Acoustic monitoring of lobster (Homarus gammarus) behavior and survival during fishery

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Forord

En stor takk utrekkes til alle på Havforskningsinstituttet i Flødevigen. Både jeg og Tonje har vært veldig takknemlige for at vi har fått bo i huset under arbeidet med oppgavene. En spesiell takk utrekkes også veiledere Even Moland, Esben Moland Olsen og Thrond Haugen, hvorav Even takkes ekstra for utveksling av røverhistorier fra de syv hav og hjelp i å forstå range-testingens skjulte finnesser. Også Alf Ring-Kleiven, Sven Erik Enersen, Hanne Sannæs, Sigurd Espeland må takkes for hjelp av fangst av hummer og gode råd underveis. Alle i Flødevigen Tritonklubb bør også nevnes, da de har bidratt med obligatorisk bading vinteren igjennom som har gjort at hverken kropp eller hode overopphetes under nitidig arbeid forran pc-skjermen.

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Abstract

Overfishing is considered as the most important threat to many harvested marine species. This is also the case for the European lobster (Homarus gammarus). The still heavily harvested Norwegian population has been exploited to a barely sustainable level. The main aim of this study was to use automated acoustic tracking to investigate lobster behavior and survival during the lobster fishery season. In August 2011, 50 male lobsters above minimum legal size (MLS) were tagged with acoustic transmitters in an area near Arendal on the Norwegian Skagerrak coast. The data gathered were used to investigate movement variables and their effects on survival of individuals. Eight lobsters were censored from further analysis due to molting/loss of signal. Out of the 42 lobsters monitored at the onset of the fishing season, 35 were confirmed harvested and only seven survived the fishery. Other main findings suggested that lobsters avoiding trap dense areas survived (p = 0.046). Also, the observed mortality rate of 83.3% (± 5.75% SE) suggests that fishing depletes the catchable lobster population at an alarmingly high rate. This puts a strong harvest selection in favor of individuals being smaller than MLS (i.e., selection for slow growth) and movement behaviors avoiding areas considered as typical lobster habitat by fishers.

Sammendrag

Overfiske er den største trusselen mot mange marine arter. Slik er det også for den europeiske hummeren (*Homarus gammarus*). Den norske bestanden, som fortsatt er hardt beskattet, nådde i år 2000 et historisk lavmål. Hovedmålet med denne studien var å følge hummerindivider og deres vandringsmønster både før og under hummerfisket ved hjelp av akustisk telemetri. Sendere ble festet på femti hannhummer over minstemål og data fra dette ble brukt til å undersøke forskjellige variabler og deres påvirkning på overlevelsessuksessen til de forskjellige individene. Trettifem individer ble fisket, mens syv individer fortsatt levde ved endt fiske. Åtte hummere skiftet skall under studien og ble derfor ekskludert fra videre analyser. Den eneste observerbare grunnen til at syv overlevde var at de klarte å unngå steder med høyt fisketrykk (p = 0.046). Videre hentyder dødsraten som var på hele 83.3% (± 5.75% SE) at fisket desimerer den fiskebare delen av hummerbestanden i skremmende høy hastighet. Dette selekterer strekt for både individer som er mindre enn minst fangbar størrelse og individer som unngår habitater de naturlig er best mulig tilpasset til.

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1. Introduction

1.1 Background

Fisheries have severe impact on marine populations (Hutchings 2000). Overfishing is a big threat to harvested marine species (Pauly et al. 1998) and affects whole marine ecosystems and ecosystem services (Worm et al. 2006). Many marine species have throughout human history been exploited to extinction, or down to a barely sustainable level (Jackson et al. 2001). The latter is the case for the European lobsters (Homarus gammarus) in Norway (Agnalt et al. 2007, Kleiven et al. 2012). Historically, Norway was one of the largest lobster fishing nation in Europe during the last 500 years (Dannevig 1936) and one of the main supplier of lobsters for continental Europe before 1950 (Agnalt *et al.* 2007). At the start of the year 2000 the Norwegian lobster population was believed to be at a historical low level, although countermeasures had already been implemented in 1964 to prevent total population collapse. In 1964 the government declared that all lobsters below 220 mm of total length were protected and had to be released when fished. The level of protection was further increased in 1992 at the Skagerrak coast to 24 cm minimum length and the year after increased to 25 cm outside Skagerrak (Anon. 2007). In 2008 the Norwegian Directorate of Fisheries (FD) introduced new restrictions; the minimum legal size (MLS) was set to 25 cm throughout Norway, egg-bearing females were declared illegal to catch and/ or land, escape-vents measuring 60 mm in diameter was set to be mandatory on all lobster traps and for the recreational fishery a maximum of 10 traps per person/boat were allowed (Fiskeridirektoratet 2011). In addition, the lobster fishing season was set to be from 1st of October to 31st of November from the Swedish border and all the way to Sogn og Fjordane County. North of Sogn og Fjordane it is still allowed to fish up until 31st of December. How these new restrictions will affect the lobster populations in Norway remains to be seen, but it is most likely that, in the long term, the population size will rise.

Legal lobster fishery is done by using lobster traps. It is a common belief among fishers that the lobster is hard to catch and far from all lobsters in a given area are available for harvest at a given time. Which lobsters are catchable and which lobsters are not has been a mystery baffling both scientists and fishers for a long time. Several studies have been conducted on home range and movement patterns of lobsters (Geraldi et al. 2009, Watson et al. 2009, den Heyer et al. 2009, Bertelsen & Hornbeck 2010, Moland et al. 2011a, Moland et al. 2011b). However, no studies have investigated how lobster activity and home range patterns relate to the lobster fishery activity. Information on how a fishery affects different individuals within a population is important in lobster science, fishery science and fishery management. As mentioned above, over-harvesting is an important reason for the observed collapse of many marine populations, meaning that the historically low lobster population numbers seen in Norway in recent years may also be a result of this. In addition, fishing imposes an artificial selection pressure on lobsters (Jury et al. 2001, Caputi et al. 2010). Thus, harvesting constitutes a selection factor acting on the genetic makeup of future lobster populations. A recent study has shown that individuals from heavily fished local lobster populations are smaller in size, on average, than lobsters in protected areas (Moland et al. in review). This is also the case for other marine species (Hutchings & Rowe 2008, Lester *et al.* 2009), one example being the spiny lobster (*Jasus edwardsii*) (Kelly *et al.* 2000). Further, it is widely recognized that fishing selects for earlier maturity and smaller size of individuals at mating within various species (Law 2000, Wright 2007, Heino & Dieckmann 2009).

In 2007 telemetry studies on lobsters were done in the Flødevigen lobster reserve, south-eastern Norway, where movement patterns of individuals within the reserve were investigated (Moland *et al.* 2011a). The present study uses lessons learned from this study as foundation for further investigating behavioral patterns in the species both before and during the lobster fishing season by help of acoustic transmitters.

Tracking lobsters with acoustics, either with receivers set up in an array or done manually by handheld tracking, is not uncommon (*e.g.*, van der Meeren 1997, Golet *et al.* 2006, Watson *et al.* 2009, Moland *et al.* 2011 a) and is thought of as being a good way of monitoring movement of individuals of this bottom dwelling species (Golet *et al.* 2006). So it should give fulfilling answers to questions posed.

1.2 Research questions

The main aim of this study was to investigate lobster behavior and survival in relation to the lobster fishery in Sømskilen, in coastal Skagerrak, south-eastern Norway. This aim was pursued by:

- 1. Using automatic tracking system to estimate individual lobster home ranges and date of fishing.
- 2. Investigate fishing pressure on lobsters by monitoring trap sets.
- 3. Investigate lobster mortality in relation to home range change, fishing pressure, lobster size and appendage wounds.

2. Material and methods

2.1 Study area

This study was conducted in the outer part of the Sømskilen area, along with outer skerries and islands (Halvorsholmene, Tjuvholmene, Skjælbergholmene, Badstuholmen, Sven Johnsens holmer, Jerkenholmen) southwest of the Institute of Marine Research in Flødevigen and west of the Flødevigen lobster reserve in southeastern Norway (Fig. 1). The river Nidelva has two of its outflows in the basin which gives a varying freshwater discharge to the uppermost layers of the sea surface in adjacent areas. Also, the area is heavy influenced by the prevailing north-east coastal current. Depth-wise the area has shallower inner south-western parts, while the outer western parts are deeper (30 m) (Olsen & Moland 2010). The area has a wide variety of geographical variation such as mud flats, eel grass beds, kelp forest, rocks and ledges of various sizes. It is believed to constitute a typical lobster habitat of coastal Skagerrak (Moland *et al.* 2011b). The area is regarded as an area with high fishing pressure upon lobsters (Kleiven, pers. comm.).

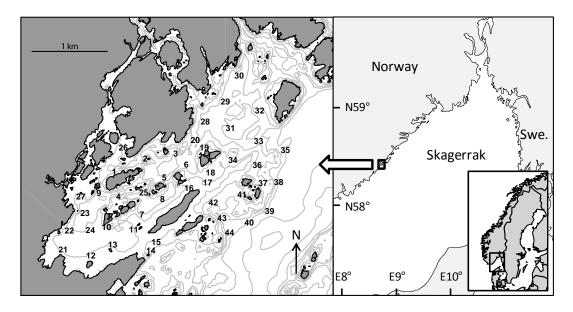


Fig. 1. Location of the study area (left panel) in south-eastern Norway (right panel). Isobaths shown are the 5, 10, 20, 30, 40 and 50 m depth contours. Numbers are positions of Vemco VR2W acoustic receivers deployed to receive signals sent by acoustic transmitters attached to lobsters.

2.2 Sampling of lobsters for acoustic telemetry

Catching lobsters began on 1 August and ended on 31 August 2011. Individuals were caught in standard 'parlour' lobster traps (Fig. 2) baited with frozen mackerel (*Scomber scombrus*). Traps were set at different sites to spread sample effort over the area, but at the same time set at locations known to harbor lobster habitat to give a sufficient yield of individuals. The soak time varied from 1 – 4 days. A total of 50 male lobsters above MLS (25 cm from tail to rostrum) were used in this study. Only males were selected to (1) ensure that tagged individuals recovered by fishers would be kept (and subsequently reported), and (2) to reduce sources of variation in statistical analysis and to keep statistical power as high as possible. Unberried females could spawn before the onset of the fishing season and thus be illegal to catch or land while undersized lobsters could escape through escape vents, and might not be fished or landed. Both groups might also behave differently than above MLS males. Catch position, carapace length (CL), total length (TL) and injuries/missing limbs (Inj) were registered for all individuals.



Fig. 2. Modern 'parlour' lobster trap used to capture lobsters in the present study. Photo: Mamut.net

2.3 Tagging lobsters with acoustic transmitters

Male lobsters above MLS were tagged with an acoustic transmitter (Vemco V13TP –L, diameter 13 mm length 36 mm, weight in seawater < 6 g, Vemco Divison, Amirix Systems Inc., Halifax, Canada). There are no indications that these devices cramp lobster behavior (Cowan *et al.* 2007, Moland *et al.* 2011a). Tags were programmed to transmit

signals (69 kHz) at 110 – 250 seconds random intervals (mean 180 seconds), coded with an ID number making it possible to distinguish individuals. Also, the transmitters were equipped with a pressure sensitive transducer that registered depth. Depth data made it possible to determine when lobsters moved around (depth varied) and more importantly when they were caught in a trap (depth constant). Following the same procedure as Moland et al. (2011a) transmitters were attached to lobsters (Fig. 3) by using a soft plastic tube as a harness in which both the acoustic and a T-bar tag was inserted. A cable tie was then treaded through two holes which were made in the plastic tubing and fitted between the denticles on the carpus of the crusher claw limb of the lobster. To heighten the return rate of tags from fishers, the T-bar tag informed fishers that a reward (NOK 50,-) would be paid if returned to the Institute of Marine Research. By doing this it was possible to confirm whether individuals were fished or not (Tag). Transmitters were lost when the lobster molted. None of the lobsters were T-bar tagged in the abdomen, as done in other lobster studies. This was to minimize potential stress on individuals. Some individuals had already been tagged during previous studies (n=16), meaning that these individuals could be recognized if the telemetry tag was lost. After tagging lobsters were released at the same location as they were caught. The total handling time was 5-15 min, dependent on the number of lobsters caught in each trap.



