Using underwater filming to study activity and fighting behavior in *Astacus astacus*

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Master thesis in Marine biology and limnology

Department of Biosciences

UNIVERSITETET I OSLO

March 2019
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Abstract

The use of remote video traps is a popular method of studying animal behavior in nature. It is an efficient, inexpensive and non-invasive way of obtaining samples from the field. In this study, I built and used video traps to look at activity and fighting behavior in the crayfish *Astacus astacus*. The aims of the project were to see if the crayfish were more active at night and if there was a relationship between activity and water temperature. I was also interested to see if bigger crayfish fought and won more than smaller crayfish and if light intensity and temperature had an effect on fighting frequency. My results showed that the activity was highest during the night, with a peak at around 11 pm to 1 am. There was a positive relationship between temperature and activity. As for fighting behavior, bigger crayfish did not fight or win more than smaller crayfish. Temperature and light intensity had no significant effect on fighting frequency.
Preface

I am really happy that I got the chance to be a master student at the Section for Aquatic biology and toxicology (AQUA). The last two years have been fantastic. I have learned more than I ever would have imagined before starting this study. The atmosphere and the people at AQUA are just amazing. Writing a master thesis has been an exciting challenge. I am proud to have accomplished such a great task.

I would like to express my sincere gratitude to my supervisors, Tom Andersen, Jan David Heuschele and Stein Ivar Johnsen. You supported me greatly and were always willing to help me. I am really grateful for all the time and effort you have spent on guiding me through this project.

Secondly, I would like to give special thanks to Kristian Norgiaard Berglund and Terje Moffat Wivestad for granting me the permissions needed to carry out my fieldwork at Store Sandungen. I really appreciate your enthusiasm towards my project. I would also like to thank Svein Erik Lillelien, Kjell Sandaas, Per-Johan Færøvig and Kim Aalborg for their contributions to this project.

Last but not least, I would like to give a deep thanks to my family for all their love, help and support.
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Introduction

*Astacus astacus*, also called noble crayfish, is a freshwater crustacean belonging to class Malacostraca within the phylum Arthropoda (ITIS). It lives in lakes, rivers, and ponds in many European countries. *Astacus astacus* is widespread throughout Europe, although it is most prominent in the northern countries such as Norway and Sweden (Edsman et al. 2010). This crayfish is a popular food resource that is highly valuable. It is harvested commercially, but many people catch them in recreational fisheries as well. They also serve as indicator species for good water quality (Zimmerman 2012).

In the last decades, Europe has experienced a drastic decrease in numbers of *Astacus astacus*. According to the IUCN Red List of Threatened Species, the global decline rate may be as high as 50-70% (Edsman et al. 2010). Many factors are responsible for this decline, including parasitic, climatic and environmental factors. The invasive signal crayfish from North America is a serious threat, mainly due to a pathogen that it carries. Negative impacts of human activities are also accountable for the decline (Bjerke et al. 2004). This is of great concern for conservation biologists who are trying to prevent *Astacus astacus* from going extinct.

The noble crayfish

As with most members of Malacostraca, *Astacus astacus* has a segmented body that consists of a head, thorax, and abdomen (Hickman et al. 2014). The head and thorax have become fused into a cephalothorax, which is covered by a carapace (Brooker et al. 2011), the dorsal section of the exoskeleton. The exoskeleton is a rigid cover that surrounds the outer parts of the animal and provides protection from predators, parasites and other environmental threats. It also functions as an attachment structure for muscles (Hickman et al. 2014). The main components of the exoskeleton are chitin, calcium carbonate, and proteins. Calcium carbonate in the exoskeleton is a characteristic feature for members of Crustacea, and adds hardness and rigidity to the cuticle (Shechter et al. 2008). At the joints, the exoskeleton is thinner and flexible, which increases the movement capabilities of the crayfish. During molting, the crayfish sheds its old exoskeleton before a new one grows in place (Wærvågen et al. 2016).

*Astacus astacus* may be confused with the North-American signal crayfish (*Pacifastacus leniusculus*) because of their morphological resemblances. However, some differences exist.
Astacus astacus has a scratchy carapace. By contrast, Pacifastacus leniusculus has a smooth carapace. Pacifastacus leniusculus also has a white spot between the chela (Zimmerman 2012). Other defining features of Astacus astacus are a small barb at the groove behind the carapace and a more brownish color compared to the signal crayfish (Direktoratet for Naturforvaltning og Mattilsynet 2007).

Ecology

Astacus astacus lives in a variety of freshwater environments, including lakes, rivers, streams, and ponds. A heterogeneous habitat is important to the crayfish (Reynolds et al. 2013). Crayfish usually prefer areas with lots of rocks, roots, driftwood, and other obstacles, as they can use them to hide from predators (Johnsen et al. 2014). A softer bottom with some sand is also ideal for the crayfish as it enables them to dig small burrows that function as shelters (Edsman et al. 2010). Astacus astacus is highly sensitive to temperature, and water temperature is a limiting factor for its distribution (Abrahamsson 1972). During late autumn and early spring, when the water temperature is relatively equal at all depths, the crayfish can stay in deep waters (10-15 meters). In spring and summer, the temperature increases, especially in the upper waters, the crayfish move towards shallower areas in the littoral zone (8-10 meters) (Taugbøl 2001).

