# Insights into lobster trap selectivity: exploring the role of local demography and behaviour for effective reserve monitoring

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SILJE MARIE ULSET

SUPERVISORS
Tonje Knutsen Sørdalen
Susanna Huneide Thorbjørnsen

**University of Agder, 2024**
Faculty of Engineering and Science
Department of Natural Sciences

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**Silje Marie Ulset**

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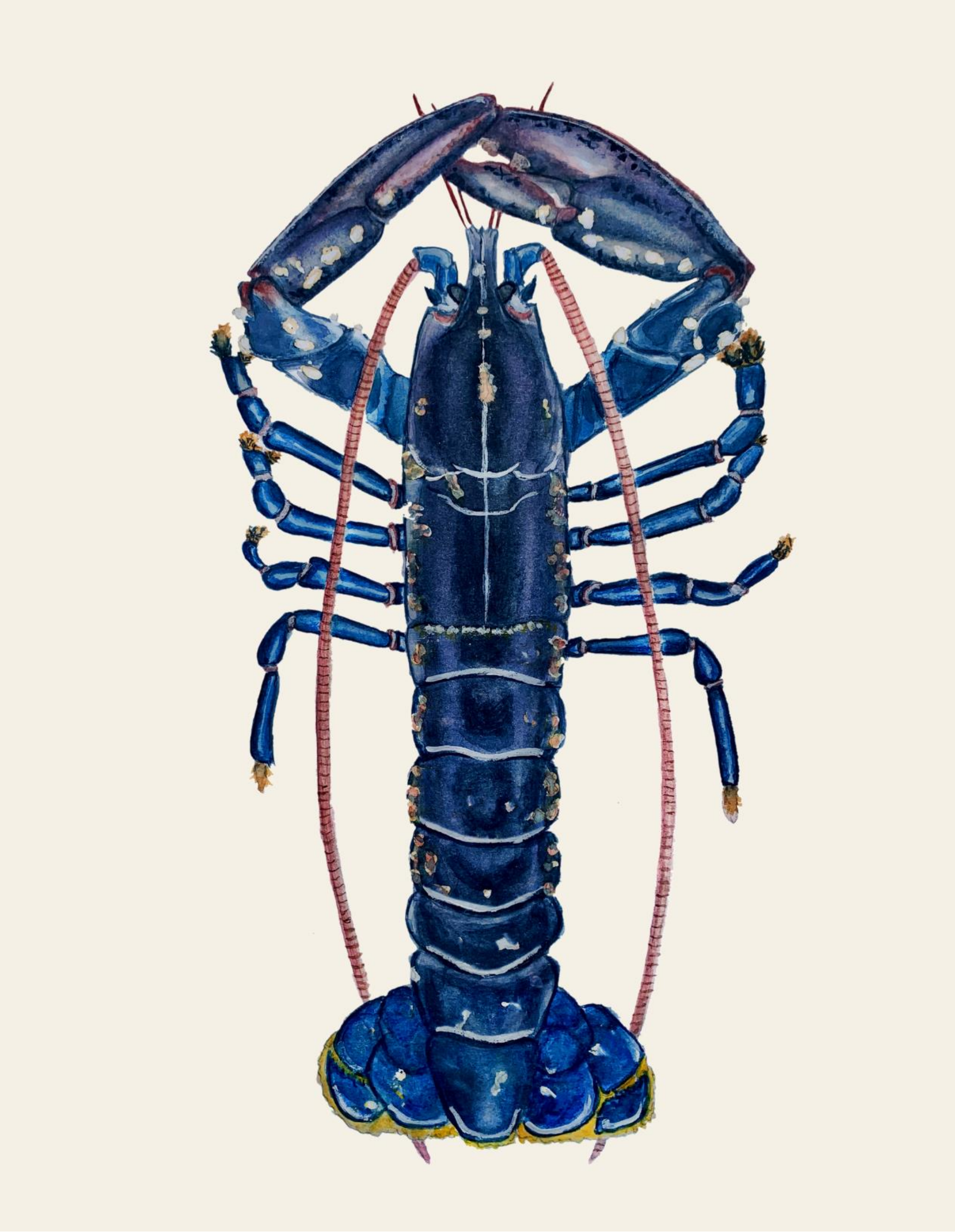

*Figure 1 Illustration made by Susanne Zazzera*

University of Agder

Faculty of Engineering and Science

Department of Natural Sciences

Gimlemoen 25

4604 Kristiansand

http://www.uia.no

# Abstract

Human activities have a major effect on the world's ecosystems including the marine environment, where harvesting practices often target individuals based on specific traits, resulting in selective fishing. This selective pressure has the potential to induce changes in the behavioural, morphological, physiological, and genetic composition of marine populations. Understanding the selectivity is important for understanding the consequences of different fisheries. The declining Norwegian catches of European lobster have led to the implementation of lobster reserves all along the Norwegian southern and western coast. These no-take zones have given researchers the opportunity to study lobster populations in the absence of selective fishing. As a part of a monitoring program, an annual trap survey has been conducted in Flødevigen lobster reserve since 2004. However, the much higher density of lobsters in the reserve area has raised concerns about the catchability and its effect on monitoring results. In this thesis, catch data from one year of the annual lobster survey is compared to a stand-alone fishing survey using a higher trap density and restraint of lobsters. This comparison aims to see how fishing with a different method influences the catches. Additionally, a behavioural experiment in the laboratory investigates the relationship between crusher claw size and behaviour in male lobsters. As males grow larger claws inside the reserve, it has been hypothesized that males with large claws have a higher catchability because of their behaviour. Results indicate that fishing with a higher trap density and restraint of lobsters leads to reduced catch per unit effort (CPUE,) decreased mean total length, a higher proportion of berried females and larger relative claws for both males and females. However, the behavioural experiment revealed no effect of claw size on behaviour. Behaviours tested were time spent in shelter, number of times entering shelter, activity, position in tank and reaction to a food box. Nonetheless, there was a notable individual behaviour among lobsters, by significant repeatability for lobster ID for all behaviours tested. These findings suggest that fishing with different methods can result in catches with different demographic compositions from the same population. Furthermore, lobsters show consistent individual behaviour in relation to shelter usage, activity, position in the tank, and reaction to food, which likely influence their attraction to baited traps and ultimately the catchability.

# Content

# Preface

Firstly, I would like to thank my supervisors Tonje Knutsen Sørdalen and Susanna Huneide Thorbjørnsen. Your support, patience and guidance have been essential. I would like to give a special thanks to Gro van der Meeren who with her expertise on lobster have given invaluable advice. I would also like to thank Stian Stiansen, Rune Johansen and Sofie Gundersen at IMR for practical help during the field work and lab experiment. I would also like to thank Tove Gabrielsen who helped me find a place to sit during the video analysis. In addition, I would like to thank Ane Timenes Laugen who gave me advice regarding the statistics.

I would like to thank Flødevigen and UIA for the opportunity to perform both a field experiment and a lab experiment. I will forever have good memories, especially from the field experiment. And I would like to thank IMR and the lobster group for providing temperature data and data from the annual lobster survey.

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Silje Marie Ulset

# 1 Introduction

Human activities have major effects on the world's ecosystems (Vitousek et al., 1997), and the marine environment is no exception. Humans can be considered a super-predator, as humans take out more marine species than all marine predators added together (Darimont et al., 2015). Marine harvesting is selective, as fishing will often remove individuals based on certain properties. For example, fishing for Sockeye salmon with gillnets in Alaska favours salmon with a certain size and shape (Hamon et al., 2000). Selective fisheries affect more than just the morphology, for example fishing selecting for larger individuals of Zebra fish resulted in earlier maturation, a smaller body size and a higher energetic investment in reproduction but lower fecundity (Uusi-Heikkilä et al., 2015). In contrast it has been found that net fishing of Atlantic salmon resulted in later maturation and a larger body size at maturation, however fishing of capelin, a salmon prey species, resulted in earlier maturation and a smaller body size of salmon (Czorlich et al., 2022). Fishery induced selection can also select for certain behaviours, for example, it has been found that fishery can affect schooling behaviour, making smaller groups more common (Guerra et al., 2020). Fishing have also been found to indirectly select for growth rate, through selection of behaviour as cray fish with a consistent bold behaviour type and a higher growth rate has been found to have a higher catchability (Biro & Sampson, 2015) Harvest selection can alter the genetic composition in a population by selecting for certain genotypes (Biro & Post, 2008). Rainbow trout with a bold and fast-growing genotype has been found to have a higher chance of being harvested compared to trout with a shy and slow growing genotype (Biro & Post, 2008).

Overall understanding how fishery selection acts on species is important for fisheries management. Several common fishery policies have been found to result in disruptive selection, however the likelihood of this depends on the life history of the species (Landi et al., 2015). Evolutionary changes caused by selective fisheries can be reversed, although it could take decades (Conover et al., 2009). This underlines the importance of understanding how fisheries select for different traits, and how this affects the population of the species and species community.

The European lobster (*Homarus gammarus*) is currently categorized as vulnerable on the Norwegian red list, due to a decline in the national population size (Tandberg et al., 2021). It is a species under high fishing pressure from both recreational and commercial fisheries (Kleiven et al., 2012), and it is a species of commercial importance and public interest.

The population decline of European lobster, and a global interest for marine protected areas, motivated the establishment of the first three lobster reserves in Norway in 2006 (Knutsen et al., 2022). Since then, additional lobster reserves have been implemented, and there are currently more than 50 lobster reserves along the Norwegian coastline (Forskrift om fredningsområder for hummer, 2024, § 5; Knutsen et al., 2022). These reserves are no-take zones for lobsters, as all fishing with nets and traps are forbidden. However, fishing with hook and line is allowed (Moland et al., 2013). An annual trap-based monitoring program investigate the effect of the reserves. Although lobsters are the main target for protection, several other species also benefit from the protection (Moland et al., 2021). Cod, brown trout and goldsinny wrasse have all become more abundant compared to control areas (Moland et al., 2021).

These lobster reserves have granted researchers the opportunity to study lobsters were fishery induced selection is absent. Research from the reserves have found that there is a higher density of lobsters in the reserves, the lobsters grow bigger and faster. And in addition, male lobsters grow bigger crusher claws compared to lobsters in non-protected areas (Sørdalen et al., 2020, 2022). This have given new insights to how the Norwegian population of lobster is affected by trap fishing.

The probability of catching fish and crustaceans in a trap is a function of abundance and catchability. Therefore, understanding the catchability of a species is necessary to calculate the abundance (Tremblay & Smith, 2001). Several factors have been found to affect the catchability of crustaceans, for example temperature, lunar cycle, sex, size, season, and moult stage (Goñi et al., 2003; Hewitt et al., 2023).

There has been a concern that as the density of lobsters are becoming high in the reserves, differences in catchability and the selectivity of the traps play a bigger role, and the results of the annual monitoring survey might not fully represent actual lobster demography and density. It is well established that traps are size selective (Miller, 1989). As lobsters in the reserve became bigger, it was decided to include bigger traps as a part of the annual survey in addition to the standard sized traps. This was implemented in 2016. However, in 2022 a study found that adding even larger fish traps resulted in higher catches of large male lobsters (Helms, 2023). The largest lobsters in the reserves were too big to enter both the standard sized traps and the bigger traps used in the annual survey, especially large males with large claws. However, these males were caught in the large fish traps and clearly showed that the size of the gear and/or entrance is correlated to the size of the individuals being caught (Helms, 2023).

There is also evidence that behavioural interactions around the traps could influence the catch. For example, it has been found that pre-stocking traps with lobsters reduces the catches (Addison, 1995). This suggests that the presence of a lobster reduces the probability that a new lobster will enter the trap. For spiny lobsters, traps loaded with large individuals reduced the catches of smaller individuals (Tuffley et al., 2021). A study done on American lobsters, saw that many lobsters interrupted their approach to the traps due to agonistic encounters (Karnofsky & Price, 1989). The same was observed in another study, were 89% of entries ended up as half entries, where the lobster retracted before fully entering, when another lobster were present in the trap (Jury et al., 2001). In comparison when there was no lobster in the trap, only 34 % of entries ended up as half-entries (Jury et al., 2001). Clawed lobsters are known for being hierarchical and aggressive animals, where subdominant lobsters will pull away from dominant lobsters (Skog, 2009). Dominant lobsters will likely scare off subdominant lobsters. There are several factors determining the dominance of lobster. Some examples are size, claw size, moulting stage, and sex. Generally bigger lobsters with bigger claws are dominant, males are dominant over females, and newly moulted individuals can lose their dominance to another previously subdominant individual (Atema, 1986; Bruce et al., 2018; Karnofsky et al., 1989).

A high density of lobsters in Flødevigen reserve could potentially mean that there is many lobsters approaching each trap, however if dominant lobsters are scaring off subdominant lobsters, they could be overrepresented in the results. If subdominant lobsters are prevented from entering the traps, this could also mean that the traps become “full” and the CPUE stagnates even though the population density continues to increase.

Male lobsters within the reserve grow larger crusher claws compared to their body size, which have also been found to be a sexually selected trait (Sørdalen et al., 2020; 2018). These results indicate that relative claw size is linked to catchability. This is supported by the findings of Moland et al. (2019) who found that males with higher relative claw size have a higher chance of being harvested. It is well known that behaviour and catchability is related (Biro & Sampson, 2015), it is possible that lobsters with larger claws have a different behaviour making them more attracted to traps or more likely to enter traps. Although claw size in lobsters have been studied in relation to aggressive behaviour (Bruce et al., 2018) it is little research investigation the relationship between claw size and non-social behaviour.

For American lobsters, trap approaching rates and capture rates have been found to vary greatly between individuals (Karnofsky & Price, 1989). This suggest that individual behaviour also determine the catchability. Lobsters have been found to display a consistency in their behaviour in the wild when it comes to home range, mean depth, depth amplitude and their cumulative distance moved (Moland et al., 2019). This supports the hypothesis that lobsters have individual behaviour that could affect their catchability. Although there is done several studies on behaviour of lobsters, few studies have investigated if lobsters have consistent individual behaviour.

## 1.1 Aim

The lobster no-take areas monitoring program utilizes a trap survey methodology, relying on CPUE (Catch per unit effort) and size distribution data to evaluate the effects of the reserves (Knutsen et al., 2022; Moland et al., 2022). By comparing the catch data from the monitoring survey with results from a fishing experiment using higher trap density and the retaining caught lobster, I aim to discern how this influences the catch metrics of body size, relative claw size, sex and CPUE. Additionally, this study aims to investigate consistent individual behaviour and explore potential relationships between behavioural and morphological traits through laboratory-based behavioural experiments. Specifically, I seek to investigate whether variations in behaviour can be attributed to morphological traits (claw size) and whether male lobsters exhibit individual behavioural patterns.

**Field experiment**

**CPUE:**

**H0:** *There will be no difference in CPUE between the two fishing experiments.*

**H1:** *There will be a lower CPUE in Week 2.*

**Body size:**

**H0**: *There will be no difference in size of lobsters between the two fishing experiments. Size of lobsters will remain the same throughout the fishing period.*

**H1**: *Lobsters will be smaller in the second fishing experiment and the mean size of the lobster catch will decrease during the four fishing days.*

**Relative claw size**:

**H0**: *There will be no difference in relative claw size between the experiments.*

**H1**: Male *lobsters in Week 1 will have a bigger relative claw size than lobsters in Week 2.*

**Sex:**

**H0:** *There will be no difference in the ratio between males, females, and egg-bearing females.*

**H1:** *There will be a higher proportion of egg-bearing females in Week 2 compared to Week 1.*

**Behavioural experiments**

**Time in shelter:**

**H0:** *Lobsters with different crusher claw index will have the same behaviour.*

**H1:** *Lobsters with a higher crusher claw index will spend less time in shelter.*

**Entering shelter:**

**H0:** *Lobsters with different crusher claw index will have the same behaviour.*

**H1:** *Lobsters with a higher crusher claw index will enter the shelter fewer times.*

**Activity:**

**H0:** *Lobsters with different crusher claw index will have the same behaviour.*

**H1:** *Lobsters with a higher crusher claw index will be more active.*

**Position in tank:**

**H0:** *Lobsters with different crusher claw index will have the same behaviour.*

**H1:** *Lobsters with a higher crusher claw index will spend more time away from the wall.*

**Reaction to food box:**

**H0:** *Lobsters with different crusher claw index will have the same behaviour.*

**H1:** *Lobsters with a higher crusher claw index will react more to the food box.*

**Individual behaviour:**

**H0:** *Lobsters will not have a consistent individual behaviour.*

**H1:** *Lobsters will have individual behaviour.*

# 2 Methods

## 2.1 Study site

The study has taken place at the research facility of the Norwegian Institute of Marine Research (IMR) in Flødevigen, Arendal (Figure 2). The fishing experiment was done in Flødevigen lobster reserve. Flødevigen lobster reserve was established in 2006 for research purposes. All types of fixed gear are banned, only hook and line are allowed fishing methods, (Knutsen et al., 2022). Flødevigen lobster reserve is monitored every year by an annual fishing survey, that also monitors a control area (Knutsen et al., 2022). Flødevigen lobster reserve has a size of approximately 1 $km^2$ and the depth varies from 0 to 50 meters (Moland, Moland Olsen, et al., 2011). The seafloor in the reserve consists of both boulders, rocky and soft sediment areas (Moland, Olsen, Andvord, et al., 2011).

## 2.2 Study species

The European lobster (*Homarus gammarus*) can be found in the Atlantic Sea from Marocco in the south to Norway in the north, as well as the Mediterranean Sea. The Northernmost breeding population is found in Tysfjorden in the northern part of Norway (Triantafyllidis et al., 2005). European lobsters are mostly found in or nearby to rocky habitats (Galparsoro et al., 2009). Lobsters in Norwegian waters live mostly at depths ranging from 0-60 meters (Moland, Moland Olsen, et al., 2011). The European lobster is a nocturnal species which is mostly active after sunset and spends most of the day in shelter. Their activity level is seasonal, with decreasing activity with decreasing temperatures (Moland, Moland Olsen, et al., 2011; Smith et al., 1998). They usually have relatively small home ranges, however some individuals may have large home ranges (Moland, Olsen, et al., 2011). Males have been found to have larger home ranges than females (D. Skerritt et al., 2015).

The European lobster is a sexually dimorphic species. When the lobsters reach maturity males will grow larger claws than the females (Debuse et al., 2001). The larger crusher claw in males is a sexually selected trait and females have been found to prefer males with larger claws (Sørdalen et al., 2018). The larger crusher claws are also used to establish dominance between males, for instance for American lobster the male with the largest claw is most likely to be dominant (Atema, 1986; Bruce et al., 2018). The size of the lobster, when they reach maturity is site dependent, lobsters have been found to reach maturity at a carapace length of 73.5-88 (mm) (Coleman et al., 2023), which translates to a total length of approximately 21-25 cm. The European lobster is a long-lived species. A female caught along the coast of England was estimated to be 72 years old, while the oldest male in the same study was estimated to be 42 years old (Sheehy et al., 1999). Lobsters grow by moulting every 1-2 years (Sørdalen et al., 2022). They mate during autumn, and egg-bearing females are found from September to December. The eggs are hatched the following summer (Agnalt et al., 2007). The lobster larvae are pelagic, they go through four stages before they become juveniles (Tully & O Ceidigh, 1987). The newly settled juvenile lobsters are rarely seen in the wild (Linnane et al., 2001). European lobsters can grow large, though the maximum size is unknown. Some large crusher claws have been found, and the original total length of the lobsters has been estimated to be at approximately 65 cm and weighing 9 kg (Wolff, 1978). Lobsters tend to appear in traps when they are about 20 cm long.  The largest lobster caught by trap in Flødevigen lobster reserve had a total length of 45 cm (Helms, 2023).

