DETERMINANTS OF HABITAT UTILIZATION PATTERNS OF EUROPEAN LOBSTERS (*Homarus gammarus*) IN THE INNER OSLO FJORD, NORWAY

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managementMaster Thesis 60 credits 2022

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Master of Science Thesis by Teyie Sharon

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Preface

I am grateful to God for seeing me through my Master of Science studies. It has been an interesting journey of fieldwork and analysis in Norway, a different continent from my home Kenya. I have had new experiences, learnt a new language, made new friends and acquired scientific writing experience supported by several people! This study was made possible thanks to the financial support from the Finn Jørgen Walvigs trust and cooperation between the Norwegian University of Life Sciences (NMBU), the University of Oslo (UiO), Drøbak station, the Frogn municipality, and SOS Oslo fjord.

Special thanks to my supervisors Jonathan Colman, Stein R. Moe, and Thrond O. Haugen.. Thrond's expertise in statistics is something I hope to match up to one day. Thank you for your patience.. Stein, you are so thorough and fast with your responses, thank you for being so kind, patient, and concerned for my wellbeing.., Thank you Jonathan for showing up during fieldwork even when you were unwell.! Nashukuru (I'm grateful)

The field study would not have been possible without the gracious and patient collaboration of all participants. To the many volunteers who contributed to the fieldwork during lobster sampling in September 2020 and 2021, and December 2021, thank you! Knut and Odd thank you for showing me how to enjoy my first ever lobster meal.

Mari, thank you for the laughter shared, it was great to have someone to talk to when frustrations hit.

Special thanks go to my OIFC family and friends as well as Mwanaisha. Thanks for always checking up on me and ensuring I stay sane. To my loving mother, Ayitso M. Jayne, my siblings, Charlotte, Shantal, Molly, Alexis, and the little ones Ayllah, Christian, and Lerato. you are more than a blessing. Thank you ladies for keeping me grounded, making me laugh amidst the questions and teary eyes, your prayers and support mean a lot to me. Echinyogora!

Abstract

Habitat type and structure influences diversity body size, recruitment, population size structure and survival of species in marine communities. There is, however, inadequate empirical evidence on what substitutes location-specific habitat structure as this tends to vary from one region to the other. This study was therefore carried out to analyze factors that determine habitat utilization patterns of European lobsters (*Homarus gammarus*) in the inner Oslo fjord, Norway. Capture-mark-recapture sampling method was employed. Data was collected in 3 seasons-September 2020, September 2021, and December 2021) in 4 zones (Middle, North, South and Northeast) for five days with 20 traps and a 24 hours soaking time. Results indicate that shallow marine hard bottoms had the most prevalent vegetation type in the fjord and the most preferred by both male and female lobsters. Zone S had the highest heterogeneity with nine out of ten benthic vegetation types. Depth utilization patterns for both male and female lobsters in the three seasons (September 2020, September2021 and December 2021) were highest between 10 m and 25 m.

Male lobsters had a positive preference for substrate grain sizes ranging between 5 - 120 mm, while females had a positive preference for grain size 120-200 mm. However, both male and female lobsters showed a negative selection ratio towards substrate grains < 5 mm. Both male and female lobsters had a negative selection ratio towards depth below 10 m. Males had a positive selection ratio towards depths of between 10 m to 20 m. Both sexes have a negative selection for depth >30 m. Catch Per Unit Effort (CPUE) decreased with depth in all zones and was highest in zones Middle and South at any depth compared to zones North and North East. They were, however, not statistically different (M and S) due to overlapping confidence bounds. Finally, this study found that depth is a major determinant in habitat utilization patterns of European lobsters. There are, however, other factors that are associated with this. Considering the differences in habitat preferences, management decisions made in line with what habitats are suitable for assigning sanctuaries should not be generalized and instead should be based on area specific data and research.

Contents

1. INTRODUCTION

Habitat type and structure have been shown to influence diversity (Witman et al., 2004), body size, (Thorbjørnsen et al., 2018), recruitment, population size structure, and survival (Friedlander et al., 2006) of species in marine communities. Species adapt to certain habitat conditions, including the movement of water, amount of light, temperature, water pressure, nutrients, availability of food, and salinity (Broms et al., 2009; Plagányi et al., 2018; Planque et al., 2010).

European lobster (*Homarus gammarus*) (henceforth called lobster) is a species with high site fidelity and limited mobility (Hinchcliffe et al., 2022). Agnalt et al. (2007) found that 84% of hatchery-reared and released lobster off the southwestern coast of Norway were recaptured within 500 m of the release site. Wiig et al. (2013) in their study on acoustic monitoring of *Homarus gammarus* found that home range sizes ranged from 43,129 to 64,1731 m2 in September and from 12,024 to 39,7348 m2 during the fishing season.

Studies indicate seasonal variation in lobster activity patterns linked to species-specific temperature requirements. Lobsters prefer temperatures from 15-18 °C (Coleman et al., 2021), as water temperature plays a significant role in their growth, survival, and reproduction. Lobsters therefore tend to move in order to achieve adequate water temperatures to meet the physiological requirements mentioned above (Cowan et al., 2006). In a study on lobsters' diel activity, Wiig et al. (2013) found that there was a peak in activity around summer and early autumn and a drop-in activity during winter and early spring. Similarly, Smith et al. (1999); Moland et al. (2011) found that lobsters spent a considerable amount of time at depths between 15 m to 35 m and moved deeper (up to 60 m) during colder months (December to March).

Werner et al. (1983) and Werner and Gilliam (1984) found that differences in habitat types, size and age affect how organisms utilize their habitat. In fragmented habitats, movements involve trade-offs between foraging benefits and predation risk (Werner and Gilliam, 1984). For species that forage in the same habitats, residing near the edge offers both shelter and proximity to spatially segregated food resources. Generally, lobsters have been found in rocky habitats (with boulders at depths down to about 60 m) (Galparsoro et al., 2009), sheltered areas, as well as muddy environments where they can burrow and co-exist with other bottom dwellers like crabs, mussels and sea urchins (Plagányi et al., 2018). Lobsters are active at night and shelter in burrows during daytime, however their preferences vary with age and size as well as depth (Galparsoro et al., 2009)

Considering the different aspects that constitute a suitable habitat, this study was carried out to analyze factors that determine habitat utilization patterns of lobsters along and near the threshold to the inner Oslo fjord. Considering that European lobsters may not have the same habitat requirements in the Oslo fjord as in other areas around the coast, the resulting knowledge from this study seeks to improve the knowledge base for decisions on where to establish local lobster sanctuaries. This contribution considers the identification of preferred seafloor characteristics by the European lobster and predicts suitable habitats for assigning sanctuaries.

Given that lobsters have been found to prefer habitat depths between 15 m to 35 m depending on the season (Moland et al., 2011; Galparsoro et al., 2009), habitat depth preferences were presumed to vary with season

Secondly, lobsters' habitat utilization patterns have been found to vary depending on the different phases that the lobsters are in (Agnalt et al., 2007), for instance, egg-bearing females are more vulnerable and would tend to seek shelter more than male lobsters. Males were presumed to utilize habitats with larger grain sizes than females.

Vegetation types vary across the sea floor. However, this does not imply that lobsters randomly utilize available vegetation types in the fjord. I therefore predicted that lobsters, both females, and males, prefer certain vegetation types. For instance, eelgrass (Zostra spp.) beds have been shown to be of the highest preference (Bekkby et al., 2013).

2. MATERIALS AND METHODS

2.1. Study area

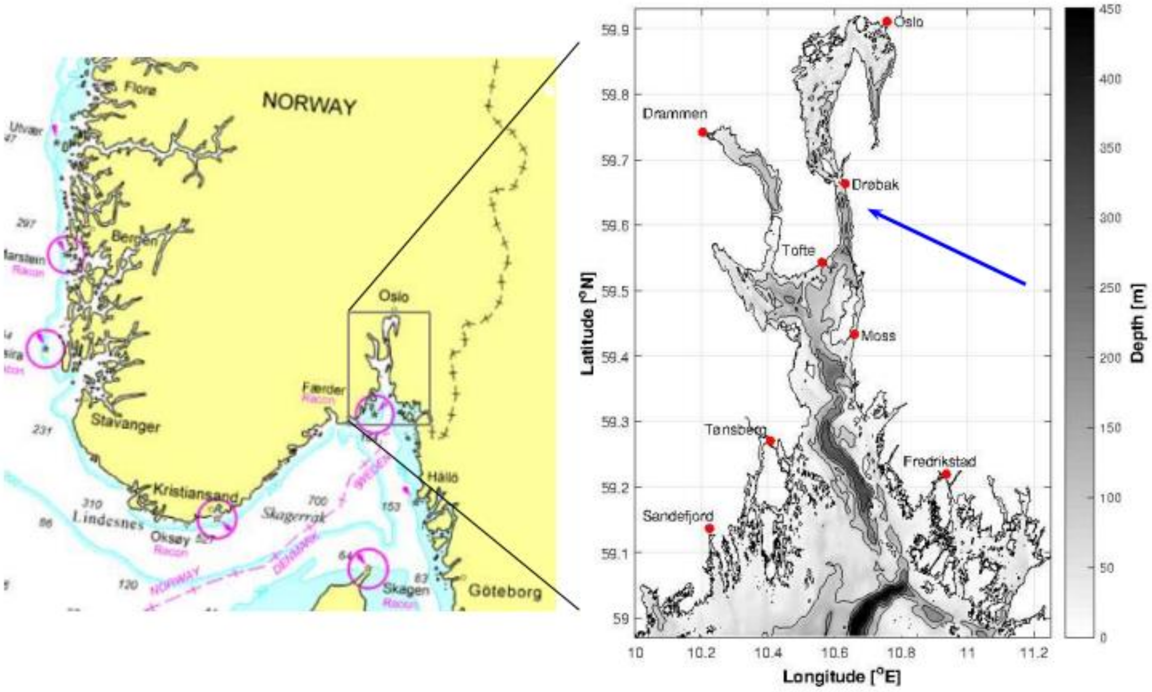

Figure 2. 1. The coastline of the Oslo fjord and its location in Southern Norway. The right-hand gray scale bar indicates depth in meters. The blue arrow points to the location of the study area (Norwegian Meteorological Institute).