The noble crayfish is an omnivore species that feeds on a variety of invertebrates and plants. Snails and midges are important animal components of the crayfish’s diet, while periphyton and macrophytes are important plant components. It is also a great consumer of detritus (Nyström et al. 1999). Astacus astacus shows an ontogenetic shift in habitat usage. This means that juveniles occupy a different habitat than adults (Reynolds et al. 2013). Juveniles often live in shallower areas containing plants, litter or gravel, where the water is warmer. This is beneficial to the juveniles because warmer water allows for higher molting frequencies and quicker growth (Renai et al. 2007). A high growth rate is important for crayfish juveniles as they are more prone to predation because of their smaller size and their less developed exoskeleton. Astacus astacus functions as prey for many predators, including fish, birds, insects, and mammals (Zimmerman 2012). Eel and perch are the most important fish predators, but pike also consumes crayfish. In waters with a great abundance of eels, the chances are that populations of crayfish are absent (Taugbøl 2001). Among the birds, fish-eating ducks consume crayfish. A few mammals also prey on crayfish. Mink is as a
significant consumer of crayfish during summer, especially in smaller streams and rivers where the mink has easy access to crayfish (Wolff et al. 2015). When population size is large and food availability is scarce, crayfish exhibit cannibalism (Seemann et al. 2014).

*Astacus astacus* plays an important ecological role and is considered to be a key species in many freshwater communities (Direktoratet for Naturforvaltning og Mattilsynet 2007). In addition to capture invertebrate prey, it is also an efficient browser. Browsing keeps the vegetation down and prevents overgrowing in the affected area. Crayfish are also important bioturbators. They mix up the bottom sediments with their bodies when excavating, walking and swimming. As a result, nutrient fluxes are changed and ecosystem conditions are enhanced (Vaeßen & Hollert 2015). In addition, crayfish are a significant consumer of detritus and therefore serve as important decomposers (Reynolds et al. 2013).

**Behavior**

*Astacus astacus* is a poikilothermic animal such that its body temperature varies with the ambient temperature (Krebs 2014). Because physiological processes are dependent on body temperature, the environment has a significant influence on the behavior of the crayfish (Zimmerman 2012). In winter, when water temperature is low (<10°C), the metabolism of the crayfish decreases, and it becomes less active. This makes catching crayfish difficult during winter. In spring and summer, the temperature is higher and crayfish resume their activity (Peay 2000). Crayfish were previously thought to be stationary animals with a very limited movement range. However, newer findings suggest that crayfish actually move more than expected in search of food and hideouts (Taugbøl 2001). The optimal thermal range for noble crayfish is between 16 to 24 °C (Renai et al. 2007). These water temperatures are achieved in the summer in Norway. In June-July, the roe hatches and juveniles molt several times. Molting frequencies decline with age. While juveniles can molt as many as 4-5 times during summer, mature crayfish only molt 1-2 times (Taugbøl 2001). When molting, crayfish shed their old exoskeleton. This makes them extra vulnerable to predation, and crayfish usually hide from predators and remain inactive during this time. This is why heterogeneous areas with lots of obstacles and shelters are important to the crayfish (Johnsen et al. 2014). *Astacus astacus* is a nocturnal species of crayfish that are more active at night than day. The reason for this might be that they are less prone to predation during the night (Musil 2010).
Astacus astacus is subject to competition from several species of animals, including its own species (Zimmerman 2012). Intraspecific competition commonly occurs when the crayfish density is high, and resources are limited. The noble crayfish forms dominance hierarchies (Goessmann et al. 2000). Aggressive behavior and fighting are normal in these societies. The biggest crayfish are usually the ones that are dominant, and these crayfish have access to the best feeding areas and hideouts. Another form of intraspecific competition that occurs at high population densities is cannibalism. A study found that cannibalism was responsible for 37% of the mortality of adult Astacus astacus. During starvation, the number increased to 94% (Gydemo & Westin 1993). Astacus astacus also has to deal with interspecific competition. Fish, such as trout, compete for the same resources as the noble crayfish (Olsson et al. 2006). However, the biggest competitor to Astacus astacus may be non-indigenous crayfish species, such as the American signal crayfish (Pacifastacus leniusculus). Compared to the noble crayfish, the signal crayfish features a larger body and chela size, faster growth, greater fecundity and better tolerance to temperature and pollution (Westman & Savolainen 2001). American crayfish are also more aggressive than European ones and they have very similar niche requirements. Because of the great niche overlap and the highly competitive properties of Pacifastacus leniusculus, the two crayfish species cannot co-exist. As a result, Astacus astacus will be outcompeted and exterminated over time (Johnsen & Taugbøl 2010).