In addition to the lobster reserves, there are several fishing regulations that aims to protect the European lobster. In Norway the lobsters are protected by a limited fishing season from 1st October until 30th November (31st December from the border between Vestland and Møre og Romsdal county and northwards) (*Reglar for Hummarfiske*, n.d.). There is a minimum landing size of 25 cm (total length) and a maximum size of 32 cm (total length). The landing maximum size is only active from the Swedish border to the border between Agder and Rogaland County. Additionally, all who fish for lobsters must be registered. There is a maximum limit of 10 traps per boat for recreational fishers, and 100 traps per boat for registered commercial fishermen. All traps must have two escape openings of 60 mm diameter. There are also regulations regarding bouyes, name tags and cotton threads which has a main function to reduce ghost fishing of lobster traps (*Reglar for Hummarfiske*, n.d.).

## 2.3 Field experiment

The first part of the research involved conducting two fishing experiments targeting lobsters in the Flødevigen lobster reserve. The first experiment, referred to as Week 1, was part of the annual lobster survey conducted by the Lobster group at the research station. The second experiment, Week 2, used a higher number of traps concentrated in a smaller area with the aim of maximizing lobster catch within that predefined limited space. Additionally, in Week 2, all lobsters were retained on land until the conclusion of the experiment for the purpose of investigating the effect of lobster removals on the subsequent catch. For both experiments two types of two-chambered parlour traps were used; standard size traps (L: 90 cm, W: 45 cm, H:

39 cm, 2 entrances: 12 cm, mesh size: 4,2 cm) and bigger traps (L: 120 cm, W: 60 cm, H: 54 cm, 2 entrances: 18 cm, mesh size: 4.2 cm).

### 2.3.1 Experiment Week 1

The annual lobster survey took place from 29.08.23 to 01.09.23 and used 25 standard-sized traps and 5 bigger traps. The traps were placed evenly throughout the lobster reserve from 5 to 24 meters depth (Figure 2). The traps were baited with half a frozen mackerel and left for 24 hours before they were hauled. The GPS position of each trap was registered. This was repeated four times. All the catches were counted, and species registered. Lobsters were measured for carapax length (mm), total length (mm), and crusher claw width (mm). For females, the abdomen width (mm) was also measured. The sex was registered, and for females, eggs were noted if present. For tagged lobsters, the tags were registered, while untagged lobsters were tagged with two T-bar tags (TBA2, 45 x 2mm; Hallprint). If lobsters were caught with only one tag, the lost tag was replaced with a new. A DNA sample was taken from untagged lobsters by cutting a piece of the pleopods. All animals were released at site of capture after being registered and measured.

### 2.3.2 Experiment Week 2

The second experiment took place the following week, from 04.09.23 to 08.09.23. The predefined area was at approximately 0.13 $km^2$. Since the highest effects of the reserves as has been found furthest away from the reserve borders (Nillos Kleiven et al., 2019), we chose to focus on the inner parts of Flødevigen lobster reserve, the Flødevigen bay, including Terneholmen (Figure 2). For Experiment Week 2, 32 standard-sized traps and 8 bigger traps were used, which is the same ratio of small to big traps as in Experiment Week 1. The traps were placed evenly in the inner parts of the reserve from 2 to 25 meters depth (Figure 2). The traps were baited with half a frozen mackerel and left for 24 hours before they were hauled. The GPS position of each trap was registered. This was repeated four times ending up in 156 hauls (4 hauls less than planned due to traps that got stuck). All the catches were counted, and species were registered. Everything but lobsters were released. Lobsters were registered and measured for carapax length (mm), total length (mm), and crusher claw width (mm). For females, the abdomen width (mm) was also measured. Tagged lobsters were registered, while untagged lobsters were tagged with two T-bar tags (TBA2, 45 x 2mm; Hallprint). If lobsters were caught with only one tag, the lost tag was replaced. A DNA sample was taken from untagged lobsters by cutting a piece of the pleopods.

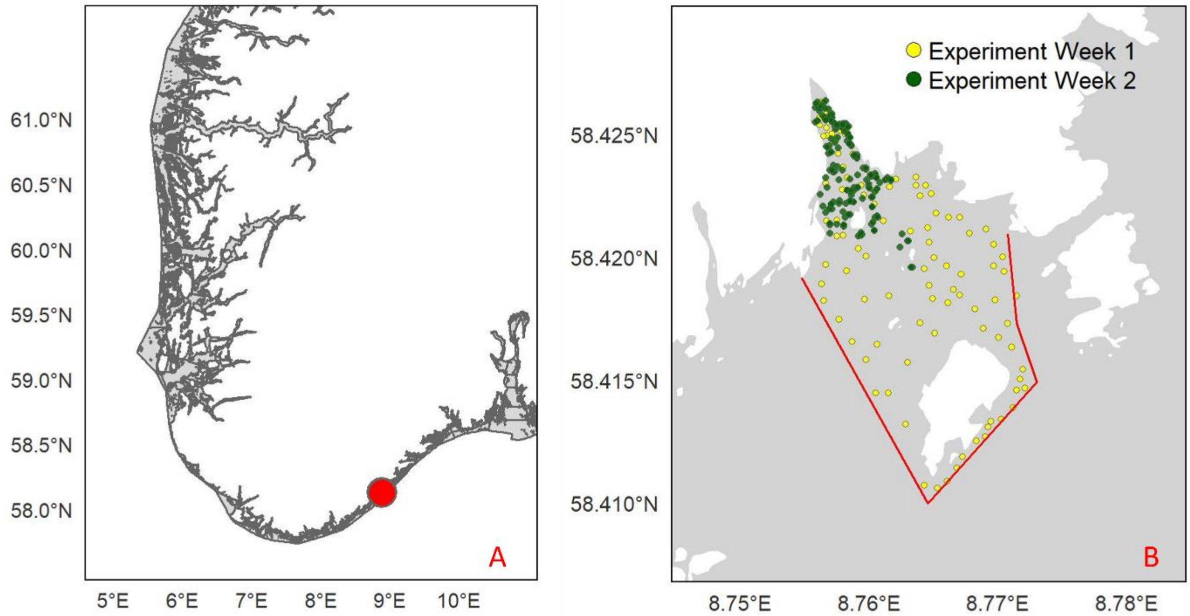


*Figure 2 Map A: The southern part of Norway, the red dot marks where the experiments took place, in Flødevigen lobster reserve. Map B: The location of the fishing experiment. The red lines mark the outer borders of Flødevigen lobster reserve. The yellow and green points marks the locations of the lobster traps in Experiment Week 1 (yellow) and Experiment Week 2 (green), respectively. These maps were made using the package tmap and sf in R-studio and map data from The Norwegian Environment Agency* (Pebesma, 2018; Tennekes, 2018).

## 2.4 Lobster husbandry

All lobsters caught in Week 2 were brought to land, where they were stored with their claws tied using elastic bands (Figure 3). Wet cotton rags were placed over the lobsters during transportation to prevent drought and daylight stress. All lobsters were registered for ID and capture location before they were stored. The lobsters were kept in two-chambered parlour traps and wrasse traps where all openings were closed. The entrance between the chambers were also closed. The lobsters were sorted by sex and size and kept in numbers of 2-3 individuals per trap chamber. Egg-bearing females were kept alone in separate chambers. The traps were placed in a semi-natural pool with seawater from 19 m depth. The water had a temperature varying between 15°C and 17°C. At the end of the last fishing day, lobsters were released back at the capture locations. However, a limited number of males within the legal fishing size were kept for the lab experiment. The lobsters used for the behaviour experiment were kept in the same pool however, in three one-chambered storage traps in groups of five or six lobsters. The bottom of the storage traps was covered with the same carpet as used in the tanks for the behavioural experiment (see 2.5.1 Experimental set up). The lobsters were not fed during storage.

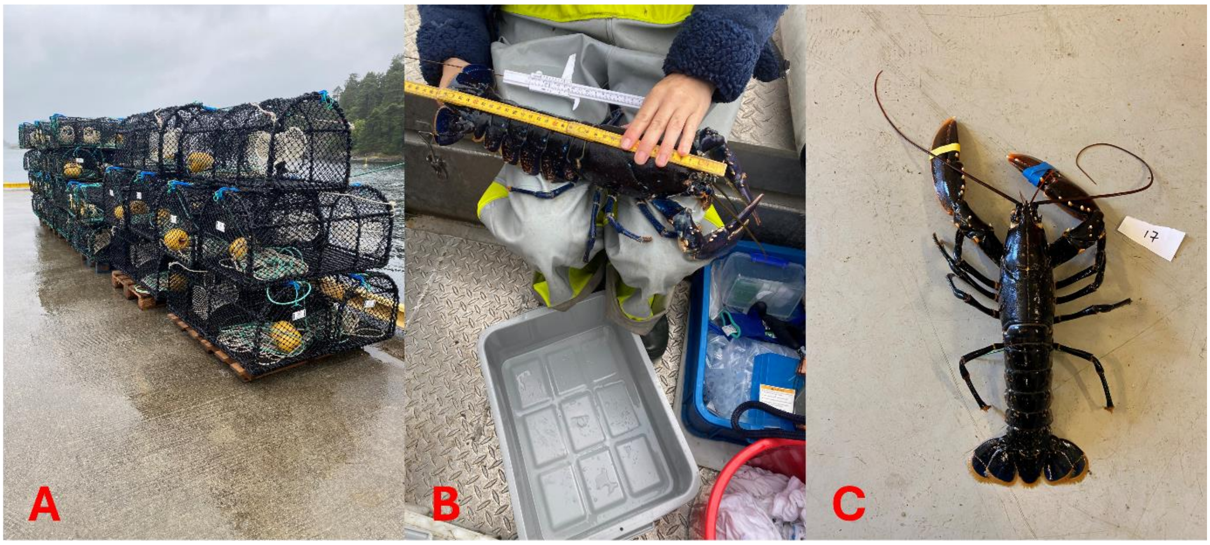


*Figure 3 Pictures from the Experiments. Picture A: The lobster traps used for the fishing experiment. The bigger traps are at the front of the picture, and the standard sized traps are further back. Picture B: A female lobster being measured for total length. Picture C: A male lobster used in the behaviour experiment ready for storage.*

## 2.5 Behavioural experiment

16 male lobsters were used for the behavioural experiment, all within a size range of 25-29 cm total length (TL). The lobsters qualified for the behavioural experiment by being males, within the legal fishing size and without injuries. Then the 16 lobsters with the narrowest size range were chosen. The lobsters were measured for total length, carapax length, claw width, claw length and claw circumference for both crusher and scissor claws. As the moulting stage has been found to affect the behaviour of lobsters (Tamm & Cobb, 1978), a sample was taken from the pleopods to test for the moulting stage. This was done by looking at the pleopods using a stereomicroscope (Figure 4). The moulting stage was determined by using the method described by Koepper et al., (2022).

*Figure 4 Pictures of two pleopods seen through the stereomicroscope. These pleopods are at two different moult stages; 0 (left) and 2-2.5 (right). Foto: Jan Henrik Simonsen*

### 2.5.1 Experimental setup

Six tanks (137x137 cm) were used for the behaviour experiment. The bottom of the tank was covered with a “grass” carpet to give the lobster some structure to walk on. The carpet was glued to the bottom of the tank using Tec 7 (Trans 7). A grid of 9 squares (45x45 cm) was drawn onto the carpet to track the movement on camera. Each tank contained a shelter built from roof tiles and paving stones with two openings. Two pavement stones formed one of the sidewalls, while a roof tile made up the roof and second sidewall. Two additional pavement rocks were placed on top to stabilize and make it difficult for the lobsters to rearrange the shelter. Additionally, a small tile was place underneath the roof tile to make up for it being slightly smaller at one end (Figure 5). To make sure the shelter was of appropriate size it was tested using some lobsters from the research station. For the food box experiment a string was attached at two of the edges of the tanks, making it crossing over the tanks. A knot was tied at the string making a loop. A perforated box with a string through the lid and with a hook in the end, was hooked at this loop during the food box experiment. The water in the tanks was seawater from 75 m depth. The inflow of water was kept at 5.5 L/min throughout the experiment. The water level was kept so that the shelters (including the pavement stones on top) were fully emerged, ca. 400 L of water in each tank. The water temperature was monitored daily and varied between 12.6°C and 14.5°C throughout the experiment. The light was kept constant throughout the experiment at 5.7 Lux measured at the water surface in the tanks. This was the lowest light level where there was still enough visibility to analyse the videos.

A camera was placed over the six tanks, filming them all at once. The camera was connected to a server where the videos were stored.


*Figure 5 Picture A: Tank set up with both shelter and food box in the tanks, the red x marks where lobsters were put in the tank, facing away from the shelter, Picture B: The food box, Picture C: The shelter.*

### 2.5.2 Experimental run

Each of the 16 lobsters was tested three times (replicates), at three days intervals. Before each run, the lobster got their claws untied for the replicate run, and then tied again before going back to storage. For each experiment session with a new set of five or six lobsters, the water was changed. This was to make sure that there would be no influence on behaviour from the past trial. The water was also changed several times before the first run. The lobsters were placed at the same spot in the tanks each time, to the right of the shelter, facing away of the shelter (Figure 5). After 19.5 h a perforated box containing a piece of frozen mackerel filet (ca. 30 g) were added to the tank at the opposite side of the shelter. After two additional hours, the experiment was over, and the lobsters were taken back to storage. The lobsters were otherwise not fed during the experimental period. The box containing mackerel were rinsed with seawater between each experiment and refilled with a new piece of frozen mackerel before being added to the tanks.

### 2.5.3 Video analysis

The videos were analysed using the program Boris (v. 8.21.8 2023-10-05) (Friard & Gamba, 2016).

For the whole experimental run, four different behaviours were measured: usage of shelter, activity, rolling and stretching. The usage of the shelter was noted by registering the time from lobsters entered the shelter until they exited the shelter. Activity was measured by counting the number of squares the lobsters entered. The squares were given numbers from 1 to 9, where the shelter is in square 2 and the food box is in square 8 (Figure 6). Every time the lobsters entered a new square this was noted, as well as the number of the square. To qualify the lobsters must have at least the claws (or tail if backing) in the square. If lobsters were walking on the line between two squares, only one was noted. Two other behaviours were also noted: rolling on the side and stretching for the water surface along the tank wall or the shelter.

During the three first and three last hours some additional behaviours were noted. Time spent moving next to the wall as well as time spent moving away from the wall was registered. In addition, the number of times the lobsters backed and the number of times they stopped and turned. Visible turns in the shelter were also noted. For the last two hours, when the food box was present, some extra behaviours were noted; time spent with the food box (minimum their claws inside the same square as the box, square 8), reaction to the food box (either attack or stopping within square 8), and times they returned directly to their shelter after reacting to food box. Attacking the food box was defined as contact and the claws "grasping" for the box.

Furthermore, the time until entering the shelter (the time from the lobster was put in the tank until it entered the shelter) and the time of the first stay in the shelter, was noted at the beginning of each experiment.

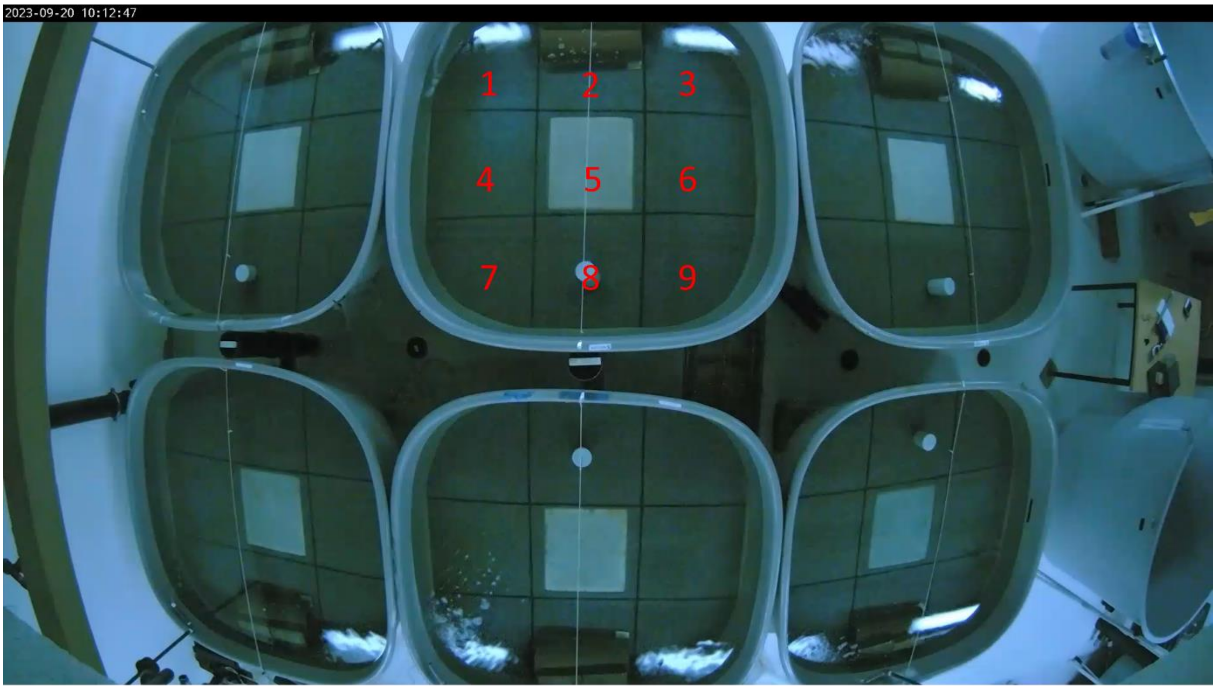


*Figure 6 Tank set-up seen from the camera when the food boxes are present. The numbers in red represent the numbers used when measuring activity in the video analysis.*

## 2.6 Statistical analyses

Data analysis has been done using R (version 4.3.2) (R Core Team, 2023) in RStudio (version 2023.12.1). To compare the data from the two fishing experiments, all traps placed outside the area of experiment Week 2 were filtered out (Figure 7). In the Flødevigen reserve there is a continuous logging of the water temperature at 1-, 19- and 75-meters depth. These data have been provided by IMR, and the water temperature at 19 meters depth have been used in the analysis.

Relative claw size is a measurement used in several studies looking at catchability and was therefore chosen for the data analysis for the field experiment. Relative claw size was calculated as described by (Sørdalen et al., 2020). This was done by calculating the residuals from the linear regression Crusher claw width ~ Total length was for each sex separately. It was assumed that the residuals would be normally distributed, and the negative residuals with a higher absolute value than the highest positive residual were removed (one male). This was to make sure that claws being small due to regeneration after claw loss were not included in the analysis.

