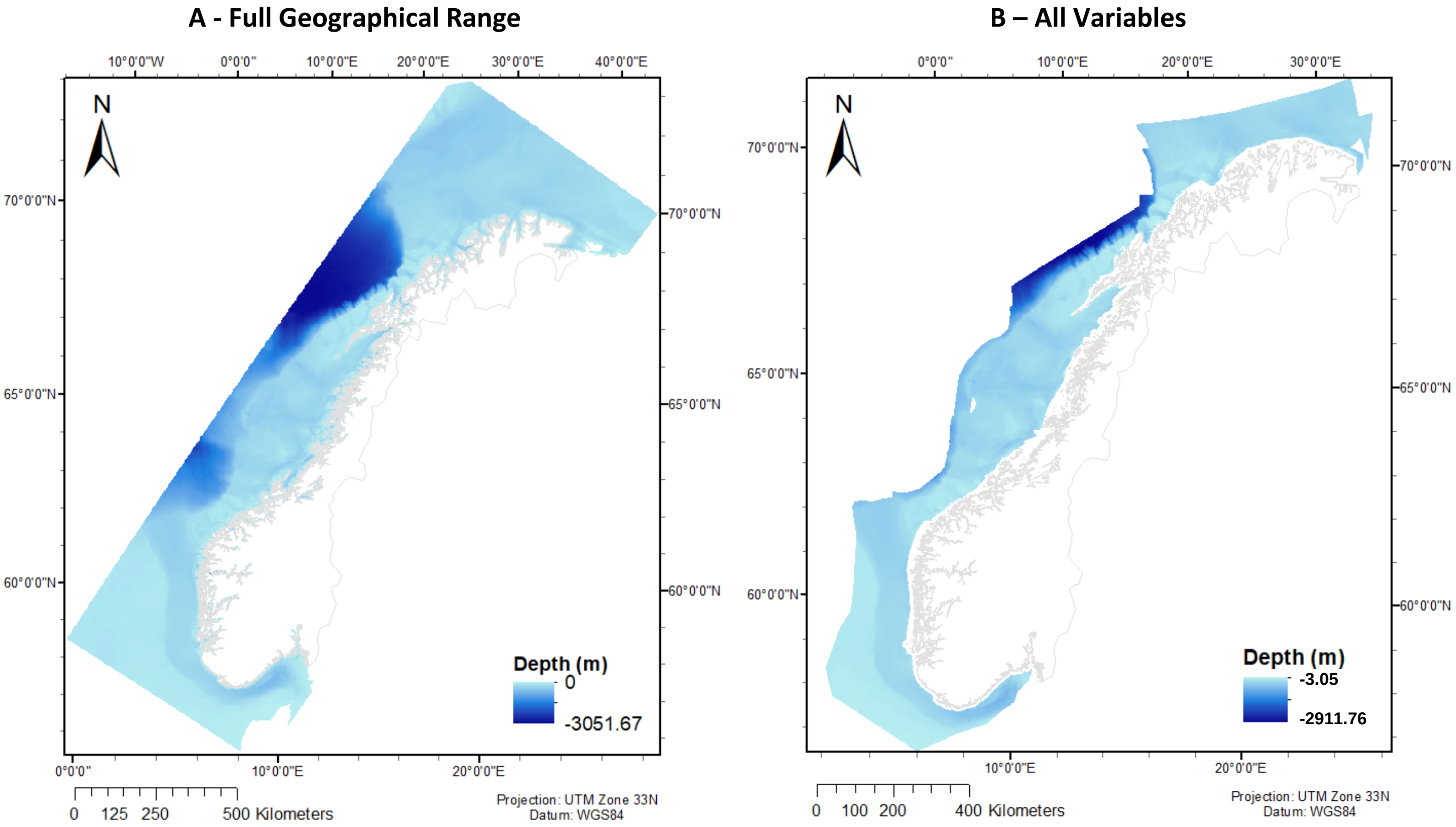
1) to create SDMs within Norwegian waters at a relatively fine spatial scale (176m) for the common CWCs *Lophelia*, *Paragorgia*, and *Primnoa* that may indicate areas with high probability of species occurrence,
2) to explore the potential of a number of environmental variables to predict the spatial distribution of these species, both individually and in combination, which could also add to our knowledge about the ecology and biology of the corals.

2. MATERIALS AND METHODS

2.1 Study Area

This study covers Norwegian waters defined by the current extent of the oceanographic model NorKyst-800. Within this area, models were created at two different scales:

1. “Full Geographical Range” (Figure 1A): extends along the entire Norwegian continental shelf, and uses all environmental layers except for sediment and marine landscape (details in section 2.2).
2. “All Variables” (Figure 1B): extends within the first study, but the range is defined by the limited extent of the included sediment and marine landscape layers.


A - Full Geographical Range

B – All Variables

Figure 1 – The two studies done, with depth in meters shown.

A – Full Geographical Range covers the entire length of the Norkyst-800 model and does not include sediment and marine landscape type, while B- All Variables” is restricted to the included sediment and marine landscape type layers. All maps in this thesis were created with ArcMap 10.5.1.

Brief Description of the Marine Geology of the Study Areas

The Norwegian seabed represents a diversity of environments ranging from the deep sea (4000 m) to shallow banks (30-50 m) and coastal areas dispersed with fjords and archipelagos (see Buhl-Mortensen et al. 2016 for a detailed description of the geological settings of the Norwegian sea floor). Glaciations has largely influenced the shape of the marine landscapes, and the distribution of sediments, excavating troughs during ice sheet expansion, and leaving moraines at the retreat of the glaciers. The broad continental shelf with troughs and banks covers most of the area. The continental shelf break occurs at the edge of the shelf. Below the shelf break is the continental slope, interspersed with canyons, leading down to the deepest depths, the abyssal plain. In addition to long-term geological processes, the distribution of sediments is also controlled by biological production in the water masses after the last glaciation. Finest sediments occur in depressions, where finer particles accumulate, such as in basins, troughs, and fjords. The sediments of the deep sea (the abyssal plain) have been less influenced by the glacial processes, and have been much more influenced by biological processes.

Oceanography in Norwegian Waters

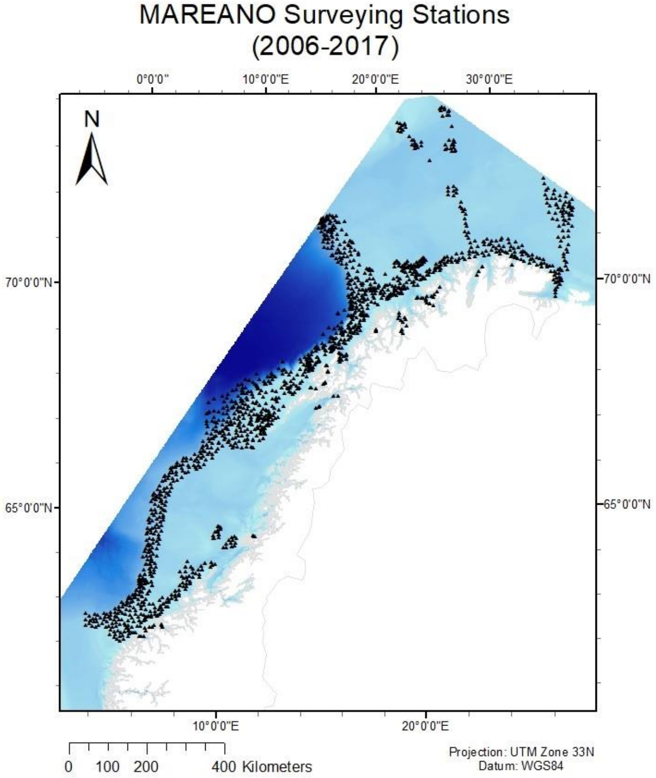
The oceanography of the study area is influenced by four water masses (Hansen & Østerhus, 2000). The northward flowing Norwegian Coastal Current is characterized by the Norwegian coastal water (NCW) with low salinity and variable temperature, which lays above the Norwegian Atlantic Current (NAC) (with Norwegian Atlantic water, NAW) like a wedge, thickest towards the coast. The NAW extends down to about 500–600 m and is part of the relatively warm and saline North Atlantic Current. Below this depth, two cold water masses occur: the Norwegian Sea Arctic intermediate water (NSAIW) and the Norwegian Sea deep water (NSDW). NSAIW has temperatures between -0.5 and 0.5°C, whereas the NSDW has a temperature range between -0.5 and -1.1°C. In the Norwegian Sea, the border between these two water masses typically occurs at around 1,300 m depth.

2.2 Data Sources

Coral Positions

Two coral presence datasets were used, the main one coming from MAREANO. MAREANO is a Norwegian national mapping program coordinated by the Institute of Marine Research, in collaboration with the Geological Survey of Norway (NGU) and the Norwegian Hydrographic Service (NHS), that aims to survey and map the Norwegian seabed. The MAREANO mapping is conducted in two parts: first, multibeam data (bathymetry and backscatter) are collected by the NHS allowing the geologists and biologists to select survey stations. Surveying stations (Figure 2) are selected based on a combined stratified and random sampling strategy, where the aim is to cover the variation in bathymetry, topography, landscapes (e.g. canyons, banks, troughs), and sediment hardness (indicated by the backscatter). The majority of stations (ca 80 %) are distributed randomly within areas of potentially similar environment (identified by unsupervised classification), whereas the remaining 20% are allocated to features of special scientific interests (Buhl-Mortensen et al. 2015).

Figure 2 - Locations of the MAREANO surveying stations, from the start of the program (2006) until spring 2017.



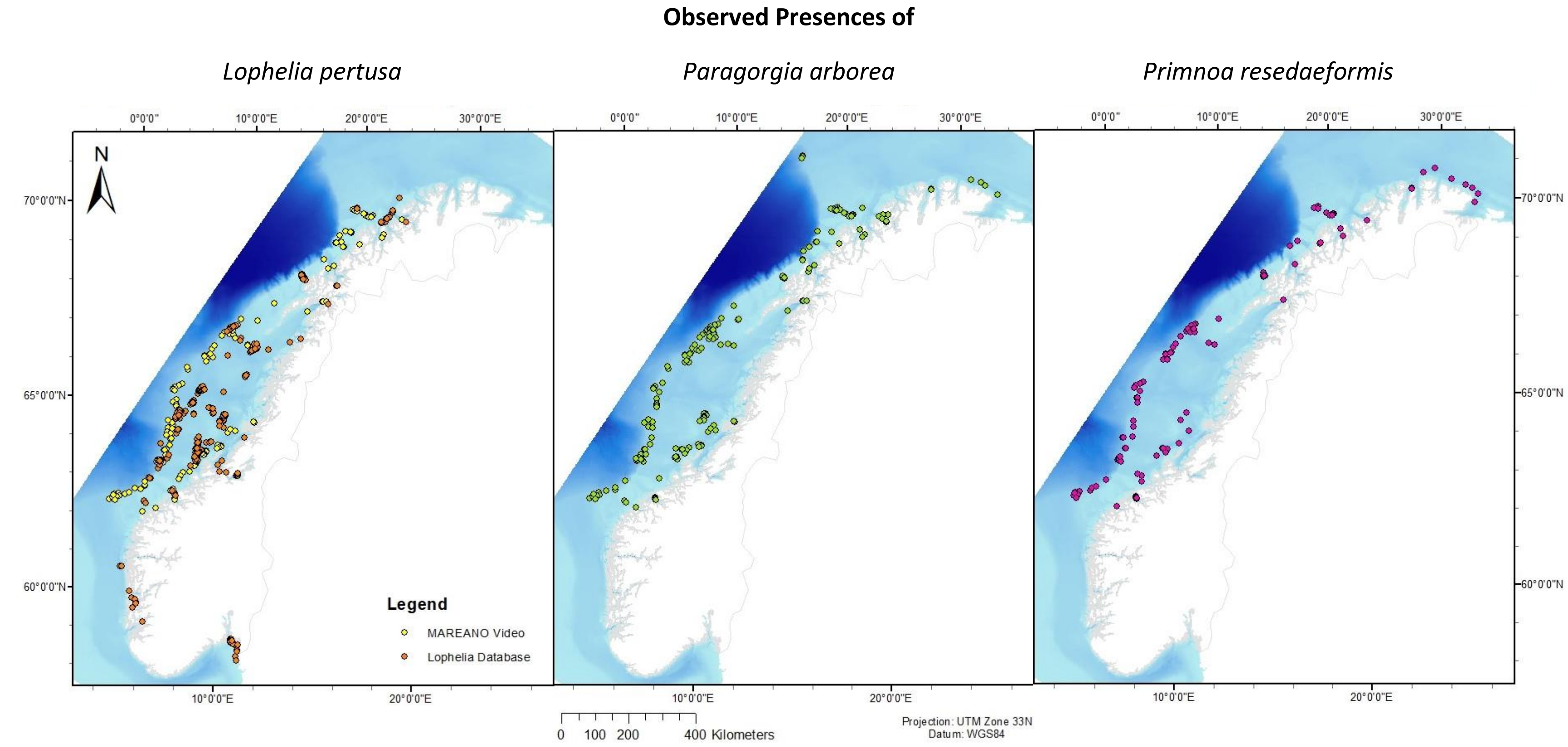
The MAREANO dataset contains presence points on all three coral species from Møre to Lofoten with high precision (±5m). Video observation points may over-account for *Lophelia* presence because, since the extent of a single *Lophelia* reef may not be possible to see, it may extend beyond the view captured by the camera and the same reef could be counted twice; thus, individual *Lophelia* points within 50m of each other were grouped together and defined as a "Coral Reef Habitat" (Table 1).

The second dataset, the IMR *Lophelia* database, is a compiled database of various sources that have observed *Lophelia* using different sampling methods (e.g. dredge, ROV/video, multibeam) since the

Table 1 - Number of coral observations by data source.

* A "Coral Reef Habitat" observation is defined as an assemblage of video point observations of *Lophelia* residing within 50m of each other

Data Sources	**# Observations *Lophelia pertusa***	**# Observations *Paragorgia***	**# Observations *Primnoa***
MAREANO Video Coral Points **"Coral Reef Habitats" ***	21356 (595)	449	238
IMR *Lophelia* Database	867	-	-



Observed Presences of

Lophelia pertusa

Paragorgia arborea

Primnoa resedaeformis

Figure 3 - Positions of observed coral for each species. Note the two sources for *Lophelia*.

1940s (Fosså et al. 2002), with observations extending further south than the MAREANO records to around Skagerrak. The presence positions have variable precision (0 – 1000m), but only points with precision within 100m or less were included in this study. Duplicates that existed between the IMR *Lophelia* database and the (newer) MAREANO video records were removed by creating a 50m radius buffer around the MAREANO video records and deleting overlapping IMR *Lophelia* database records. *Figure 3* shows observed presence points for each coral so far.

Bathymetry/Depth Data

The following Digital Terrain Model (DTM) bathymetry basemaps were downloaded as ESRI ASCII files from the European Marine Observation and Data Network (EMODnet) portal: B1, B2, C1, C2, D1, and D2 (EMODnet Bathymetry Consortium, 2016). Source resolution of these layers is 1/8 x 1/8 arc minute and the datum is WGS 1984.

NorKyst-800 Oceanography Data

Point data on bottom temperature, salinity, and currents was obtained from the ocean modelling project NorKyst-800 (Norwegian Coast 800m), which models oceanographic data at 800m resolution based on 10 years of monitoring data along the Norwegian coast from the Swedish border to Russia (Albretsen, et al., 2011). The extent covers the entire length of the coral presence data. Modeled variables from the NorKyst-800 model are within 10% of the actual bottom depth.

Surface Chlorophyll a Concentration

Ocean color image raster layers, with approximately 4km^2 resolution, indicating annual averages of sea surface chlorophyll *a* concentration (mg/m^3) from 2002 to 2016 were obtained from the Ocean Biology Processing Group (OBPG) at NASA's Goddard Space Flight Center (NASA Biology Processing Group, n.d.).

Sediment and Marine Landscape Types

Shapefile "regional" and "continental shelf" layers on seabed sediment classification from NGU were obtained from the Geonorge public map catalogue. Sediment type is classified by grain size as seen in Table 2, which is based on and modified from (Folk, 1954). The "regional" shapefile layer shows the sediment of the seabed's upper layer (0-50cm) within mapped regions of the Norwegian shelf in the MAREANO study area and in Skagerrak. Classification is based on sediment sampling analysis, backscatter data analysis and interpretation, and seismic data interpretation, with support from video observations and bathymetry data (Buhl-Mortensen et al. 2016). The "continental shelf" shapefile layer also indicates the sediment of the seabed's upper layer and extends over Norwegian waters from

Grain Size	Definition/Description	Code
Clay	Clay:silt ratio >2:1 and clay+silt >90%, sand <10%, gravel <2%	10
Organic mud	Clay:silt ratio from 1:2 to 2:1 and clay+silt >90%, sand <10%, gravel <2%. High content of organic material.	15
Mud	Clay:silt ratio from 1:2 to 2:1 and clay+silt >90%, sand <10%, gravel <2%	20
Mud with sediment blocks	Mud alternating with blocks of hard sediments	21
Sandy clay	Clay:silt ratio >2:1 and clay+silt >50%, sand <50%, gravel <2%	30
Sandy mud	Clay:silt ratio from 1:2 to 2:1 and clay+silt >50%, sand <50%, gravel <2%	40
Silt	Clay:silt ratio <1:2 and clay+silt >90%, sand <10%, gravel <2%	50
Sandy silt	Silt:clay >2:1 and clay+silt >50%, sand <50%, gravel <2%	60
Clayey sand	Sand >50%, clay:silt ratio >2:1 and clay+silt <50%, gravel <2%	70
Muddy sand	Sand >50%, clay:silt ratio from 1:2 to 2:1 and clay+silt <50%, gravel <2%	80
Silty sand	Sand >50%, silt:clay ratio >2:1 and clay+silt <50%, gravel <2%	90
Fine sand	Sand >90%, includes fine and very fine sand (Wentworth, 1922)	95
Sand	Sand >90%, clay+silt <10%, gravel <2%	100
Coarse sand	Sand >90%, includes medium, coarse and very coarse sand (Wentworth, 1922)	105
Gravelly mud	Sand:silt+clay ratio <1:9, gravel 2-30%	110
Gravelly sandy mud	Sand:silt+clay ratio from 1:9 to 1:1, gravel 2-30%	115
Gravelly muddy sand	Sand:silt+clay ratio from 1:1 to 9:1, gravel 2-30%	120
Gravelly sand	Sand:silt+clay ratio >9:1, gravel 2-30%	130
Muddy gravel	Gravel 30-80%, sand:silt+clay ratio <1:1	140
Muddy sandy gravel	Gravel 30-80%, sand:silt+clay ratio from 1:1 to 9:1	150
Sandy gravel	Gravel 30-80%, sand:silt+clay ratio >9:1	160
Gravel	Gravel >80%	170
Gravel and cobbles	Dominant grain sizes are gravel and cobbles.	174
Gravel, cobbles and boulders	Dominant grain sizes are gravel, cobbles and boulders.	175
Cobbles and boulders	Dominant grain sizes are cobbles and boulders.	180
Sand, gravel and cobbles	Dominant grain sizes are sand, gravel and cobbles.	185
Diamicton	Sediment containing particles of a wide range of sizes. Unsorted or very poorly sorted.	200
Mud/sand with cobbles/boulders	Bimodal bottom type where cobbles and boulders occur frequently in the areas dominated by fine-gained sediments.	205
Mud and sand with gravel, cobbles and boulders	Fine-grained sediments with varying content of coarser grain sizes.	206
Cobbles/boulders covered by slam/sand	Very coarse sediments covered by fine material.	210
Sand, gravel, cobbles and boulders	Sand, gravel, cobbles and boulders in frequent interchange.	215
Compacted sediments or sedimentary bedrock	Submarine outcrop of compacted sediments or sedimentary bedrock.	300
Bioclastic material	Mud, sand and gravel of biological origin.	500
Thin or discontinuous sediment cover on bedrock. Sediments with varying grain size.	Lateral variation of small basins with sediments and exposed bedrock, and/or bedrock with thin/discontinuous sediment cover. Sediments in small basins may have varying grain size.	1
Exposed bedrock	Areas without sediment cover.	5
Unspecified	Grain size is not specified.	0

Table 2 - Seabed Sediment Classification taken from *(NGU/MAREANO, n.d.)*, modified from *(Folk, 1954)*. Code numbers of the categories are used in the Maxent analysis.

Svalbard to Skagerrak, but is much coarser and is based on drawings from the National Atlas for Norway in 1991 (Vorren & Vassmyr, 1991).

The seabed can also be classified into marine landscape types, which are defined as large geographical regions (can be mapped with a scale of 1:500 000) that have a uniform appearance. MAREANO (2016) defines them using the parameters 1) relative relief (difference of 50m in height within a $1 km^2$ area is set as a cut-off point), 2) slope angle, 3) terrain variation (e.g. ruggedness), and 4) relative position (BPI). The marine landscape types identified within Norwegian waters are listed in Table 3. A shapefile of marine landscape types was also obtained from Geonorge.

Landscape (Original Norwegian Name)	**Landscape (English Translation)**	**Code**
Strandflate	Strandflat	1
Jevn kontinentalskråning	Smooth continental slope	21
Marint gjel	Marine canyon	22
Marin dal	Marine valley	31
Fjord	Fjord	32
Dyphavsslette	Deep sea plain	41
Kontinentalskråningslette	Continental slope plain	42
Kontinentalsokkelslette	Continental shelf plain	43
Grunn marin dal	Shallow marine valley	431

Table 3 – Marine landscape types as defined by MAREANO (2016). Code numbers of the categories are used in the Maxent analysis.

2.2 Environmental Variable Preparation in ArcGIS

The first part of the analysis involved data processing and visualization with the ArcGIS 10.5.1 program. The two main types of data are coral position layers from above and environmental variable raster layers. All layers were projected with the World Geodetic System 1984 (WGS 84) datum and the Universal Transverse Mercator (UTM) Zone 33N projection, so distances are measured in the metric system and cells are of equal sizes across the region. All layers were clipped to the same extent as the Norkyst-800 oceanographic layers, and snapped to and cell size resampled to 176 x 176m to match the final bathymetry layer Bathymetry_EMODNET_176.

Bathymetry Raster Layer (Depth)

The EMODnet layers were merged together with the Mosaic to New Raster tool in the Data Management ArcToolbox using the “Blend” mosaic operator, with a 32-bit floating point pixel type, one band, no colormap, and the remaining settings left as default. The merged raster layer was reprojected to WGS84 UTM33 with the Project Raster tool in Data Management using the “Nearest” resampling technique in order to maintain the cell values, resulting in a cell size of 176.5137701 x 176.5137701m. The reprojected raster layer was clipped to the same extent as an outline polygon of the Norkyst-800 extent with the Clip tool in Data Management, using the Norkyst-800 outline polygon for clipping geometry, maintaining the clipping extent, and setting a Norkyst-800 raster layer (max salinity) as snap raster. Finally, the clipped raster layer was resampled to an integer cell size of 176 x 176m with the Resample tool in Data Management using the “Nearest” resampling technique, resulting in the final bathymetry layer Bathymetry_EMODNET_176.

Creating Benthic Terrain/Geomorphometric Raster Layers

Layers of various geomorphometric measurements of the bathymetry layer were created. The Benthic Terrain Modeler (BTM) plug-in (Wright, et al., 2012) was used to create slope, broad and fine bathymetric position indices (BPI), ruggedness, and statistical aspect (northerness and easterness), and the Spatial Analyst ArcToolbox was used to create aspect. Each resulting layer has the same cell size as the bathymetry layer.

Slope is defined as the vertical rate of change for each cell, and the resulting slope raster is in degree units (Wright, et al., 2012).

BPI is a measure of the concavity or convexity of a location in reference to the surrounding location, a modification from the terrestrial topographic position index (TPI) (Wright, et al., 2012). Positive BPI values indicate convex terrain (mounds), while negative BPI values indicate concave terrain (troughs). The broad BPI layer was calculated with a 3-cell inner radius and 49-cell outer radius, resulting in an 8,624m (49 x 176m) search radius. The fine BPI layer was calculated with a 3-cell inner radius and 9-cell outer radius, resulting in a 1,584m (9 x 176m) search radius. The BPI layers were standardized with the BTM plug-in.

Ruggedness is a measure of the terrain complexity (rugosity) in terms of slope and aspect within a specified neighborhood; the neighborhood chosen here is 3 x 3 cells. Ruggedness values vary from 0 (no terrain variation) to 1 (complete terrain variation), with values typically ranging from 0 to 0.4 (Wright, et al., 2012). The raw ruggedness layer produced at this scale showed very small values (from 0 to 0.14), so a natural logarithm transformation of the layer (omitting values of 0) was created to separate out the values and better analyze relative difference in terrain ruggedness.

Aspect identifies the compass heading that the downhill slope surface faces, in degrees. Surfaces that are flat are given a value of -1. Since regular statistics cannot be done on the degree values (taking the mean of 1° and 359° would become 180°, while in actuality it should be 0°, close to North), the statistical aspect layers were also created; these are the decomposition of the degree aspect into the Sine (Easterness) and Cosine (Northerness) of the angle, giving two relative distances on a unit circle (Wright, et al., 2012). A Sine aspect value of 1 means absolute East, while -1 means absolute West. A Cosine aspect value of 1 means absolute North, while -1 means absolute South.

NorKyst-800 Oceanography Raster Layer

The point data from the NorKyst model was interpolated using the Inverse Distance Weighted (IDW) interpolation tool in the Spatial Analyst toolbox to create raster layers with 800m cell resolution. The output cell size was set to 800, number of points used for search distance was set to one, maximum search distance set to 800m, and all other settings left as default.

