Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natral Resource Management (INA)

Master Thesis 2015
60 credits

Diel cavity use in wild European lobster (*Homarus gammarus*): behavior and implications for management

Julianne Island

Preface

The lobster's popularity becomes evident each autumn as the attention from the media increases. Working with a species that receives such amounts of attention and that many people relates to, has made the work with the thesis extra exciting, and there has never been a lack of interest when I have told what my master thesis deals with. The project was carried out at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences (NMBU). A special thanks to the marine biologist Sondre Ski at for making the lobster house, placing it in the Oslo fjord and back up of data. Also, a sincerely thanks to my supervisors Thrond O. Haugen and Ronny Steen for helping me with everything from changing SD cards to sorting out statistical tangles. I am truly grateful for your generosity with sharing your time and given me constructive feedback during the entire process. Thank you Jessica Marks for helpful comments on the manuscript and for correcting my English, perhaps the most overwhelming task of them all, and Oddbjørn Pettersen at NIVA for providing water temperature and salinity data. And of course, thank you my dear friends for putting out with me these past months.

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Julianne Island

Ås, May, 2015

Abstract

Knowledge and understanding of an animal's diel activity and temporal and spatial positioning within a habitat is important if we want to understand the pattern behind an animal's movement and behavior. Information about normal behavior and activity in the field is vital for managing the species. From the 1950s through the 1970s, there was a dramatic decline in the catches of European lobster (*Homarus gammarus*). The number of lobsters is now so low that the species is registered as "near threatened" on the Norwegian "red list". In this study, diel cavity use was analyzed in relation to season and environmental factors such as water temperature and light conditions. Further, I explored patterns of cavity use throughout the day for two years. A custommade cavity was placed at ca. 20 m depth in the Outer Oslofjord and monitored with a CCD camera from November 2012 to November 2014. For each lobster observed, activity was recorded as entering or exiting the cavity, time entered or exited, and under what light conditions the activity occurred. Data analysis using generalized linear mixed effect models (GLMM) and linear mixed effect models (lme), showed that the lobster was most active under low light conditions and that lobster activity level was positively correlated with water temperature. Also, the overall impression was that there was a higher activity level in the summer and early autumn, and a drop in the activity through the winter. As the lobster's activity is correlated with temperature, climate change with corresponding rising sea temperatures might lead to changes in lobster behavior and refugee use. The possible resulting changes in catchability and the effect it will have on the exploitation of lobster stocks should be further explored to ensure a sound foundation for decision making, and potentially make changes in the duration of today's fishing season.

Sammendrag

Kunnskap og forståelse om et dyrs døgnaktivitet og temporale og romlige habitatbruk er viktig om vi skal kunne forstå dets bevegelsesmønster og atferd. Informasjon om hva som er normal aktivitet er essensielt for forvaltningen av arter. Fra 1950 og gjennom 1970 var det en dramatisk nedgang i fangstene av europeisk hummer (*Homarus gammarus*). Bestandsestimatene er nå så lave at arten er karakterisert som nært truet på Norske rødliste. I dette studiet er skjulbruken gjennom døgnet analysert i forhold til miljømessige faktorer som vanntemperatur og lysforhold. Videre ønsket jeg å se på hvordan hummer bruker skjulesteder gjennom døgnet og gjennom året. Et spesiallaget skjulested ("hummerhus") ble plassert på 20 m dyp i Ytre Oslofjord og overvåket med et CCD kamera fra november 2012 til november 2014. Hummerens aktivitet ble notert som "entre" eller "forlate" skjulestedet, tiden den gikk inn eller ut og hvilke lysforhold det var. Ved bruk av "generaliserte lineære blandet effekt" modeller (GLMM) og "lineære blandet effekt" modeller (lme), ble det funnet at hummeren var mest aktiv når det var mørkt, og at aktivitetsnivået korrelerte positivt med vanntemperaturen. Det ble funnet et høyere aktivitetsnivå på sommerstid og tidlig vår, og lavest aktivitet gjennom vinteren. Fordi hummerens aktivitet er korrelert med temperatur, er det mulig at klimaendringer, med høyere havtemperatur, fører til endringer i hummerens atferd. Den mulige endringen i fangbarhet som kan resultere fra økt aktivitet, og effekten dette vil ha på utnyttelsen av hummerpopulasjoner, bør utforskes videre for å kunne gi et godt vedtaksgrunnlag, og muligens bør dagens fangstperiode kortes noe inn.

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Introduction

The niche concept plays a central role in ecology and has aided ecologists in explaining the coexistence of multiple species within the same spatio-temporal habitat. The niche, as defined by George Evelyn Hutchinson (1958), is a multidimensional concept entailing environmental factors and resources, including space and time. Over time, a specie's niche can change through natural selection (Macarthur & Levins 1967), and only suitable parts of the spatial niche, the fundamental niche, is used (Hutchinson 1958). An animal's local distribution is further limited by the presence of, and competition from, other organisms, described through the Volterra-Gause principle (Hutchinson 1958), limiting the fundamental niche to the realized niche (Hutchinson 1958).

Time constitutes an important niche limitation, restricting the animal to its temporal niche (Carothers & Jaksic 1984 and references herein). Roth and Huber (1986) proposed that diel activity is an important contributing factor to a species ecological niche. Hence, knowledge and understanding of an animal's diel activity and temporal positioning within the habitat is important if we want to understand the pattern behind the animal's movement and behavior. When habitat changes, some animals are not able to adapt sufficiently quickly and therefore inhabit only a portion of their potential habitat range (e.g. Fabry et al. 2008). This will also influence the activity pattern, and information about the normal activity is an important tool for managing the species (e.g. Alós et al. 2012; Olsen et al. 2012; Roth & Huber 1986).

Time series from the Swedish west coast, dating back to 1875, reveal a slight decline in the catches of European lobster (*Homarus gammarus*) over the first 80 years, followed by a dramatic decline in the catches from the 1950s through the 1970s (Sundelöf et al. 2013). The same was observed in the Norwegian catches, where post 1980s landings declined to lower than 10% of the pre-1960 level (Olsen & Kleiven 2014). As a consequence, the lobster is now registered as "near threatened" (NT) in the Norwegian "red list" (Lindgaard et al. 2012). The decision is based upon time series from Skagerrak, western Norway and total catches. Today's harvesting regime has a major impact on the lobsters' ecology, as it may lead to high mortality of dominating males and the movement of "beta-males" from low quality habitats (Wiig et al. 2013). To fully understand the process behind the long-term decline in lobster populations, and construct a sustainable harvesting program it is important to understand this species' niche, both spatially and temporally.

The Norwegian Directorate of Fisheries (NDF) has implemented protection measures (NDF 2011). Fishing for lobsters is permitted along shore from the Swedish boarder to Sogn and Fjordane County from the 1st of October until the 30th of November. For the rest of the country, the lobster fishery is open from October 1 through December 31. There is a "no-take" policy for berried (egg-bearing) females, and the minimum legal size for harvestable lobsters is 25 cm, measured from the eyes to the end of the carapace, i.e. the carapace length (CL) (NDF 2011).

In addition to fisheries regulation, another attempt to restore the declining lobster stock has been to stock cultured lobsters into the wild (Addison & Bannister 1994; Bannister et al. 1994; Jørstad et al. 2008). Both *Homarus americanus* (American lobster) and *H. gammarus* have on several occasions been released into American and European waters, respectively (Addison & Bannister 1994). Results from the East coast of England show that three-month old hatchery-reared lobsters survived for up to eight years in the wild, and were later caught by commercial fishermen (Bannister et al. 1994). From 1990 to 1994, there were hatchery-reared lobsters introduced into waters outside Kvitsøy in Rogaland (Jørstad et al. 2008). The first hatchery-reared lobsters were caught by local fishermen after 3-4 years, and the introduced lobster individuals from 1990-1994 were still present in the 2005 and 2006 catches.

Marine protected areas (MPA), and the resulting prohibition of fishing within these areas, is yet another method to restore and protect the lobster populations (Halpern & Warner 2003; Moland et al. 2013a). Much of the published information on behavior of the European lobster is gained studying it in MPAs (Moland et al. 2011a; Moland et al. 2011b; Moland et al. 2013b). These reserves offer opportunities for long-term studies on species under natural conditions, without being affected by harvest mortality and disturbance of fishing gear (Moland et al. 2011b). The reserves offer the possibility for gaining knowledge regarding population dynamics, behavior, and the development of local lobster populations (Moland et al. 2011a). Moland et al. (2011a and 2011b) conclude that, in some cases, even small costal reserves (≈ 1 km^2 in size) may protect relevant fractions of European lobster populations.

According to Norwegian legislation, the management goal for species is that "the species and their genetic variety are to be protected in a long-term scenario" (Naturmangfoldloven § 5). Further law § 8 states that "public decisions affecting the biological diversity shall, within all practical means, rest upon scientific knowledge about the species population situation" (Naturmangfoldloven § 8). Information on fine-scale behavior of the European lobster under natural conditions is scarce (but see: Agnalt et al. 2007; Hallbäck & Warén 1972; Moland et al. 2010; Moland et al. 2011a; Smith et al. 2001). The shortage of detailed information on lobster behavior in the wild reflects the difficulties of observing nocturnal marine animals. Through the use of video cameras, the aim of this study is to register and quantify diel cavity use, and map out the lobsters' diel activity in the wild. This is knowledge that is required in order to have grounds for sustainable management of lobster populations, based among others upon the lobsters' ecology, including its temporal niche. In this study, diel cavity use was analyzed in relation to season and environmental factors. I examined how lobster behavior may be affected by environmental factors such as water temperature and light conditions. Specifically, I aim at exploring cavity use by lobsters in relation to time of day and season.

Material and methods

Study area

A cavity (artificial shelter or lobster house) was custom made, with 35×35×20 cm walls of stone bricks, and a concrete flagstone as a roof (Figure 1). The opening measured 30×15 cm. It was located in the outer Oslofjord (Figure 2), about 200 meters from the Drøbak shore (Euref89 UTM32 6614801N 591551E) as a part of an ongoing project in collaboration with the drøbak Aquarium. It was located at about 20 meter below sea level, in an area dominated by sublittoral sediments and mud (Rinde et al. 2009).

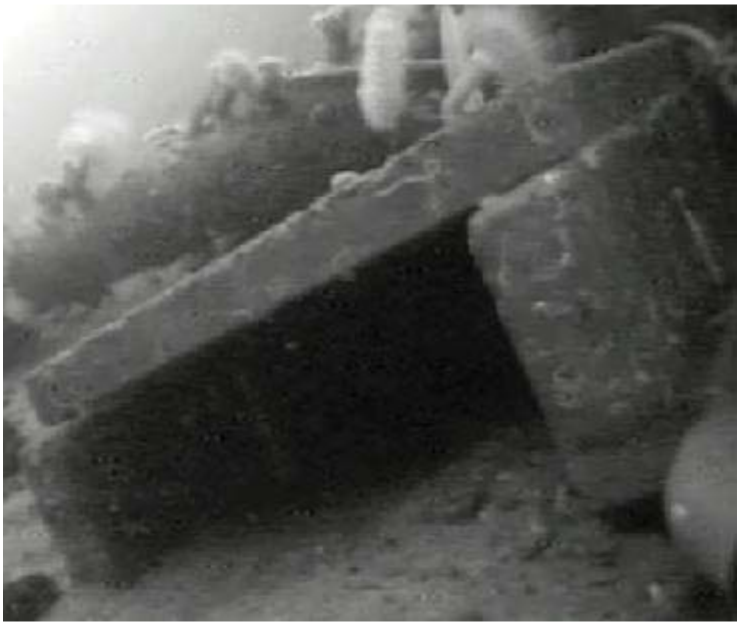

Figure 1. The artificial lobster cavity used in this study, with its 35x35x20 cm walls of stone bricks and the concrete flagstone roof.

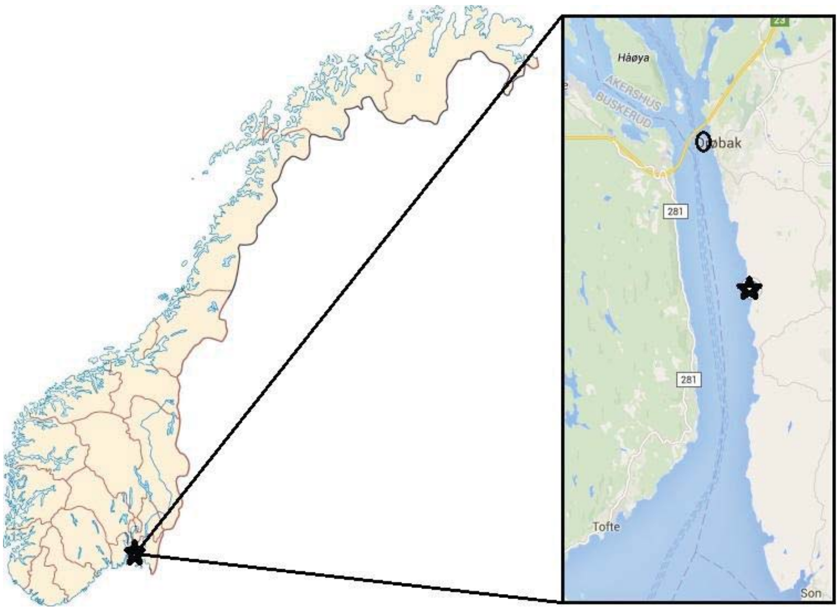

Figure 2. Map of Norway with a circle indicating the study area (with the lobster cavity), and the star indicating the NIVA Research Facility where the temperature data were collected, both located in the outer Oslofjord. The maps are based on Gyldendal (2015) and Google (2015).

Study species

The geographical distribution of the European lobster extends from north-western Norway south to the Atlantic coast of Morocco (Triantafyllidis et al. 2005). Sheehy et al. (1999) were able to determine age of wild lobsters through a calibration based on the natural rate of lipofuscin accumulation in an eyestalk ganglion of European lobsters. The oldest lobster recorded in the study from the Yorkshire fishery (United Kingdom), was a 72±9 years old female (Sheehy et al. 1999). The oldest male was 42±5 years. The average age of males and females (150-170 mm CL (Figure 3)) were 31 and 54, respectively. The lobsters maximum total body length is about 60 cm (5-6 kg), but large-sized specimens are usually 23 to 50 cm (Holthuis 1991). Agnalt et al. (2007) found that females moult every two years, immediately after their eggs hatch, increasing and average of about 7 mm at each moult. Lobsters are poikilothermic (the body temperature fluctuates according to that of the surroundings) ((Waterman 1960), tend to move more at higher water temperature (Moland et al. 2011b). They are mainly nocturnal (Moland et al. 2011b) but a considerable activity level has been observed during daytime in August, September and November (Smith et al. 1999). Smith et al. (1999) also found indications that the diel timing of lobster movement is largely governed by changes in the light level. The activity was greatest during summertime, and as the activity level decreased during the winter, the diel pattern disappeared (Smith et al. 1999). This was thought to be a response to the low water temperatures.