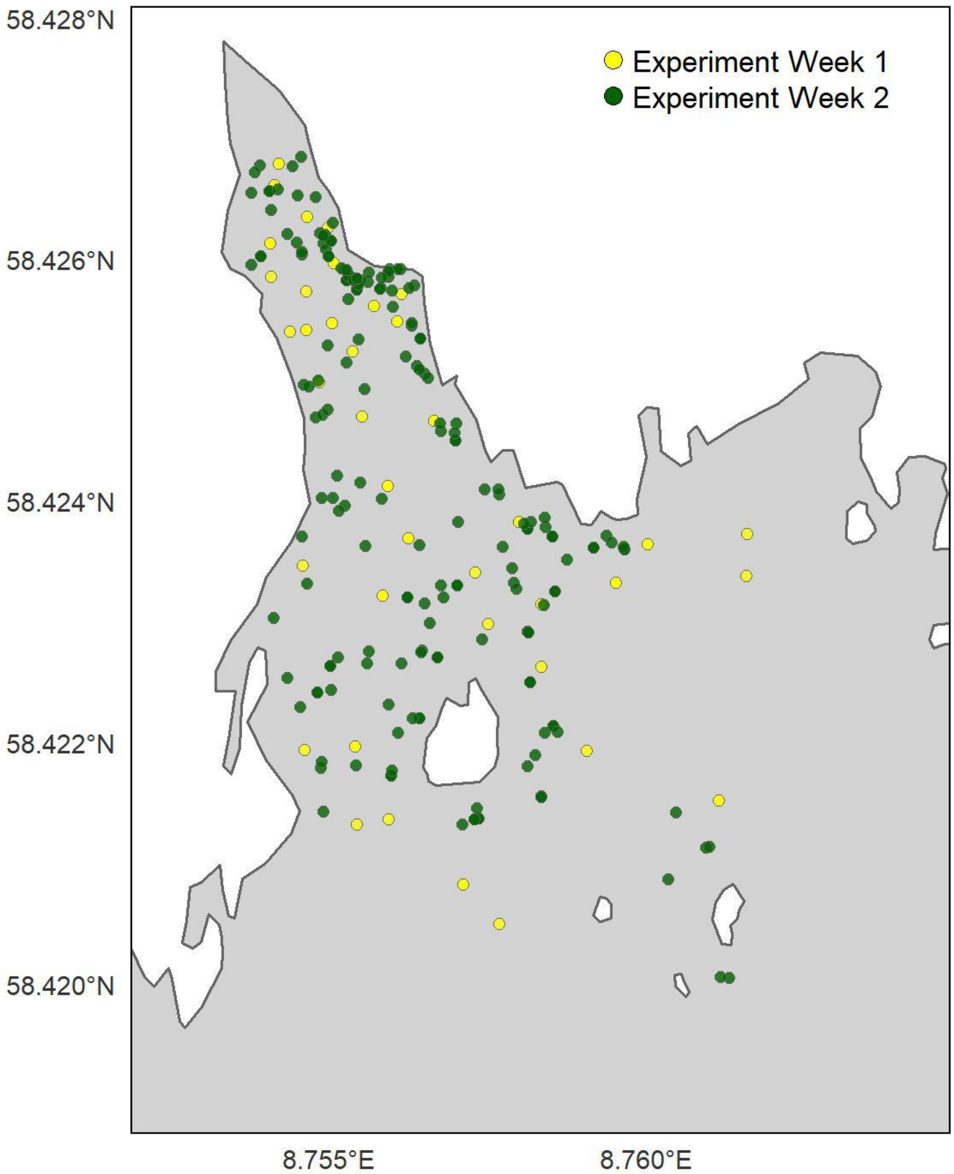


*Figure 7 Map of the inner parts of flødevigen lobster reserve. The points mark the locations of the lobster traps in Experiment Week 1 and experiment Week 2. Note here traps from experiment Week 1 have been removed to match the coverage of experiment Week 2 The maps were made using the package tmap and sf in R-studio and map data from The Norwegian Environment Agency* (Pebesma, 2018; Tennekes, 2018).

### 2.6.1 Models fishing experiment

The models for the fishing experiments were made using the *lm() and glm()* functions in the stats package (R Core Team, 2023). All the models were designed based on our research questions which included an interaction effect. All models were compared to an simplified model without the interaction effect, and the best fit models were chosen based on AIC-values using the *AIC()* function in the stats package (R Core Team, 2023). The advanced model needed to have an AIC that was more than 2 values lower than the simplified model, or else the simplified model was chosen. To evaluate that the assumptions were met, the function *check_model()* in the performance package were used (Lüdecke et al., 2021), or the *plot()* function in the graphics package (R Core Team, 2023) . The diagnostics plots were then evaluated visually and can be found in the Appendix (Figure A 1, Figure A 2, Figure A 3, Figure A 4, Figure A 5).

**CPUE**

Catch per Unit Effort (CPUE) was calculated by number of lobsters caught divided on number of hauls. This calculation was performed per day per week. A generalized linear model with a Poisson distribution was chosen. To test the hypothesis on a reduction in CPUE during the experimental weeks, and to test the difference between the weeks, we chose to look at CPUE as a function of Week and Day with an interaction effect. We also corrected for temperature as this has recently been shown to influence the lobster catches (Sørdalen, pers. comm.).

$$CPUE \sim Week \times DAY + Temperature$$

**Egg bearing females**

During initial data exploration, a hypothesis regarding berried females was formed. A generalized linear model with a binomial distribution was used to test if there was a difference in number of berried females between the two weeks, and to see if it increased over the 4 fishing days. Temperature was added as a variable for correction.

$$\text{Number of berried females} \sim Week \times Day + Temperature$$

**Body size**

To test the hypothesis that lobsters would be smaller in Week 2 and that there would be a reduction during the week, the following linear model was tested:

$$\text{Total length} \sim Week \times Day + \text{Trap type}$$

Trap type is included to correct for a higher proportion of bigger traps in Week 1.

**Relative claw size**

To test the hypothesis that lobster would have a smaller relative claw size in Week 2 compared to Week 1, and that there would be a reduction during the week, the following linear model was tested for each sex separately:

$$\text{Relative claw size} \sim Week \times Day$$

### 2.6.2 Model selection for the behaviour experiment

Unfortunately, some video files were damaged and could not be analysed. A total of five files were damaged (Table A 1 (Appendix)). To correct for this the missing time has been subtracted from the total duration for the relevant observations. However, the results showed that time spent in the shelter and activity measured in the number of squares entered is related to the time of the day (Figure 14), which this correction does not account for.

For the behavioural analysis generalized mixed effect models were used to look at the different behavioural traits with lobster ID and tank as random effects. Lobster ID was included to check for consistent individual differences in behaviour, while tank was included to correct for any tank effect. Replicate, temperature and Total length were added as fixed effects to all models to correct for any effects. This was in addition to Crusher claw index which were added to test our hypotheses. These models were made using the lme4 package in R (Bates et al., 2015). The models were then compared to simplified models, and the best fit model was chosen by comparing AIC using the *anova()* function from the stats package (R Core Team, 2023). The advanced model needed to have an AIC that was more than 2 values lower than the simplified model, or else the simplified model was chosen. Firstly, the starting model was compared to models without random effects. Then the model was compared to a model where the fixed effect with the highest p-value were removed. Finally, the best fit model was compared to a model without fixed effects. A full list of models and AIC values can be found in the appendix (Table A 2, Table A 3, Table A 4, Table A 5, Table A 6). The models were evaluated using the DHARMa package in R (Hartvig, 2022). All models were checked for overdispersion, the residuals were plotted in a qq-plot and it was checked for patterns in the residuals. Diagnostics plots can be found in the appendix (Figure A 6, Figure A 7, Figure A 8, Figure A 9, Figure A 10, Figure A 11, Figure A 12).

Claw index has been used in the models as a measurement that accounts for both length and circumference of the claws, therefore a more detailed measurement than relative claw size. Claw index was calculated following the method by Van Der Meeren & Uksnøy, (2000): *Claw index = Claw length (mm) × Claw circumference (mm)*

**Time spent in shelter**

To test the hypothesis that lobsters with bigger crusher claws spends less time in shelter a binomial distribution was chosen, comparing time in shelter with time out of shelter. Time spent in shelter = sec in shelter / sec out of shelter.

Full model:

*Shelter ~ Total length + Crusher Claw Index + Temperature + Replicate + Random: Tank + Random: Lobster ID*

**Number of times entering the shelter**

Number of times entering the shelter was divided by total duration of the trial, resulting in number of times entering shelter per hour. To test whether this depends on morphologic measurements as claw size and total length, a linear mixed effect model was used, as the response variable was normally distributed.

Full model:

*Number of times entering shelter per hour ~Total length + Crusher claw index + Temperature + Replicate + Random: Tank + Random: Lobster ID*

**Activity**

Every time a lobster entered a new square this were noted as a measure of activity. The 1.5 first hours were removed, as lobsters had a very high activity at the beginning of each experiment. The two last hours were also removed, as when measuring activity, the response to the food box were not of interest. Number of squares entered were then divided on time, to correct for missing files. Activity per hour was log-transformed to achieve normality. To test if activity could be explained by morphologic measures the following linear mixed effect model was used:

Full model:

*log(Activity per hour) ~Total length + Crusher Claw Index + Temperature + Replicate + Random: Tank + Random: Lobster ID*

**Position in tank**

Time spent moving next to the wall vs away from the wall were measured for the three first and three last hours. To investigate if the position in the tank could be explained by claw size and total length a generalized linear mixed effect model with a binomial distribution were chosen. Here, seconds moving next to the wall is compared to seconds moving away from the wall. Position in tank = sec. next to wall/sec. away from wall.

Full model:

*Position in tank~ Total length + Crusher Claw Index + Temperature + Replicate + Random: Tank + Random: Lobster ID*

**Reactions to the food box**

Reaction to the food box was defined as entering the same square as the food box when the food box was present (Figure 6). A generalized linear model with a Poisson distribution was chosen. For this model, "day" was chosen instead of replicate as one of the predictor variables. Number of day in trial gives a better estimate of potential hunger, as all the same replicates were not done on the same day. To test if number of reactions to the food box could be explained by morphologic measurements, the following model was used:

Full model:

*Number of reactions to food box ~ Total length + Crusher Claw Index + Temperature + Day + Random: Tank + Random: Lobster ID*

### 2.6.3 Repeatability

Repeatability (R) is a standardized measurement used in behaviour analysis to quantify how much of the variation is explained by the individual (Dingemanse & Dochtermann, 2013). Repeatability is defined by Equation 1, where $V_{ind}$ represent the among individual variance and $V_e$ represent the within individual variance (Dingemanse & Dochtermann, 2013):

$$repeatability = V_{ind}/(V_{ind} + V_e) \quad \text{(Eq. 1)}$$

The ID of the lobster was added as a random effect for all behaviours. A trait was considered to have a significant repeatability when inclusion of the random effect improved the model (AIC-value reduced by >2). ICC stands for Intraclass Correlation Coefficient and is calculated using the same equation as for repeatability (Lüdecke et al., 2021). ICC-values are presented in the model summaries for the behaviour models and was calculated using the *icc()* function in the package performance (Lüdecke et al., 2021).

# 3 Results

## 3.1 Field experiment

In Week 1, where all catches were released on site, and the trap density was lower, 39 hauls were conducted within the inner part of the reserve (Figure 7). This effort yielded the capture of 64 lobsters, consisting of 59 individuals as five lobsters (2 females and 3 males) were caught twice. Of the captured lobsters, 29 were males and 35 were females, with nine of the females having eggs. During experiment Week 2, 156 hauls were conducted resulting in 104 lobsters. Among these, 46 were males and 58 were females, with 26 of the females having eggs. Because all captured lobster was retained, no lobsters in experiment Week 2 were caught more than once, however 28 lobsters previously captured during Week 1 were re-captured in Week 2.

The model selection resulted in the following model:

*CPUE ~ Week + Day + Temperature*

The average number of lobsters per trap was higher in Experiment Week 1 (mean= 1.64) compared to Week 2 (mean= 0.67, p-value <0.001) (Table 1). Both Week 1 and Week 2 showed a decline in lobster catch over the four-day period, however the decrease was not statistically significant (p-value = 0.11) (Figure 8).

*Table 1 Summary output of the generalized linear model for CPUE.*

| **Model: CPUE ~ Week + Day + Temperature** | | | | |
|---|---|---|---|---|
| **Coefficients:** | **Estimate** | **Standard error** | **Z value** | **p-value** |
| **Intercept** | -1.57 | 3.83 | -0.41 | 0.68 |
| **Week 2** | -0.84 | 0.20 | -4.13 | **<0.001** |
| **Day** | -0.16 | 0.10 | -1.60 | 0.11 |
| **Temperature** | 0.15 | 0.25 | 0.61 | 0.54 |

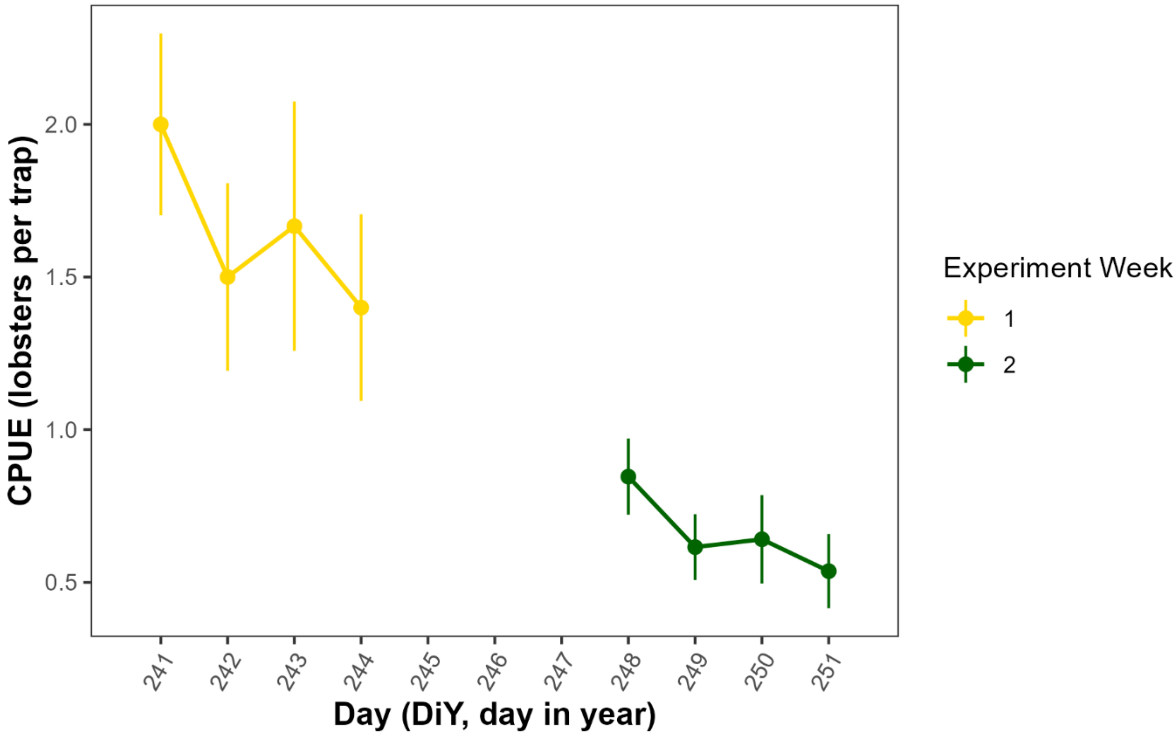


*Figure 8 Lobsters per trap for the four fishing days for Experiment Week 1and 2. The vertical lines represent the Standard error.*

### 3.1.1 Sex

The model selection resulted in the following model:

*Proportion of berried females ~Week + Day + Temperature*

The proportion of males and females was similar in both weeks (Week 1; 0.55:0.45 females to males, Week 2; 0.56:0.44 females to males). However, in Week 2, there was significantly higher proportion of berried females compared to Week 1 (p-value = 0.026) (Table 2). Additionally, there was no effect of day on the proportion of berried females.

*Table 2 Summary table for Proportion of berried females.*

| **Model: Proportion of berried females ~Week + Day + Temperature** | | | | |
|---|---|---|---|---|
| **Coefficients** | **Estimate** | **Standard error** | **Z value** | **p-value** |
| **Intercept** | -20.81 | 13.19 | -1.57 | 0.11 |
| **Week 2** | 1.49 | 0.67 | 2.22 | **0.026** |
| **Day** | -0.18 | 0.32 | -0.56 | 0.58 |
| **Temperature** | 1.24 | 0.84 | 1.47 | 0.14 |

### 3.1.2 Size

In Week 1 lobsters ranged from 193 mm to 391 mm in total length, with a mean of 311.4 ± 5.3 (mm ± SE). Females had a mean size of 306.2 ± 7.9 (mm ± SE), while males had a mean size of 317.6 ± 6.7 (mm ± SE). In Week 2 total length of lobsters ranged from 170 mm to 387 mm, with a mean of 286.8 ± 5.0 (mm ± SE). Females had a mean size of 290.5 ± 6.0 (mm ± SE), and males had a mean size of 282.1 ± 8.4 (mm ± SE) (Figure 9, Figure 10).

The model selection resulted in the following linear model:

*Total length ~Week + Day + Trap type*

This model was used to investigate how total length differed between the weeks if it changed during the four days. There was no effect of day but lobsters were significantly bigger in Week 1 (p-value 0.0019) (Table 3).

*Table 3 Model summary output:* ***Total length ~Week + Day + Trap type***

| **Model: Total length ~Week + Day + Trap type** | | | | |
|---|---|---|---|---|
| **Coefficients** | **Estimate** | **Standard error** | **t value** | **p-value** |
| **Intercept** | 309.16 | 10.15 | 30.46 | **<0.001** |
| **Week 2** | -23.99 | 7.58 | -3.16 | **0.0019** |
| **Day** | -0.69 | 3.25 | -0.21 | 0.83 |
| **Trap type** | 12.91 | 8.34 | 1.55 | 0.12 |

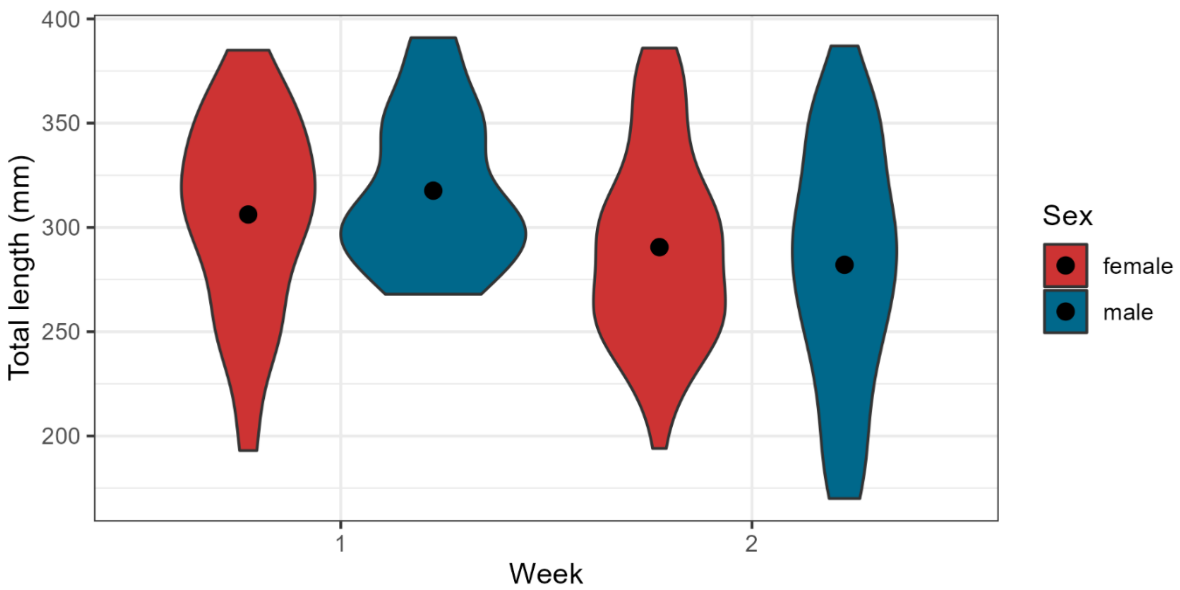


*Figure 9 A violin plot with Week on the x-axis and Total length (mm) on the y-axis. Females are plotted in red and males are plotted in blue. The mean for each group is visualized by a black dot*

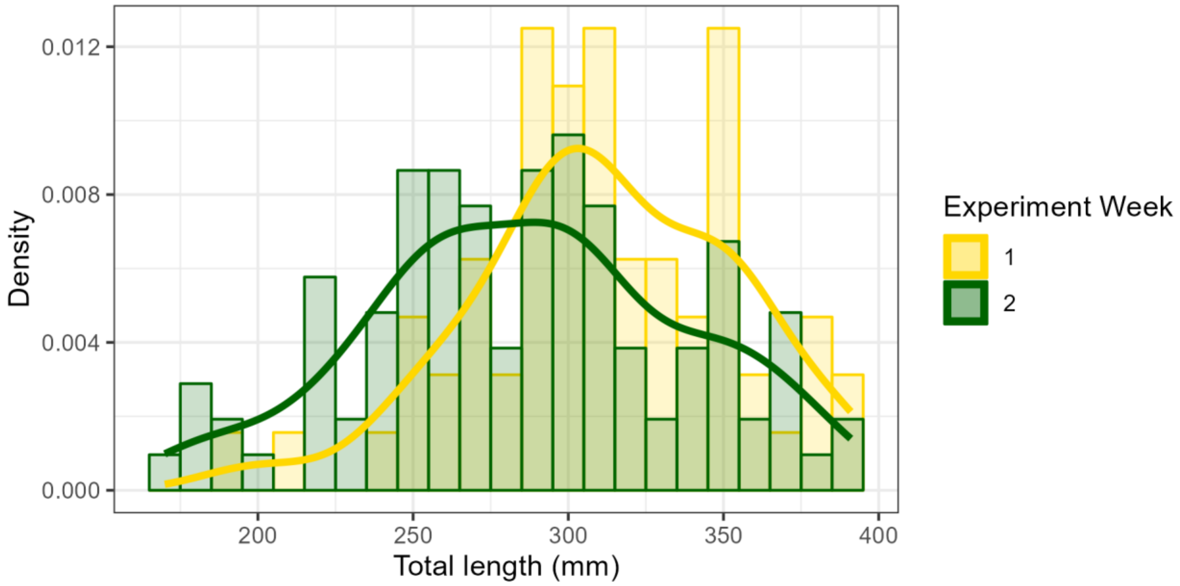


*Figure 10* Density *plot and histogram with total length of lobsters caught in Experiment Week 1 (yellow) and 2 (green).*

### 3.1.3 Relative claw size

In Week 1 female crusher claw width ranged from 29 mm to 72 mm with a mean of 49.29 ± 1.53 (mm ± SE). Male crusher claw width ranged from 47 mm to 91 mm, with a mean of 65.14 ± 2.42 (mm ± SE). In Week 2 female crusher claw width ranged from 30 mm to 67 mm width a mean of 49.39 ± 1.26 (mm ± SE). Male crusher claw width ranged from 19 to 96 mm, width a mean of 58 ± 2.91 (mm ± SE). The model selection resulted in the following model:

*Relative claw size ~ Week + Day*

The relative claw size (calculated as the residuals from the regression line: Crusher claw width ~ Total length) did not decline during the four fishing days for neither males or females, but the relative claw size was larger in Week 2 for both sexes (Table 4) (Figure 11).