This study was conducted between the outer and inner Oslo Fjord (Figure 2.1). The Oslo fjord is an inlet in the South-East of Norway that stretches 100 km and is part of the Skagerrak strait (Vølstad et al., 2021). The inner part of the fjord is made up of two basins, VestFjord and Bunnefjord. They are separated from the outer fjord at Drøbaksundet, where a submarine ridge forms a threshold with depths from 0 to 19.5m (Alve & Nagy, 1990). The maximum depth of the fjord is approximately 250 m, while the minimum depth is approximately 0-20 m (Baalsrud & Magnusson, 2002). The currents entering the Oslo fjord originate from the North Sea through Skagerrak. There are also several rivers and brooks draining into the fjord. The mixture of water sources into the fjord influences the environmental properties such as temperature, nutrient concentration, and salinity (Sætre et al, 2007), as well as the topography of the fjord (Baalsrud & Magnusson, 2002). Several other parameters influence the physical and chemical parameters of the fjords in Skagerrak, which include salinity, wind, and tidal forces (Sætre et al, 2007). The Norwegian coastal current originates from brackish and freshwater from the Baltic Sea which increases its salinity and while meeting the Atlantic water, it will decrease its stratification.

2.2. Study species and fishing regulations

The species of interest in this study is the European lobster (*Homarus gammarus*). It is a long-lived benthic decapod crustacean of significant ecological and commercial importance (Triantafyllidis et al., 2005.). It is distributed from the Atlantic in areas stretching between Norway (Lofoten islands) to the Azores and Morocco (Swift & Koltermann, 1988). They are known for their long-life span (several decades) (Moland et al., 2013), their culture (Olson et al., 2014), and their commercial (Bondad-Reantaso et al., 2012) importance. Lobsters prefer boulder fields or burrows as suitable habitat for defense purposes and can grow to a total body length of up to 500 mm and attains sexual maturity at 220 – 250 mm (Kleiven et al., 2019). Studies indicate that lobsters have high site fidelity and rarely move far from their preferred habitats (Moland et al., 2013). Sørdalen et al. (2018) found that egg-bearing females made minimum movements and were within 500 m of their release sites. A study by Agnalt et al. (2013) found that most recaptures of lobsters within a given size range were made within approximately 4 km of the release position, although not all lobsters were recaptured. A finding that Sørdalen et al. (2020) attribute to the need for shelter from disadvantageous environmental conditions. In Norway, lobsters have been found to occur in depths up to 60 m (Galparsoro et al., 2009). They however tend to move to shallow waters in summer due to better food availability, while warmer surface temperatures enhance metabolism, incubation of eggs, and maturation (Plagányi et al., 2018).

European lobster has been described as an omnivore with a diet mainly consisting of crustaceans (Pagurus sp.), gastropods (e.g., Gibbula sp., Buccinum sp.), and polychaets (e.g., Nereis sp.), but also of fish, bivalves, echinoderm, algae, and eggs Hallbäck and Warén (1972).

In 1964, the Norwegian government stated that lobsters less than 220 mm in total length were protected and had to be released when captured (Penn et al., 2018). Protection levels increased in 1992 at the Skagerrak coast to 240 mm minimum length (measured from the eyes to the end of the carapace, i.e., the carapace length - CL) and further to 250 mm outside Skagerrak a year later

(Moland et al., 2013). The Norwegian Directorate of Fisheries announced new regulations in 2008, stipulating that throughout Norway, the minimum legal size will be 250 mm, all egg-bearing females were illegal to capture and land, all lobster traps to have mandatory 60 mm diameter escape-vents, and a maximum of 10 traps per person/boat for recreational fishing (Fiskeridirektoratet 2011). In 2017, a gazette notice stipulated a new maximum size limit of 320 mm CL for lobster caught along the Norwegian Skagerrak coastline (Neufeldt et al., 2018). The fishing season was restricted to between 1st of October to 31st of November from the Swedish border and all the way to Sogn and Fjordane County. North of Sogn, Fjordane, and the rest of the country, the fishing season extends to the 31st of December (NDF 2011).

2.3. Sampling lobsters

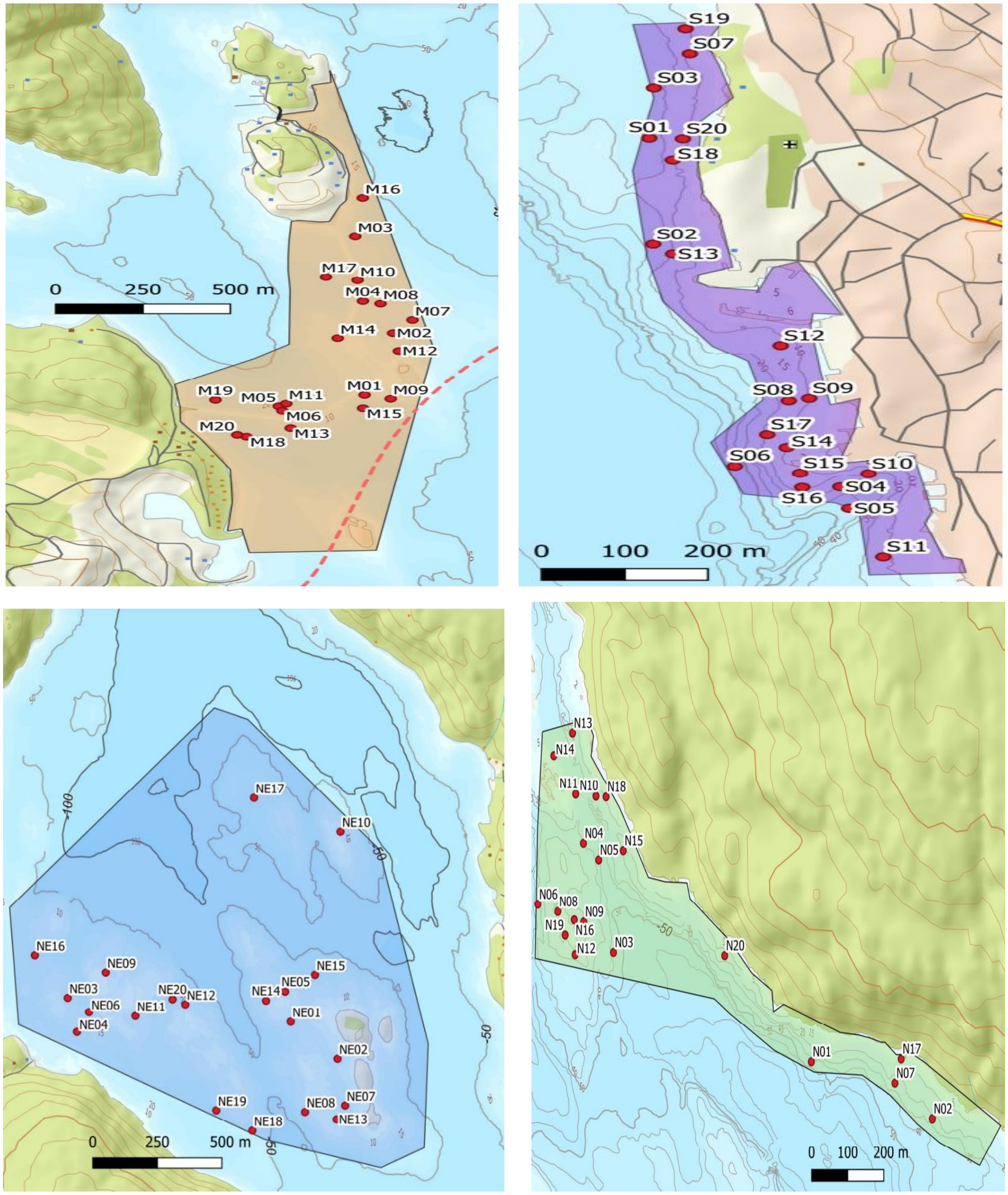

Figure 2. 2. Map showing locations of trap placements in the four selected zones denoted with letters pointing towards the area's location in cardinal directions (M=Middle, S-South, NE-North-East, N-North). N was not used in the statistical analysis for 2021, as there was no data for that Zone in 2021.

Lobsters were caught using a modern parlour trap (Fig. 2.3) (900 ´ 450 ´ 400 mm with 120 mm openings), meeting the Norwegian Directorate for Fisheries standards (Norwegian Fisheries Directorate), but our obligatory escape vents were closed. Non-buoyant rope was attached to traps and surface buoys on opposite ends. The surface buoys were numbered and labelled "Experimental fishing" with contact information. Defrosted Atlantic mackerel (*Scomber scombrus*) was used for bait.

Capture-mark-recapture sampling methods were employed. A stratified random distribution design was used to set up the traps to avoid bias (2 layers of depth intervals at 5-20 m and 20-50 m, 10 traps per layer, in total each zone had 20 traps) (Fig.2.2). A minimum of 30 m horizontal distance between traps was drawn using the "random-points-inside-polygon" tool in QGIS.

A handheld GPS (Garmin 78s) GPs was used to upload trap location coordinates daily. Even though efforts were made to attain consistent trap locations, traps may drift several meters away from the dropping points. Additionally, in some cases, human error with hand-held GPS may have caused variation to trap locations.

One to one and a half mackerel were used to bait traps before deploying the traps, which were allowed to soak for 24 hours approximately. Sampling was conducted three times; once in 2020 (round one from 17th to 21st of September) and twice in 2021 (round two from 16th to 20th of September and round three from 5th to 9th December). (Directorate of Fisheries, 2011). Sampling rounds consisted of 5 days of fishing (i.e., a sampling effort of 20 traps x 5 days per site per sampling session).

Figure 2. 3. Modern ‘parlour’ lobster trap used to capture lobsters during the study.