The European lobster's main food items are snails and other bottom dwelling organisms, mainly Malacostraca, Gastropoda and Polychaeta (Hallbäck & Warén 1972). Hallbäck and Warén (1972) found no difference in food preference between males and females, nor did they find any difference in preferred food between lobsters caught along the Swedish coast. Although, they found that the preferred diet does differ throughout the year. During the summer, the diet consists of more shallow living blue mussels (*Mytilus edulis*), while it consist of horsemussels (*Modiolus* spp) during the winter.

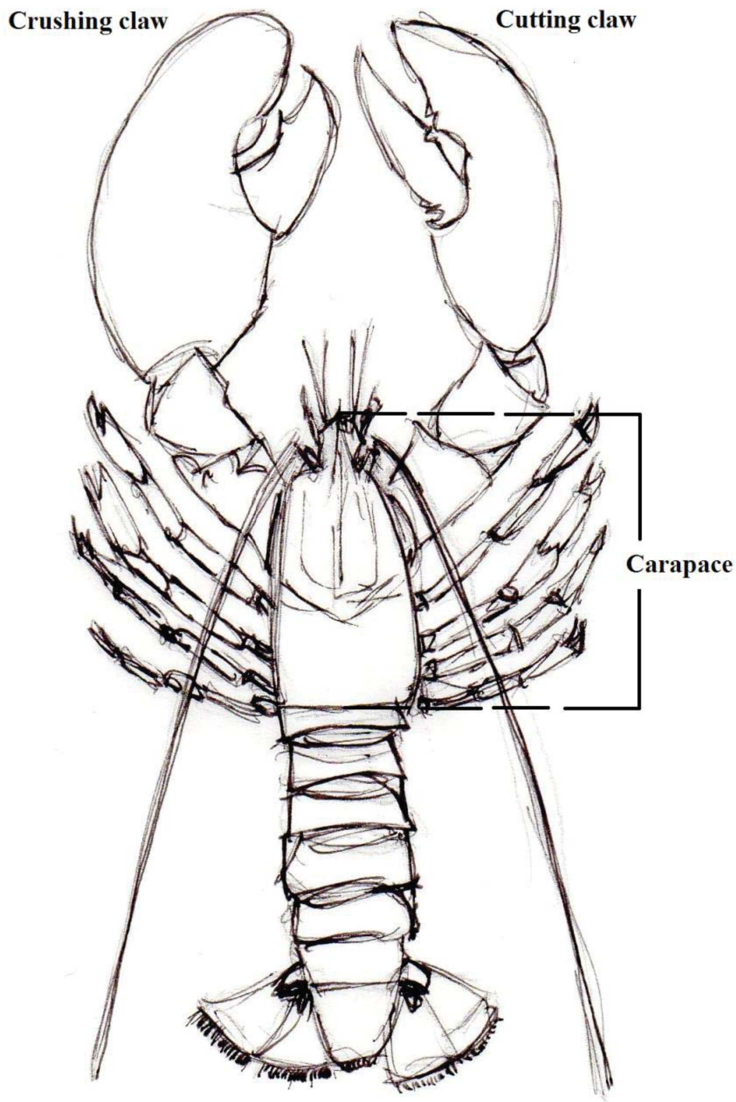

Figure 3. The lobster, drawn after a figure given in Holthuis (1991).

Lobsters are primarily stationary, and most do not move very far during the year (Bannister et al. 1994; Moland et al. 2011a; Moland et al. 2011b). Smith et al. (2001) found that most recaptures of lobsters in the size range 50-85 mm CL where made within 3.8 km of the release position. However, it should be mentioned that a considerable proportion of the lobsters were not recaptured. Agnalt et al. (2007) found that berried female moved even less, and remained within 500 meters from the release site. It is suggested that lobsters keep to areas where the water conditions are satisfying, and therefore do not move further than they have to (Smith et al. 2001). Howard (1980) argues that the limited movement may also be because of the need for shelter from disadvantageous environmental conditions, such as tidal currents.

In Norway, lobsters normally occur at depths between 15 to 35 meters (Moland et al. 2011b). When surface waters warm up in May, lobsters move into shallower areas (Moland et al. 2011b). Moland et al. (2011b) explain this behavior by greater food availability in shallow areas as temperatures increase, combined with the lobsters seeking warmer water to accelerate metabolism, incubation of eggs or maturation of internal gonad tissue.

Data collection and data processing

The cavity and video monitoring system

The cavity was monitored from November 2012 to the beginning of November 2014. I grouped June, July and August into a single period, Summer, while November and December were the basis for the period called Winter. A color CCD camera was placed in a custom-made casing, facing the opening of the lobster cavity, and an IR illumination was placed in a separate casing to enable night time footage. The IR illumination turned on automatically during dark hours, as it was equipped with a sensor. A 200 m cable was used to supply power and video signal, which was transmitted to the Drøbak Aquarium on the mainland. At the Aquarium, the video signal from the cable was connected to a mini DVR. For technical details about the monitoring equipment, see Steen and Ski (2014).

A frame rate of 10 pictures per second was chosen (resolution 704×560 pixels), and date and time were automatically recorded. Changes in the monitoring area (either made by the lobster itself or other organisms) were sensed by a built-in video motion-detection (VMD) sensor in the mini digital video recorder (DVR). When such changes occurred, the event was automatically recorded on the 32 GB SD card used. The sensitivity level that triggers the recording was set by displaying the percent change in the monitoring area when the lobster moved. To initiate recordings when movement occurred, a threshold level of 10-15 % was found to be sufficient. The detection area only covered the entrance area, and the recording time for each event was set to 5 seconds.

The data stored on the SD card were transferred to a laptop. To analyze the data, the multimedia viewer XnView version 2.13 was used. XnView makes it possible to view several video snap shots in chronological order, and the video material can be processed in an effective way, as files with lobster activity easily were separated from files with unwanted recordings. During the processing of the material, “time in”, “time out”, “lobster ID” and “light condition” were recorded.

Measured variables

A lobster was recorded as inside the cavity if it was inside the fixed camera view. A lobster could stay outside the cavity, but still be recorded as "inside", because it was visible in the picture. Hence, point of entry was recorded as the time a lobster entered the picture, or the sensor detected movement for the first time. Point of exiting was when a lobster exited the view of the fixed camera. A lobster entering the cavity was given the status "IN", and, similarly, a lobster exiting the cavity was given the status "OUT".

Marking individual lobsters was outside the scope of this study, for practical reasons, the lobsters were not marked. However, individual lobsters were fairly easy to identify, based on a series of distinguishing characteristics from the photo series recorded. I used several morphological characteristics to individually identify each lobster: the number of spikes were counted on the crusher claw and cutter claw (Figure 4); whether the crusher claw was the left or right claw; whether any claw was missing and if so, which claw it was (left/ right, crusher/ cutter); and, the lobsters relative size. The relative size groups were Big, Medium and Small. Additionally, some lobsters had special identifying characteristics, which were noted. Such a characteristic could for example be "upper crusher claw broken". The first lobster recorded was given the identification "ID1" and all data and comments for this individual was recorded. The number of spikes was not recorded for each picture, but rather for a single lobster. A lobster was identified as the same individual during a continuous observation. When a new lobster entered the picture, it was compared to the other lobsters recorded, and if it did not match any characteristics, it was identified as a new lobster.

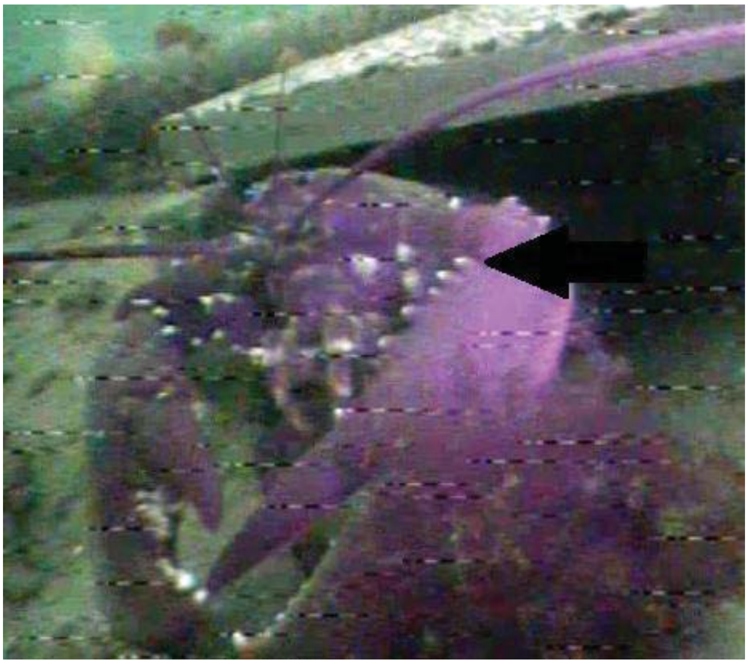

Figure 4. The number of spikes were recorded on the crusher claw and the cutter claw. The figure shows lobster H2, with 5 spikes on its crusher claw.

The identified lobsters were then compared file by file, to see whether any lobsters could be the same, or any files consisted of more than one lobster. This way, I could make sure that all the lobsters were appropriately identified.

“Light condition” was recorded for the point in time a lobster entered or exited the cavity. The five light conditions from the beginning of the recording to the middle of August 2014, were L1, light (Figure 5), L2, dark light (Figure 5), L3 (Figure 5), L4 light dark (Figure 5) and L5, dark (Figure 5).

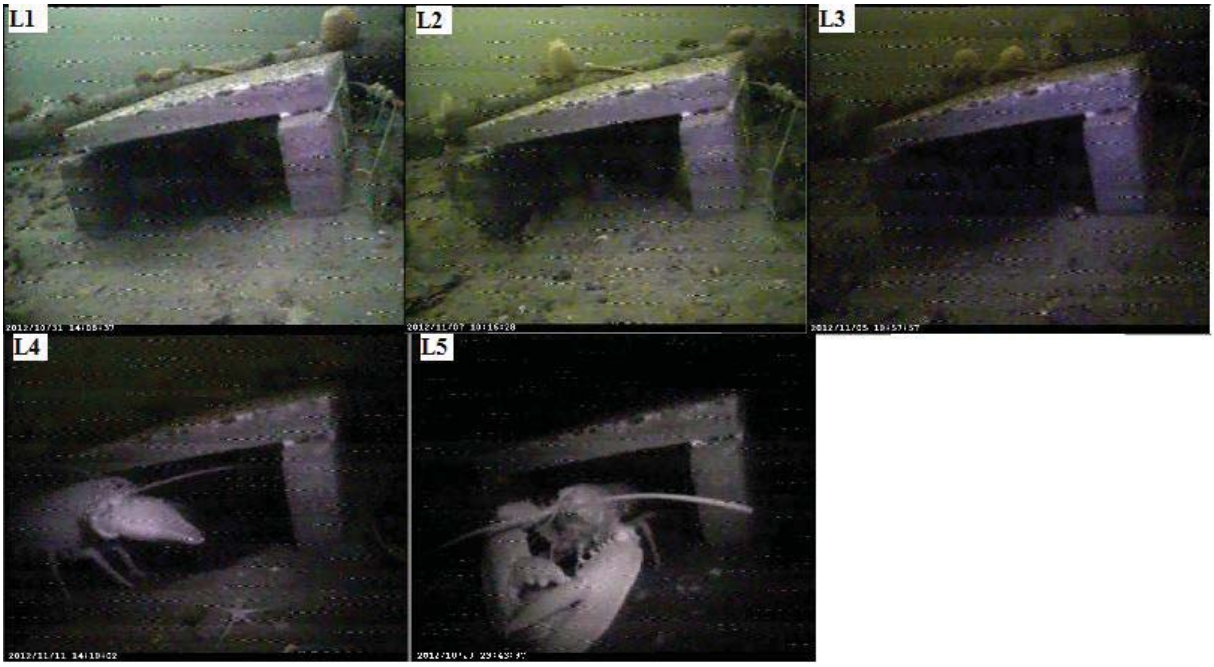

Figure 5. Light conditions for comparison before 2014/ 08/ 16.

After the 16th of August 2014, the picture was only black and white, and the five light conditions were as shown in figure 6.

Figure 6. Light conditions for comparison after 2014/ 08/ 16.

Temperature data were collected from the NIVA Research Facility at Solbergstrand, just south of Drøbak. The temperature was measured in ^{o}C at 1 m and 60 m depth outside the research facility and recorded once an hour. Where there was a lack of data, the values were interpolated. If there was a gap of more than 3 hours, the temperature was set to NA. The time of sunrise and sunset was collected from a data base containing meteorological information (Time and date 2015). The time of sunrise and sunset for the 15th each month was used.

To investigate the degree that lobsters dominate the cavity, I applied the Simpson diversity index, as described by Hunter and Gaston (1988). This index is given by calculating the sum of the proportion of individuals entering the cavity during a month, and subtracting it from 1, giving an index ranging from 0 (low dominance) to 1 (high dominance). The Simpson diversity index gives an indication of the dominance level of the lobsters. A high index means no dominant lobster or a high turnover rate in the cavity.

The time and date when the lobster entered and exited the cavity and the duration during which the cavity was occupied (the lobster was present either inside the cavity or in close proximity to the entrance) was used to calculate a "cavity-use" index (CUI). The CUI was the magnitude which the cavity was occupied across hour blocks (24 hour blocks through the day) for each month, controlled for monitoring time (see Skalak et al. 2012). The CUI was defined as:

$$\mathrm{CUI} = \sum_{\bar{e}}^{t} P^{*}$$

Where the CUI was calculated by summing the amount of time (t) the lobster was present at the cavity (P^*) for each hour block and dividing it by the video monitoring effort in minutes.