*Table 4 Model summary for Relative claw size ~ Week + Day, for males and females*

| **Model: Relative claw size ~ Week + Day** | | | | | |
|---|---|---|---|---|---|
| **Males:** | **Coefficients** | **Estimate** | **Std. error** | **t value** | **p-value** |
| | Intercept | -0.97 | 1.27 | -0.76 | 0.45 |
| | Day | -0.59 | 0.45 | -1.31 | 0.20 |
| | Week 2 | 3.74 | 1.04 | 3.61 | **<0.001** |
| **Females:** | | | | | |
| | Intercept | -0.63 | 1.23 | -0.52 | 0.61 |
| | Day | -0.39 | 0.40 | -0.99 | 0.32 |
| | Week 2 | 2.62 | 0.92 | 2.85 | **0.005** |

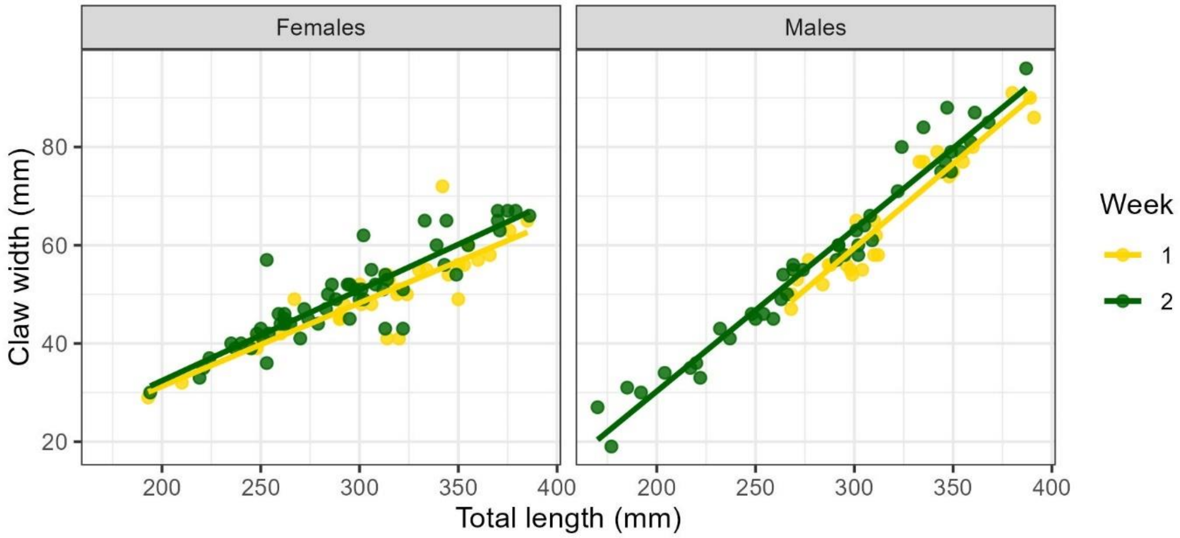


*Figure 11 A scatter plot with Total length (mm) on the x-axis and Claw width (mm) on the y-axis for Week 1 (yellow) and Week 2 (green). Regression lines have been added using the stat_smooth() function in ggplot in R. The left panel is for females and the right for males.*

## 3.2 Behavioural experiment

For the behavioural experiment we used male lobsters with a total length within the legal fishing size range (250 mm - 320 mm). After removing lobsters with injuries, we were left with 17 lobsters in the size range: 252 mm to 287 mm. For simplicity, the lobsters were given a number between 1 and 17, in addition to their tags. However, one of the lobsters (number 8) were not used in the behavioural experiment. Therefore number 8 is excluded from the following results. 16 lobsters went in the behavioural experiment three times, resulting in 48 trials. All the lobsters had newly moulted and were at moult stage 0, except for lobster 15 who were at moult stage 2 or 2.5 (Koepper et al., 2022)(Table 5).

*Table 5 Morhological measurements of lobsters used in the behavioural experiment*

| Lobster ID | Total length (mm) | Carapace length (mm) | Crusher Claw width (mm) | Crusher claw length (mm) | Crusher claw circumference (mm) | Moult stage |
|---|---|---|---|---|---|---|
| **1** | 266 | 96 | 52 | 116 | 134 | 0 |
| **2** | 274 | 98 | 54 | 121 | 140 | 0 |
| **3** | 267 | 97 | 54 | 120 | 139 | 0 |
| **4** | 270 | 96 | 52 | 127 | 131 | 0 |
| **5** | 256 | 91 | 51 | 121 | 133 | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **6** | 252 | 88 | 49 | 116 | 126 | 0 |
| **7** | 261 | 91 | 55 | 123 | 145 | 0 |
| **9** | 254 | 86 | 47 | 116 | 123 | 0 |
| **10** | 278 | 101 | 52 | 124 | 137 | 0 |
| **11** | 278 | 99 | 57 | 134 | 144 | 0 |
| **12** | 269 | 93 | 48 | 116 | 130 | 0 |
| **13** | 256 | 89 | 45 | 112 | 117 | 0 |
| **14** | 266 | 89 | 44 | 107 | 114 | 0 |
| **15** | 275 | 101 | 53 | 127 | 134 | 2-2.5 |
| **16** | 287 | 102 | 55 | 133 | 140 | 0 |
| **17** | 283 | 100 | 51 | 129 | 137 | 0 |

### 3.2.1 Shelter

Whenever lobsters entered the shelter, time was noted until they exited. These times have then been added together and divided by the total time of the trial. This was to correct for missing video files. The lobsters spent on average 86.8 % ± 0.037 (SE) of the trial in the shelter, however 6 observations spent between 0.6 % and 65.6% of time in shelter. The remaining 42 observations spent between 84.4% and 99.7% of the time in shelter (Figure 12).

For the statistical analysis, time spent in shelter was compared to time spent outside the shelter, for 48 observations divided on 16 lobsters. The final simplified model was a generalized mixed effect model with the following structure:

*Shelter ~ Temperature + Replicate + Random: Tank + Random: Lobster ID*

There was no effect of either the total length or size of the crusher claw. However, there was a significant negative effect of temperature (p-value <0.001) and a positive effect of replicate (p-value <0.001). Lobsters spent less time in shelter when the temperature was higher, and more time in shelter in subsequent replicates. Repeatability was significant for lobster ID (R=0.47). Inclusion of tank as a random effect also improved the model, but the effect was relatively small (R=0.05) (Table 6).

The diagnostics plot for the model showed patters in the residuals (Figure A 6). Therefore, an alternative model without outliers were fitted. This model gave the same results for the fixed effects, significant effect of temperature and replicate, and no effect of total length or crusher claw index. However, the repeatability for lobster ID (R = 0.16) and tank (R = 0.019) was lower (Table A 7). Nevertheless, this model also showed patterns in the residuals (Figure A 7).

*Table 6 Model summary output for shelter usage without outliers. 95% confidence intervals and p-values were computed using a Wald z-distribution approximation.*

| **Model: Shelter ~ Temperature + Replicate + Random: Tank + Random: Lobster ID** | | | |
|---|---|---|---|
| | | | |
| **Model Fit:** | | | |
| Pseudo-$R^2$ (fixed effects) = 0.08 | | | |
| Pseudo -$R^2$ (total) = 0.55 | | | |
| | | | |
| **Fixed effects:** | **Estimate** | **95% CI** | **p-value** |
| **Intercept** | 22.16 | (20.70, 23.62) | **<0.001** |
| **Temperature** | -1.50 | (-1.58, -1.42) | **<0.001** |
| **Replicate** | 0.82 | (0.77, 0.88) | **<0.001** |
| | | | |
| **Random effects** | **Variance** | **Standard deviation** | |
| **Lobster ID** | 3.16 | 1.78 | |
| **Tank** | 0.32 | 0.57 | |
| | | | |
| **Repeatability:** | | | |
| **Group** | **Groups** | **ICC** | |
| **Lobster ID** | 16 | 0.47 | |
| **Tank** | 6 | 0.05 | |

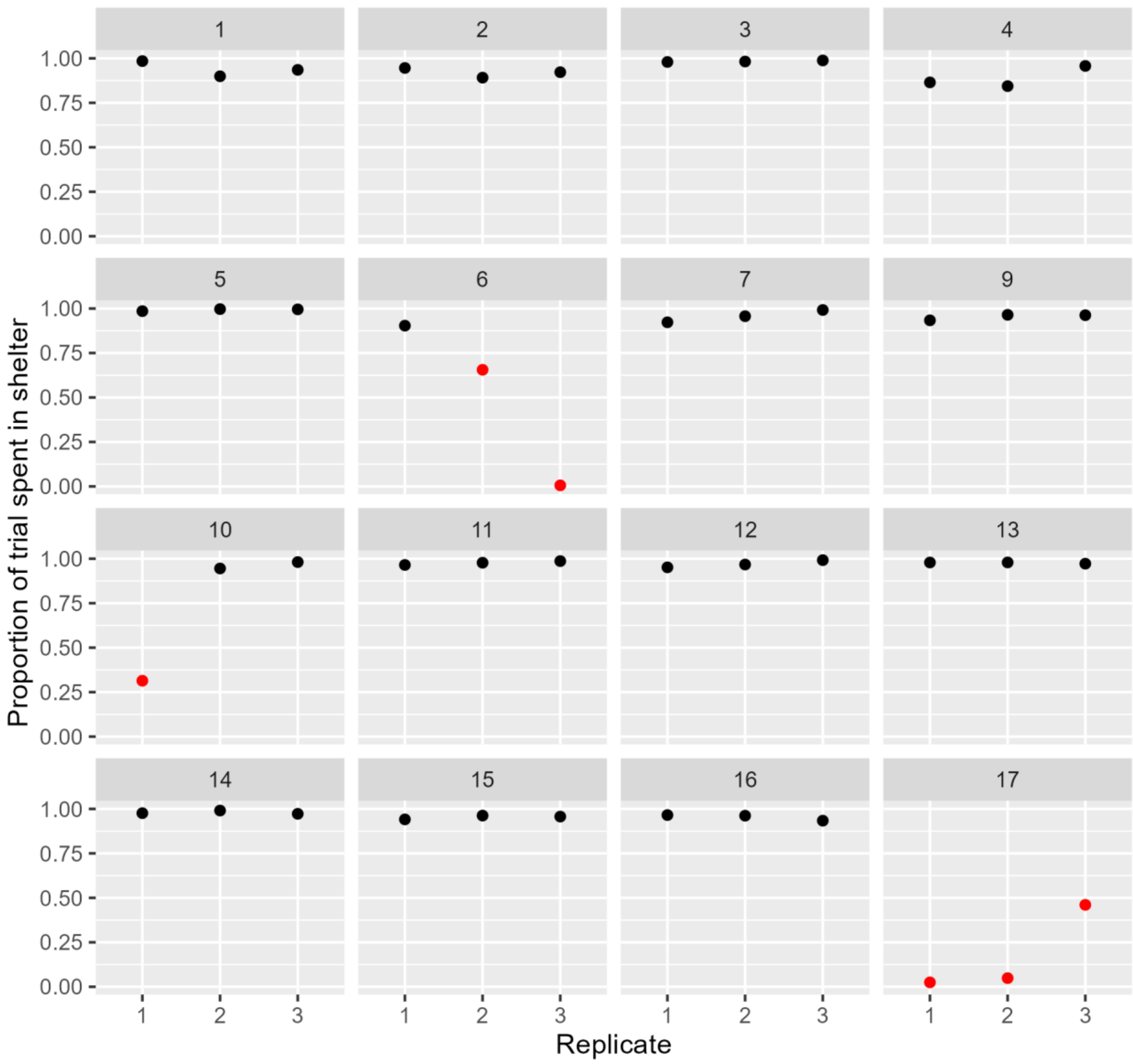


*Figure 12 A scatter plot with replicate on the x-axis and proportion of time spent in shelter on the y-axis. The different panels represent the different lobsters. The red points are outliers, these were included in the presented model, however they were removed in an alternative model that can be found in the appendix (Table A 7).*

### 3.2.2 Number of times entering shelter

Number of times entering shelter per hour ranges from 0.44 to 5.0 (Figure 13). Lobsters entered shelter on average 2.1 ± 0.15 (SE) times per hour. For the statistical analysis 48 observations were used divided on 16 lobsters. The model selection resulted in the following simplified model:

*Number of times entering shelter per hour ~ Replicate + Random: Tank + Random: Lobster ID*

There was no effect of Total Length, crusher claw index or temperature. However, there was a significant negative effect of replicate. Lobsters entered shelter less often in subsequent replicates (p-value: 0.037) (Table 7). Repeatability was significant for lobster ID (R = 0.44) but not for tank.

*Table 7 Model summary table for number of times entering the shelter. 95% Confidence intervals and p-values were computed using a Wald t-distribution approximation*

| **Model: Number of times entering shelter ~ Replicate + Random: Tank + Random: Lobster ID** | | | | |
|---|---|---|---|---|
| | | | | |
| **Model Fit:** | | | | |
| Pseudo-$R^2$ (fixed effects) = 0.05 | | | | |
| Pseudo -$R^2$ (total) = 0.47 | | | | |
| | | | | |
| **Fixed effects:** | **Estimate** | **d.f.** | **95% CI** | **p-value** |
| **Intercept** | 2.71 | 45.8 | (2.01, 3.41) | **<0.001** |
| **Replicate** | -0.30 | 31 | (-0.58, -0.02) | **0.037** |
| | | | | |
| **Random effects** | **Variance** | **Standard deviation** | | |
| **Lobster ID** | 0.49 | 0.70 | | |
| **Residual** | 0.63 | 0.79 | | |
| | | | | |
| **Repeatability:** | | | | |
| **Group** | **Groups** | **ICC** | | |
| **Lobster ID** | 16 | 0.44 | | |

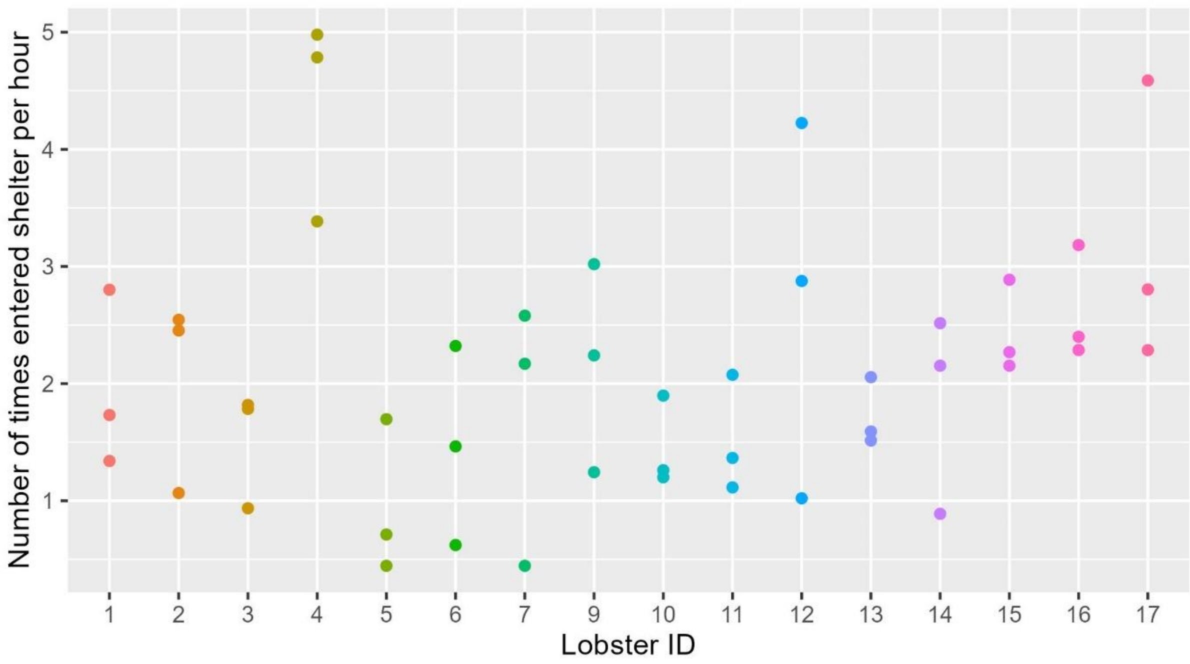


*Figure 13 A scatterplot with lobster ID on the x-axis and Number of times entered shelter per hour on the y-axis.*

#### 3.2.3 Activity

The activity of lobsters varied during the day, with the highest activity the first 1.5 hours after entering the tank (Figure 14).