Fig. 3. Tagging of lobster with an acoustic transmitter (Vemco V13TP, length: 13mm, diameter: 36 mm). Photo: Even Moland

2.4 Monitoring lobster movement with Vemco VR2W System

To follow lobster movement, 44 acoustic receivers (VR2W, Vemco Divison, Amirix Systems Inc., Halifax, Canada) (Fig. 4) attached to subsurface buoys were moored at 3 m depth throughout the study area. Receivers were positioned to maximize monitoring capability for acoustic tags not only attached to lobsters but also cod (*Gadus morhua*) and eel (*Anguilla anguilla*) (Olsen & Moland 2010, Simpfendorfer *et al.* 2012). Detection range of receivers were checked by a special purpose range test tag transmitting with the same signal strength as the tags used in the study, but with a fixed 5 second interval between signals. The range test tag was lowered down to the sea floor at selected Global Positioning System (GPS) positions (n=616) at approximately 200 m distance to each other throughout the study area. Lowering positions were set on a map before range testing was conducted. This made it possible to pinpoint areas throughout the study area where lobster were less likely to be detected by acoustic receivers. It also provided a good indication of the maximum listening range of receivers.

To check status of both tags and hydrophones data were manually downloaded from hydrophones over several days in September. To download data from hydrophones, each one had to be pulled from the water and set in data transmission mode with a magnetic key. Data were then transferred via Bluetooth to a laptop PC. Receivers' internal clocks were reset and synchronized before the buoys were lowered into the water at the same position. Also, hydrophones, buoys and ropes were cleansed for barnacles and other fouling organisms which had settled on the gear. Lastly, small floating buoys attached to four meter long sinking ropes were attached to the buoys to ease retrieval of receivers at the end of the experiment.

The system is based on omni-directional hydrophones that are deployed relative to each other so that their detection ranges overlaps and one signal can be received by multiple hydrophones. A receiver's probability to detect a signal omitted by an acoustic transmitter is linearly related to its distance to the receiver (Simpfendorfer *et al.* 2002, Heupel *et al.* 2006), meaning that the number of receptions over a set time period (often between 5-60 minutes) is higher the closer the source signal is to the hydrophone. When a signal is detected by more than one hydrophone (preferably at least three) it is possible to calculate signal source distance relative to each hydrophone by counting how

many detections of a device each hydrophone receives. This gives an estimate of the transmitter position over the set time period. The more signals received by the more hydrophones, the more accurate the position (Simpfendorfer *et al.* 2002). Movement patterns and home ranges for tagged individuals can then be constructed by using this data. In the present study lobster positions were estimated by the method described above (termed position averaging ['PAV']) for 30 minutes time bins. Meaning, if a lobster was continuously heard by one or more hydrophones, a single position for that lobster would be estimated each 30 minutes throughout the study whenever an animal was in range of receivers. When the 2011 lobster fishing season had ended, data were downloaded from the receivers.



 Fig. 4.
 VR2W Acoustic receiver (length: 308mm, diameter: 78mm) which were used to monitor lobster activity.

 Photo:
 Vemco Ltd.

2.5 Registration of traps

Starting on the second day of the lobster fishing season (2 October), positions of all observed lobster traps in the study area set by recreational and commercial fishers were registered and their positions recorded with a handheld GPS (Garmin 78xc). Trap registration continued throughout the fishing season three times per week in October and two times per week in November. For days when counting were not conducted, an estimate for trap numbers were made using the previous day's trap count. The last day of registration was 28 November 2011. Alongside maps showing trap positions each day of the fishery (Fig. 14, Appendix 3), a map showing areas with overall fishing pressure for the whole season were made (Fig. 15). This map was made by making a kernel estimation for all traps, so that a utilization distribution (UD) for the traps was made. Isoclines were plotted from 5 to 100% UD for each 5% interval. Kernels were constructed within the R software version 2.12.1 (R-project.org) by using the package "adehabitat" (Calenge 2006) and further development of R-scripts made by Simpfendorfer, Olsen, Heupel, Moland & Espeland (Moland *et al.* 2011 a, Olsen & Moland 2010). The smoothing parameter for kernel calculation (h) was set to 50 (Worton 1989, Gitzen *et al.* 2006, Kie *et al.* 2010).

2.6 Communication with local fishers

Media coverage through a front-page article in the local newspaper (Agderposten) on 3 October informed lobster fishers about the project. Fishing regulations state that it is mandatory to mark trap buoys with name and telephone number, enabling identification of trap owners. All owners of traps registered the first day of the fishery were contacted by phone and informed about the ongoing study. Contact with lobster fishers was also established in the field throughout the study and whenever fishers returned telemetry tags to Flødevigen research station. Fishers were in general positive to the project, and willingly provided information on when and where lobsters were caught.

2.7 Home range estimation and lobster activity

As recommended by Rogers & White (2001) and done by Simpfendorfer *et al.* (2006) and Moland *et al.* (2011a) a home range (HR) was defined as the smallest area containing 95% of the utilization distribution (UD) of an individual, i.e. the area within which an individual can be expected to be found 95% of its time. By setting the UD to 95 one removes outliers from the home range and only includes the area most used by the individual (Rogers & White 2001). Core areas of the home range set to be 50% of UD were also estimated.

When calculating home ranges one must also set a smoothing parameter (*h*). Setting the smoothing parameter is crucial and is the most important aspect in kernel home range analysis (Kie *et al.* 2010). There are several ways to determine *h*. One, being the least

square cross validation (LSCV), where a smoothing parameter is calculated for each single home range (Gitzen *et al.* 2006). However, the LSCV method made home ranges for some lobsters very "thin" while others were clearly much "fatter". Therefore, in the present study, a compromise were made and a shared smoothing parameter (h=50), which gave relatively meaningful home ranges for most individuals, were used for all lobsters. This meant that most home ranges were undivided and at the same time not too wide in areas having a high number of positions and narrow in areas having few positions. Using a shared smoothing parameter was important because it eased comparison of home range sizes between individuals and it were especially important when calculating the experienced trap exposure for each individual. The standardization was also made to ensure reproducibility.

Separate home ranges were estimated for September and October/November, making it possible to distinguish behavior before and under the fishing season. Home ranges for lobsters were constructed within the R software version 2.12.1 (R-project.org) by using the R package "adehabitat" (Calenge 2006) and altering of the same script as used for the traps (see section 2.5). Because of molting, tag malfunction or dispersion, separate home ranges during September and under lobster fishing season were constructed for only 37 of the 50 individuals (see Table 1, Figure 12 and Appendix 1).

To check whether lobsters were philopatric and remained in their home range throughout the fishery all location data in the fishing months for that specific individual were compared to its September home range. Total number of positions given during the fishery that fell within the individual's September home range was divided by the total number of positions under the fishery, giving a proportion of the degree to which the lobster remained within its September home range through the fishery, *i.e.*, a degree of philopatry (Ph).

The following mutually exclusive fates (Fate) of all lobsters at the end of the fishing season were determined: (1) *fished*, (2) *molted/signal loss*, (3) *dispersed out of study area*, (4) *survived within study area*.

2.8 Estimation of individually experienced trap exposure

For each lobster the experienced trap exposure (ETE) was estimated as the accumulated number of traps within their respective 95% UD (home range) during the fishing season (T_n) divided by the number of total traps (d) the lobster possibly could encounter until it was fished or fishing ended. This gave the following equation:

$ETE = T_n / d$

By using this equation it was possible to compare trap exposure between lobsters that were fished at different dates and take into account the fact that traps were far more numerous in the beginning of the fishing season (Fig 13 and 14). For lobsters that were fished, only traps counted up and till the last day of survival for that individual were included in the estimate. For lobsters that survived the fishery all traps were included.

2.9 Investigation of lobster fate

An estimation of overall lobster mortality was done by using Kaplan-Meier analysis (Kaplan & Meier 1958). The estimation of mortality rate is a very important parameter for harvested species and usually difficult to estimate (Heupel & Simpfendorfer 2002).

A timeline based on vertical movement patterns of each individual were made. This timeline gave a good view of the activity pattern of the lobsters, and, alongside with the raw data, showed when individuals entered a trap and were subsequently fished. Although fishing moment was given when tags were returned, the timeline and its raw data gave a more accurate point in time when a lobster entered a trap. This is because traps were not hauled by fishers each day, meaning that lobsters could be locked within a trap for several days before the trap got hauled. A lobster was set to be fished at the earliest point in time it was evident that the lobster had been caught in a lobster trap (*i.e.*, from cessation of any vertical movement). It is also important to note that by using timelines, it was possible to estimate fishing moment for individuals which were not reported to be fished. This was done for four individuals. If any doubt of when a lobster entered a trap were raised, fishing point (date) was set to be the time reported by the fisher.

To check for factors affecting lobster survival probability, the effects of various independent variables on the fates of lobsters were investigated by logistic regression (Janzen & Stern 1998). The variables used as predictors for the fate were carapace length (CL), September home range size (HR), degree of philopatry (Ph), experienced relative fishing pressure (ETE) and injured limbs (Inj). Variables with p > 0.05 were manually backward step-wise excluded from the analysis to find the variable(s) having significant effect on survival. The analysis was done in R with the GLM function in the AOD library(R-project.org).

3. Results

3.1 Range testing

66 of the 616 test positions (10.7%) were not detected by the receivers. Most of the undetected positions were in the outer parts of the study area (Fig. 5).

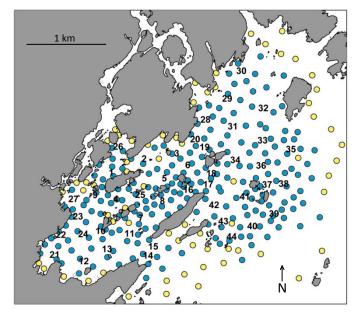


Fig. 5. Results from listening range testing of acoustic receivers. Numbers 1-44 is position of receivers. Yellow circles indicate testing positions which were not detected by receivers (n=66). Blue positions were detected by one or more receivers (n=550).

3.2 Lobster data

Different lobster data that were gathered are presented in Table 1. Lobster size ranged from 250 – 315 mm total length (TL) and 87 – 116 mm carapace length (CL). The lobsters had a mean TL of 272 mm (± 2.4 mm SE) while mean CL was 97.2 mm (± 1 mm SE). Twelve of the lobsters were registered as having various minor injuries like partially regenerated claws (chelae), loss of antennae, and loss of one or more walking legs. Seven injured lobsters were fished and five injured lobsters molted. Seven lobsters survived the fishery, 35 lobsters were confirmed fished and eight lobsters were censored from the survival analyses due to molting tag malfunction (loss of signal within study area prior to the onset of the fishing season). Thirty-two tags were returned from fishers, meaning that mortality were inferred for three individuals by investigating depth data. Depth data for a few selected individuals are shown in Figs. 6-11, while depth data for all individuals are shown in Appendix 2.