Statistical analyses

Statistical analysis was performed with the software R, version i386 3.0.2 (R Development Core Team 2015b) with the use of generalized linear mixed effects models (GLMM) in the lme4 package (R Development Core Team 2015a). The candidate models were ranked according to a corrected version of Akaike's Information Criterion (AIC) (Akaike 1974), AICc values, and the model with the lowest value was considered the most supported among the candidate models. However, if the difference in AICc (ΔAIC) between the most supported model and other candidate models was larger than 2.0, these models were taken in account as well when discussing the results (Burnham & Anderson 1998). In the analysis of diel cavity use, the periodic component of time series were represented by pairs of sine and cosine functions (Nelson et al. 1979; Pita et al. 2011). As an indicator of activity, a binomial response variable was also established based on whether the lobster entered or exited the cavity. The fixed explanatory variable 'time of the day' (i.e. 0 to 24 hours) was fitted with the cosinor method (Nelson et al. 1979; Pita et al. 2011) to test whether there were oscillating patterns. In addition, water temperature and light conditions were included as fixed covariates. Multiple observations of the same specimens were accounted for by including ID as random effect in the model. Each observed hour was the sample unit.

The cosinor models were specified as:

$$M_0 = logit\big(f(x)\big) = a_0$$

$$M_1 = logit\big(f(x)\big) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24})$$

$$M_2 = logit\big(f(x)\big) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24})$$

$$M_3 = logit\big(f(x)\big) = a_0 + (a_1 \cos\frac{2\pi x}{24} + b_1 \sin\frac{2\pi x}{24}) + (a_2 \cos\frac{2*2\pi x}{24} + b_2 \sin\frac{2*2\pi x}{24}) + (a_3 \cos\frac{3*2\pi x}{24} + b_3 \sin\frac{3*2\pi x}{24})$$

With x expressing ‘time of the day’. In addition, temperature and light conditions were included as fixed effects and lobster ID and year as random effects. In total, I tested for 17 different combinations (see Appendix).

When testing for whether there was a difference between entering and exiting the cavity throughout the day, each model fit (M_1-M_{16}) was assesed by using AICc values compared with a model including only the random term (M_9). After running the models, it was discovered that M_0 and M_9 was the same, so M_0 was removed, making M_9 the “simplest” model.

A linear mixed effect model (lme) from the nlme package (Pinheiro & Bates 2000) was used when testing the effect of different variables on the length of time spent inside the cavity, and when testing the potential effect of temperature on the total cavity use. When testing which variables best explained the length of time spent inside the cavity, the response was time inside the cavity (hours) and month, days since midsummer, temperature and temperature^2 were explanatory variables. Also here models were assessed using AICc compared with a model including only the random term, and the model fit was ranked in accordance to the AICc values.

Results

From November 2012 to November 2014, the cavity was monitored (i.e. the camera worked and could make recordings) for 12,773 effective hours (Table 1). Out of this, the cavity was occupied 3,154 hours by 37 different lobsters. The lobster cavity was not monitored the whole time due to the changing of SD cards, technical failure and blocking of the cavity by seaweed or sea stars and sea urchins. June and August 2013 and January, August and November 2014 had less than 300 hours monitoring, while June 2014 had only 59 hours of monitoring. This should be kept in mind when reading the results.

Table 1. The number of hours the cavity was monitored and occupied each month, and the number of lobsters occupying it (37 unique IDs).

Year	Month	Number of hours monitored	Number of hours occupied by lobsters	Number of lobsters occupying the cavity
2012	November	665.0	598.2	3
	December	735.8	324.5	1
2013	January	739.9	5.6	4
	February	667.9	0.0	0
	March	744.0	7.0	2
	April	698.4	0.0	1
	May	558.8	205.2	4
	June	261.9	149.2	7
	July	638.1	173.2	5
	August	221.8	70.8	10
	September	361.6	119.7	11
	October	720.8	367.2	7
	November	701.2	103.3	5
	December	358.7	280.6	4
2014	January	226.0	10.1	2
	February	672.0	0.0	0
	March	737.1	0.0	0
	April	717.2	0.0	1
	May	744.0	129.3	5
	June	59.1	31.8	1
	August	284.3	211.7	5
	September	584.9	317.3	4
	October	444.9	10.9	1
	November	229.6	37.8	2
Total		12772.9	3153.5	85 (37 ID)

The cavity use in November was relatively high (Figure 7). Circle indicates the proportion of each month (dark color) being monitored (Figures 7-10). There was no registered activity at the cavity during February 2013 (Figure 8) and February and March 2014 (Figure 9). During summer, the cavity-use index was higher at midday, and during winter it was relatively even throughout the day (Figure 10).

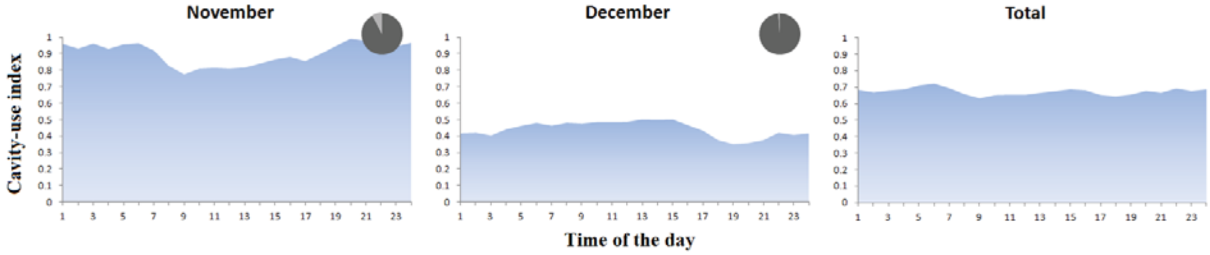

Figure 7. Cavity-use index as a function of time of day in 24-hour time blocks for 2012. The circle indicates the proportion of each month that was monitored (dark grey: time monitored and light grey: total time in a month).

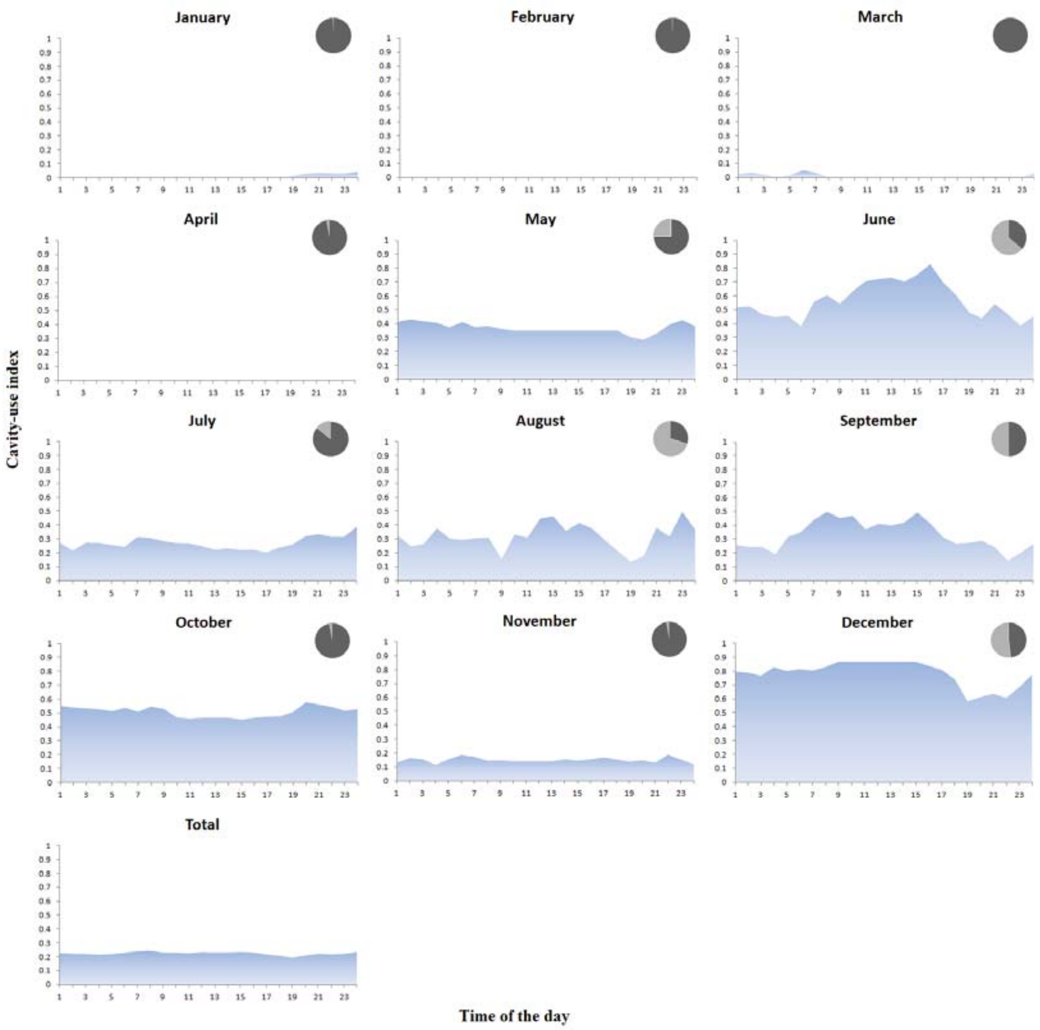

Figure 8. Cavity-use index as a function of time of day in 24-hour time blocks for 2013. The circle indicates the proportion of each month that was monitored (dark grey: time monitored and light grey: total time in a month).

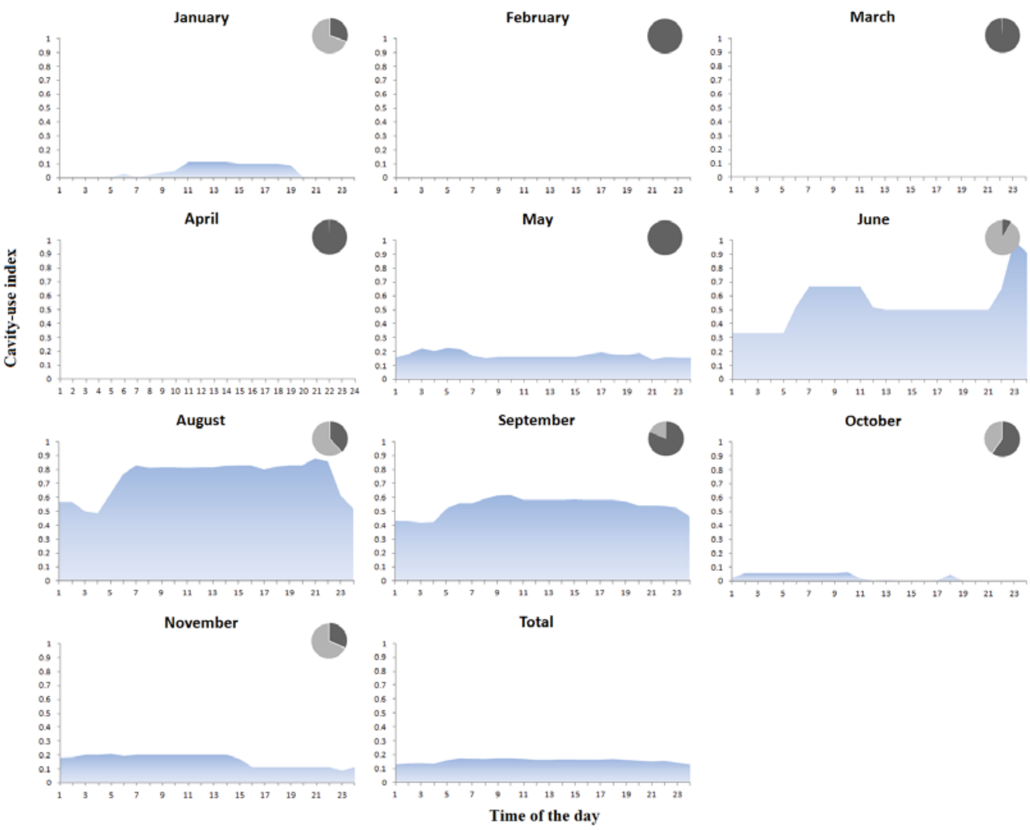

Figure 9. Cavity-use index as a function of time of day in 24-hour time blocks for 2014. The circle indicates the proportion of each month that was monitored (dark grey: time monitored and light grey: total time in a month).

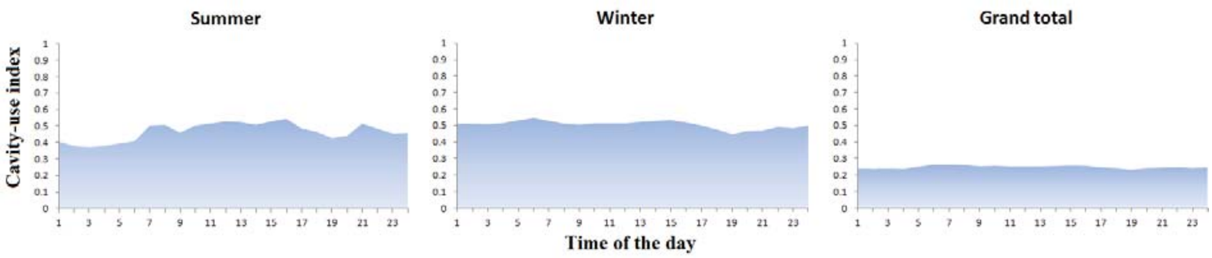

Figure 10. Cavity-use index as a function of time of day in 24-hour time blocks for the periods Summer and Winter, and for the whole period monitored.

When testing if there was a difference between time of entering or exiting the cavity as a function of time of day, light conditions, or temperature, the most supported GLMM model included the effect of temperature (Table 2). Since there were two models within ΔAIC < 2, the simpler model 9, including only ID and Year as random effects, must also be taken into account. The effect of temperature was almost non-existent, leading to the conclusion that there was no difference in probability of whether the lobsters entered or exited the cavity as a function time of day, light conditions or temperature. Most importantly, a lack of difference in periodicity between the two activities (i.e. entering vs. exiting the cavity) means that the lobster was as likely to leave the cavity as enter the cavity for a given time of the day, under different light conditions and temperature. For model including the effect of temperature (model 5), there was only a small variation in between years, and no variation in between individuals. There was no variation neither between individuals nor years for model 9 (Table 3). Table 3 displays the parameter estimates of models 5 and 9. For the full table, models and model parameter estimates, see the Appendix.