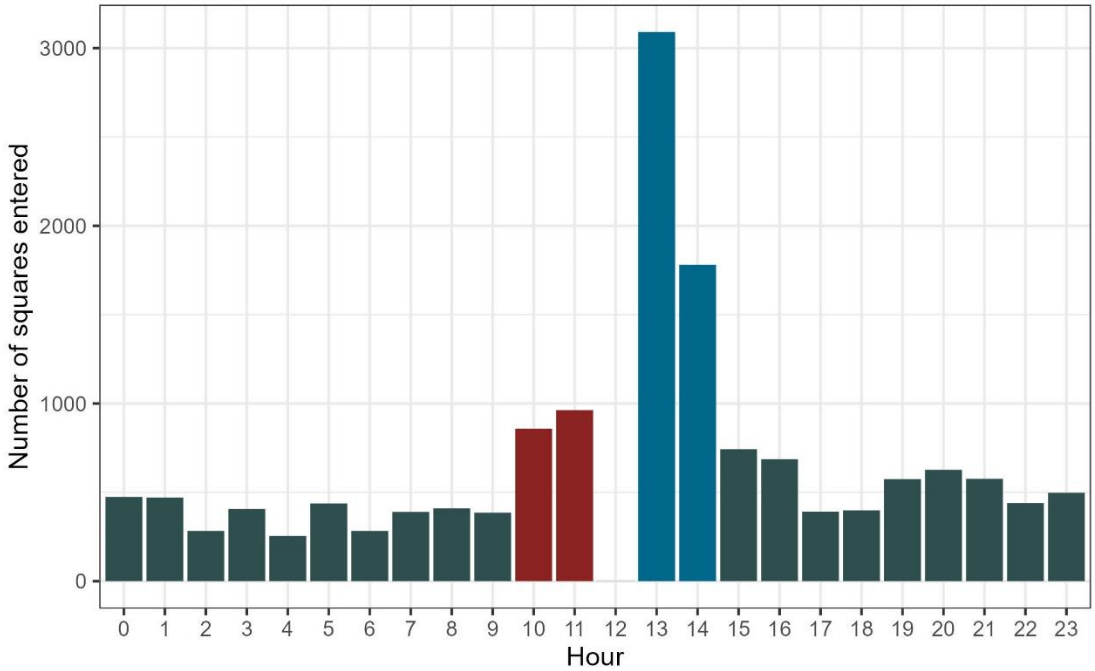


*Figure 14 A bar plot with hour at the x-axis and number of squares entered on the y-axis. The hours represent the time of the day, for example hour 10 = 10:00-10:59. The red bars (10 and 11) is when the food box is present. The blue bars represent the first 1.5 hours of the experiment. Number of squares entered for hour 13 has been doubled, as the experiment started 13.30 and not 13.00.*

To look at their “normal activity” the first 1.5 hours, and the last two hours (when the food box was present) were removed from the analysis. The total number of squares was then divided by the total duration. 48 observations distributed among 16 individual lobsters were used for the analysis. Activity ranged from 0.37 to 47.38 squares entered per hour (Figure 15). A lobster entered on average 9.85 ± 1.27 (± SE) squares per hour. The model selection resulted in the following linear mixed-effect model:

*log(Activity per hour) ~   Random: Lobster ID*

There was no effect of total length, crusher claw index, temperature, or replicate. However, the repeatability for lobster ID group is 0.47, indicating that 47% of the variation in the response variable is explained by Lobster ID (Table 8).

*Table 8 Linear mixed effect model summary table for activity. 95% confidence intervals and p-values were computed using a Wald t-distribution approximation*

| **Model: Number of times entering a square ~ +1 + Random: Tank + Random: Lobster ID** | | | | |
|---|---|---|---|---|
| | | | | |
| **Model Fit:** | | | | |
| Pseudo-$R^2$ (fixed effects) = 0.00 | | | | |
| Pseudo -$R^2$ (total) = 0.47 | | | | |
| | | | | |
| **Fixed effects:** | **Estimate** | **d.f.** | **95% CI** | **p-value** |
| **Intercept** | 1.96 | 15 | (1.60, 2.32) | **<0.001** |
| | | | | |
| **Random effects** | **Variance** | **Standard deviation** | | |
| **Lobster ID** | 0.36 | 0.60 | | |
| **Residual** | 0.41 | 0.64 | | |
| | | | | |
| **Repeatability:** | | | | |
| **Group** | **Groups** | **ICC** | | |
| **Lobster ID** | 16 | 0.47 | | |

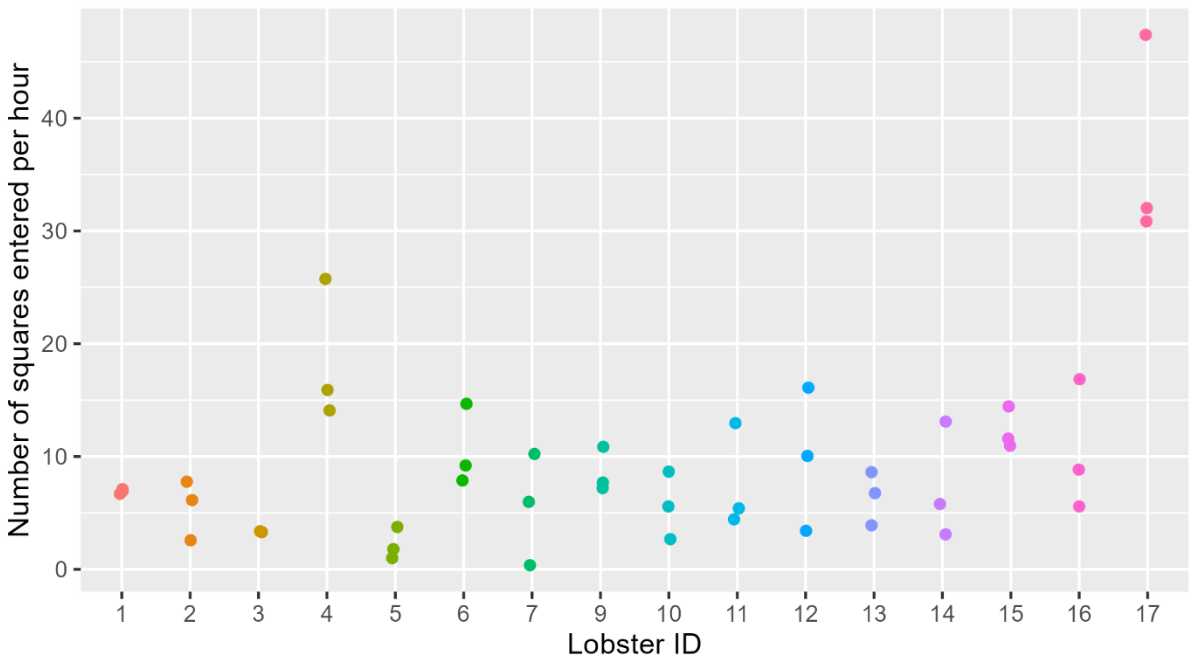


*Figure 15 Plot with number of squares entered per hour on the y-axis and lobster ID on the x-axis.*

### 3.2.4 Position in tank

Minutes moving next to the wall ranged from 1.17 to 155.6, while minutes moving away from the wall ranged from 0.83 minutes to 302.8 minutes (Figure 16, Figure A 14). Lobsters spent on average 17.4 ±4.4 (SE) min next to the wall and 34.7 ± 9.3 (SE) minutes away from the wall. The model selection gave the following generalized mixed-effect model:

*Position in tank~ Temperature + Replicate + Random: Tank + Random: Lobster ID*

There was no effect of total length or crusher claw index, however, there was a significant effect of both replicate (p-value: < 0.001) and temperature (p-value: < 0.001) (Table 9). The temperature had a positive effect of moving next to the wall, while replicate had a negative effect. Repeatability was significant for lobster ID (R= 0.14), and for tank (R= 0.04).

When running diagnostics plot for the model for position in tank, some patterns were detected in the residuals (Figure A 10). Therefore, an alternative model was fitted without outliers, this model gave the similar results for the fixed effects (effect of replicate and temperature, and no effect of Crusher claw index and total length), and a slightly lower repeatability for ID (R=0.10) and tank (R=0.03) (Table A 8). For this model the diagnostics plot showed no patterns in the residuals (Figure A 11).

*Table 9 Model summary for position in tank. 95% confidence intervals and p-values were computed using a Wald z-distribution approximation.*

| **Model: Position ~ Temperature + Replicate + Random: Tank + Random: Lobster ID** | | | |
|---|---|---|---|
| | | | |
| **Model Fit:** | | | |
| Pseudo-$R^2$ (fixed effects) = 0.01 | | | |
| Pseudo -$R^2$ (total) = 0.18 | | | |
| | | | |
| **Fixed effects:** | **Estimate** | **95% CI** | **p-value** |
| **Intercept** | -6.09 | (-6.78, -5.48) | **<0.001** |
| **Temperature** | 0.43 | (0.40, 0.46) | **<0.001** |
| **Replicate** | -0.18 | (-0.20, -0.16) | **<0.001** |
| | | | |
| **Random effects** | **Variance** | **Standard deviation** | |
| **Lobster ID** | 0.56 | 0.75 | |
| **Tank** | 0.14 | 0.37 | |
| | | | |
| **Repeatability:** | | | |
| **Group** | **Groups** | **ICC** | |
| **Lobster ID** | 16 | 0.14 | |
| **Tank** | 6 | 0.04 | |

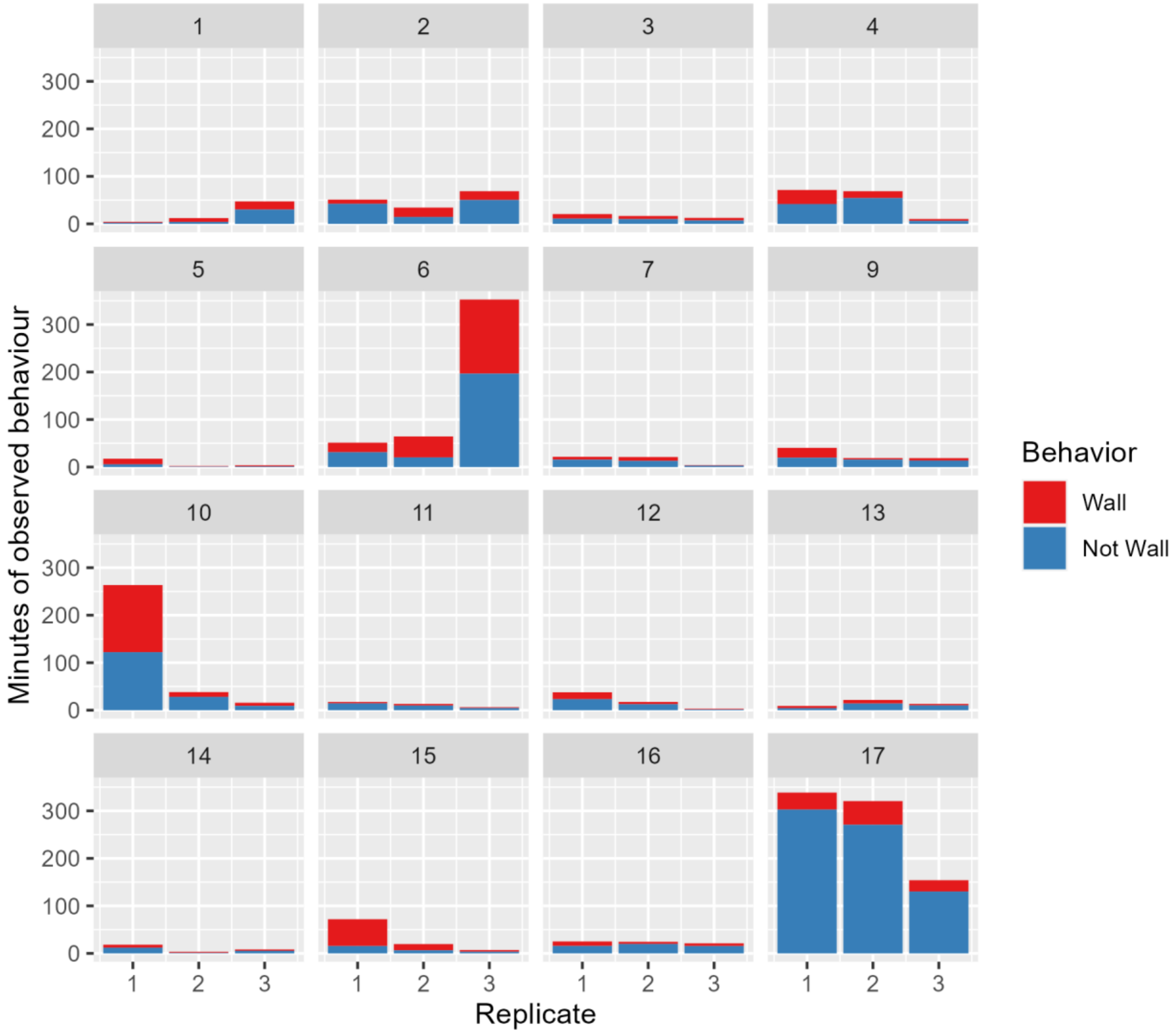


*Figure 16 A stacked bar plot with minutes of observed behaviour on the x-axis and replicate on the y-axis. The panels represent the different lobster IDs.*

### 3.2.5 Reaction to food box

Number of reactions ranged from 0 to 16 reactions. In 22 observations there were 0 reactions. 2 individuals (lobster 5 and lobster 14) did not react at all during the three replicates (Figure 17). The overall mean was 2.8 ± 0.58 (SE) reactions per trial. The model selection gave the following generalized mixed-effect model:

*Number of reactions to food box~ +1 + Random: Tank + Random: Lobster ID*

This model includes 48 observations divided into 16 individual lobsters were used. There was no effect of either day, temperature total length or crusher claw index. However, there was a significant repeatability for lobster ID (R = 0.54) and tank (R = 0.068) (Table 10).

*Table 10 Model summary for reactions to food box. 95% confidence intervals were computed using a Wald z-distribution approximation*

| **Model: Number of reactions to food box ~ +1+ Random: Tank + Random: Lobster ID** | | | |
|---|---|---|---|
| | | | |
| **Model Fit:** | | | |
| Pseudo-$R^2$ (fixed effects) = 0.00 | | | |
| Pseudo -$R^2$ (total) = 0.74 | | | |
| | | | |
| **Fixed effects:** | **Estimate** | **95% CI** | **p-value** |
| **Intercept** | 0.36 | (0.35, 0.36) | <**0.001** |
| | | | |
| **Random effects** | **Variance** | **Standard deviation** | |
| **Lobster ID** | 1.36 | 1.17 | |
| **Tank** | 0.14 | 0.37 | |
| | | | |
| **Repeatability:** | | | |
| **Group** | **Groups** | **ICC** | |
| **Lobster ID** | 16 | 0.54 | |
| **Tank** | 6 | 0.06 | |

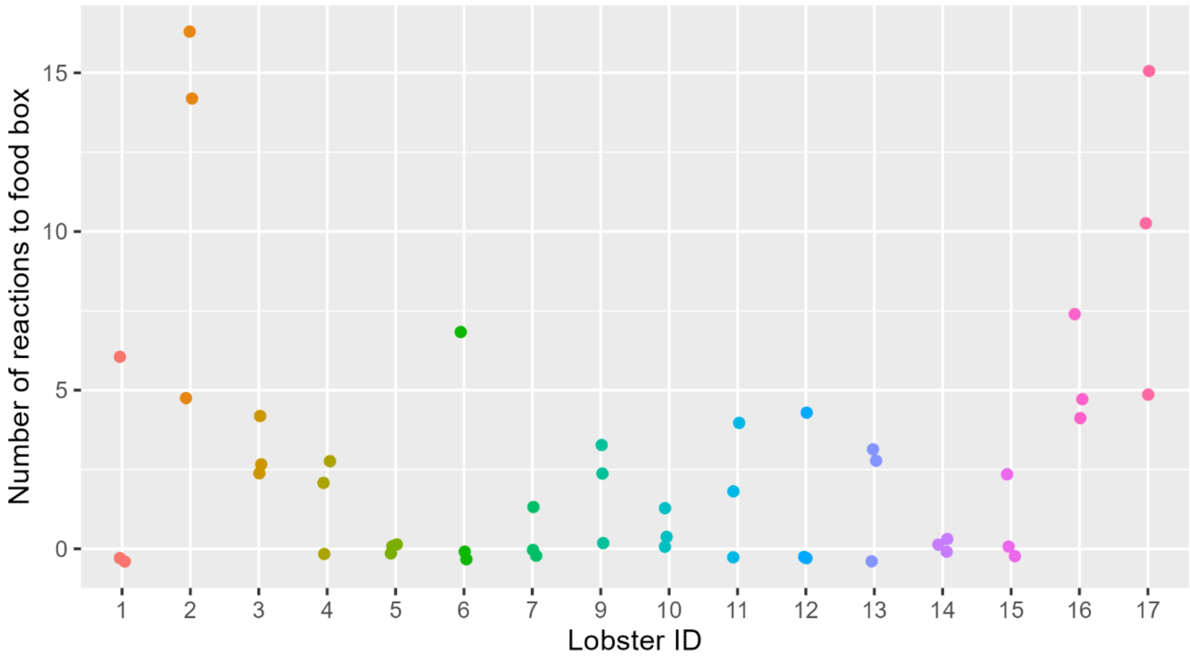


*Figure 17 Plot of Number of reactions to the food box on the x-axis and Lobster ID on the x-axis.*

# 4 Discussion

This study aimed to investigate if fishing with two different methods would give different catches. This was done by comparing the catches of the annual lobster survey in Flødevigen reserve to a fishing experiment with a higher trap density and restraint of lobsters. In addition, this study aimed to investigate the relationship between lobster behaviour and crusher claw size.

## 4.1 Field experiment

Fishing with a higher trap density and not putting lobsters back, resulted in a higher number of smaller lobsters, larger relative claw size, as well as a higher proportion of berried females.

Catch per unit effort (CPUE) was different for the two fishing experiments with a higher CPUE in Week 1. This is as expected due to the increase in fishing effort in Week 2. Neither of the CPUE's declined significantly during the fishing days, however both had a negative slope. We expected a significant decline in Week 2 as there would be fewer lobsters left in the area. However, it is possible that we underestimated the number of lobsters in this area. Lobsters seems to get a reduced catchability immediately after being caught (Kleiven,, pers. comm.), this could explain why we see a non-significant decline in Week 1. This could for example be due to the stress of handling or because they have fed on the bait and have less motivation to approach the traps. However, they would still have been able to participate in behavioural interactions. Lobsters remember each other from recent agonistic interactions, and sub-dominant lobsters will retract from dominants to avoid a second fight (Karavanich & Atema, 1998). It is possible that when lobsters are put back in Week 1, they could still be around the trap and hinder subordinate lobsters from entering the trap.

Fishing with baited traps two weeks in a row could interfere with "catchability patterns" as lobsters feed on the bait in Week 1 and might have a reduced motivation to seek the baited traps in Week 2. It is well known that lobsters enter the traps, feeds, and then escapes without being caught, or manages to feed without entering at all (Jury et al., 2001). It is therefore possible that a higher number of lobsters, higher than the number caught in Week 1 fed of the bait. If lobsters that fed the bait in Week 1 were not random in terms of size distribution, sex, or relative claw size, this can have affected the catch in Week 2.

### 4.1.1 Smaller lobsters in Week 2

Lobsters had a larger total length in Week 1 compared to Week 2. There was no decline in total length over the four fishing days, for neither of the experiments. This indicates that in Week 2, smaller lobsters were caught from day 1. This is most likely due to the high trap density, as the effect of not putting back lobsters would not be applicable for the first day. The high trap density is likely causing less behavioural interactions around the traps. As the presence of a lobster inside the trap have been found to reduce catches (Addison, 1995), and it has been observed that the presence of a larger lobster can scare off a smaller lobster, preventing it from entering (Jury et al., 2001). It may be that a higher trap density reduces the chance of these interactions, resulting in a higher number of smaller lobsters. However, the relationship between behavioural interactions and catchability is not clear. D. J. Skerritt et al. (2020) preloaded traps with lobsters and found no effect on lobster catches, however preloading traps with lobsters resulted in lower catches of brown crabs and velvet crabs. This suggests that there are also interspecific interactions affecting the catchability of crustaceans.