The variables used in this study are: mean bottom temperature (°C) of March through May, the months observed as the coldest three months from coral positions; mean bottom temperature (°C) of October through December, observed as the warmest three months from coral positions; minimum, mean and maximum bottom salinity (PSU); mean and maximum bottom current speed (m/s); and mean bottom current direction (° compass heading). Current direction was also decomposed into Northerness and Easterness using the Raster Calculator in Spatial Analyst, as follows:

- Northerness: Cos (NK800_currentdirectionmean_176 * (math.pi / 180.0))
- Easterness: Sin (NK800_currentdirectionmean_176 * (math.pi / 180.0))

Current-aspect angle: this additional variable was created to examine the interaction between bottom currents and the terrain's slope. The current-aspect angle measures the angle made by the bottom current's heading in respect to the terrain aspect heading. Cells of aspect that were flat (aspect value of -1) were left as -1 in the new raster. This variable was processed with the Raster Calculator and Math tools in the Spatial Analyst ArcToolbox, as follows:

- If Current-Aspect Angle ≤ 180°, Current-Aspect Angle = abs (Current∡ - Aspect∡)
- If Current-Aspect Angle > 180°, Current-Aspect Angle = abs (abs (Current∡ - Aspect∡) - 360)).

The conditions are set as above because the aspect is the direction of a flat surface facing one way, and the angle made by the current direction in respect to the flat surface's direction is the value being examined; thus, for values greater than 180°, the inverse angle is calculated. The following interpretations can thus be made; if the current-aspect angle value

= 0°, this indicates that the current and aspect headings are the same, so the current passes over the terrain slope exactly;

< 90°, the current passes over the terrain;

= 90°, the current runs parallel to the terrain;

> 90°, the current meets/hits the terrain.

= 180°, the aspect and current directions are entirely opposite, so the current meets the terrain exactly.

Surface Chlorophyll a Concentration Layer

A new raster averaging the 15 raster layers was created using the Raster Calculator tool in Spatial Analyst.

Sediment and Marine Landscape Layers

The "regional" and "continental" shapefile layers were combined into one shapefile using the Union tool in the Analysis ArcToolbox; the "regional" sediment layer was ranked as first, and the "continental" sediment layer thus supplemented in areas that the "regional" sediment layer did not cover. The sediment class "Bioclastic material" (500) was removed since analyzing the sediment cover classified as biological material results in a circular argument for analyzing the sediment type that the coral species settle on.

Sediment and marine landscape shapefile layers were converted to raster layers using the "Polygon to Raster" tool in the Conversion ArcToolbox with the maximum combined area cell assignment type.

2.3 Statistics, Maxent Preparation, and Modeling

Statistics

The values of the environmental variable layers at each coral point was extracted using the "Extract Multi Values to Points" tool in the Spatial Analyst ArcToolbox. Distribution for all 20 variables was demonstrated with histograms plotted with Microsoft Excel, visually comparing the difference between the three coral species.

Maxent is reasonably robust in regards to covarying variables, and the "machine learning approach" suggests that all variables should be included and the algorithm will decide which are important via regularization, explained below (Phillips, Anderson, & Shapire, Maximum entropy modeling of species geographic distributions, 2006). However, some a priori variable selection is good to reduce covariation and better understand variable importance (Davies & Guinotte, Global Habitat Suitability for Framework-Forming Cold-Water Corals, 2011). The coral point layer with environmental variable values appended was put into the "Scatterplot Matrix for Table" tool in the Marine Geospatial Ecology Tools 0.8a68 (MGET) plug-in (Roberts, Best, Dunn, Treml, & Halpin, 2010) to test for correlation of numerical variables with the Spearman's rank test (Appendix I). One of the pair of covarying variables was eliminated, trying to keep a variety of variables for the modeling. At $\rho(1971) \geq 0.75$ ($p<0.01$) and $\rho(2147) \geq 0.75$ ($p<0.01$), those eliminated were max current speed, ruggedness, and mean temperature for October through December.

Maxent

Background on Maxent

Maxent version 3.4.1 Java application was used for SDM. Maxent creates a *probability distribution*/geographic range of a species (species distribution) that has maximum entropy, i.e. the distribution that is most uniform, subject to some *constraints* (Phillips, Anderson, & Shapire, Maximum entropy modeling of species geographic distributions, 2006). These constraints are that the expected value for each *feature* (raw environmental variables and simple transformations thereof) of points within a study area should equal, or approximate, the average of feature values at species presence points (Phillips, Anderson, & Shapire, Maximum entropy modeling of species geographic distributions, 2006), (Phillips, Anderson, Dudík, Schapire, & Blair, 2017).[1]

The distribution of values for features at species presence points and at background points is termed the *probability density* of features. Finding the probability distribution/geographic range/species distribution of maximum entropy means that the difference in probability density at species presence points and at background points is minimized (see Figure 4 for a clear explanation). This makes sense because the background probability density is a null model for species distribution; without the constraints from species presence points we could not predict a better species distribution than that the species occupies environmental conditions proportionally to their availability in the landscape sampled (Elith, et al.,

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[1] The 2nd law of thermodynamics states that without outside influence, processes move in a direction that maximizes entropy; so in the absence of influences other than those constraints determined by the environmental variables (factors), the geographic distribution of species will tend toward the distribution of maximum entropy. A distribution with higher entropy involves more choices, i.e. is less constrained. (Phillips et al. 2006).

2011). This gives as uniform a probability distribution as possible, giving the largest possible range size that is consistent with the data (Merow, Smith, & Silander, 2013).

Data used by Maxent is three-fold (Phillips et al. 2004; Phillips et al. 2006):

1) Study area: cells of an area upon which the Maxent probability distribution is defined. Non-negative probability is assigned to each pixel in the study area, which add up to 1.
2) Sample points: cells within the study area with known species presence. Species presence points are used to train the model, but a fraction can be chosen to test the model as well.
3) Features: various environmental variables which have been measured within the study area and transformations made on these raw variables. Species' response to environmental variables may

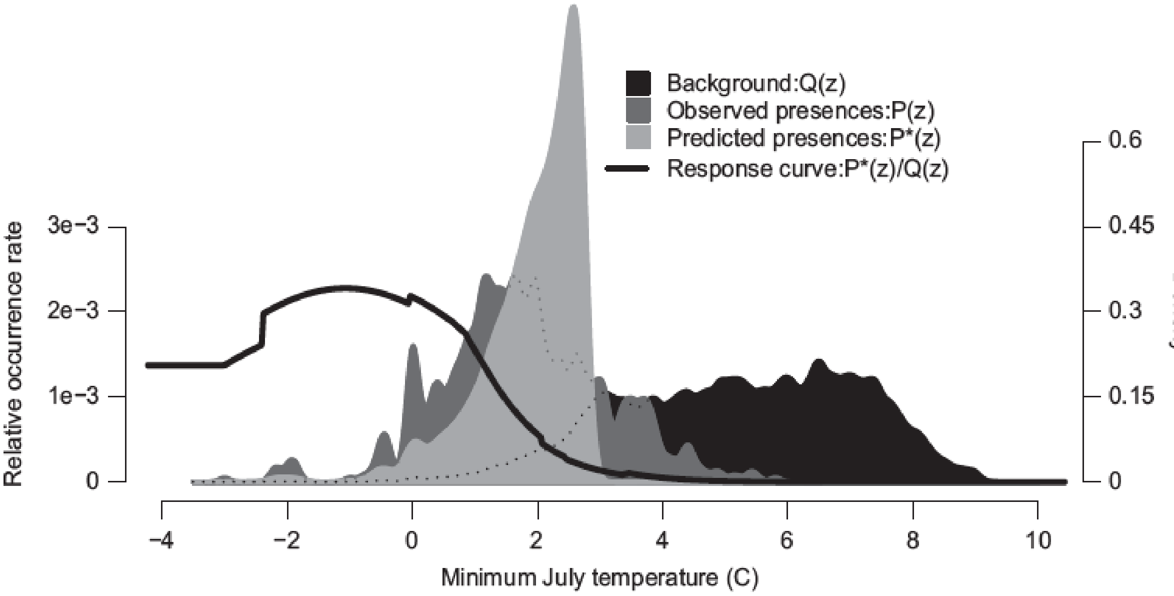


Figure 4 – Image taken from *(Merow, Smith, & Silander, 2013)*, explaining the calculation made to create a predicted probability density of an environmental variable and to model the response of a species to this variable.

The image shows the probability density distributions of background data (black), observed presences (dark gray), and predicted presences (light gray) for the environmental variable "Minimum July temperature" for a test species. Default settings in Maxent were used for the model run.

Maxent creates the predicted probability density based on a ratio of the probability density of observed presences to the probability density of background data. A response curve (the black line), a smoothed estimate of the ratio, shows the prediction model, i.e. the response of the species to minimum July temperature.

The predicted probability density can be seen to have a similar mean to the variable's observed probability density, but the mode is shifted towards the mode of the background probability density. This illustrates the effect of minimizing the difference between predicted and background density while meeting the constraints of observed data, i.e. maximizing the entropy of the prediction *(Merow, Smith, & Silander, 2013)*.

be complex, so some transformations of the raw variables are made, and the ones available in Maxent are:

a. Linear: the variable itself. The mean value of the variable at areas of predicted occurrence should approximately match the mean value of the variable at observed occurrences.
b. Quadratic: the quadratic of the linear (raw) variable equation. The variance of the variable is constrained.
c. Product: all possible pairings of variables, representing simple variable interactions. The covariance of variable pairings is constrained. Product features are omitted in this study because product features have shown to not improve model performance much and can make simpler models with simpler response curves (Phillips, Anderson, Dudík, Schapire, & Blair, 2017).
d. Threshold: a continuous binary prediction defining a feature as 0 below set thresholds and 1 above the thresholds; this can be good to use if e.g. there is a known biological tolerance limit to species survival (Merow, Smith, & Silander, 2013). Threshold (step-function) is also omitted because this also seems to give smoother and simpler models (Phillips, Anderson, Dudík, Schapire, & Blair, 2017).
e. Hinge: a linear function with steps, similar to threshold, which allows a linear function to have sudden changes, steps, in the response (Elith, et al., 2011).
f. Categorical: splits a predictor with *n* categories into *n* binary features. A feature is defined as 1 when the feature is present and 0 when not.

Many features can be chosen to obtain a complex, highly nonlinear model, or fewer features can be chosen for a simpler, more linear model, with simpler response curves (Merow, Smith, & Silander, 2013).

Strictly presence-only data estimates a probability density (distribution) of the environmental variables at presence locations (species presence response to predictor environmental variables) within a study area, but cannot approximate species distribution probability on its own, as is the case without absence data; so instead, background data is used to model probability density (distribution) of environmental variables where species records does not exist (area/random background point response to predictor environmental variables). This presence/background environmental response data allows us to estimate the relative occurrence rate (relative probability that a cell contains a presence), which is Maxent's "raw output" (Elith, et al., 2011). The relative suitability in cells across the study area has to sum to one (Merow, Smith, & Silander, 2013). This means that the relative probability is predicted, and not the actual occurrence rate (number of individuals in cells), for which the population size of presence data would need to be known, which it usually is not in presence-only data such as here (Merow, Smith, & Silander, 2013). This study thus only predicts the probability of presence in cells within the study areas, not the probability distribution of individuals.

The Maxent model is a log-linear model, similar in form to a GLM (Elith, et al., 2011). Maxent calculates coefficients ("lambdas") to the model from features in order to fit the constraints made by sample features means, together with a standard error bound based on the variation in sample feature values (Elith, et al., 2011).

Choosing the Output Format

There are four format output types in Maxent: raw, cumulative, logistic, and the newer complementary log-log (cloglog). Each gives the same model fitting results but are just scaled differently to create different visual interpretations of species distribution (Elith, et al., 2011). The raw output is Maxent's original exponential function P(x) and can be interpreted as a model of relative abundance (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). It gives the probability of occurrence between 0 and 1 in each cells within the study area, with all cells' probabilities adding up to 1 in the trained model. This means each cell's probability is really small, making the SDM map hard to read, so using a log scale can help better interpret the distribution (Phillips, Anderson, & Shapire, Maximum entropy modeling of species geographic distributions, 2006). In the cumulative output, the value of a cell is the sum of the raw value output of that cell and all other cells with equal or lower value, multiplied by 100; it can omit presences that are below a chosen threshold of presence/absence (Merow, Smith, & Silander, 2013). The logistic output is a logistic transformation of the raw function,

(1) $P(x) = 1 / (1 + \exp(-x))$

which assigns the same probabilities to cells (0 to 1) but scaled up in a non-linear way, making the map easier to read (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). Lastly, the cloglog output is a transformation again of the raw function,

(2) $P(x) = 1 - \exp(-\exp(x))$

and can be interpreted as the probability of presence of at least one individual in each cell, instead of relative abundance like in the other outputs. Cloglog shows slightly higher predictions than the logistic output, especially for higher probabilities (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). This is the default setting in Maxent version 3.4.1 and is used in this study because of its higher discrimination power compared to the logistic output and because the goal is to simply estimate the areas of high probability of CWC occurrence and not relative abundance.

Regularization

Regularization on the coefficients makes sure the model does not overfit. Regularization does this by 1) ensuring the model does not fit too closely to observed mean and variance, and by 2) shrinking the magnitude of coefficients so that the smaller coefficients become zero and the rest closer to zero (Merow, Smith, & Silander, 2013). The larger the variance of a feature, the more likely its coefficient value will become zero. This means that the model shrinks coefficients that do not have as much predictive power, and thus selects the coefficients that contribute most to model fit, which allows the model to both accurately predict and generalize (Elith, et al., 2011).

Extrapolating outside observed values

Another setting, extrapolation, allows Maxent to extrapolate or restrict output outside the observed values of environmental variables for the training data, which can be seen in response curves. “Clamping” maintains the suitability response observed at the extremes of the training data steady, while no clamping lets the response curve continue on the same trajectory as seen towards the limits of the training data (see Figure 5). Clamping was chosen in order to be conservative with predictions outside observations.

Running the Model

Data layers imported into and created with ArcGIS were prepared so that the Maxent application could read the data. The coral presence data was saved as comma-delimited files. The environmental variable raster layers were converted to ASCII files.

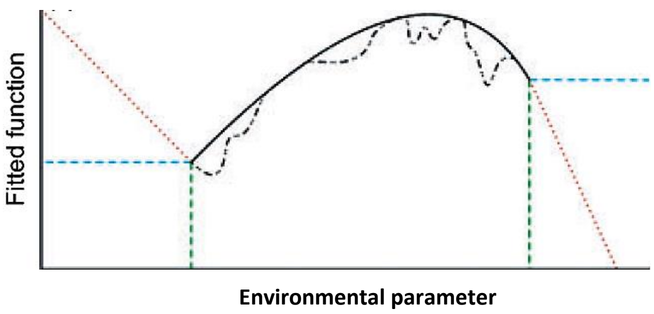


Figure 5 – Image 8a in *(Webber, et al., 2011)* showing methods to deal with predicting model response beyond values of environmental variables observed in training data in Maxent.

Green dashed lines: no extrapolation. No estimates of model response are made outside of the training data limits.

Dashed blue lines: clamping. This type of extrapolation makes the model maintain a flat response to values based on the extreme values in training data.

Dashed red lines: no clamping. The model response continues on the same trajectory as seen towards the extremes of training data.

The following settings were used:

- “Create response curves”, “Make pictures of predictions”, and “Do jackknife to measure variable importance” were enabled.
- Output format: kept as the default Cloglog (complementary log-log).
- Regularization multiplier: left as the default of 1 leaving the regularization coefficients as default.
- Features: linear, quadratic, and hinge.
- “Remove duplicate presence records”: sometimes more than one coral observation will lie within a 176 x 176 m cell, but since the point is to understand species response to environmental variables just based on how it is at coral presence data, keeping just one of the records within a cell is fine. The aim is not to look at relative abundance, but probability of presence, which the cloglog output shows well.
- 10x cross-validation**:** presence data is split into 10 groups, and each group is left out while the rest of the data is used to train the model. The trained model is then tested with the omitted group (the “test data”). This method is good as it uses all data to test the model (Philips, 2017).
- With a bias grid: a layer showing the sampling effort within the study area, which in this study are the MAREANO station locations; the bias grid does not include sampling effort of the *Lophelia* database. A raster layer was created in ArcGIS using the Point Density tool from the Spatial Analyst toolbox, using a 1km radius, the same length, and the longest, of the video transects from the first MAREANO cruise in 2006 (Buhl-Mortensen L. , Buhl-Mortensen, Dolan, & Holte, 2015). The values in the Point Density raster were added with a value of 1 with the Raster Calculator to avoid having null values, as per Maxent specification for the bias grid (Elith, et al., 2011). The resulting raster layer measures the point density of MAREANO stations within a 1km radius around each station and therefore indicates sampling effort from MAREANO.

The following runs were done:

1) Full Geographical Range. NGU sediment and marine landscape variables were left out because these two variables did not cover the entire Norwegian shelf area
2) All Variables. Includes the NGU sediment and marine landscape variables, so the extent is defined by these two.

Model Evaluation

Maxent evaluates the model's accuracy with the Area under the Receiver Operating Characteristic (ROC) curve, the AUC. The ROC curve is a continuous plot showing the true positive rate (correctly predicting presence over falsely predicting absence) vs. false positive rate (falsely predicting presence over correctly predicting absence) of the model, like a confusion matrix, as the choice of discrimination threshold changes (Lobo, Jiménez-Valverde, & Real, 2008). Normally the AUC is used to evaluate how well models discriminate between presence and absence points, when absence data is available (Phillips et al. 2006). Instead, Maxent evaluates the model's ability to discriminate between presence and the randomly chosen background points. Background points are sometimes also called "pseudo-absences", which can contain presences or absences (Merow, Smith, & Silander, 2013).

Each of the 10 model runs also produce a "gain", a measure of goodness of fit like in GAMs and GLMS. The training gain is created while the model is being run with the training points and gives the likelihood ratio of finding presence point over background points; the test gain is the same for predicting the test points over background points. For example, if the gain is 2, the average likelihood of presence at a presence point is $e^2 \approx 7.4$ times greater than at a background point (Phillips, Anderson, Dudík, Schapire, & Blair, 2017).

3. RESULTS

3.1 Environmental Characteristics of Observed CWC Locations

The distribution of the three coral species at presence locations for all environmental variables (all benthic, except for surface chlorophyll a concentration) collected are presented below as histograms, showing the number of occurrences within intervals. The interval sizes were selected to visually compare observations for the species between each other, so notice that over- and underflow bins are often used. The number of observations (n) together with the mean ($\bar{x}$), standard deviation (s), maximum, and minimum values are noted as well. Maps of the variables are also displayed. *Table 4* shows the same summary statistics for the continuous variables (all variables except for sediment and marine landscape) at MAREANO sampling stations for reference.

3.1.1 Depth

A wide range of depth was sampled, from 33.7 to 2721.73m, while the study area depth ranges from 0 to 3051.67m (*Table 4*). The distribution of coral occurrences with depth shows a similar pattern for all three species, although the gorgonians extended deeper (max for *Paragorgia*: 769.25m, max for

Table 4 - Summary table of the count (n), mean ($\bar{x}$), standard deviation (s), maximum, and minimum observed values for each continuous environmental variable at MAREANO sampling stations.

Environmental Variable	n	$\bar{x}$	s	Max	Min
Depth (m)	1610	432.46	409.29	2721.73	33.70
Slope (°)	1610	1.75	2.80	31.41	0.00
Broad BPI	1546	-17.98	223.70	1489.00	-1961.00
Fine BPI	1600	-5.88	115.19	1240.00	-764.00
Ln Ruggedness	1553	-11.13	2.43	-3.91	-15.94
Aspect Easterness	1610	-0.20	0.68	1.00	-1.00
Aspect Northerness	1610	0.46	0.60	1.00	-1.00
Mean Temp March-May (°C)	1610	4.26	2.43	7.50	-0.63
Mean Temp October-December (°C)	1610	5.06	2.91	10.69	-0.67
Max Salinity (PSU)	1610	35.19	0.12	35.97	34.42
Mean Salinity (PSU)	1610	34.96	0.17	35.23	33.69
Min Salinity (PSU)	1610	17.52	0.08	17.65	16.97
Max Current Speed (m/s)	1610	0.53	0.29	1.89	0.09
Mean Current Speed (m/s)	1610	0.11	0.05	0.33	0.02
Current Direction Easterness	1610	0.21	0.62	1.00	-1.00
Current Direction Northerness	1610	0.46	0.60	1.00	-1.00
Current-Aspect Angle (°)	1610	85.76	44.63	179.83	-1.00
Surface [Chlor *a*] (mg/m^3)	1575	1.32	0.36	4.48	0.78

Primnoa: 714.87m) than *Lophelia* (max: 715.45m) (*Figure 6*). This is also reflected in the mean depths, with 281 ± 77.12m for *Lophelia,* 343.50 ± 107.08m for *Paragorgia* and 339.62 ± 118.04m for *Primnoa*; thus *Primnoa* also varies the most in its distribution. *Figure 6* also indicates that the corals have two peaks of depth occurrence, the shallower peak being particularly distinct. Most occurrences of *Lophelia* are found around 250m, and the deeper peak occurs at around 325m. For the gorgonians, the shallow peak is at 325m, the same depth as the deeper *Lophelia* peak. The deeper peaks for *Paragorgia* and *Primnoa* are not very pronounced, but occur at depths of around 425 to 500m.

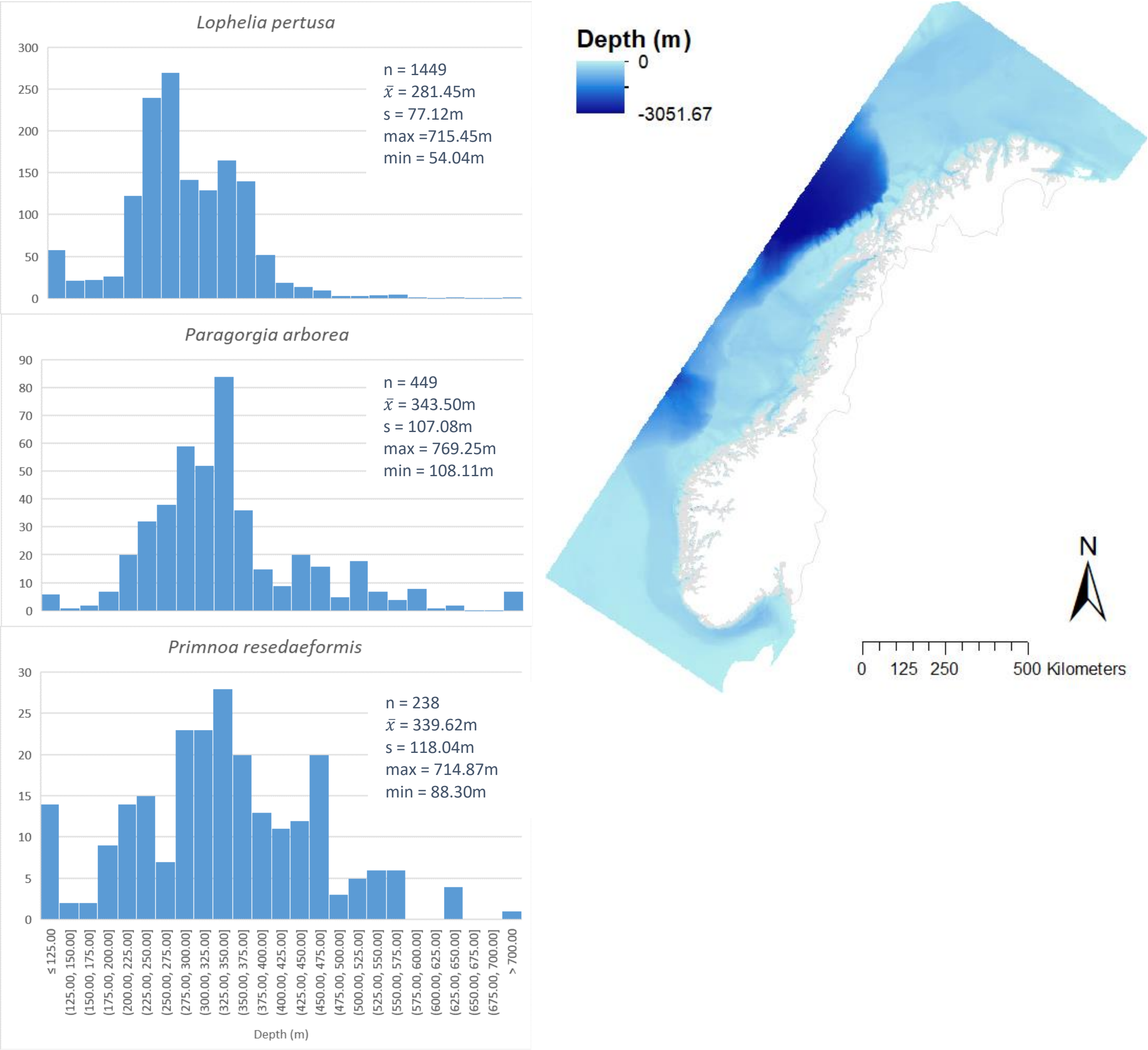


Figure 6 - Histograms showing depth distribution per coral species. Next to it is the bathymetry map within the Norwegian study showing the spatial distribution of depth.

3.1.2 Terrain Variables

In general, BPI (both broad and fine) and the natural logarithm of ruggedness have a unimodal distribution, more or less centered around the mean (Figure 8, Figure 9, and Figure 10). Slope differs from this pattern, resembling a Poisson distribution, with most occurrences clustering around at the lowest slope values and a logarithmic decline in number of occurrences with increasing values (Figure 7).

Slope (*Figure 7*) means are quite similar for all corals (*Lophelia* = 2.15°, *Paragorgia* = 3.35°, *Primnoa* = 3.17°), but *Primnoa* shows greatest variation (s = 5.75°, compared to s = 3.16° for *Lophelia* and s = 4.46° for *Paragorgia*), and *Lophelia* has the highest maximum slope record at 38.24° (compared to 35.00° for the gorgonians).

For broad BPI, *Lophelia* is unique in that it shows two peaks of occurrences, one around -50 to 100 (slight depressions and elevations in the terrain) like the gorgonians, and the other in more negative (trough) values (*Figure 8*). Broad BPI varied the most for *Paragorgia* (s = 303.76, compared to s = 180.99 for *Lophelia* and s = 145.07 for *Primnoa*), which the range of values also reflects (from -1260.00 to 1220.00, compared to a range from -937.00 to 700.00 for *Lophelia* and from -542.00 to 448.00 for *Primnoa*). *Lophelia* had a slight tendency to negative broad BPI values with a mean of -39.64, while *Paragorgia* had a mean of 15.17 and *Primnoa* a mean of 33.73, indicating slightly more preference to a larger terrain area that protrudes. Similar patterns can be seen for fine BPI (*Figure 9*). One noteworthy point about the distributions for fine BPI is that observations are more clustered around the smaller BPI values than they are for broad BPI, within a similar range (-100 to 100), indicating more uniformity at local, smaller-scale variations in terrain.