Table 2. Model selection based on AIC. The response was the lobsters entering or exiting the cavity. The random effects ID and Year were included in all the models.

Model	Fixed effects	Number of cosinor harmonics	Delta AICc
mod 5	Temperature	—	0.000
mod 9	—	—	0.774
mod 6	Temperature	1	3.748
mod 10	—	1	4.573
mod 7	Temperature	2	7.606

Table 3. The parameter estimates of the best fitted models of the difference between entering and exiting the cavity (n = 1576, random effects were ID = 36 (0) and year = 3 (4.00E-14 ± 2.00E-08), n = 1640, random effects were ID = 36 (0) and Year = 3 (0) for models 5 and 9, respectively).

Model		Estimat	SE	z value	Pr(>|z|)
Model 5	(Intercept)	-0.01	0.15	-0.07	0.95
	Mediantemp	0.00	0.01	-0.02	0.98
Model 9	(Intercept)	-0.01	0.05	-0.20	0.84

Using the 15th each month as the basis, sunrise and sunset from November 2012 to November 2014 is displayed in Table 4. Lobsters most often enter the cavity before sunrise and exit after sunset (Figures A1 and A2).

Table 4. The sunrise and sunset at the 15th each month from November 2012 to November 2014 in Drøbak.

Year	Month	Sunrise	Sunset
2012	November	08:14	15:49
	December	09:12	15:14
2013	January	09:02	15:52
	February	07:54	17:10
	March	06:34	18:20
	April	06:02	20:35
	May	04:42	21:47
	June	03:57	22:39
	July	04:24	22:21
	August	05:33	21:09
	September	06:46	19:38
	October	07:56	18:09
	November	08:14	15:50
	December	09:12	15:14
2014	January	09:03	15:52
	February	07:55	17:09
	March	06:35	18:19
	April	06:03	20:34
	May	04:43	21:47
	June	03:58	22:37
	July	04:24	22:22
	August	05:33	21:09
	September	06:45	19:39
	October	07:56	18:10
	November	08:13	15:50

Plotting the raw data illustrates that the lobsters had a tendency to both enter and exit the cavity during the late evening and at night (Figure 11). The highest level of activity was recorded from June through September, peaking with lobsters entering 18 times at 5 AM in the morning in September, and exiting 20 times at 10 PM in the evening in August (Figures A1 and A2).

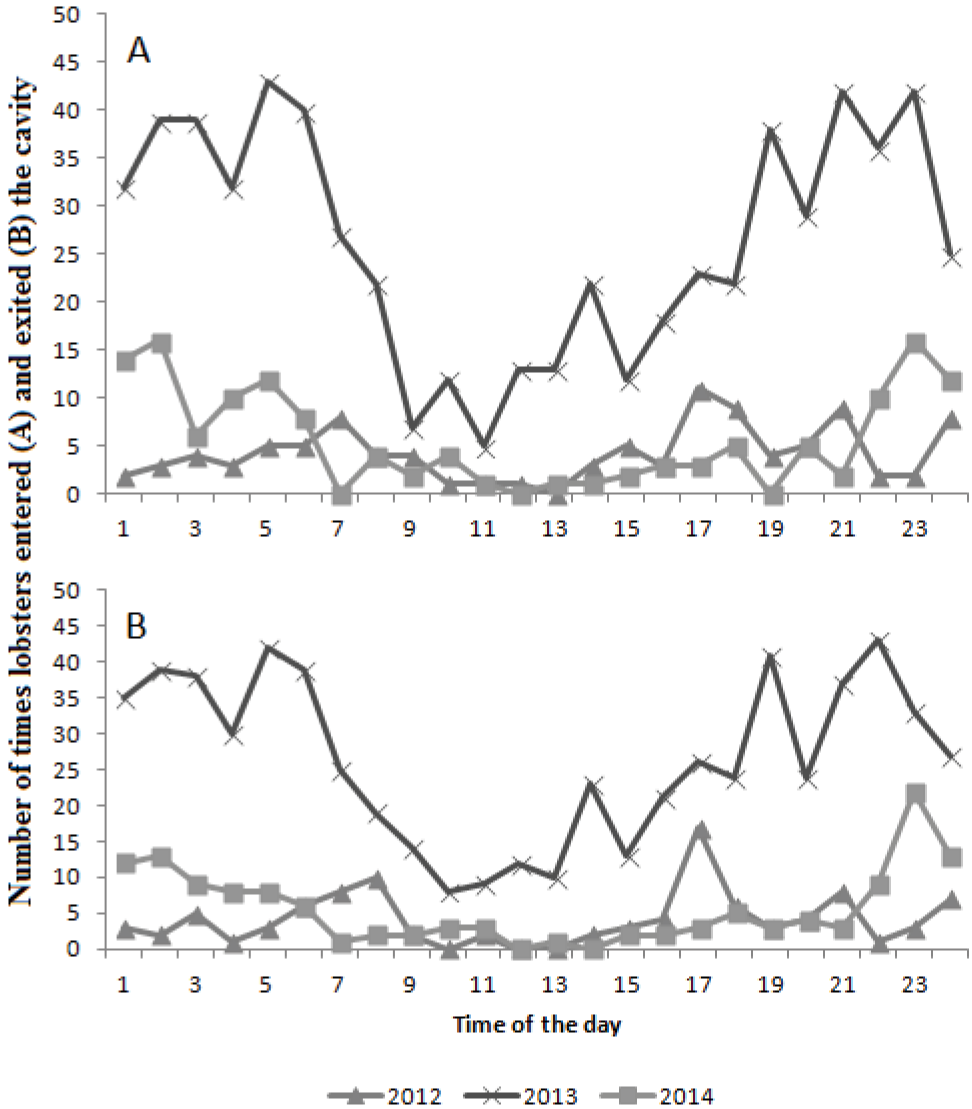

Figure 11: Number of times per hour slots lobsters enter (A) and exit (B) the cavity through the day (n= 102, 633 and 137 for entering in 2012, 2013 and 2014 respectively, n= 100, 632 and 134 for exiting in 2012, 2013 and 2014 respectively).

The lobsters most often both entered and exited the cavity under the light conditions L5, dark (Figure 12). The number of times exiting and entering the cavity were nearly identical, with lobsters entering the cavity 95 times and exiting it 94 times under dark light conditions in 2012, and entering/ exiting 429/ 427 and 112/ 112 times in 2013 and 2014, respectively. Lobsters both enter and exit the cavity most often under the dark light condition (L5) independently of month (Figure A3 and A4).

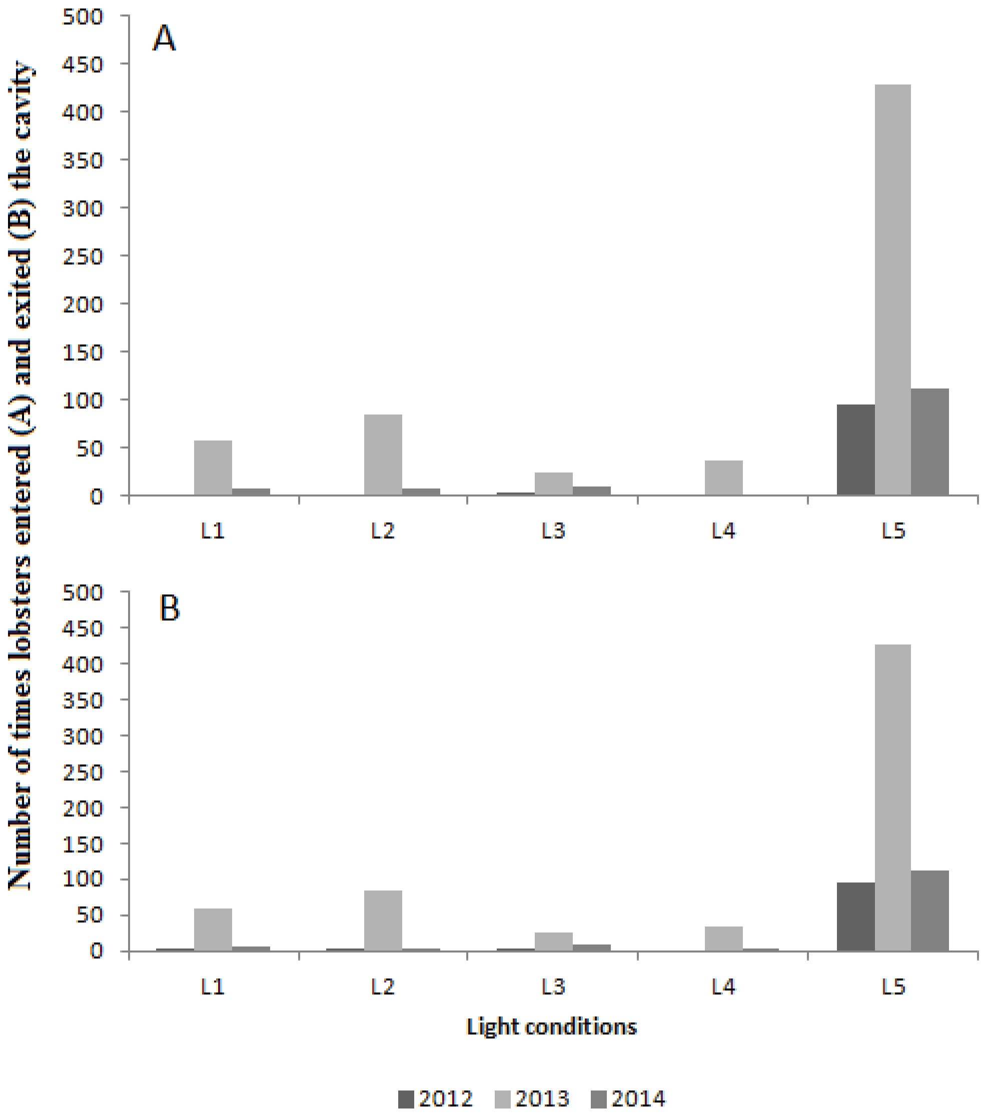

Figure 12. Number of times lobsters entered or exited the cavity under the different light conditions in 2012, 2013 and 2014 (n=102, 633 and 137 for entering in 2012, 2013 and 2014 respectively, n=100, 632 and 134 for exiting in 2012, 2013 and 2014 respectively).

Throughout the summer period, the number of times lobsters entered the cavity was more evenly distributed among the five categories of light conditions, while they in the winter period were concentrated to the L5 category (Figure 13).

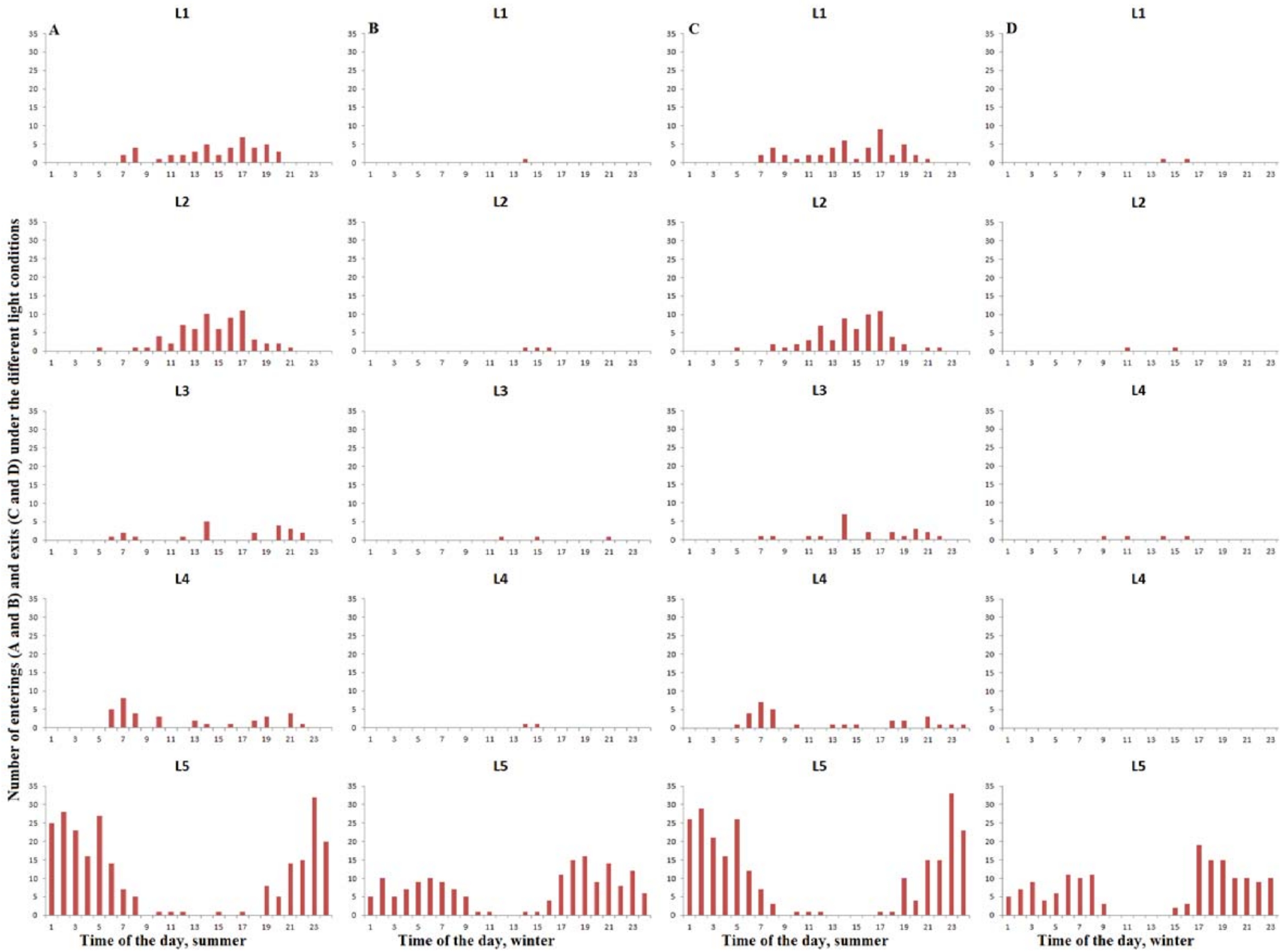

Figure 13. The aggregatd number of times lobsters entered and left the cavity under the different light conditions during summer (June, July and August) and winter (November and December). N = 409 and 175 for summer and winter respectively.