Astacus astacus in Norway
Astacus astacus is the only native species of crayfish in Norway. It is believed that the species first appeared in Sweden and later migrated to Norwegian lakes (Direktoratet for Naturforvaltning og Mattilsynet) However, many of the contemporary populations of crayfish are a result of introduction events performed by humans. Today, Astacus astacus is most abundant in the Southeastern parts of the country. The crayfish is a valuable highly sought-after resource. It is a culinary delicacy, and many people are paying high prices for them. The noble crayfish has a higher consumer price than any other freshwater species (Mattilsynet 2014). The commercial value of Astacus astacus was 4-8 million NOK in 2009, and this number is probably even higher today (Johnset et al. 2009). In addition to being an important source of income (Skurdal et al. 2002), Astacus astacus is also used for recreational purposes and as a bioindicator (Kuklina et al. 2014).
Crayfish catching is a popular event that takes place annually between August 6 and September 14 in many Norwegian lakes and rivers. It is a long-known tradition that is still going on today. In the 1960s, 40 tons of crayfish were caught every year. Today the catch has been reduced by a significant amount and only 10-12 tons are caught annually (Direktoratet for Naturforvaltning og Mattilsynet 2007). Private stakeholders own most of the catching areas. To participate in the catching, a catching license is required. However, some sites are open to everyone and do not require a license. One of the most popular sites is Steinsfjorden. *Astacus astacus* was first introduced to Steinsfjorden in 1850. It was heavily exploited by fishermen during the first 8 decades in the 20th century. In 1979, regulations were made to limit the catching (Skurdal et al. 2014).

The total number of *Astacus astacus* in Norway has decreased dramatically in the last 40 years. Reports from The IUCN Red List suggest a decline rate as high as 61% within three generations (Edsman et al. 2010). Today, *Astacus astacus* is an endangered species and is included on the Norwegian red list. According to the Norwegian species data bank, there were about 470 Norwegian populations of *Astacus astacus* remaining in 2014 (Henriksen & Hilmo 2015). The drastic decrease in numbers of crayfish is of great concern to Norwegian conservation biologists, as it may have considerable negative ecological and economic effects (Johnsen et al. 2009).

**Causes of population decline of *Astacus astacus***

Many factors are accountable for the decline in numbers of *Astacus astacus*. Decrease in water calcium levels, invasion of alien species, habitat loss and pollution are some of the most important factors (Johnsen & Taugbøl 2010, Hessen et al. 2017).

Crayfish are highly dependent on calcium to grow a strong exoskeleton. A sturdy exoskeleton is critical to the crayfish as it provides protection against predators and parasites as well as having other important functions (Hickman et al. 2014). The last 30 years there has been an evident decline in calcium levels in Norwegian lakes and rivers (Hessen et al. 2017). This decline is a result of acidification and other processes. Deposition of sulfuric acid (H$_2$SO$_4$) due to pollution from human activities is a main factor that causes acidification in lakes and rivers (Gałuszka & Migaszewski 2013).
Invasion of the North-American signal crayfish (*Pacifastacus leniusculus*) is a serious problem for *Astacus astacus*. Due to the great niche overlap and the highly competitive properties of the signal crayfish, *Astacus astacus* is at risk of being outcompeted (Westman & Savolainen 2001). However, the biggest threat to the noble crayfish is the pathogen *Aphanomyces astaci* (Johnsen 2014). *Aphanomyces astaci* is an oomycete that the signal crayfish carries. It is lethal to *Astacus astacus*. Infection of a population usually results in extinction of all the associated individuals (Taugbøl 2001). *Aphanomyces astaci* is the main factor that is responsible for the decline in numbers of the noble crayfish in Norway and Europe (Johnsen & Vrålstad 2010).

Habitat loss affects many species around the world (Department of the Environment and Heritage 2004). For freshwater animals like *Astacus astacus*, regulation of watercourses has a negative effect on habitat quality (Larsen et al. 2012). The building of dams in conjunction with hydropower plants causes fragmentation. River fragmentation can alter physical and chemical parameters in a way that causes habitat degradation (Uzunova et al. 2012). In addition, repeatedly changing water levels may increase erosion in the littoral zone where the crayfish live. Increased erosion over a long time can cause a reduction in nutrient and shelter availability for crayfish and other animals living in this zone (Arnekleiv et al. 2006).

Anthropogenic pollution is a threat to the environment and animal life. Excessive fertilizing from farming activity is a problem for many freshwater species, including crayfish. Nitrogen and phosphorus from fertilizers leak into rivers and lakes. This eutrophication results in algal blooms. When the algae die, large amounts of sediment build up at the bottom. The sediments smother the crayfish’s hiding places, making them more exposed (Taugbøl 2001). Another consequence of algal bloom is oxygen deficiency. *Astacus astacus* has high oxygen demands and requires oxygen-rich waters to survive (Laggis et al. 2017). Algal blooms can lead to hypoxia and mass death of crayfish in the affected area (Pitcher & Calder 2000).
Project focus, aims, and hypothesis

Because of the decline, we need to know more about the behavior of this species in the field. The purpose of this project was therefore to use underwater filming to study crayfish behavior in their natural environment. I examined how temperature and light intensity affect crayfish activity. I also looked at crayfish fighting behavior and how this is affected by temperature and light.

I chose to use a self-built underwater filming rig to study crayfish behavior. It is an inexpensive way of collecting samples, which is not prone to depth or time limitations associated with diving. Another benefit is that video sampling is a non-destructive technique that is suitable for use in protected areas containing endangered species (Cappo et al. 2004). Video sampling techniques are relatively accurate and reliable. In recent years, the quality of the equipment has improved greatly thanks to new technology (Stobart et al. 2015). By using underwater filming techniques, one can study several aspects of crayfish that is not possible using only traditional methods, such as mark-recapture. It also makes it easy to study behavior in the animal’s natural environment.