The natural log of ruggedness is quite similar for the species, as expected with the small variation in the ruggedness layer created (*Figure 10*). The means -9.95 (*Lophelia*), -9.54 (*Paragorgia*), and -9.81 (*Primnoa*) actually equate to approximately 0.00005, which is very low terrain ruggedness. In addition, the corals, particularly *Lophelia*, extend almost across the entire range of ruggedness seen in the map.

Wind charts were created to visualize the angular aspect distribution (Figure 11), while the summary statistics for the statistical aspect values, northerness and easterness, are shown. There is a tendency towards slopes facing west for all three corals (reflected by the negative easterness means, i.e. west), and northwest for the gorgonians (positive northerness means, i.e. north), while *Lophelia* resides mostly on a range from southern to northwestern slopes.

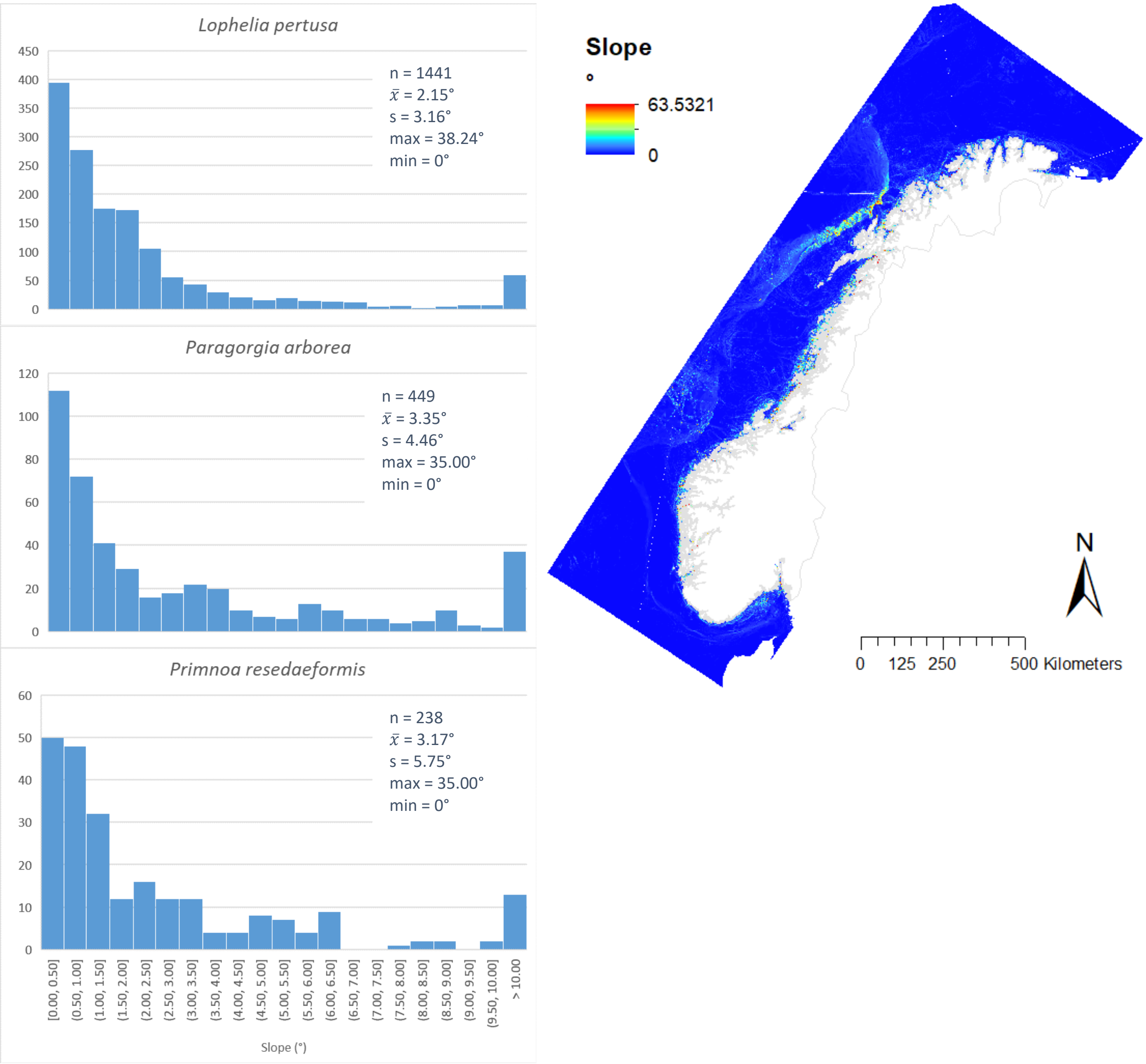


Figure 7 - Histograms showing slope distribution per coral species, with a map of the variable within the Norwegian study.

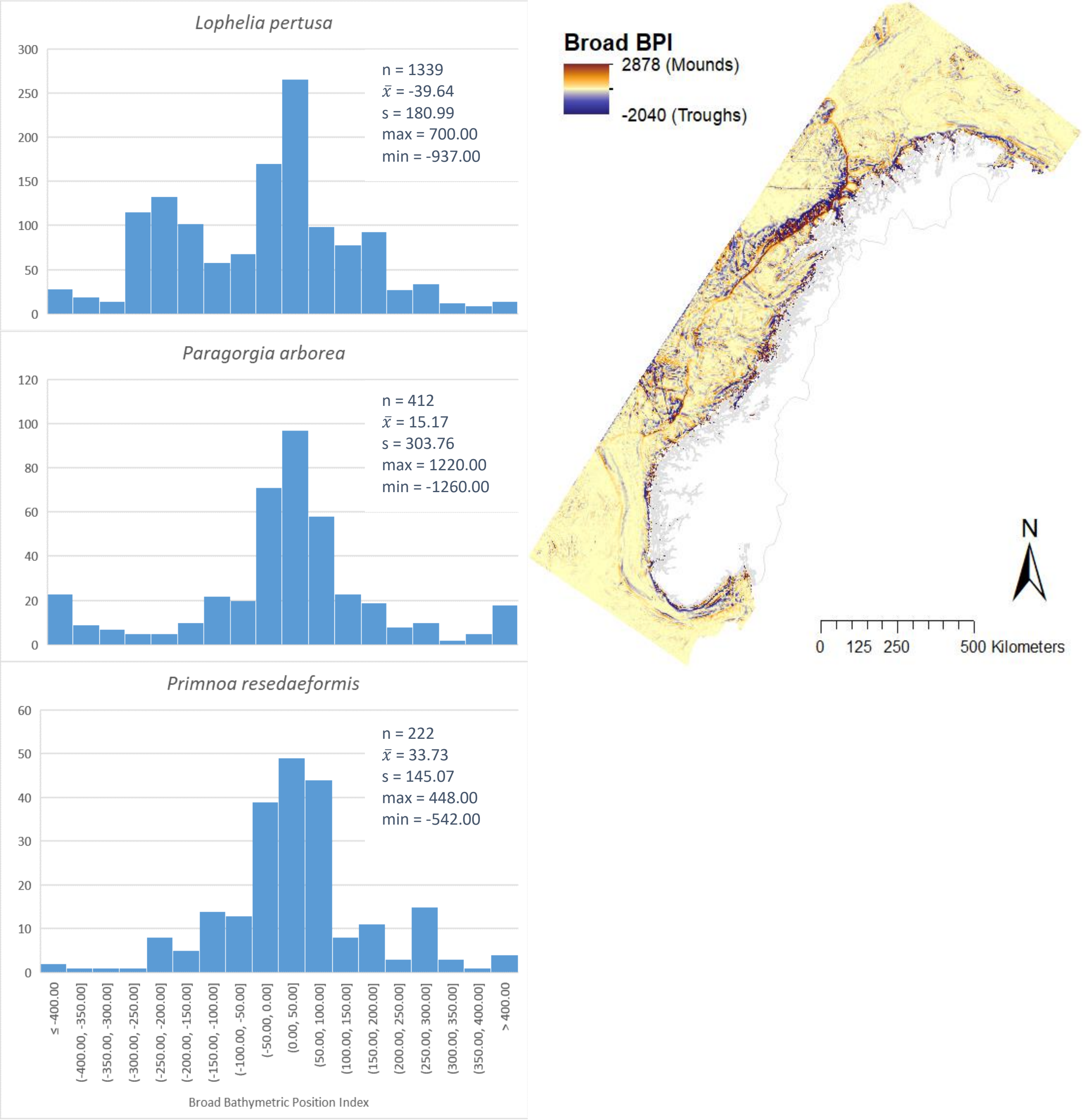


Figure 8 - Histograms showing broad BPI distribution per coral species, with a map of the variable within the Norwegian study.

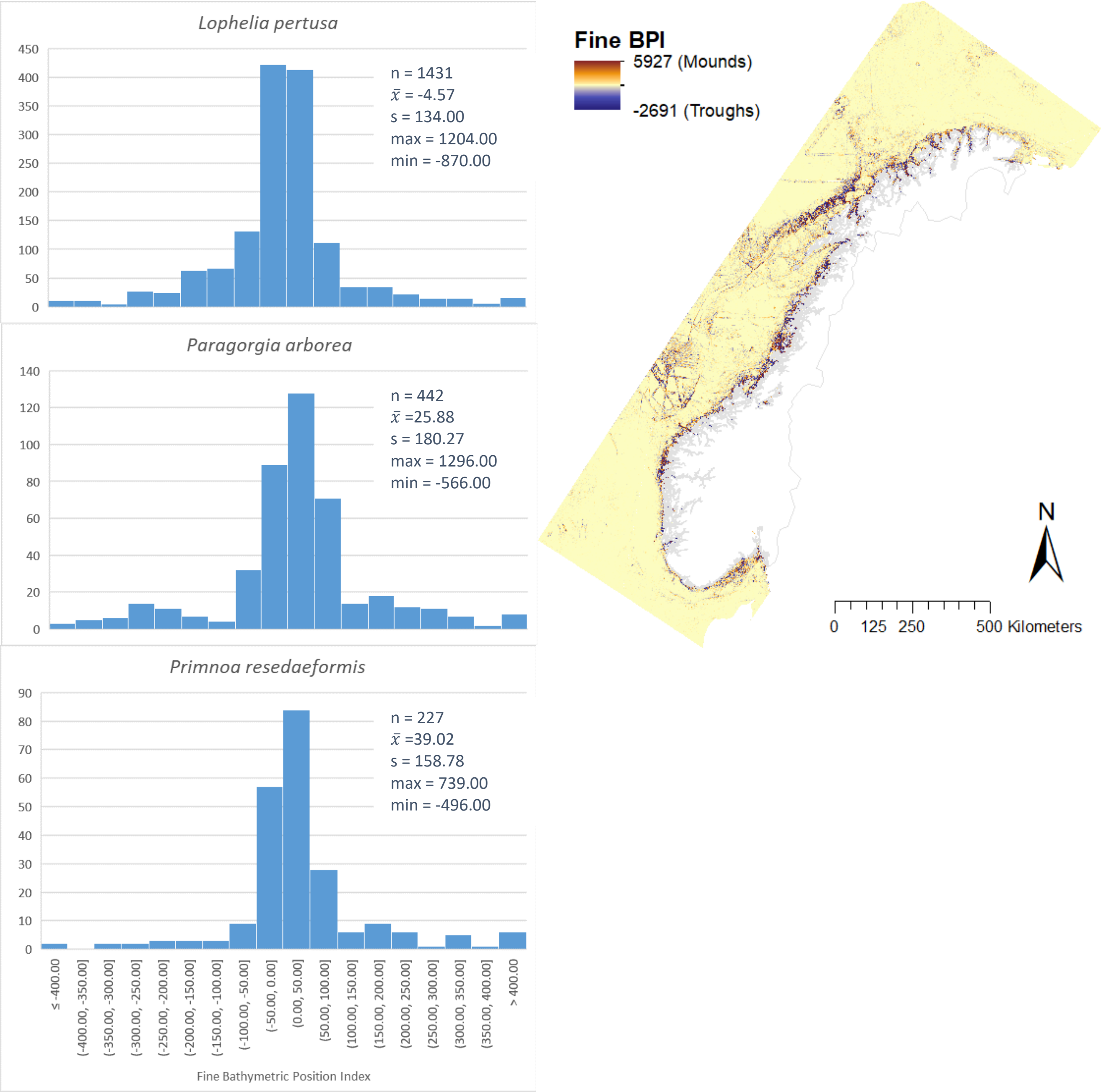


Figure 9 - Histograms showing fine BPI distribution per coral species, with a map of the variable within the Norwegian study.

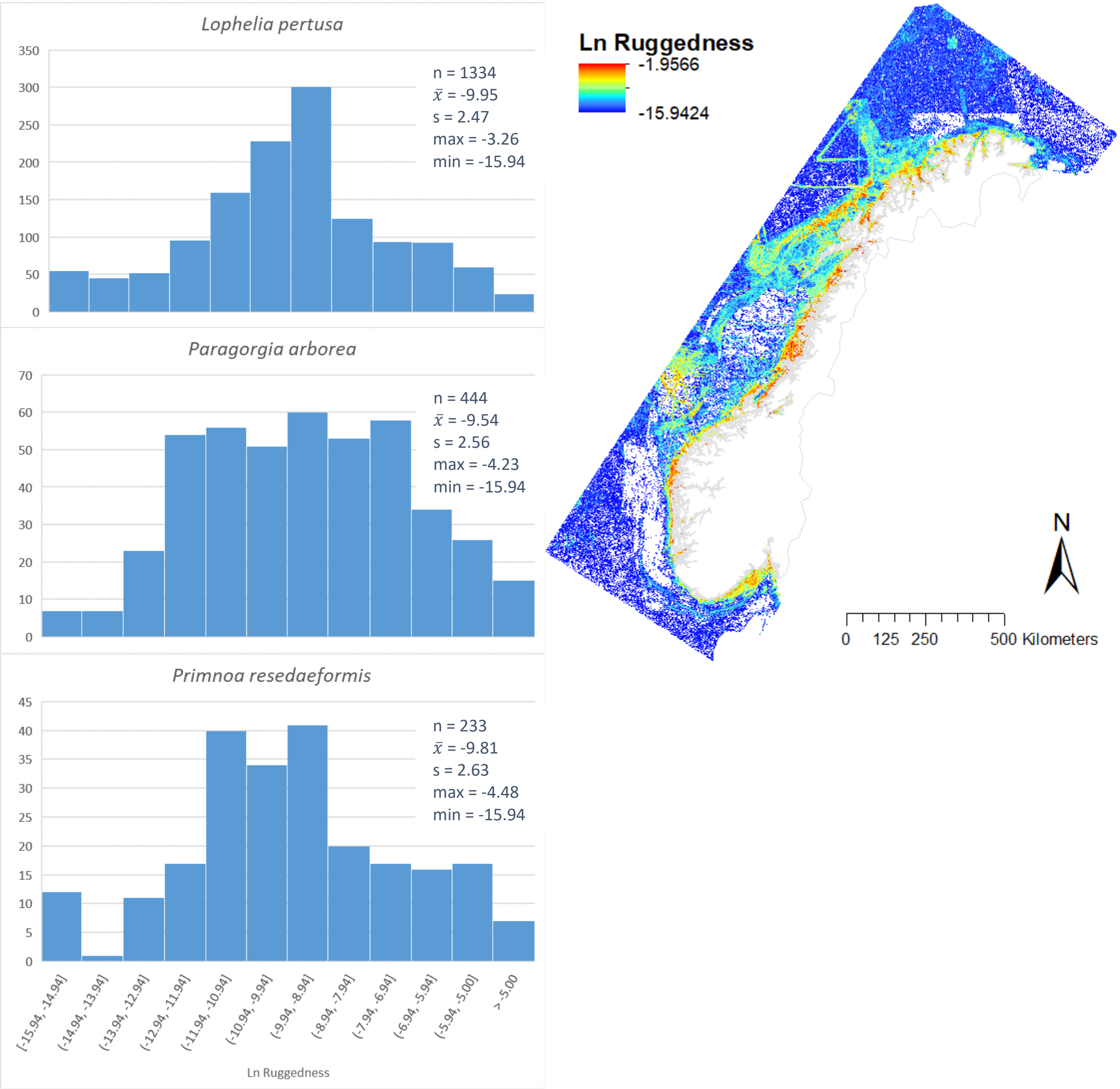


Figure 10 - Histograms showing the natural logarithm of ruggedness distribution per coral species, with a map of the variable within the Norwegian study. White areas in the water are areas without value, a consequence of leaving out original ruggedness values of 0 before taking the natural logarithm.

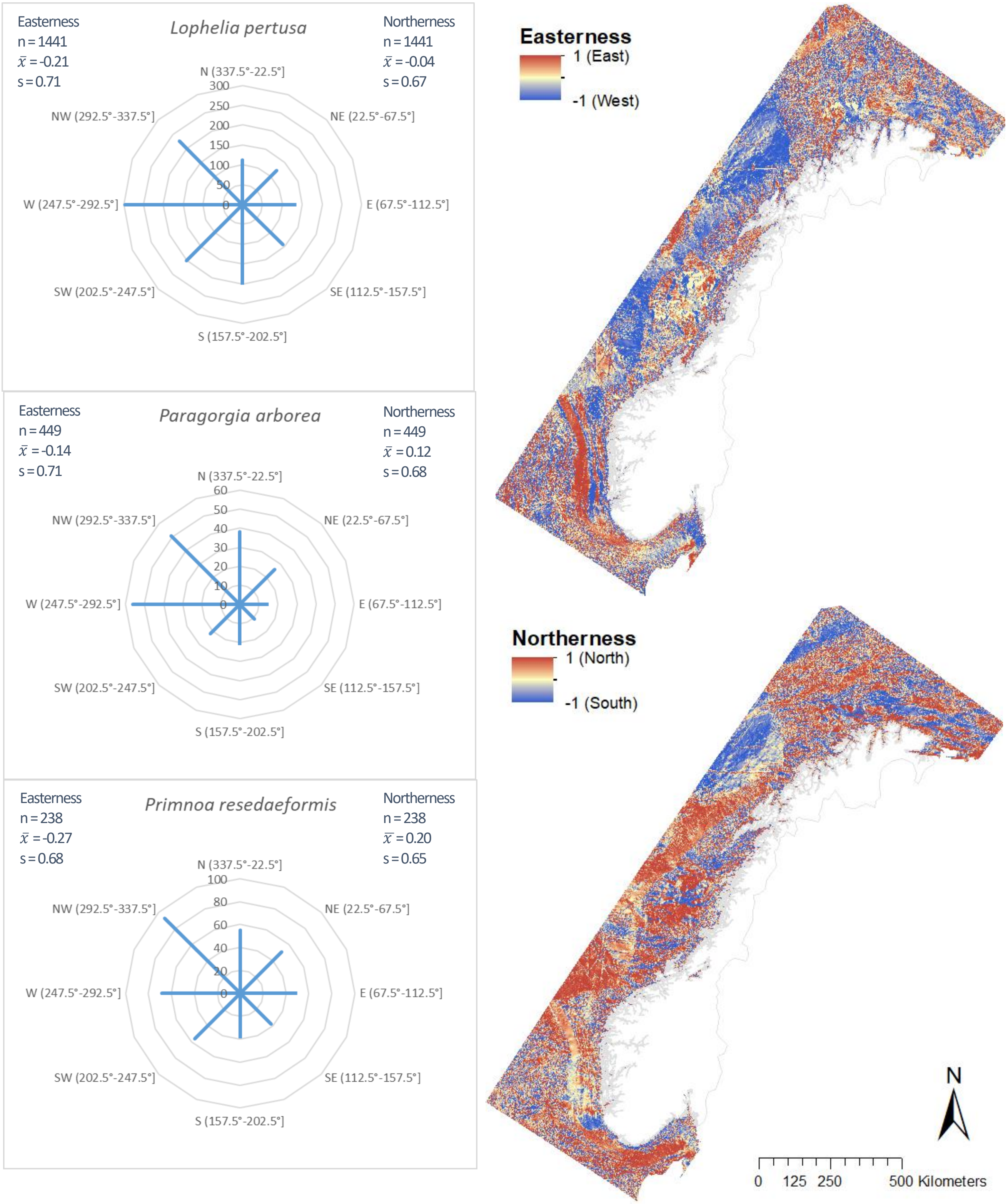


Figure 11 - Wind charts showing aspect direction distribution per coral species, together with summary statistics for the angle's decomposed variables, easterness and northerness. The upper map shows easterness and the lower map shows northerness within the Norwegian study area.

3.1.3 Oceanographic Variables

The mean temperature distribution in the "cold season" (*Figure 12*), from March to May, for *Lophelia* shows a clear peak at 6-6.5 °C, while the gorgonians have a wider range of temperatures, dropping suddenly at 4.5 °C and then slowly decreasing as temperature decreases. In the "warm season" (*Figure 13*), from October to December, *Lophelia* again has a sharp peak, at 7.5-8 °C, a second one at 6.5-7 °C, and then dropping suddenly at 5 °C. *Paragorgia* also shows a sudden drop at 5 °C, but otherwise the distribution is shifted towards colder temperatures compared to *Lophelia,* as it is for *Primnoa*. The gorgonians also have second, smaller peak at the colder temperatures of 3.5-4 °C.

In terms of salinity, all corals are mostly within 35.2-35.3 PSU for the average maximum (though *Primnoa* also has a small peak at 35.05-35.10 PSU) (*Figure 14*); at 34.95 PSU and above for mean salinity (with a maximum mean salinity of 35.26 PSU for *Lophelia*, 35.28 PSU for *Paragorgia*, and 35.23 PSU for *Primnoa*) (*Figure 15*); and mostly within 17.5-17.65 PSU for minimum salinity (*Figure 16*), which must be due to short bursts of low-saline downwelling currents. Thus, the corals are within quite restricted windows of salinity.

In regards to current speed, most coral presences for each species occur within maximum speeds of 0.2-0.7 m/s, with some occurrence throughout at greater speeds (*Figure 17*). For mean current speed (*Figure 18*), all corals tend towards bimodality, most clearly seen with *Lophelia* (which has the greatest number of presence points), with peaks at around 0.08 and 0.2 m/s.

The wind charts for mean current direction (*Figure 19*) indicate *Lophelia* prefers currents heading west, *Paragorgia* north/northeast, and *Primnoa* north. All have a great tendency for currents heading north, as seen with the northerness means of 0.55 for *Lophelia*, 0.39 for *Paragorgia*, and 0.45 for *Primnoa*, reflecting the prevailing direction of the Norwegian Coastal Current explained in section 2.1.

The "experimental" variable current-aspect angle (*Figure 20*), showing the angle made by currents relative to the aspect direction, shows for all species that very few reside in areas where the current directly flows over the slope (angle 0°) or directly into the slope (angle of 180°). Corals are mostly distributed with angles that are in between, but especially angles of 90°, meaning the current runs perpendicular to the slope.

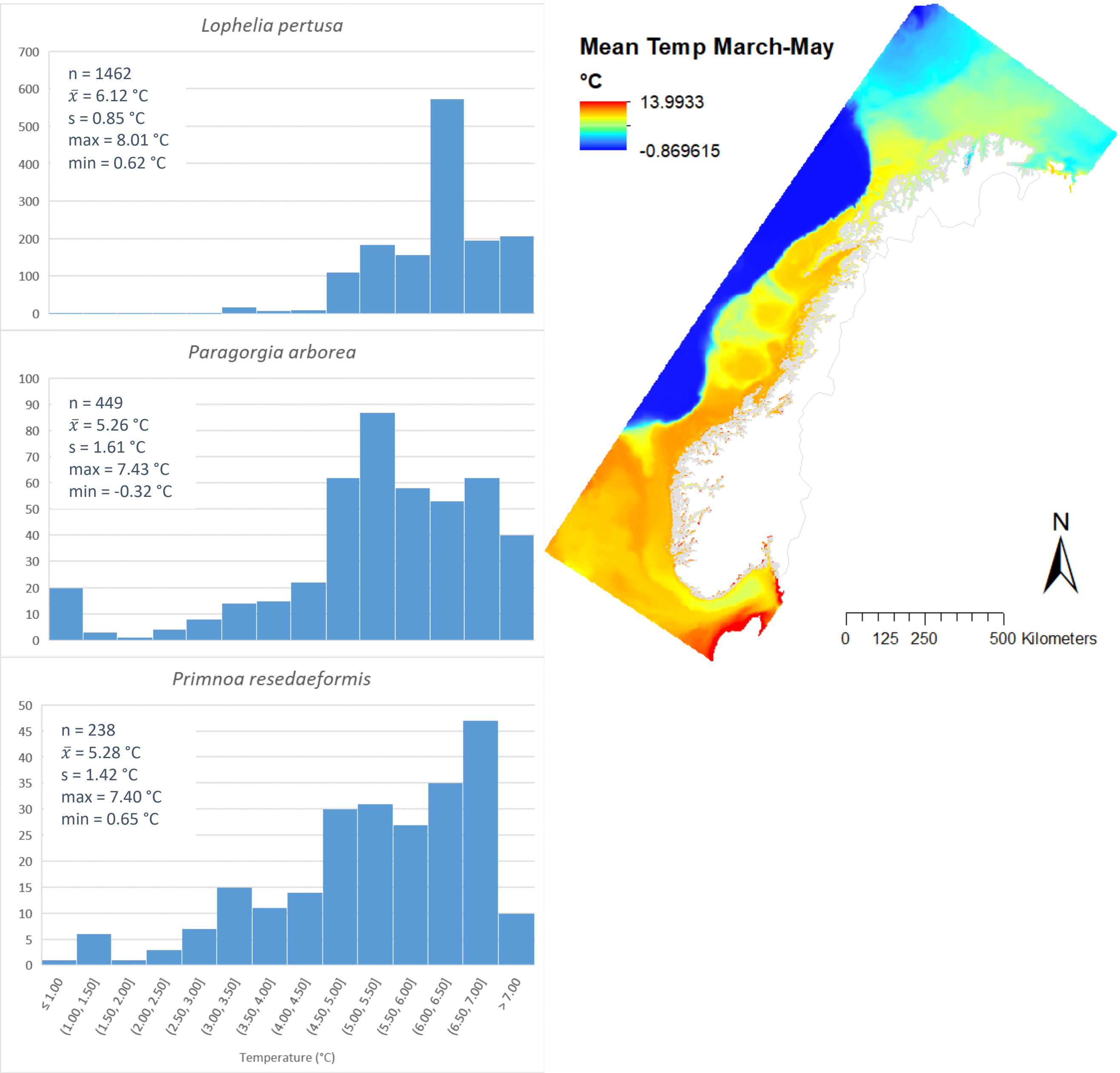


Figure 12 - Histograms showing mean temperature distribution for March through May, per coral species, with a map of the variable within the Norwegian study.