2.4. Tagging lobsters

For every trap haul the information on lobster sexual orientation; total length; tag number and recaptures were recorded. Additionally, trap number and sampling area was also noted. Sex was determined by examination of the first pair of pleopods (Fig. 2.5). TL was measured from the rostrum to the posterior end of the telson. Each lobster got tagged with 60 mm white T-bar tags (FD-94, T-bar, Floy-tag Inc) in the thorax before we released them back into the fjord. The T bar was marked with individual numbers, and contact information. A tag applicator was used to insert the T bar through the thoracoabdominal membrane located between the cephalothorax and the first abdominal segment.

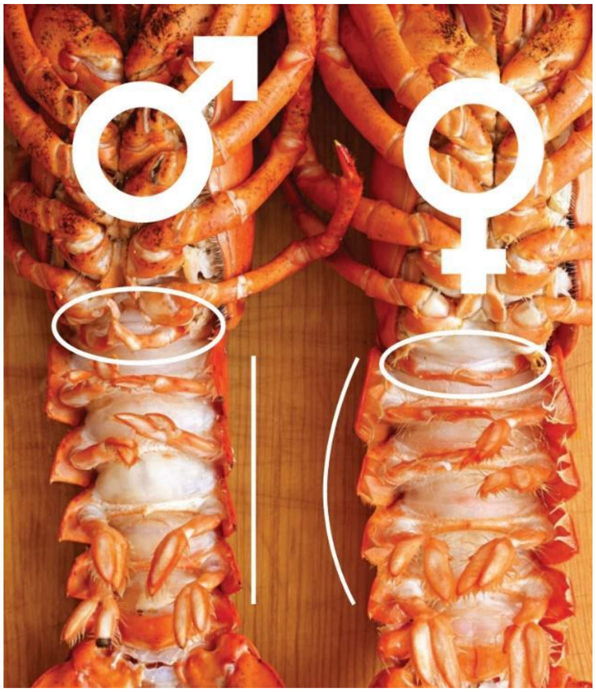

Figure 2. 4. Sex of lobsters (left-male, right-female).

2.5. Data preparation and analysis

Preparation of data and construction of the input-file was performed in Microsoft Excel, while the visual presentation of results in plots was made using R software. Habitat data for seafloor vegetation and substrate size data were obtained and used with authorization from the Norwegian Institute of Water Research (NIVA) (http://www.indre-oslofjord.no/) (Fig.2.6 and 2.7). However, this was not verified in the field.

The input dataset (depth (m), zone (Middle, South, North East, and North), sex (male and female), season (September 2020, September 2021, December 2021), Vegetation type, and substrate size) was the basis for a logistic regression model predicting the catch of lobster in the study area, with the lobster presence or absence as a binary response variable.

CPUE estimates obtained were used as a proxy for lobster abundance in this study. I assumed that lobsters have a similar catchability in baited traps that are deployed within their home range. Data used in analyses of CPUE were limited only to traps that were in the water for 24 hours. CPUE values are thus presented as the number of lobsters per trap per day.

Akaike's Information Criterion (AIC) was used in model selection to find the best fit of 27 different regression models explaining the most variation in the data and was

calculated as: $AIC = -2\log\text{- likelihood} + 2(p+1)$
where p is the number of parameters in the model,
and +1 is added for the estimated variance (Crawley, 2007).
By adding $(p+1)$ to the deviance, AIC removes superfluous variables. The best fit model with the lowest AIC was found through the step-function in R. The model generated was used to predict utilization patterns.

Information on selected marine habitat types in the Oslo fjord was obtained from the mapping of prioritized marine nature types in the Oslo fjord (2021) from the Norwegian Institute for Water Research (NIVA) using the NiN habitat classification system. Table 2.1 is a key extract of the overview of the mapped habitat types. The dominant vegetation types are indicated in bold, while the less dominant vegetation types are in normal font.

Table 2. 1. Overview of NiN code types pre-mapped during modeling and their explanation.

NiN-code	**Explanation**
M.1	Grunn marin fastbunn (shallow marine hard bottom)
M.2	Afotisk fast saltvannsbunn (aphotic hard saltwater bottom)
M.3.(4-6)	Blæretang, spiraltang, sauetang- blåskjell- og rurbunn (litt beskyttet) *Fucus vesiculosus*, *Fucus spiralis*, (Pelvetia, mussel and barnacle bottom, slightly protected area)
M.4	Eufotisk marin sedimentbunn (Euphotic marine sediment bottom)
M.4.1	Grunn sandbunn (shallow sandy bottom)
M.4.13	Løs mudderbunn i rødalgebeltet (loose muddy bottom between 13-30 m where production is still greater than decomposition)
M.4.15	Finmaterialrik sedimentbunn i rødalgebeltet (tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition)
M.5	Afotisk marin sedimentbunn (Aphotic marine sediment bottom)
M.5.1	Sandbunn i øvre sublittoral (Sandy bottom in the upper sublittoral)
M.5.4	Finmaterialrik sedimentbunn i øvre sublittoral (Tiny/fine particle rich sediment bottom in the upper sublittoral)

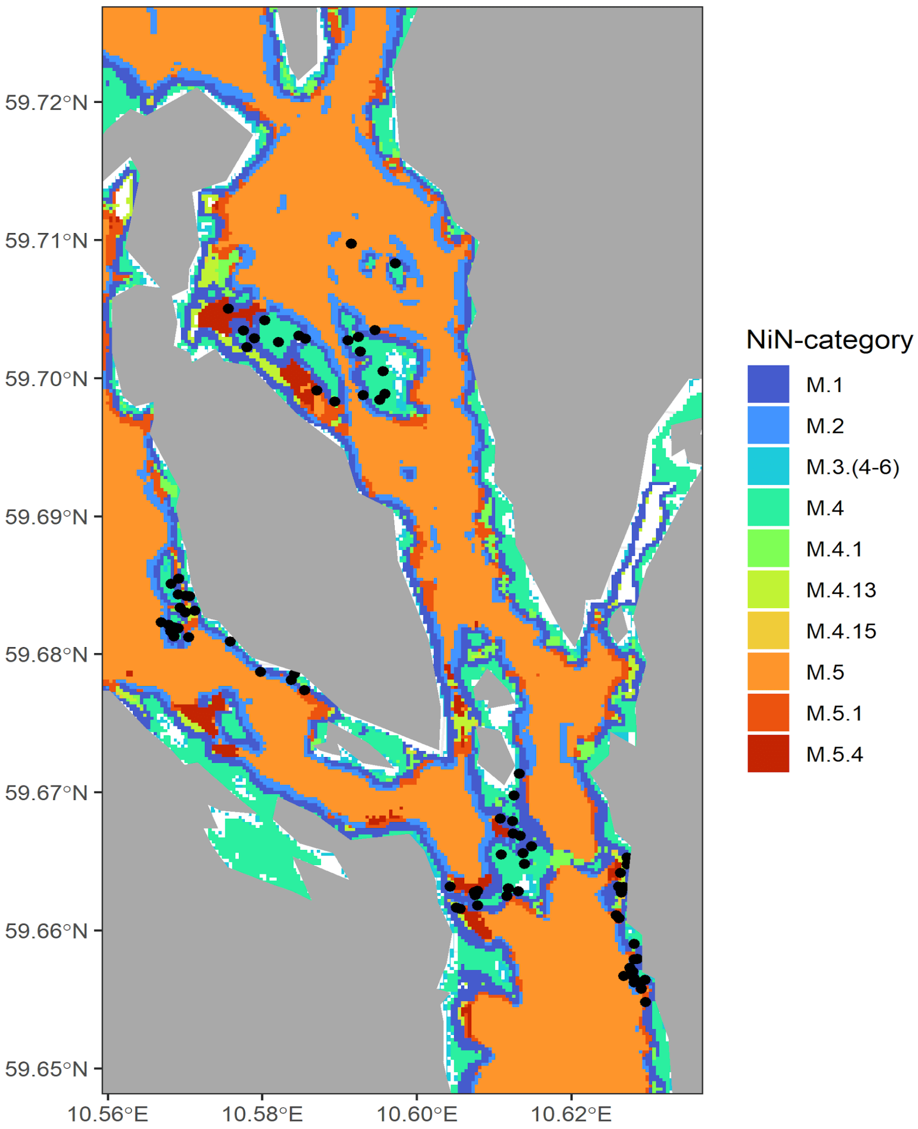

Figure 2. 5. Map showing an overview of vegetation types modelled for the areas of trap placement (shallow marine hard bottom (M.1), aphotic hard saltwater bottom (M.2), Pelvetia, mussel and barnacle bottom, slightly protected area (M.3(4-6)), Euphotic marine sediment bottom (M.4), shallow sandy bottom (M.4.1), loose muddy bottom between 13-30 m where production is still greater than decomposition (M.4.13), tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15), Aphotic marine sediment bottom (M.5), Sandy bottom in the upper sublittoral (M.5.1) and Tiny/fine particle rich sediment bottom in the upper sublittoral (M.5.4))based on the NiN model 2020 performed by NIVA). Lines of latitude and longitude denoted as ^{0}*N-North and* ^{0}*E-East. Appendix 2 has a detailed pre-mapped model.*