Temperature & activity

According to the literature, Astacus astacus is more active when the water temperature is higher (Peay 2000, Zimmerman 2012). Activity is mainly connected to food searching, although other factors such as mating and shelter searching might contribute too (Brown & Bowler 1977). Because of the poikilothermic nature of crayfish, an increase in water temperature causes the metabolic rate to increase as well (Ackefors 1999). An increased metabolic rate results in an increased need for food. As a result, the animal has to spend more time searching for food. This might explain why crayfish are more active in summer when the temperature is higher. It should also be noted that although crayfish are more active at higher temperatures, a study from Croatia showed that crayfish can be active the whole year, even at water temperatures as low as 1°C (Faller et al. 2006).
Light intensity & activity

*Astacus astacus* is a nocturnal species of crayfish (Musil 2010). This means that it is more active during the night when light intensity is low. A study performed by Styrishave et al. showed an increase in heart rate, locomotor activity, and oxygen consumption levels during nighttime in *Astacus astacus* (Styrishave et al. 2007). The reason for this nocturnal activity pattern might be that they are less prone to predation during the night (Musil 2010). Interestingly, the noble crayfish is able to adapt to the presence of a predator by changing its diel peak activity towards times of low predator activity. It also displays seasonal shifts in diel locomotor activity, with lower nocturnal activity in winter and higher nocturnal activity in summer (Hamrin 1987).

Crayfish fighting behavior

Just as with many other animals, crayfish fight to get access to food, shelter, mates and other resources. *Astacus astacus* forms dominance hierarchies (Gherardi & Daniels 2003). The purpose of these hierarchies is likely to decrease the time needed for fighting, so that they can spend more energy on collecting resources (Goessmann et al. 2000). Crayfish establish dominance by aggressive behavior, ritualized displays, and fighting. The consequences of such interactions are often non-lethal, as the intention is not to kill but to establish dominance (Moore 2007). The biggest crayfish are usually the ones that are dominant, and these crayfish have access to the best feeding areas and hideouts. Fights between crayfish of markedly different size are often short and of low intensity, while fights between crayfish of similar size are more aggressive (Sato & Nagayama 2012). Fighting is more likely to occur when the crayfish density is high and resources are scarce. Resources that are more valuable will frequently cause longer and more intense fights compared to less valuable resources (Moore 2007). Competition for food is an important cause of fighting. However, field observations and laboratory experiments suggest that crayfish fight more for shelter than food. They also suggest that fights for shelters are longer and more intense than fights over food resources (Bergman & Moore 2003).
Hypotheses

Based on the literature referred to in the previous sections, I hypothesize that:

1) Crayfish activity is highest during the night
2) Crayfish activity increases with decreasing light intensity
3) Crayfish activity increases with increasing water temperature
4) Larger crayfish are more likely to win over smaller combatants
5) Crayfish fight more when the water temperature is higher
6) Crayfish fight more when the light intensity is lower
**Materials and methods**

To film crayfish, I used three custom filming setups based on Raspberry Pi Zero microcontrollers. I put the Pis in waterproof enclosures, which I bought from JMRobotics. The enclosures were made of acrylic tubes\(^1\) with transparent dome end caps\(^2\). I placed a Romoss 10000 mAh battery and a PiNoir camera module in each of the tubes. The components were held in place by three 3D printed plastic plates (see assembly illustrations in Appendix D for more details). To provide the cameras with light during nighttime, I equipped the cameras with two Luxorparts 1W infrared LED lights (see wiring diagram for LEDs in Appendix D for more details). Because crayfish dislike white light, I used infrared light to prevent scaring them. Just as with the cameras, I had to put the LEDs in waterproof enclosures. The JMRobotics enclosures were made of aluminum tubes\(^3\) with transparent dome end caps\(^4\). To power the LEDs, I used two 4400 mAh lithium-ion battery packs wired in parallel. I attached the cameras and LEDs to a metal frame. The metal frame was made of Dexion slotted angle steel strips that I screwed together with bolts and nuts. I used three fittings as attachment structures for the camera and the LEDs. The bottom of the frame consisted of chicken wire mesh. I strapped a crayfish trap to the mesh using plastic strips. As bait, I chose to use chicken wings. To attach the bait, I used a steel wire or the built-in safety pin in the crayfish traps.

\(^1\) Product number: WTE3-P-TUBE-12-R1-RP  
\(^2\) Product number: WTE3-P-DOME-R1-RP  
\(^3\) Product number: WTE2-M-TUBE-6-R1-RP  
\(^4\) Product number: WTE2-P-DOME-R1-RP
I made three metal frames. Each frame carried one camera and two LEDs. I connected a three-meter rope to each of the frames. At the end of the rope, there was a buoy, to which I attached a laminated document containing the crayfish permit. I also equipped each frame with a HOBO temperature and light intensity logger.

The Raspberry Pis were controlled using scripts in the Python programming language. To start the filming, I connected to the Pi using the Secure Shell protocol (SSH). In this way, I could access the terminal and run a script to start the filming. To access the internet, I used the internet sharing option on my phone. I programmed the Pis to film for 2-hour intervals with a total run time of 24 hours. In this way, 12 smaller files were made. If one of the recordings failed, I would still get many working recordings. I used a 64 GB SD card to store my data. As my video settings, I used a resolution of 1280×720 pixels, a frame rate of 24 frames per second and a bit rate of 3 megabits per second. To prevent the script from stopping when quitting SSH, I utilized the “Screen” program for Linux based devices. This was necessary because the internet connection disappeared when I lowered the frames into the water.