Table 1. Information on 50 lobsters tagged in Sømskilen, south-eastern Norway, in autumn 2011. ID: *id of individual*, Date: *date of tagging*, TL: *total length*, CL: *carapace length*, DA: *days alive during fishing season*, HR: *September home range*, Ph: *degree of individual philopatry*, Di: distance *between tagging position and harvest position if harvested*, Tr: *number of traps within home range during fishing season*, ETE: *experienced trap exposure*, Inj: whether individuals were injured, Fate: *fate*, Tag: *whether tag were returned by fisher*.

ID	Date	TL	CL	DA	HR	Ph	Di	Tr	ETE	Inj	Fate	Tag	Comments
15646	26.08	253	90	6	-	-	1222.1	8	-	Yes	Fished	yes	Signal lost 04.09
15647	26.08	276	100	3	399672	0.778	61.7	13	0.040	Yes	Fished	yes	
15648	26.08	270	97	-	-	-	-	-	-	Yes	Molted	-	Molted 14.09
15649	24.08	260	92	6	118230	0.969	394.8	33	0.048	Yes	Fished	yes	Captured with fyke net
15650	24.08	278	98	-	-	-	-	-	-	No	Molted	-	Molted 29.08
15651	22.08	250	91	22	149468	0.973	208.2	8	0.003	No	Fished	yes	Defect depth 13.10
15652	24.08	298	105	61	151762	0.983	-	75	0.016	No	Survived	-	
15653	25.08	255	92	5	166595	0.894	211.9	35	0.063	No	Fished	yes	
15654	25.08	268	101	11	-	-	-	-	-	Yes	Fished	no	Signal lost 23.09
15655	25.08	272	95	61	101122	0.940	-	71	0.015	No	Survived	-	-
15656	15.08	252	89	3	113644	0.955	226.0	13	0.040	No	Fished	yes	
15657	23.08	256	90	-	-	-	-	-	-	Yes	Molted	-	Molted 17.09
15658	23.08	257	89	-	-	-	1189.2	-	-	No	Fished	yes	Signal lost 27.09
15659	22.08	280	101	23	128451	0.977	119.6	76	0.027	Yes	Fished	no	U
15660	22.08	283	107	17	-	-	-	-	-	Yes	Molted	-	Molted 17.09
15661	18.08	251	88	55	200836	0.991	42.0	128	0.028	No	Fished	yes	Defect depth sensor
15662	15.08	252	87	-	-	-	-	-	-	Yes	Molted	-	Molted 03.09
15663	22.08	290	103	61	74190	0.962	-	57	0.012	No	Survived	-	
15664	15.08	258	91	45	339505		1346.5		0.065	No	Fished	yes	
15665	16.08	275	105	3	110545		197.7		0.022		Fished	yes	
15989	5.08	289	104	61	370686		-	69	0.014	No	Survived	-	
15990	4.08	280	101	13	129133		46.1				Fished	yes	
15991	31.08	280	99	29	46013		923.4		0.014	No	Fished	yes	
15992	8.08	297	104	29	62664		97.1		0.013	No	Fished	yes	
15993	8.08	258	93	14	63925		138.2	6	0.003	No	Fished	yes	
15994	10.08	300	108	13	226094		214.4		0.030		Fished	yes	
15995	9.08	292	105	61	211151			78	0.016	No	Survived	-	
15996	9.08	272	92	2	43129		420.5	5	0.023	No	Fished	yes	
15997	9.08	297	106	6	113502		227.4	27	0.039	No	Fished	yes	
15998	9.08	251	89	19	221209		182.0	46	0.020	No	Fished	yes	
15999	11.08	250	87	61	-	0.021	- 102.0		- 0.020	No	Molted	- -	Molted 17.09
16000	11.08	281	98	24	268498	0.861	150.4	219	0.076	No	Fished	yes	Molica 17.00
16000	10.08	262	92	- 27	200430	0.001	- 150.4	213	0.070	Yes	Molted	- -	Molted 25.08
16002	10.08	250	89	61	44113	0.067	-	45	0.009	No	Survived	-	Molieu 20.00
16002		297	107	10	274736		713.0		0.003	No	Fished		
16003	11.08			36	173208				0.035		Fished	yes	
16004	12.08		100	30 8	61448		314.0		0.030		Fished	yes	
16005	12.08		91				272.1		0.007			yes	
				20	279500 47840				0.044		Fished	yes	
16007	12.08		92	3			155.4	1			Fished	yes	
16008	12.08		92	4	178434		304.0	5	0.011		Fished	yes	
16009	17.08		101	2	43621	0.945	383.7	9	0.042		Fished	yes	Singel leat 00.00
16010	15.08		99 100	33	-	-	15750	-	-	No	Fished	yes	Singal lost 08.09
16011	19.08		100	42	219734	0.327	319.5	82	0.021	No	Fished	yes	Maltad 27.00
16012	19.08		91	-	-	-	-	-	-	No	Molted	-	Molted 27.09
16013	12.08		88	6	-	-	-	-	-	No	Fished	yes	Signal lost 21.09
16014	8.08		116		641731		979.6	29	0.052		Fished	yes	
16015	8.08		99	1	211189		522.9		0.028		Fished	no	
16016	5.08		93	61	233993		-		0.007		Survived	-	
16017	8.08		95	35	48829		118.6		0.003		Fished	yes	
16018	5.08	281	105	12	46013	0.939	257.3	123	0.082	Yes	Fished	yes	

3.3 Home Ranges and lobster activity patterns

Lobster 16010 was reported harvested outside Flostadøya 15.75 km from its release position (Easting 495669, Northing 6486207), making calculations of a home range inaccurate for this individual. Several other individuals also traversed outside the listening range of the receivers, making it difficult to calculate accurate home ranges for those individuals as well. Further, a few individuals started to transmit a constant depth signal some time after tagging. This was most likely due to molting or loss of crusher claw. For these reasons 13 lobsters were excluded from further home range analysis (see Table 1).

Altogether, 37 lobsters were included in further analyses. Home range estimates for September (Table 1) and during the fishing season are shown in Fig. 12 and Appendix 1. Individuals showed a high degree of philopatry and mostly stayed within their September home range during the fishing season or until time of harvest (Table 1). On average, 90.3% (± 0.3% SE) of positions calculated for October and November were found within each individual's respective September home range. However, individuals 15989 (18.3%), 15992 (69.4%), 15998 (62.1%) and 16011 (32.7%) had relatively few positions from the fishing season within their September home range and lowered this mean.

Home range sizes ranged from 43129 to 641731 m² in September and from 12024 to 397348 m² during the fishing season. The average home range size in September was 170660 m² (\pm 20635 SE) while the average home range size during the fishing season was 123004 m² (\pm 12974 SE).

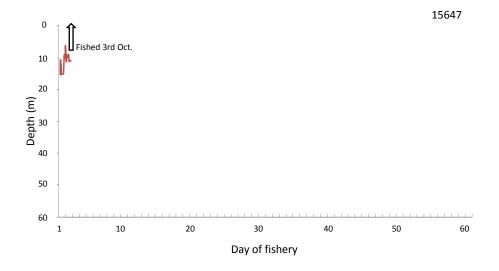


Fig. 6. Vertical movement pattern of lobster 15647 until it was harvested in Sømskilen, south-eastern Norway, in autumn 2011.

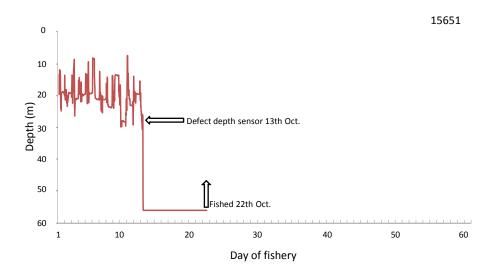


Fig. 7. Vertical movement pattern of lobster 15651 until it was harvested in Sømskilen, south-eastern Norway, in autumn 2011. Note that depth sensor malfunctioned on the 13 October.

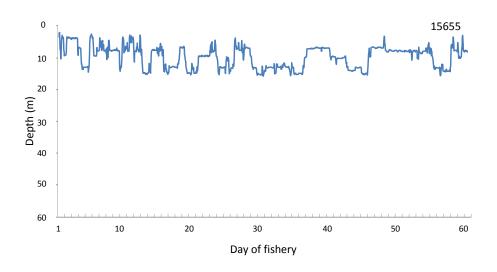


Fig. 8. Vertical movement pattern of lobster 15655 which survived the fishery in Sømskilen, south-eastern Norway, in autumn 2011.

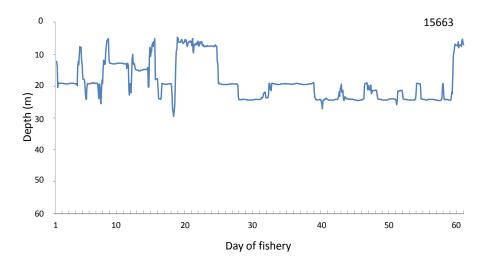


Fig. 9. Vertical movement pattern of lobster 15663 which survived the fishery in Sømskilen, south-eastern Norway, in autumn 2011.

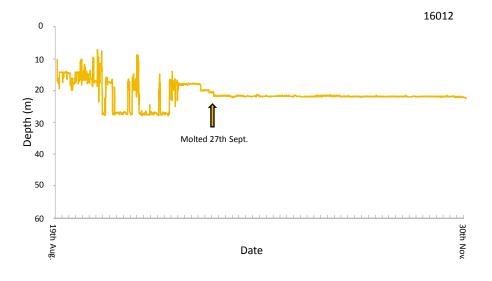


Fig. 10. Vertical movement pattern of lobster 16012 which molted and thus had an unknown fate in Sømskilen, south-eastern Norway, in autumn 2011.



Fig. 11. Vertical movement pattern of lobster 15646 which dispersed out of the study area before it was fished on day six of the fishing season in Sømskilen, south-eastern Norway, in autumn 2011.

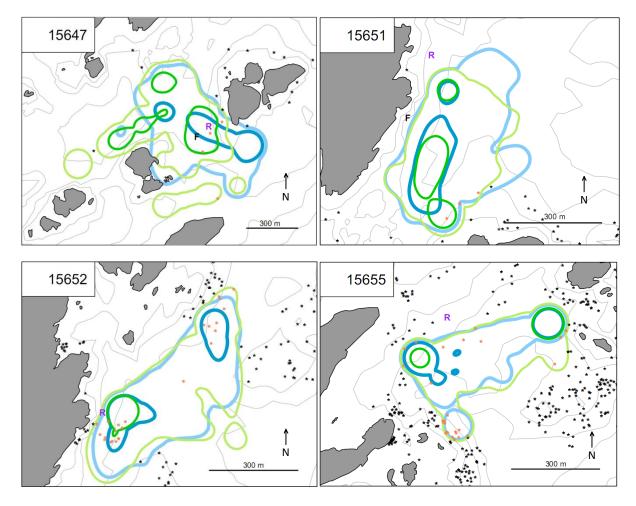


Fig. 12. Home ranges estimates for four selected lobsters in Sømskilen, south-eastern Norway, in autumn 2011. ID numbers 15647 and 15651 are lobsters that were fished. 15652 and 15655 survived the fishery. Blue home ranges are home ranges estimated for September, whereof light blue is the 95% kernel UD and dark blue is the 50% kernel UD. Green home ranges are home ranges estimated for October and November, whereof lighter green is the 95% kernel UD and darker green is the 50% kernel UD. "R" denotes the release position, e.g., the place the lobster were first tagged with an acoustic transmitter and subsequently released. "F" denotes the position reported as harvested by fishers. If a harvest position was not provided by the fisher, the last known position of the lobster was used. Stars are lobster traps, whereof the light red stars are traps within the lobsters 95% kernel UD during the fishing season used to estimate experienced trap exposure.