Lobsters above 40 cm where not caught in this study. However, they are known to be present in the reserve. Helms (2023) studied the relationship between trap size and the size of lobsters caught in the traps in Flødevigen reserve. It was found that large fish traps caught lobsters that were too big to enter traps that correspond to the standard sized and big trap used in the present study. In Week 2, an important aspect of the method was to remove dominant lobsters from the fished area, to see if this resulted a higher amount of smaller and assumed subdominant lobsters. Large lobsters have been observed "taking control" over the traps, even though they are too large to enter (Hummerteina live). It is possible that large lobsters with big claws could have been present around the traps participating in behavioural interactions, and scaring of smaller individuals, but being too large to enter themselves. If this was the case, it would have interfered with our attempt to remove big lobsters which scares off smaller, and less dominant lobsters. This could be a part of the reason why we did not get a significant reduction in size in Week 2. However, it is also possible that fishing for four days was not sufficient to get this effect. Nor was there a significant decline in CPUE during Week 2, which also suggest that four days of fishing was not sufficient.

### 4.1.2 A higher proportion of berried females in Week 2

The proportion of captured males and females where the same in Week 1 and 2. However, there was a higher proportion of berried females in Week 2. It has been suggested that egg-bearing females have a lower catchability as they have been found to have a lower food consumption than males and unberried females (Branford, 1979). Agnalt et al. (2007) also suggests that berried females have a lower catchability, as adult females are berried every 2 years, berried females should constitute 50 % of the caught adult females, however the catches of berried females were lower. Nevertheless, Laurans et al., (2009) found no difference in the catchability of berried and unberried females, indicating that the catchability of berried females is not fully understood. Berried and unberried females differs in their behaviour with berried females being more aggressive (Figler et al., 2004). However, it is reasonable that berried females would avoid agonistic interaction, as they have eggs to protect. The higher catch rate of females with eggs in Week 2 could be due to the high trap density. A higher density makes it more likely that a berried female can approach a trap without having an agonistic interaction. Our results clearly show that fishing with different methods gives a different ratio of berried and unberried females, suggesting that they have a different catchability. Understanding the catchability of berried females is important for understanding the demography of a lobster population. If berried females have lower catchability than unberried females, this could result in incorrect sex ratio estimations when using data from a trap survey.

### 4.1.3 Relative claw size

The method of fishing in Week 2 was designed in attempt to catch lobsters with a lower catchability by reducing the effect of behavioural interaction. However, as opposed to our hypothesis, lobsters had a higher relative claw size in Week 2, both for males and females (Figure 11). There was no effect of day on relative claw size, suggesting that there was no decline in claw size during the fishing period, although there was a negative slope. Males with a higher relative claw size have been hypothesized to have a higher catchability. Lobsters are hierarchical animals where large males with large claws usually is the most dominant lobster (Atema et al., 1979; Bruce et al., 2018). Dominant lobsters have been observed chasing off subdominant lobsters from both shelters and traps (Jury et al., 2001; Karnofsky et al., 1989), this likely gives male lobsters with large claws a higher catchability as they will take control of the traps. Females prefer dominant males, and male claw size is a secondary sexual trait (Sørdalen et al., 2018). This could also mean that dominant males are more voracious as sexually selected traits are energetic costly (Kotiaho et al., 1998) and it is therefore possible that lobsters with bigger claws could have a higher motivation to seek food, and therefore also baited traps. This is supported by the fact that male lobsters in reserves, where fishery selection is absent, have bigger crusher claws (Sørdalen et al., 2020), and that lobsters with bigger crusher claws have been found to have a higher chance of being harvested (Moland et al., 2019). However, in a stock enhancement study on the west coast of Norway, lobsters with double scissor claws have been found to be overrepresented in the catches (Agnalt et al., 1999), suggesting that the absence of crusher claws gave a higher catchability. This was believed to be due to the difficulty for lobsters with no crusher claw to eat hard shelled food, making their access to food restricted. A trap baited with soft food would therefore be attractive for lobsters with double scissors (van der Meeren, pers. comm). Although lobsters with double scissors are less common among wild born lobsters (Agnalt et al., 1999), this shows that the relationship between catchability and claws are not fully understood.

It is important to note that the relative claw size of females also was larger in Week 2 compared to Week 1. Female relative claw size does not differ between lobster reserves and fished areas (Sørdalen et al., 2020). It is therefore reasonable to assume that female claw size is a trait that does not affect catchability to the same degree as males. However, females have also been observed chasing off subdominant individuals and can be highly aggressive (Karnofsky et al., 1989; Skog, 2009), having larger claws could be an advantage for females as well. However, for females there are also other aspects affecting their dominance and aggression. Berried females will for instance outcompete non-berried females for shelters, this has also been observed when the berried female has a size-disadvantage (Figler et al., 1998). All of this suggests that the relationship between female lobster catchability, morphology and dominance is not fully understood.

## 4.2 Behavioural experiment

In the laboratory behavioural experiment 16 males went in the behavioural experiment for 22.5 hours three times. There was overall no effect of crusher claw size or total length on behaviour. However, for some of the behavioural traits the models with the highest support included temperature and/ or replicate as fixed effects. There was a significant repeatability for lobster ID for all behavioural traits, indicating that lobsters have consistent individual behaviour. There was also a significant repeatability for tank; for time spent in shelter, position in the tank and reaction to the food box.

### 4.2.1 Usage of shelter

In the wild, lobsters are highly dependent of their shelters. As soon as the lobster larvae settle, they will seek shelters (Botero & Atema, 1982). Lobsters spend most of the daytime in their shelter and will often have more than one shelter (Karnofsky et al., 1989). The shelters are important for protection, especially during moulting. Lobsters have been observed barricading their shelter during moulting (Karnofsky et al., 1989). The only time more than one lobster occupies a shelter, is during mating, where the female enters the shelter of the male (Atema et al., 1979; Karnofsky et al., 1989). Lobsters have been observed fighting over shelters. Generally, a lobster will approach an already inhabited shelter, and then evicts the resident, or loses and pulls away. Larger lobsters often win, although smaller lobsters have been observed winning if they are the defender (Karnofsky et al., 1989).

The lobsters spent a high proportion of the trial in shelter, which closely resemble what Konecny et al. (2024) found for adult lobsters in the wild. In addition, Konecny et al. (2024) observed that the likelihood of American lobsters being in a shelter increased with larger body size. On the other hand, Konecny et al. (2024) also conducted a short-term experiment where they observed the opposite trend: the probability of being in a shelter decreased with increasing body size. Nevertheless, in our study we kept the size range as narrow as possible to avoid effect of size, but rather look for an effect of crusher claw size. In spite of this, no effect was found, either for time spent in shelter or number of times entering shelter. For juvenile lobsters in a laboratory experiment number of times entering shelter and time spent in shelter were negatively correlated with size (Mehrtens et al., 2005). In the study of Mehrtens et al., (2005), lobsters spent 1-10 % of the time in shelter, much less time compared to the present study. This could be due to the difference in behaviour of juvenile and adult lobsters. Overall, this indicates that the relationship between shelter usage and lobster length is not fully understood and may be influenced by additional factors.

There was a significant negative of temperature for time spent in shelter. The water in the trial came from 75 meters depth, and the temperature varied between 12.6°C and 14.5°C. Ideally the water temperature should have been constant throughout the experimental period, as temperature was not a part of our objective, but are known to affect behaviour (Branford, 1979).

Overall, lobsters spent a high proportion of the trial in shelter. However, three lobsters (lobster 6, 10, and 17) differed from the rest. The model for time spent in shelter showed patterns in the residuals, and it was therefore fitted an alternative model without outliers

(Figure 12, Figure A 6). This model gave similar results for the fixed effects (replicate and temperature) but a much lower repeatability (R=0.16) (Table A 7). This suggests that the high repeatability is driven by lobster 6, 10 and 17 which spent much less time in shelter compared to the rest. However, this alternative model still had patterns in the residuals, therefor the results must be interpreted with caution. Although some of the datapoints differ from the rest and can be considered outliers, these are real observations of behaviour, and filtering them out make little sense in a behavioural perspective. Behavioural outliers are a known phenomenon and have been observed in other experiments as well (Fraser et al., 2001).

### 4.2.2 Activity

Lobsters are typically nocturnal with studies showing the highest activity occurring 0.5-4 hours after sunset (Smith et al., 1998). Although this was not tested explicitly herein, observations suggest a deviant from this pattern in this study. Instead, lobsters were most active during the first 1.5 hours of the trial (13:30-15:00) and the last two hours (10:00-12:00) (Figure 15) However, the handling stress, introduction to a new environment, limited acclimation time and the introduction of the food box may overshadow their natural activity rhythms. Additionally, the consistent low light levels during the experiments, despite the lobsters experienced a natural night – day cycle during storage, could have influenced their behaviour.

Adult American lobster have been found to be more active with increasing length (Konecny et al., 2024), while juveniles have been found to be less active with increasing length (Mehrtens et al., 2005). However, in this study there was no effect of body size, nor crusher claw size we hypothesized. Nevertheless, there was a significant effect of repeatability of lobster ID, suggesting that the activity is mainly driven by the individual. Activity has been linked to catchability, were more active individuals have a higher catchability (McLeese & Wilder, 1958). Individuals with a higher activity will have a higher probability of encountering a trap (Alós et al., 2012). A part of the activity in the wild is related to foraging behaviour (Karnofsky et al., 1989), suggesting that high activity levels could be correlated with voraciousness. There are some limitations of the activity measure in this study, instead of measuring distance moved, which gives an accurate measurement, squares entered have been counted. It is possible that restless lobsters which moves short distances but crosses the lines in the tank often have been measured to similar activity levels as active lobsters exploring the whole tank.

### 4.2.3 Position in tank

Lobsters in laboratory environments have been found to seek the wall or other solid objects when released in a tank (van der Meeren, 2001) ). In this study lobsters spent on average 39% of the time next to the wall and 61% of the time away from the wall. There was large variation between individuals. For example, lobster 15 spent on average 66% of the time by the wall, while lobster 17 spent 14% of the time by the wall. It is possible that the lobsters spending more time away from the wall, could have a more exploratory behaviour and spend more time in open habitats. In the wild, lobsters in open habitat have been found to have a higher catchability than lobsters in rocky habitats (Tremblay & Smith, 2001). When lobsters are caught in traps, many will be released back to sea as they are not within the legal fishing size, or they are berried females. When they are released, they will likely try to find their home shelter or site (Karnofsky et al., 1989; Meeren, 1997). Lobsters walking through open habitats will likely return faster than lobsters walking along solid structures. Although walking along solid structures might be less risky, good shelters can be taken if lobsters leave them for too long. However, one should be cautious transferring observations in a laboratory environment to assumptions about behaviour in the wild. It would have been interesting to have followed our males after release and see if their lab behaviour was similar to their behaviour in the wild.

### 4.2.4 Reactions to food box

The number of reactions to the food box varied between individuals, where some individuals never reacted while others showed strong reactions (eg. lobster 2 had a count of 35 reactions). The type of reaction varied; some attacked the food box, while others approached the box without any physical contact. Since no lobsters were fed during the experimental period, they could have had an increased motivation to feed as the experiment progressed, however there was found no effect of day (number of days in trial).

Increased food consumption in lobsters have been related to a higher catchability (Branford, 1979), suggesting that individuals that are more voracious, by reacting more to the food box will have a higher catchability. This has been found for cray fish where voracious behaviour was positively correlated to catchability. (Biro & Sampson, 2015). The food box could also be seen as a novel object as both the box and the food were introduced. This suggests that reaction to food box also contains an element of exploratory behaviour. The introduction of the food box in the experiment resembles the introduction of a trap in the wild, a novel object with a bait. It is possible that those lobsters that reacted more to the food box, would approach a trap more often, compared to lobsters with few reactions.

### 4.2.5 No effect of crusher claw size

Claw size of male lobsters have been linked to dominance (Atema, 1986) as well as catchability (Moland et al., 2019), lobsters with bigger claws are more dominant and have a higher catchability. This difference in catchability could be explained by differences in behaviour. We therefore hypothesized that there could be a difference in behaviour explained by claw size. However, no effect was found for neither of the behavioural traits. It is possible that there was not enough variance in the claw size, as we had a relatively small sample size. All our lobsters were also caught with traps suggesting that there is a catchability-bias. As our lobsters are caught by traps, they may have a higher catchability than for example lobsters collected by divers.

### 4.2.6 Effect of Habituation

There was a significant effect of replicate for three of the behavioural traits tested, time spent in shelter, number of times entering shelter and position in tank. This indicates that there is an effect of habituation. Habituation can be defined "as decreased response to repeated stimulation" (Groves & Thompson, 1970) . In this study lobsters spent more time in shelter with increasing replicate, entered the shelter fewer times and spent more time away from the wall, compared to being by the wall. Spending more time in shelter and entering the shelter fewer times can be considered a decreased response as they spend less time exploring the new environment. Lobsters have been observed to prefer walking along the wall or solid objects when introduced to a tank (van der Meeren, 2001). Walking less along the wall could be because the lobsters become more familiar with the tank design. Although it could also be seen as an increase in risk taking behaviour. Reduced behavioural response with increasing replicate have been found in other behavioural studies (Martin & Réale, 2008). It has been suggested that habituation could affect the repeatability. However, the number of observations per individual has been found not to affect the repeatability (Bell et al., 2009).

### 4.2.7 Consistent individual behaviour in lobsters

For all behavioural traits tested, there was a significant repeatability for lobster ID. This indicates that lobsters have consistent individual behaviour. Around 35 % of the variation in animal behaviour has been found to be due to individual differences (Bell et al., 2009). The repeatability in this study were mostly higher, between 0.44 and 0.54. However, for position in tank the repeatability was at much lower (0.14). Repeatability has been found to vary between behavioural traits, typically being higher for behaviours related to aggression, mating behaviour and habitat selection, and lower for activity (Bell et al., 2009).

Moland et al. (2019) measured repeatability for four different behavioural traits for lobsters: depth amplitude, cumulative distance, mean depth, and home range. In this study the repeatability's varied between 0.55 and 0.76, which is higher values compared to our study. However, this study was done in the wild, and behaviours studied in the wild have been found to result in a higher repeatability than behaviours studied in the laboratory (Bell et al., 2009). This could maybe be explained by the expression of behaviours related to habitat, or the maybe the absence of handling stress.

Although efforts were made to make the tanks as identical as possible there was a significant repeatability for tank for time spent in shelter, position in tank and reaction to food box, suggesting that there was a tank effect. Both, time spent in shelter and reaction to food box are behavioural traits related to specific elements of the tank design, there was likely small differences between the shelters and the food boxes, although the intention was to make them as similar as possible. For position in tank, there could be differences between the tanks, or for instance in the carpet glued to the bottom of the tank, making a tank effect. However, these values were markedly lower for tank than for lobster id.

Our study supports the hypothesis that lobsters show individual differences in behaviour and may further have individual differences in motivation to approach a trap. Lobsters that spend more time in shelter or are less active will likely encounter fewer traps (Alós et al., 2012). Also, lobsters that react more to the smell of food will more likely approach a baited trap, this has been found for cray fish were voracious animals also had higher growth rate as well as higher catchability (Biro & Sampson, 2015). This is also supported by Sørdalen et al. (2022) who found that lobsters in reserves have higher growth rates compared to control areas. Lobsters that are more exploratory and is more likely to enter open habitats will also likely have a higher catchability, which is supported by the findings of (Tremblay & Smith, 2001).

## 4.3 Implications for future monitoring of the reserves

As long as reserves are monitored by a trap-survey, there will be an effect of trap selectivity. The field experiment in this study shows that fishing with a higher trap density and restraint of lobsters gives a catch of lobsters with a shorter mean length, a higher proportion of berried females and a larger relative claw size. Adjusting the method of the annual monitoring program by fishing with a higher trap density likely gives less behavioural interaction, and therefore a more random sample.

The result from the behavioural experiment supports the hypothesis that lobsters have consistent individual differences in behaviour, which in turn can result in differences in catchability. This emphasizes the complexity of trap selectivity and catchability and the necessity of more research to fully understand this concept.

Overall, a trap survey will never give a perfectly random sample, but testing adjusted methods as the lobster populations in the reserves grows and changes will give more insights into weaknesses in the current design. In addition, it can provide useful information that can be used when interpreting the results from the annual survey.

# 5 Conclusion

In summary, fishing with a higher trap density and retainment of lobsters, resulted in a lower CPUE, a lower mean total size, a higher proportion of berried females and larger relative claws for both males and females, compared to the fishing method of the annual lobster survey in Flødevigen reserve. This suggests that fishing with different methods can give catches with a different demographic composition from the same population. As demography changes over time in a lobster reserve, long term monitoring data may not fully portray changes in density and demography. In this study, there was a smaller mean length and higher proportion berried females, suggesting that small lobsters and berried females might be underrepresented in the catch from the monitoring program. In the behavioural experiment there was no effect of claw size, but there was a significant individual repeatability for all behavioural traits tested. This suggests that lobsters have consistent individual behaviour. Their individual behaviour in relation to shelter usage, activity, position, and reaction to food is likely giving them an individual catchability. All of this underlines the complexity of trap selectivity and catchability.