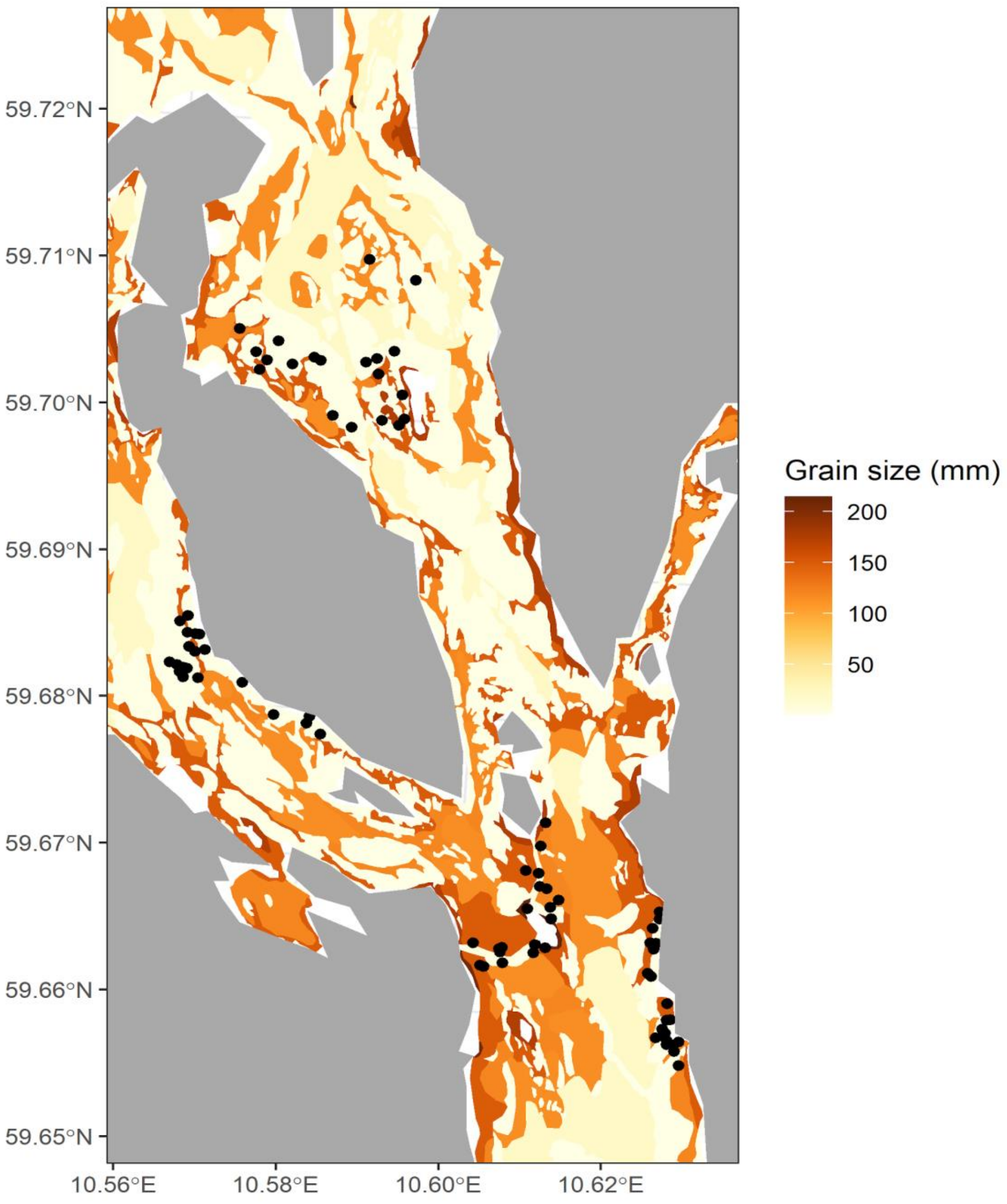

Figure 2. 6. Map showing an overview of grain sizes modelled for the areas of trap placement based on the NiN model 2020 performed by NIVA. Lines of latitude and longitude are denoted as ^{0} N-North and ^{0}E-East. Appendix 2 has a detailed pre-mapped model.

3. RESULTS

3.1. Vegetation types and utilization

Out of 29 available vegetation types (Appendix, Table 1), 10 vegetation types were utilized (Table 2.1).

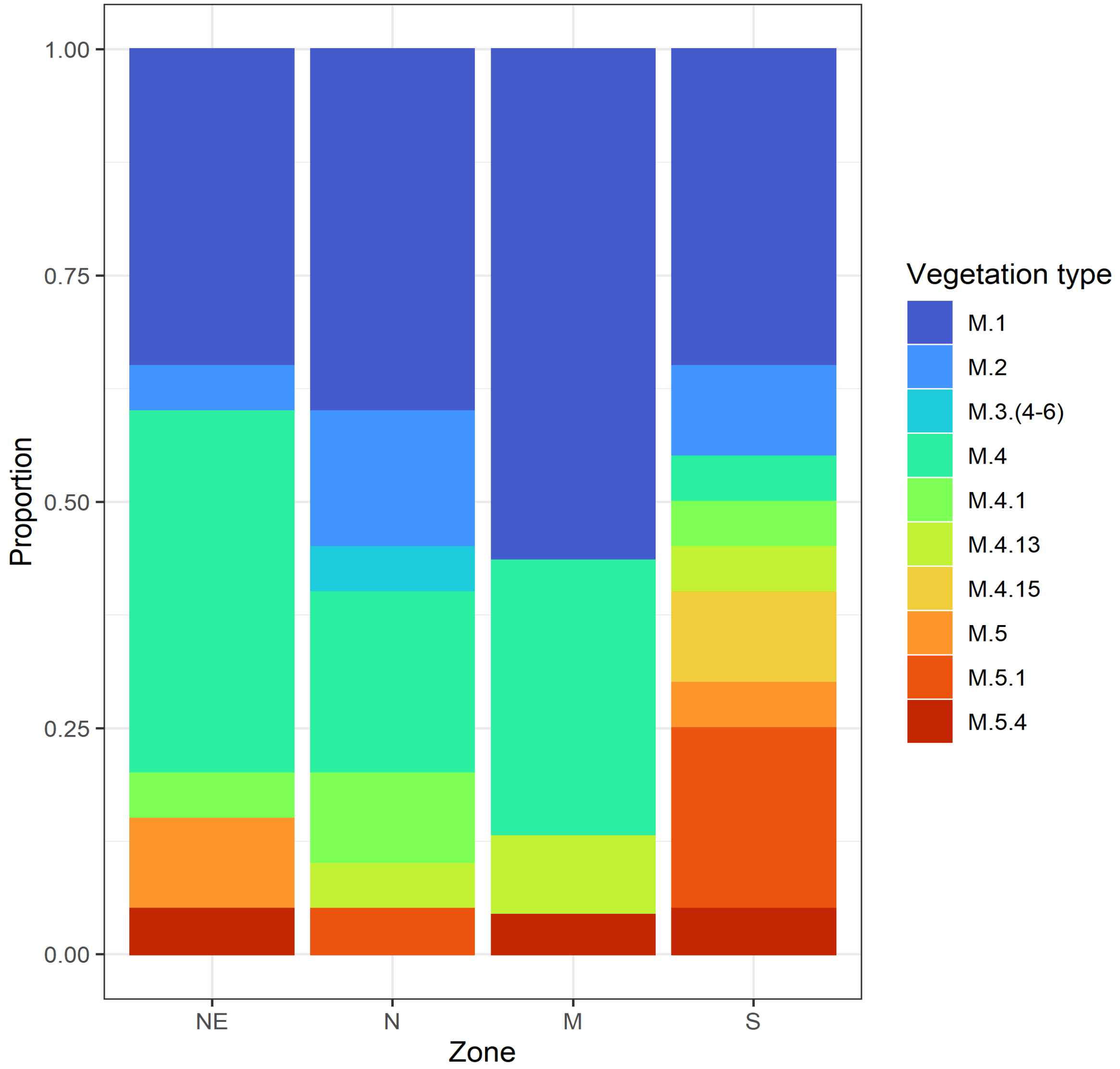

Figure 3. 1. Figure showings the proportion of available benthic habitat types found on the beds of trap placements, shallow marine hard bottom (M.1), aphotic hard saltwater bottom (M.2), Pelvetia, mussel and barnacle bottom, slightly protected area (M.3(4-6)), Euphotic marine sediment bottom (M.4), shallow sandy bottom (M.4.1), loose muddy bottom between 13-30 m where production is still greater than decomposition (M.4.13), tiny/fine particle rich sediment

bottom between 13-30 m where production is still greater than decomposition (M.4.15), Aphotic marine sediment bottom (M.5), Sandy bottom in the upper sublittoral (M.5.1) and Tiny/fine particle rich sediment bottom in the upper sublittoral (M.5.4) in the different zones (NE=North-East, N=North, M=Middle, S=South) based on the NiN model category 2020 performed by NIVA.

Shallow marine hard bottom (M.1) was found to be the most prevalent vegetation type in all zones other than Zone NE which had Euphotic marine sediment bottom (M.4) as the most prevalent vegetation type (Fig. 3.1). Euphotic marine sediment bottom (M.4) is the second predominant habitat type in zones N and M, while Zone Shad Sandy bottom in the upper sublittoral (M.5.1) as the second most predominant habitat type (Fig. 3.1).

Zone S had the highest heterogeneity with nine vegetation types: shallow marine hard bottom (M.1 aphotic hard saltwater bottom (M.2),Euphotic marine sediment bottom (M.4), shallow sandy bottom (M.4.1), loose muddy bottom between 13-30 m where production is still greater than decomposition (M.4.13), tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15), Aphotic marine sediment bottom (M.5), Sandy bottom in the upper sublittoral (M.5.1) and Tiny/fine particle rich sediment bottom in the upper sublittoral (M.5.4)vegetations types followed by Zone N, Zone NE and Zone M (Fig 3.1).