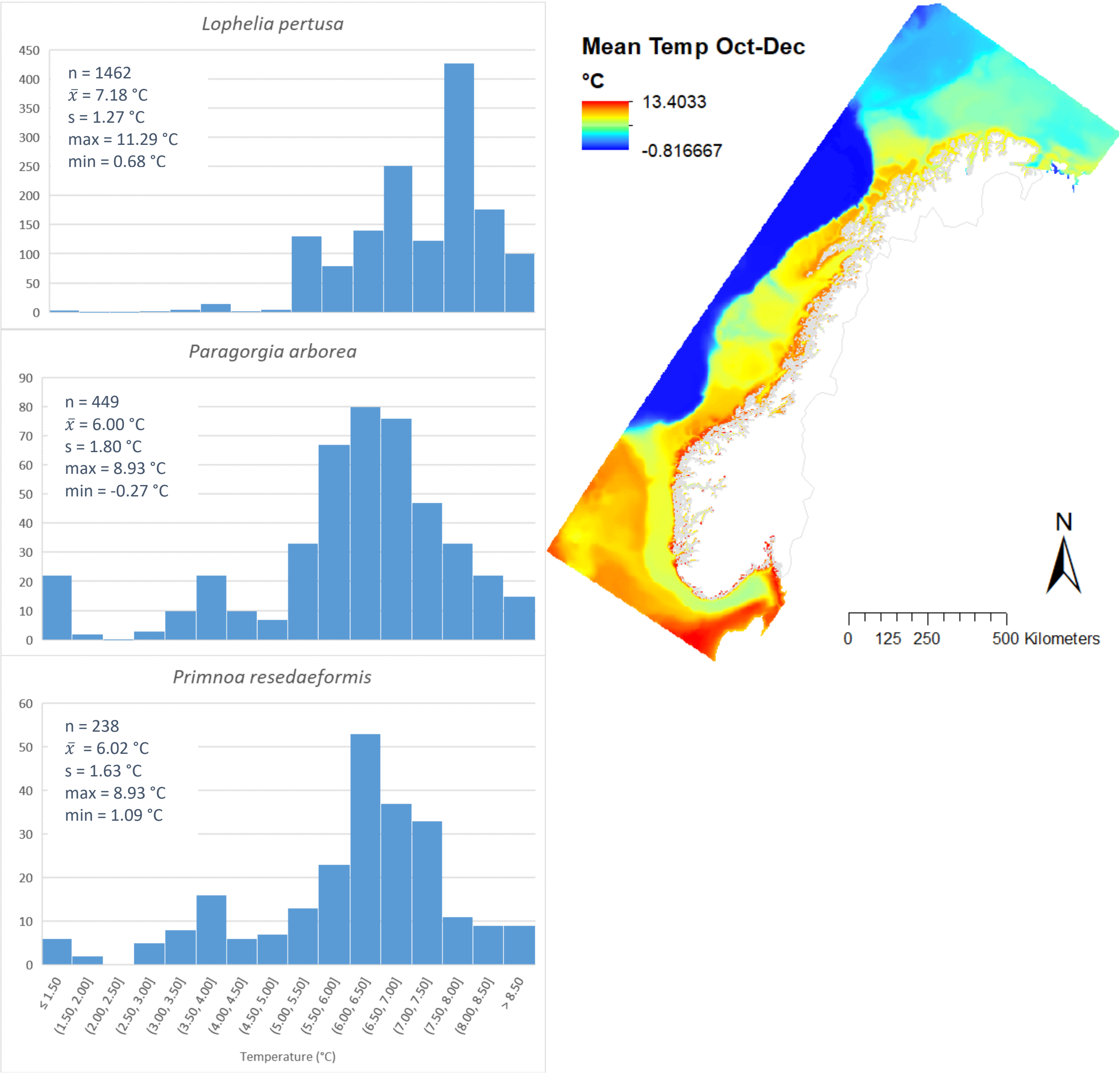


Figure 13 - Histograms showing mean temperature distribution for October through December, per coral species, with a map of the variable within the Norwegian study.

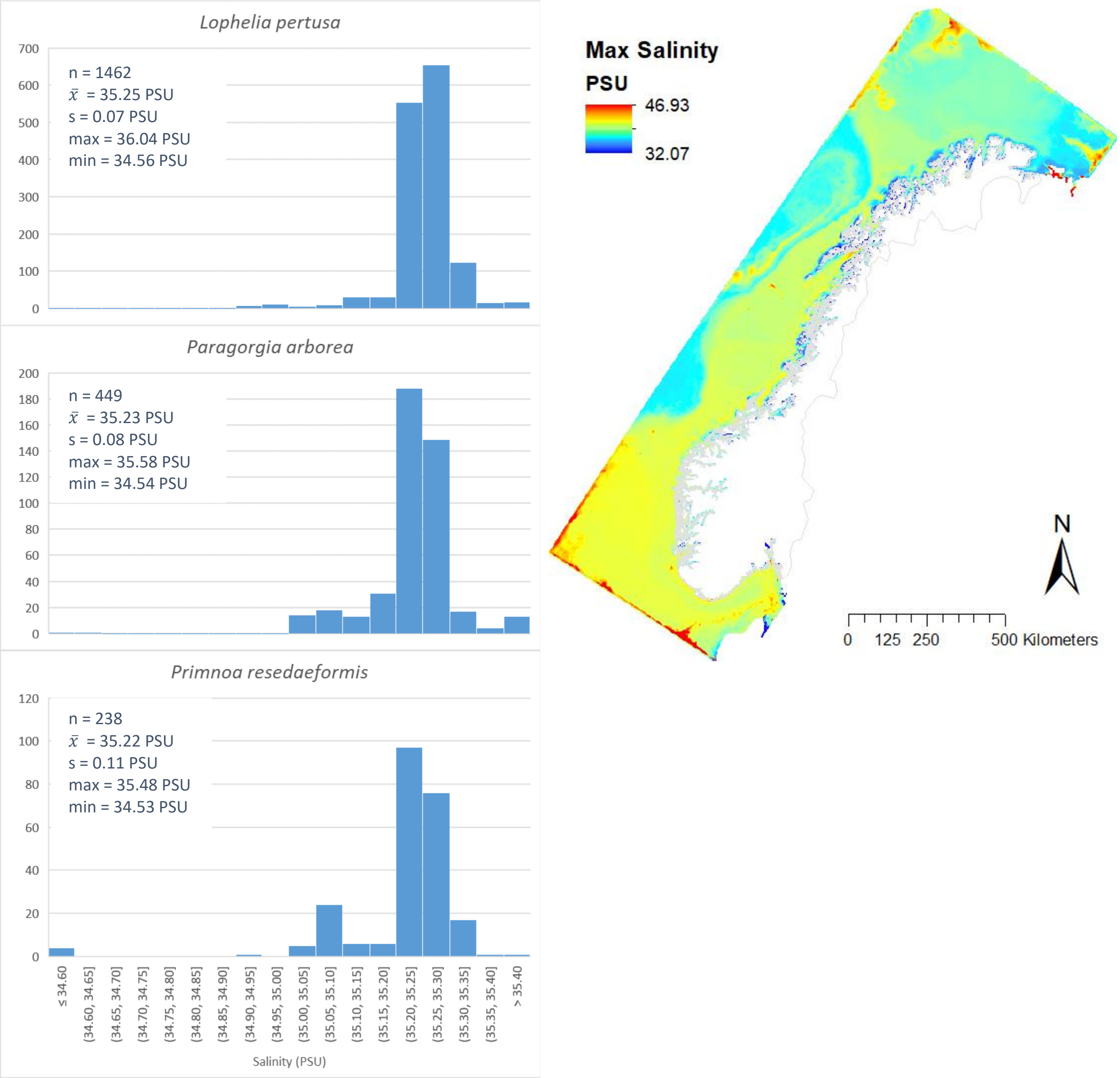


Figure 14 - Histograms showing maximum salinity distribution per coral species, with a map of the variable within the Norwegian study.

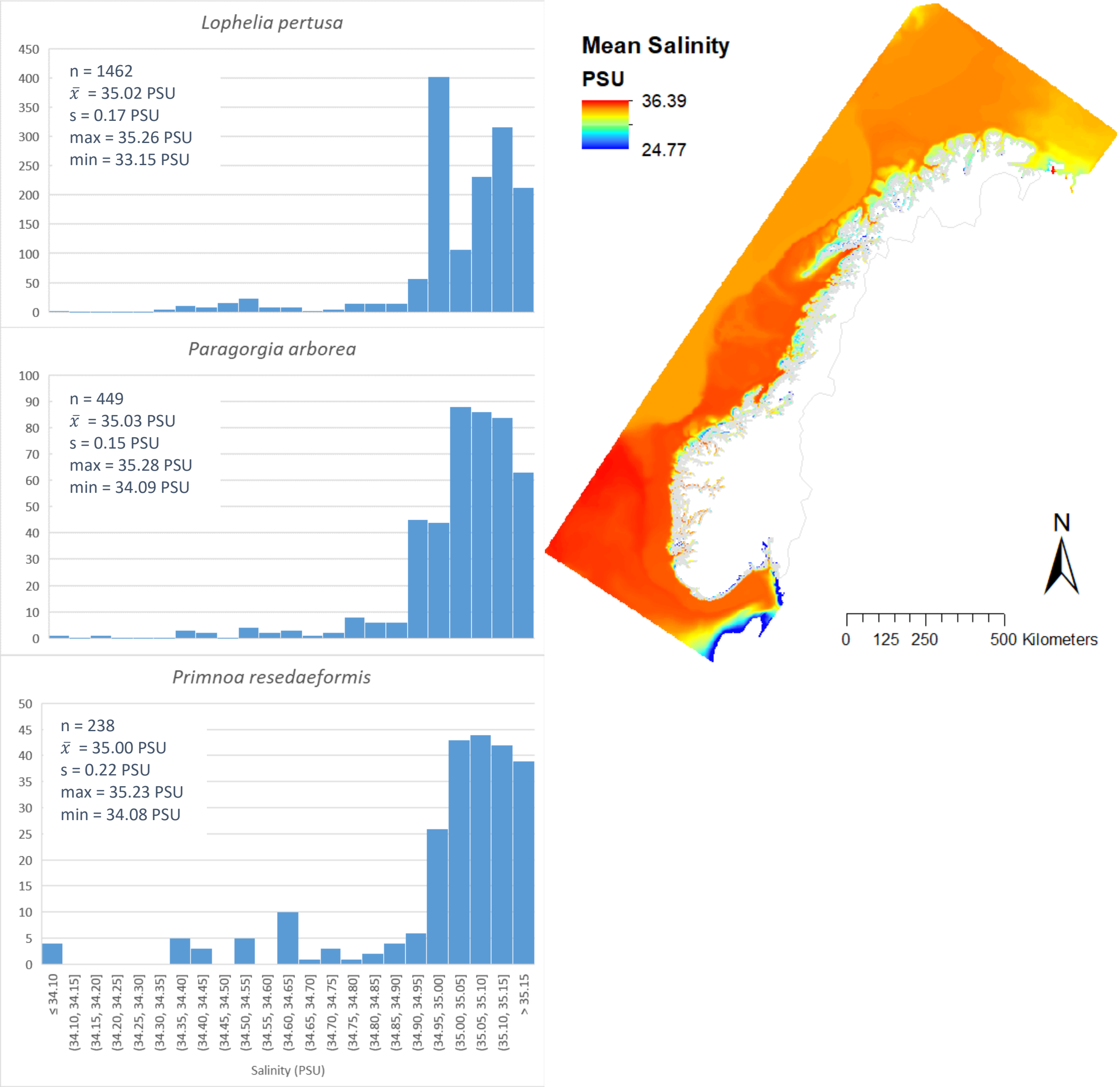


Figure 15 - Histograms showing mean salinity distribution per coral species, with a map of the variable within the Norwegian study.

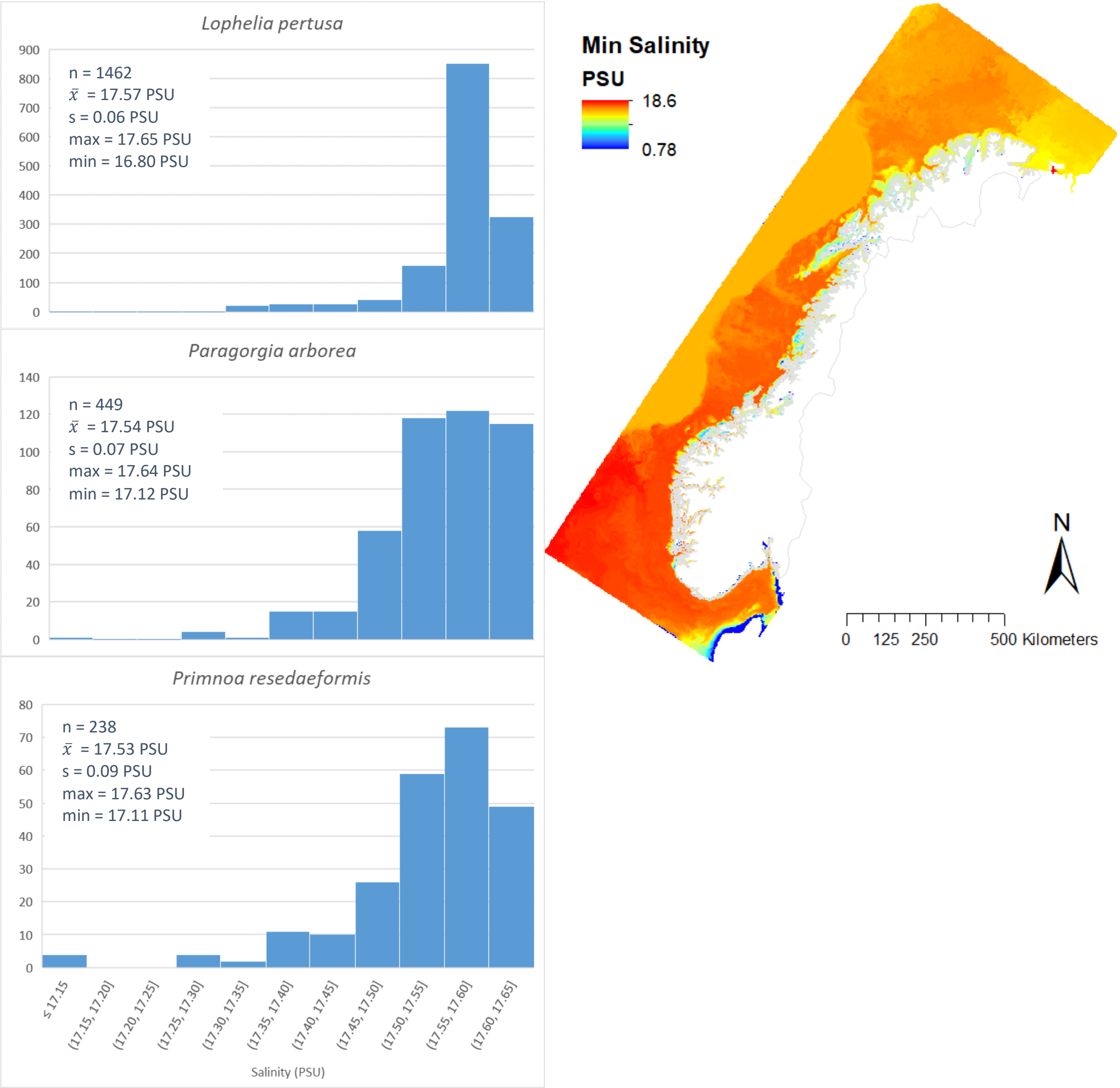


Figure 16 - Histograms showing minimum salinity distribution per coral species, with a map of the variable within the Norwegian study.

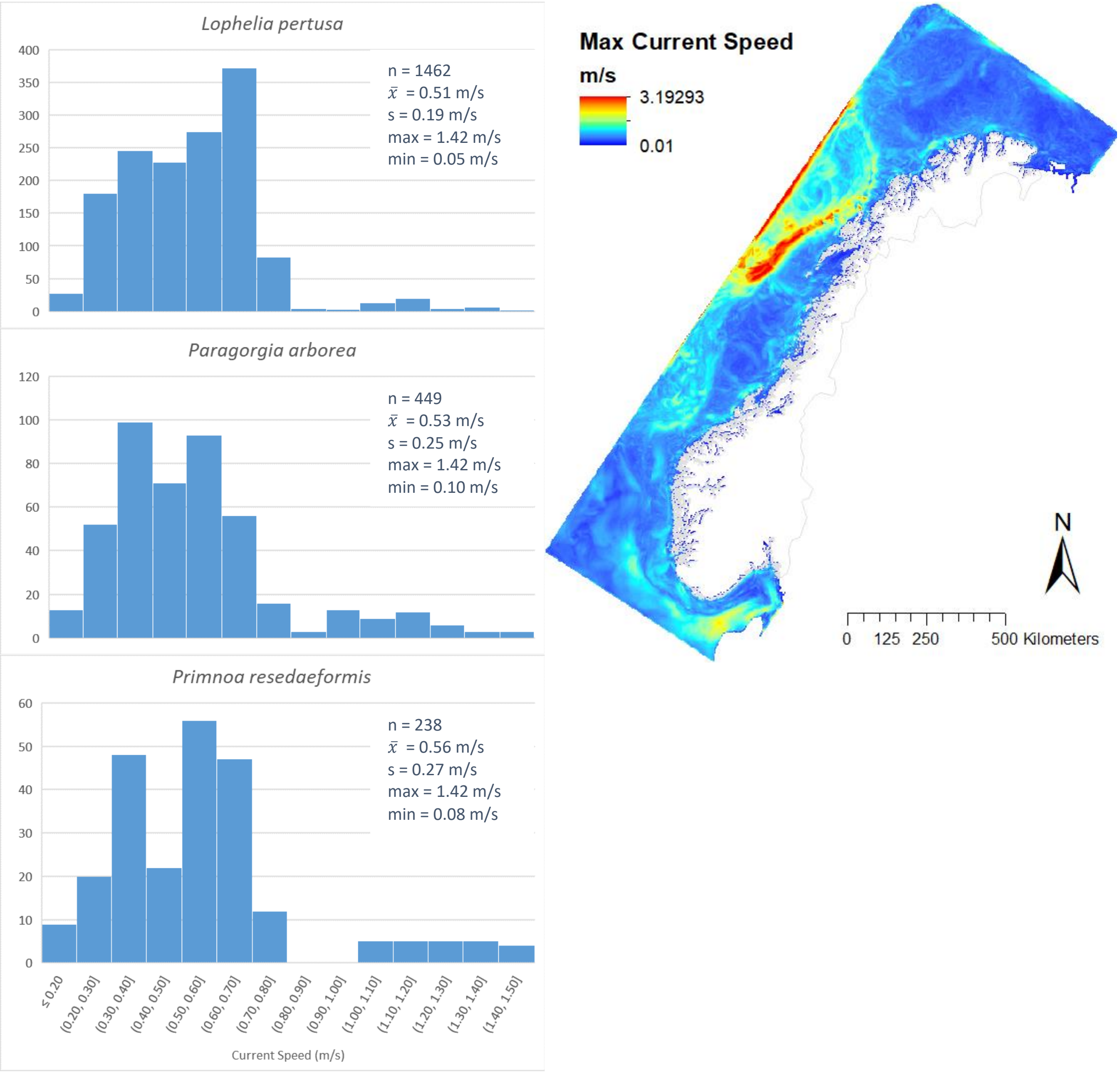


Figure 17 - Histograms showing maximum current speed distribution per coral species, with a map of the variable within the Norwegian study.

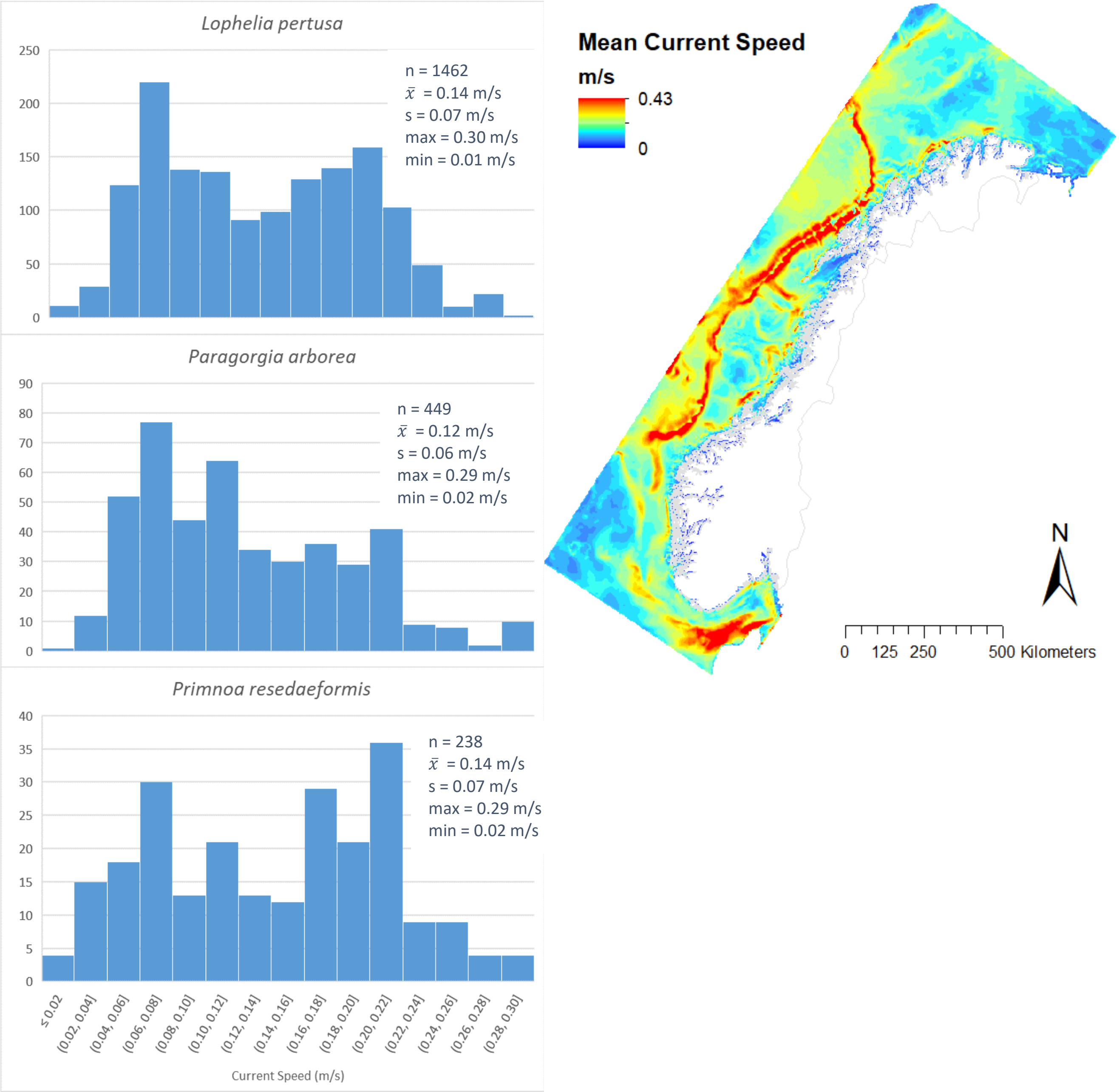


Figure 18 - Histograms showing mean current speed distribution per coral species, with a map of the variable within the Norwegian study.