Catching crayfish in Store Sandungen requires a permit. With the help of my co-supervisor, Stein-Ivar Johnsen from the Norwegian Institute for Nature Research (NINA), I got a permit from the county governor in Oslo and Akershus. The permit allowed me to catch crayfish outside of the official crayfish-catching season. It also allowed me to use a rowing boat. In
addition to the crayfish permit, I had to get a driving permit from the landowner. As my equipment was really big and heavy, I had to transport it by car. I got the permit from Kristian Berglund from Løvenskiold.

I used a small rowing boat to deploy the traps. Before lowering them into the water, I attached a crayfish trap to the bottom mesh of two of the frames. I used one 12 mm and one 21 mm trap. The third frame was left open with no trap attached to it. I turned on the cameras and LEDs and attached them to the frame. I then deployed the traps such that the distance between them was 10-15 meters. To randomize the design, I moved the traps around to new locations every day within the same area. I retrieved the traps after 24 hours and brought the cameras and LEDs home for data extraction and battery charging.

![Diagram](image.png)

**Figure 2:** An illustration of the setup showing the differences between the traps.

When pulling up the frames, I measured the length and determined the sex of the crayfish caught in my traps. I wrote down all information about size, sex, filming start time and weather conditions in a field report form for later use. I then released the caught crayfish back into the lake again. The fieldwork was conducted over a period of about two months, from the end of June to the end of August 2018, resulting in 15 deployments with 43 successful recordings.
Building and testing equipment

Building and testing equipment was a highly time-consuming process that required a lot of work. I spent a lot of time ordering components, 3D printing parts, soldering my LEDs and assembling all the parts. The 3D printing took 1-48 hours to finish depending on the size and design of the components.

When I had finished assembling all the parts, I had to test the equipment to see if it was working properly. The first task I had to do was to see if the tubes were waterproof. After putting them in my bathtub, I realized that they were leaking. Fortunately, this was easy to fix. The next task was to find the correct distance such that the camera was focused on the bait. To test this, I used a 38 by 38 cm sheet of paper and placed the camera at different distances until I could see the whole sheet. By doing this, I would make sure that I could see the crayfish trap when filming in the field. For every distance tried, I had to take a picture and then connect the Raspberry Pi to my computer to view it. After finding the correct distance, I had to test the cameras and the lights in a dark room. I used a bike handle as my test object and placed it about 40 cm away from the camera. The Raspberry Pi has an adjustable lens that adjusts the focus of the camera. By using a pair of pliers, I gently gripped the lens and turned it a few degrees. I then took a picture to see if the image was sharp or not. When the focus was set right, I tried to put the LEDs at different distances and angles to see when the illumination was best. I ended up placing them 55 cm away from the object.

The next step of the testing procedure was to start testing my equipment in the field. This phase of the project was especially troublesome. I encountered several problems that slowed my progression. Barriers blocking the road, LED tubes that would not close completely, camera tubes that opened in the water, unstable internet connection and failed recordings were some of the problems I had. During the final stages of testing, I realized that I needed a bigger boat to work with. The canoe I had brought was just too small and unsteady when working with the big and heavy traps. To get a boat, I had to fetch one that was located at my cabin.

Building and testing equipment took about 6 months to finish. The original plan was to start the fieldwork in the beginning of May. However, due to all the trouble I had been experiencing with my equipment, I was not able to begin the fieldwork until the end of June. This was much later than expected. Figure 3 shows a flowchart with the different problems I encountered and the time it took to fix them.
After about a week of work in the field, I began watching the recordings. The video quality was not very good and the video was a bit blurry. The field of view was also smaller than expected. I also realized that the illumination from my LEDs was not as good as I had expected. The LEDs were also draining more power than expected such that they did not last the whole night. When I was testing the camera at home, everything looked much nicer. I discussed my issues with my supervisor. It turned out that my pictures became blurry because of refraction, or bending of light in water. Regarding the LEDs, the problem was that infrared light is highly absorbed by water. As I did not know anything about these issues from before, I did not consider them when testing my equipment. I also realized that I had made a big mistake by only testing my components in air and not in water. Because it was too late to change things at this point, I just had to carry out with my current equipment and try to make the best out of it. Although not great, the video quality was good enough for my purposes.
Figure 4: Screenshots showing the quality of the videos. The left picture is from the 21 mm trap and the right from the open trap.

Data preparation

Analyzing the video footage was an important part of this project. To acquire the data, I first had to extract the videos from the Raspberry Pis and save them on my computer. The total file size of the videos was 10-40 GB. Because the capacity of my SD cards was only 64 GB, I had to transfer the videos to my computer after every filming session. I transferred the files using Wi-Fi. After the transferring process was completed, the next step was to start analyzing the 43 sets of video recordings. Every video was 24 hours long, giving a total runtime of 1032 hours. To speed up the process, I changed the playback speed to 32. I used the information gathered from the videos to make three different datasets. The datasets contained information about size, fighting behavior, and crayfish activity.