3.4 Fishing pressure

A total number of 4781 trap sets were registered throughout the fishing season with a mean of 78 traps per day. Overall fishing pressure was highest early in the season, with the highest count of traps registered the day 10 and 11 (145 traps) and the least registered the three last days with 10 traps each day (Fig. 13 and 14). The highest density of traps was found to be around outer laying islands and skerries (Fig. 15).

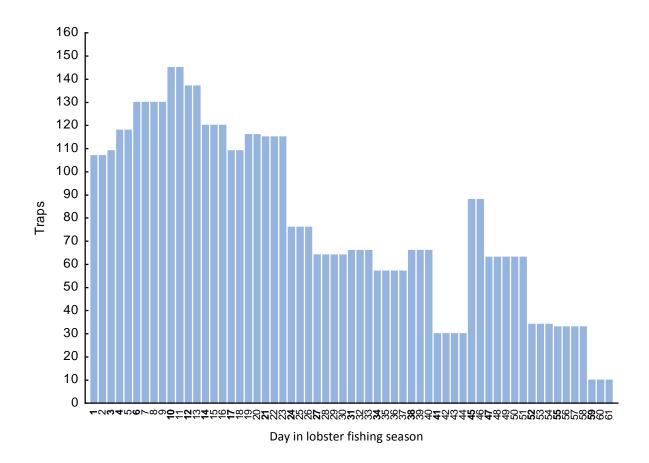


Fig. 13. Number of lobster traps counted each day in Sømskilen, south-eastern Norway, in autumn 2011. Days in bold are true trap numbers, while the following day(s) are estimates of true trap numbers (actual trap counting were not done these days).

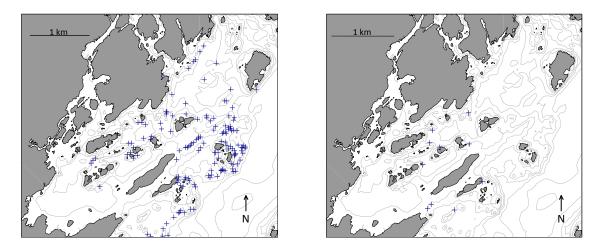


Fig. 14. Lobster traps in Sømskilen, south-eastern Norway, in autumn 2011. Left: Lobster traps registered on the day 10 of the fishing season. Right: Traps registered on day 58 of the fishing season.

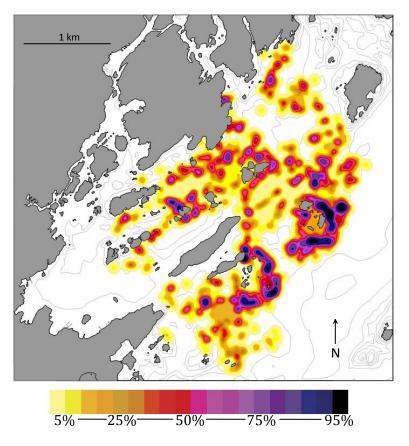


Fig. 15. Lobster trap density throughout the lobster fishing season in Sømskilen, south-eastern Norway, in autumn 2011. The darker the color, the higher the chance there was a trap at any given position within the area.

3.5 Fate of lobsters

A Kaplan-Meier analysis was done on lobster mortality (Fig. 16). Eight lobsters (15648, 15650, 15657, 15660, 15662, 15999, 16001, 16012) were censored due to molting or tag malfunction (see Table 1). Lobsters were censored when signal disappeared or lobsters sent out constant vertical and horizontal position over an extended period of time before signal loss. The first lobster was harvested on the first day in the fishing season, while the last lobster was fished on day fifty-five, six days before the season ended (Table 1). At the end of season seven lobsters were confirmed survivors. The mortality rate for the study period was 83.3% (±5.75% SE) (Fig. 16). During the first week of the fishing season sixteen individuals were harvested, with the most harvestheavy day being the fifth day when four individuals were caught. If all lobsters with unknown fate survived the fishery, the total number of survivors would be 15 which would reduce the mortality rate to 70%.

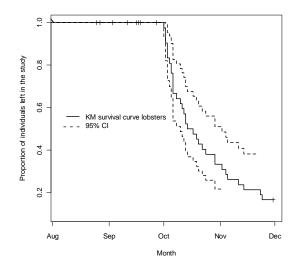


Fig. 16. Mortality rate of 50 tagged male lobsters in Sømskilen, south-eastern Norway, in autumn 2011. Vertical lines indicate censoring of a lobster.

The logistic regression analysis revealed that individual trap exposure was the only variable which had a significant effect on the fate of individuals (p = 0.0461) (Table 2). E.g., an experienced trap exposure of 0.003 is predicted to result in a survival probability of 0.5. While on the other side of the scale an experienced a trap exposure of 0.082 would result in a predicted survival probability of 0.001.

Table 2. Logistic regression analysis of fate of 50 lobsters (fished or survived at end of fishing season)caught in Sømskilen, Norway. Analysis were done by testing the dichotomous variable fate (harvested vs.survived) in relation to the selected independent variables being CL: carapace length, HR: September homerange, Ph: philopatry of individual, ETE: experienced trap exposure and Inj: loss of limbs. Selection ofsignificant variable was done by manual backward stepwise regression. Parameter estimates are providedon logit scale.

	AIC	Estimate	SE	Z-value	P-value
Model 1	36.56				
Intercept		-1.147	0.074	-1.068	0.285
CL		-0.118	0.088	1.085	0.278
HR		0.000	0.000	1.196	0.232
Ph		-0.209	2.575	0.081	0.935
ETE		-158.1	84	-1.883	0.060
Inj		-15.40	2438	-0.006	0.995
Model 2	33.074				
Intercept		-0.287	0.839	-1.145	0.252
CL		0.122	0.109	1.123	0.262
HR		0.000	0.000	1.292	0.197
Ph		-	-	-	-
ETE		-170.7	81.67	-2.09	0.037
Inj		-	-	-	-
Model 3	32.761				
Intercept		0.2588	0.781	0.331	0.74
CL		-	-	-	-
HR		-	-	-	-
Ph		-	-	-	-
ETE		-84.942	42.59	-1.994	0.046
Inj		-	-	-	-

4. Discussion

4. 1. Home ranges and lobster activity

The average home range size of lobsters in September was 170 660 m². On one side of the scale the smallest home range size was 43 129 m², while the largest was 641 731 m². There was no correlation between size of individual lobsters and their home range size. Lobster activity varied. The most active lobster dispersed out of the study area and was caught 15.75 km away from its tagging/release position. However, most fished lobsters were fished close to their original tagging position (see Table 1, Fig 12. and Appendix 1) and were fished within, or not far outside, their respective home ranges. This indicates that lobsters usually are philopatric and don't stroll far from their respective home ranges. Smith *et al.* (1998) also found that most lobsters were caught not far from their tagging spot, while some individuals exhibit a more adventurous character. Such extremes are far from the norm, but are a well known phenomenon in ecology (Krebs 2001). Variations in lobster activity are well illustrated by the depth data Figs. 6 - 11, but no analysis of these patterns was done. This could be investigated in future studies.

In estimations of kernel home ranges, the same smoothing parameter was used for all individuals. Attempts to use cross square validation for choosing a smoothing parameter for the home range analysis were done, but it did not give a clear advantage (*e.g.*, clearly less fragmented home ranges) compared to a fixed kernel method. Negatively, it caused a bias by giving some lobsters an artificially "fatter" home range than others and for some individuals an artificially "thinner" home range. In practical terms this gave individuals with a larger h-value a higher amount of traps within their home ranges than individuals with small h-values, causing a possible bias. Choosing a set smoothing parameter at h=50 for all individuals gave a reasonably fair basis for comparing home range sizes and number of traps each lobster had within its home range during the fishing season.

Moland *et al.* (2011a) found that male lobsters in Flødevigen Lobster reserve had a mean home range size of $21250 \pm 2224 \text{ m}^2$, which greatly contrasts the larger home ranges of individuals in this study. At the same time, catch per unit effort of lobsters was higher inside the Flødevigen lobster reserve than in the control area where many of the individuals used in this study were fished. Lobsters must defend their shelter more

actively if they live in lobster dense areas (Steneck 2006). Lobsters not hampered by intra-specific competition might therefore have the opportunity to have larger home ranges than their relatives living in denser areas. Having large home ranges may heighten fitness, because it gives better chance to find food and mate with more females. This could be an explanation for why there are much larger home ranges for individuals in this study compared to the sizes found by Moland *et al.* (2011a).

A second explanation for the larger home ranges, also being biological, could be that the autumn of 2011 was unusually warm and this caused heightened lobster activity. Activity in lobsters is positively correlated with water temperature (Smith *et al.*1999, Karnofsky *et al.* 1989, Moland *et al.* 2011b) and this could cause them to be more adventurous and have larger home ranges than under colder conditions.

Lastly, the observed differences could stem from the fact that two different tracking methods were used in each study. Moland *et al.* (2011a) tracked lobsters manually and even if they tracked individuals during all hours, they could not monitor lobsters continuously and thus some of the home range area could be lost. Oppositely, perhaps the acoustic monitoring array made artificially large home ranges because they "dragged" lobster positions towards listen buoy positions. This could happen for example if only one receiver buoy picked up transmitted signals over a longer period. If so the position average would be at the position of the buoy.

Some individuals had small compact home ranges, some had long slender ones, some had more patchy ones and some had spread out ones. These variations could be explained by different behavioral patterns among individuals. Also the topography of the sea bottom could play a role, where for example lobsters walk along or on top of rock or pebble reefs which gives long slender home ranges. Golet *et al.* (2006) found that movement rates among American lobsters (*Homarus americanus*) were not dependent on size but rather dependent on life stage. However, in the present study all lobsters were more or less from the same life stage (*e.g.,* mature males at 250 to 314 mm CL), so this could not be verified here.

4.2. Fishing pressure

The overall fishing pressure was highest in areas thought by fishermen to be the best lobster habitat, meaning the outer laying skerries and islands with rocky habitat (Fig. 15). This corresponds to the findings of Smith *et al.* (2001) who found that lobsters preferred rocky habitat. Individuals which had home ranges within areas with high relative fishing pressure were harvested. Individuals who experienced less fishing pressure survived. This was significant at the 95% confidence level with a p-value of 0.046 (Table 2). This also concurs with the findings of Smith *et al.* (1999) who found that the activity of individual lobsters influence their catchability. Further, Smith *et al.* (1999) found a connection between fishing pressure and fishing mortality, meaning that the more traps there are, the more lobsters are fished. Since fishers set traps in areas which they believe are lobster habitat and they fish up a high amount of the present catchable individuals there, fishing selects for those individuals that not only are under minimum catch size, but also those individuals which avoid areas which are regarded as the best lobster habitat by fishers.