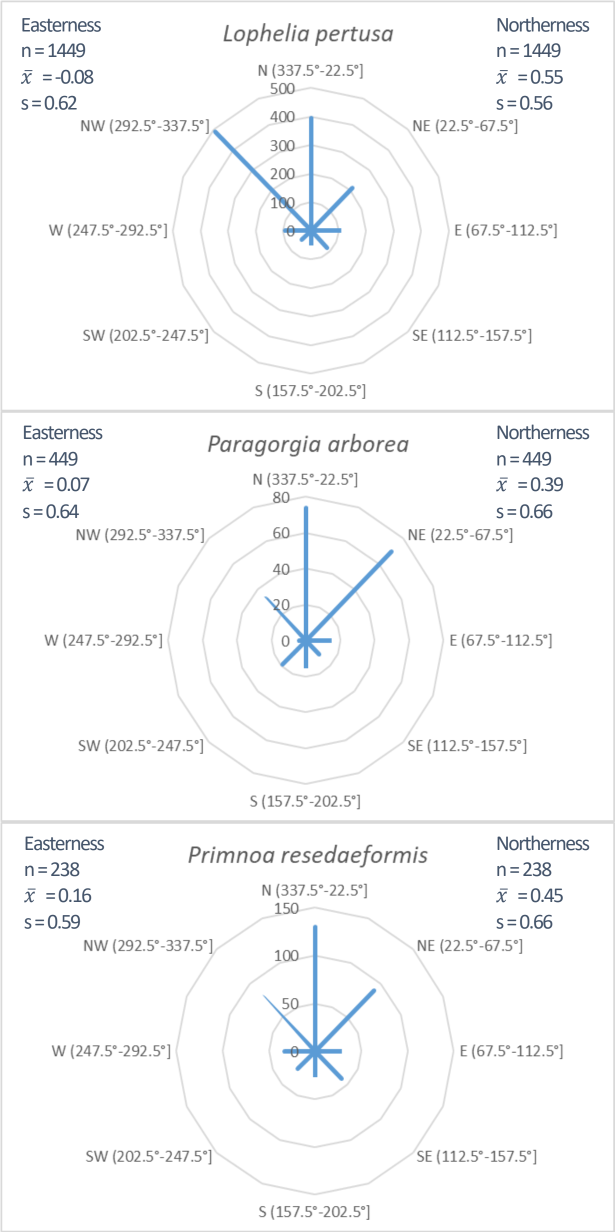
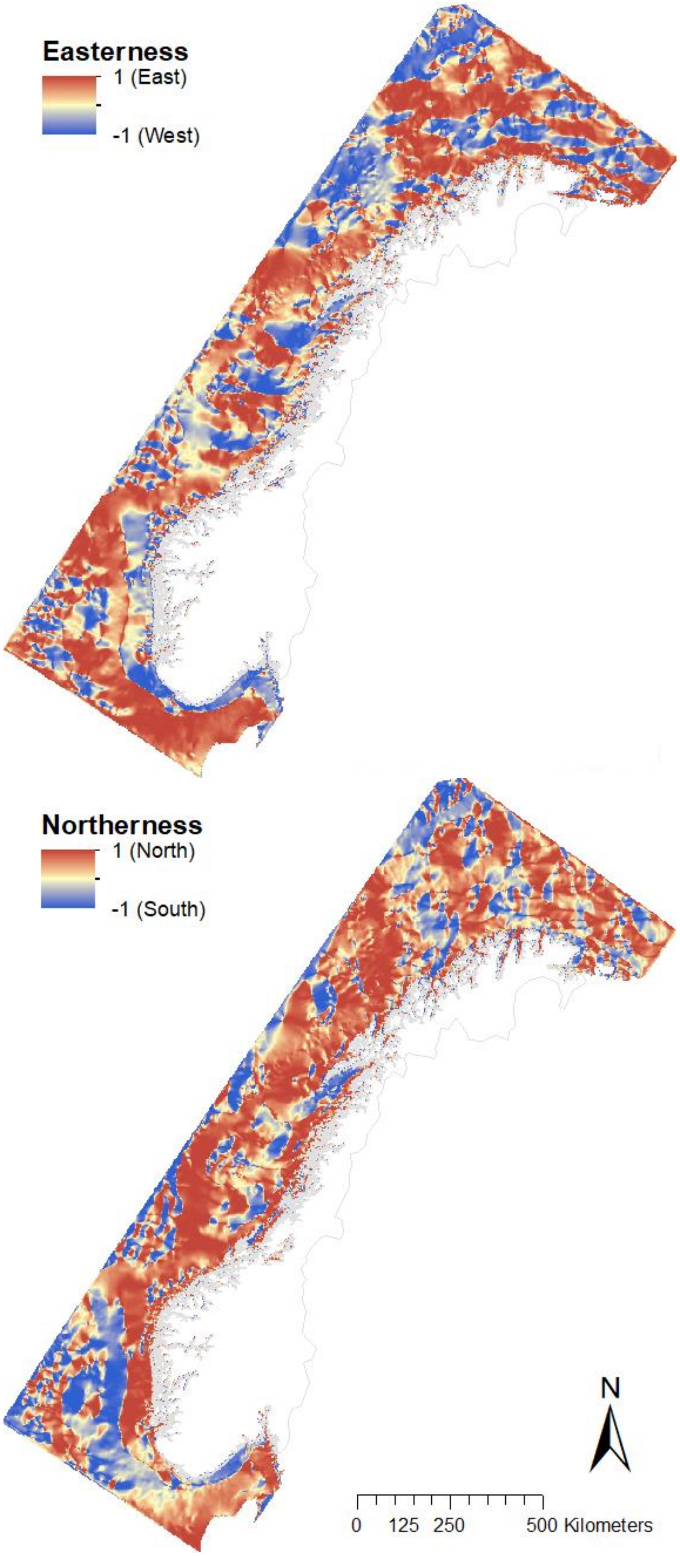


Figure 19 - Wind charts showing mean current direction distribution per coral species, together with summary statistics for the angle's decomposed variables, easterness and northerness.



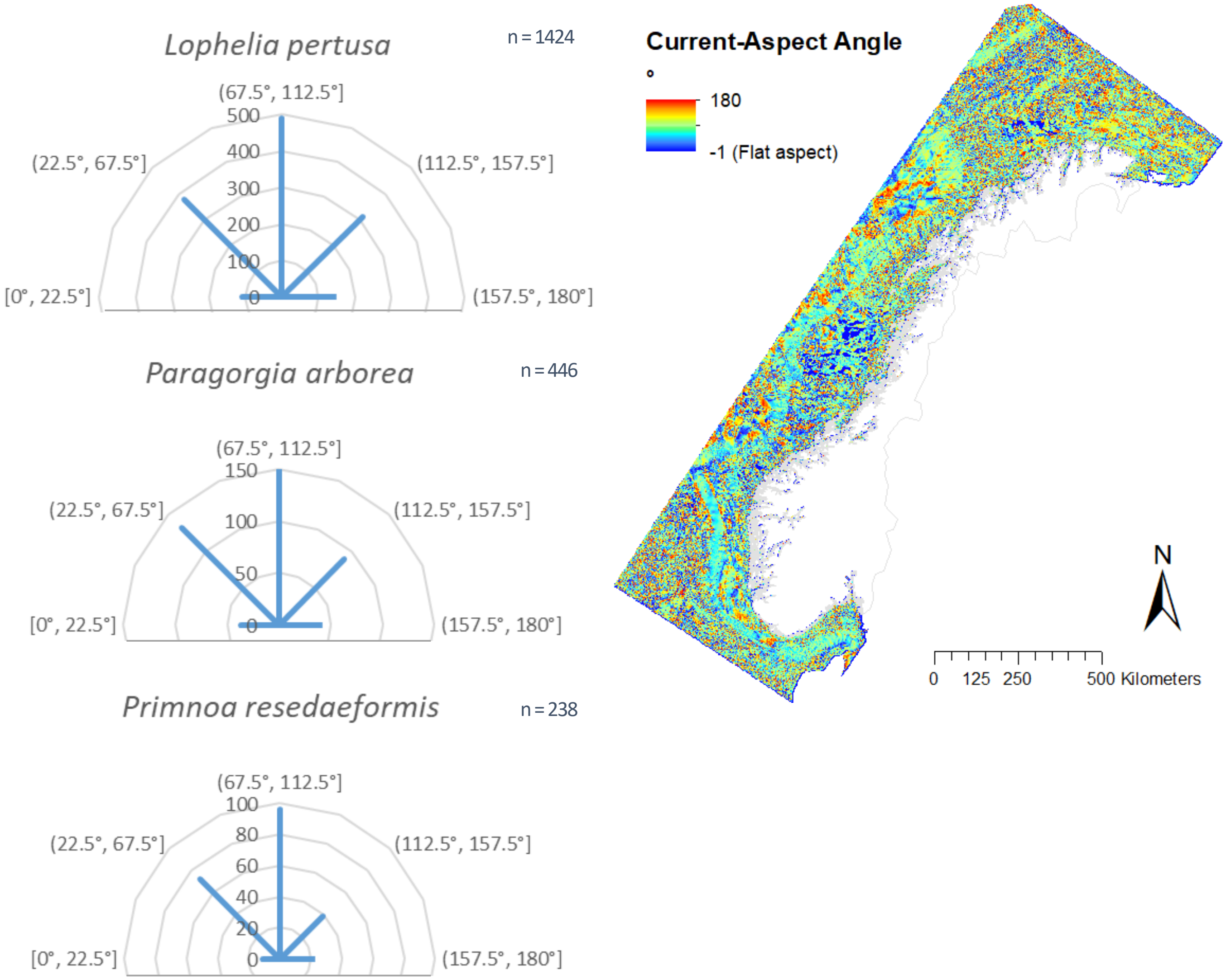


Figure 20 - Half wind charts showing current-aspect angle distribution per coral species, with a map of the variable within the Norwegian study. The variable range is from 0 to 180°, but areas in dark blue on the map are areas with flat terrain/no slope (-1), meaning the current-aspect angle was not calculated here.

3.1.4 Surface Chlorophyll *a* Concentration

The distribution for surface chlorophyll *a* concentration varies a lot for each species. *Lophelia* has a clear peak at 1.35-1.4 mg/m^3, and a higher mean of 1.60 mg/m^3 compared to 1.39 mg/m^3 for *Paragorgia* and 1.28 mg/m^3 for *Primnoa*. But *Lophelia* also greater variation (s = 2.05 mg/m^3) compared to *Paragorgia* (s = 0.74 mg/m^3) and *Primnoa* (s = 0.49 mg/m^3), and a much greater range, with a maximum of 20.59 mg/m^3 compared to 4.76 mg/m^3 for *Paragorgia* and 4.75 mg/m^3 for *Primnoa*.

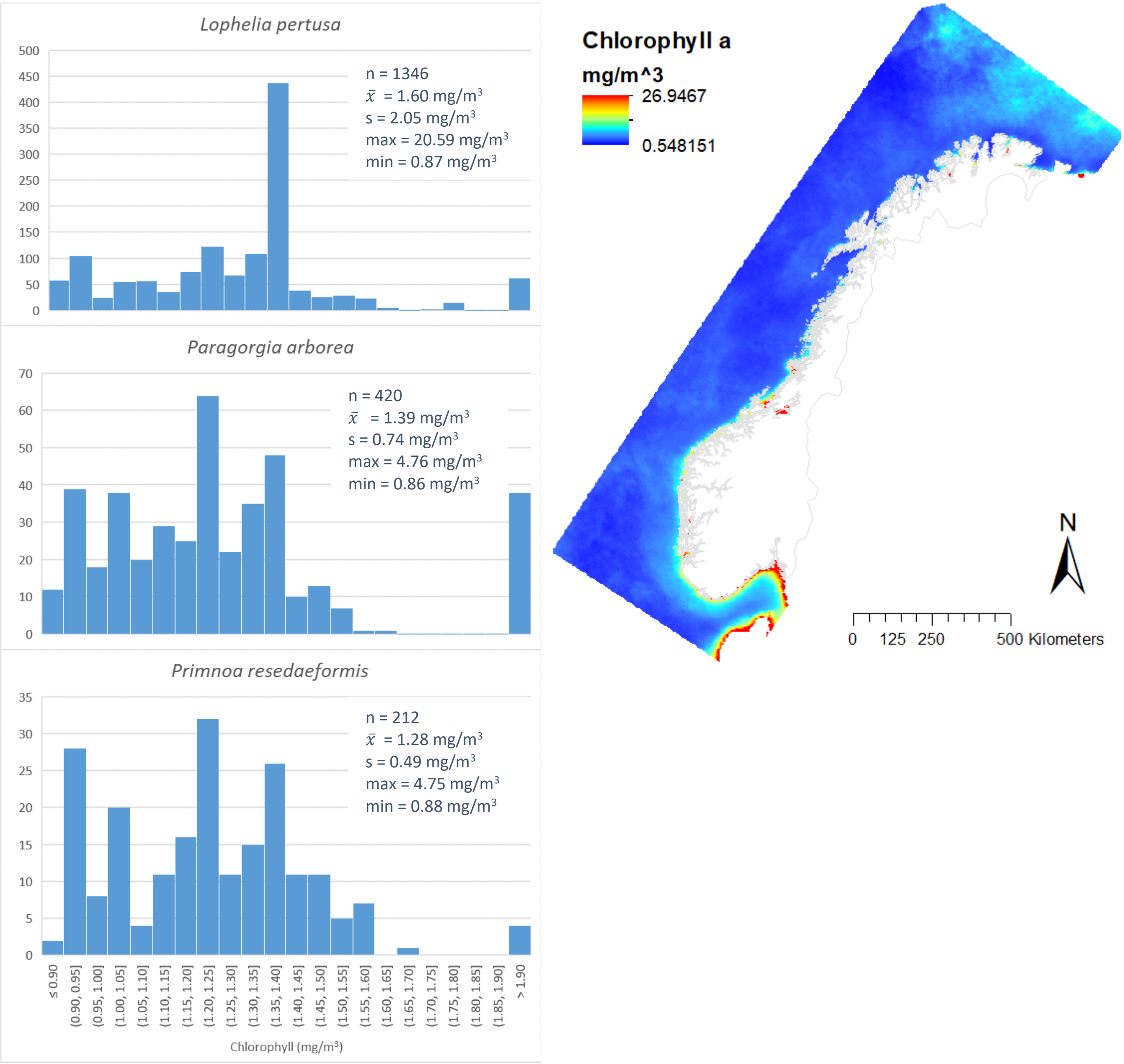


Figure 21 - Histograms showing mean surface chlorophyll a concentration per coral species, with a map of the variable within the Norwegian study.

3.1.5 Sediment

The bar graphs in *Figure 22* show the relative frequency of each coral species within the sediment categories defined as above in Table 2; the upper graph, NGU Records, indicates the sediment as defined by the sediment map in Figure 22, and the lower graph, Video Observation, indicates sediments recorded in the video logs for coral presence data. According to the video data, gorgonian corals have the highest presence on coral, i.e. *Lophelia* reefs. The most closely related category in the NGU records, “Bioclastic material”, was deleted as explained in section 2.2. The sediments “gravelly muddy sand” and “sandy gravel” are frequent for all three corals in the NGU records, as is “gravelly sand” in the video records.

Lophelia observations are most abundant in “gravelly muddy sand” sediment in the NGU records, while for the video data they are most abundant in “gravelly sand”, two very similar sediments. *Paragorgia* is mostly observed at both “sandy gravel” and “gravelly muddy sand” in the NGU records, but mostly just “gravelly sand” according to the video logs. Lastly, *Primnoa* also occurs mostly in “gravelly muddy sand” and “sandy gravel” in the NGU records, while video logs indicate *Primnoa* to be most abundant on “exposed bedrock”.

3.1.6 Marine Landscape

The bar graph in Figure 23 show the relative frequency of each coral species within the marine landscape categories defined as above in Table 3, as well as the map showing the broad classification of the landscape within Norwegian waters.

The graph shows that “smooth continental slope”, “marine valley”, and “shallow marine valley” are the most frequent for all three species. *Lophelia* has the highest frequency of shallow marine valley landscape, *Paragorgia* of marine valley landscape, and *Primnoa* of smooth continental slope. Strandflat has very low/no frequency for all.

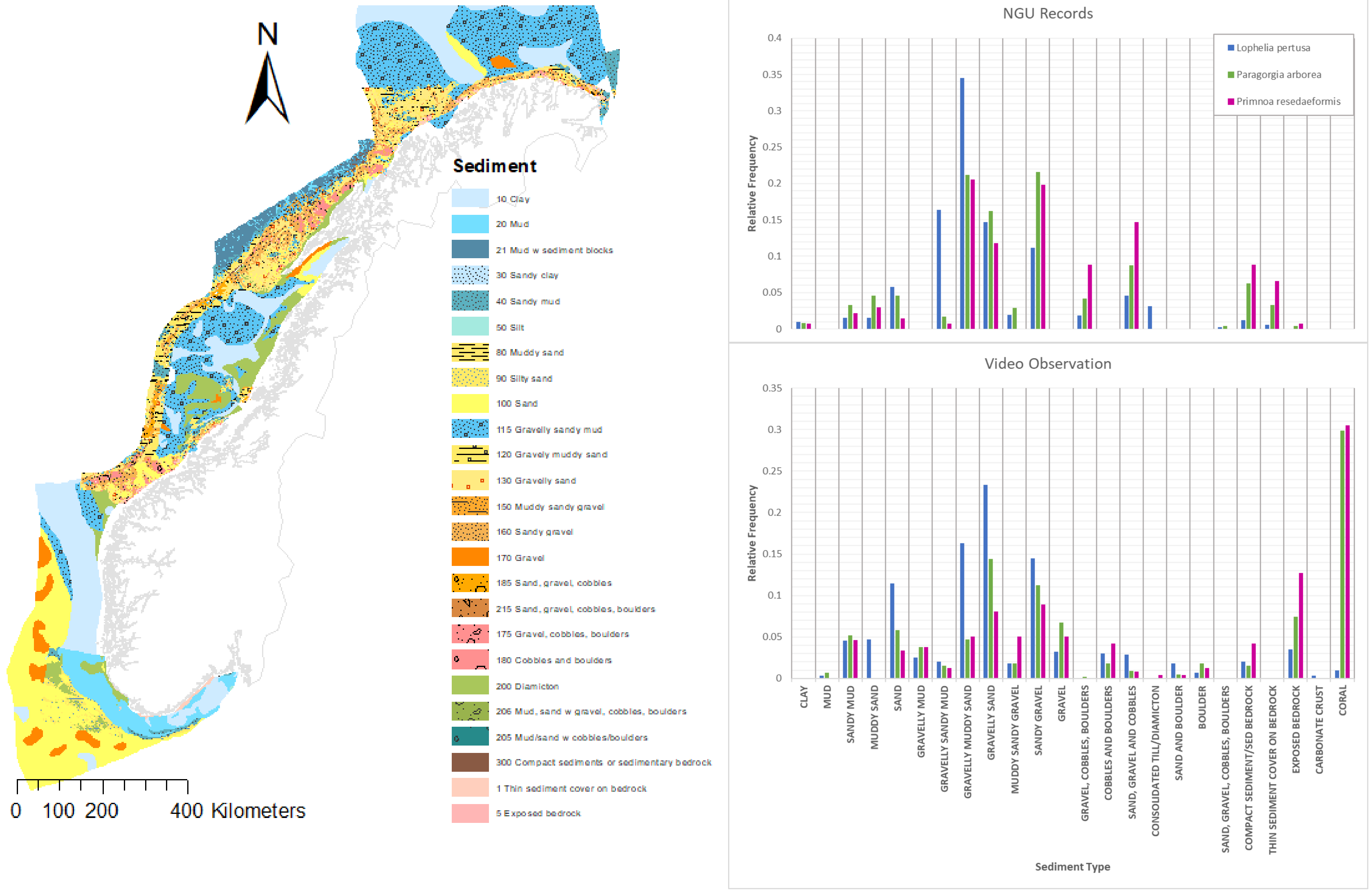


Figure 22 - Bar charts showing relative frequency of sediment type per coral species, from the NGU classification (also pictured in the map) and from MAREANO's coral video records.

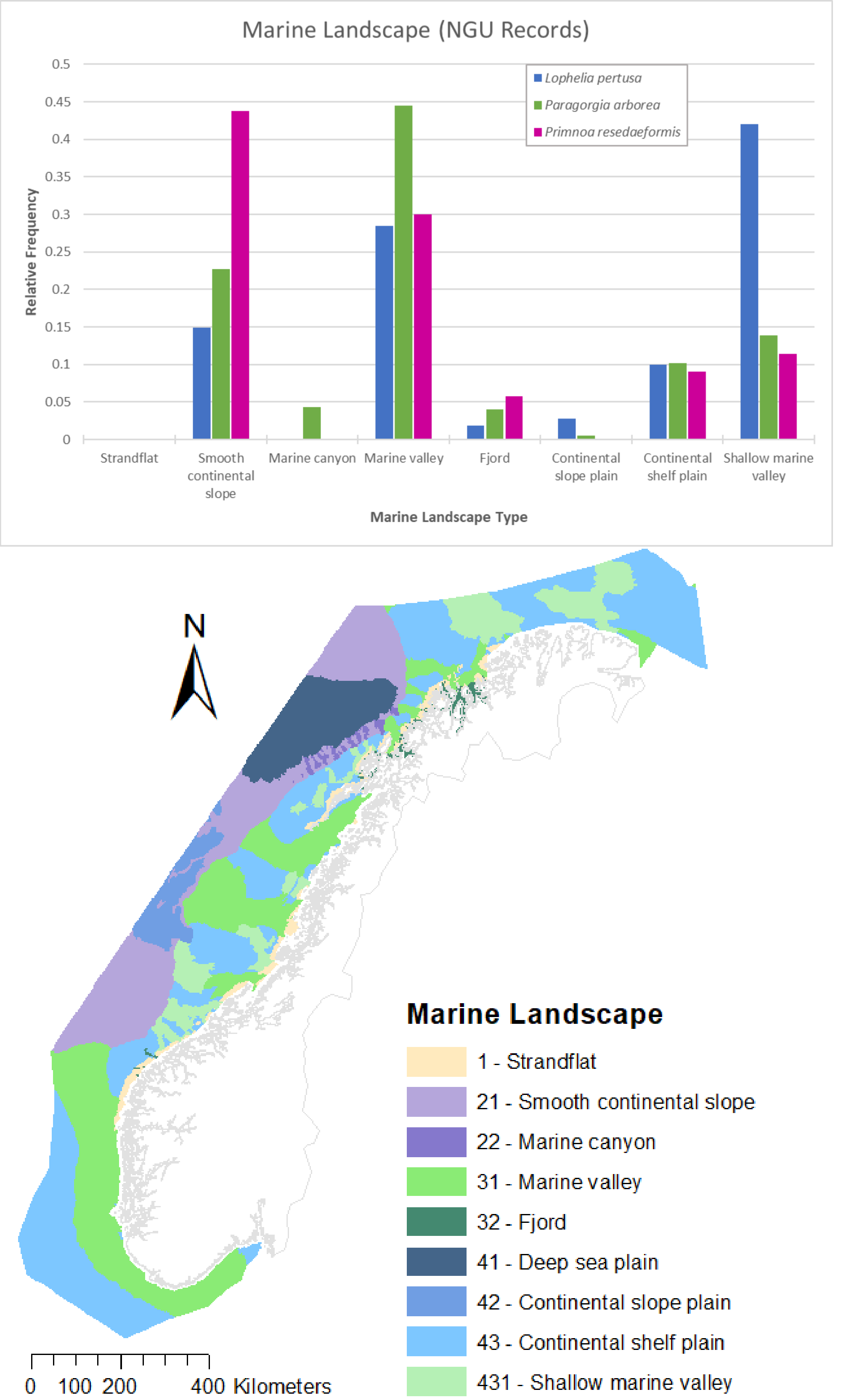


Figure 23 - Bar charts showing relative frequency of marine landscape type per coral species from the NGU layer (pictured).

3.2 Maxent Analysis Results

3.2.1 Full Geographical Range

Species Distribution Models based on 10 Cross-Validated Replications

Results extend to the full Norkyst-800 range because the sediment and marine landscape variables were omitted. Maxent automatically created separate results for *Lophelia*, *Paragorgia*, and *Primnoa*. After 10 runs of the model with the chosen variables except for sediment and marine landscape, SDMs with the mean, standard deviation, median, minimum, and maximum presence probability at each grid cell was produced. *Figure 24* shows the mean SDM for (A) *Lophelia,* (B) *Paragorgia*, and (C) *Primnoa*.

The SDM output shows a continuous scale of probability values. Areas colored in red indicate high probability of presence, area in green have conditions that are typical for where species presence, and blue areas indicate lowest probability of presence. The predicted distribution for *Lophelia* is the most widespread out of all three coral species, with predicted typical conditions covering most of the Norwegian continental shelf and western and southern Norway. Areas that were found to have high probability of *Lophelia* presence are (names based on identified "svært sårbare områder"):

1) Large parts of the entire edge of the continental shelf ("Eggakanten") from Møre og Romsdal to Tromsøflaket;
2) Large parts of the Norwegian coastal regions in the Norwegian and North Seas;
3) Northern extent: northern Lofoten region up to western part of Tromsøflaket, and the eastern Tromsøflaket region "Loppahavet" outside Alta in Finnmark;
4) Specifically within the Norwegian Sea: southwestern part of the continental shelf outside Lofoten/Vestfjorden region (includes the Røst Reef), Froan region with the Sula Reef, Iverryggen, and in the Trondheimsfjord;
5) And specifically within the North Sea: mouth of Korsfjorden, a small part of Karmøyfeltet, the areas Listastrendene and Siragrunnen, the Norwegian part of Skagerrak, and the outer Oslo fjord area.

Some areas of particularly low probability of presence are the coastal region in the Barents Sea at the northernmost point of continental Norway, western part of Vestfjorden running along the Lofoten archipelago, as well as Sklinnabanken and Haltenbanken on the continental shelf.

Predicted areas of high probability of presence for the gorgonians *Paragorgia* and *Primnoa* also includes the entire Eggakanten, but extending from Møre all the way to within the Barents Sea. Other high probability areas also include the area on the continental shelf southwest of Lofoten/Vestfjorden, as well as the Skagerrak area and a smaller part of the Oslo fjord. *Paragorgia* also showed high probability along the Hordaland coastal region (including Korsfjorden) and in the Boknafjord around Stavanger, while *Primnoa* had high probability for the northern Danish coast in Skagerrak and in the Trondheimsfjord. A slight probability was also observed for the gorgonians around the northern Norwegian coast in the Barents Sea, unlike for *Lophelia*. The presence of typical regions is not as widely distributed for *Paragorgia* and *Primnoa*, the least for *Primnoa,* with low probability particularly on the continental shelf and in the whole western Norway region.