I started by looking at crayfish activity. To do this, I wrote down the number of crayfish arriving for every hour of the day in the videos. For the open traps, I also recorded the number of crayfish leaving every hour. Information from all three trap types was included in this dataset. To make the size and fighting behavior datasets, I only used information from the open traps. I monitored the first five crayfish arriving in every video, from their moment of arrival to their moment of departure. I wrote down information about arrival time, residence time, crayfish size, number of fights, outcome of the fights, and size of the opponents. Body size was measured as the total carapace area. I would like to emphasize that body size (carapace area) referred to in this and the next section is not the same a body length, which is mentioned later.
Because measuring the actual crayfish size out in the field was not possible with the open traps, the only way was to do it digitally. To do this, I took a screenshot for every five crayfish and their opponents. I then used a digital image analysis program called Fiji to measure the carapace area as a number of pixels. I also measured the mesh size of the chicken wire using the same method. To find the actual carapace area, I used the formula:

\[ \text{Carapace area} = \frac{C_p}{M_p} \times M_c, \]

where Carapace area = actual carapace area (cm\(^2\)), \(C_p\) = measured carapace area in pixels, \(M_p\) = chicken wire mesh area in pixels and \(M_c\) = chicken wire mesh area in cm\(^2\). The chicken wire mesh size \((M_c)\) was specified in the product dimensions. In my case, it was 1 cm\(^2\).

In addition to the three datasets already mentioned, I collected a fourth dataset in the field. This dataset contained directly observed crayfish body lengths and sex of the individuals caught in the traps. To determine the sex of the crayfish, I looked at the abdomen. Males have a characteristic sperm-transfer organ that females lack. I measured the length from the head end of the carapace to the tip of the middle tail fan. This is a common way of measuring crayfish length. Body length referred to in this dataset is not the same as body size (carapace area) measured in the previous section. Carapace area was calculated digitally, while body length was measured directly in the field. All three datasets contained temperature and light intensity data extracted from the loggers attached to the traps. I had programmed the loggers to measure temperature and light intensity for every hour of the day. As there were three loggers, I used the median temperature and light intensity of all three of them in the datasets.

I uploaded the datasets to figshare, which is an online open access repository where researchers can share their research output. My datasets can be accessed at https://figshare.com/s/334d91b00cea66d32af7, DOI: 10.6084/m9.figshare.7861916.

Statistics and choice of methods
I used four different datasets for the statistical analyses. As mentioned earlier, the datasets contained information about length and sex, size and fighting behavior and crayfish activity. I made the statistics with RStudio, a free and open-source integrated development environment for R, which is a programming language for statistical computing and graphics (R Core Team 2019). For most of the data, I chose to utilize a generalized linear model (GLM). Generalized
linear models are more flexible than linear regressions because they can handle data from other distributions than the Gaussian.

For my data, I chose to use a Poisson model, which is based on the Poisson distribution. I used it frequently when looking at the number of fights each crayfish was involved in. I also used it when looking at the number of crayfish arriving and leaving my traps. The reason why I chose a Poisson model is that my dependent variable consists of count data. However, a problem with the Poisson model is its inability to deal with overdispersion. Overdispersion is when the residual variation in your dataset is higher than what would be expected from the Poisson model alone. When you have overdispersion, the standard errors of model parameters will be underestimated, which increases the risk of Type I error. If an excess of zero-valued observations is the cause of the overdispersion, then quasi-Poisson, zero-inflated Poisson or negative binomial models are possible options. In my case, my data displayed overdispersion and contained many zeroes. For the sake of simplicity, I decided to use the quasi-Poisson model. A quasi-Poisson model assumes that variance is proportional to, but not necessarily equal to, the mean (Ver Hoef & Boven 2007). This differs from the Poisson model, which assumes that variance is exactly equal to the mean. By using a quasi-Poisson model, I would prevent getting over-optimistic standard errors for my estimates.

Although I mostly used generalized linear models, I also utilized a generalized additive model (GAM) from the mgcv package in R (Wood 2019). GAMs are useful when the relationship between the variables is expected to be of a more complex form, not easily fitted by standard linear or non-linear models (BCCVL). They are flexible models that have a wide range of use.

In addition to using different models, I also used various other statistical tests. These included Welch’s t-test, Pearson correlation test, overdispersion test and likelihood ratio test. Welch’s t-test compares the means of two groups of samples (Whitlock & Schluter 2015). The Pearson correlation test is a parametric test that measures the linear dependence between two variables (STHDA). The overdispersion test checks for overdispersion in your data. Finally, the likelihood ratio test compares the goodness-of-fit of two models (McDonald 2014). This test is useful when you want to see if a more complex model fits your data better than a simpler model. The likelihood ratio test only works when comparing nested models (IBM).
Study area

The fieldwork was conducted in Store Sandungen (60°7′N, 10°38′E), a lake in Asker municipality, about 40 kilometers outside of Oslo. It is an oligotrophic, soft-water lake with a pH-value of slightly less than 7 (Källqvist et al. 2003). The water is clear with a low content of total organic carbon (TOC). The area of the lake is about 0.64 km² (Skiforeningen). Bottom conditions are quite variable and range from a hard, rocky bottom to a soft and muddy one. Closer to land, the bottom is often rockier due to rockslides from the steep hills surrounding the lake. These rocky areas are well suited for crayfish catching. Due to the clear water, the lake is a popular area for swimming and camping. Previously, Store Sandungen served as drinking water for Asker municipality. At that time, swimming and fishing were not allowed. In 2007, the prohibition was repealed (Asker municipality).