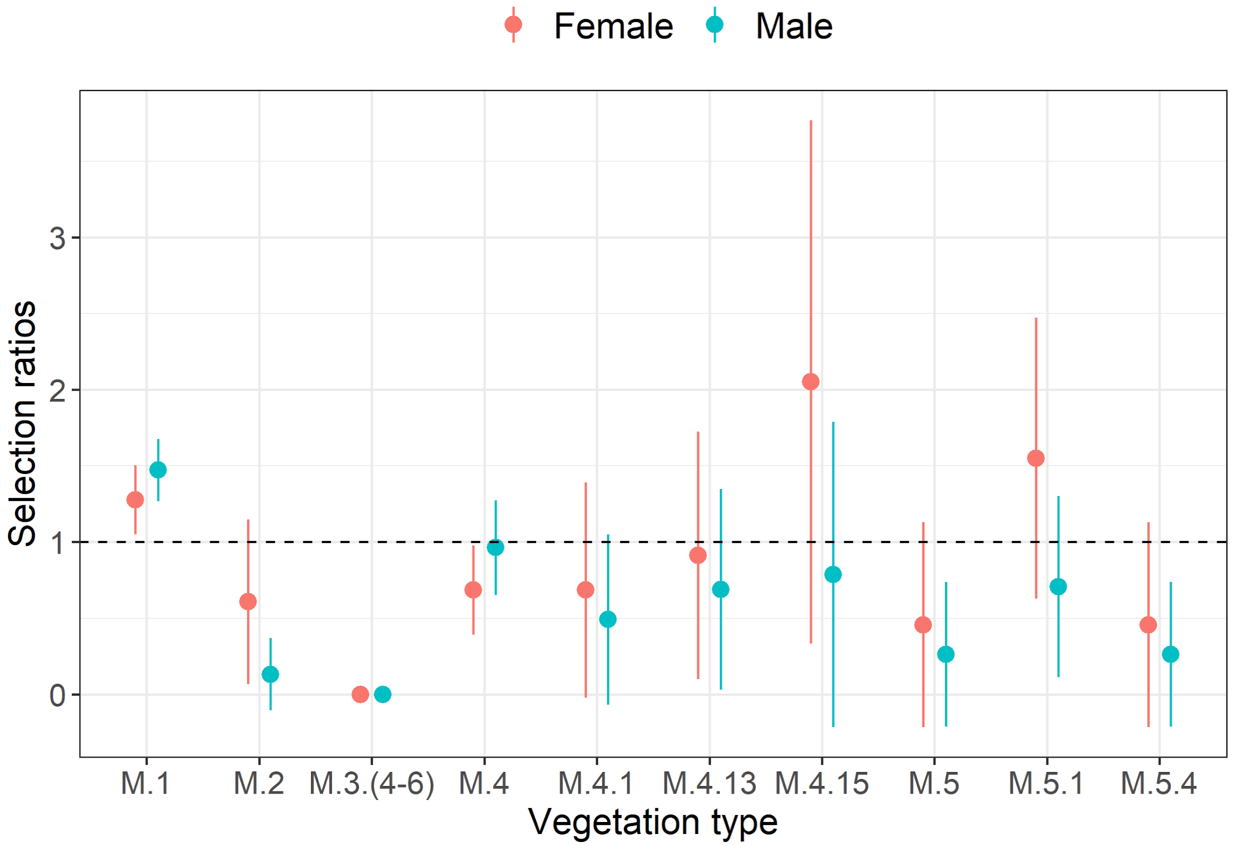

Figure 3. 2. Selection ratios (± 95 % confidence intervals) of 10 marine habitat types. Ratios >1 and <1 indicate a positive selection (preference) and negative selection (avoidance), respectively for male and female lobster for the time period 2020 September and 2021 September and December. Vegetation types: Shallow marine hard bottom (M.1), aphotic hard saltwater bottom (M.2), Pelvetia, mussel and barnacle bottom, slightly protected area (M.3(4-6)), Euphotic marine sediment bottom (M.4), shallow sandy bottom (M.4.1), loose muddy bottom between 13-30 m where production is still greater than decomposition (M.4.13), Tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15), Aphotic marine sediment bottom (M.5), Sandy bottom in the upper sublittoral (M.5.1) and Tiny/fine particle rich sediment bottom in the upper sublittoral (M.5.4)

Both males and females positively selected shallow marine hard bottom (M.1), (Fig. 3.2). Both male and females negatively selected Pelvetia, mussel and barnacle bottom, slightly protected area (M.3(4-6) and was not used at all. Negative selection was used (less than expected) for males on the aphotic hard saltwater bottom (M.2). Tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15) and Sandy bottom in the upper sublittoral (M.5.1) had a positive female selection ratio and a negative male selection ratio.

Tiny/fine particle-rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15*)* had the highest positive selection ratio for female lobster while Shallow marine hard bottom (M.1), *was* the only habitat with a positive selection ratio for males.

3.2. Substrate grain size availability versus use

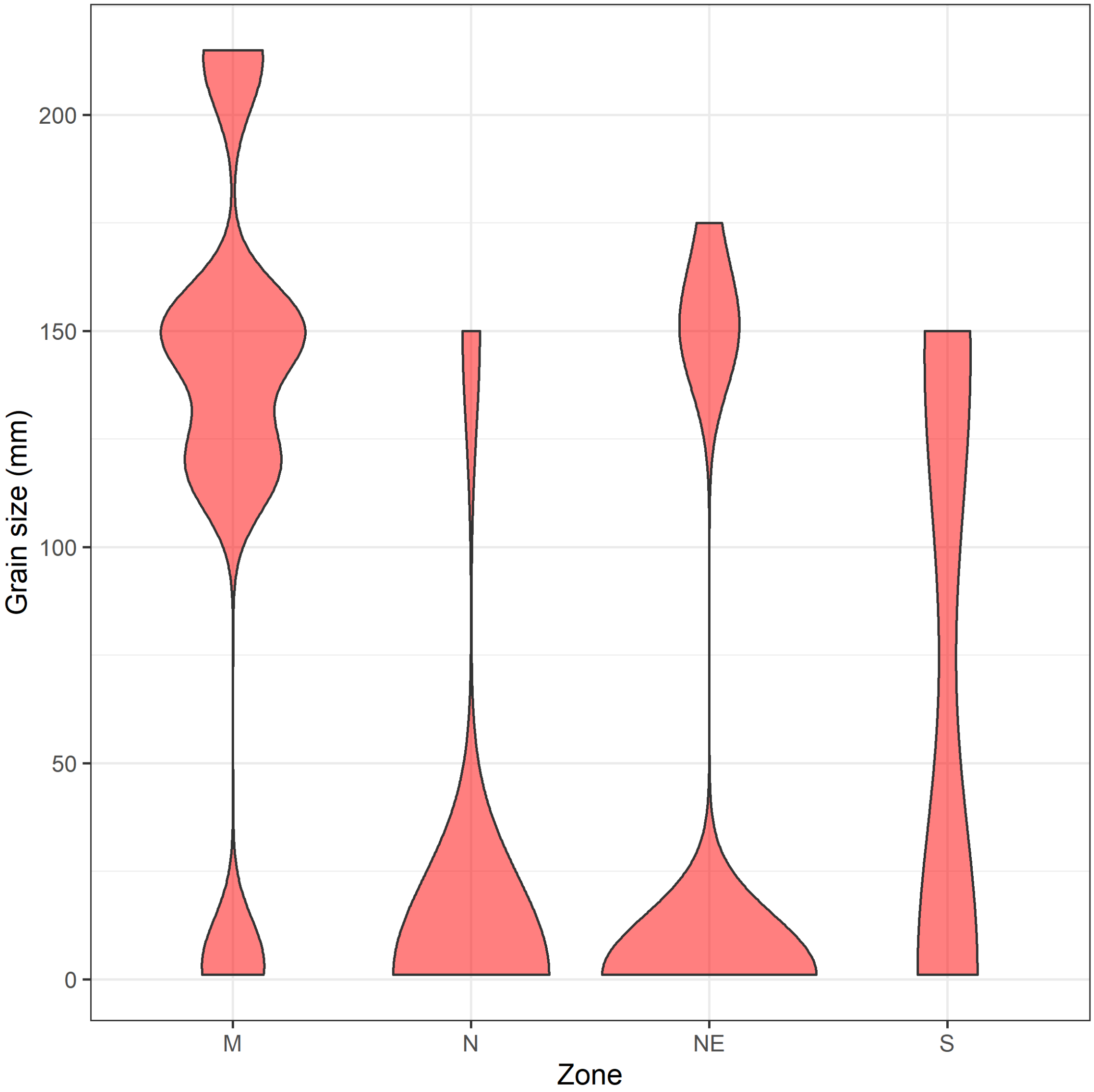

Figure 3. 3. Available substrates grain sizes (mm) in the different zones (M=Middle, N=North, NE=North-East, and *S=South) in the Oslo fjord.*

All zones had grain sizes ranging from 0-50 mm (Fig. 3.3). However, M had much larger grain sizes with a range of 0-250 mm compared to N which had relatively small grain sizes 0-150 mm. NE had either small or big grain sizes. S had an almost even distribution of all grain sizes.

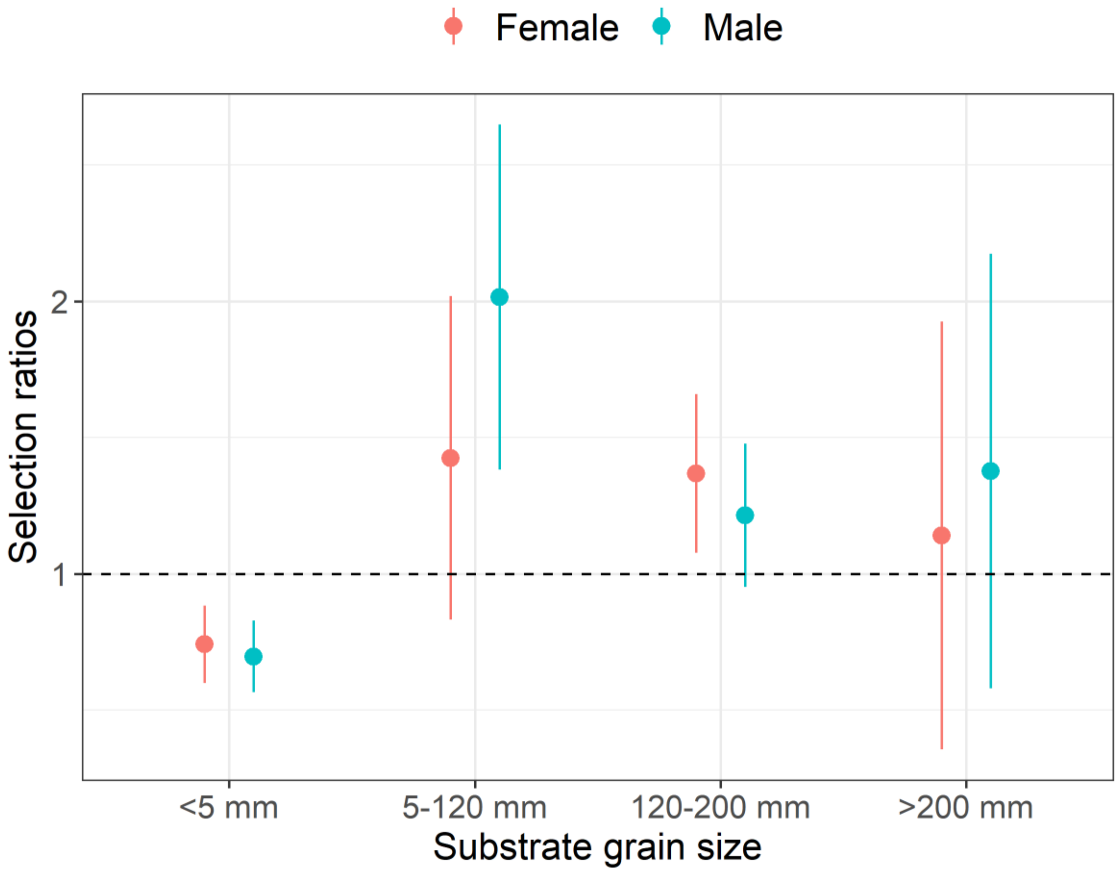

Figure 3. 4. Selection ratios of substrate grain size (mm) by different lobster sexes. Ratios *>1 and <1 indicate positive selection (preference) and negative selection (avoidance), respectively.*

Both male and female lobsters showed a negative selection ratio towards substrate grains <5 mm (Fig. 3.4). Male lobsters had a positive preference for substrate grain sizes ranging between 5-120 mm, while females have a positive preference for grain size 120-200 mm.