Temperature measured at 1 m depth varied from -1.5 ^{o}C in January and February to 25 ^{o}C in July. The mean monthly temperatures at 1 m varied from 20.9 ^{o}C in August 2014 to 1.7 ^{o}C in February 2014 (Figure A5). The measured temperatures at 60 m were more stable, with mean monthly temperatures varying from 6.7 ^{o}C in April 2013 to 11.0 ^{o}C in September the same year (Figure A6). Figure 11 shows how temperatures differ throughout the year, and the oscillation of the lobster cavity use. The temperatures at 1 m tended to be low from January to February, as was the lobster cavity use index, but the temperatures at 60 m were higher (Figure 14). Likewise were the temperatures at 1 m and the cavity use higher from June to September, and the temperature at 60 m lower.

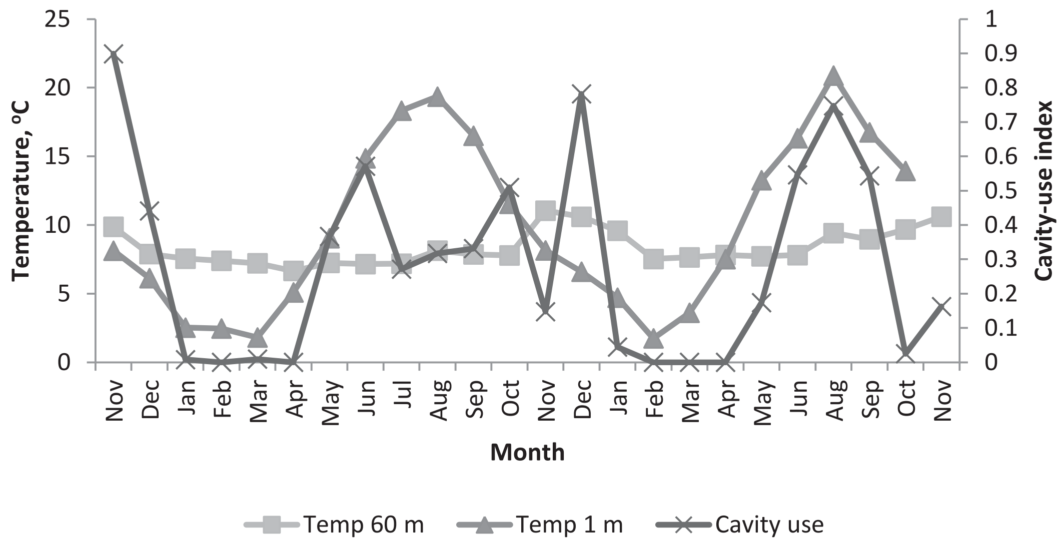

Figure 14. The average temperature at 1 m and 60 m and total cavity use (the time spent inside pr time monitored) from November 2012 to November 2014 (n= 22).

Logistic regression showed a relation between the total cavity-use index (range 0-1) and the temperature at 1 m (Table 5, Figure 15), indicating that the cavity use increases as the temperature at 1 m increases. There was not run a test on whether there was a relation between total cavity use and the temperature at 60 m depth as the cavity was placed on 20 m and was thought not to be affected by the (stable) temperature at 60 m.

Table 5. Logic parameter estimates of the logistic regression of total cavity use as a function of temperature at 1 m (n = 23, random effect was year = 3 (0)).

	Estimate	SE	z value	Pr(>|z|)
(Intercept)	-2.530	1.144	-2.211	0.027
Temperature	0.155	0.087	1.788	0.074

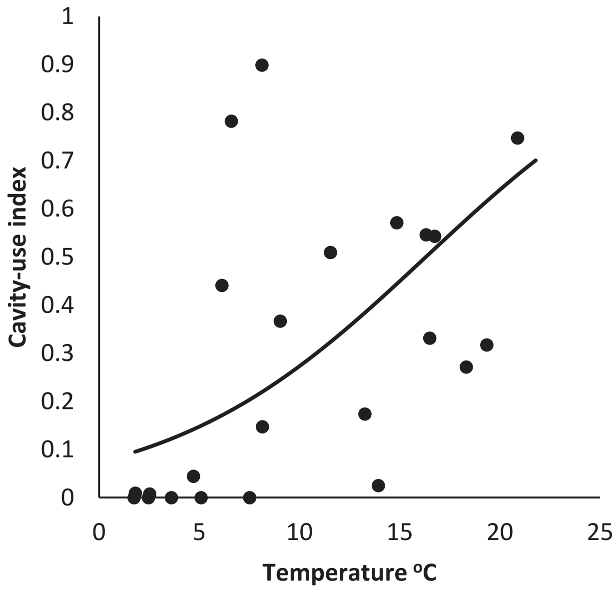

Figure 15. The predicted cavity-use index as a function of temperature at 1 m. predictions were estimated from the logistic regression model reported in Table 5.

Figure 16 shows the cavity-use index and the predicted cavity use as a function of temperature. The model did describe the changes in cavity use throughout the season quite well, as the actual cavity-use index and the predicted cavity-use index shows the same oscillatory pattern.

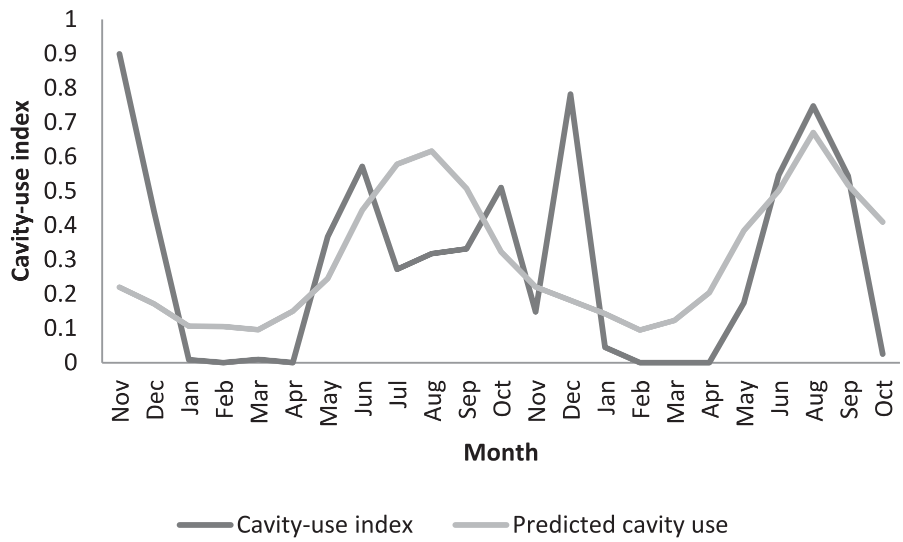

Figure 16. The recorded total cavity-use index and the predicted cavity use index from the logistic regression model reported in Table 5.

When testing for what had an effect on the duration of time spent inside the cavity for each unique visit, month was the most supported explanatory variable, followed by temperature (Table 6). The response variables were log transformed (natural logarithm) to get a normal distributed model, and the parameter estimates for the best model are presented in Table 7. For the parameter estimates for all the models, see the Appendix. January through April monitoring dates were not included in the test material, as there were few or no lobsters occupying the cavity during these months.

Table 6. The model selection when testing the effect on the duration of time spent inside the cavity of different variables, based on AIC. The response was the time spent inside the cavity (hours). N=789, random effects were ID and Year.

Model	Fixed effects	Δ AICc	Random effect ID	Random Effect Year
Model 3	Month	0	28.70±5.35	1.01E-12±1.01E-06
Model 1	Temperature	27.2	26.98±5.19	0.00
Model 4	—*	30.2	1.49±1.22	0.31±0.56
Model 2	Days since midsummer	34.2	26.60±5.17	0.00

* Only intercept and random effects

Table 7. Parameter estimates of the most supported model when testing which factors best explained time spent inside the cavity. Month has the strongest effect. The response variables

were log transformed (natural logarithm) to get a normal distributed model. N= 789, random effects were ID = 33 (28.70±5.35) and year = 3 (1.01E-12±1.01E-06).

	Estimate	SE	t-value
August (Intercept)	1.18	1.38	0.86
December	4.91	2.19	2.25
July	2.83	1.70	1.66
June	-0.20	1.45	-0.14
May	8.36	2.44	3.43
November	5.17	1.86	2.78
October	5.36	2.01	2.68
September	1.70	1.26	1.35

Individual lobsters spent the least amount of time inside the cavity in June, July and August (Figure 17), with an average of only 1 hour in June and August. In October, November and December, lobsters spent an average of > 6 hours inside the cavity. May, October and November were significantly different from June, July and September (Figure 17).

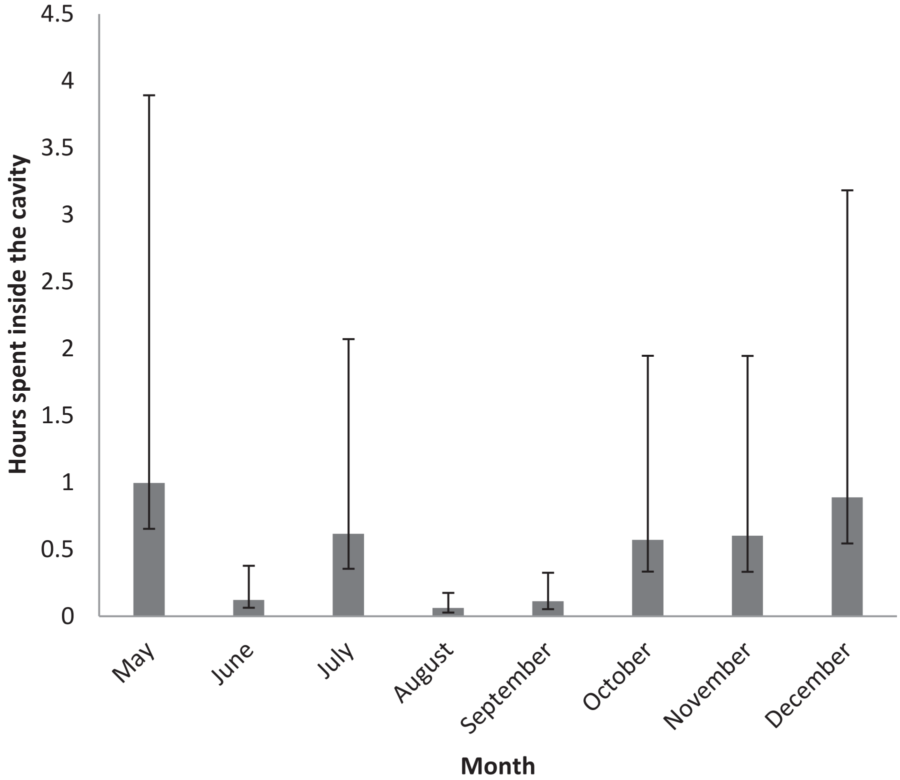

Figure 17. Predictions from the best fitted model, the number of hours lobsters spend inside the cavity from May to December, with a 97.5 % upper CI and a 2.5 % lower CI. Predictions were estimated from parameters provided in Table 7. Note: the CI intervals are back transformed from the parameter estimates.

There were the greatest number of lobsters in the cavity per monitored hour from May to October overall for all years (Figure 18), when looking at the raw data. August and September 2013 were the months with the highest number of lobster individuals, 10 and 11 respectively, and were also the months with most lobsters in 2014, with respectively 5 and 4 lobsters.

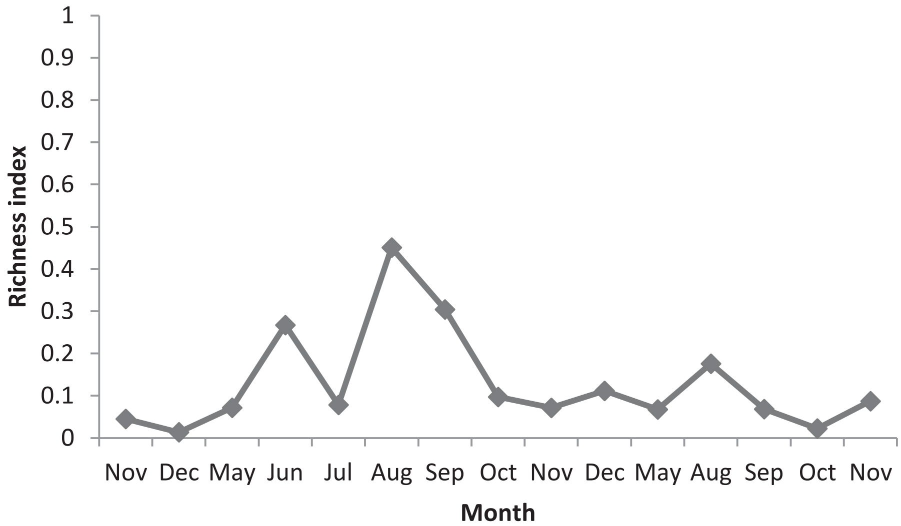

Figure 18. The number of individuals per number of hours monitored giving the richness index from November 2012 to November 2014.

When calculating the richness and Simpson Diversity index, 14 lobsters were taken out of the test material due to lack of monitoring connected to the changing of SD cards. Only the months of May to November (except June 2014) were used as these were the ones with sufficient amounts of data.

As the Simpson diversity index gives an indication of the dominance level of the lobsters, the high index in August and September both in 2013 and 2014 (Figure 19), indicated a high turnover in occupation of the cavity and no dominant lobster. The median was 0.47 ± 0.26.