Figure 5: A photo of Store Sandungen. The orange buoys are marking my rigs.
The climate in Store Sandungen is temperate, with four distinct seasons. Summers are warm, while winters are cold. The summer of 2018 was exceptionally warm and dry. Figure 7 shows the mean summer temperature at Store Sandungen for the last 30 years. We can see that the temperature was significantly higher in 2018 compared to previous years. In June, the temperature was 2.3°C warmer than normal. In July, it was an astonishing 5.1°C above normal. In August, it was 0.8°C above normal. Precipitation numbers were also much lower. In June, there was 37% less precipitation than normal. In July, the reduction was 91%, while in August it was 60%.
Figure 7: Monthly mean temperatures at Store Sandungen. The currently used normal period is 1961-1990. The weather data was collected from eKlima, a weather and climate data service provided by The Norwegian Meteorological Institute. The weather station used was located in Sem in Asker municipality.
Results

Sex & length distribution

Figure 8 shows the sex distribution of crayfish from the 12mm, 21mm, and open traps. There were more females than males in all traps. The number of crayfish caught was highest for the 12 mm traps and lowest for the open traps. There was no difference in sex ratio between the various trap types (see Table 1 for details).

![Crayfish sex distribution](image)

**Figure 8:** A bar graph showing the total number of caught crayfish based on sex and trap type.
Table 1: A generalized linear mixed model showing the difference in sex ratio between the various trap types.

<table>
<thead>
<tr>
<th>glmerMod</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family: binomial (logit)</td>
</tr>
<tr>
<td>Formula: Gender01 ~ Mesh + (1</td>
</tr>
<tr>
<td>Data: df</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>AIC</th>
<th>BIC</th>
<th>logLik</th>
<th>deviance</th>
<th>df.resid</th>
</tr>
</thead>
<tbody>
<tr>
<td>345.5</td>
<td>360.3</td>
<td>-168.7</td>
<td>337.5</td>
<td>295</td>
</tr>
</tbody>
</table>

Scaled residuals:

<table>
<thead>
<tr>
<th>Min</th>
<th>1Q</th>
<th>Median</th>
<th>3Q</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>-3.223</td>
<td>-0.722</td>
<td>0.305</td>
<td>0.583</td>
<td>1.961</td>
</tr>
</tbody>
</table>

Random effects:

<table>
<thead>
<tr>
<th>Groups</th>
<th>Name</th>
<th>Variance</th>
<th>Std.Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>(Intercept)</td>
<td>2,505</td>
<td>1.583</td>
</tr>
</tbody>
</table>

Number of obs: 299, groups: Date, 39

Fixed effects:

| Estimate | Std.Error | z value | Pr(>|z|) |
|----------|-----------|---------|---------|
| (Intercept) | 0.456     | 0.456   | 1.002   | 0.316   |
| Mesh21mm  | -0.174    | 0.692   | -0.251  | 0.802   |
| Meshopen  | 0.580     | 0.842   | -0.689  | 0.491   |

Correlation of Fixed Effects:

<table>
<thead>
<tr>
<th>(Intr)</th>
<th>Mesh21mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesh21mm</td>
<td>-0.658</td>
</tr>
<tr>
<td>Meshopen</td>
<td>-0.541</td>
</tr>
</tbody>
</table>

Figure 9 displays the length distribution of males and females for different trap types. The average length of males was 9.32 cm. Females were slightly smaller with an average size of 9.27 cm. A Welch’s t-test showed that the difference in size between sexes was not bigger than what would be expected from chance alone (p-value = 0.548; see Table 2 for details). In addition, there was no difference between the traps and no interaction between sex and trap type (see Table 3 for details).
Figure 9: A boxplot showing the crayfish length distribution for different trap types.
### Table 2: Results of the Welch’s T-test used to test for difference in size between sexes.

<table>
<thead>
<tr>
<th>t</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>-0.602</td>
<td>247.640</td>
<td>0.548</td>
</tr>
</tbody>
</table>

alternative hypothesis: true difference in means is not equal to 0

95 percent confidence interval:

| -0.227 | 0.121 |

Sample estimates:

<table>
<thead>
<tr>
<th>Mean of x</th>
<th>Mean of y</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.271</td>
<td>9.324</td>
</tr>
</tbody>
</table>

### Table 3: Summary statistics of a linear model showing the difference in length between the traps and the interaction between sex and trap type.

\[
\text{lm(formula = Length ~ Gender * Mesh, data = field_df)}
\]

<table>
<thead>
<tr>
<th>Coefficients:</th>
<th>Gendermale</th>
<th>Mesh21mm</th>
<th>Meshopen</th>
<th>Gendermale: Mesh21mm</th>
<th>Gendermale: Meshopen</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>9.104</td>
<td>0.207</td>
<td>0.342</td>
<td>-0.336</td>
<td>-0.261</td>
</tr>
</tbody>
</table>

### Length change during summer

To examine if the crayfish grew bigger throughout the summer, I ran a linear regression (Figure 10). The results showed that the relationship between length and date was not statistically significant (p-value = 0.521; see Table 4 for details). I used a likelihood ratio test to test if there was a difference between sexes. The results were not statistically significant (see Table 5 for details).
Figure 10: A linear regression showing crayfish length change during summer for males and females. Dotted red lines are confidence bands.
Table 4: Summary statistics of a linear model showing the relationship between length and date.

