UNIVERSITY OF OSLO

Department of Biology

The Faculty of Mathematics and Natural Sciences

Demography, habitat suitability modelling and local ecological knowledge of European lobster (*Homarus gammarus* (L.)) in coastal Skagerrak: Valuable tools in identifying potential marine reserves?

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Master thesis

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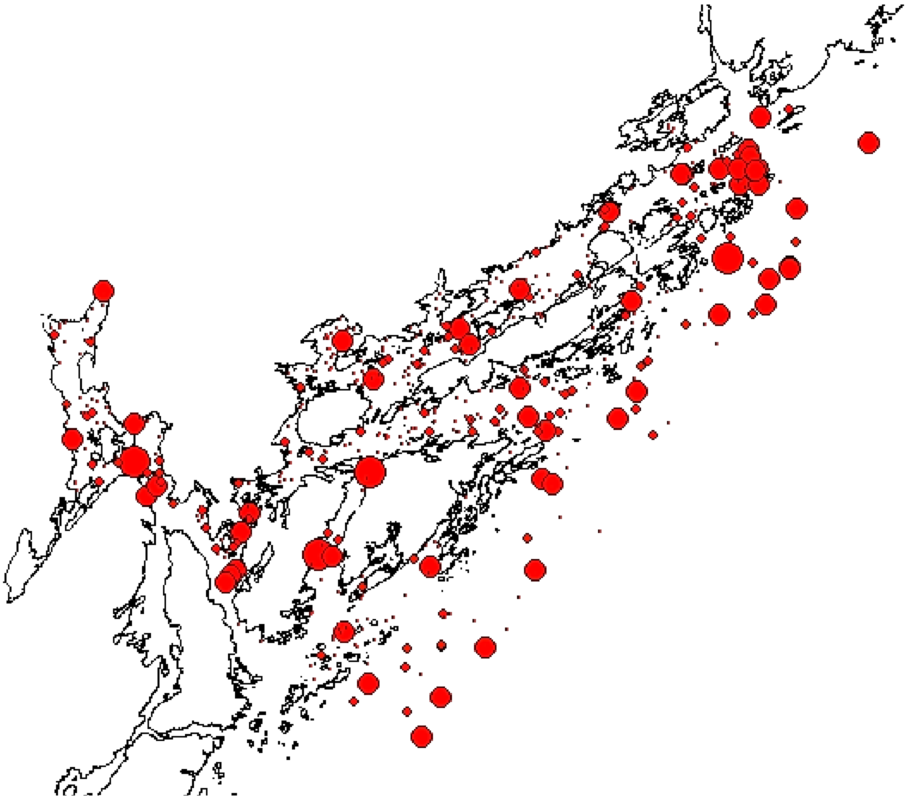

Preface

I grew up in a small village next to the sea in the municipality of Tvedestrand, and the ocean has always fascinated me. This fascination became greater when discovering life aquatic through diving, and it was after a day of snorkelling with whale sharks in the Philippines I realised that marine biology was my path. When I started my biology studies I was determined to go back to the Philippines and study these stunning creatures during my master thesis, but in my studies I learned that marine biology is more than natures extremes presented by Sir David Attenborough. The state of the ocean and marine management caught my interest, and I saw an opportunity of doing something exiting and meaningful during my master thesis when I read about the experimental lobster reserves in coastal Skagerrak by the Institute of Marine Research (IMR). After contacting the research group at IMR, Flødevigen, and discussing a potential master thesis related to their studies, I realised that my exotic plan of studying whale sharks in the Philippines had to be discarded for the benefit of lobster studies in Tvedestrand, where I grew up. I certainly do not regret this, and the whale sharks will always be there, hopefully.

I would like to thank Jan Atle Knutsen for letting me do my master thesis at Flødevigen, introducing me for the research group and being my head supervisor until he stepped into a leave for being chief of environmental protection department in the County of Aust-Agder in 2010. I was privileged to have a group of excellent scientists supervising me at Flødevigen. Esben Moland Olsen (head supervisor since January 2010), Alf Ring Kleiven, Even Moland and Sigurd Heiberg Espeland guided me through all phases of my master thesis; aiming the research questions, planning and conducting mapping surveys and experimental fishing, analysing the results and writing my thesis. I would also thank Torstein Olsen, at Flødevigen, for helping me in all GIS related challenges. Thank you all for supporting me and believing in me.

This study could not be implemented without funding from the project “Active management of marine resources in the coastal zone” and the municipality of Tvedestrand. The municipality of Tvedestrand also provided a boat with a crew (captain Johan Colbjørnsen and Asbjørn Aanonsen).

I thank my friends Terje Marcussen and Morten Feltstykke and my dear Nina Follo for assisting me in the experimental fishing in the weekends. Nina also encouraged me, and shared good times with me, in my writing phase in Copenhagen.

I owe my parents great thanks for making my life easy when I was home doing field studies or working at Flødevigen.

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Jon Kristian Haugland
Copenhagen, March 30, 2011

Contents

Abstract

The use of species habitat suitability (HS) modelling is increasing as an approach in detecting important areas in integrated coastal zone management. European lobster (*Homarus gammarus*) is currently listed as near threatened in the Norwegian red list, according to IUCN (International Union for Conservation of Nature) criteria. Past management regimes were insufficient to rebuild the lobster population after a considerable decline that mainly occurred in the 1960s and -70s. Catch per unit effort (CPUE) has indicated rapid population increase in experimental lobster reserves in Skagerrak, suggesting that marine reserves can be an effective management tool in successful rebuilding efforts. In the process towards establishing full-scale marine reserves, new methods are addressed to supplement experimental fishing surveys. This study reveals important topographical factors for lobster habitats through modelling of randomly designed experimental fishing. Bathymetric lope, depth and exposure were good environmental predictors for habitat suitability (HS). A HS map was generated to predict lobster habitats, hence possible areas for placing reserves. The data obtained were compared with local lobster fishers' placement of traps to assess local ecological knowledge and the possibility of using mapping of trap distribution as a tool to verify good lobster habitats. Based on the individuals sampled in the experimental fishing surveys a description of the lobster population demography in the municipality of Tvedestrand is given. Using lobster as a model, this contribution uncovers the potential of habitat suitability and LEK as a tool in the process of implementing marine reserves in coastal Skagerrak.

1 Introduction

Predictive habitat distribution modelling is becoming a common tool in management of natural resources. It relates the distribution of the target species with different environmental conditions; hence the species niche (Guisan and Zimmermann, 2000; Hirzel and Guisan, 2002). In the marine environment, the seafloor condition can be obtained, in high resolution, through mapping by multibeam echosounder (Wilson et al., 2007). A study by Galparsoro et al. (2009) on European lobster in the Bay of Biscay used the ENFA (Ecological-Niche Factor Analyses) approach, which compares the presence data (not the absence) of a species with environmental conditions (Guisan and Zimmermann, 2000). A conclusion was made towards a requirement for randomized sampling (Galparsoro et al., 2009). Habitat suitability (HS) modelling has also been used on spiny lobster (*Panulirus argus*) (Bello et al., 2005) and squat lobster (*Munida* sp.) (Wilson et al., 2007).

The use of marine reserves as a management tool has increased considerably the last decades. The popularity is partially resulting from a global problem of overfished marine resources, and the perceived failing of traditional fisheries management to prevent overexploitation (Pauly et al., 2002). General effects inside protected areas are expected to be lower fishing mortality and higher density, -biomass and -mean size of target species, which again may lead to a spillover effect of juvenile and adult individuals out of the area, and increased recruitment as a result of higher production of propagules (eggs/larvae) (e.g., Russ, 2002; Lubchenco et al. 2003). Lubchenco et al. (2003) emphasize the value of large spanning reserve *networks*, as they provide greater protection for marine communities than a single reserve.

In 2006, four experimental European lobster (*Homarus gammarus* (L.)) reserves were implemented along the Norwegian Skagerrak coastline. The intention for the reserves was to assess the effects of small-scale protection on local lobster populations and to test whether marine reserves are appropriate tools for lobster management (Pettersen et al., 2009). The Institute of Marine Research (IMR) monitors three of these reserves, the fourth being left out since it did not meet the predetermined biological criteria (see Pettersen et al., 2009). After four years of protection the reserves showed more than two-fold average increase (245 %) in catch per unit effort (CPUE, lobster per trap day^{-1}), while average change in CPUE in the control areas was modest (87 % increase) (Moland et al., in prep). The study suggests that marine reserves can be a helpful management- and conservation tool in rebuilding portions of the depleted European lobster population in Norwegian waters. The rapid response to conservation is supported by former studies of lobsters in marine reserves; e.g., American lobster (*Homarus americanus*) (Rowe, 2002), spiny lobster (*Jasus edwardsii*) (Kelly et al., 2000), Caribbean spiny lobster (*Panulirus argus*) (Acosta, 2002), spotted lobster (*P. guttatus*) (Acosta and Robertson, 2003) and European lobster (*H. gammarus)* (Hoskin et al., 2011).

In Norway, the European lobster is a common pool resource and lobster fishing has been intensive. In the period from 1960 to 1980 the lobster population had a major setback. The official landings declined to a level of <10 % of the pre-1960 landings, and have remained low (Agnalt et al., 2007). However, official landing statistics have to be treated with caution. A study from Southern Norway revealed that only 7 % of the total landings were included in the official landings statistics, due to recreational fisheries and underreporting from commercial fishers (Kleiven, 2010). Furthermore, the reduced lobster population in Norway is described for CPUE, estimated from standardised logbook reports in Skagerrak and the North Sea west coast of Norway. CPUE decreased from 0.15 - 0.2 before the 1950s to 0.05 - 0.07 the last decade (in 2007) (Pettersen et al., 2009). The European lobster entered the Norwegian red list in 2006 and is currently categorized as near threatened by the IUCN (International Union for Conservation of Nature) criteria (Oug et al., 2010).

Ecological knowledge is essential in the interpretation and hence in management of ecosystems. Good knowledge of ecosystems may be obtained from local people that utilise the ecosystems for different purposes and therefore have a substantial knowledge about it. Olsson and Folke (2001) argue that “Local ecological knowledge (LEK) is knowledge held by a group of people about their local ecosystems”. LEK has proven to be an important resource in the understanding of ecosystems at different levels (Olsson and Folke, 2001). A successful example of lobster conservation through LEK is found on the Newfoundland Eastport Peninsula, where local lobster fishers have cooperated with scientists and the government to prevent overfishing of lobster stocks (*H. americanus*) (Rowe and Feltham, 2000). Another study in the Bay of Biscay showed that local fishermen demonstrated good knowledge of preferred lobster habitat (*H. gammarus*) (Galparsoro et al. 2009).

Involving local stakeholders in the implementation process is considered important factor for the success of a marine reserve (Houde et al 2001; Sweeting and Polunin, 2005; Pettersen et al., 2009).

In Norway, several municipalities along the Skagerrak coastline have taken initiatives to implement local marine reserves, with lobster as one of the target species. A considerable amount of work is required to verify an area as suitable lobster / marine reserve, and new methods may be useful in this process. HS modelling and considering LEK may be two approaches to verifying lobster habitats, hence potential reserves, and may also give valuable information about lobster ecology and the utilisation of the lobster population.

The aim of this study was to (1) give a characteristic of the lobster population in the study area, (2) reveal important topographical factors for lobster presence through randomly designed experimental fishing, (3) predict lobster habitats based on modelling of the experimental fishing and linked environmental predictors, and (4) test if LEK could be used as a reliable tool to verify good lobster habitats.

2 Materials and method

2.1 Study area

The study area was the municipality of Tvedestrand (N 58° 60´, E 9° 05´) (Fig. 1), located in southeast Norway on the Skagerrak coast. Glacial scouring has shaped the topography, resulting in a small fjord system (approximately 8 km in length) with several sills and basins. The fjord stretches perpendicularly towards the outer coastline. An outer, submerged, glacial moraine runs parallel to the coastline. Several large (> 3 km long) islands and smaller skerries stretches parallel along the mainland and form more or less sheltered areas with a few deeper basins. Tvedestrand has been, and still is, used in several projects related to marine biological diversity, habitat mapping and marine reserves. “Active management of marine resources in the coastal zone” is a collaboration project, led by IMR, implemented to develop methods to map marine habitats, fish resources and its exploitation. One of the project aims is to implement a zoning plan in the municipality of Tvedestrand.