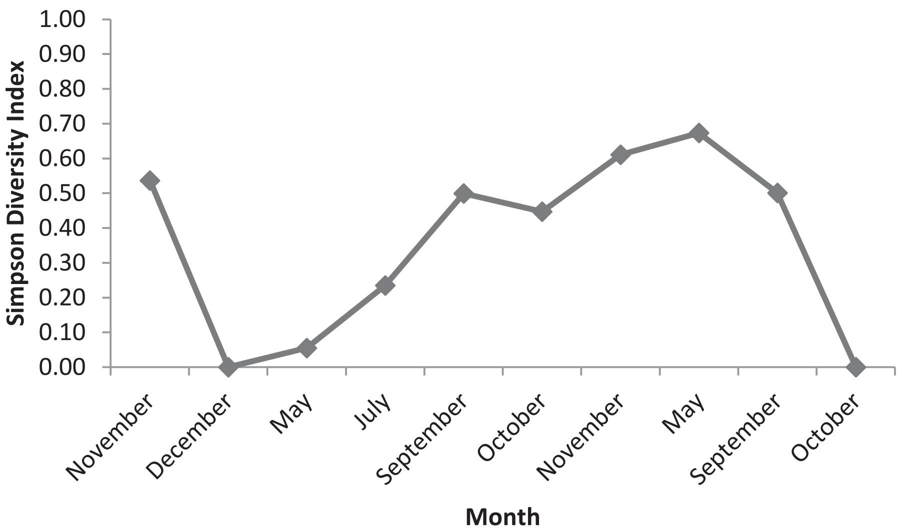

Figure 19. The dominance relationship, where 0 is one lobster dominating, indicating a low turnover rate in occupation of the cavity, and 1 indicate a high turnover rate (i.e. no dominant lobster). The sum of the proportion of individuals inside the cavity subtracted from 1, gave the Simpson Diversity index, for months being monitored for greater than 50 % of the time (from November 2012 to November 2014).

Discussion

This study has demonstrated that there was a peak in cavity use around summer and early autumn, and a drop in the cavity use through winter and early spring, with no cavity use recorded at all in the mid-winter month of February. This is consistent with earlier findings on the European lobster (Moland et al. 2011b; Smith et al. 1999) when considering cavity use as an indicator of lobster activity. Moland et al. (2011b) found that lobsters spent most time at depths from 35-15 meters, but that during December to March, they were found as deep as 50 meters, indicates a migration to deeper seas. This could explain the lack of recorded lobsters in this study in February 2013 and February and March 2014, as the lobster cavity was situated at 20 m depth. The movement to deeper water is perhaps as a way to avoid oscillatory water movement (Smith et al. 1999), which Howard and Nunny (1983) demonstrated could impair lobster activity, using flume experiments. In a telemetry study, Smith et al. (1999) found that lobster overwintering in a cove became inactive, remaining in the same location for months. I observed the same tendencies in this study, as lobsters stayed inside the cavity for longer periods in the months up until and after winter. Such inactivity could further explain the lack of recordings midwinter, as lobsters are dormant other places than near the monitored cavity. The temperature at 60 m near my study site is relatively stable throughout the year.

Being cold-blooded, the lobster is likely to move towards warmer water, a trend I present here, that supports earlier observations by Moland et al. (2011b) in marine protected areas and Smith et al. (1999) in the wild. It may be more optimal for lobsters to stay in deeper waters from November to April, as the temperature was higher then, and from May until November to stay in more shallow waters to benefit from the higher temperatures here. A way of testing whether lobsters migrate into deeper waters, could be to place cavities at several depths, each installed with a sensor measuring the temperature. Then one could test for differences in cavity use as a function of time of the year, and whether there is a correlation between activity and temperature, as seen in these results. Tagging the lobsters (e.g. Bannister et al. 1994) would solve the problem of non-independent data from the same individuals, and enable more complex questions to be addressed. A reliable test would be to tag lobsters and use telemetry (Agnalt et al. 2007; Smith et al. 1998) with temperature and depth sensors, but this is also a more expensive experiment.

The understanding that the European lobster (e.g. Moland et al. 2011b) and the American lobster (Golet et al. 2006; Jury et al. 2005) are nocturnal was further verified by my findings that lobsters both entered and exited the cavity at nighttime, during low (dark) light conditions and before sunrise and after sunset. Since there is a lack of published information on European lobster, the American lobster's life history, ecology and behavior is often applied. Van der Meeren (2003) warned against applying data from one species to another, implying that there might be significant differences between the two species. This further emphasizes the need for data on the European lobster.

When testing whether there was a difference in entering or exiting the cavity, I found that there was no pattern, indicating that lobsters were as likely to exit the cavity for any given time of the day, under different light conditions and seawater temperature. Despite no differences in the two activities, both occurred most frequently before sunrise and after sunset, during the night and under dark light conditions, emphasizing that lobsters were most active during the darkest hours. A telemetry study in an artificial reef consisting of blocks made of concrete or cement-pulverized fuel-ash, showed that movement by adult *H. gammarus* was predominantly nocturnal (Smith et al. 1998). In the same study, the activity was found to increase around midnight, peaking in the early part of the night and declining to low levels before dawn. Through telemetry in the same artificial reef, Smith et al. (1999) found a negative relation between midday illumination and activity level. Using SCUBA, Karnofsky et al. (1989) did not observe any lobsters outside their shelters during the day, and Spanier et al. (1998) found, when studying juvenile American lobsters in a laboratory, that foraging took place almost exclusively at night. However, video surveillance of an enclosed mesocosm revealed that American lobster expressed patterns of activity that were quite variable (Golet et al. 2006). Most lobsters were active during the night, but some were diurnal, or had no preference at all, and all lobsters could switch from nocturnal one day to diurnal the next.

The number of times lobsters entered and exited the cavity was more evenly distributed among the five light levels during Summer, and more concentrated to the lowest light levels during Winter. Erkert and Kappeler (2004) proposed that animals not living near the equator require flexibility in their diel activity patterns, as they experience seasonal changes in day length. When observing the world's northernmost lobster population in Tysfjord and Nordfolda, Agnalt et al. (2009) found that lobster adapted to the light from the midnight sun, and were active in shallow waters at daytime during the summer. Using SCUBA and divers, up to 10 lobsters were seen walking on the seabed at depths between 10 and 2 m (Agnalt et al. 2009). By attaching acoustic transmitters to lobsters and releasing them into a study area covered with receivers mounted in a triangulation network, the lobsters' position when not in the cavity would be known, and more detailed information on the diel activity would be revealed, as well as the lobster's movement during daytime (e.g. Wiig et al. 2013).

August and September were the months with the highest recorded number of individuals occupying the cavity, the highest richness index, the highest Simpson diversity index and the lowest number of hours spent inside the cavity per visit. Together, these data indicate a high activity level throughout these months. There were many lobsters recorded near the cavity and there was a high turnover rate in the occupation of the cavity. During the next two months, lobsters are exposed to fishing pressure, raising the question of what impact today's fishing regime has on the lobster population. Whether the richness index was significantly lower in October/ November than in June/ July (as a reaction to fishing), could be tested if several lobster cavities were monitored simultaneously. The low Simpson diversity index in December could be due to fewer lobsters present in the area, as they tend to move towards deeper waters this time a year (Moland et al. 2011b; Smith et al. 1999).

Wiig et al. (2013) show, in a study from the Norwegian Skagerrak coast, that the coastal fishery can be highly effective although findings indicates that only a small proportion of both the European lobster (Agnalt et al. 2009; Moland et al. 2013b) and the American lobster (Karnofsky & Price 1989; Watson et al. 2009) that encounter traps, enter them. Wiig et al. (2013) argued that lobster mortality rate estimated from their study to be about 83% was artificially high due to the relatively low sample size, and referred to English studies with lower mortality rates. These studies, done by Smith et al. (2001) and Bannister and Addison (1986), still reported relatively high mortality rates, of 26% - 52% and 35% - 55%, respectively. More studies like the one done by Wiig et al. (2013) should be conducted to see what effect the coastal fishery has on the population size and dynamics, and whether the impact is the same along the entire Norwegian coast. Such studies are important, and comprise the basis for sustainable regional management.

In this study, algal growth on the lobsters was not registered. When studying 7 tropical crab species along the eastern coast of the Gulf of Thailand, Becker and Wahl (1996) suggested that the best antifouling mechanisms were behavioral mechanisms. By being nocturnal, algal growth was suppressed by shading and nigh activity. Becker and Wahl (1996) further predict that residing into deeper water offers protection from fouling because the water is less illuminated, as increased algal growth leads to decreased visibility and darker light conditions (Lindström 2000). Algal growth was also thought to have an effect on lobster cavity use in the outer Oslofjord in July 2011 (Steen & Ski 2014). Hence, algal growth might be one key to understanding the lobster's behavior, and should be included in further studies. Another important abiotic factor that may have been overlooked in the present study is current speed and lobster behavior, as proposed by Howard and Nunny (1983). One strength of this study is that it is based on two years of data collection, facilitating the possibility of monitoring many different lobsters, gathering a relatively large sample size.

Through the use of video monitoring, I was able to monitor the lobster and its behavior without disturbing it, in contrast to studies that employ diving or capture (see Vecchione & Roper 1991). Already in 1974, Altmann concluded that observing ones study object using instantaneous sampling in the object's natural environment gives better insight in its real-life situation, than studying it in captivity (Altmann 1974). Steen and Ski (2014) point out that the event-triggered recordings are dependent on the sensitivity settings of the mini-DVR, and hence on the magnitude of movements, and that this should be kept in mind when choosing this kind of recording tools. One of the problems in my study, was that I did not watch and analyze the recorded material simultaneously as the recordings were made, so if there were any problems, for example when the cavity entrance was blocked with a fishing net, I could not take immediate action, but had to wait to see whether the mistake was corrected.

The European lobster's diel activity was positively correlated with seawater temperature, and hence it was most active during the late summer and early autumn, when the temperature was highest. As the water is warming up due to climate change (Belkin 2009; IPCC 2013), it will be interesting to see how the lobster will react to this. For the north Europe and Scandinavia, the prospect is warmer and wetter winters (IPCC 2013). Schmalenbach and Franke (2010) found that European lobster larvae that were hatched under laboratory conditions had a reduced incubation time, early date of hatching and low temperature at hatching time when the temperature during incubation increased. In accordance with the match-mismatch hypothesize (Cushing 1972; Green et al. 2014 and refrences herein), earlier release of larvae would lead to problems for lobsters in a warming North Sea, as larvae will not have enough food upon hatching, and will experience a prolonged stay in early larval stages (Schmalenbach & Franke 2010). Seeing as algal proliferation also is temperature dependent (Skreslet & Borja 2003), it is reasonably to think that also these organisms will "start the season" earlier, and meet the lobster larvae's need. Perhaps lobsters will become more active also throughout the winter months and have a prolonged growth period, as an increase in the temperature has been shown to lead to an increase in activity. Further, catchability has been shown to increase with increased temperature for both *H. gammarus* (Smith et al. 1999) and *H. americanus* (McLeese & Wilder 1958). An increase in catchability, especially early in the season when the fishing activity peeks (Wiig et al. 2013), might lead to over exploitation of the stock, as there are no restriction on the total number of lobster pr house hold throughout the season (NDF 2011). It seems, on the other hand, that lobster traps become saturated (lobsters won't enter the trap when it is occupied), and the effective catch rate is relatively low (Addison 1995). The possible change in catchability and the effect it will have on the exploitation of lobster stocks should be further explored to make a sound foundation for decision making, and conceivably make changes in the duration of today's fishing season.

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Appendix

The models used when testing if there was a difference between entering and exiting the cavity throughout the day were as follows:

```
M1:glmer(Status~Lightcondition+(1|ID)+(1|Year)

M2:glmer(Status~Lightcondotions+I(cos(2*pi*Hour/24))+
      I(sin(2*pi*Hour/24))+(1|ID)+(1|Year)

M3:glmer(Status~Lightconditions+I(cos(2*pi*Hour/24))+
      I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
      I(sin(2*2*pi*Hour/24))+(1|ID)+(1|Year)
M4:glmer(Status~Lightconditions+I(cos(2*pi*Hour/24))+
      I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
      I(sin(2*2*pi*Hour/24))+I(cos(3*2*pi*Hour/24))+
      I(sin(3*2*pi*Hour/24))+(1|ID)+(1|Year)
M5:glmer(Status~Mediantemp+(1|ID)+(1|Year)

M6:glmer(Status~Mediantemp+I(cos(2*pi*Hour/24))+
      I(sin(2*pi*Hour/24))+(1|ID)+(1|Year)

M7:glmer(Status~Mediantemp+I(cos(2*pi*Hour/24))+
```

```
     I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
     I(sin(2*2*pi*Hour/24))+(1|ID)+(1|Year)
M8:glmer(Status~Mediantemp+I(cos(2*pi*Hour/24))+
     I(sin(2*pi*Hour/24))+ I(cos(2*2*pi*Hour/24))+
     I(sin(2*2*pi*Hour/24))+ I(cos(3*2*pi*Hour/24))+
     I(sin(3*2*pi*Hour/24))+(1|ID)+(1|Year)
M9:glmer(Status~(1|ID)+(1|Year)
M10:glmer(Status~I(cos(2*pi*Hour/24))+
     I(sin(2*pi*Hour/24))+(1|ID)+(1|Year)
M11:glmer(Status~I(cos(2*pi*Hour/24))+
     I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
     I(sin(2*2*pi*Hour/24))+(1|ID)+(1|Year)
M12:glmer(Status~I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
     I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
     I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24))+
     (1|ID)+(1|Year)
M13:glmer(Status~Lightconditions+Mediantemp+(1|ID)+(1|Year)
M14:glmer(Status~Lightconditions+Mediantemp+
    I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+(1|ID)+(1|Year)
M15:glmer(Status~Lightconditions+Mediantemp+
     I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
     I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
     (1|ID)+(1|Year)
M16:glmer(Status~Lightconditions+Mediantemp+
     I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+
     I(cos(2*2*pi*Hour/24))+I(sin(2*2*pi*Hour/24))+
     I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24))+(1|ID)+(1|Ye
     ar)
```

Table A1. The model selection based on AIC. The response was if the lobster exited or entered the cavity (i.e. testing if there was a difference in entering and exiting the cavity as a function of temperature, light conditions and time of the day). N=766. The random effect ID and year were included in all the models.

Model	Fixed effects	Number of cosinor harmonics	Δ AICc
mod 5	Temperature	—	0.000
mod 9	—	—	0.774
mod 6	Temperature	1	3.748
mod 10	—	1	4.573
mod 7	Temperature	2	7.606
mod 13	Light and Temperature		7.803
mod 11	—	2	8.406

mod 1	Light	—	8.565
mod 8	Temperature	3	11.240
mod 14	Light and Temperature	1	11.659
mod 12	—	3	11.988
mod 2	Light	1	12.467
mod 15	Light and Temperature	2	15.571
mod 3	Light	2	16.335
mod 16	Light and Temperature	3	19.207
mod 4	Light	3	19.901

Table A2. Parameter estimates of the models for testing if there was a difference in entering and exiting the cavity as a function of temperature, light conditions and time of the day. L1-L5 were light conditions L1-L5. N= 766, random effects were ID = 36 and year = 3.