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# 7 Tables and figures

## Figures:

**Appendix:**



## Tables:

**Appendix:**

# 8 Appendix

*Table A 1 An overview of missing files and affected lobsters.*

| Lobsters | Replicate | Missing time | Missing hours (hh:mm) |
|---|---|---|---|
| **13-17** | 1 | 60 min | 00:27-01:27 |
| **7-12** | 2 | 120 min | 17:37-19:37 |
| **13-17** | 3 | 68 min 10 sec | 13:30-14:38 |

## 8.1 Diagnostics plot Field experiment models

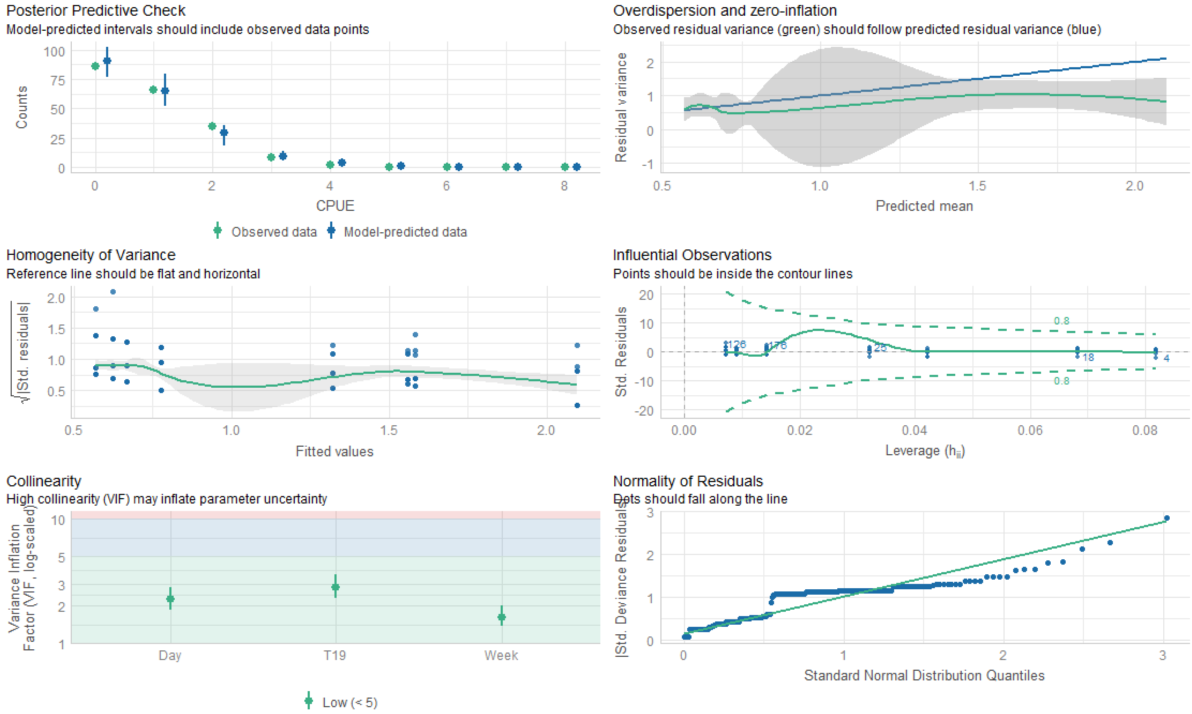


*Figure A 1Diagnostics plot for the CPUE model*

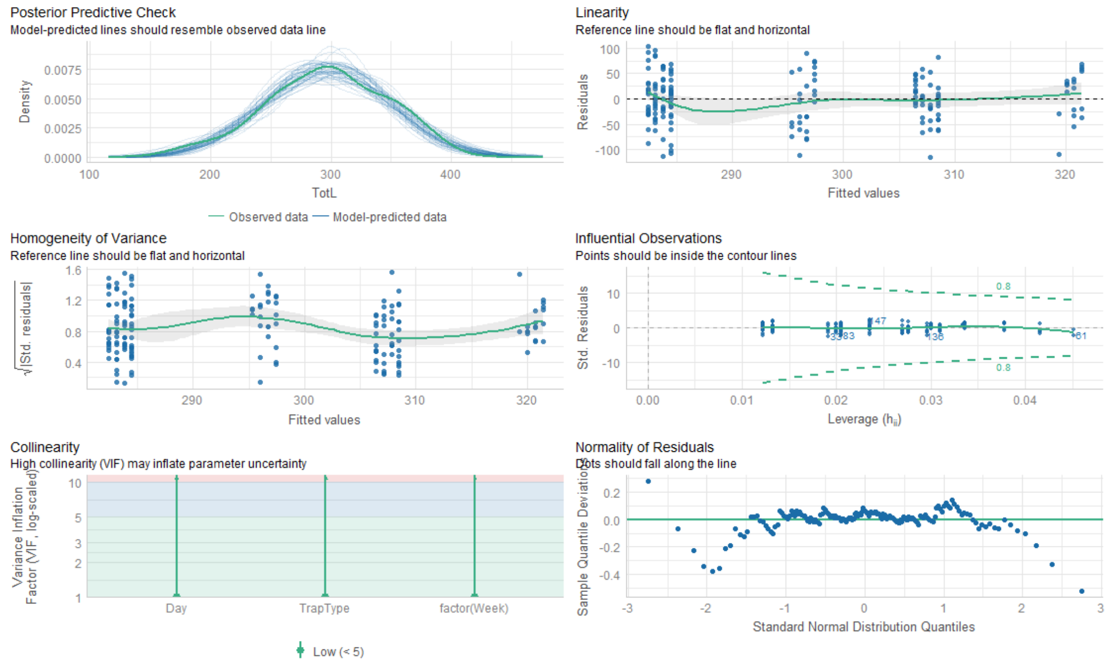


*Figure A 2 Diagnostics plot for the total length model*

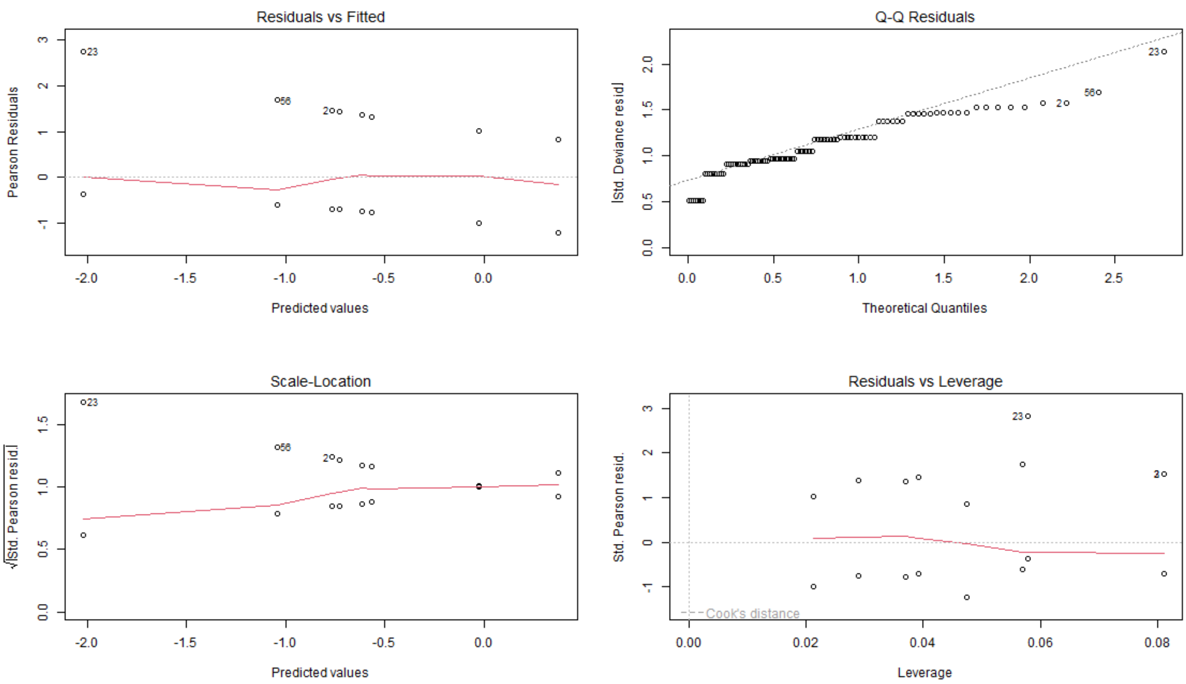


*Figure A 3 Diagnostics plot for the model for berried females*

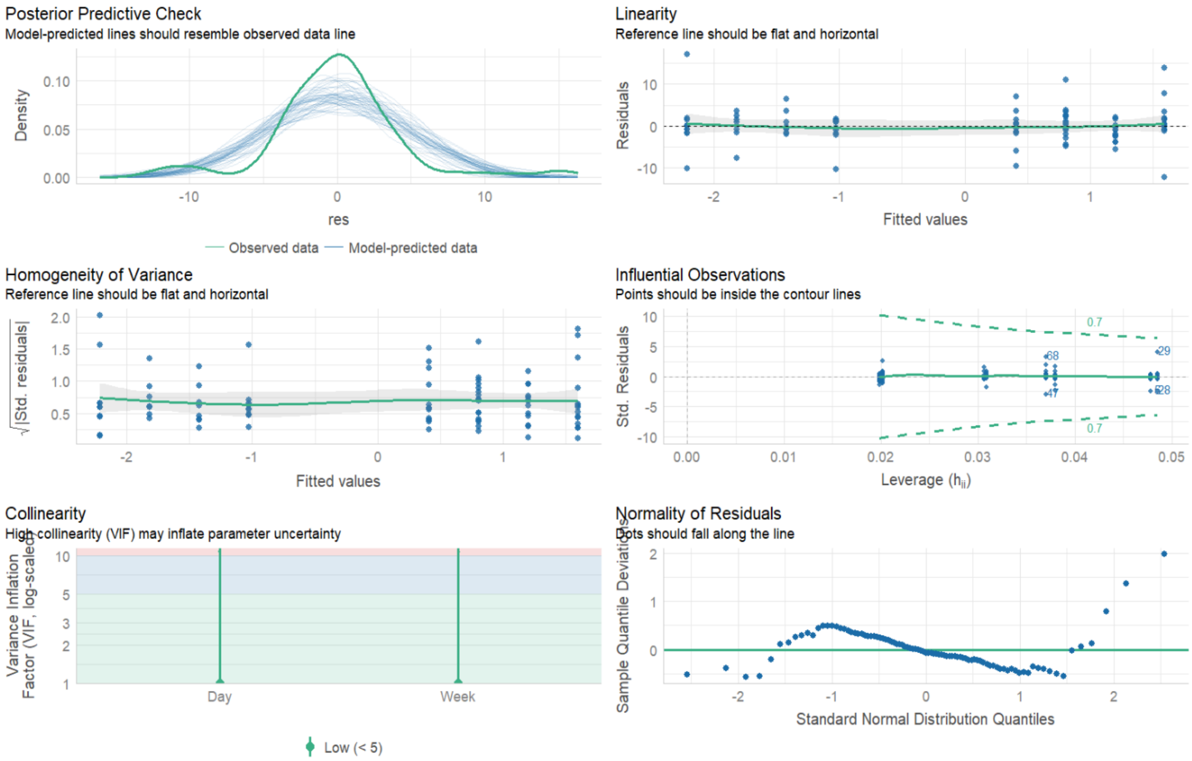


*Figure A 4 Diagnostics plot for the relative claw size model for females*

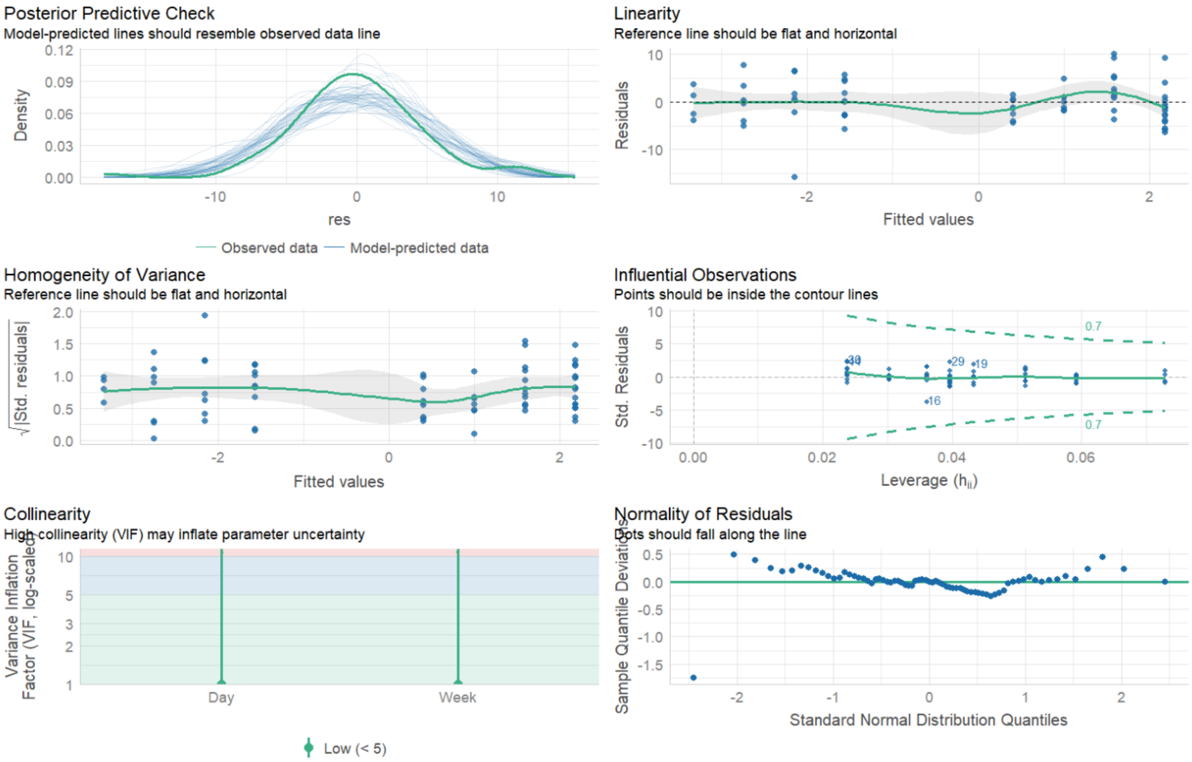


*Figure A 5 Diagnostics plot for the Relative claw size model for males*

## 8.2 Model selection tables

*Table A 2 Complete list over models that were tested in the model selection process for time spent in shelter. The final model is marked with bold.*

| Models | AIC |
|---|---|
| Shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id+ random: Tank | 4503.8 |
| Shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Tank | 22398.3 |
| Shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id | 5357.0 |
| Shelter ~ Total length + Temperature + Replicate + random: Lobster ID+ random: Tank | 4501.8 |
| **Shelter~ Temperature + Replicate + random: Lobster ID+ random: Tank** | **4501.2** |
| Shelter ~ Temperature + random: Lobster ID+ random: Tank | 5550.1 |
| Shelter ~ Replicate + random: Lobster ID+ random: Tank | 6093.1 |
| Shelter ~ +1 + random: Lobster ID+ random: Tank | 6276.0 |

*Table A 3 Complete list over models that were tested in the model selection process for number of times entering shelter. The final model is marked with bold.*

| Models | AIC |
|---|---|
| Number of times entering shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id+ random: Tank | 140.0 |
| Number of times entering shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Tank | 145.2 |
| Number of times entering shelter ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id | 140.2 |
| Number of times entering shelter ~ Total length + Crusher claw index + Replicate + random: Lobster id | 139.0 |
| Number of times entering shelter ~ Total length + Replicate + random: Lobster id | 138.0 |
| **Number of times entering shelter ~ Replicate + random: Lobster id** | **138.9** |
| Number of times entering shelter ~ +1 random: Lobster id | 141.4 |

*Table A 4 Complete list over models that were tested in the model selection process for activity. The final model is marked with bold.*

| Models | AIC |
|---|---|
| Activity ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster ID+ random: Tank | 121.2 |
| Activity ~ Total length + Crusher claw index + Temperature + Replicate + random: Tank | 124.4 |
| Activity ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id | 119.2 |
| Activity ~ Total length + Crusher claw index + Replicate + random: Lobster id | 117.2 |
| Activity ~ Total length + Replicate + random: Lobster id | 117.8 |

| | |
|---|---|
| Activity ~ Total length + random: Lobster id | 118.3 |
| **Activity ~ +1 + random: Lobster id** | **119.3** |

*Table A 5 Complete list over models that were tested in the model selection process for position in tank. The final model is marked with bold.*

| **Models** | **AIC** |
|---|---|
| Position in tank ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id+ random: Tank | 2455.9 |
| Position in tank ~ Total length + Crusher claw index + Temperature + Replicate + random: Lobster id | 4622.7 |
| Position in tank ~ Total length + Crusher claw index + Temperature + Replicate + random: Tank | 9574.8 |
| Position in tank ~ Total length + Temperature + Replicate + random: Lobster ID+ random: Tank | 2454.2 |
| **Position in tank ~ Temperature + Replicate + random: Lobster ID+ random: Tank** | **1183.3** |
| Position in tank ~ Replicate + random: Lobster ID+ random: Tank | 3125.0 |
| Position in tank ~ Temperature + random: Lobster ID+ random: Tank | 2715.7 |
| Position in tank ~ + 1 + random: Lobster ID+ random: Tank | 3151.1 |

*Table A 6 Complete list over models that were tested in the model selection process for number of reactions to the food box. The final model is marked with bold.*

| **Models** | **AIC** |
|---|---|
| Number of reactions to food box~ Total length + Crusher claw index + Temperature + Day + random: Lobster id+ random: Tank | 216.3 |
| Number of reactions to food box~ Total length + Crusher claw index + Temperature + Day + random: Lobster id | 220.9 |
| Number of reactions to food box~ Total length + Crusher claw index + Temperature + Day+ random: Tank | 273.4 |
| Number of reactions to food box~ Total length + Temperature + Day + random: Lobster id+ random: Tank | 214.4 |
| Number of reactions to food box~ Total length + Temperature + random: Lobster id+ random: Tank | 212.7 |
| Number of reactions to food box~ Total length + random: Lobster id+ random: Tank | 211.12 |
| **Number of reactions to food box~ +1+ random: Lobster id+ random: Tank** | **212.74** |