A relatively small marine area within the municipality was excluded from the study area because of its low salinity and its inaccessibility (area inside red line in Fig. 1). The outer boundary of the study area was vague, but the field studies were mostly conducted inside the municipality jurisdiction line, which cover approximately 65 km^2.

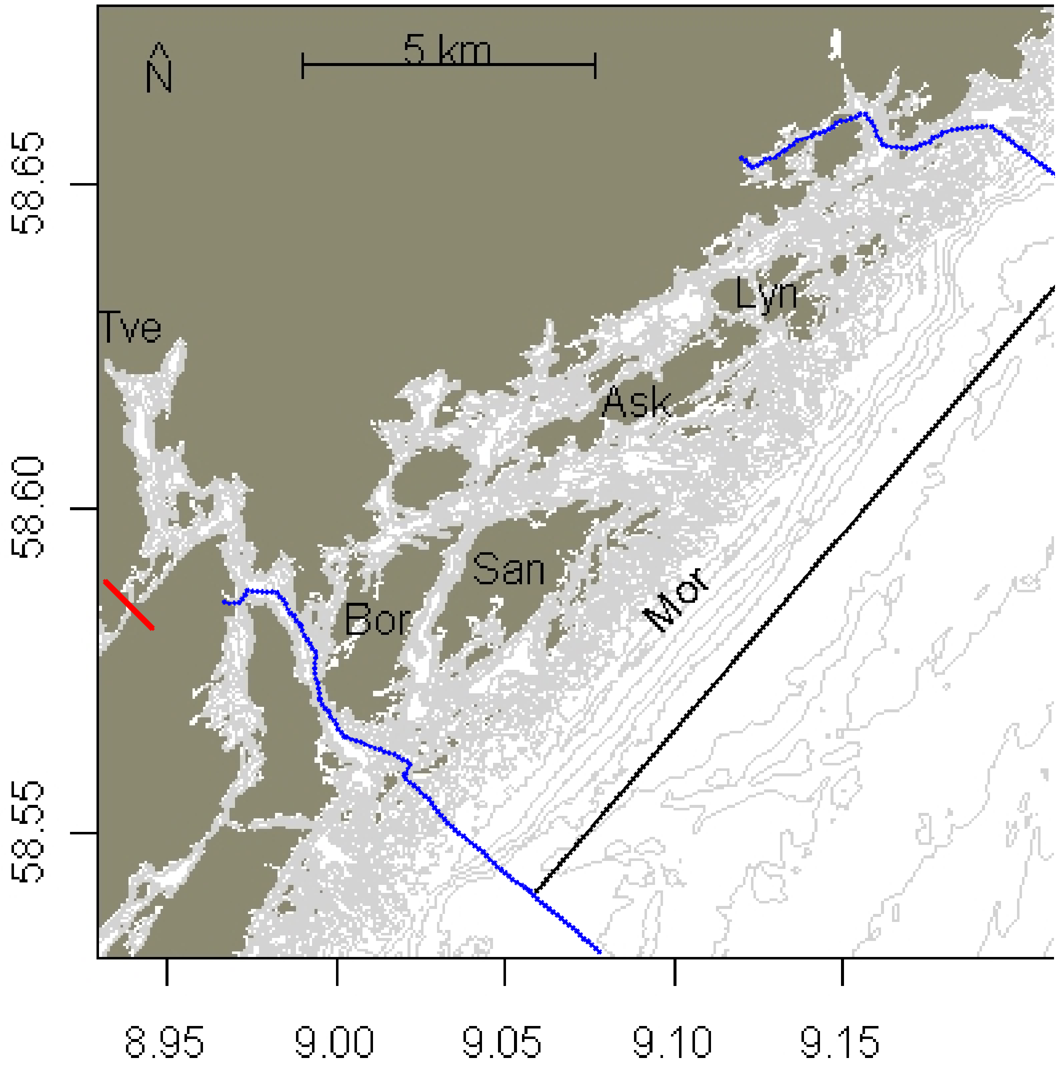

Fig. 1. Study area. The marine area in the municipality of Tvedestrand (within dotted blue lines), estimated to cover 65 km^2 inside the jurisdiction line (black, dotted line). The area southwest of red line was not included in the study area. Longitude and latitude along the axis are given in WGS84 decimal degrees. Grey lines are depth contours, and names of essential places are shortened: Tve = Tvedestrand, Bor = Borøya Island, San = Sandøya Island, Ask = Askerøya Island, Lyn = Lyngør archipelago, and Mor = moraine ridge (follows depth contours).

2.2 Study species

The European lobster is known to prefer habitats of bedrock, rocks and boulders (Dybern, 1973; Howard, 1980; Smith et al., 2001), within a depth range of 10 – 40 meters (Dybern, 1973; Moland, 2010). A study of European lobster in the Bay of Biscay found an inverse relationship between lobster presence and distance to rock, and that mean bathymetric slope value for lobster presence was 6° (Galparsoro et al., 2009). The European lobster is also a species with high site-fidelity. Smith et al. (2001) found that 95 % of the European lobsters moved less than 3.8 km from the release sites in a mark-recapture study on the south coast of England. Similar results were found by Agnalt et al. (2007), where 84 % of released European lobsters off the southwestern coast of Norway were recaptured within 500 meters from the release site. Results from Moland et al. (in press) suggest an even stronger site-fidelity, in their study of home ranges of European lobster in a marine reserve in Norwegian Skagerrak. They found that the lobsters had a mean home range of 19 879 m^2 (± SE = 2 152 m^2).

The feeding ecology of European lobster in Skagerrak was described by Hallbäck and Warén (1972). They described the adult European lobster as an omnivore with a diet mainly consisting of crustaceans (e.g., *Pagurus* sp.), gastropods (e.g., *Gibbula* sp., *Buccinum* sp.) and polychaets (e.g., *Nereis* sp.), but also of fish, bivalves, echinoderm, algae and eggs. The wide range of prey animals implicates the potential impact and importance of adult lobster presence as a predator in an ecosystem (Moland, 2010).

The lobster has historically been of commercial significance in coastal communities in Norway (Agnalt et al., 2007), and is consequently also an important component of the culture along the Norwegian coast (Knutsen et al., 2009). The most recent modification of the lobster fishing legislation in Norway was made in 2008. Lobster fishing in Skagerrak is now restricted to a two months season (1 October - 30 November), fishing for lobster is legally conducted with baited traps with escape vents of 60 mm, the minimum legal size is set to a carapace length (CL) of 90 mm, capture of ovigerous females is banned and the maximum number of traps is 10 for recreational fishers and 100 for commercial fishers (Directorate of fisheries, 2011).

2.3 *Experimental fishing*

Experimental fishing was conducted from 18 – 31 August 2010 by J. K. Haugland and researchers from IMR. On weekdays a vessel with crew from the municipality of Tvedestrand was used. The vessel (ProCat 1000) is 11 meters long and equipped with a power block and an echo sounder (Raymarine DSM 300). In weekends a smaller boat (Buster L) from IMR with a pot hauler and an echo sounder (Hummingbird) was used.

The lobster traps were standard ‘parlour’ traps used for standardized experimental fishing by IMR (900 × 450 × 400 mm with 120 mm openings), and the escape vents were closed. Minimum 35 meters of non-buoyant ropes were attached to the traps, with surface buoys in the opposite ends. The surface buoys were numbered, and marked with “Experimental fishing” and contact information. Frozen Atlantic mackerel (*Scomber scombrus*) used for bait was bought from a local fish delivery.

Lobster fishing in the given area is restricted to a two-month season from 1 October – 30 November (Directorate of Fisheries, 2011), hence a permission was required to conduct the experimental fishing in the given period. An application for experimental fishing in the given area and period was sent to the Norwegian Directorate of Fisheries, and the permission was given before the experimental fishing started.

All areas within 10 – 30 m depth in the study area, a reasonable depth to catch European lobster (Dybern 1973; Moland, 2010), were isolated with a geographical information system (ArcGIS, version 9.3.1). The areas within this depth interval were used in the further modelling of the experimental fishing design. In order to make the experimental fishing personal-independent, coordinates were picked randomly from the GIS software within the defined study area. The exposed outer areas covered a substantial part of the study area and after some test modelling the fishing effort was deliberately skewed towards the inner area to ensure sufficient data from both areas. A borderline between the inner and the outer areas was drawn along the outermost islands, and the effort was set to 80 % in inner areas and 20 % in outer. Fifty plotted coordinates were given for each day, including back-ups, which were used if a plotted position was unsuitable (due to heavy boat traffic, under piers, etc.) or if the weather stopped us from deploying traps in the specific area. The nearest back-up plot was used when an original plot was omitted.

Coordinates for all traps for each particular day, and the previous, were uploaded to a hand-held GPS (Garmin 78s) to get exact positions for deploying and locating traps. Every trap was baited with approximately one half mackerel, and deployed with high precision according to the given coordinates. The traps were soaked for one day, approximately 24 hours, although some traps were soaked for two days due to bad weather. When traps were hauled, a waypoint was made and depth was recorded when the rope tightened vertically. This was done to get an exact position of where each trap was hauled, in case of drifting or other reasons for traps being moved. Plastic cable ties sealed the traps to control for the possibility that traps were hauled and emptied by unauthorised persons. This precautionary measure was dropped after five days, as ‘looting’ did not seem to be a problem.

For every trap haul the following information was recorded: date of deployment; date of haul; depth; position and number of edible crabs (*Cancer pagurus*) (males and females). For every lobster caught the following information was recorded in addition to trap number: sex; total length (TL); carapace length (CL); tag number; genetic sample number and egg sample number. Sex was determined by examination of the first pair of pleopods. TL was measured from the rostrum to the posterior end of the telson, while CL was measured from the rear of the eye-socket to the posterior margin of the carapace. Each lobster was tagged with a T-bar anchor tag, coded with individual numbers, contact information and reward (50 or 500 NOK), inserted with a tag applicator through the thoracoabnominal membrane between the cephalothorax and the first abdominal segment. This was done to record fishing intensity and estimate population size at time of recovery. This tagging procedure prevents tag loss during moulting (Agnalt et al., 2007). Genetic samples were collected from the first 99 individuals, from the fifth pair of pleopods, for future genetic analysis. Egg samples were taken from ovigerous females. The lobsters were released at the same position they were captured. Neither the tagging data nor the genetic data was used in this thesis.

After six days of experimental fishing (phase one), with many traps deployed on mud bottom with low catch rates, the design was modified in the inner area towards a higher fishing effort in areas with bottom topography steeper than, or equal to, 8 degrees (≥ 8°). This modification was made in order to get sufficient data from these particular areas, covering a smaller area compared to muddy and sandy planes in the inner basins. Approximately 80 % (27 of 32 traps per day) were placed in areas ≥ 8° slope for the remaining experimental fishing. The experimental fishing design was not modified in the outer area.

Experimental fishing lasted for 14 consecutive days, with 13 trap hauls. Fishing effort (E) was measured in trap days (traps soaked for 24 h, hence a trap soaked for two days counted as two trap days). The total fishing effort was 486 trap days, distributed on 477 hauled traps (Table I). In all, 204 lobsters were caught, resulting in a CPUE of 0.42. Proportions of males, females, indeterminate sex and ovigerous females were 0.60, 0.39, 0.01 and 0.23, respectively. Total mean CL (mm) was 93.6.

Table I. Summary of the experimental fishing for European lobster (*H. gammarus*) conducted 18 – 31 August 2010. Number of traps are independent replicates (n); trap days are the fishing effort (E); CPUE (catch per unit effort, lobster per trap day^{-1}) is calculated with trap days; proportion of ovigerous females (Ovig.) is calculated from the total number of females in the given area; and mean CL is referring to carapace length.