It is important to note that lobster trap fishing normally does not catch all individuals in an area. The phenomenon is well known among lobster fishers and also supported by studies. Jury et al. (2001) found in studies done on American lobsters that only six percent of lobsters which entered a trap were subsequently caught. They concluded that lobster traps are ineffective and catch only a small proportion of lobsters present in a certain area. Other studies that strengthen this theory have been done by Lovewell *et al.* (1988) and Watson et al. (2009). Lobsters even above MLS can easily escape from traps unless they have entered the innermost 'parlour' chamber. It is only these individuals or those present in the bait chamber ('kitchen') at hauling that are caught. Another important factor behind the observed low effective catch rates is saturation of traps, e.g., if a lobster is already caught in a trap it is more unlikely that another will enter (Smith et al. 1999). This study also notes that interaction between conspecifics and other species outside the traps have a major impact on individuals' catchability. As larger individuals usually fend of smaller ones from a food source, smaller individuals could be fended off from traps. This means that intra-specific competition could select for survival of smaller individuals in fished populations. In the present study this phenomenon could

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heighten the number of traps an individual had to encounter to be fished and because of bait attraction also affect lobster movement behavior under the fishing season.

4.3. Lobster mortality

The fishing mortality of the 50 lobsters in this study was 83.3% (Fig. 16). Mortality was highest in the first two weeks of the fishery, coinciding with the highest number of traps being set early in the fishing season (Figs. 10 and 16). No other studies have reported a mortality rate this high in any lobster species. In comparison, mark/recapture studies done by Smith *et al.* (2001) and Bannister & Addison (1986) on lobsters in southern England reported mortality rates of 26, 49 and 52% and 35 - 55%, respectively.

The reason for the observed high mortality rate could stem from the fact that Sømskilen is known among locals to be a heavily fished area under the lobster season. The high mortality rate might not be representative for the lobster population along the Skagerrak coast, but may rather be higher than the norm.

On the more technical side, both Smith *et al.* (2001) and Bannister & Addison (1986) operated with much larger sample sizes than used in this study and their estimates may thus be more representative for a lobster population as a whole. It is also important to note that the lobster population in Southern England has not plummeted as the Norwegian population has and this may also have had an effect on the different results obtained.

Another technical bias could be that all lobsters in this study except one were caught by the use of lobster traps, meaning that forty-nine individuals were already prone to enter traps. This "selectivity of traps problem" is also mentioned by Smith & Tremblay (2003) and is a reoccurring problem in lobster science. Further, we do know from studies done on American lobster, that by setting traps one facilitates for lobsters to walk intro traps (Bowlby *et al.* 2007). The effect of this is so significant that it's even thought to maintain an unnaturally large lobster population in Maine (Saila *et al.* 2002). This especially applies for berried females, which are protected, and individuals below MLS. Both groups get a free meal when entering traps because they leave through escape vents or are released if caught. Thus, it could be that the capture method used in this study also

conditioned the forty-nine lobsters to walk into traps, because they had already been "rewarded" before the study started. Ideally, all lobsters studied should be caught by using other methods, but this was impossible to accomplish.

As noted above, the fishery observed in this study most likely selects for survival of smaller individuals. Wynne & Côté (2007) found the same in a study done on spotted spiny lobsters (*Panulirus guttatus*) in Anguilla. Selective fishing is a major problem in marine conservation biology and has a negative effect on populations, biodiversity and whole ecosystems (Fenberg *et al.* 2008, Garcia *et al.* 2012). A natural environment selects for larger body size while fishing usually targets these large individuals (Carlson *et al.* 2007). Fishing of large individuals means that harvested stocks are better off if they grow slowly, meaning that we impose a strong artificial selection on exploited populations. One can imagine how strong this effect is on European lobsters if over 83% of the catchable population is harvested annually.

Alarmingly, if it is so that the mortality rate of 83.3% observed in this study is representative of a given catchable lobster population it would mean that after just a few years fishers would deplete the catchable part of a population completely and thus artificially suppress lobster populations so that they mainly consist of individuals below MLS.

4.4. Use of equipment

The main reason of the range testing (Fig. 5) was to quality check the VEMCO buoy system and its ability to detect an individual should it be present in the study area. In another study using 25 similar buoys as in this study, Olsen & Moland (2010) found that 92% of the signals deployed were detected by one or more receivers. Many factors affect the possibility that an acoustic signal will be logged by a receiver. This could be vegetation, different sensitivities and powers between pieces of equipment, signal overlap due to large numbers of tagged animals present in an area, noise from biological (*e.g.*, benthic organisms) and human sources (*e.g.*, boat motors). All of these factors tend to reduce the linearity in the relationship between the number of signals received and the distance from a receiver (Simpfendorfer *et al.* 2002). Having said so, it is safe to say if a lobster is present within the system for some time, it would be detected due to the

high detection rates of range testing tag deploys. However, some shallow inner areas close to land had bad reception, but this was hard to work around due to the geography of the area.

Van der Meeren (1997) also found that tracking lobsters in their natural habitat was difficult because of varied bottom structure. The fact that many lobsters hide in dens during the day may also interfere with signals and even make false signals because of reflections from rock surfaces). Smith *et al.* (1998) also commented on this being a particular problem. Further, Watson *et al.* (2009) found that positions given by receivers can be highly erroneous and under their study on American lobsters chose to exclude 46% of the positions given by the acoustic array. Contrastingly, the present study used 95% of the positions given to calculate home ranges, as done by Moland *et al.* (2011a). However, Watson *et al.* (2009) did a more fine-scaled study on movement patterns and not a home range study. Hopefully by removing 5% of the positions one would also exclude occasional strolls done by individuals and pings detected by only one receiver, whereof the last would place positions exactly at the position of the receiver.

Many individuals dispersed out of the study area and were fished south of the outermost receivers around Tjuvholmane (between receiver 15 and 43, 44). These individuals were excluded from the analysis. The area around Tjuvholmane is thought of as prime lobster habitat and is popular lobster fishing grounds as shown by the fishing pressure map (Fig. 15). A few lobsters also had home ranges in outer laying areas, meaning that these home range sizes could be underestimated. Van der Meeren (1997) and Watson *et al.* (2009) also comments on this problem, whereof Watson *et al.* (2009) removed several lobsters from their analysis because they stayed in the outer vicinity of the study area. To overcome this problem Golet *et al.* (2006) suggested to limit off *in situ* areas by constructing a mesocosm where caught individuals were placed. However, this was never an option here due to the large geographical scale of this study and as we aimed to monitor natural behaviors in the natural habitat of the tagged population

Mainly because of the small dataset, and a loss of eight individuals due to molting, a choice was made to include all possible lobsters in the analysis even if their home ranges were in the study area's outer parts.

5. Conclusion

In the lobster fishing season of 2011 in Sømskilen, south-eastern Norway, estimates suggest that 83.3% of the catchable male population may have been harvested. This gives a survival estimate of only 16.7%. Further, because lobster traps are often set in habitat believed to be favorable for lobsters, lobster fishing selects for individuals settling in what can be less favorable habitat, because as shown, survival seem to depend mostly on individuals' experienced trap exposure. Out of 50 observed individuals, only those seven which were exposed to the least degree of fishing pressure were confirmed to survive the lobster fishery. These survivors may, because they avoided typical lobster habitat, be less fit in their natural environment than their harvested conspecifics. If a survival estimate of 16.7% is representative for the whole catchable population for three consecutive years, one would end up with only 0.47% of the original cohorts entering the legal size limit in any given year due to the fishery alone. This indicates that fishing strongly select for survival of size classes below MLS (slow growth) and, somewhat awkwardly, for behaviors avoiding what is thought to be typical lobster habitat by the human predator.

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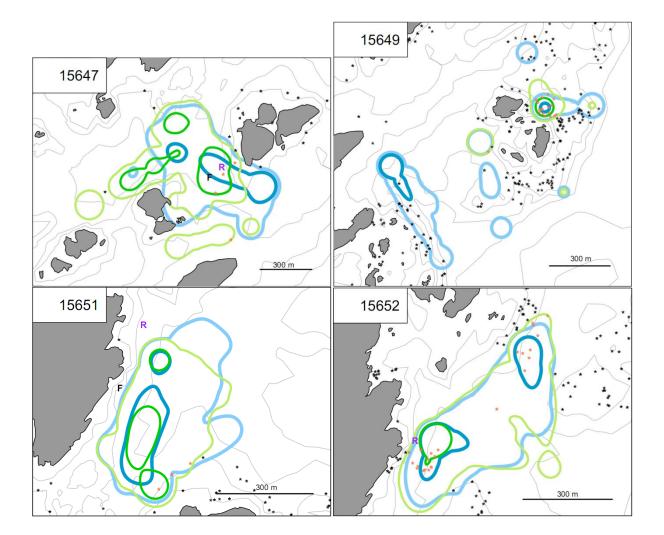
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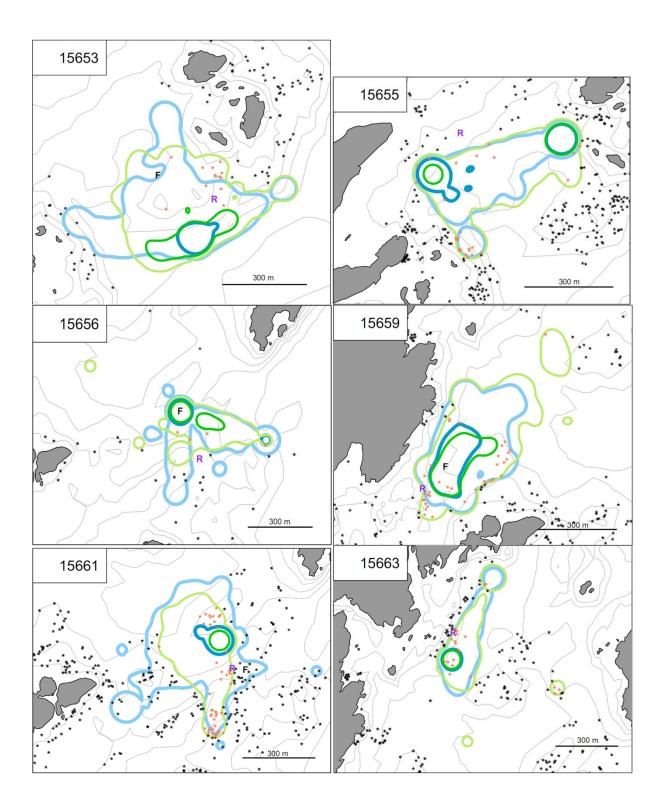
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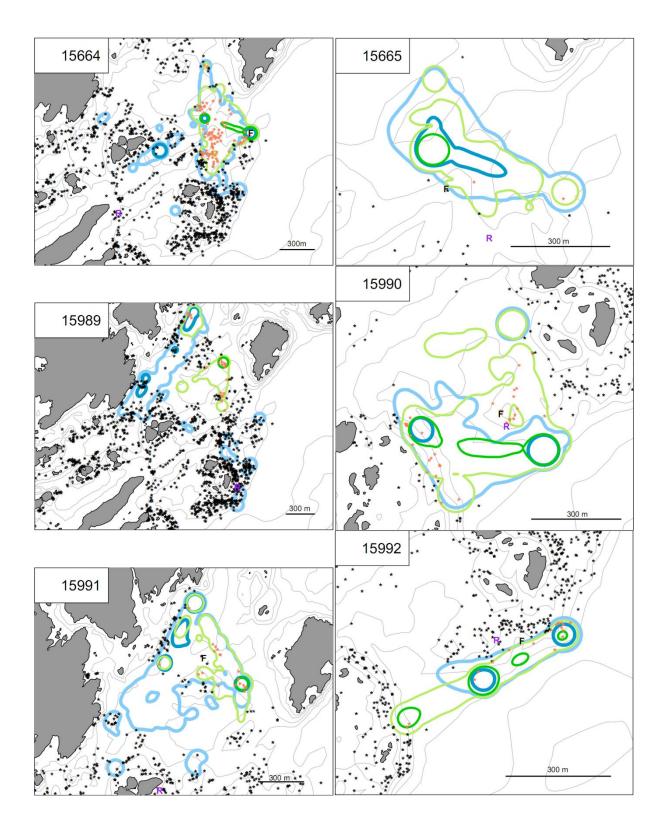
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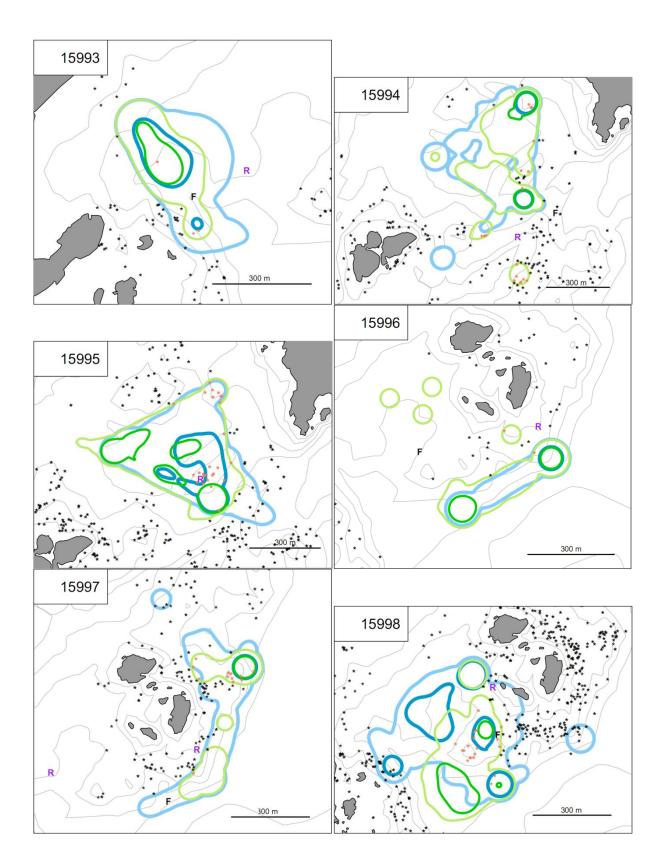
Appendix 1