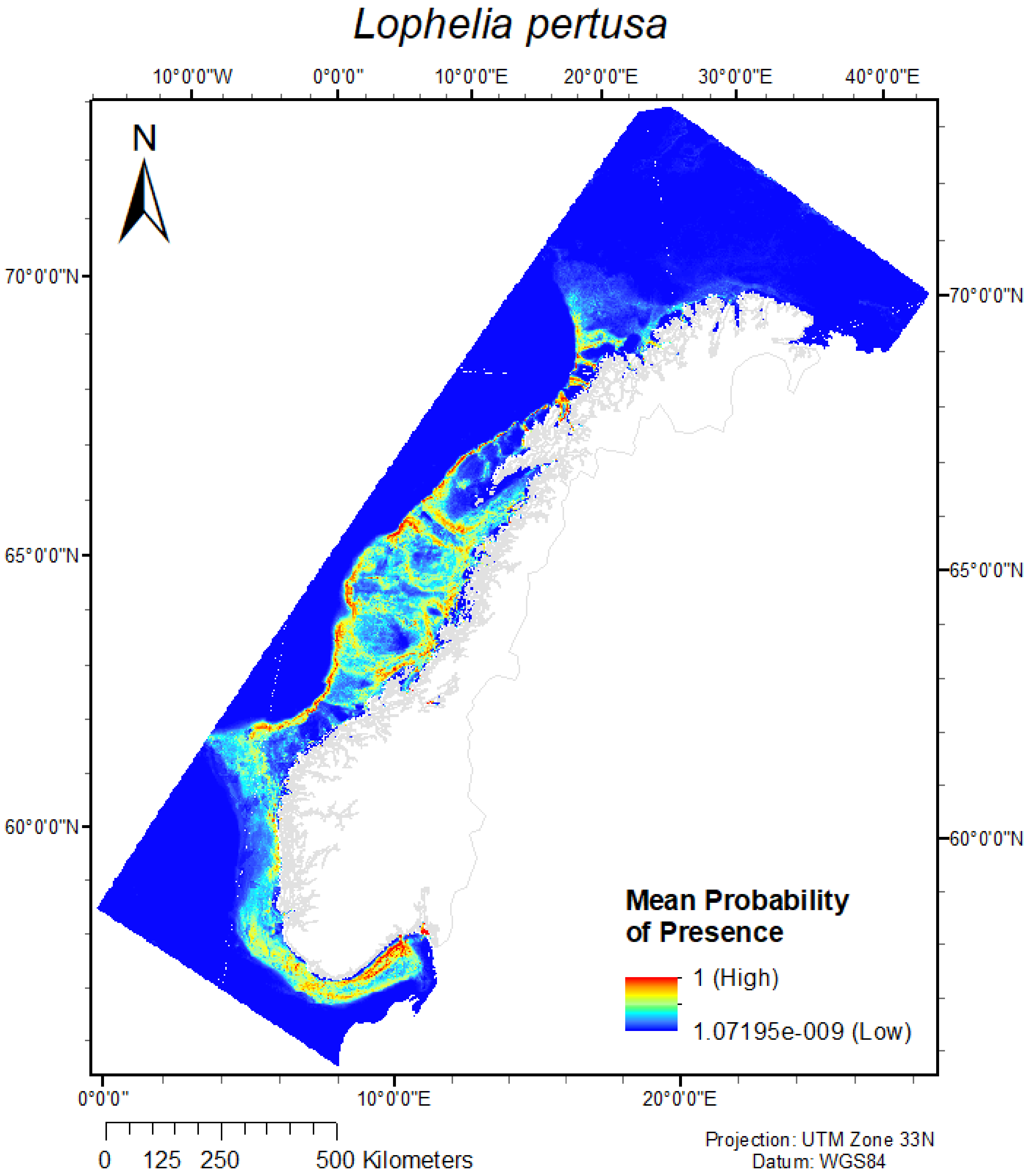


Figure 24A - Species distribution model showing mean probability of presence in each 176m cell within the Norwegian-wide study area, for *Lophelia pertusa*.

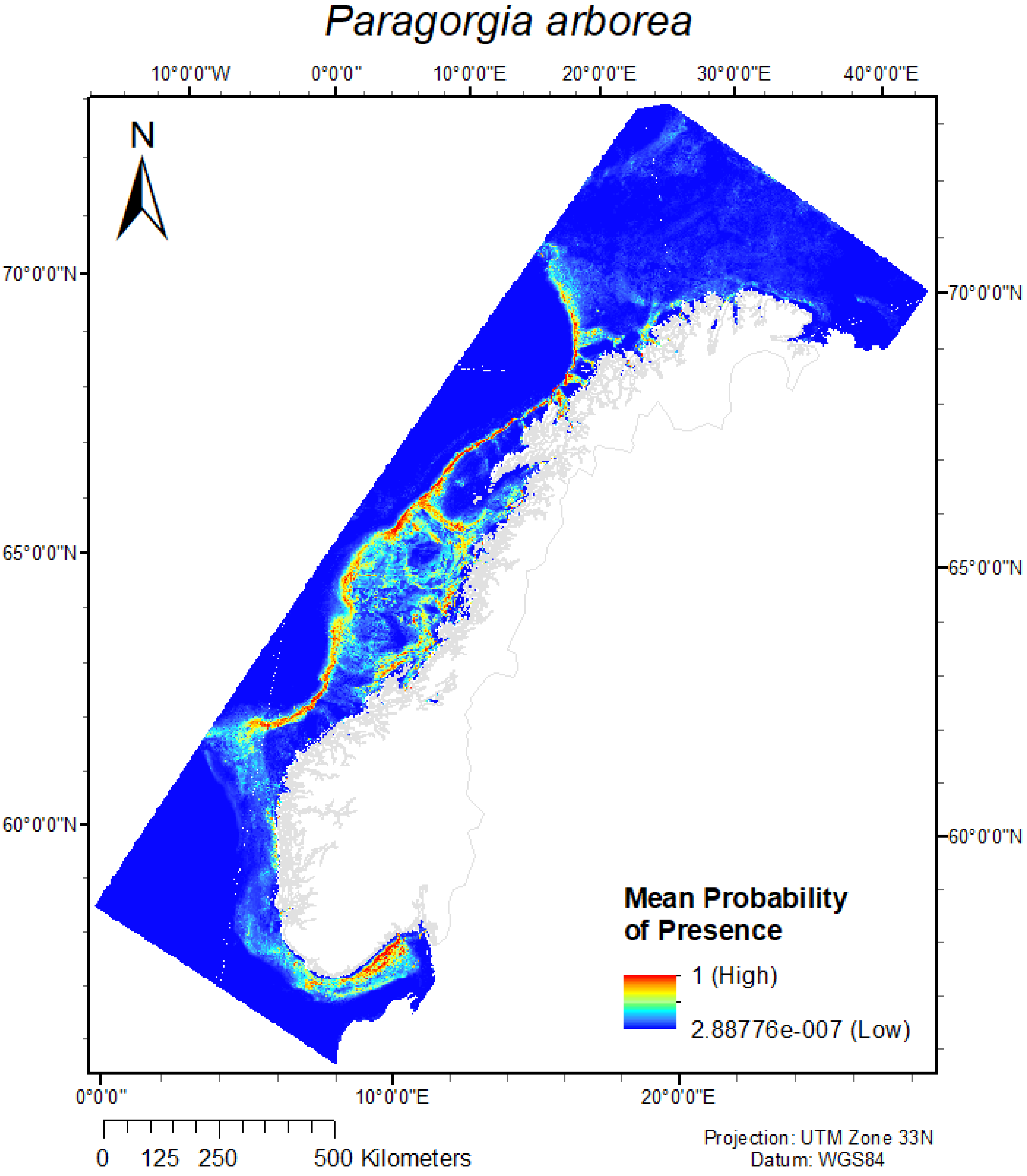


Figure 24B - Species distribution model showing mean probability of presence in each 176m cell within the Norwegian-wide study area, for *Paragorgia arborea*.

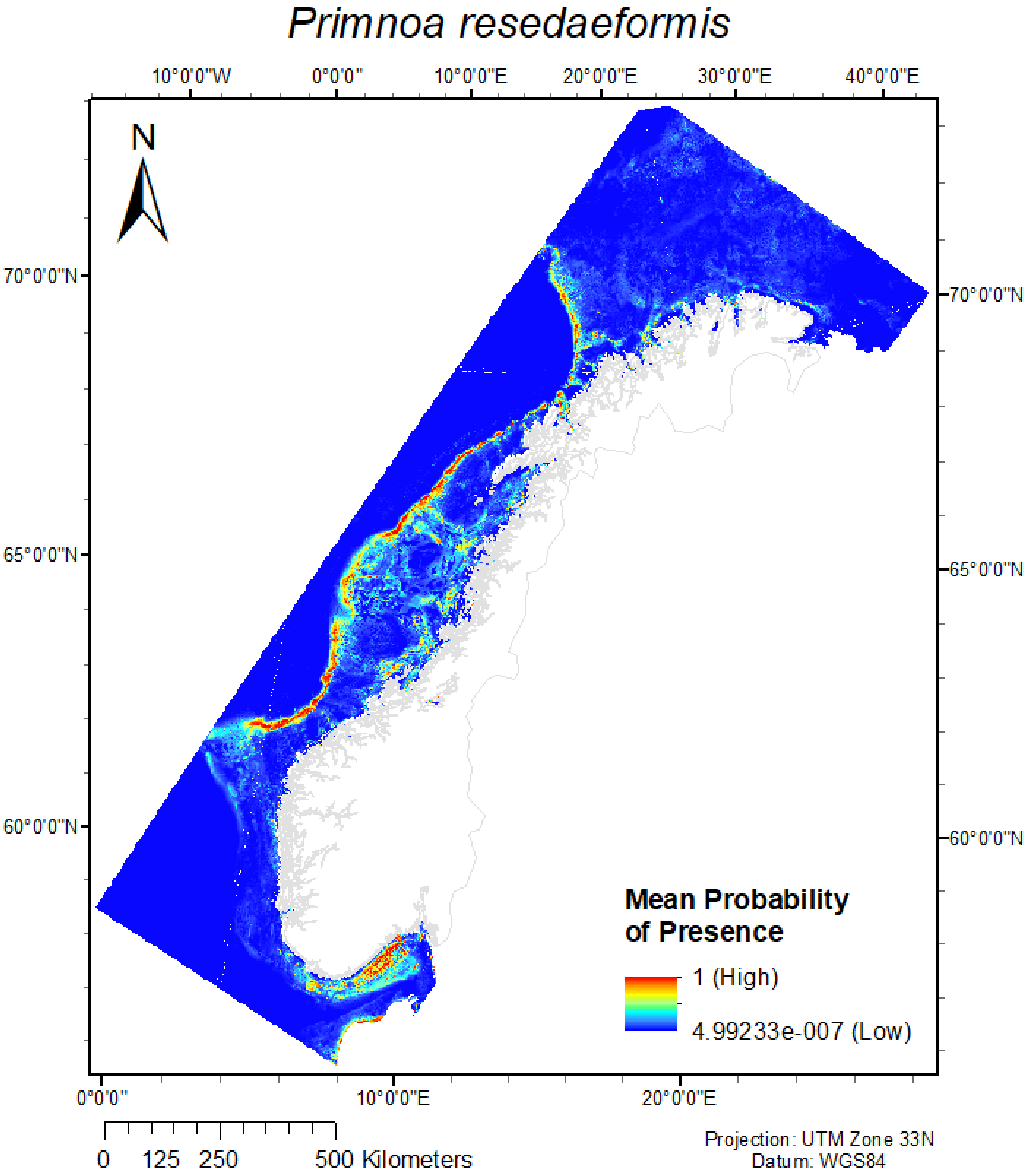


Figure 24C - Species distribution model showing mean probability of presence in each 176m cell within the Norwegian-wide study area, for *Primnoa resedaeformis*.

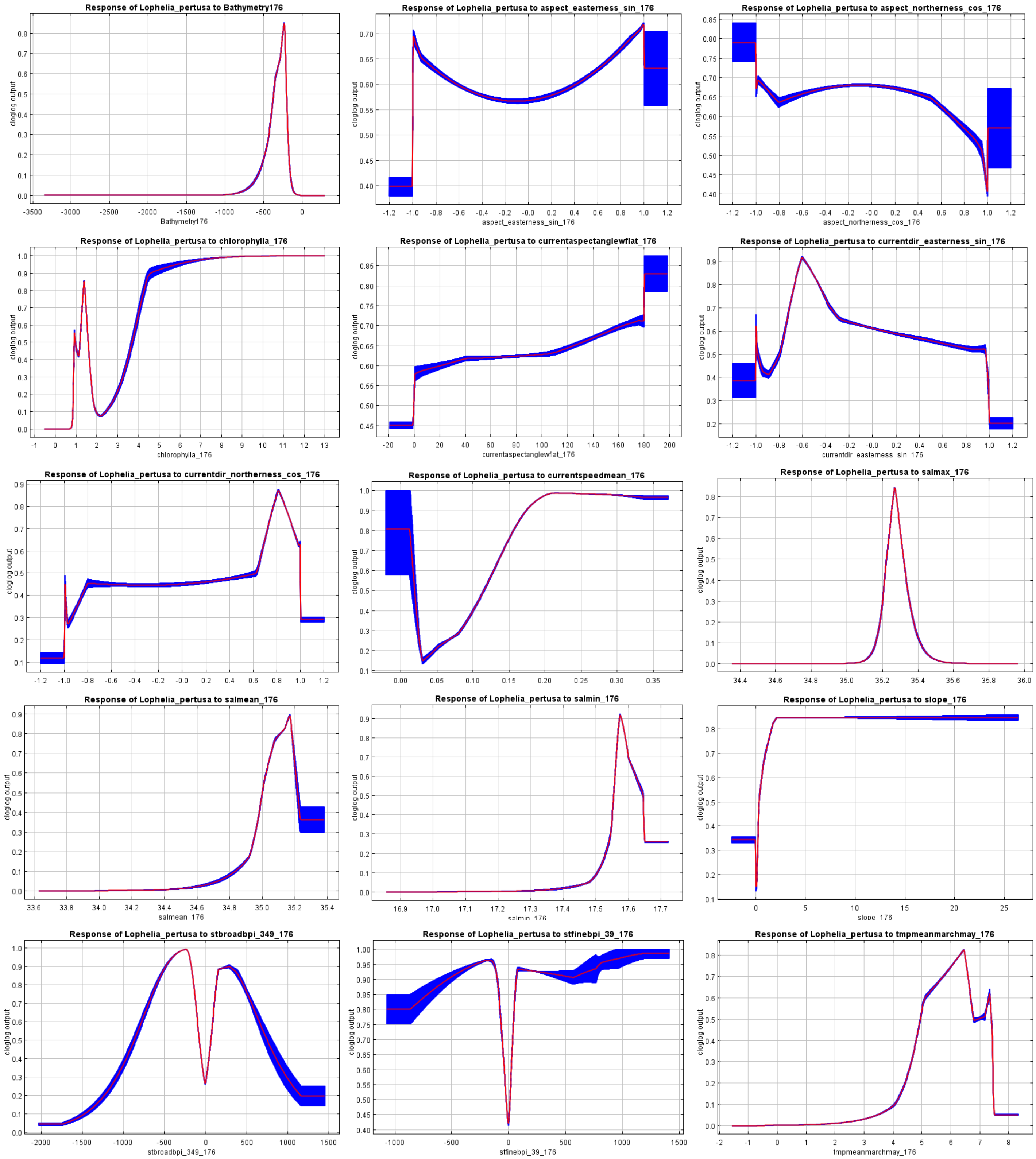
Model Response to the Predictor Variables

The response curves show how the model predictions are affected by each variable, how probability of presence changes as a variable changes. Two types of response curves are given by Maxent, the marginal response and the individual variable response. The marginal type shows model response to a variable while all other variables are maintained at their average values. This can mask the actual effect of a variable if it is correlated to any of the other variables (Appendix I). Thus, the response curves of individual variables are shown here to better understand the unique response to each predictor variable. The curves show the mean response (red line) ± one standard deviation (blue shaded area) from 10 replicates for *Lophelia* in *Figure 25*, *Paragorgia* in *Figure 26*, and *Primnoa* in *Figure 27*. The flat extremes are due to extrapolation with clamping, conservative predictions of responses outside of observed ranges in the study. Extrapolation does not apply to the northerness and easterness variables for aspect and current direction outside of -1 and 1, to the current-aspect angle outside of 0° and 180°, and to slope below 0° because these are the absolute extremes for these variables.

Terrain characteristics: Depth preference is quite uniform within the range of sampled depths; *Lophelia* depth preference appears to peak at about 250m, *Paragorgia* has two peaks at around 300m and 600m, while *Primnoa* has a similar shape to *Paragorgia* but peaks at around 550m. All corals appear to sit more on eastern or western-facing slopes, *Lophelia* also on more southern-facing slopes, in terms of northerness and easterness. A sharp increase in preference of slope angle at around 2° can be seen for *Lophelia,* a more gradual increase in preference as slope angle increases for *Paragorgia*, and something in between for *Primnoa*, as well as possible preference in steeper slopes for all but with some uncertainty as slope angle increases, especially for *Primnoa.* There is also a preference for small mounds (positive BPI) and troughs (negative BPI) in the landscape for all species, with a sharp drop in preference for specifically flat terrain (BPI = 0), concurring with slope results. *Paragorgia* preference is clearly maintained even for more extreme BPI, i.e. higher mounds and deeper troughs, with less certainty for troughs than mounds at smaller scales (negative fine BPI). *Lophelia* preference is also maintained at more extreme fine BPI values than at extreme broad BPI values, and slightly more at positive fine BPI values, which shows that 1) large-scale changes in terrain elevation (broad BPI) is more of a limiting factor than small-scale changes, and that 2) *Lophelia* prefers a greater range of small-scale mounds than small-scale deep troughs. But, in general, there is little difference in the preference of mounds vs. troughs, so the main conclusion is that the corals simply prefer a sloped terrain over a flat one.

Oceanographic characteristics: *Lophelia* seems to strongly prefer currents heading north-west, *Primnoa* also but less pronounced, while *Paragorgia* prefers both northerly and southerly currents. All corals also prefer areas with stronger average current speed, especially reaching a plateau at 20 m/s, though *Lophelia* also seems to tolerate no current, perhaps reflecting the fact that it appears in areas with current periodicity. All corals have a sharp peak at 35.2-35.3 PSU as their maximum salinity tolerance, 35.0-35.2 PSU for their mean salinity tolerance, and around 17.6 PSU for their minimum salinity tolerance. The minimum salinity layer is very low and must be due to short pulses of currents bringing in fresher waters to the depths. *Lophelia* mostly prefers temperatures between 5 °C and 7.3 °C (especially 6.5 °C), *Paragorgia* has three peaks at around 0.7 °C, 5.5 °C and 7.3 °C, *Primnoa* at around 5.3 °C and 7.3 °C, and even a small jump at 0.7 °C. *Lophelia* therefore shows preference for strictly higher temperatures, while the gorgonians appear to have two general areas of preference, probably reflecting the depth preferences illustrated earlier.

Chlorophyll *a*: All corals appear to prefer two different chlorophyll *a* concentrations, around 1-1.5 mg/m^3 and then at all ranges above around 4 mg/m^3. Perhaps this is a result of varying primary productivity at locations throughout the year, resulting in varying surface production of food and transport to the benthic layer.


Response of Lophelia_pertusa to Bathymetry176

Response of Lophelia_pertusa to aspect_easterness_sin_176

Response of Lophelia_pertusa to aspect_northerness_cos_176

Response of Lophelia_pertusa to chlorophylla_176

Response of Lophelia_pertusa to currentaspectanglewflat_176

Response of Lophelia_pertusa to currentdir_easterness_sin_176

Response of Lophelia_pertusa to currentdir_northerness_cos_176

Response of Lophelia_pertusa to currentspeedmean_176

Response of Lophelia_pertusa to salmax_176

Response of Lophelia_pertusa to salmean_176

Response of Lophelia_pertusa to salmin_176

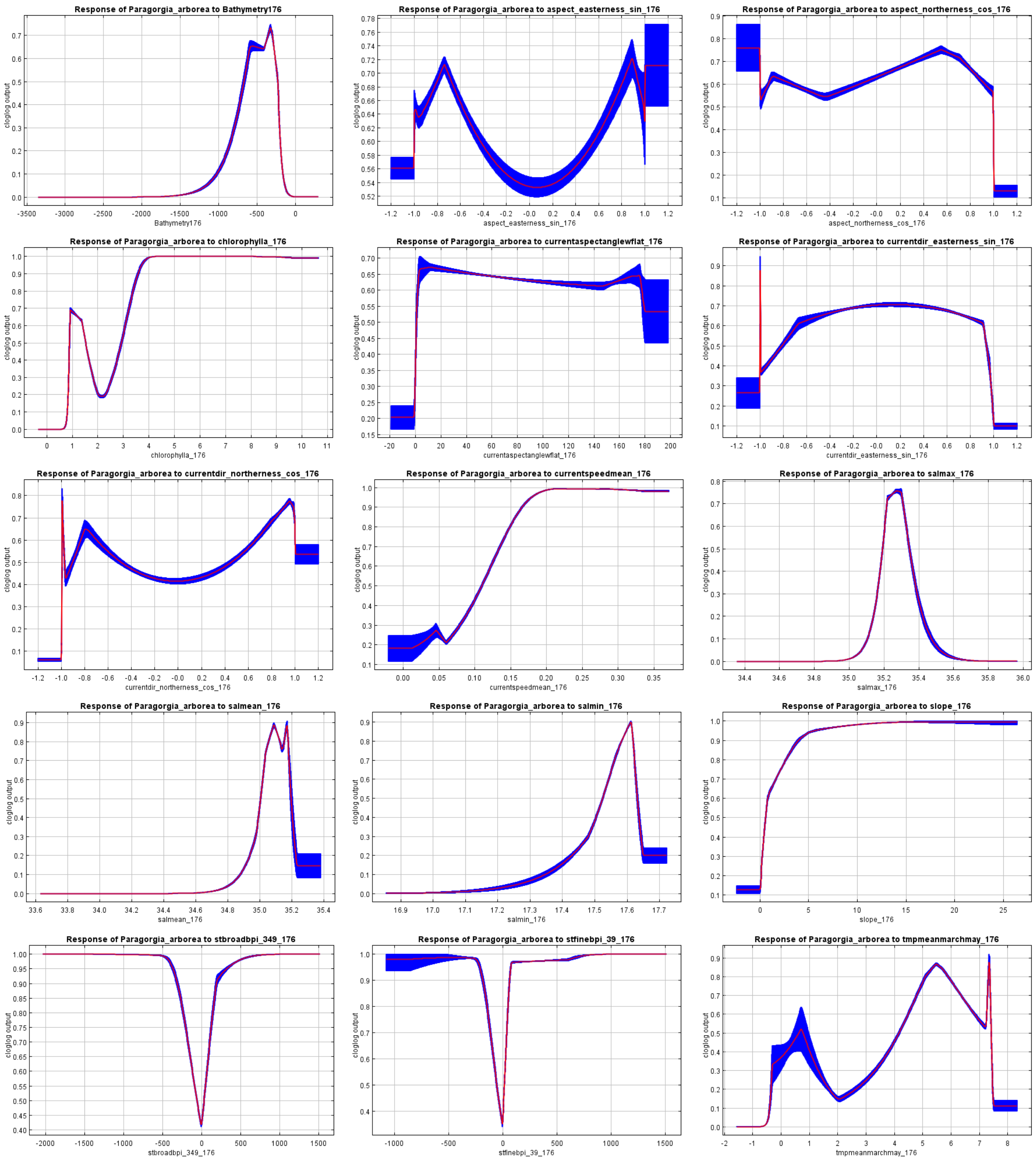
Response of Lophelia_pertusa to slope_176

Response of Lophelia_pertusa to stbroadbpi_349_176

Response of Lophelia_pertusa to stfinebpi_39_176

Response of Lophelia_pertusa to tmpmeanmarchmay_176

Figure 25 - Individual response curves showing the *Lophelia pertusa* model response to all variables except sediment and marine landscape.


Response of Paragorgia_arborea to Bathymetry176

Response of Paragorgia_arborea to aspect_easterness_sin_176

Response of Paragorgia_arborea to aspect_northerness_cos_176

Response of Paragorgia_arborea to chlorophylla_176

Response of Paragorgia_arborea to currentaspectanglewflat_176

Response of Paragorgia_arborea to currentdir_easterness_sin_176

Response of Paragorgia_arborea to currentdir_northerness_cos_176

Response of Paragorgia_arborea to currentspeedmean_176

Response of Paragorgia_arborea to salmax_176

Response of Paragorgia_arborea to salmean_176

Response of Paragorgia_arborea to salmin_176

Response of Paragorgia_arborea to slope_176

Response of Paragorgia_arborea to stbroadbpi_349_176

Response of Paragorgia_arborea to stfinebpi_39_176

Response of Paragorgia_arborea to tmpmeanmarchmay_176

Figure 26 - Individual response curves showing the *Paragorgia arborea* model response to all variables except sediment and marine landscape.

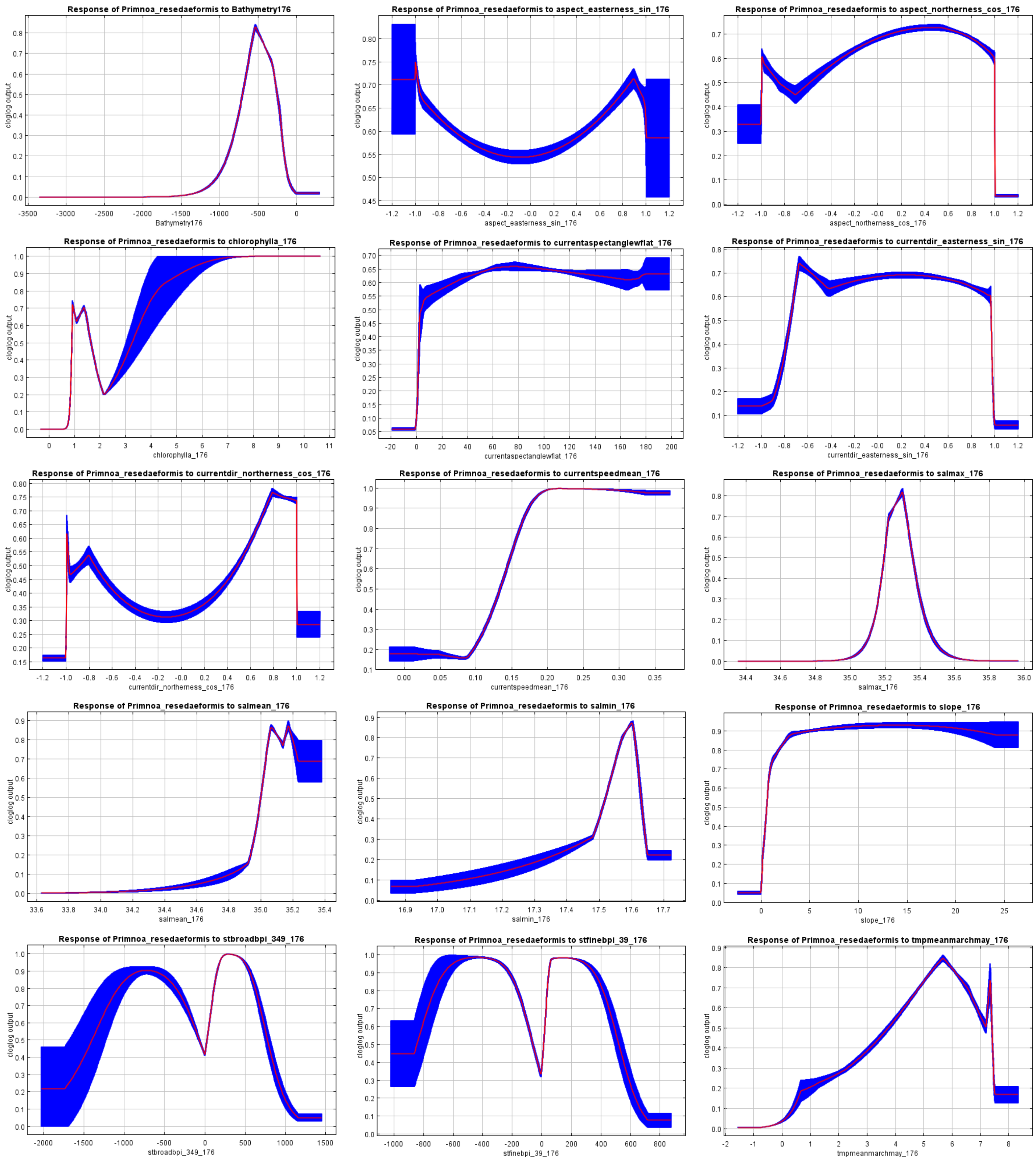


Figure 27 - Individual response curves showing the *Primnoa resedaeformis* model response to all variables except sediment and marine landscape.