Model		Estimat	SE	z value	Pr(>|z|)	Random effects ID	Random effects Year
Model 5	(Intercept)	-0.01	0.15	-0.07	0.95	0.00	4.00E-14±2.00E-07
	Mediantemp	0.00	0.01	-0.02	0.98		
Model 9	(Intercept)	-0.01	0.05	-0.20	0.84	0.00	0.00
Model 6	(Intercept)	0.00	0.15	0.00	1.00	0.00	0.00
	Mediantemp	0.00	0.01	-0.05	0.96		
	I(cos(2*pi*Hour/24))	-0.03	0.08	-0.42	0.68		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.47	0.64		
Model 10	(Intercept)	0.00	0.05	-0.06	0.95	0.00	0.00
	I(cos(2*pi*Hour/24))	-0.04	0.08	-0.45	0.65		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.43	0.67		
Model 7	(Intercept)	0.00	0.16	0.00	1.00	0.00	0.00
	Mediantemp	0.00	0.01	-0.06	0.96		
	I(cos(2*pi*Hour/24))	-0.03	0.08	-0.39	0.70		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.47	0.64		
	I(cos(2*2*pi*Hour/24))	0.00	0.08	0.02	0.99		
	I(sin(2*2*pi*Hour/24))	0.01	0.07	0.08	0.94		
Model 13	(Intercept)	0.02	0.25	0.07	0.94	0.00	0.00
	LysforholdL2	-0.05	0.23	-0.21	0.83		
	LysforholdL3	0.04	0.29	0.13	0.89		
	LysforholdL4	-0.10	0.29	-0.33	0.74		
	LysforholdL5	-0.03	0.19	-0.15	0.88		
	Mediantemp	0.00	0.01	-0.02	0.99		
Model 11	(Intercept)	0.00	0.05	-0.04	0.97	0.00	0.00
	I(cos(2*pi*Hour/24))	-0.04	0.08	-0.45	0.66		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.39	0.69		
	I(cos(2*2*pi*Hour/24))	0.00	0.07	0.03	0.97		
	I(sin(2*2*pi*Hour/24))	0.00	0.07	-0.05	0.96		
Model 1	(Intercept)	0.02	0.17	0.09	0.93	0.00	0.00
	LysforholdL2	-0.05	0.23	-0.21	0.83		

	LysforholdL3	0.04	0.29	0.13	0.90		
	LysforholdL4	-0.09	0.29	-0.33	0.75		
	LysforholdL5	-0.02	0.18	-0.13	0.90		
Model 8	(Intercept)	-0.01	0.16	-0.06	0.96	0.00	0.00
	Mediantemp	0.00	0.01	0.02	0.99		
	I(cos(2*pi*Hour/24))	-0.01	0.09	-0.14	0.89		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.38	0.71		
	I(cos(2*2*pi*Hour/24))	-0.02	0.08	-0.22	0.82		
	I(sin(2*2*pi*Hour/24))	0.00	0.08	0.06	0.96		
	I(cos(3*2*pi*Hour/24))	0.09	0.08	1.21	0.23		
	I(sin(3*2*pi*Hour/24))	-0.02	0.07	-0.29	0.78		
Model 14	(Intercept)	-0.07	0.28	-0.26	0.79	0.00	0.00
	LysforholdL2	-0.06	0.23	-0.27	0.79		
	LysforholdL3	0.06	0.29	0.21	0.84		
	LysforholdL4	-0.04	0.30	-0.13	0.89		
	LysforholdL5	0.07	0.23	0.31	0.76		
	Mediantemp	0.00	0.01	0.21	0.84		
	I(cos(2*pi*Hour/24))	-0.08	0.12	-0.68	0.50		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.49	0.63		
Model 12	(Intercept)	0.00	0.06	-0.02	0.99	0.00	0.00
	I(cos(2*pi*Hour/24))	-0.02	0.08	-0.22	0.83		
	I(sin(2*pi*Hour/24))	-0.02	0.07	-0.29	0.77		
	I(cos(2*2*pi*Hour/24))	-0.02	0.08	-0.20	0.84		
	I(sin(2*2*pi*Hour/24))	-0.01	0.08	-0.07	0.94		
	I(cos(3*2*pi*Hour/24))	0.09	0.08	1.16	0.25		
	I(sin(3*2*pi*Hour/24))	-0.02	0.07	-0.21	0.83		
Model 2	(Intercept)	-0.03	0.18	-0.18	0.86	0.00	0.00
	LysforholdL2	-0.06	0.23	-0.26	0.80		
	LysforholdL3	0.05	0.29	0.19	0.85		
	LysforholdL4	-0.04	0.29	-0.15	0.88		
	LysforholdL5	0.06	0.22	0.30	0.77		
	I(cos(2*pi*Hour/24))	-0.08	0.11	-0.72	0.47		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.45	0.66		
Model 15	(Intercept)	-0.07	0.28	-0.26	0.80	0.00	0.00
	LysforholdL2	-0.06	0.23	-0.28	0.78		
	LysforholdL3	0.06	0.29	0.22	0.83		
	LysforholdL4	-0.03	0.30	-0.11	0.91		
	LysforholdL5	0.07	0.23	0.31	0.75		
	Mediantemp	0.00	0.01	0.20	0.85		
	I(cos(2*pi*Hour/24))	-0.08	0.13	-0.67	0.51		
	I(sin(2*pi*Hour/24))	-0.04	0.07	-0.48	0.63		
	I(cos(2*2*pi*Hour/24))	0.01	0.08	0.11	0.91		
	I(sin(2*2*pi*Hour/24))	0.00	0.07	0.06	0.95		
Model 3	(Intercept)	-0.03	0.18	-0.18	0.85	0.00	0.00
	LysforholdL2	-0.06	0.23	-0.27	0.79		
	LysforholdL3	0.06	0.29	0.20	0.84		

	LysforholdL4	-0.04	0.30	-0.13	0.90		
	LysforholdL5	0.07	0.22	0.32	0.75		
	I(cos(2*pi*Hour/24))	-0.09	0.12	-0.74	0.46		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.41	0.68		
	I(cos(2*2*pi*Hour/24))	0.01	0.08	0.18	0.86		
	I(sin(2*2*pi*Hour/24))	0.00	0.07	-0.05	0.96		
Model 16	(Intercept)	-0.11	0.28	-0.38	0.71	9.35E-21±9.67E-11	2.64E-15±5.14E-08
	LysforholdL2	-0.06	0.23	-0.26	0.79		
	LysforholdL3	0.10	0.30	0.33	0.75		
	LysforholdL4	-0.03	0.30	-0.10	0.92		
	LysforholdL5	0.10	0.24	0.41	0.68		
	Mediantemp	0.00	0.01	0.31	0.76		
	I(cos(2*pi*Hour/24))	-0.07	0.13	-0.56	0.58		
	I(sin(2*pi*Hour/24))	-0.03	0.07	-0.38	0.70		
	I(cos(2*2*pi*Hour/24))	-0.01	0.08	-0.12	0.90		
	I(sin(2*2*pi*Hour/24))	0.00	0.08	0.03	0.98		
	I(cos(3*2*pi*Hour/24))	0.10	0.08	1.28	0.20		
	I(sin(3*2*pi*Hour/24))	-0.02	0.07	-0.27	0.78		
Model 4	(Intercept)	-0.04	0.18	-0.24	0.81	0.00	3.22E-15±5.68E-08
	LysforholdL2	-0.06	0.23	-0.25	0.80		
	LysforholdL3	0.08	0.29	0.29	0.77		
	LysforholdL4	-0.03	0.30	-0.11	0.91		
	LysforholdL5	0.08	0.22	0.38	0.70		
	I(cos(2*pi*Hour/24))	-0.07	0.12	-0.60	0.55		
	I(sin(2*pi*Hour/24))	-0.02	0.07	-0.31	0.76		
	I(cos(2*2*pi*Hour/24))	0.00	0.08	-0.05	0.96		
	I(sin(2*2*pi*Hour/24))	-0.01	0.08	-0.08	0.94		
	I(cos(3*2*pi*Hour/24))	0.09	0.08	1.20	0.23		
	I(sin(3*2*pi*Hour/24))	-0.02	0.07	-0.23	0.82		

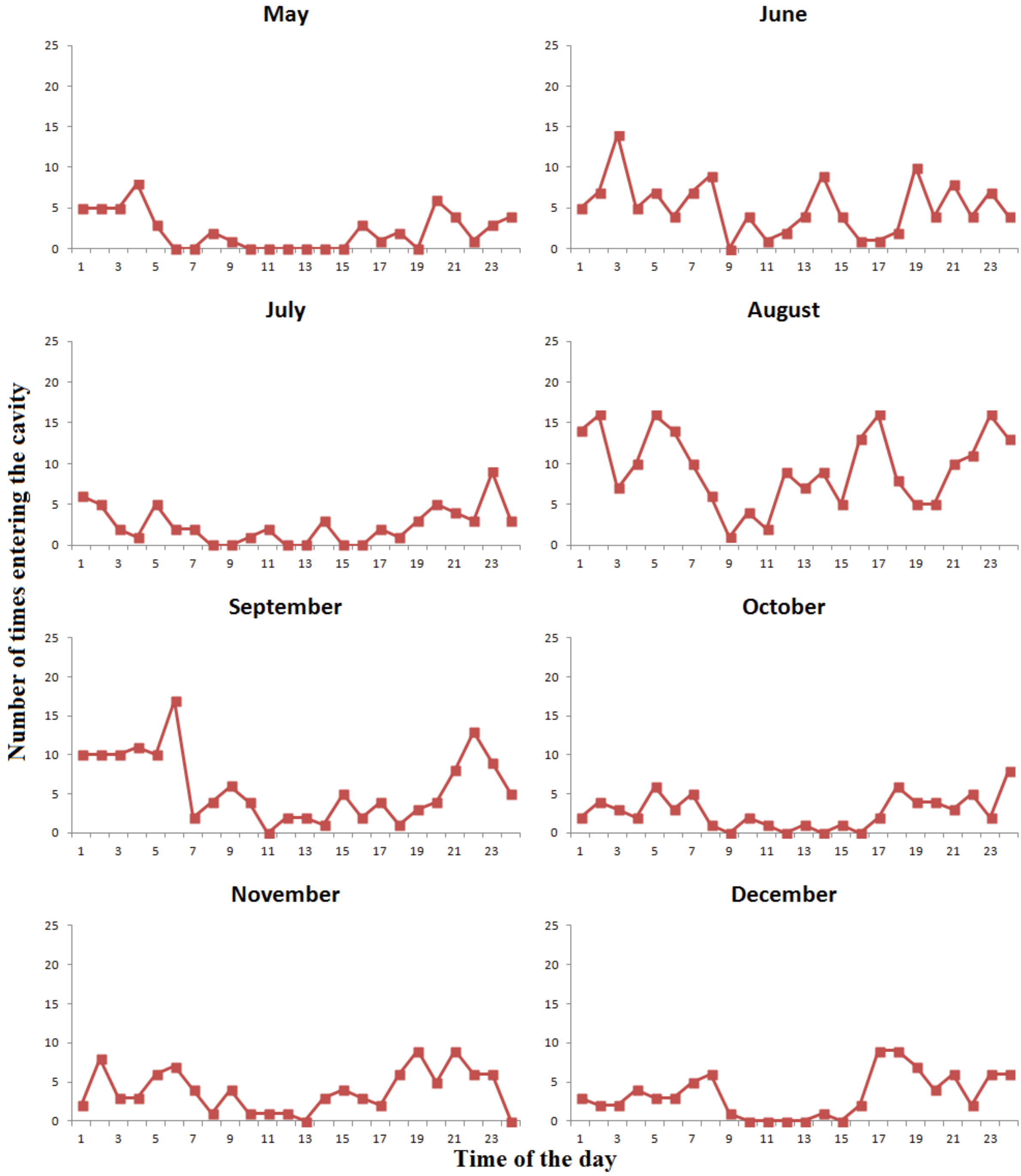

Figure A1. The aggregated number of times the lobster is entering the cavity from May to December as a function of time of the day. N= 15.

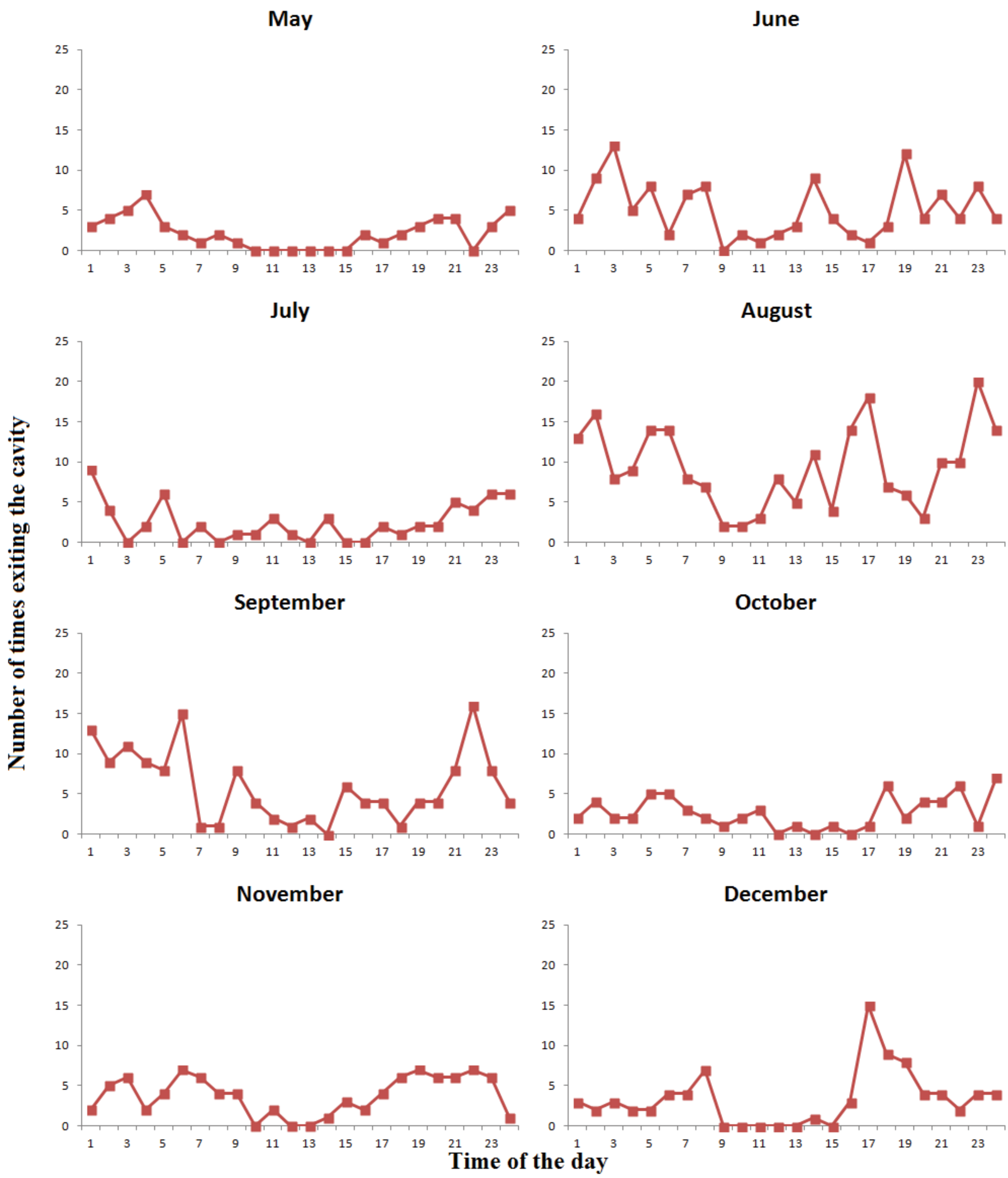

Figure A2. The aggregated number of times the lobster is exiting the cavity from May to December as a function of time of the day. N= 15.