Area	**# of traps**	**Trap days**	**# of lobsters**	**CPUE**	**Proportion of**				**Mean CL (mm)**
					Males	**Females**	**Indet.**	**Ovig.**	
Inner (ph. 1)	164	164	42	0.26	0.60	0.40	0	0.08	93.5
Inner <8°	55	56	10	0.18	0.70	0.30	0	0.00	95.6
Inner ≥8°	201	201	95	0.47	0.59	0.40	0.01	0.32	92.0
Inner tot.	420	421	147	0.35	0.60	0.39	0.01	0.22	92.7
Outer	57	65	57	0.87	0.60	0.37	0.03	0.24	96.1
Total	477	486	204	0.42	0.60	0.39	0.01	0.23	93.6

2.5 Local ecological knowledge

In 2009, a public questionnaire inquiring about how people use the ocean and its resources was carried out by IMR in the municipality of Tvedestrand. Among other relevant issues local and cabin (summer house) residents replied where they optimally fish for lobster. 47 % reported that they fished lobster, and 52 persons filled in their favourite lobster fishing grounds (Torstein Olsen, unpublished data). They did this by marking their favourite lobster fishing grounds in a map. Replies were loaded into

GIS software, and a map (Fig. 2) was generated in order to describe the most popular lobster fishing grounds. This can be considered as the LEK about high-quality lobster habitats.

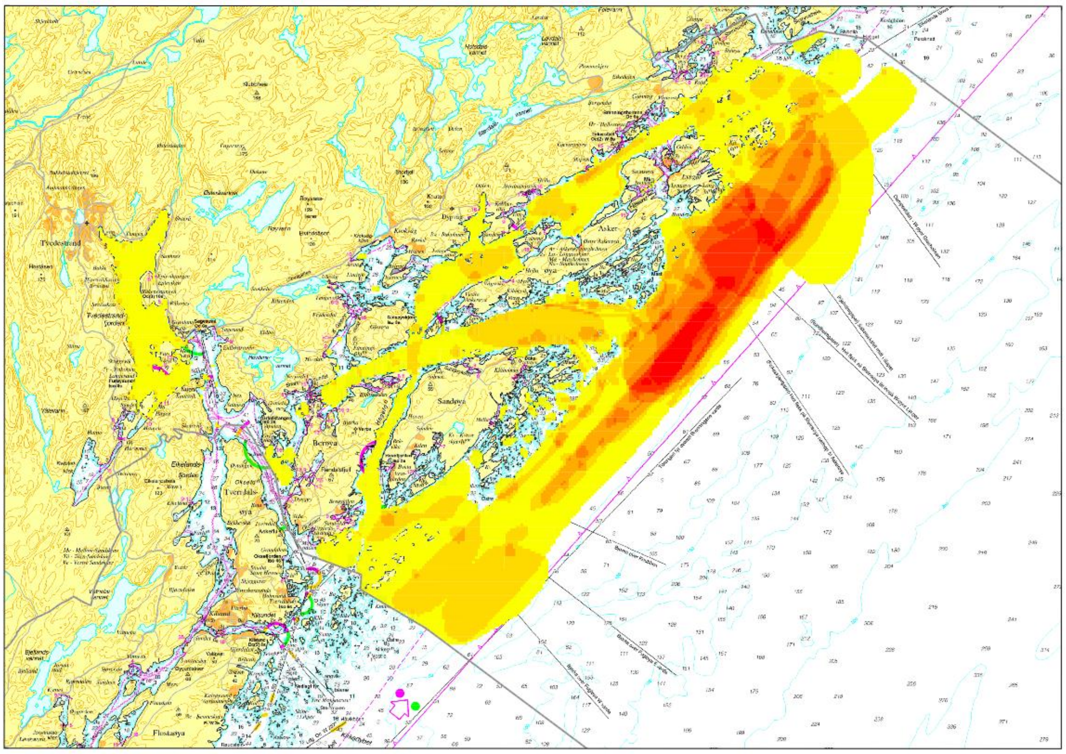

Fig. 2. A map of favourable fishing grounds for lobster (*H. gammarus*) in the municipality of Tvedestrand, based on 52 respondents in a questionnaire inquiry. A colour scale, ranging from yellow to red, indicates increasing popularity. Map is made by-, and used with authorization from Torstein Olsen, IMR.

Another approach in assessing the LEK was to examine fishing pressure in the study area. An assumption was made that lobster fishers do not place their traps randomly; hence their placement reflects their LEK about lobster habitats. In total, three field surveys were conducted. The first survey was conducted from 5 to 9 October 2009, while survey number two and three were conducted in 2010, from 2 to 7 October 2010, and 9 to 12 October 2010, respectively (Table II). The surveys were done by plotting the positions of lobster traps, by entering waypoints on a hand-held GPS (Garmin 78s) while positioned next to the surface buoys. Two GPSs were used to distinguish between recreational and commercial fishers. The commercial fishers were recognised by the specific licence code painted on their trap buoys (registration number of fishing vessel).

The study area was relatively large (~ 65 km^2), thus several days (4 – 6, depending on weather conditions) were needed to cover it all. Surveying was done systematically and the tracking function on the GPS aided in navigating through areas of high trap density, or in the outer area with few reference points, without missing or plotting traps twice.

Table II. Summary of mapping of fishing pressure in the municipality of Tvedestrand.

Survey	Date	# of commercial traps	# of recreational traps	Total # of traps
One	5 – 9 Oct. 2009	1024	320	1344
Two	2 – 7 Oct. 2010	1428	379	1807
Three	9 – 12 Oct. 2010	1459	335	1794
Total	-	3911	1034	4945

2.6 Data analysis

In order to test for significant differences in CPUE between different areas in the experimental fishing Tukey’s post hoc test (TukeyHSD in the software R, version 2.12.1) was used. The test incorporates an adjustment for sample size that produces sensible confidence intervals for slightly unbalanced designs (Crawley, 2007), like the ones in this study. Tukey’s post hoc test compares means with every other means and identifies where differences are significant. The test assumes independent observations with equal variance (homoscedasticity). Homoscedasticity was tested for with the Cochran test (cochran.test in R).

To test for sex-specific differences in mean CL, Welch’s Two Sample (two-tailed) *t*-test, was used. The test defines the statistics *t* by the following formula:

$$t = \frac{\overline{X}_1 - \overline{X}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

where $\overline{X}_1$, s_1^2, and n_1 are the mean CL, CL variance and sample size for males, respectively, and $\overline{X}_2$, s_2^2, and n_2 are the corresponding values for females. A two-tailed Welch's Two Sample *t*-test tests the null hypothesis that two population means are equal. The null hypothesis is rejected if the given p-value is lower than the significance level. Welch's Two Sample *t*-test assumes normal distribution, but the two samples may have unequal variance. A quantile-quantile plot was used to confirm normal distribution.

The Tukey's post hoc test was applied to the variables bathymetric slope, depth and exposure in the predicting model in order to examine potential isolated effects on CPUE. Exposure was incorporated as a factor variable, but slope and depth had to be converted to factor variables in order to conduct this significant test. Both slope and depth were then grouped in intervals of five (degrees and meters, respectively). If presence or absence of edible crabs (*Cancer pagurus*) and number of edible crabs affected CPUE was also tested with Tukey's post hoc test.

Catch result (CPUE), and variables depth, days since the experimental fishing started, bathymetric slope, and exposure value (Table III) was specified at each coordinate for the experimental fishing. Slope was found with the slope-function in ArcGIS, which identifies rate of maximum change (in degrees) within cells in a 10 × 10 meter grid. Exposure values, ranging from 1 to 7 within cells within a 100 × 100 grid, were obtained from a model made by-, and used with authorization from NIVA (Norwegian Institute for Water Research), based on fetch (distance to nearest shore, island or coast), wind strength and -direction. The input dataset was the basis for a logistic regression model predicting the catch of lobster in the study area, with lobster presence or absence as binary response variable. Presence and absence were selected, rather than CPUE, because the data were zero inflated and non-normal distributed. Prior to the modelling a correlation matrix was made to reveal potential correlating variables. The predictor variables *depth*, *slope and exposure* were allowed to interact, while *day* was modelled as an additive effect, hence the initial model was:

$$LP = slope \times depth \times \exp osure + day$$

where LP is lobster presence, × indicates interaction between variables, and + indicates additive variable.

Table III. Summary of variables in input data for the logistic regression model, obtained by 477 independent traps, during experimental fishing for lobster (*H. gammarus*), conducted 18 – 31 August 2010.

Variable	**Min.**	**First Qu.**	**Median**	**Mean**	**Third Qu.**	**Max.**
Slope	0.24	5.90	10.93	11.97	16.69	35.19
Depth	6.00	14.00	18.00	18.91	24.00	38.00
Exposure	3.00	3.00	5.00	4.549	6.00	7.00
Day	1.00	4.00	7.00	7.145	10.00	13.00

Akaike's Information Criterion (AIC) was used in model selection. AIC is a penalized log-likelihood, which considers the trade-off between goodness of fit and number of parameters in the model, and hence finds the most parsimonious model. The AIC is described:

$$AIC = -2\log - likelihood + 2(p+1)$$

where *p* is 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 most parsimonious model with the lowest AIC, was found through the step-function in R.

The model generated from the experimental fishing was used to predict catch, hence the HS in the study area, based on a 100 × 100 meter grid with average bathymetric slope and –depth, and exposure. The predicting variable *day* was excluded in the HS model, as the period the experimental fishing lasted (14 days) probably was to short to explain seasonal changes in CPUE. Prior to the HS modelling, all areas with predicting variable values outside the intervals obtained by the experimental fishing were left out. A habitat suitability (HS) map was generated from the prediction model.

3 Results

3.1 Description of the lobster population demography

Size distribution, given in CL from all 204 individuals caught in the experimental fishing, was normally distributed, and ranged from 57 to 128 mm (Fig. 3). The total mean CL was 93.6 mm (SE = 0.9 mm). Sex-specific mean CL was 94.3 mm (SE = 1.2 mm) for males and 92.7 mm (SE = 1.4 mm) for females. The sex specific difference in size was not significant (p = 0.39) following Welch's Two Sample (two-tailed) *t*-test.

In total, 69 % (141 individuals) were over the minimum legal size (MLS). Fortynine % (100 individuals), 74 % (151 individuals) and 88 % (180 individuals) were within one, two and three mean moult increments from MLS (larger or smaller), respectively, according to a mean moult increment of 7 mm (estimated for females) (Agnalt et al., 2007). By using this mean moult increment 34 % (69 individuals) was recruited to the fishery after their last moult according to the MLS. Of the total catch, 33 % was one-, 18 % was two-, 9% was three-, and 3 % was four moult increments larger than MLS. Based on this declining proportions of catches greater than zero-, one-, two-, three and four moult increments greater than MLS (69 %, 33 %, 18 %, 9 % and 3 %, respectively), an approximate estimate of mortality (M) from one moult to the next, after reaching MLS, is M = 0.5. Following this mortality, the probability of surviving through four moults, to a size of 111 mm CL, after reaching MLS is 0.125.

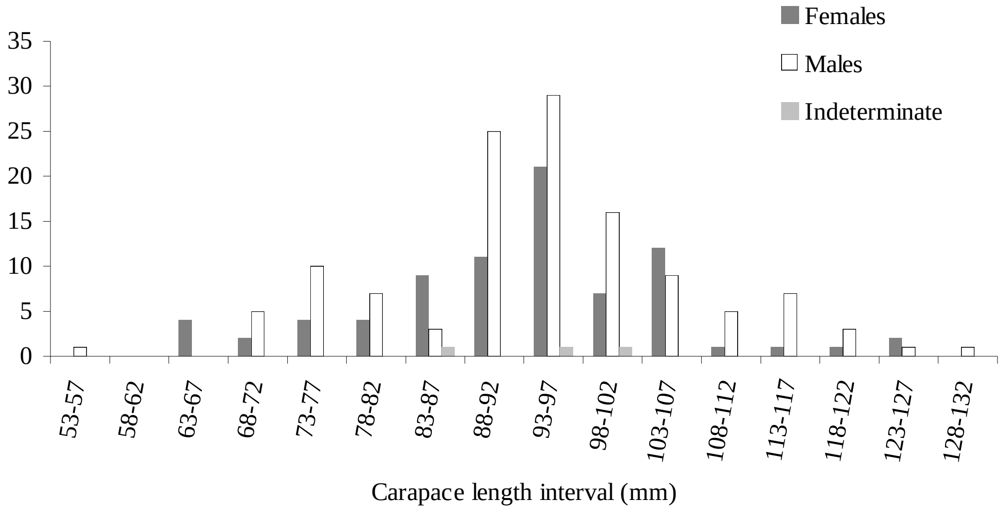

Fig. 3. Sex-specific size distribution given in carapace length (CL) intervals of 4 mm, obtained from 204 individuals during experimental fishing for lobster (*H. gammarus*) in the municipality of Tvedestrand conducted 18 – 31 August 2010.