Estimates of Variable Contribution to the Models

There are different ways that Maxent measures the relative contribution of a variable, or variable importance, to the overall model as the model is being created (Halvorsen, 2012). These are listed below, averaged by the 10 replicated models. All variable contribution analyses should be treated with caution when variables are correlated (Philips, 2017).

Percent contribution: during training runs on the point data, the increase in gain is calculated and added (or subtracted if gain is negative) for each variable to its percentage contribution. This measure should especially be interpreted with caution because the percent contribution values are heuristically calculated, and the path chosen to the final model can differ, giving varying end results (Halvorsen, 2012; Philips, 2017). Results are in *Table 5* show that the top three variables in terms of percent contribution to the model for *Lophelia* are mean temperature (tmpmeanmarchmay_176), mean current speed (currentspeedmean_176), and depth (Bathymetry176); for *Paragorgia* are mean temperature, slope (slope_176), and mean current speed (currentspeedmean_176); for *Primnoa* are mean current speed, slope, and depth.

Permutation importance: during the reruns, the values of one of the variables for training presence and background data is randomly permuted/changed (Halvorsen, 2012). The model with the permuted variable is compared with the model where the variable has not been permuted, and the resulting drop in AUC is reported as a percentage, as seen in *Table 5*. The three variable permutations that affected the

Table 5 – Measures on the % contribution and permutation importance of each variable per coral species. The top three variables for % contribution and for permutation importance for each species are highlighted in bold.

	Lophelia pertusa		***Paragorgia***		***Primnoa***	
Variable	% Contribution	Permutation Importance (%)	% Contribution	Permutation Importance (%)	% Contribution	Permutation Importance (%)
Bathymetry176	**11.5**	**10.9**	14.4	**24.6**	**10.1**	**16.6**
aspect_easterness_sin_176	0.2	0.2	0.4	0.3	1.5	0.9
aspect_northerness_cos_176	0.4	0.1	1.1	1.2	0.8	0.6
chlorophylla_176	0.8	3.2	1.3	1.6	1	1.3
currentaspectanglewflat_176	0.2	0.4	1.1	1.3	1.1	0.9
currentdir_easterness_sin_176	0.4	0.5	1.1	1.1	2.5	3.2
currentdir_northerness_cos_176	0.2	0.4	1	1.4	0.7	0.6
currentspeedmean_176	**15.6**	4.7	**16.2**	11.6	**33.7**	**11.3**
salmax_176	4.9	**31.7**	5.9	**18.3**	3.3	10
salmean_176	1	2.1	0.3	0.2	0.2	1
salmin_176	0.4	0.3	0.6	1.4	1	2.7
slope_176	9.6	1.5	**23.8**	4.4	**17.8**	2.7
stbroadbpi_349_176	0.6	0.7	2.5	1.9	0.4	0.3
stfinebpi_39_176	1.8	1.5	3.1	3.7	5.1	5.5
tmpmeanmarchmay_176	**52.4**	**41.9**	**27.2**	**27**	21	**42.4**

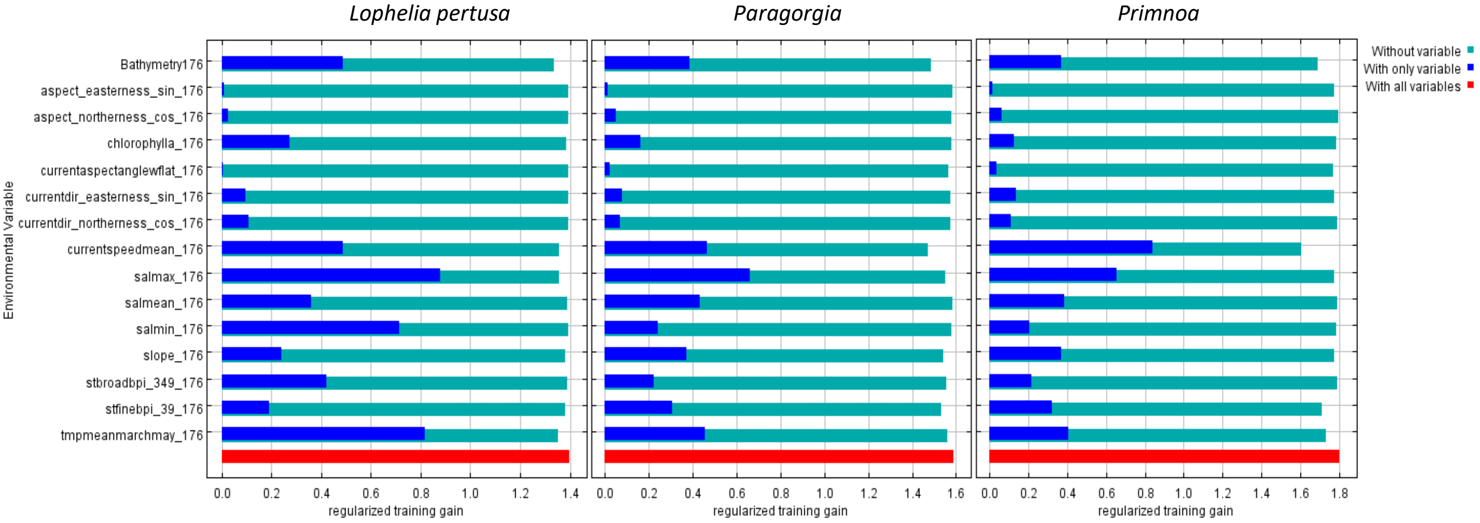
model most for *Lophelia* are mean temperature, maximum salinity (salmax_176), and depth; for *Paragorgia* are mean temperature, depth, and maximum salinity; and for *Primnoa* are mean temperature, depth, and mean current speed.

Jackknife tests: two variable contribution analyses are made with the optional Jackknife tests. In one part of the test, one of the variables is omitted in each rerun and the drop in overall model performance because of this is measured with loss in training gain, test gain, and test AUC. This shows which variables have the most unique information for the model that is not present in the other variables. In the other part of the test, only one variable is used in each rerun. The difference between this single-variable model and the overall model is measured again with the loss in training gain, test gain, and test AUC. The variables with the smallest drop thus have the most useful information for the model by themselves (Philips, 2017). The training gain Jackknife results are shown in *Figure 28* and test AUC results in *Figure 29*.

The Jackknife tests show that for

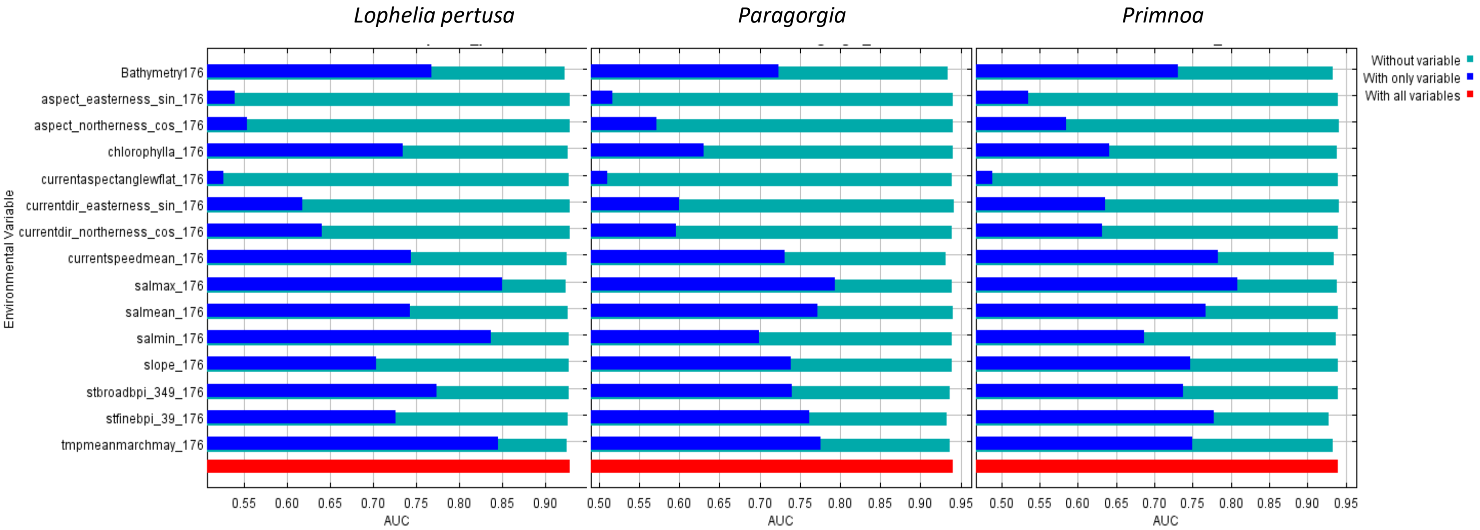
1) *Lophelia*: maximum salinity, mean temperature, and minimum salinity are the variables that give the highest training gain *and* test AUC alone, but omitting one of any variable does not decrease the gain or AUC much.

Figure 28 – Average Jackknife regularized training gain results from 10 models. Blue lines indicate average training gain when only one variable is used, teal lines when only one variable is omitted, and the red line for the whole model.



Lophelia pertusa *Paragorgia* *Primnoa*

Figure 29 - Average Jackknife test AUC results from 10 models.



2) *Paragorgia*: maximum salinity, mean current speed, and mean temperature give the highest training gain, while mean salinity replaces mean current speed among the three highest test AUC contributors. Training gain visibly decreases slightly when depth or mean current speed is omitted.

3) *Primnoa*: mean current speed, maximum salinity, and mean temperature give the highest training gain, while fine BPI (stfinebpi_176) replaces mean temperature among the three highest test AUC contributors. Training gain decreases by 0.2 when mean current speed is omitted, and also slightly when depth, fine BPI or mean temperature is omitted.

3.2.2 Modeling with All Variables

This study adds the categorical variables sediment and marine landscape, restricting the output to the combined extent of these two variables. 10 models were run again, and the mean SDMs for each species is shown in *Figure 30*.

Again, coastal areas in the Norwegian and North Seas as well as the Eggakanten show high probability of presence for all three species. The gorgonians additionally have high probability of presence this time in the Barents Sea at the coastal area close to the Russian border. *Lophelia* also appears to have high probability of presence in fjord landscape areas (see Figure 23 in section 3.1.6), e.g. at the mouth of the Geirangerfjord at Ålesund.

The range of “typical presence” is much more restricted now than it was for all corals without sediment and marine landscape. This is noticeable as large parts of low probability appearing on the continental shelf around the middle of Norway, but also outside western Norway and in Skagerrak. Otherwise, *Paragorgia* and *Primnoa* are almost entirely excluded on the continental shelf between Eggakanten and the coast along the middle of Norway.

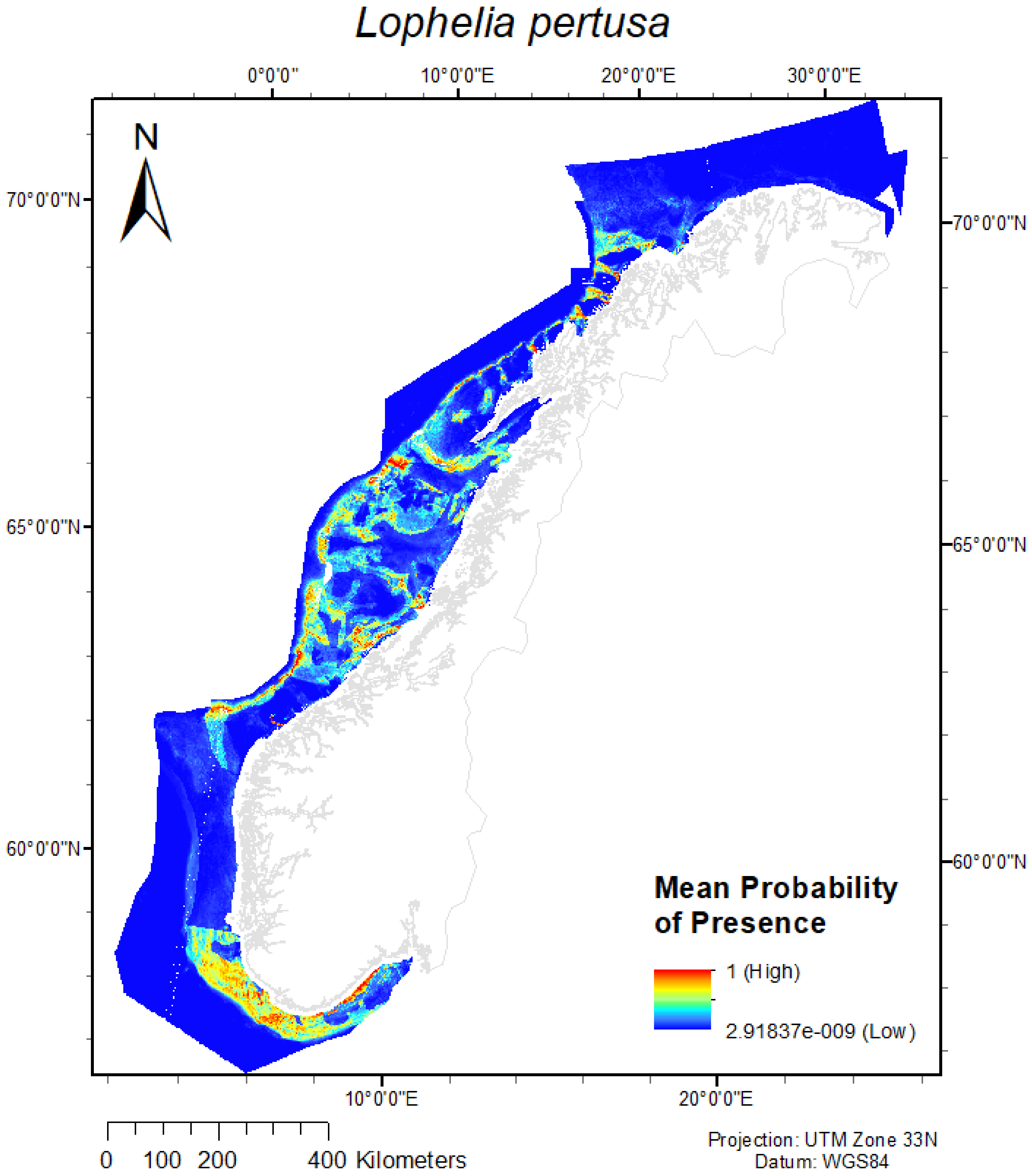


Figure 30A - Species distribution model showing mean probability of presence in each 176m cell within the MAREANO study area, for *Lophelia pertusa*.

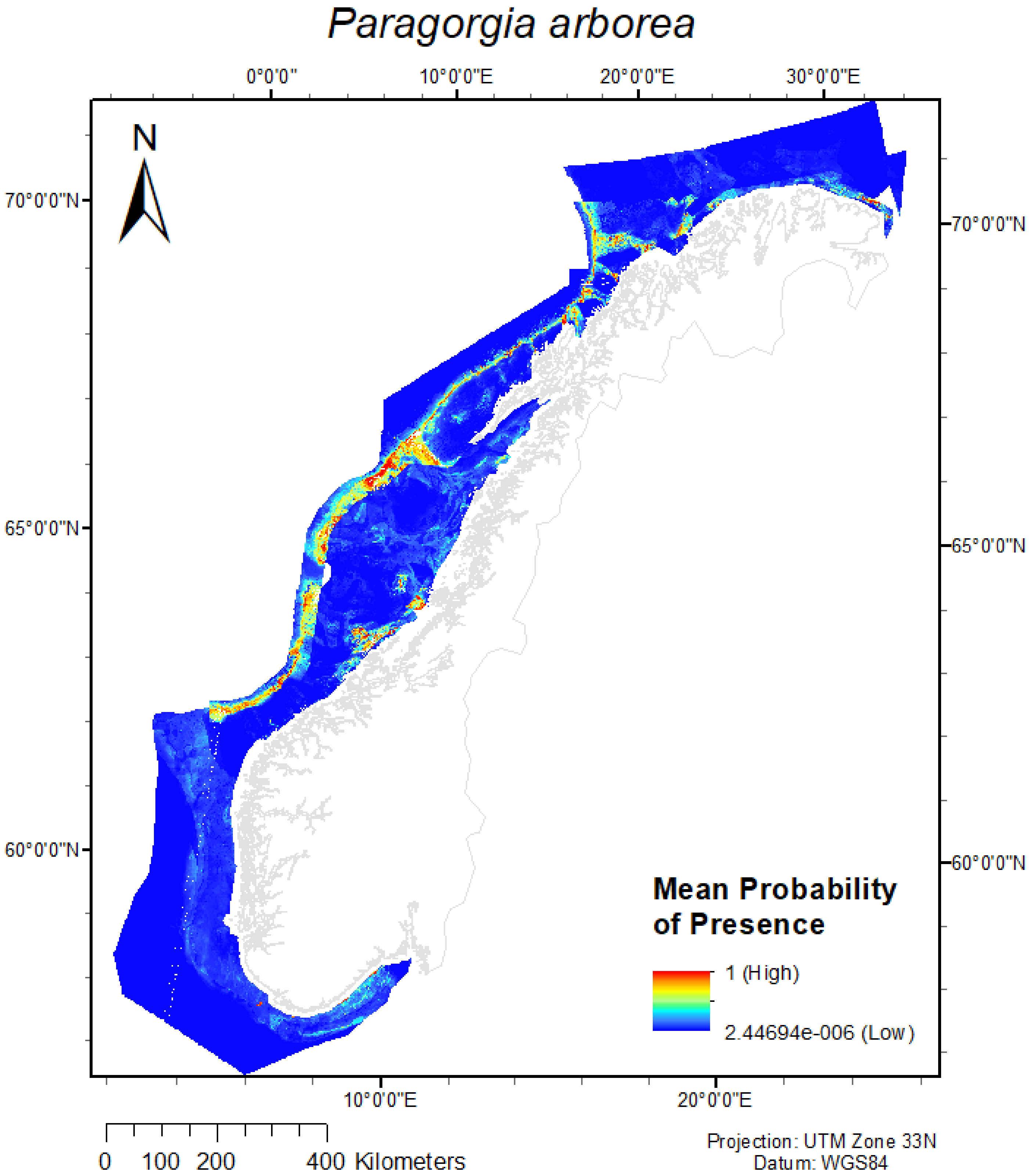


Figure 30B - Species distribution model showing mean probability of presence in each 176m cell within the MAREANO study area, for *Paragorgia arborea*.

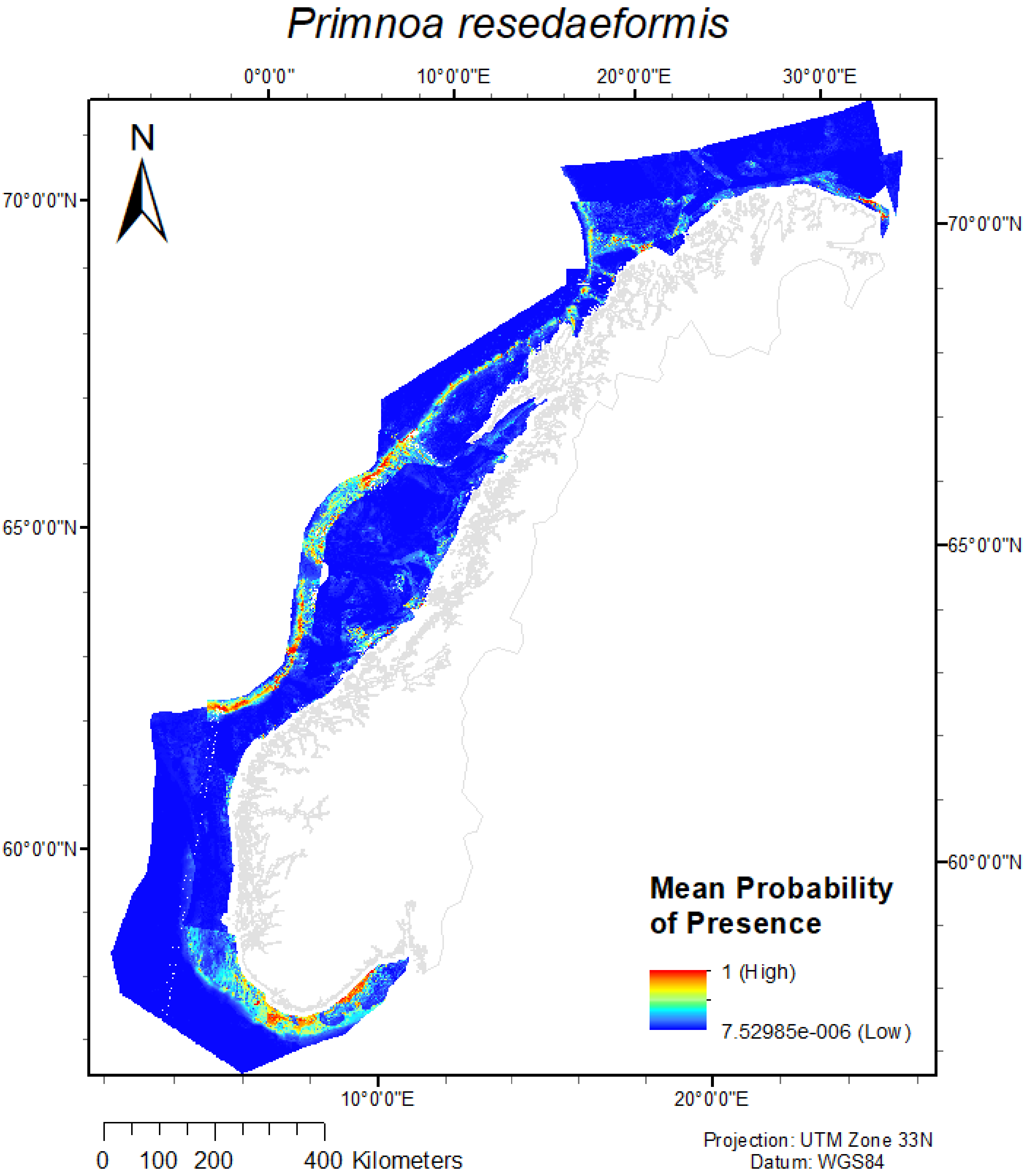


Figure 30C- Species distribution model showing mean probability of presence in each 176m cell within the MAREANO study area, for *Primnoa resedaeformis*.

Model Response to Marine Landscape and Sediment Variables

Response curves of variables in these models that had been used in the Full Geographical Range models were similar. In terms of marine landscape preference (*Figure 31*A), *Lophelia* appears to prefer marine valleys (31), shallow marine valleys (431), and fjords (32), while the gorgonians prefer the smooth continental slope (21) and marine valleys (31), but *Paragorgia* also prefers marine canyons (22).

The corals appeared at a variety of the sediments classified by NGU (*Figure 31*B), but were especially rarely seen at sediments with clay (10), as seen in the SDMs above, or mud in them (e.g. 20, 115). Specific preferences are as follows:

1) *Lophelia*: “gravelly muddy sand”, “sand, gravel, cobbles”, and “sand, gravel, cobbles, boulders”.
2) *Paragorgia*: “exposed bedrock”, “sand, gravel, cobbles”, “sand, gravel, cobbles, boulders”, and “compact sediments or sedimentary bedrock”.
3) *Primnoa*: also preferred “exposed bedrock”, “sand, gravel, cobbles”, and “compact sediments or sedimentary bedrock”, as well as “thin sediment cover on bedrock”.