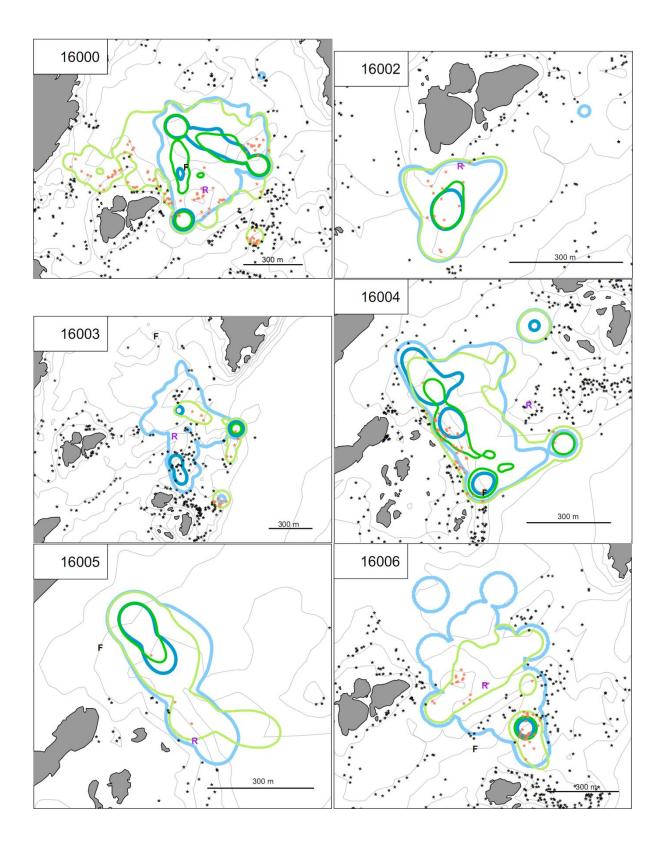
Home ranges for all lobsters which still transmitted position data up until either they were fished or fishery ended (N=37). All lobsters except 15652, 15655, 15663, 15989, 15995, 16002 and 16016) were fished. Blue home ranges are home ranges calculated for September, whereof light blue is 95% kernel and dark blue 50% kernel. Green home ranges are home ranges calculated during October and November, whereof lighter green is 95% kernel and darker green is 50% kernel. "R" is the release position e.g. the place the lobster were first tagged with acoustic transmitter and released. "F" is the position reported by fishers that the lobster was fished. If fishing position were not given by fishers, the last known position of the lobster was used. Stars are lobster traps, whereof the light red traps are traps within the lobsters 95% kernel during fishery.

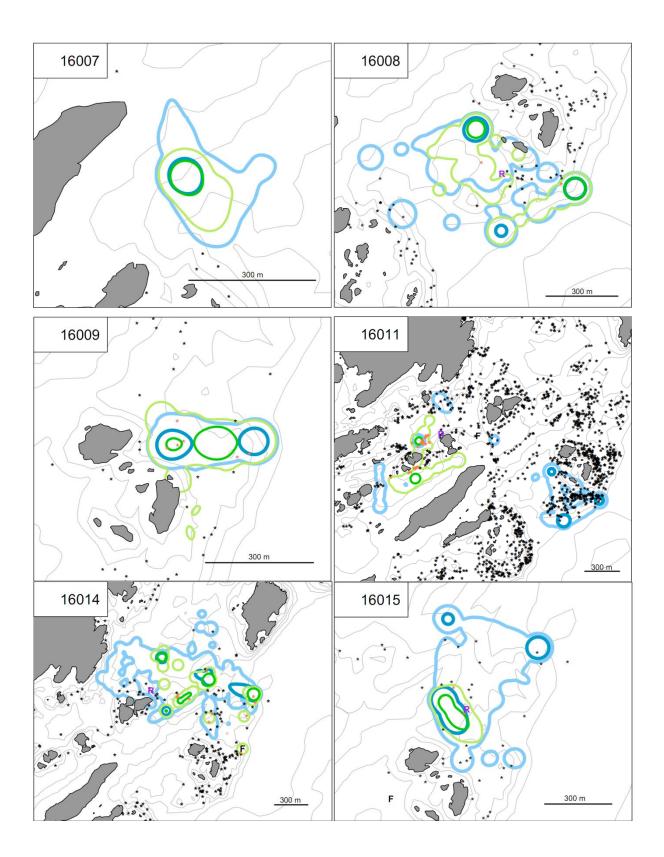


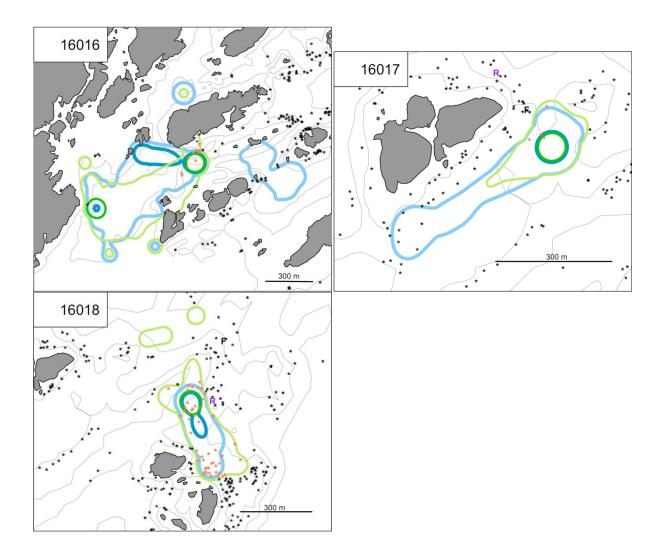






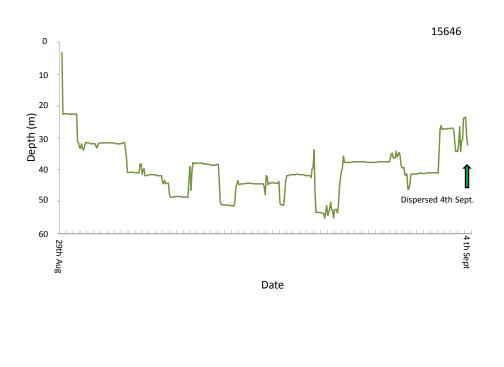


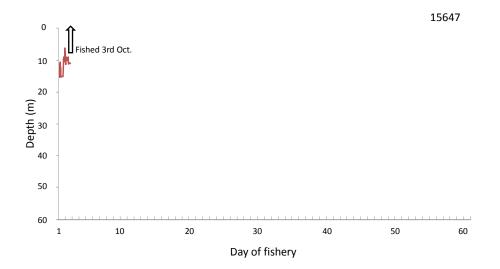


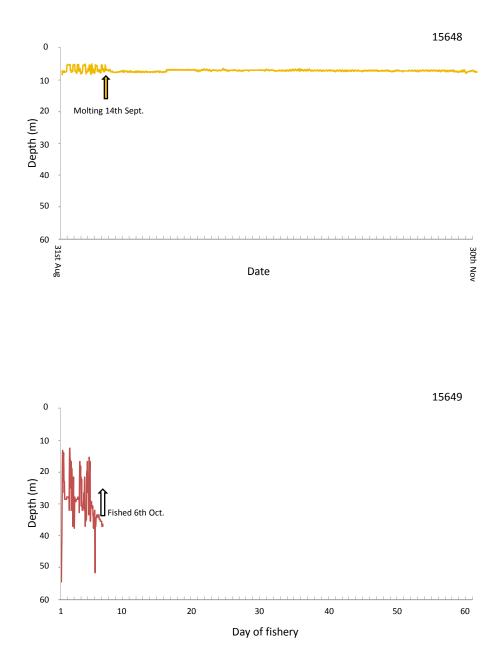


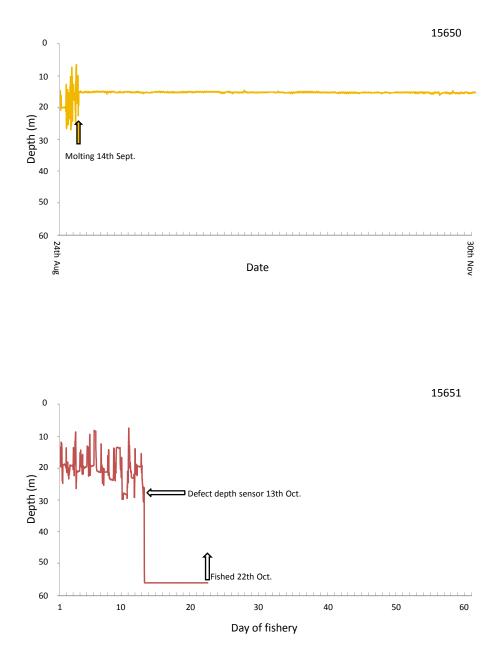
Appendix 2

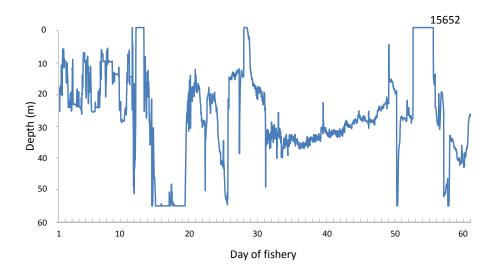
Vertical movement patterns (depth) for all lobsters. Fished lobsters are given in red, alive lobsters are given in blue. Molted lobsters are orange. Lobsters which signals were lost for unknown reason are given in grey. Lobsters which dispersed out of the study are are in green. The maximum depth that could be registered by transmitters were 55meters, meaning that if a lobster ventured below this depth, 55meters were registered. Also not that for lobster 15652, the depth sensor malfunctioned around ten days within the fishery and erroneous depth data were given.