There were a higher proportion of males in the catches. However, there were no difference in sex distribution between the inner and the outer areas (Table I). In the inner area the distribution of sex was proportioned (females / males / indeterminate) 0.40 / 0.59 / 0.01. In the outer area the distribution was 0.37 / 0.60 / 0.03. The total distribution of sex in the experimental fishing was proportioned 0.39 / 0.60 / 0.01.

No difference in proportion of ovigerous females, out of the total sample size of females (n = 79), was found between the inner and the outer areas (Table 1). The proportions were found to be 0.224 (13/58) in the inner area, 0.238 (5/21) in the outer area, and 0.227 (18/79) for the entire fishing experiment.

CPUE in different areas during the experimental fishing revealed significant variation (Table IV, Fig. 4 and 5). In fact, all areas except the inner area in phase one and the inner area < 8° slope (adj. p = 0.89) were significantly different from each other. The most obvious, and essential, difference was the difference between the total inner- (CPUE = 0.35) and the outer area (CPUE = 0.87). Lowest CPUE was found in the inner area with a flattened slope (< 8°, CPUE = 0.18), followed by the inner area in phase one before the subdivision of the slope categories (CPUE = 0.26), and then the inner area with a steeper slope (≥ 8°, CPUE = 0.47). Total CPUE throughout the experimental fishing was 0.42. Geographical distribution of catch is given in Fig. 6.

Table IV. Differences in CPUE for different areas during the experimental fishing (18 – 31 August 2010), given in adjusted p-values.

Area	**Inner ph. one**	**Inner < 8°**	**Inner ≥ 8°**	**Outer**
Inner ph. one	-	-	-	-
Inner < 8°	0.8901	-	-	-
Inner ≥ 8°	<0.05	<0.05	-	-
Outer	<0.0001	<0.0001	<0.0001	-
Inner total	-	-	-	<0.0001

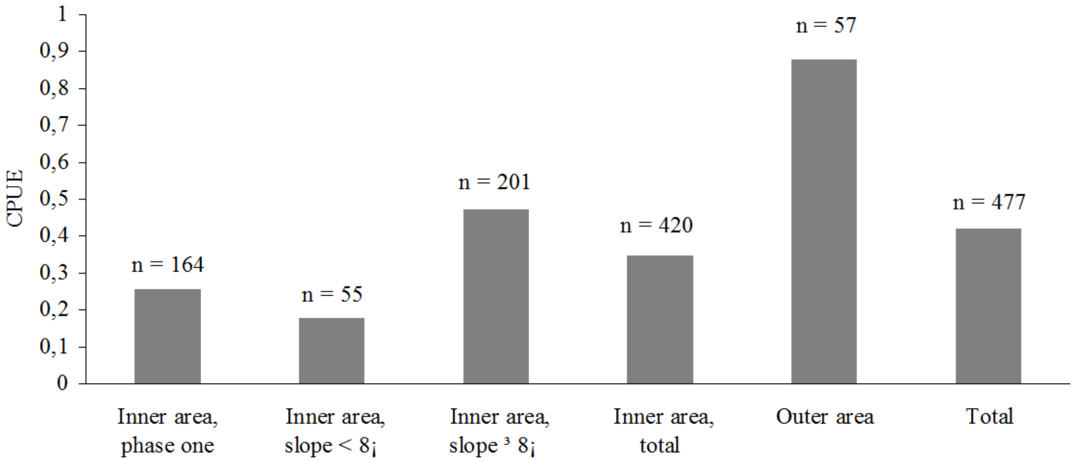

Fig. 4. CPUE (catch per unit effort, lobster per trap day^{-1}) in different areas during the experimental fishing for lobster (*H. gammarrus*), conducted 18 – 31 August. Number above bars: sample size (n, number of traps)

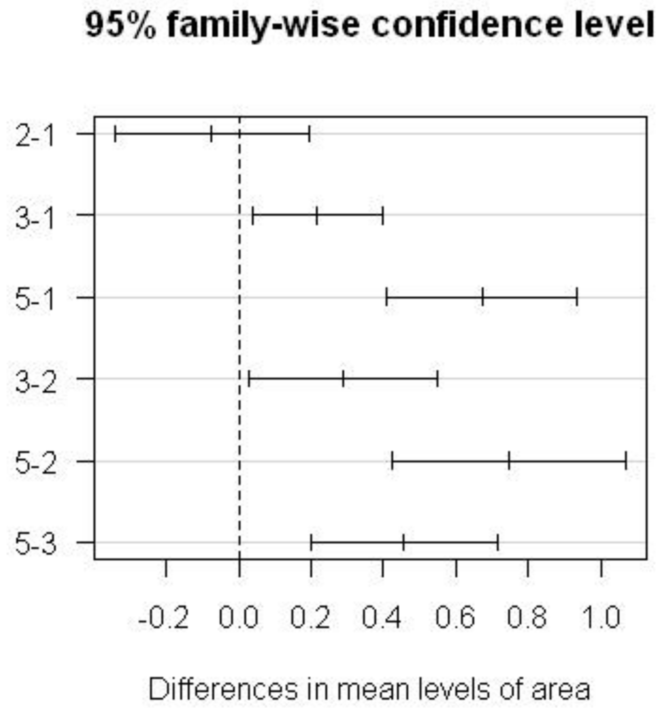

Fig. 5. Pairwise differences in CPUE between areas (1 = Inner ph. one, 2 = Inner area, slope < 8°, 3 = Inner area, slope ≥ 8°, 5 = Outer area) in experimental fishing for lobster (*H. gammarus*), based on Tukey's post hoc test. The differences are significant (at a 5 % level) if the confidence interval (bracket lines) does not overlap zero (dotted vertical line).

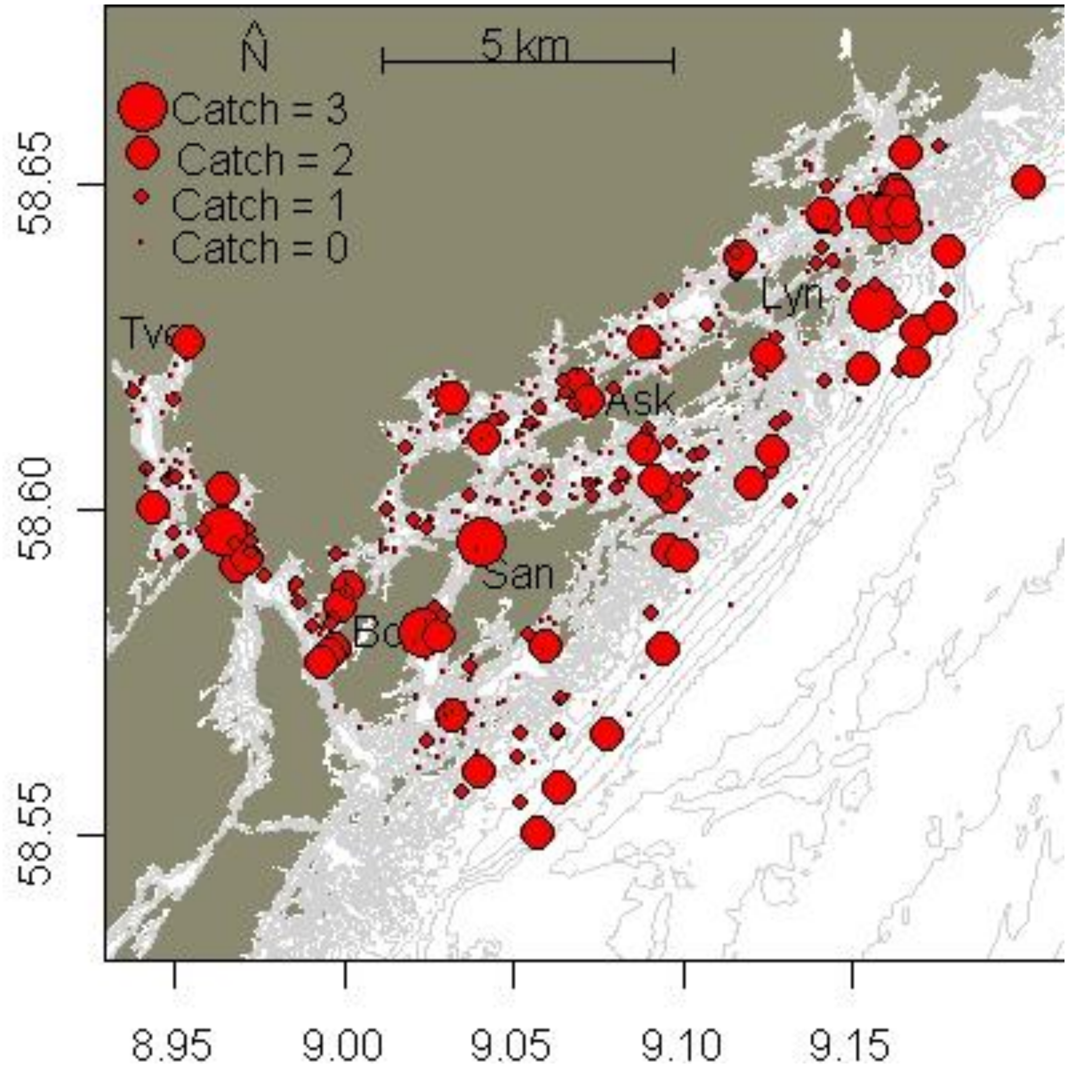

Fig. 6. Geographical catch results from the experimental fishing for lobster (*H. gammarus*) in the municipality of Tvedestrand conducted 18 – 31 August. Catch is given in number of lobsters in each trap (not CPUE) with circles of increasing size indicating 0, 1, 2 and 3 lobsters (see scale in upper right corner).

Even though CPUE in inner areas ≥ 8° were significant higher than inner areas < 8° (adj. $p < 0.05$), mean slope within cells in 10 × 10 meter grid did not show significant influence on CPUE when compared in intervals of five degrees (Fig. 7 A), but a slight tendency of higher CPUE within cells with mean slope greater than 10 degrees was observed (Fig. 8).