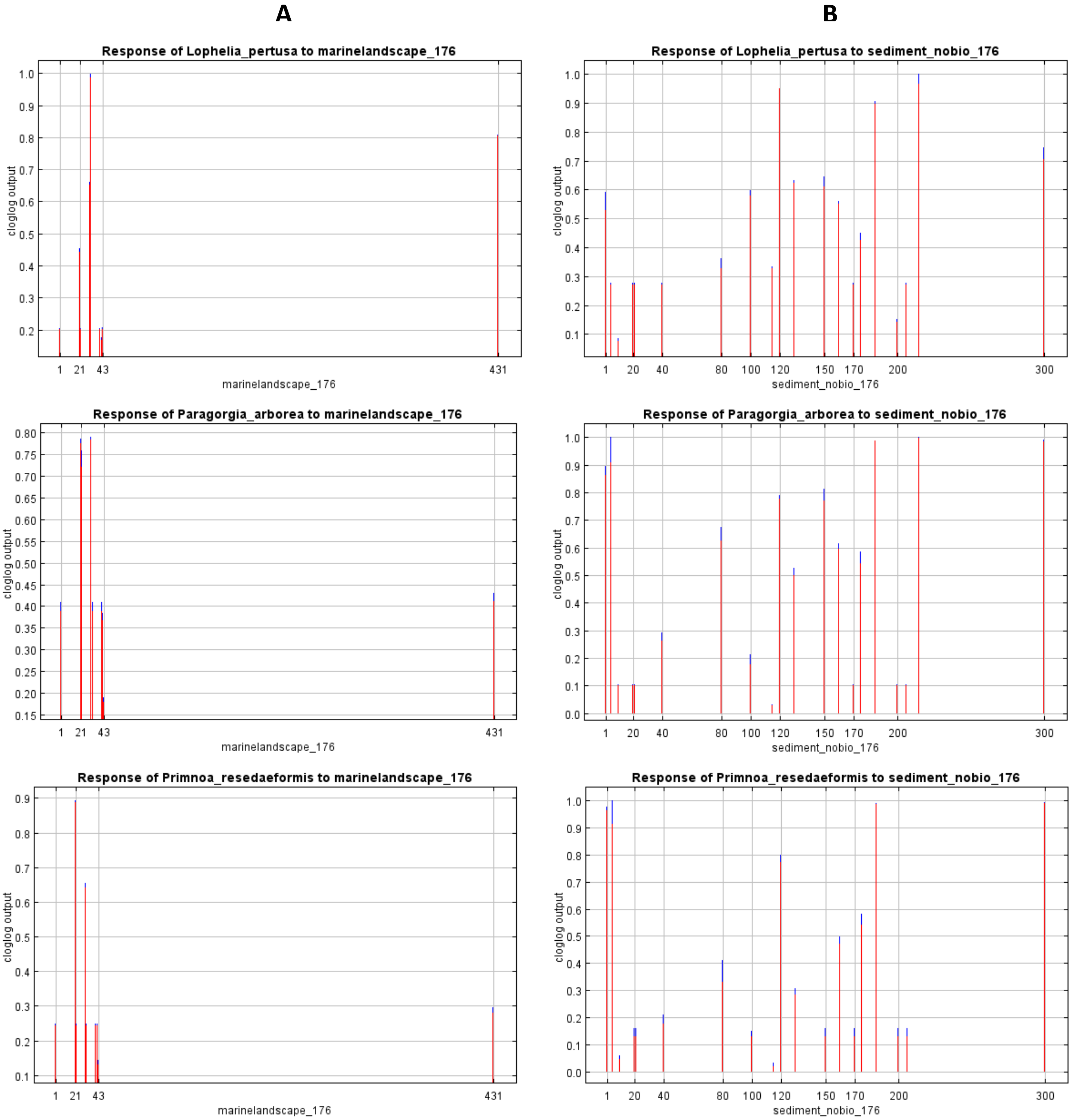
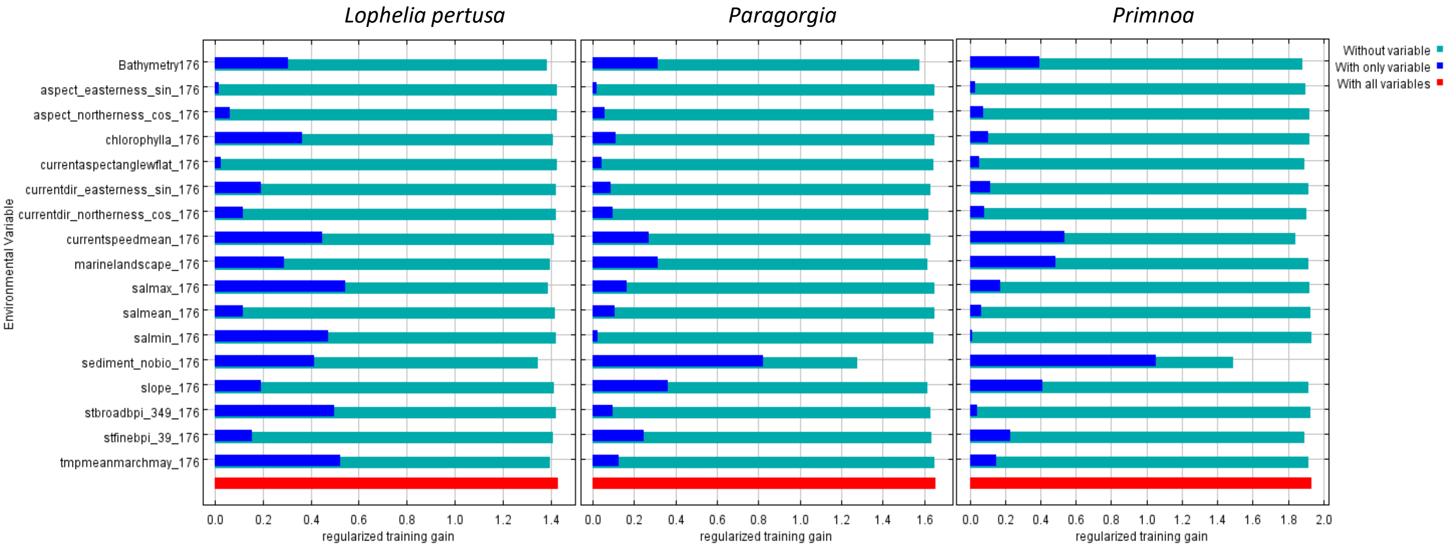


Figure 31 - Individual responses per species to (A) marine landscape and (B) sediment (with the bioclastic sediment removed). See Figure 23 and Figure 22 and in section 3.1 for an explanation of numbers for marine landscape and sediment, respectively.

Figure 32 – Average Jackknife regularized training gain results from the 10 MAREANO models.

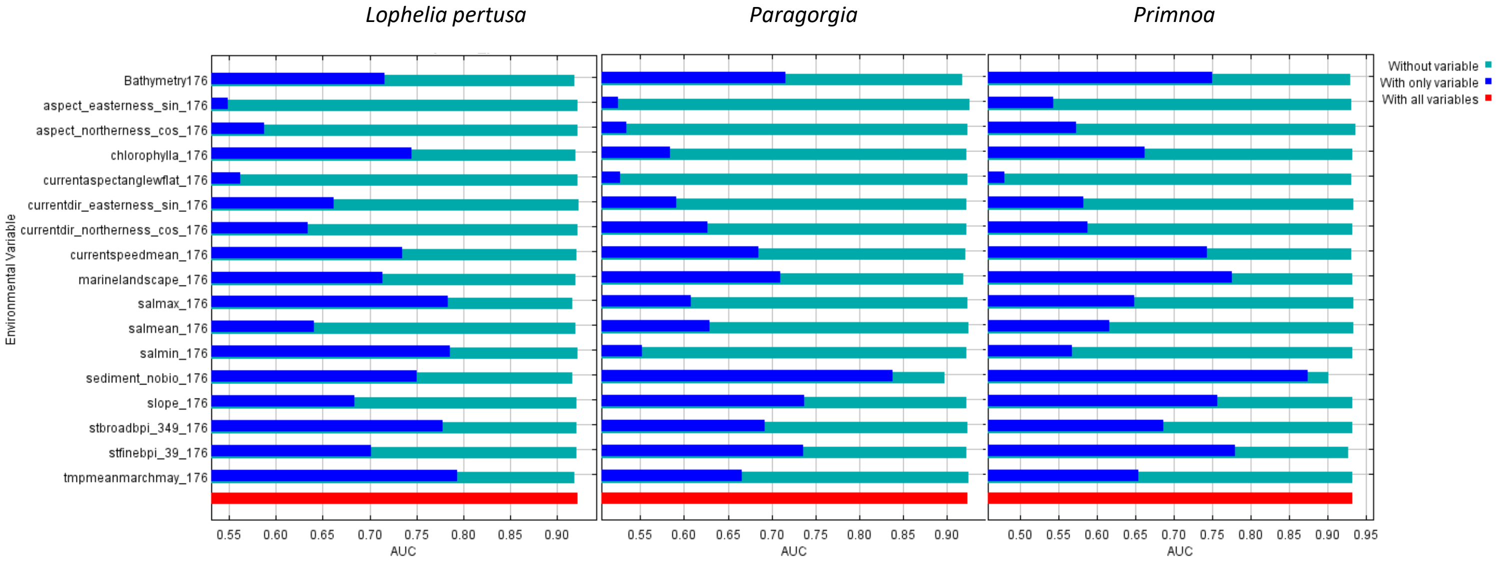


Estimates of Variable Contribution to the Models

The Jackknife tests including marine landscape and sediment variables show that for

1) *Lophelia*: maximum salinity, mean temperature, and broad BPI are the variables that give the highest training gain alone, together with minimum salinity for test AUC alone. Omitting sediment decreases the gain.
2) The gorgonians: sediment clearly gives the highest training gain and test AUC alone, and decreases the gain and AUC significantly if omitted.

Figure 33 - Average Jackknife test AUC results from the 10 MAREANO models.



3.2.3 Model Evaluation

The average test AUC, training, and test gain values for both the Full Geographical Range study and the All Variables study are listed in *Table 6*. The high test AUC values for both the Full Geographical Range and MAREANO studies show that these models have high discriminatory power between the test points, which were the presence points left out to test each replicate model, and background data within the study area; see points on interpreting this below in the discussion. The average training and test gain were highest for *Primnoa* in both studies, indicating that the model concentrates around the presence points for *Primnoa* the most, perhaps because this species has the fewest presence points out of the three species and/or because this species is more restricted in its distribution.

Table 6 – Test AUC, training gain, and test gain values averaged over 10 replicate models for the Norwegian-wide study and for the MAREANO study.

	3.2.1 Full Geographical Range			**3.2.2 All Variables**		
	Test AUC	Approx. Training Gain	Approx. Test Gain	Test AUC	Approx. Training Gain	Approx. Test Gain
Lophelia pertusa	0.928 ± 0.009	1.4	1.6	0.923 ± 0.010	1.42	1.6
Paragorgia	0.940 ± 0.013	1.6	1.73	0.924 ± 0.029	1.65	1.6
Primnoa	0.940 ± 0.018	1.8	1.92	0.933 ± 0.020	1.92	1.88

4. DISCUSSION

This study looked at the characteristics of 18 environmental variables at locations where *Lophelia*, *Paragorgia,* and *Primnoa* have been found along the Norwegian continental shelf, and assessed the predictive power of 17 variables (using northerness and easterness as proxies for aspect and current direction) to model the potential distributions of these CWCs.

Range of Sampled Environmental Conditions Within the Study Areas

MAREANO has sampled the seabed over a wide range of depth and terrain (Table 4, Figs 6-14). However, the full range of bottom slope angles has not been represented, and only seabed with slope < 31.41° has been sampled. The actual range within the study area is 0 - 63.53°Such steep bottoms are of course challenging to sample, but more sampling effort in steeper terrain would cover the gradient better and probably increase the model performance, especially in the area on the continental margin north of Lofoten, which appears to have a very steep slope (Figure 7). The same applies for ruggedness, which in this area is high (Figure 10). The natural log ruggedness for seabed sampled by MAREANO stops at a maximum of -3.91, while values in the study area extend to -1.96. Broad-scale mounds and depressions (identified over an 8,624m search radius as explained in section 2.2) have been sampled quite well (Figure 8). However, fine BPI in the study area had a much smaller range than the range present in the study area, possibly another issue that could be solved by sampling the area north of Lofoten (see Figure 9), but it is harder to fully capture terrain elevation differences at the shorter distances (1,584m). However, to successfully model a species' habitat distribution, more than sampling the full environmental range of the areas, it is important that the full range of the species niche is covered. Unfortunately, for most environmental variables, this is not known.

With regards to the oceanographic data from the NorKyst-800 model, a much broader range of mean temperatures was sampled (Figures 12 and 13). Than ever recorded near locations with any of the three corals (Buhl-Mortensen et al. 2015). The range of salinity at MAREANO stations overall, however, was considerably smaller than the study area's total range (Figures 14, 15, and 16); though, the area with extremely low minimum and mean salinity values is at the edge of the study area around Denmark closer to the brackish Baltic Sea (Figures 15 and 16). A large part of the mean current speed (Figure 18) range was sampled, but less so for maximum speed (Figure 17), which may be difficult due to speeds changing over time.

Sampled surface chlorophyll *a* concentrations stopped at 4.48 mg/m^3, while values range up to 26.95 mg/m^3 in the study area; areas of very high surface productivity is mainly restricted to the southern coasts in Kattegat (Figure 21). Finally, as stated previously, the MAREANO stations are selected to cover a wide range of terrain, so a variety of sediment types and the eight types of marine landscape within the study are covered (Figures 22 and 23).

Accuracy of Data Used

Errors and uncertainty can arise with any model, and the modeled data used in this study is no exception. Firstly, the process of interpolating the Norkyst-800 oceanography data points into a raster layer in ArcMap created new, continuous values in between the 800m-separated points, which may not reflect actual conditions between the points. Another important note to add is that the oceanographic and chlorophyll *a* layers were resampled from their 800 x 800m and 2 x 2km resolutions, respectively, to match the 176 x 176m resolution set for the bathymetry layer. This does not create new values, but it was a necessary step to create layers with cells of equal size and position for the Maxent program to analyze. The process of converting the shapefiles of sediment and marine landscape type into raster layers with the same resolution loses some information on the true extent and presence of terrain and landscape types, especially for the smallest vectors, since the maximum combined area cell assignment type was used. This is a small inconvenience when the sediment and marine landscape type that covers most of a cell's location is chosen.

Choice of resolution comes with trade-offs; the larger the cell size used, the less processing capacity required, but the more data is lost. Davies et al. (2008) had the problem when modelling with ENFA that the model indicated temperatures outside of *Lophelia*'s known tolerance window because the grid resolution was not high enough, and the temperature may change at short distances. This was noticeable at some presence points in this study as well. Some observed temperatures were outside the known tolerance range of the corals, e.g. points of *Paragorgia* had temperature around -0.3 °C; selecting these points in ArcMap indicated they were located on the continental margin. This can mean that the large differences present at a short horizontal distance at the continental margin may not be captured within a 176m grid cell (or the original 800m for the oceanographic data), potentially assigning the values from the deeper area to the cells where the coral points were.

Another visible aberration of the environmental layers is that the bathymetry maps and the derived terrain maps (slope, ruggedness, aspect, and BPI) in some places have artefacts (appearing as long thin lines), which is due to collected data being different between different ship surveys (Gunleiksrud &

Hodnesdal, 2013). This is due to differences in sampling precision and not difference in the actual terrain. These errors give changes in the depth and terrain variables at locations where they should not be, an important consideration when looking at the effect of these variables on the SDMs.

Lastly, the detectability of corals during sampling may also affect the quality of presence data (Elith, et al., 2011), e.g. poor visibility while video recording the benthos can affect the number of presences recorded.

Predicted Distributions and Importance of Variables Identified by the Models

From observed environmental characteristics at species points (section 3.1) and at randomly selected background points (which could be either presence or absence points), Maxent estimates a variable's "true" general prediction on species distribution. This help us understand the unique environmental preference for the coral species, their niche, in relation to the available range of values for that variable within the study area, which was explained in Figure 4 in terms of density distributions. This helps us predict where the species may be found in general within the study area.

The global models of Davies & Guinotte (2011) indicated that most of suitable scleractinian coral habitat is on continental shelves and slopes of the Atlantic, South Pacific, and Indian Oceans. Knowledge of *Lophelia* distribution within the Norwegian waters so far shows that the highest densities are observed on the continental shelf north of Stadt up to Lofoten, and along the coasts and fjords of Møre og Romsdal and Trøndelag (Järnegren & Kutti, 2014). The models in this study substantiate these observations, indicating high probability of presence for all three coral species on the continental margin Eggakanten from Møre og Romsdal up to Tromsøflaket, and slightly further north into the Barents Sea for the gorgonians *Paragorgia* and *Primnoa*. Large areas on the continental shelf southwest of Lofoten indicate high presence probability, an area which includes the Røst Reef, the largest known *Lophelia* reef found thus far (Fosså, et al., 2005). The models picked up large parts along the Norwegian coast, too, specifically around the northern Lofoten/Tromsøflaket region near the Eggakanten and Loppahavet, the Froan region with the Sula Reef (Freiwald, et al. 2002). Fjords were also areas of high probability, specifically within the Trondheimsfjord, as well as outside the Geirangerfjord, Korsfjorden, and the outer Oslo fjord (for which the environmental data layers do not extend *into*). Only *Paragorgia* had low probability in the Trondheimsfjord. Overall, the models confirm present observations of these species (MAREANO, n.d.).

When including the sediment and marine landscape variables, extent of high probability presence for the gorgonians extended along the northern coastal area in the Barents Sea towards the Russian border.

Presence probability decreased to very low for all three coral species in many areas broadly characterized as having clay sediment (#10) (compare Figure 30 in section 3.2.2 and Figure 22 in section 3.1.5), including waters along the middle of Norway as well in the general region outside western Norway. Clay sediment showed very low response for all three coral species (the third line from the left in Figure 31B), indicating this is too soft a substrate for the corals to settle on. Part of the region defined as clay in southern Norway/Skagerrak region still shows high presence probability of *Lophelia* and *Primnoa*, however, so a combination of other factors is making this region particularly suitable. The broad characterizations seen in the sediment map, however, originate from the "continental shelf" layer, which are coarse drawings made in the National Atlas from 1991 (see section 2.2), so this may not capture the true variation in seabed sediment. Lastly, *Lophelia* has also been observed to grow on oil platforms in the North Sea (Bell & Smith, 1999), so even if natural substrate may not be suitable outside Western Norway, a combination of other suitable conditions together with even man-made structures may provide settling opportunities for *Lophelia,* and possibly *Primnoa*.

The models indicated that *Lophelia'*s preferred depth range is indeed shallower than that for *Paragorgia* and *Primnoa* as stated in the literature (Brooke & Järnegren, 2013; Buhl-Mortensen et al. 2015), approximately 100 to 500m for *Lophelia*, and up to 1000m for the gorgonians. The preferred temperature ranges also extended to colder degrees for the gorgonians, approximately 7.3 down to 0.7 °C, compared to *Lophelia*'s window of 7.3 to 4 °C. Preferred slope angle shows to be around 2°, but the response did not drop with steeper slopes, possibly reflecting, as previously stated, that the corals are able to settle on steep, even vertical, terrains. Though it was expected that corals would grow on more elevated terrain (Mohn, et al., 2013), i.e. there would be a greater response to positive BPI values than negative BPI values, this was not found. Instead, there was simply a general preference for non-flat terrain (BPI value of 0). All corals prefer exposure to a relatively high mean current speed, especially around 0.20 m/s, confirming that having a flow of water in their habitat is important, for e.g. feeding and resuspension of sediment disposition (Davies et al. 2009). The angle at which the current hits the slope that the corals are settled on, the variable "current-aspect angle", did not show a particular response to any angle in relation to the rest of the study area. The wind charts in section 3.1.3, however, show that the corals sampled for all three species resided mostly in areas with currents flowing perpendicular to the aspect direction, meaning currents that flow parallel to the terrain, in comparison to the fewest observations having been made for currents that hit (180°) or pass over (0°) the slope directly. Perhaps this indicates that not directly incoming or outgoing currents is a better condition for the corals, or it is simply an artifact of the dynamics of current-slope interaction.

Sediment type was a clearly important predictor for CWC distribution for all species according to the Jackknife results, but especially so for the gorgonians, with clear losses when this variable was omitted to the goodness of fit of the trained model (training gain) and to presence-background discrimination when using data set aside to test the trained model (test AUC). Training gain and test AUC also decreased the least for the gorgonians when only sediment type was used, meaning sediment type alone could predict gorgonian presence pretty well. Thus, overall, sediment type seems much more essential in predicting the gorgonian corals' distributions than for *Lophelia*. Surface productivity on the other hand had a greater gain increase for *Lophelia* than for the gorgonians, meaning surface productivity has a considerate effect on *Lophelia* presence; this species does have a varied diet, ranging from ingesting copepods to utilizing dead particulate matter, so it can benefit directly from particulate matter brought down to the surface (Frederiksen et al. 1992; Mortensen et al. 2001; Mortensen 2001). Maximum salinity and mean temperature alone also increased training gain more for *Lophelia* than for the gorgonians. Otherwise, values of depth, mean current speed, marine landscape, and slope were important individual indicators of presence for all.

Accuracy of the Models

Maxent is a useful modeling tool because it only requires presence data and it produces a continuous probability distribution output so that fine distinctions can be made of suitable areas; though, binary predictions can also be made if some biological threshold that can distinguish between presence from absence is known. However, since it is newer than e.g. GLM or GAM, so there are not as many estimates of the model's accuracy. Evaluating the model's accuracy with only AUC should be done with caution, especially if the AUC is very high. If only background points are used when absence data is lacking, there is a higher degree of uncertainty of the probability of absence than there is for presence. False prediction of absences is therefore more likely to occur than false prediction of presences (Lobo et al. 2008), meaning the model could potentially be over-predicting. However, it is better to over-predict slightly than to under-predict, since observations of predicted areas of high suitability can be made to verify the results; such field validation will also improve model accuracy (Davies & Guinotte 2011).

The greatest challenge when modeling with Maxent is the potential for sampling bias. If the range of sampled depth is e.g. only between 0 and 500m while true values range between 0 and 1000m in the study area chosen, we would not know if a species actually prefers depths within 0 and 500m, or if it is an artifact of having overwhelmingly sampled this depth range. Thus, sampling bias can disguise the actual biological response of species' distributions to environmental characteristics behind the sampling distribution**.** Maxent assumes uniform sampling in terms of the environmental conditions sampled are in proportion to their availability within the study area (Merow, Smith, & Silander, 2013). The MAREANO stations cover a good range of conditions as explained previously, and indicating the extent with the sampling bias grid helped the model take sampling bias further into account (Buhl-Mortensen et al. 2015).

Another bias is the potential for presence points to cluster, known as spatial auto-correlation, which violates Maxent's assumption of independent sampling (Phillips et al. 2006). Spatial auto-correlation is an artifact of uneven sampling; sampling intensity and sampling methods can vary across the study area. Presence points from the MAREANO video records are from video transects that are 700-1000m long (Buhl-Mortensen et al. 2015), meaning records made along this transect will cluster around the sampling stations. Individual *Lophelia* points were pragmatically grouped together into "reef habitats" because of the potential to over-sample the same *Lophelia* reef, since it is a colonial framework-forming species (Davies et al. 2008). Regarding the *Lophelia* database, sampling methods varied (dredge, video, multibeam data), as did the precision of the geographical location, but the precision variation was accounted for by including only points with more precise location. Additionally, presences recorded in the *Lophelia* database that were within 50m of the MAREANO video records were removed, reducing the likelihood of duplicates. Lastly, the Maxent setting of removing duplicate points within a cell was used (Fourcade et al. 2014), reducing the potential to over-predict the importance of conditions when multiple sampled points are within a 176 by 176m cell. The purpose of this study was to model the relative suitability for CWC presence within the range of sampled environmental conditions is the study, which the cloglog output gives, rather than relative frequency, so not including the abundance of samples within each cell is fine (Phillips et al. 2017).

The choice of background points also affects the predictive power of the model. Increasing the number of background points in number will increase the AUC because there is a greater chance of selecting points that are different from sampled presence locations, so the model easily discriminates between the presence and background points (Acevedo et al. 2012) but causes over-prediction (Chefaoui & Lobo, 2008). Decreasing background points decreases AUC because there are fewer background points to contrast with presence points, and as a result creates a more diffuse SDM. Most SDM studies keep the default of 10,000 background points (Fourcade et al. 2014), which was done in this study too. The extent from which background points are chosen is also important to consider; with a larger area, there can be a wider range of environmental values, which can again increase the contrast between presence and background points (Merow, Smith, & Silander, 2013). For example, if more of the abyssal plain would have been included in the bathymetry layer, the depth curve response could have been even more uniformly distributed than it was in this study because of a larger range of possible non-suitable environmental conditions. The geographical extent from which background points will be chosen should reflect the area accessible to the species, e.g. by considering physical barriers and the species' dispersal strategies. *Lophelia* is a gonochoristic broadcast spawner and produces long-living planua larvae that can disperse far (Brooke & Järnegren, 2013; Larsson, et al., 2014); *Primnoa* is also a broadcast spawner, but with high early-life mortality, and *Paragorgia* a brooder with fewer recruits, which can limit their dispersal (Lacharité & Metaxas, 2013).

Finally, the choice of the regularization multiplier, the control on the effect and number of factors used to create coefficients to the model, was left with the standard of 1. The default regularization values (0.050 for linear and quadratic factors, and 0.500 for hinge factors) are chosen based on testing with a range of taxonomic groups (Phillips & Dudík 2008). A lower regularization multiplier would give too many constraints to the model and make the model overfit and, thus, be less able to extrapolate to conditions outside of those observed at species presence points than a simpler, more regularized model would do. Conversely, the regularization multiplier was not raised because the model would predict more diffusely with fewer constraints (Philips, 2017).

Management Implications and Recommendations for Future Studies

The models created in this study should serve as a guidance to deciding on areas that may contain *Lophelia*, *Paragorgia*, and *Primnoa* so that conservation efforts can be better targeted. Exploring these areas closer with bottom cameras will help verify these models. The modeled distributions could also be limited in their prediction due to e.g. physical barriers limiting coral dispersal, or bottom trawling may have destroyed and removed corals from areas that are actually suitable conditions; the actual realized distribution could therefore be more limited (Elith 2000). Future studies could also explore other variables not included in this study that may better predict the species' niche and create more realistic predicted distributions (Phillips et al. 2006). One example is calcite and/or aragonite saturation state, which were found to contribute greatly to models for suborders of Alcyonacea (Yesson et al. 2012) and for *Lophelia* (Davies et al. 2008; Davies & Guinotte 2011). Another is measures of oxygen (Yesson, et al. 2012; Yesson et al. 2015). Perhaps the depth could be left out next time since, like in the study of Yesson et al. (2012), many variables utilized the bathymetry layer. Ideally, different regularization values should be explored, too, and the resulting models compared to obtain the best model that is simple and predicts accurately at the same time (Merow et al. 2013).

A combination of threats from bottom trawling, release of suspended particles industries from the oil and mining industries, to ocean acidification and ocean warming (resulting in decreased oxygen solubility and vertical water mixing) put CWC reefs under pressure, especially those living near their tolerance threshold. About 30% of all known *Lophelia* occurrences so far are on the Norwegian continental shelf (Järnegren & Kutti, 2014). Thus, Norway has a great responsibility in leading the conservation of CWCs, so the hope is that this study will aid in targeting conservation efforts for *Lophelia*, *Paragorgia*, and *Primnoa*.

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APPENDIX I

Scatterplot matrix produced with the MGET plug-in for ArcGIS on all coral presence points for all continuous variables. The Spearman's Rank ρ value for each variable pairing is in the upper right half, distribution of each variable in the diagonal, and a scatterplot with a line of best fit in the lower left half.