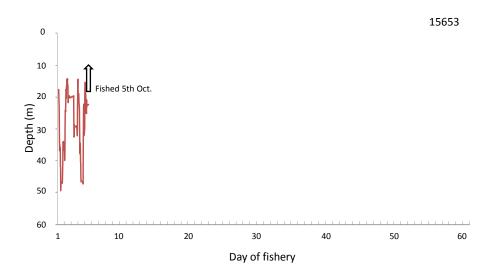


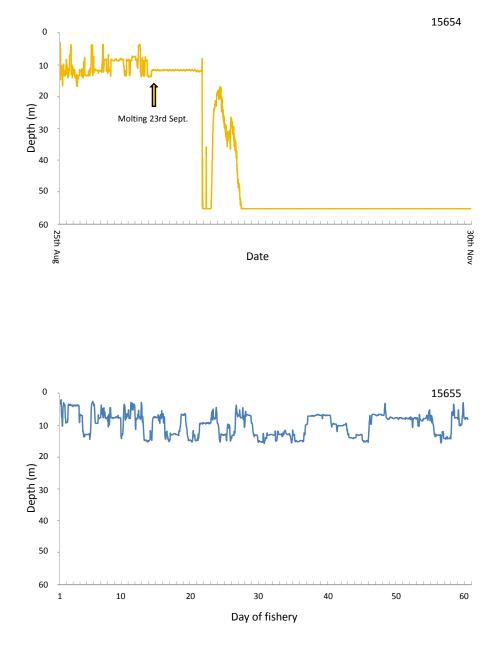


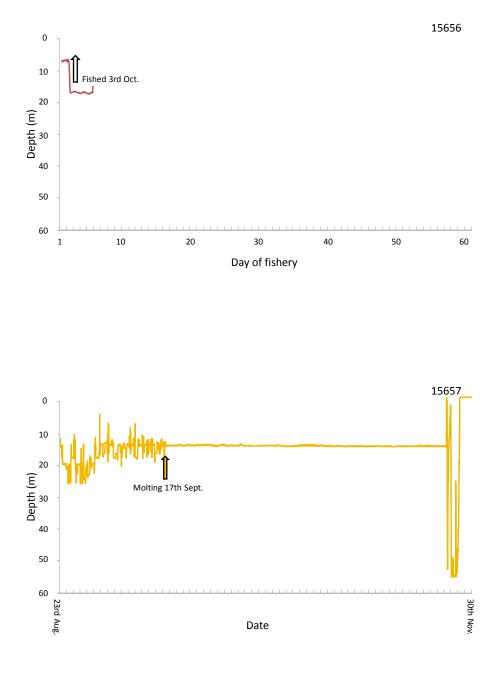


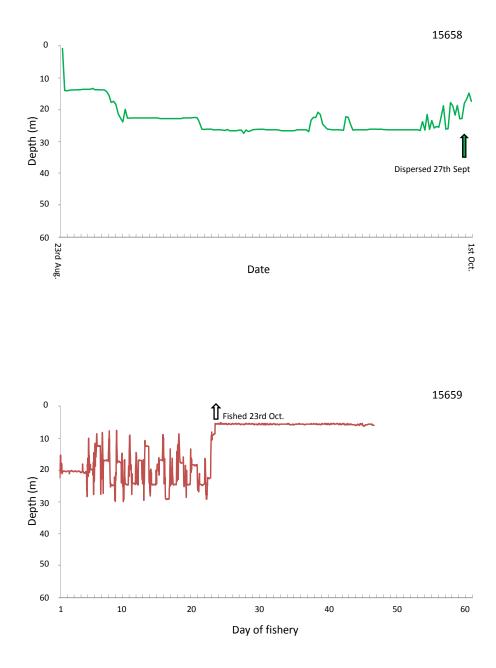


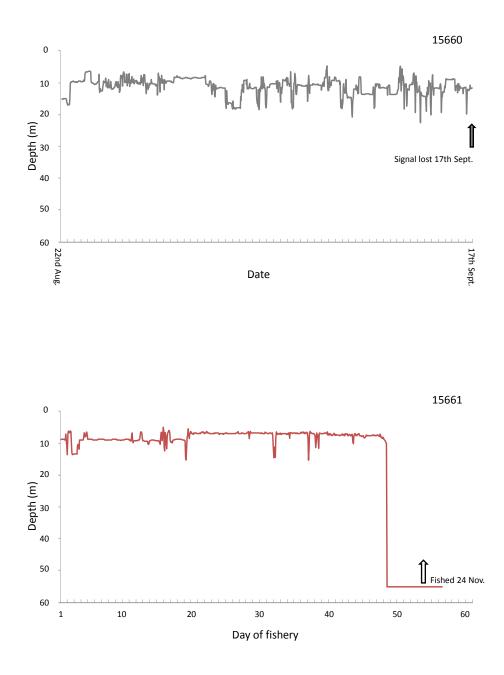


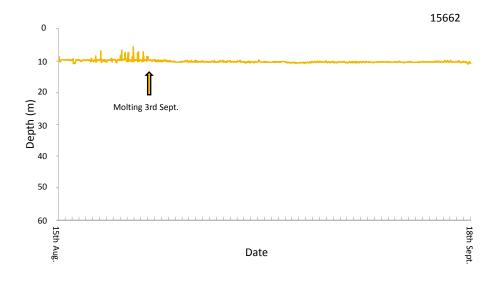


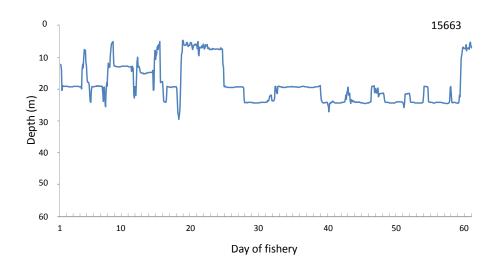


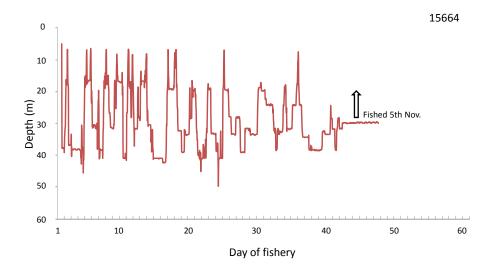


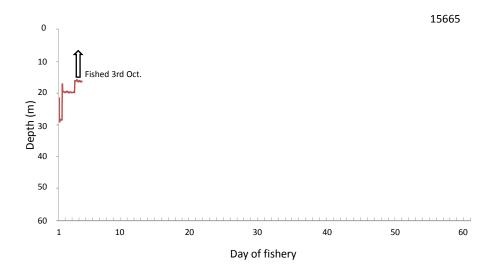


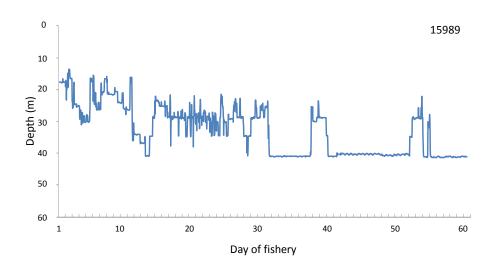


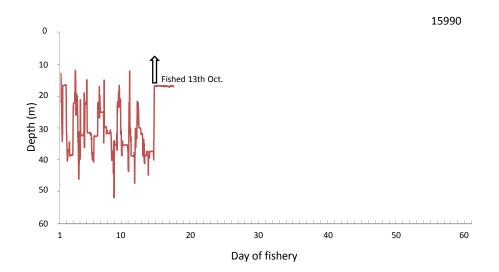


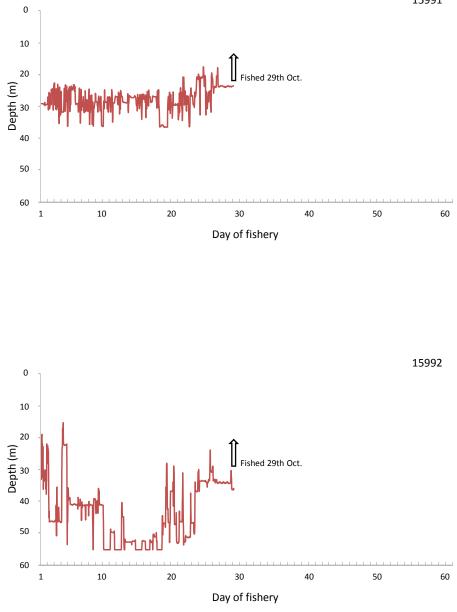


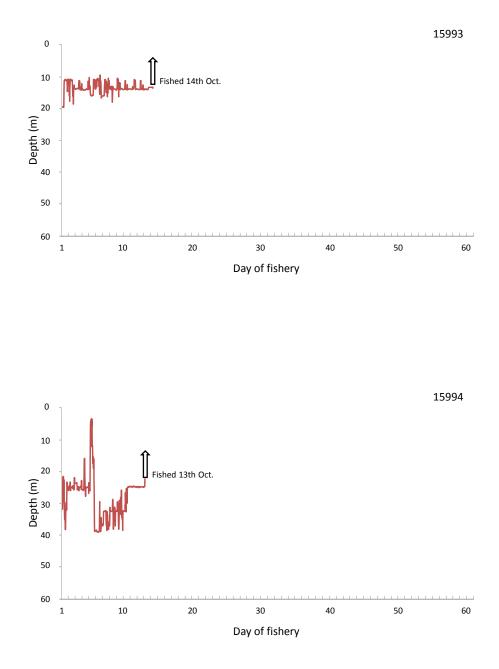


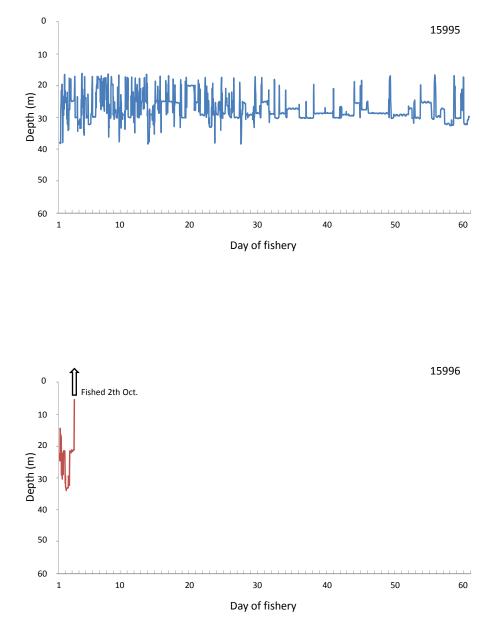


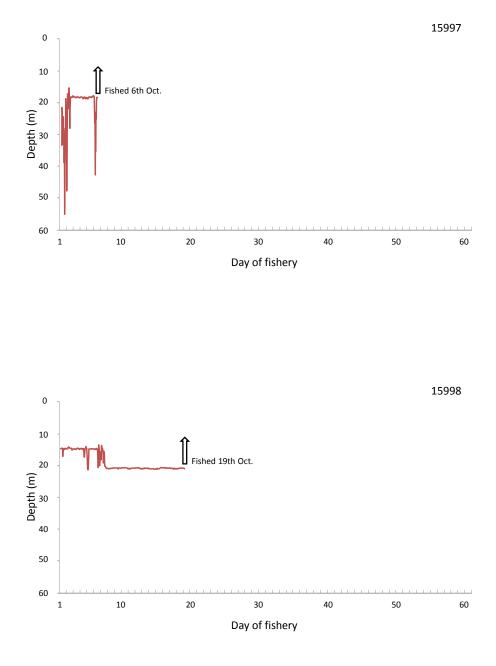