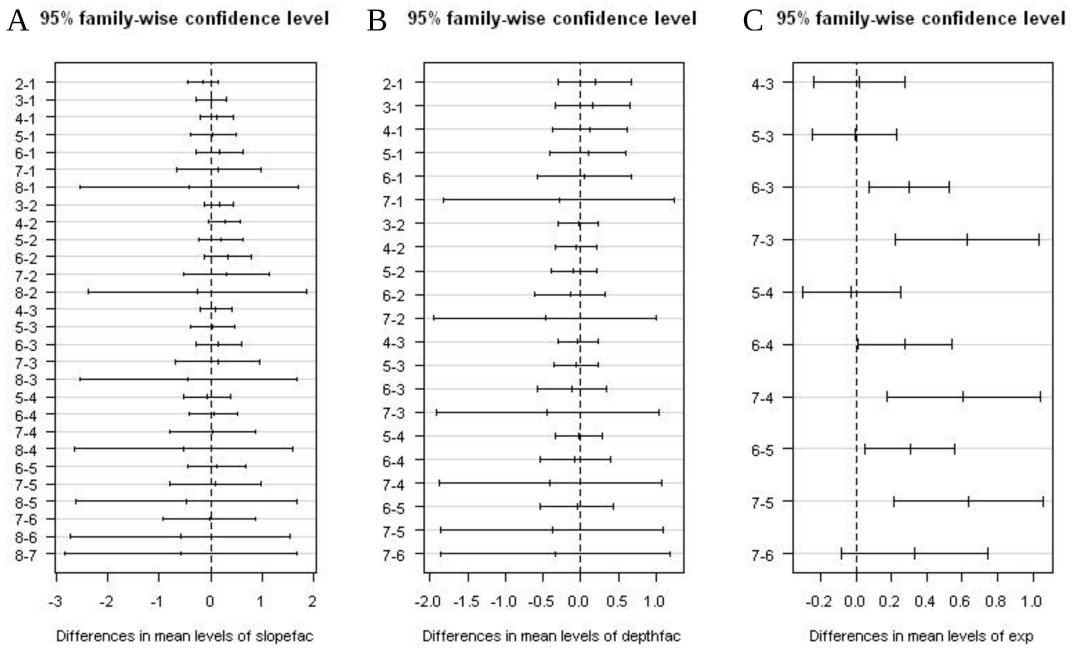

Fig. 7. Pairwise differences in CPUE based on Tukey's post hoc test between variables. The differences are significant (at the 5 % level) if the confidence interval (bracket lines) does not overlap zero (dotted vertical line). Panel A illustrates differences in CPUE between slope intervals of 5° (1 = 5° ≤ 10°, 2 = 10° ≤ 15°, … , 8 = 35° ≤ 40°). Panel B illustrates differences in CPUE between depth intervals of 5 meters (1 = 5 m ≤ 10 m, 2 = 10 m ≤ 15 m, … , 7 = 35 m ≤ 40 m). Panel C illustrates differences in CPUE between exposure values (3 – 7).

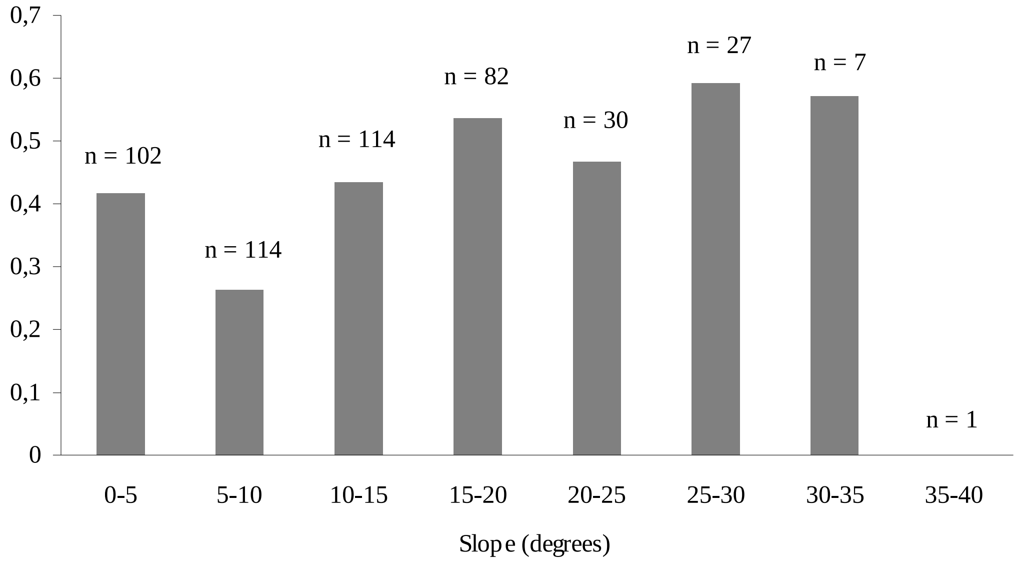

Fig. 8. CPUE (catch per unit effort, lobster per trap day^{-1}) within slope intervals of 5 degrees, based on mean slope in a 100 × 100 meter grid. Number above bars: sample size (n, number of traps).

Lobsters were caught in depths between 7 and 34 meters (Fig. 9). Fig. 9 implies a slightly higher CPUE at 13 – 14 and 15 – 16 meters, but the Tukey's post hoc test did not reveal significant differences in CPUE between different 5-meter depth intervals (Fig. 7 B).

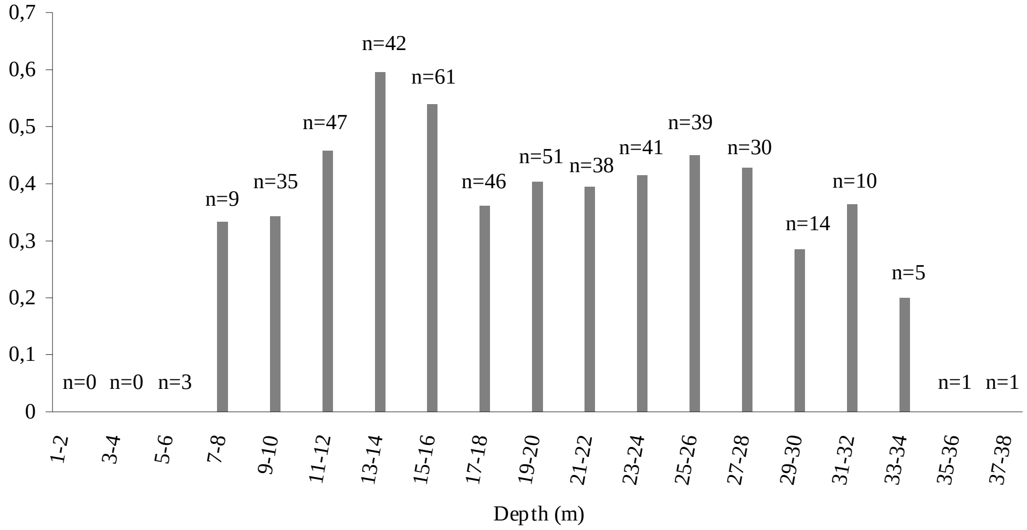

Fig. 9. CPUE (catch per unit effort, lobster per trap day^{-1}) at different depths for 204 individuals sampled in an experimental fishing for lobster (*H. gammarus*) in the municipality of Tvedestrand 18 – 31 August 2010. Number above bars: sample size (n, number of traps).

The randomized experimental fishing design placed traps in exposure values from 3 to 7, and a higher CPUE was observed in the two most exposed categories (Fig. 10). This is supported by Tukey's post hoc test, which revealed significant differences in CPUE between the highest exposure categories (6 and 7, separately) and the lower categories (3, 4, and 5, separately), but no significant differences between the highest categories or between the lower categories (Fig. 7 C).

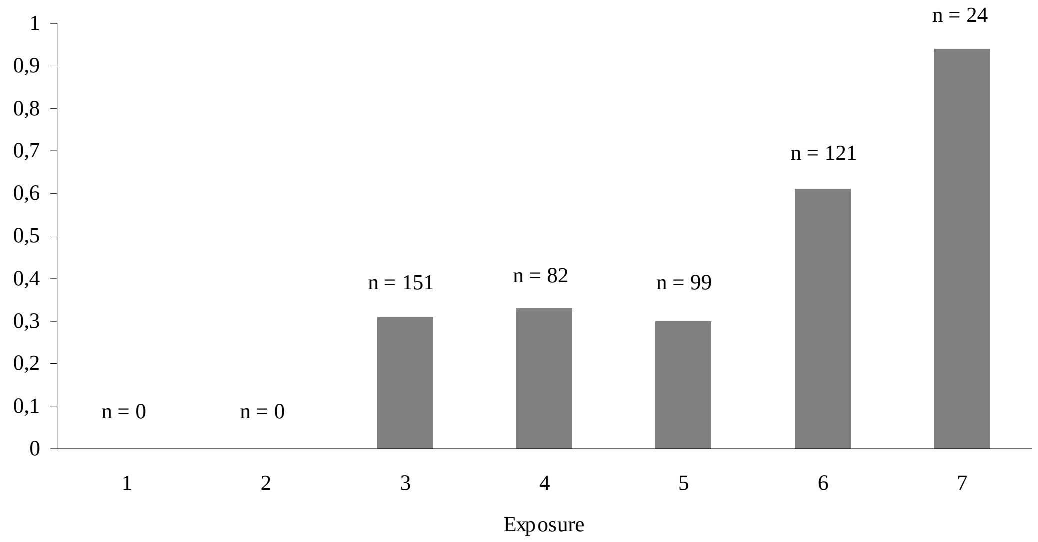

Fig. 10. CPUE (catch per unit effort, lobster per trap day^{-1}) at different exposure values for 204 individuals sampled in experimental fishing for lobster (*H. gammarus*) in the municipality of Tvedestrand 18 – 31 August 2010. Number above bars: sample size (n, number of traps).

Number of lobsters in the traps was not significantly affected by presence or absence of edible crab (*Cancer pagurus*) (adj. $p = 0.76$), nor was the number of edible crabs ($p = 0.98$) (Fig. 11). Out of the total number of traps (477), 202 traps caught edible crabs, ranging from one to ten individuals. Mean number of lobsters in traps with crab absence was 0.41, while mean number of lobsters in traps with crab presence (1-10) was 0.45. The difference in CPUE of lobsters between crab presence and absence was not significant ($p = 0.76$), and the CPUE lobster and presence of crabs was not correlated (Pearson's $r = 0.01$).

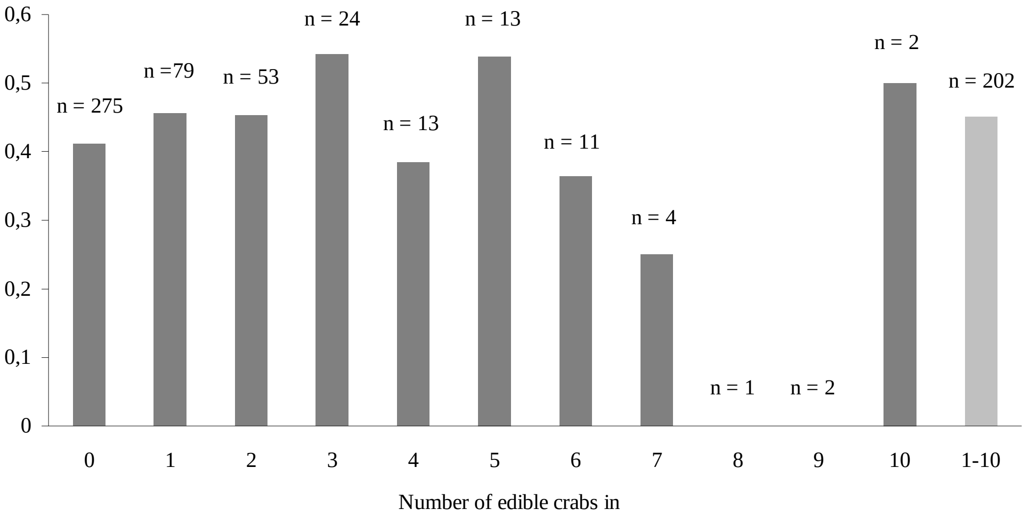

Fig. 11. Number of lobsters in traps in relation to number of edible crabs (*Cancer pagurus*) in traps during experimental fishing for lobster (*H. gammarus*) in the municipality of Tvedestrand 18 – 31 August 2010. Sample size (n) is shown above bars. The bar designated "1-10" shows number of lobsters in traps with *presence* of edible crabs.

3.2 Habitat suitability modelling

The most parsimonious linear regression model for lobster presence, the one with the lowest AIC-score was:

$$LP = \beta_0 + x_i\beta_1 + x_j\beta_2 + x_k\beta_3 + x_l\beta_4 + x_{ik}\beta_5 + x_{jk}\beta_6 + \varepsilon_{ijkl}$$

where *LP* is lobster presence, β_0 is the intercept, $x_i\beta_1$ is the inner product between the vector x for slope i and the coefficient for slope β_1, $x_j\beta_2$ is the inner product between the vector x for depth *j* and the coefficient for depth β_2, $x_k\beta_3$ is the inner product between the vector x for exposure *k* and the coefficient for exposure β_3, $x_l\beta_4$ is the inner product between the vector x for number of days since the experimental fishing started *l* and the coefficient for day β_4, $x_{ik}\beta_5$ is the inner product between the vector x for slope *i* and exposure *k* and the coefficient for the interaction of slope and exposure β_5, $x_{jk}\beta_6$ is the inner product between the vector x for depth *j* and exposure *k* and the coefficient for the interaction of depth and exposure β_6, and ε_{ijkl} is the error term for slope *i*, depth *j*, exposure *k* and day *l*.