3.3.Catch per Unit Effort/Density

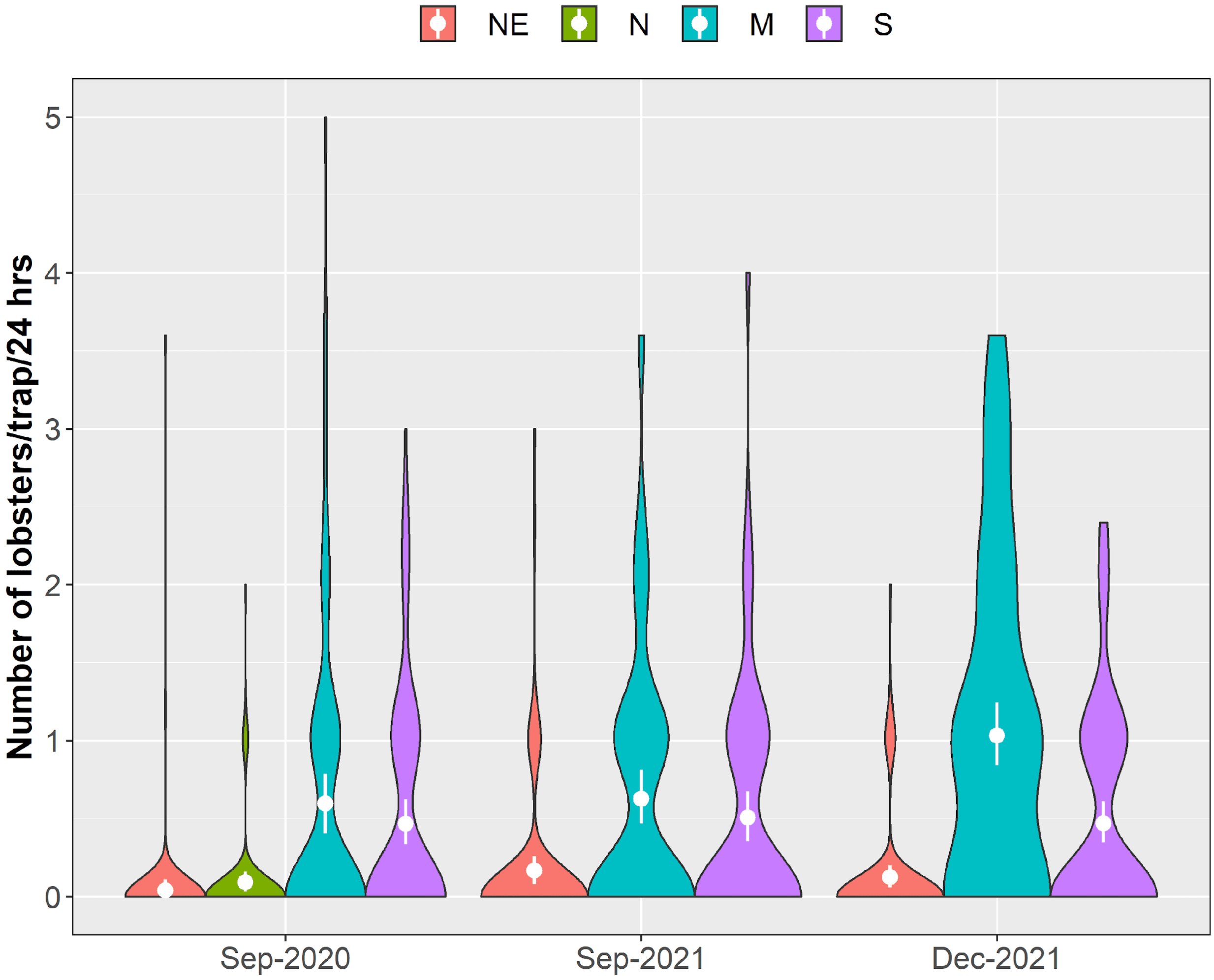

Figure 3. 5. Number of lobsters caught per trap every 24 hours (CPUE) for each season (September 2020, September 2021 and December 2021) and Zone (M=Middle, S=South, N=North, NE=North-East).

CPUE increased in M and S from September to December 2021, but decreased in NE between these two months (Fig.3.5).

M had the highest CPUE in all seasons compared to other zones, as well as a more even distribution in the catch.

Out of the 27 models, model 7 had the highest support of 57%. Depth and the interaction between zone and round were significantly associated with the CPUE response ($p<0.0001$).

CPUE relates to depth in different ways in different zones as can be seen from the subsequent figures

Table 3. 1. Parameter estimates (A) and corresponding test statistics (B) for the best *model (Depth+Zone*Round). Estimates, standard errors and p-values for variables describing lobster presence in the study area.* Depth (m) *zone ((M=Middle, S=South, N=North, NE=North-East) in three rounds (September 2020, September 2021 and December 2021) against the depth level in meters.*

Table. A

	log (CPUE + 1)		
Predictors	Estimates	CI	p
(Intercept)	0.10	-0.02 – 0.21	0.095
Depth	-0.00	-0.01 – -0.00	**0.035**
Zone [N]	0.06	-0.07 – 0.19	0.365
Zone [M]	0.32	0.20 – 0.45	**<0.001**
Zone [S]	0.28	0.15 – 0.41	**<0.001**
Round9-2021	0.09	-0.01 – 0.19	0.092
Round12-2021	0.05	-0.05 – 0.15	0.283
ZoneM: Round9-2021	-0.05	-0.19 – 0.09	0.482
ZoneS: Round9-2021	-0.07	-0.21 – 0.07	0.349
ZoneM: Round12-2021	0.16	0.02 – 0.30	**0.023**
ZoneS: Round12-2021	-0.04	-0.18 – 0.10	0.549
Random Effects			
σ^2	0.13		
$\tau_{00\ \text{TrapID}}$	0.02		
ICC	0.11		
N_{TrapID}	81		
Observations	989		
Marginal R^2 / Conditional R^2	0.170 / 0.262		

Table. B

	B Effect	**Chisq DF**	**P-value**
Depth	4.4671	1	P = 0.035
Zone	63.4201	3	P = 1.092 e^{13}
Round	10.5531	2	P = 0.005
Zone: Round	13.6499	4	P = 0.008

Depth and round (September 2020, September 2021 and December 2021) estimates were negative (Table 3.1). Fig. 3.6 shows the interaction between negative estimates of depth and round on CPUE, CPUE decreases with depth in all seasons.