## 8.3 Diagnostics plot behavioural models

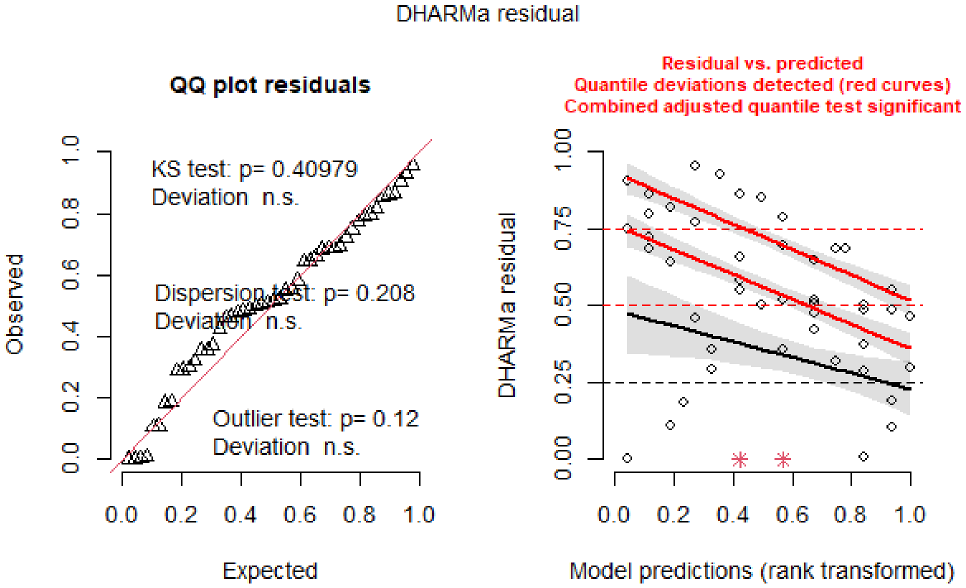


*Figure A 6 Diagnostics plot for time spent in shelter*

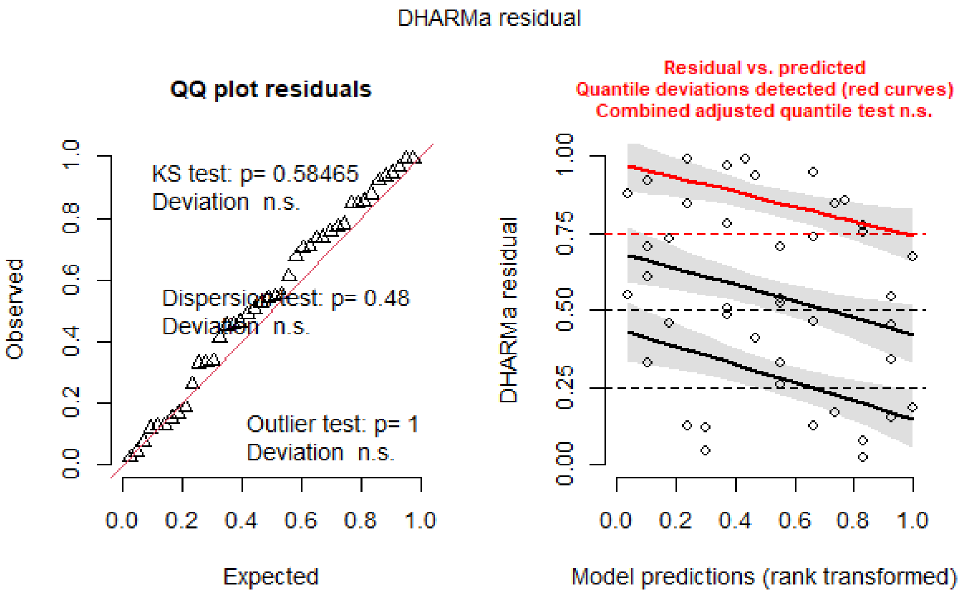


*Figure A 7 Diagnostics plot for time spent in shelter without outliers*

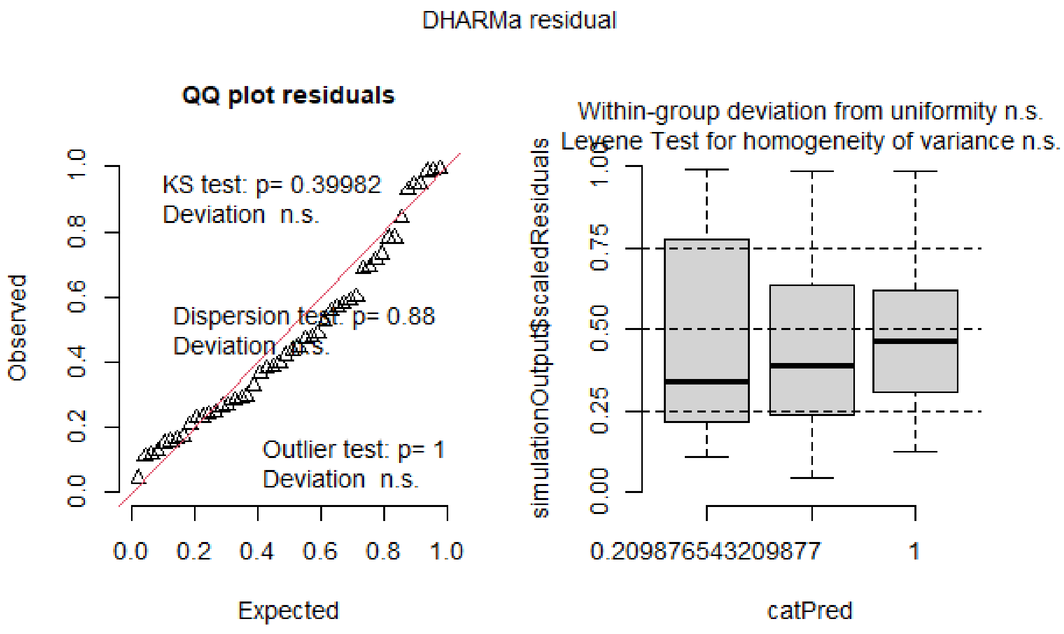


*Figure A 8 Diagnostics plot for number of times entering shelter*

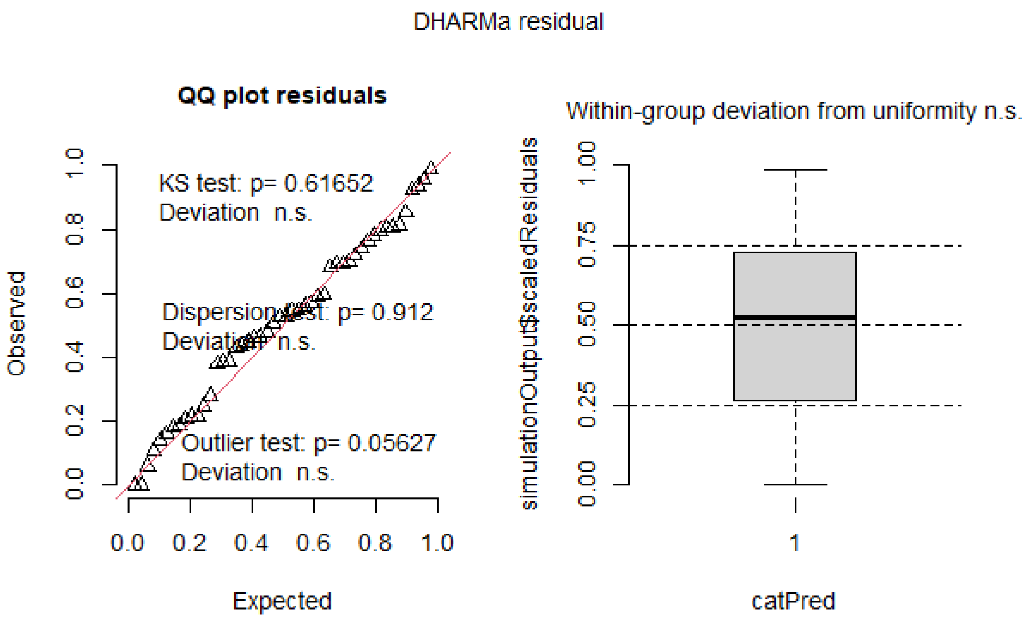


*Figure A 9 Diagnostics plot for activity*

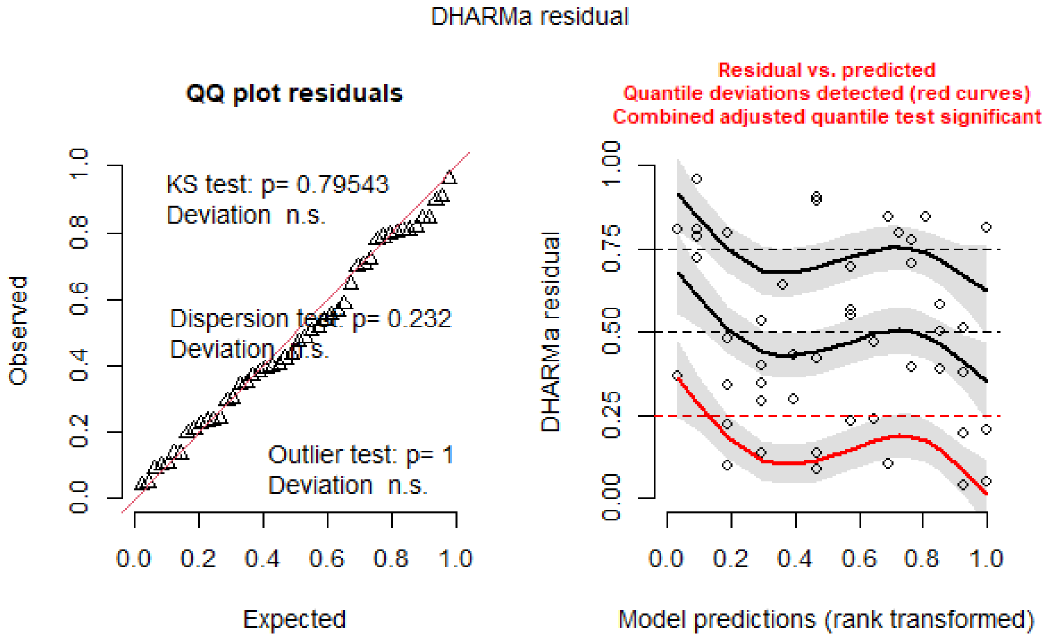


*Figure A 10 Diagnostics plot for position in tank*

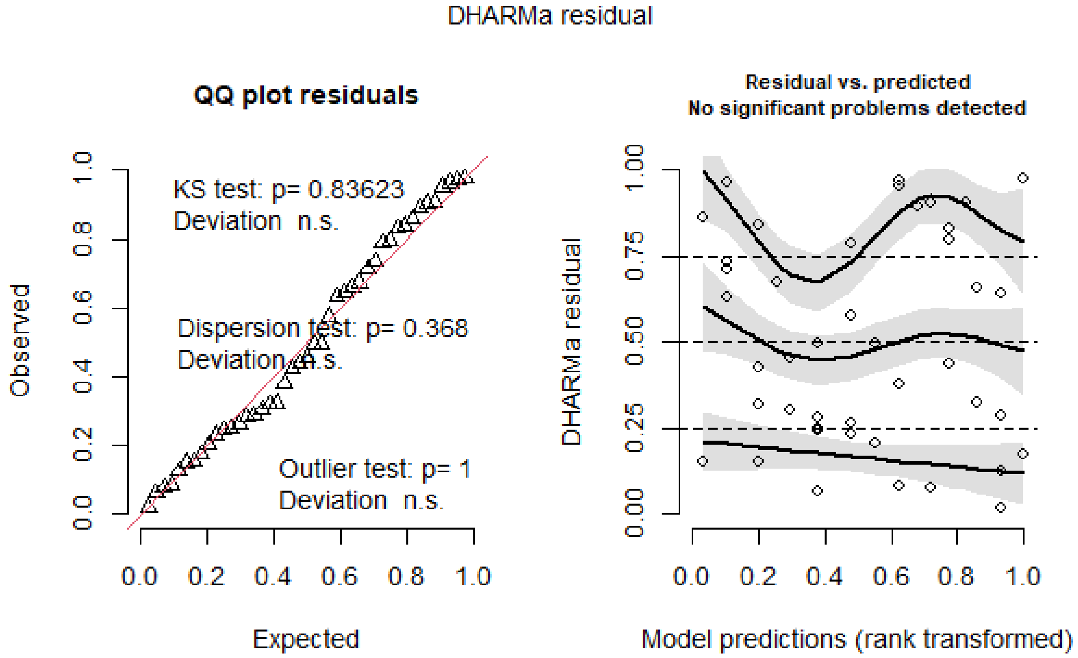


*Figure A 11 Diagnostics plot for position in tank without outliers*

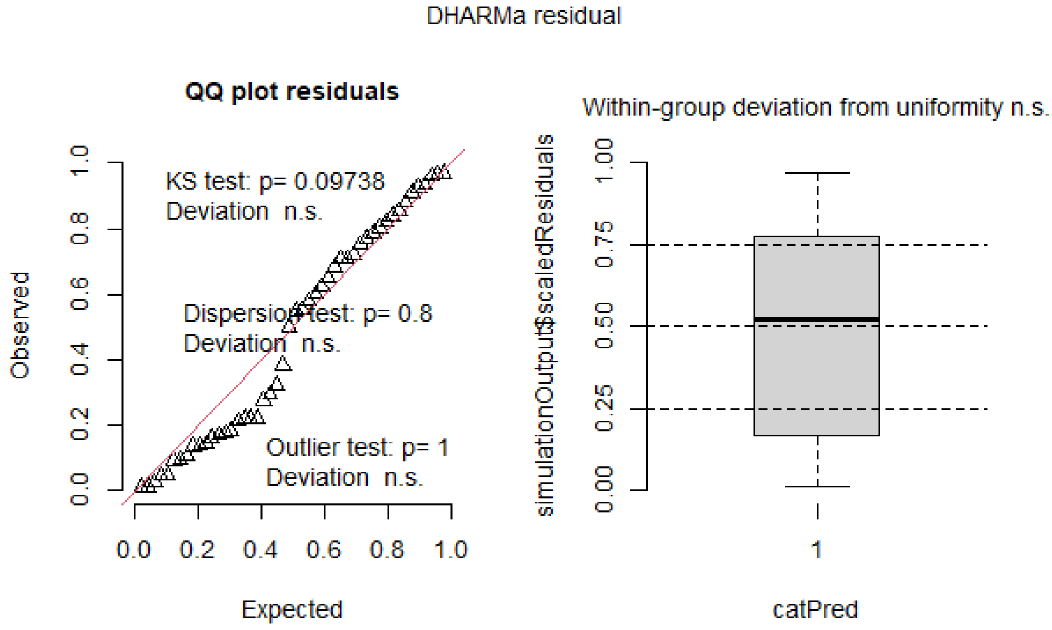


*Figure A 12 Diagnostics plot for number of reactions to food box*

## 8.4 Summary tables alternative models

*Table A 7 Model summary for time spent in shelter without outliers. Standardized parameters were obtained by fitting the model on a standardized version of the dataset. 95% confidence intervals (CI) and p-values were computed using a Wald z-distribution.*

| **Model: Shelter ~ Temperature + Replicate + Random: Tank + Random: Lobster ID** | | | |
|---|---|---|---|
| | | | |
| **Model Fit:** | | | |
| Pseudo-$R^2$ (fixed effects) = 0.02 | | | |
| Pseudo -$R^2$ (total) = 0.19 | | | |
| | | | |
| **Fixed effects:** | **Estimate** | **95% CI** | **p-value** |
| **Intercept** | 8.83 | (7.37, 10.30) | **<0.001** |
| **Temperature** | -0.45 | (-0.55, -0.34) | **<0.001** |
| **Replicate** | 0.31 | (0.24, 0.38) | **<0.001** |
| | | | |
| **Random effects** | **Variance** | **Standard deviation** | |
| **Lobster ID** | 0.62 | 0.79 | |
| **Tank** | 0.075 | 0.27 | |
| | | | |
| **Repeatability:** | | | |
| **Group** | **ICC** | | |
| **Lobster ID** | 0.16 | | |
| **Tank** | 0.019 | | |

*Table A 8 Model summary for position in tank without outliers. Standardized parameters were obtained by fitting the model on a standardized version of the dataset. 95% confidence intervals (CI) and p-values were computed using a Wald z-distribution.*

| **Model: Position in tank ~ Temperature + Replicate + Random: Tank + Random: Lobster ID** | | | |
|---|---|---|---|
| **Model Fit:** | | | |
| Pseudo-$R^2$ (fixed effects) = 0.01 | | | |
| Pseudo -$R^2$ (total) = 0.15 | | | |
| **Fixed effects:** | **Estimate** | **95% CI** | **p-value** |
| **Intercept** | -6.13 | (-6.78, -5.48) | **<0.001** |
| **Temperature** | 0.44 | (0.44, 0.48) | **<0.001** |
| **Replicate** | -0.22 | (-0.25, -0.19) | **<0.001** |
| **Random effects** | **Variance** | **Standard deviation** | |
| **Lobster ID** | 0.41 | 0.63 | |
| **Tank** | 0.11 | 0.35 | |
| **Repeatability:** | | | |
| **Group** | **Groups** | **ICC** | |
| **Lobster ID** | 15 | 0.10 | |
| **Tank** | 6 | 0.03 | |

## 8.5 Other Figures

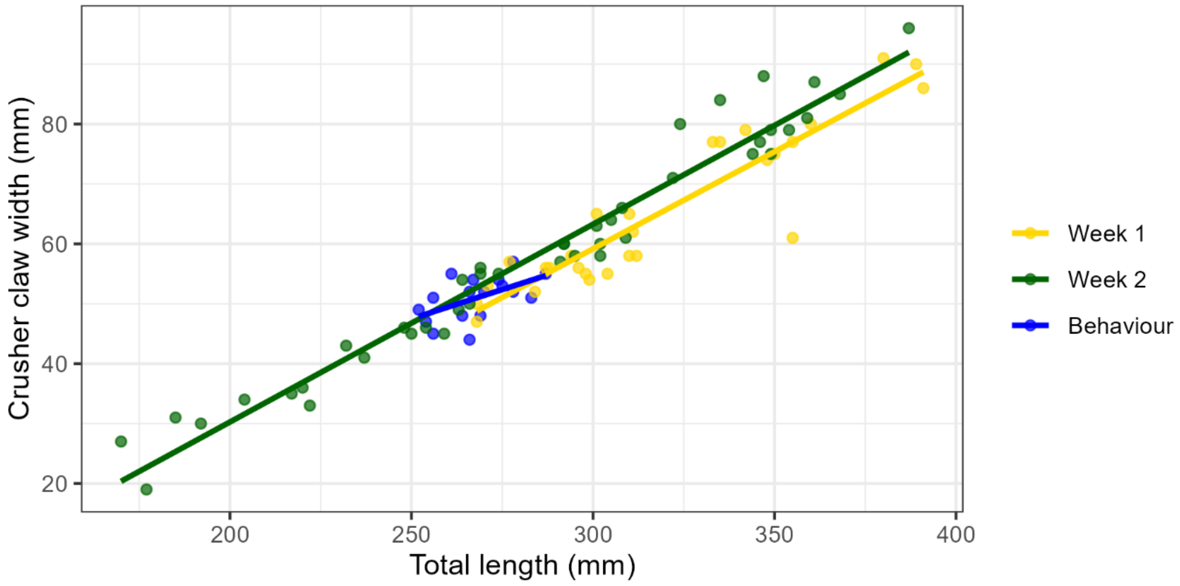


*Figure A 13 A scatter plot with Total length of male lobsters on the x-axis and crusher claw width on the y-axis. The colours represent lobsters caught in Week 1 (yellow), Week 2 (green) and the blue points and line represent lobsters used in the behaviour experiment. Regression lines have been added using the stat_smooth() function in r.*

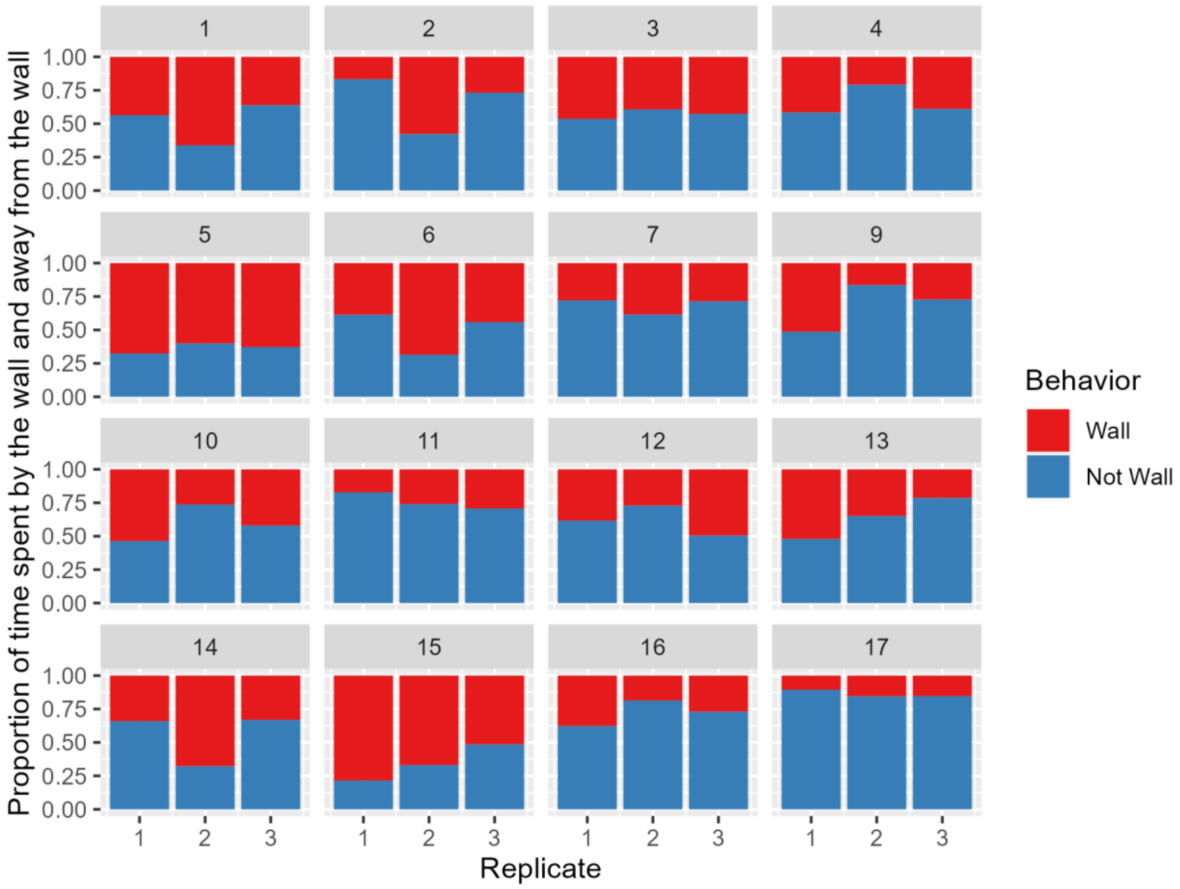


*Figure A 14 A bar plot with proportion of time spent by the wall (red) and away from the wall (blue) on the y-axis and replicate on the x-axis. Each panel represent a lobster ID.*