Table V. Estimates, standard errors and p-values for variables describing lobster presence in the study area. Significance levels are designated by asterisks (significant codes: `*´ = p <0.05, `** ´= p <0.01).

Coefficients	Estimates	Std. Error	p-value
β_0 (*Intercept*)	–1.32063	1.49849	0.37815
β_1 (*slope*)	0.16489	0.05303	0.00187 **
β_2 (*depth*)	–0.22118	0.06966	0.00150 **
β_3 (*exposure*)	–0.05113	0.29939	0.86441
β_4 (*day*)	0.06738	0.02919	0.02100 *
β_5 (*slope:exposure*)	–0.02589	0.01089	0.01744 *
β_6 (*depth:exposure*)	0.04238	0.01387	0.00225 **

The linear regression model for lobster presence gave five significant variables at the 5 % level (Table V). β_1 and β_2 were significant, β_1 with a positive and β_2 with a negative relation to lobster presence. β_3 alone was not significant, but the interaction between slope and exposure, β_5, was significant with a weak negative relation to lobster presence. β_6 was significant with a slightly positive relation to lobster presence. The last variable, β_4 was also significant in the regression model with a positive relation to lobster presence. β_4 is not able to predict habitat suitability or seasonal changes in this study, due to the relatively short experimental fishing period of 14 days, but it reveals an increased catch through the fishing period and explain significant variance in the experimental fishing (Fig. 12).

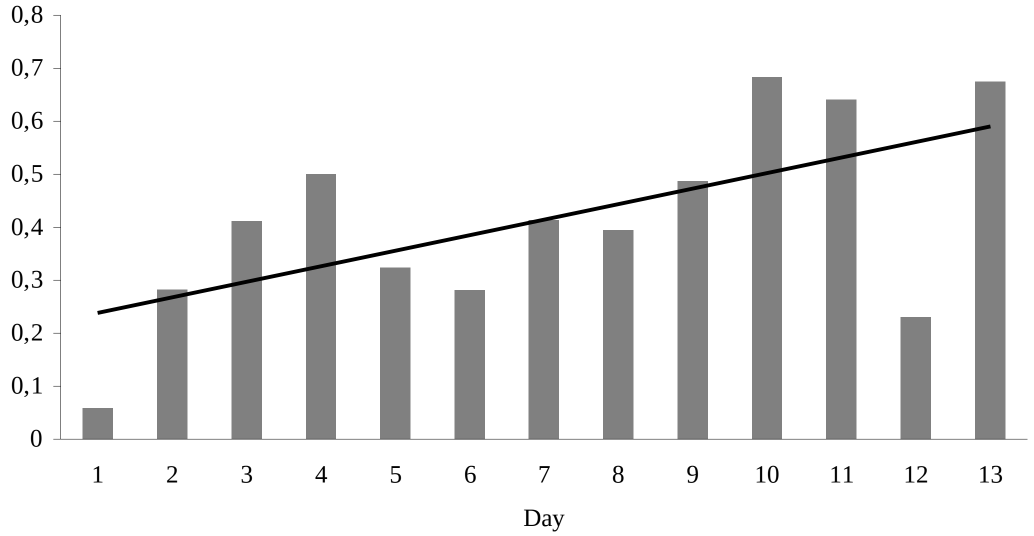

Fig. 12. CPUE (catch per unit effort, lobster per trap day^{-1}) for each day during the experimental fishing (18 – 31 August 2010) in the municipality of Tvedestrand. A trendline indicates increasing CPUE throughout the fishing period.

The prediction model gave a considerable higher habitat suitability value in the outer areas (Fig. 13), in particular along the ridges of the moraine. In the inner areas one can see a pattern of higher HS along the shoreline and around the islands, and a lower HS in inner basins.

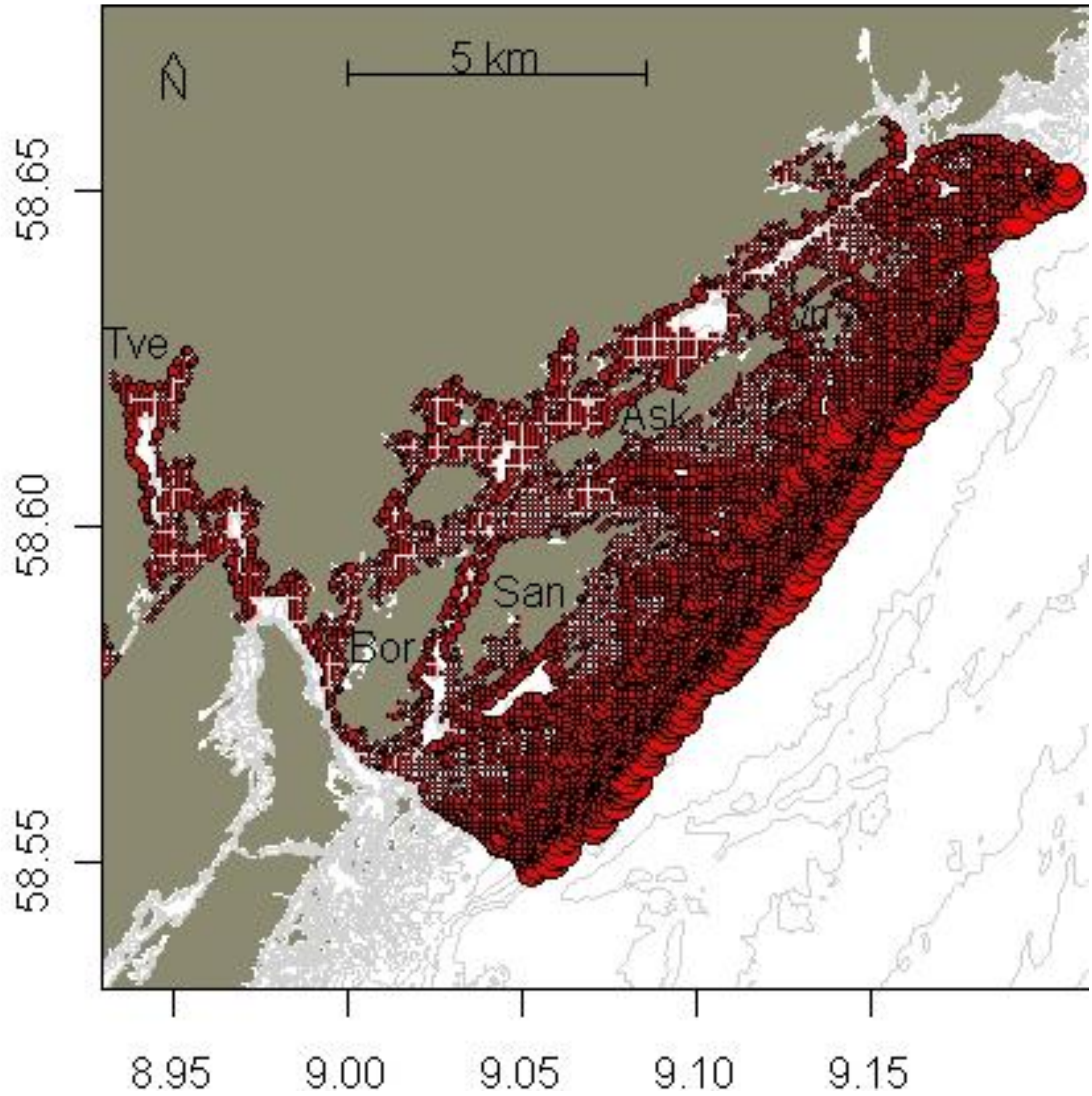

Fig. 13. Habitat suitability (HS) map for European lobster (*H. gammarus*) in the municipality of Tvedestrand. Increasing circle size indicates higher HS for lobster. The HS was predicted from the model, $LP = slp + dep + \exp + slp:\exp + dep:\exp$, from experimental fishing, and transferred to mean values of depth and bathymetric slope and exact values of exposure in a 100 × 100 meters grid. Grey lines are depth contours, and names of essential places are shortened: Tve = Tvedestrand, Bor = Borøya Island, San = Sandøya Island, Ask = Askerøya Island, and Lyn = Lyngør archipelago.

3.3 Local ecological knowledge

The map generated from the questionnaire inquiry (Fig. 2) revealed that lobster fishers prefer to place their traps in the outer area, especially along the moraine. Most of the area is preferred to some extent with a few more popular spots mostly towards the more exposed areas, but also in sheltered inner areas.

A total of 4939 traps (21 % commercial) were registered during the three surveys. The map showing the density of trap distribution illustrates that lobster fishers placed their traps more or less in the whole study area (Fig. 14). Trap placement was clearly clustered in particular areas, the most evident being more or less sheltered areas around Lyngør, the sheltered area stretching from Askerøya through the fjord between Borøya and Sandøya until trap density decreases in the more exposed areas southwest off Sandøya, and some spots along the shoreline in the fjord towards Tvedestrand. In the outer area a tendency of higher trap density followed the moraine ridge. Further inward the trend seemed to be higher density of traps closer to islands and skerries, along the shoreline, and lower in centres of basins.

Even though a general trend of lower densities of traps in the most exposed areas was insinuated by the map, proportions of total number of registered traps revealed that that nearly half (0.48) of the traps were found in areas with exposure values of 6 (0.38) and 7 (0.10) (Table VI and Fig. 15). The highest density of traps was found in areas with exposure value 5 (1.08 trap per cell), and areas of exposure values of 3 or 4 also showed relatively high densities (0.70 and 0.83, respectively).

Table VI. Summary of trap and cell data for different exposure values (1 – 7), plotted during mapping of fishing pressure in the municipality of Tvedestrand through three surveys, conducted 5 – 9 October 2009, 2 – 7 October 2010, and 9 – 12 October 2010.

Exposure	Number of traps	Number of cells	Mean number of traps per cell	Proportion of total traps
1	0	78	0.00	0.00
2	4	253	0.02	0.00
3	884	1256	0.70	0.18
4	547	656	0.83	0.11
5	1181	1098	1.08	0.24
6	1875	2306	0.81	0.38
7	474	2306	0.21	0.10