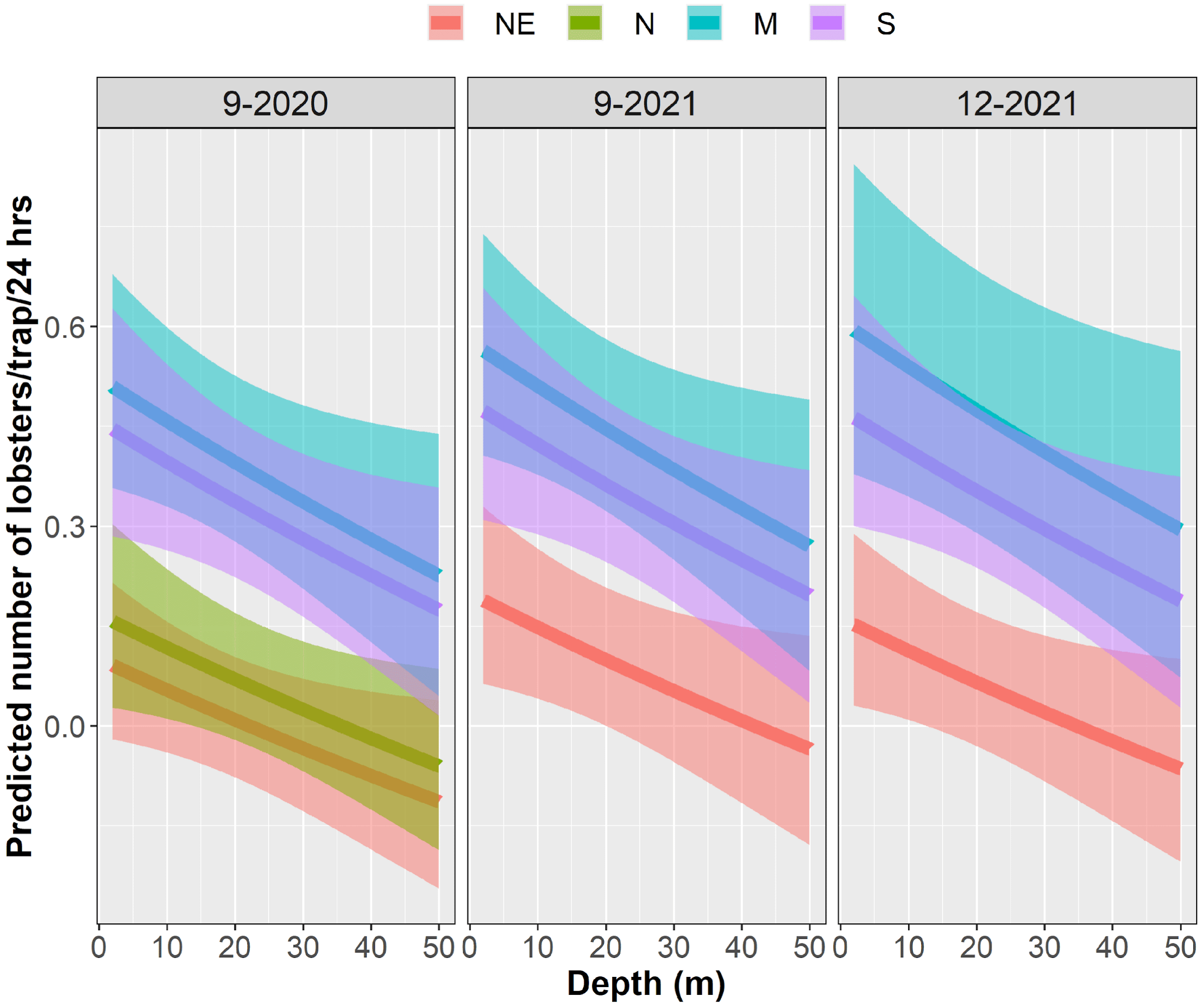

Figure 3. 6: Prediction plot for model presented in Table 3.1. Plot of the predicted number of lobsters catch per trap per 24 hours in each zone ((M=Middle, S=South, N=North, NE=North-East) in three seasons (September 2020, September 2021 and December 2021) against the depth level in meters.

CPUE decreases with depth in all zones and is higher in zones M and S at any depth compared to zones N and NE (Fig. 3.6).

They are however not statistically different (M and S) due to overlapping confidence bounds.

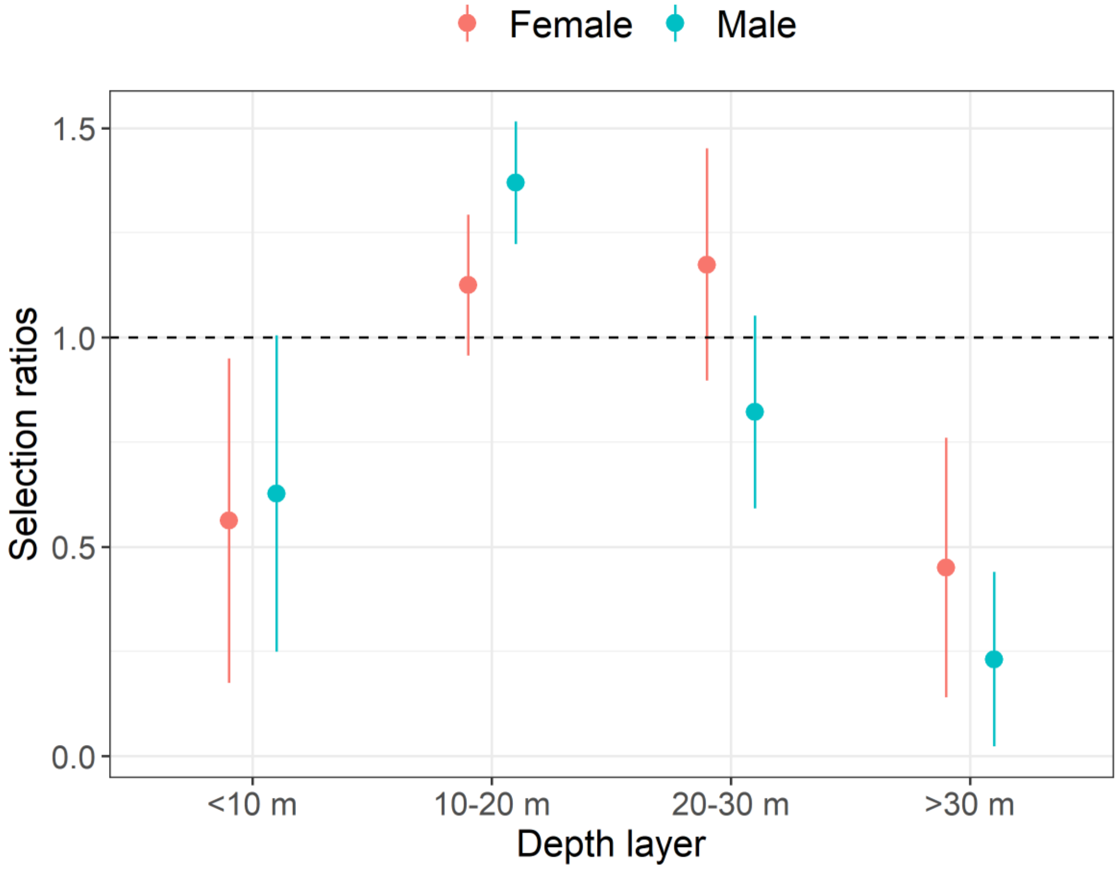

Figure 3. 7. Depths (m) selection ratio of different lobster sexes. Ratios *>1 and <1 indicate positive selection (preference) and negative selection (avoidance), respectively*

Both male and female lobsters had a negative selection ratio towards depth below 10 m.

Males had a positive selection ratio towards depths of between 10 m to 20 m. Both sexes have a negative selection for depth >30m (Fig.3.7).

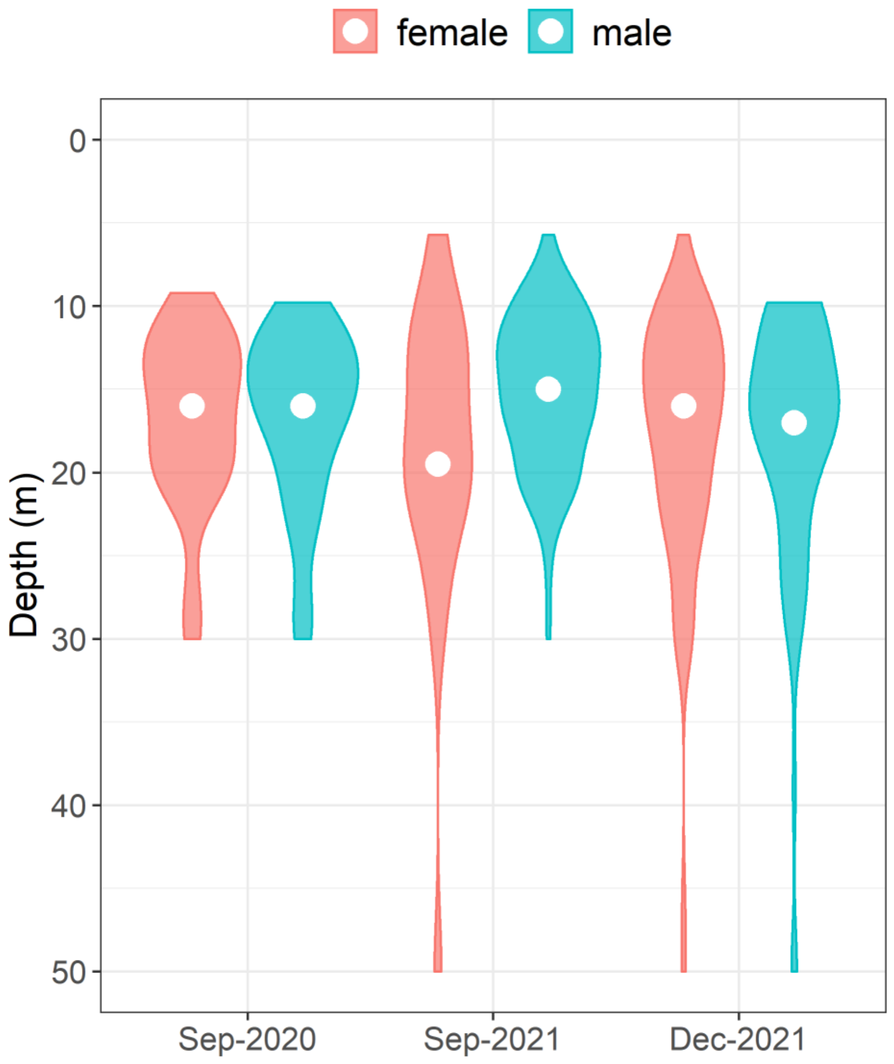

Figure 3. 8. Density per sex of lobsters caught at different depths (m) for each season (September 2020, September 2021 and December 2021) and Zone (M=Middle, S=South, N=North, NE=North-East).

Depth utilization patterns for both male and female lobsters in the three seasons (September 2020, September -2021 and December 2021) were highest between 10 m and 25 m (Fig.3.8).

4. DISCUSSION

4.1. Vegetation type and utilization

Results from the study confirmed the predictions that both female and male lobsters prefer certain vegetation types. Even though the study area was modelled to have ten types of vegetation available, lobsters preferred specific types(Shallow marine hard bottom (M.1), aphotic hard saltwater bottom (M.2), Euphotic marine sediment bottom (M.4), shallow sandy bottom (M.4.1), loose muddy bottom between 13-30 m where production is still greater than decomposition (M.4.13), Tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15), Aphotic marine sediment bottom (M.5), Sandy bottom in the upper sublittoral (M.5.1) and Tiny/fine particle rich sediment bottom in the upper sublittoral (M.5.4)). Furthermore, they utilize habitats with different species of seaweed. Previous studies indicate similar differences in utilization patterns with regards to available vegetation types. For instance, Bologna & Steneck (1993) established experimentally that kelp beds positively influenced the density of local lobster population. In a different study, Acosta et al. (1999) found that spiny lobsters would migrate among mangrove and coral reef habitats that were surrounded by seagrass meadows.

Johns & Mann, (1987) in their study found that juvenile lobsters *Homarus americanus* preferred seaweed habitats (Irish moss *Chondrus crispus* Stackhouse) more frequently than habitats without. Preference for Shallow marine hard bottom (M.1) and Euphotic marine sediment bottom (M.4) could be attributed to factors such as biochemical cues from the living algae (Johns & Mann, 1987), light avoidance responses (Milewski et al., 2021) and by seeking shelter from predators (Selgrath et al., 2007) and water currents.