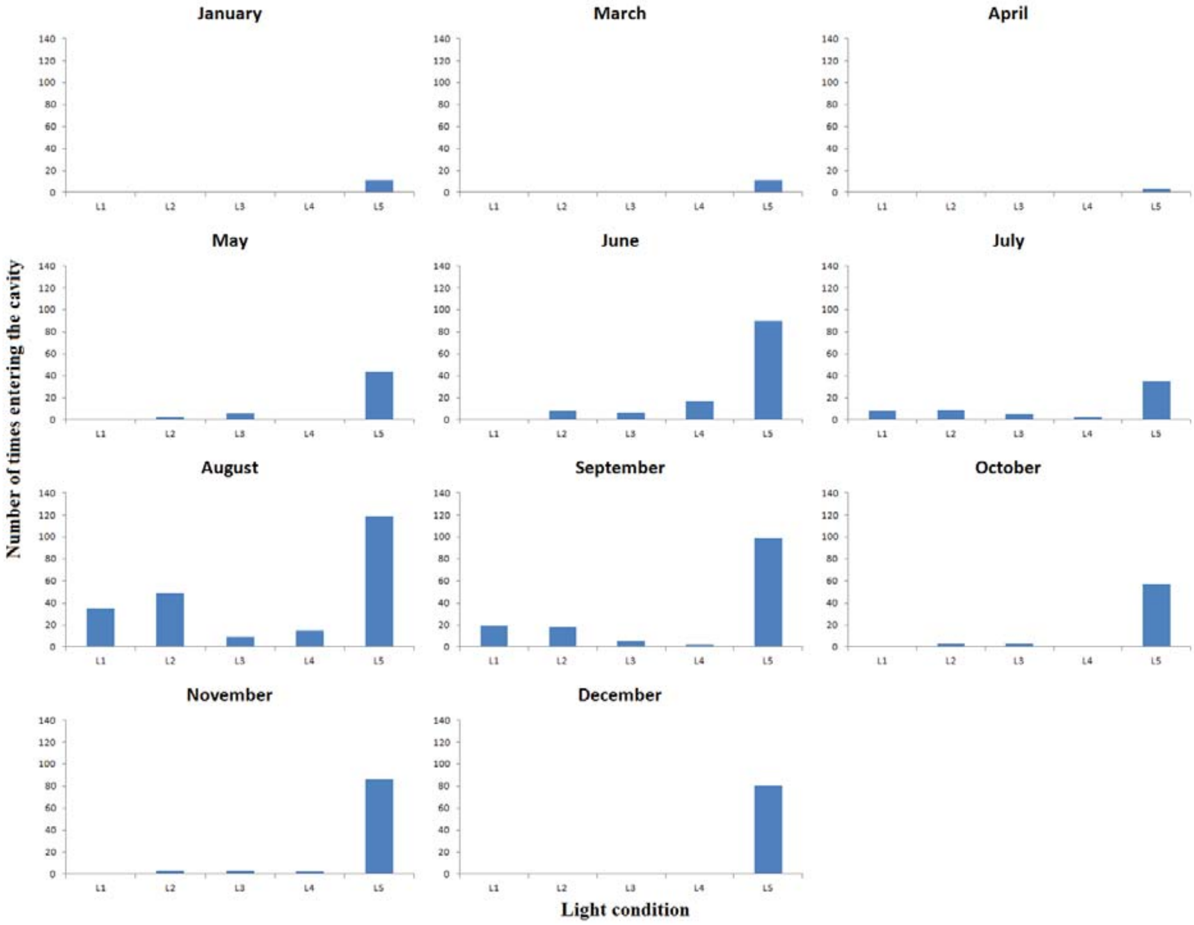

Figure A3. The aggregated number of times the lobsters enter the cavity under the different light conditions. N = 873

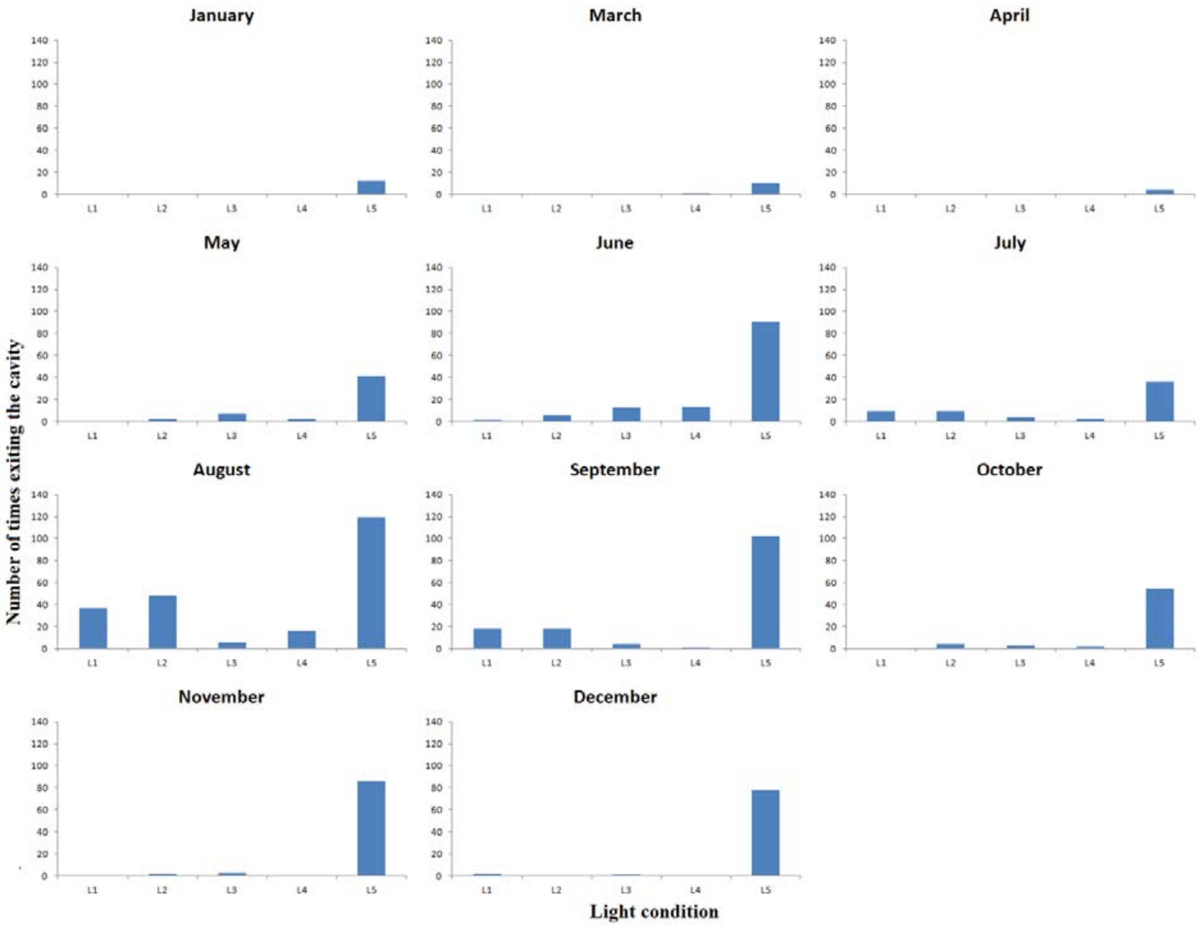

Figure A4. The aggregated number of times the lobsters are exiting the cavity under the different light conditions. N = 867

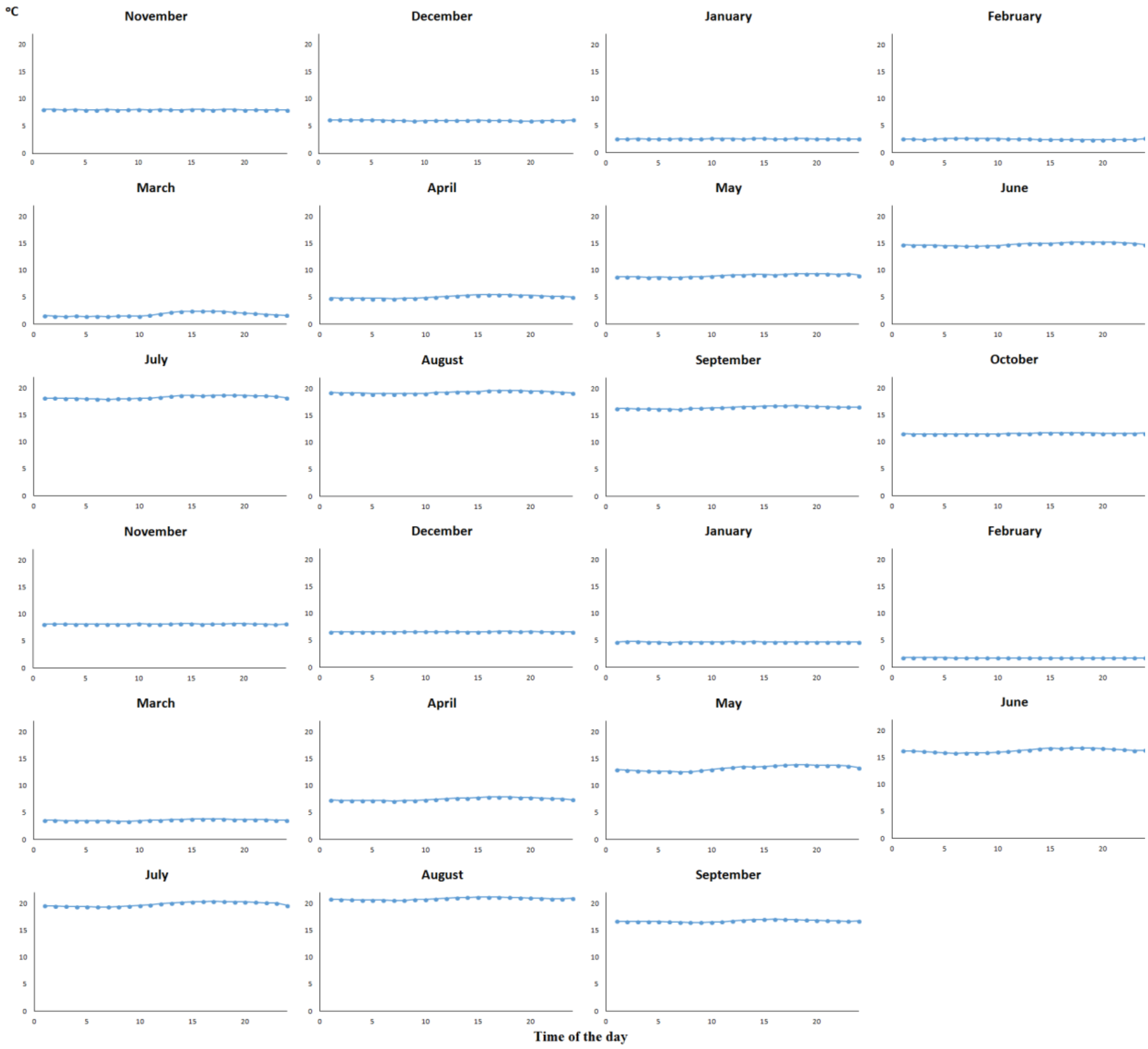

Figure A5. The temperature at 1 m from November 2012 to September 2014 as measured at NIVA Research Facility at Solbergstrand, Frogn Municipality.

Figure A6. The temperature at 60 m from November 2012 to November 2014 as measured at NIVA Research Facility at Solbergstrand, Frogn Municipality.

Table A3. Parameter estimates for the models when testing if temperature and month had an effect on the duration of time spent inside the cavity. Model 3, month, was the best. DSMc was days since midsummer. N= 788, random effects were ID = 33 and year = 3

Model		Estimate	SE	t-value	Random effect ID	Random Effect Year
Model 3	August	1.18	1.38	0.86	28.70±5.35	1.01E-12±1.01E-06
	December	4.91	2.19	2.25		
	July	2.83	1.70	1.66		
	June	-0.20	1.45	-0.14		
	May	8.36	2.44	3.43		
	November	5.17	1.86	2.78		
	October	5.36	2.01	2.68		
	September	1.70	1.26	1.35		
Model 1	(Intercept)	8.64	2.02	4.29	26.98±5.19	0.00
	Temperature	-0.31	0.11	-2.78		
Model 4	(Intercept)	-1.20	0.45	-2.67	1.49±1.22	0.31±0.56
Model 2	(Intercept)	1.57	1.53	1.03	26.60±5.17	0.00
	DSMc	0.03	0.01	2.24		

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