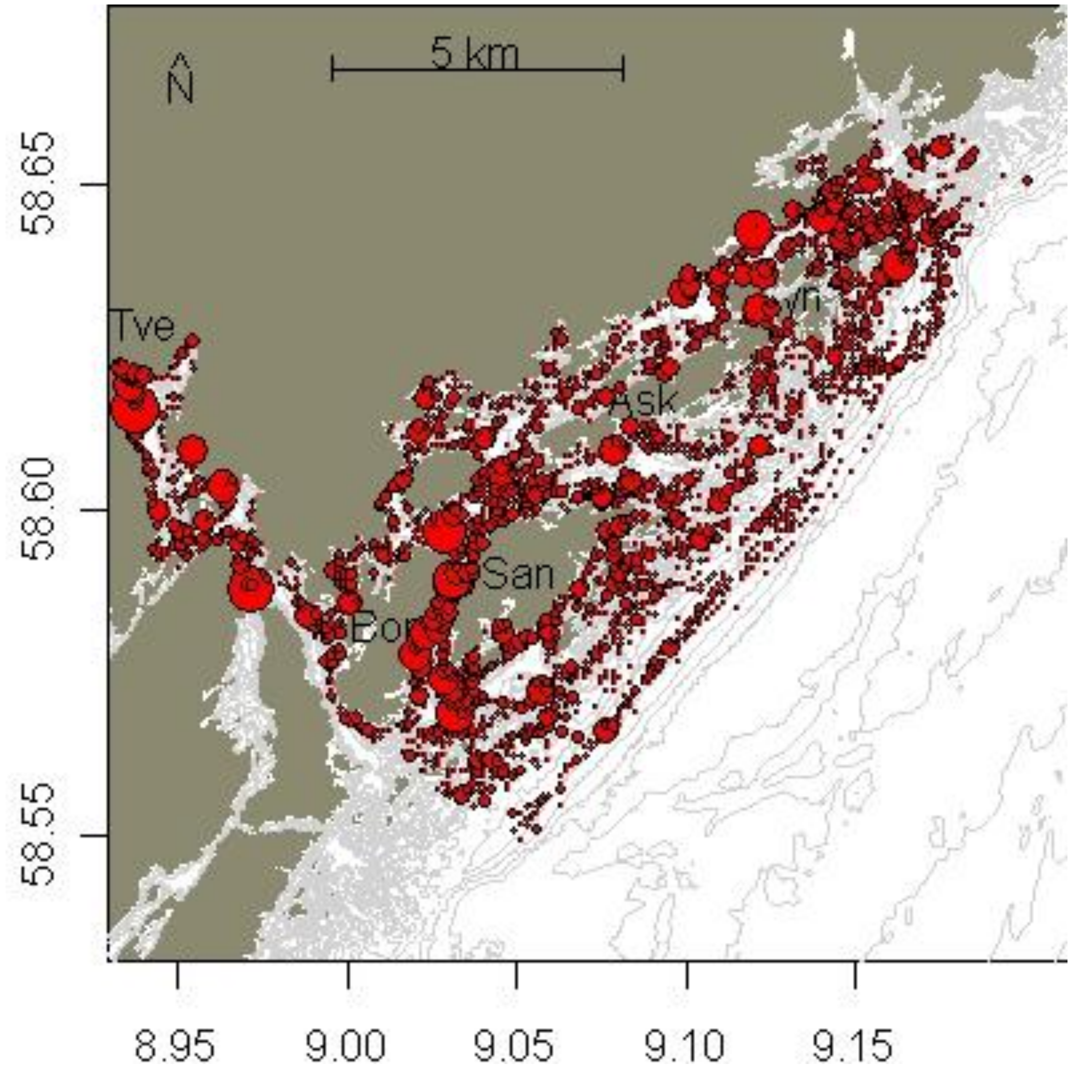

Fig. 14. Density of lobster traps in the municipality of Tvedestrand through three surveys (5 – 9 Oct., 2009, 2 – 7 Oct. and 9 – 12 Oct., 2010) based on number of traps plotted in cells in a 100 x 100 meter grid. Increasing circle size indicates higher density of traps. Grey lines are depth contours, and names of essential places are shortened: Tve = Tvedestrand, Bor = Borøya Island, San = Sandøya Island, Ask = Askerøya Island, and Lyn = Lyngør archipelago.

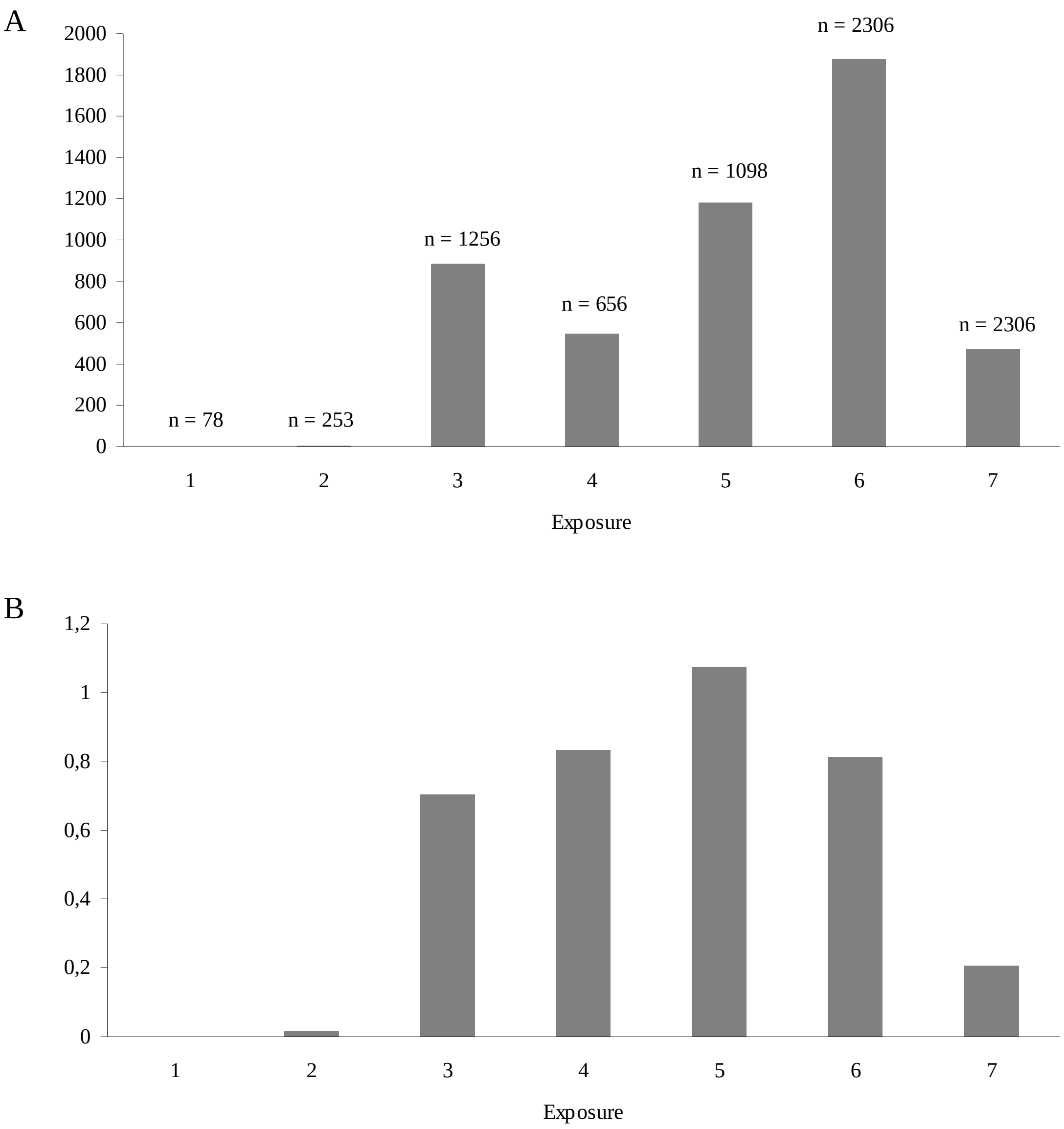

Fig. 15. Density of traps in cells with different exposure values, during three mapping surveys (5-9 Oct. 2009, 2-7 Oct, and 9-12 Oct. 2010). Increasing exposure value indicates higher exposure. Panel A illustrates number of traps in each exposure value, with number of cells in each exposure value as independent variables above bars. Panel B compensates for number of cells within the given exposure value by dividing number of traps by number of cells with the exposure value (relative trap count).

4 Discussion

The sample of the lobster population in Tvedestrand in this study was normally distributed around a mean CL of 94.3 mm, with no significant difference in CL between females and males. Based on decreasing portions of the sample with increasing size mortality (M) after reaching MLS was estimated to M = 0.5. The catch was biased towards a higher proportion of males (60 %) than females (39 %), and 23 % out of the female sample was ovigerous.

CPUE was significantly higher in the outer areas, and in the inner areas ≥ 8° bathymetric slope. Statistical testing did not reveal isolated effects of slope or depth on CPUE, but exposure showed significant differences between the two most exposed areas (6 and 7) and the more sheltered (3, 4, and 5). Presence-, or number of edible crabs (*Cancer pagurus*) did not affect CPUE significantly.

The most parsimonious linear regression model for lobster presence contained five significant variables; slope, depth, exposure, day, slope:exposure and depth:exposure, and one not significant; exposure. Day was not included in the prediction model. This model predicted a general higher HS in the outer areas, and lower HS in inner areas in centres of basins.

LEK through questionnaire inquiry reveals that the most popular fishing grounds are towards and in the outer area, particularly on the moraine ridge, but nearly the entire area is popular to some extent. Mapping of fishing pressure uncovered that the density of traps was generally higher in inner areas, but proportions of total number of traps were nearly the same in the two most exposed (6 and 7) categories combined and the three more sheltered (3, 4 and 5).

4.1 Description of the lobster population demography

Sex-specific difference in CL was not significant ($p < 0.05$) in this study, and the size distribution was normal. Why this normal distribution occurs when fishing without escape vents needs an explanation, as the population most certainly consists of more individuals below MLS. According to a pilot study on circular escape vents, 81 % of the lobster below 24 cm TL (former MLS, ~ 88 mm CL) managed to escape from the trap with 60 mm escape vents (IMR, unpublished data). Assuming that escape vents prevent catch of lobster below MLS (90 mm CL), mean CL growth at moulting is 7 mm (Agnalt et al., 2007), and exploitation is high, the reason for this distribution probably is that lobster boldness increases with size. Lobsters are territorial and cannibalism occurs (Skog, 2008), also in this study, hence it is reasonable to suggest that smaller lobsters do not take the risk of approaching and entering a baited lobster trap. The boldness assumption is evident on the left side of the CL distribution (Fig.

7), where the number of individuals gradually decreases. The CL distribution peaks within the 93 - 97 mm interval (Fig. 3), more precisely at 94 mm. The individuals recruited to the fishery in 2010 probably caused this peak, as the peak consisted of individuals growing over MLS after their last moult. However, the observed CL peak above MLS does not correspond with the size composition found on the east coast of England, which was predominantly below the MLS (Addison and Lovewell, 1991).

This study does not reveal any differences in the sex-specific distribution or proportion of ovigerous females, between the inner and outer area (Table I). However, the observed general sex-specific difference of catchability may seem contradicting. It is interesting that only 39 % of lobsters were females when capture of ovigerous females has been prohibited since 2008 (Directorate of fisheries, 2011), two years prior to the experimental fishing. In this study 23 % of the caught females were ovigerous (in late August), hence optimally protected from being taken out during lobster fishing, a moderate estimate compared with the 50 % suggested by Agnalt et al. (2007). Their study of berried European lobster off southwestern Norway found that proportions of (wild) ovigerous females in successive surveys were 39, 58, 56 (spring), 47 and 19 % (during autumn) (Agnalt et al., 2007). Assuming a considerably higher removal of males in two lobster-fishing seasons prior to the experimental fishing, one would expect a higher proportion of females than males in the catches, but the opposite was observed. Moland et al. (2010) showed that European lobster females exhibit higher survival probability, but lower recapture probability than males. They linked this to the different behaviour and life expectancy between the sexes caused by natural selection and sex-specific trade offs between survival and future reproduction, and further proposed that a male-biased difference in catches could be explained by a higher propensity for sheltering behaviour in females (e.g., while brooding), and territorial- and risk taking behaviour of males. Agnalt et al. (2007) also found that > 90 % of females followed a biennial reproductive cycle (moulting – ovigerous – moulting), implying that approximately every second female lobster caught should be ovigerous. This means, according to my data, that ovigerous females have an even lower catchability, approximately reduced by 50 % (22.7 % were ovigerous). The effects of higher exploitation of males, considering lower catchability of females and ban of capturing ovigerous females, on the population are interesting. The population may end up in a state of lacking males, but this will, hopefully, not occur as long as lobster fishers respect the MLS.

The part of the lobster population in Tvedestrand sampled in this study mainly consisted of individuals within few moults from the MLS (larger and smaller), and that mortality was approximately M = 0.5. This indicates high fishing pressure, as no predators on adult European lobsters is known (Skog, 2008). It is well documented for many marine species that large females are known to be more fecund and produce offspring of higher quality (e.g., Russ, 2002; Birkeland and Dayton, 2005), and the following studies reveal the same tendencies for European lobster: The size of the female lobster clearly affects the number of eggs produced, and the relationship is close to linear with size (Agnalt, 2008). Agnalt (2008) found that number of eggs varied from ~4000 for a female of 74 mm CL, all individuals under 88 mm CL had fewer than 11 000 eggs, up to ~40 000 for a female of 151 mm CL in European lobsters off southwestern coast of Norway. Moland et al. (2010) emphasized the effects of higher female size on the offspring in European lobster in Skagerrak, with higher mean egg size, lower sibling size variation and higher mean larval size at hatching with increasing female size. Hence, the lobster population in Tvedestrand may be adversely effected by the lack of large female individuals.