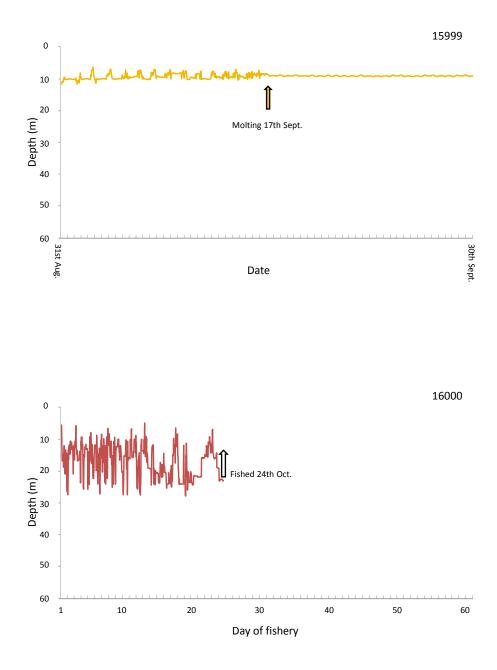


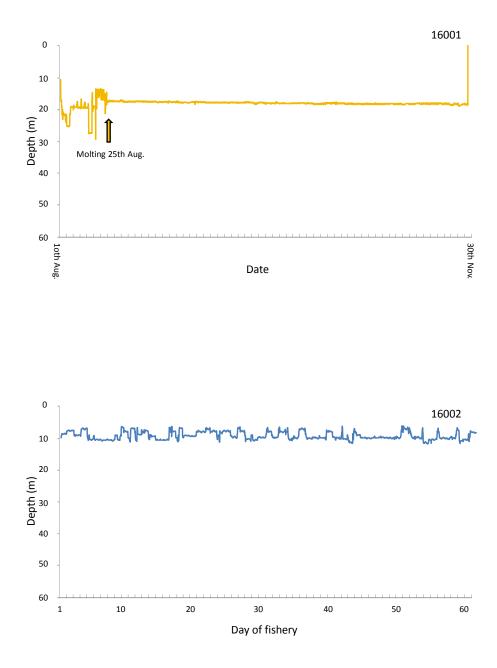


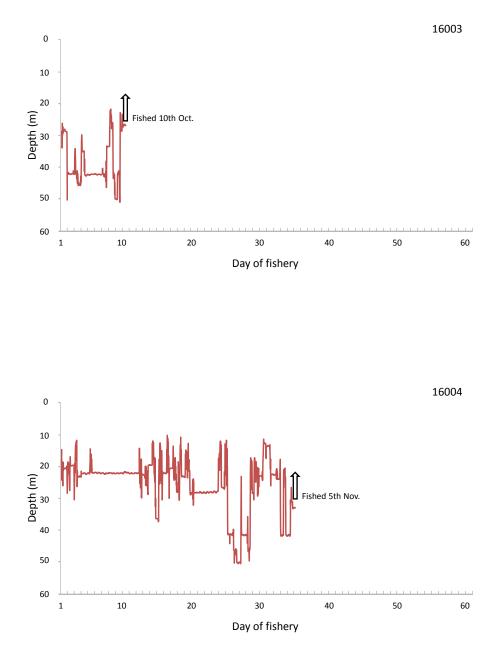


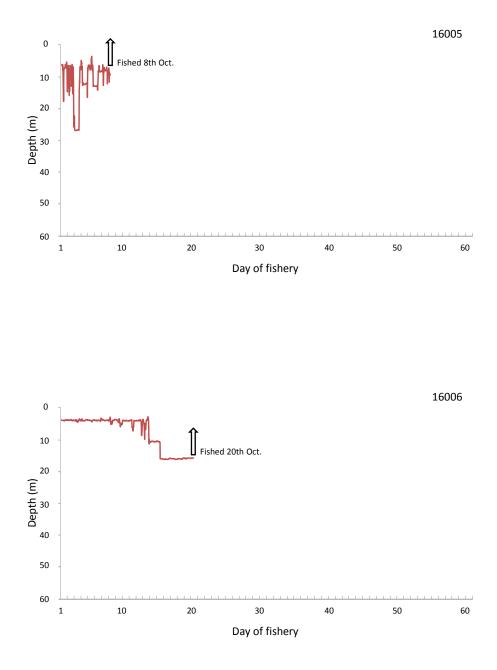


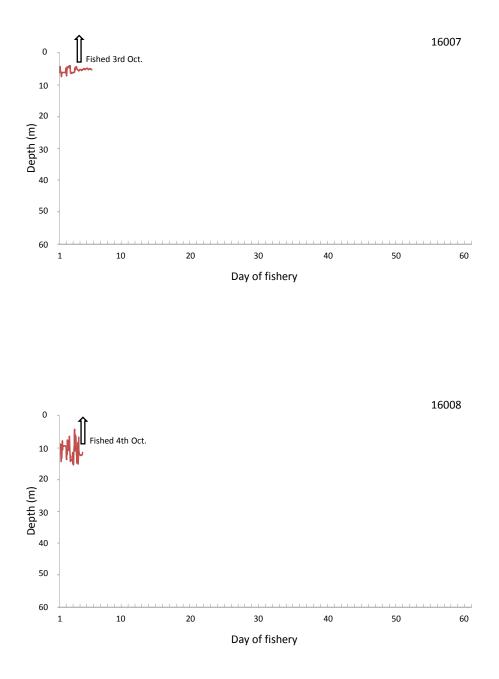


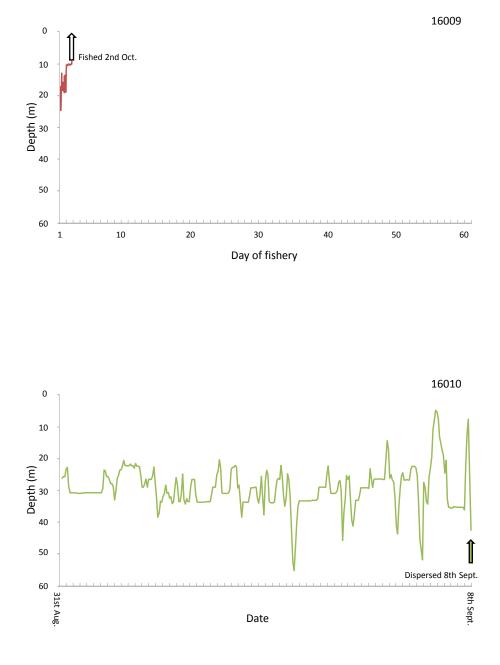


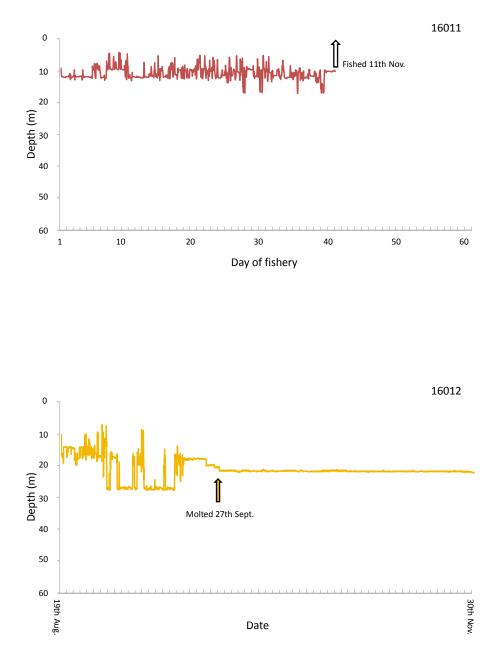


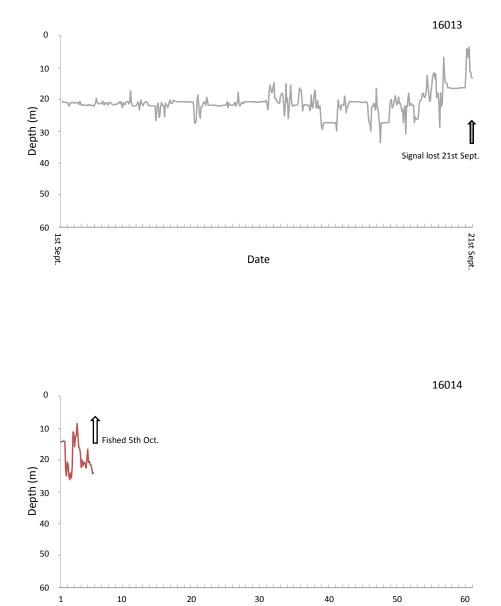






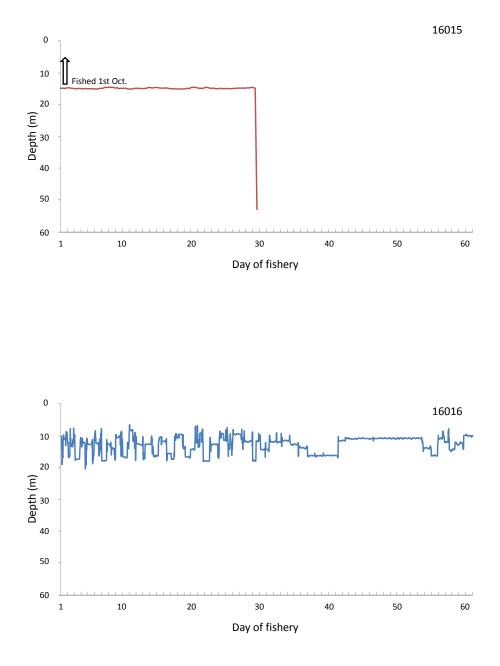


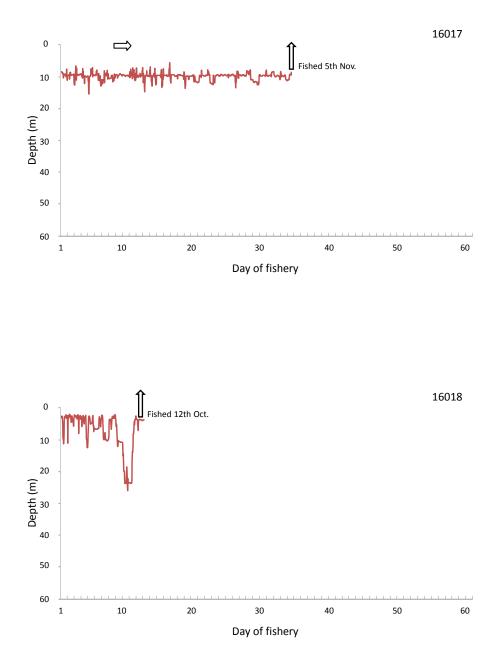




Day of fishery

71





Appendix 3

Trap positions registered during the fishery. Days when traps were not registered an estimation of numbers and positions were done by using the trap positions from the day before.