I found that male and female lobsters utilized for instance unlike males, females had a positive selection ratio for Tiny/fine particle rich sediment bottom between 13-30 m where production is still greater than decomposition (M.4.15) and Sandy bottom in the upper sublittoral (M.5.1). This could be attributed to different life stages that the lobsters were in, the size of the lobster as well as age. Egg bearing lobsters as well as molted lobsters tend to be more vulnerable and would tend to seek shelter compared to their male counterparts (Wallace et al., 1998).

M.4.15-Finmaterialrik sedimentbunn i rødalgebeltet (red algae) was found to be preferred by female lobsters more than male lobsters and represents the exact depth that had the most lobster

13-30 m. Even though previous studies indicate benefits associated with inhabiting red algae such as increased growth rate and costs of close proximity to already settled benthic juveniles from predators (Bologna & Steneck, 1993).

4.2. Substrate grain size availability and use

Contrary to my predictions, male lobsters utilize habitats with a wider range of grain sizes ranging from 5 mm to grain sizes above 200 mm, while female lobsters preferred habitats with grain sizes above 120 mm. Both male and female lobsters had a negative selection ratio towards substrate grains <5mm. A study by Botero & Atema, (1982) found that spiny lobsters can successfully exploit different substrates, however, only juvenile lobsters were found to burrow in mud and would gradually find alternative habitats as they matured. They found that spiny lobsters preferred rocks and sand, followed by mud substrates. In a different study, Galparsoro et al. (2009) found that European lobsters preferred habitat in locations between sedimentary- and rocky-bottoms. However, there were other factors associated with the choice of habitats like seafloor depressions such as steep slope, and medium. Other factors that influence selectivity include sexual differences, catchability, or behavior induced factors (Andersen et al., 2018).

4.3. Catch per unit effort as an indicator for lobster abundance

Catch per unit effort can be influenced by seasons (temperature, waves and turbidity) behavior and size of lobsters (Johnsen & Iilende, 2007). For instance, lobsters' vulnerability varies seasonally depending on the cycle phase (molted or egg bearing females) (Wallace et al., 1998). Contrary to the predicted outcome, CPUE was found to be stable in the different seasons. Increase was recorded from September 2021 to December 2021 in the zone M, and tends to stabilize in zones S and NE. This could be attributed to recruitment of lobsters from other areas to fill the niche that was created after fishing other than zone M where no fishing occurred. Alternatively, this increase in abundance could also be attributed to ease in catchability in December considering lobsters are territorial, having high site fidelity with a limited home range (Lees et al., 2020) and the temperature being low in December reduced their catchability by reducing their mobility (Moland et al., 2013) (Wiig et al., 2013). Studies have also found lobsters to be less mobile during molting (their exoskeleton is soft) which makes them more vulnerable (Agnalt et al., 2007.), a finding that could be partly attributed to catchability in September 2021 when molting occurs. Catch per unit effort (CPUE) can be influenced by seasons (temperature, waves and turbidity) behavior and size of lobsters (Johnsen & Iilende, 2007). For instance, lobsters' vulnerability varies seasonally depending on the cycle phase (molted or egg bearing females) (Wallace et al., 1998).

Similar to other studies (Galparsoro et al., 2009; Moland et al., 2011), CPUE decreased with increase in depth in all seasons and zones. Previous studies carried out in Norway indicate that lobsters normally occur at mean depths of 12 m. They normally move to warmer surface waters a phenomenon attributed to greater food availability in shallow areas as temperatures increase, combined with the lobsters seeking warmer water to accelerate metabolism, incubation of eggs or maturation of internal gonad tissue. However, during the winter, lobsters seek deeper water (50–60 m) (Galparsoro et al., 2009) within the constraints of their home range location. This supports the trend recorded in this study (Fig 3.6) season December 2021 which had relative abundance at the depth >40 m compared to the other seasons.

Contrary to expectation that depths preferences between sexes will vary, I found that both male and female lobsters had a negative selection ratio towards depth below 10 m and above 30 m. A finding that corroborates with findings from other studies (Galparsoro et al., 2009; Moland et al., 2011). This could be attributed to both sexes preferring the same depth range.

Depth utilization patterns varied between seasons (September 2020, September 2021 and December 2021). The recorded utilization pattern can be attributed to changes in seasons between slightly warmer months of September to colder months of December. Howard (1980) attributes the shift to deeper waters as a need for shelter from disadvantageous environmental conditions, such as extreme temperatures and tidal currents. (Galparsoro et al., 2009) in his study also found that European lobsters preferred water depths of 35 m-40 m as a means to seek cover during too high wave energy conditions. Additionally, depth has also been found to vary and influence European lobsters' activities. They have been found to be more nocturnal in shallow waters compared to deeper water where they are generally more active. In their review, Childress & Jury (2006) concluded that one of the major benefits of this diel activity pattern is perhaps reduced predation risk and increased prey obtainability at night.

5. CONCLUSION

The study was done to ascertain factors that determine habitat utilization patterns of European lobsters (*Homarus gammarus*) in the inner Oslo fjord in Norway. My results show that depth is a major determinant in habitat utilization patterns of European lobsters. However, the results contradicted most predictions made, for instance there was no statistical difference is depth selection ratio for both sexes as well as both sexes registering a negative selection for depth >30m.In the end my results show that determinants of habitat utilization patterns of European lobsters (*Homarus gammarus*) are area specific. Considering the differences in habitat preferences, management decisions made in line with what habitats are suitable for assigning sanctuaries should not be generalized and instead should be based on area specific data and research..

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Appendix 1

Table 1. AIC model selection table for lobster data from the Drøbak area from September 2020 to December 2021. Grain Size (mm), Depth (m), 4 zones (NE=North East, N= North, M=Middle, and S=South) Round (September 2020, September 2021 and December 2021).

Model	**K**	**AICc**	**Delta_AICc**	**AICc Wt**	**Cum. Wt**	**LL**
depth+Zone*Round	13	859.62	0	0.56	0.56	-416.62
log(grainSize)+depth+Zone*Round	14	861.57	1.95	0.21	0.78	-416.57
log(grainSize)*Round+depth+Zone*Round	16	862.11	2.49	0.16	0.94	-414.77
depth+Zone+Round	9	864.97	5.35	0.04	0.98	-423.39
depth+Zone*Round+vegetationType	22	869.02	9.41	0.01	0.98	-411.99
depth*Zone*Round	22	869.37	9.76	0	0.99	-412.16
depth*Zone+Round	12	870.92	11.3	0	0.99	-423.3
log(grainSize)+vegetationType+depth+Zone*Round	23	871.11	11.5	0	1	-411.99
depth+Zone	7	871.23	11.62	0	1	-428.56
vegetationType+Zone*Round	21	872.1	12.48	0	1	-414.59
vegetationType+log(grainSize)+Zone*Round	22	874.18	14.57	0	1	-414.58
vegetationType+depth+Zone*Round	19	876.39	16.78	0	1	-418.8
vegetationType+log(grainSize)+Round+depth+Zone	19	876.39	16.78	0	1	-418.8
depth*Zone	10	877.15	17.53	0	1	-428.46
vegetationType*depth+Zone*Round	29	879.53	19.91	0	1	-409.86
vegetationType*Round+depth+Zone*Round	38	880.03	20.41	0	1	-400.46
log(grainSize)+vegetationType*depth+Zone*Round	30	881.45	21.84	0	1	-409.76
log(grainSize)*vegetationType+depth+Zone*Round	30	882.8	23.18	0	1	-410.43
vegetationType*log(grainSize)+Round+depth+Zone+Round	26	887.85	28.24	0	1	-417.2
log(grainSize)*depth*Zone*Round+vegetationType	51	895.71	36.09	0	1	-394.02
log(grainSize)*vegetationType*depth+Zone*Round	40	895.75	36.14	0	1	-406.15
vegetationType*depth*Zone+Round	43	907.46	47.84	0	1	-408.73
vegetationType*Zone*log(grainSize)	35	912.19	52.58	0	1	-419.82
vegetationType+log(grainSize)+depth	14	915.54	55.92	0	1	-443.55
Depth	4	916.57	56.95	0	1	-454.26
CPUE.models4	3	926.73	67.11	0	1	-460.35
vegetationType*log(grainSize)*depth	31	941.06	81.44	0	1	-438.49

Appendix 2

Table 2. Overview of NiN code types of premapped during modeling and their explanation.

1	M1	Grunn marin fastbunn
2	M1-1	Grønnalgebunn
3	M1-2	Rødalgebunn
4	M1-4	Sagtangbunn
5	M1-5	Stortareskog
6	M14-2	Sterkt endret eller ny fast saltvannsbunn
7	M15-2	Sterkt endret eller ny marin sedimentbunn
8	M2	Afotisk fast saltvannsbunn
9	M3	Fast fjærebeltebunn
10	M3-(4-6)	Blæretang, spiraltang, sauetang- blåskjell- og rurbunn (litt beskyttet)
11	M3-10	Bunn dominert av filamentøse alger
12	M3-4	Blæretangbunn
13	M4	Eufotisk marin sedimentbunn
14	M4-1	Grunn sandbunn
15	M4-13	Løs mudderbunn i rødalgebeltet
16	M4-14	Grus og steinbunn i rødalgebeltet
17	M4-15	Finmaterialrik sedimentbunn i rødalgebeltet
18	M4-16	Finsedimentbunn i rødalgebeltet
19	M4-18	Algegytjebunn i rødalgebeltet
20	M4-3	Grunn fin til middels grusbunn
21	M4-4	Grunn grovere blandet sandbunn

22	M4-5	Grunn finsedimentbunn
23	M4-7	Grunn grus- og steinbunn med finmateriale
24	M5	Afotisk marin sedimentbunn
25	M5-1	Sandbunn i øvre sublittoral
26	M5-2	Løs mudderbunn i øvre sublittoral
27	M5-4	Finmaterialrik sedimentbunn i øvre sublittoral
28	M7	Marin undervannseng
29	M7-4	Salt undervannseng i sublittoral