CPUE in different areas throughout the experimental fishing showed clear differences (Fig. 4 and Fig. 5). This was supported by significant testing (Table IV) and the trend was higher CPUE in the outer area, and higher CPUE in inner areas with a steeper slope (≥ 8 °). Significant higher CPUE with high exposure values (6 and 7) also reveals this trend, as these values are mostly in the outer areas. Some of the explanation for higher CPUE in the outer area lies in the bottom bathymetry, which is expected to be more homogenous than in the inner areas, due to the smooth bottom of the end moraine. There is most likely higher probability of hitting a lobster habitat with random placement of traps in the homogenous bottom habitat in the outer area than the in inner areas with more fluctuating bathymetry. Some of the variance is likely to be caused by the latter argument, however, the difference in CPUE between the outer and the inner area was so obvious that one should expect a general higher CPUE in the outer area. If this is caused by lower exploitation of lobsters in this area, or if the outer area simply contains more suitable lobster habitat is a matter of discussion. This study predicts higher HS in the outer area (Fig. 13) and lower density in the most exposed areas (Table VI), but the HS may be a slightly circular argument because it predicts for the same area as the data are obtained in, so I will leave this question open.

For the inner areas, CPUE was higher on slopes than on flat bottom. A wide range of literature has already stated lobsters affinity for slopes (e.g., Dybern, 1973; Galparsoro et al., 2009; Moland et al., in press). This is probably of higher importance in sheltered areas, as the sedimentation rate is higher due to weaker currents and more sedimentation agents. This argument is also related to lobsters affinity for rocky substrates (Dybern, 1973; Howard, 1980; Smith et al., 2001; Galparsoro et al., 2009, Moland et al., in press), hence the quality of a lobster habitat is decreased by too much sedimentation, which is more likely in flattened, inner, sheltered areas. However, slope intervals did not affect CPUE (Fig. 7 A).

Lastly, the number of lobsters in traps was not affected by number-, or presence, of edible crabs. In fact, the number of lobsters was slightly higher in traps with crab presence (Fig. 11), but the presence of the two crustaceans was not highly correlated. European lobster and edible crab have overlapping habitat niches and are believed to compete for territories and resources, and the lobster is in general dominant. Number of edible crabs was registered to look at any effects in CPUE, but no such effect was revealed. The reason is probably, not surprisingly, that they thrive in the same habitat.

4.2 Habitat suitability modelling

Exposure alone is not significant in the linear regression model, but the Tukey's post hoc test post hoc test revealed significant differences in CPUE between exposure values. Knowing this and that the CPUE in the outer and most exposed areas were considerably higher than the inner areas, the variance described by this variable is presumably covered in the significant interacting variables β_5 (*slope:exposure*) and β_6 (*depth:exposure*). The significance of the interaction variables imply that exposure explain some of the variance together with depth and slope. The interpretation of the variables slope and depth interacting with exposure is somehow the same. A highly exposed location is not necessarily good lobster habitat, but exposure is able to explain part of the lobster presence if depth and slope are within a favourable range of values.

Some of the variance caused by bathymetric slope, is not explained by slope alone. One possible reason is that the effect of slope on lobster presence is clearer in the exposed areas, where a stronger current prevents sedimentation. In addition sedimentation agents are fewer in the outer, exposed areas. In the inner sheltered areas, where the exposure is low, sandy and muddy substrates are easily formed. If assuming that these substrates decrease an area's suitability as a good lobster habitat, then it is logical that the slope-exposure-interaction can explain parts of the lobster presence.

In the interaction variable *depth:exposure* the biological arguments are somehow similar to the *slope:exposure*. Depth alone is highly significant in the model but one can easily understand that *exposure:depth* explains some of the variance. In the outer and exposed areas the bottom bathymetry is more homogenous than the inner sheltered areas. Sheltered areas might have entirely different habitats at a given depth (regarding to particle size of substrate, vegetation, slope etc.), while it is more likely that similar habitats are found at specific depth in the outer area. This means that predicting lobster presence at different depths is dependent on exposure. Hence, it is logical to end up with the interacting variable as significant in the model.

The significance of *depth* in the model is worthy of attention. Not because good lobster habitats are independent of depth, but because our experimental fishing caught lobsters at nearly the whole depth range (Fig. 9). The post hoc test did not reveal significant differences in CPUE between depth intervals, indicating that the entire depth range is within the lobster niche. This statement is supported by literature, such as Dybern (1973) and Moland (2010).

Probability of lobster presence is increasing with steeper slope according to the linear regression model. This is as expected from a wide range of literature (e.g., Dybern, 1973; Galparsoro et al., 2009), but this study did not reveal a clear optimal slope for lobster presence (Fig. 8), and no slope interval was significantly different from others (Fig. 7 A). This may have been due to the method used for identifying slope, but it seems reasonable to consider the area around the coordinates and use maximum change as a measure.

Day is also significant in the explanatory model, with a positive relation to catch, indicating an increasing catch during the experimental fishing (Fig. 12). This trend is probably caused by two mechanisms, the first being modification of the design towards increased trap placements on steeper sites after five days of trap hauling. Second, the plastic- and chemical odour from the new traps the first days of fishing may have repelled the lobsters. Lobsters are, like other crustaceans, extremely sensitive to their chemical environment (Skog, 2009), and a synthetic smell might affect lobster behaviour and thereby reduce the probability of lobster to go into the trap (van der Meeren, pers. comm.). This may be a source of error in this study, as the first couple of days in the experimental fishing may have given misleading results.

If this HS model was the basis for implementing of a lobster reserve, the most obvious place would be somewhere in the outer area covering parts of the moraine, but also the semi-sheltered areas in the northeast of the study area would be suitable following the HS model. A lobster reserve network of smaller reserves in the inner areas should follow mainland, islands and include skerries, e.g., the west side of the fjord towards Tvedestrand, both sides of the area between Sandøya and Borøya, outside Sandøya, Askerøya and Lyngør.

The HS model was generated from catch of individuals from 57 to 128 mm CL, 88 % were within three moult increments from (smaller or larger) than MLS, 60 % were males and 23 % of the females were ovigerous. A weakness of the HS model may be that, even if the model is strong for lobster presence, the model is based on the given sample covering a rather narrow size range, thus it might not predict HS for the part of the lobster population not present in the sample. If a HS model is used in identification of potential reserves protecting the entire population it should also predict HS for juvenile individuals, the older ones, and equally for sex and proportions of ovigerous females.

The power of the HS generated in this study is hard to evaluate. The optimal test would be to transfer the predicting model to another area to test if the prediction holds in a targeted experimental fishing. This is likely to be conducted, but before this is implemented one should include more predictors in the model, i.e., those potentially obtained by a multibeam echosounder survey in the study area. This is planned for the spring, 2011. By incorporating more predictors (e.g. particle size, distance to rock, vegetation coverage, etc.) a stronger model could be generated and it would be essential to test the power of such a model in a corresponding study area. The results and methodology of this contribution hopefully forms a basis for further development of habitat suitability modelling in coastal Skagerrak, a tool of great potential in identification of marine reserves.

4.3 Local ecological knowledge

The map of favourable lobster fishing grounds generated from the questionnaire inquiry (Fig. 2) is consistent with the predicted HS in the same areas (13) and the CPUE results from outer areas compared with the inner area in the experimental fishing (Table I and IV). Number of traps in the most popular areas is also rather high (Fig. 14). However, some precautions have to be taken. Respondents may be over-represented in some areas, which will result in a skewed popularity in their neighbouring fishing grounds. They also replied for other fishing activities, hence some may not have emphasized lobster fishing in the inquiry. Undoubtedly, residents of Tvedestrand harbour substantial LEK about lobster habitats in their coastal waters, but a dialogue with local lobster fishers, both recreational and commercial, is probably a better approach instead of a questionnaire inquiry. A direct dialogue would involve the fishers more, and if a marine reserve was planned to be established they would be a part of the implementation process. In this process they may influence what area to protect, and securing the involvement of locals is important for the success of a reserve (Houde et al 2001; Sweeting and Polunin, 2005; Pettersen et al., 2009). In contrast, a questionnaire inquiry may feel as a breach of trust for the respondents if the LEK is used to restrict their resources.

The map of favourable fishing grounds does not reflect the actual fishing activity. Only 10 % of the traps were placed in areas with the highest exposure value (7), indicating popular fishing grounds. The interpretation of mapping of fishing pressure has to be considered a combination of LEK, availability and risk assessment. Even though a lobster fisher would prefer to place his traps on his favourite spots on the moraine ridge where he strongly believe in great catches, it may be time consuming to take his boat out to the moraine, and he may risk losing gear and even his own life in bad weather. Thus, the mapping of fishing pressure is to complex to reflect LEK alone.

4.4 Comparison of habitat suitability and local ecological knowledge.

The HS map (Fig. 13) and the trap density map (Fig. 14) did follow some of the same patterns. They gave high values along the shorelines (mainland and around the islands) and lower values towards the centres of the inner basins and fjords. Some areas with high trap density correspond with the HS map (e.g., the northeastern cluster in the inner area, and, to some extent, in the inner part of the fjord near

Tvedestrand), but in other areas the HS map predicts high HS in areas with low trap density. Although some patterns comply in the two maps on a detailed level, the overall impression is that they don't overlap that much, due to high HS in the outer area where trap density is relatively low (e.g., the exposed area northeast off Sandøya, (see Fig. 14)). However, some common patterns occur in both maps in the outer area, as well. They both show high values along the ridges of the moraine, and reach approximately the same distance out from shore.

High trap densities may be considered a cost in the implementation process of establishing marine reserves, as high trap densities in a potential reserve may be the basis for conflict between the authorities and the lobster fishers. Areas with low trap densities and high HS have high potential as marine reserves due to little conflict with lobster fishers, and suitable habitats for the lobster. Comparing the trap density map and the HS map in this study a general advice would be to place lobster reserves in the outer areas. These areas are also covering a large area, and protecting parts of this area would still leave considerable areas open for fishing.

5 Conclusions and implications

The demography of the lobster population, sampled in this study, reveals high mortality (M = 0.5) after reaching MLS, indicating high fishing pressure in the municipality of Tvedestrand, and suggests that lobster boldness increases with size. Females, especially ovigerous females, possess a general lower catchability, and considering the ban of capturing ovigerous females, the lobster population may suffer from lack of males in the future if MLS not is respected. The significant higher catch rates in the outer areas may function as a buffer against depletion of the lobster population in the municipality in Tvedestrand.

The most parsimonious linear regression model for lobster presence revealed that bathymetric slope, exposure and depth were good predictors in predicting lobster presence. These predictors should be included when predicting HS for adult European lobster.

This study suggest that habitat suitability modelling through randomized experimental fishing may be a useful tool in the identification of potential marine reserves as a supplement to experimental fishing in defined areas. The HS modelling will add weight to an argument for placement of a reserve. Moreover, the model presented herein could be improved by incorporating predictors from a multibeam echosounder survey.

Finally, LEK is an important resource and this study indicates that it may be used in verifying lobster habitats to some extent. This study approached LEK in two different ways, through questionnaire inquiry and mapping of fishing pressure. Both have their strengths and weaknesses in verifying lobster habitats. The questionnaire inquiry, summarised in a map of favourable fishing grounds, did comply with the results from the experimental fishing and the HS model, but was poorer in verifying lobster habitats on a more detailed scale. The mapping of fishing pressure is not only strictly reflecting LEK, but may also give good information on lobster habitats on a detailed level, although it probably fails in revealing the major patterns. Together, the two methods may be a supplement in identification of lobster habitats, hence identifying potential marine reserves.

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