<table>
<thead>
<tr>
<th>lm(formula = Length ~ Onlyday, data = field_df)</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Residuals:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Min</td>
</tr>
<tr>
<td>-2.456</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Coefficients:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimate</td>
</tr>
<tr>
<td>(Intercept)</td>
</tr>
<tr>
<td>Onlyday</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Residual standard error</th>
<th>Multiple R-squared</th>
<th>Adjusted R-squared</th>
<th>F-statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.7659 on 297 DF</td>
<td>0.001</td>
<td>-0.002</td>
<td>0.413 on 1 and 297 DF</td>
<td>0.521</td>
</tr>
</tbody>
</table>

Table 5: Summary of likelihood ratio tests used to test for differences in length between sexes.

| Res.Df | RSS   | Df | Sum of Sq | F     | Pr(>|F|) |
|--------|-------|----|-----------|-------|---------|
| 1      | 297   |    | 174.220   |       |         |
| 2      | 296   | 1  | 174.090   | 0.135 | 0.230   | 0.632   |
| 3      | 295   | 1  | 173.660   | 0.424 | 0.720   | 0.397   |

Size and fighting behavior

One of the things I wanted to look at was whether bigger crayfish fight more than smaller crayfish. I performed a quasi-Poisson regression to examine the relationship between body size (carapace area) and the number of fights. As mentioned previously, body size is different from body length. To find the best model, I used a likelihood ratio test to compare different models. The models contained interactions between the number of fights and body size, temperature, light intensity, arrival time, and residence time. I calculated the correlation coefficients for every pair of independent variables (see Table 6 for details). If the correlation coefficient was high (>0.5), this would indicate a high degree of multicollinearity (Zuur et al. 2010). In such cases, it is difficult to separate the effects of the two variables. A solution to
this could be to only include one of the variables in the model. In my case, none of the
correlation coefficients was bigger than 0.5. The results from the likelihood ratio test showed
that none of the more complex models were any better than the simplest model (see Table 7
for details).

<table>
<thead>
<tr>
<th>Table 6: Correlation coefficients for every pair of independent variables.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
<tr>
<td>Size</td>
</tr>
<tr>
<td>MeanTemp</td>
</tr>
<tr>
<td>HourLux</td>
</tr>
<tr>
<td>Residence_time</td>
</tr>
<tr>
<td>Arrival_time</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 7: Results from a likelihood ratio test comparing different models.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model 1:</strong> Number_of_fights ~ Size + MeanTemp * HourLux + Arrival_time + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 2:</strong> Number_of_fights ~ Size + MeanTemp + HourLux + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 3:</strong> Number_of_fights ~ Size + MeanTemp + Arrival_time + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 4:</strong> Number_of_fights ~ Size + HourLux + Arrival_time + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 5:</strong> Number_of_fights ~ Size + HourLux + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 6:</strong> Number_of_fights ~ Size + MeanTemp + offset(log(Residence_time))</td>
</tr>
<tr>
<td><strong>Model 7:</strong> Number_of_fights ~ Size + Arrival_time + offset(log(Residence_time))</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Resid. Df</th>
<th>Resid. Dev</th>
<th>Df</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>29</td>
<td>52.959</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>31</td>
<td>70.146</td>
<td>-2</td>
</tr>
<tr>
<td>3</td>
<td>31</td>
<td>62.898</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>31</td>
<td>67.088</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>32</td>
<td>71.207</td>
<td>-1</td>
</tr>
<tr>
<td>6</td>
<td>32</td>
<td>70.318</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>32</td>
<td>68.244</td>
<td>0</td>
</tr>
</tbody>
</table>

I decided to follow the principle of Occam’s razor and choose the simplest model, which only
included body size and the number of fights. I also chose to include offset(log(residence time)
in the model because I was interested to see how many fights per unit of time (hour) that the
crayfish were involved in during their stay and how this was related to body size. Figure 11
shows the regression. The summary from Table 8 concluded that the results were not
statistically significant (quasi-Poisson glm p-value = 0.988; see Table 8 for details). Bigger crayfish did not fight more than smaller crayfish. I also ran a test to see whether an individual did fight or not was related to size. The results were not statistically significant (binomial glm p-value = 0.603; see Table 9 for details).

**Figure 11:** A GLM showing the relationship between body size and the number of fights. The dotted red lines are prediction bands.
Table 8: Summary statistics of a generalized linear model showing the relationship between size and number of fights.

```r
glm(formula = Number_of_fights ~ Size + offset(log(Residence_time)),
    family = quasipoisson, data = d)
```

<table>
<thead>
<tr>
<th>Deviance residuals</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Min</td>
<td>1.954</td>
<td>-1.047</td>
<td>-0.510</td>
<td>1.212</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.330</td>
</tr>
</tbody>
</table>

| Coefficients:      | Estimate | Std. Error | t value | Pr(>|t|) |
|--------------------|----------|------------|---------|---------|
| (Intercept)        | -3.408   | 2.506      | -1.360  | 0.183   |
| Size               | 0.009    | 0.585      | 0.015   | 0.988   |

(Dispersion parameter for quasipoisson family taken to be 18.630)

<table>
<thead>
<tr>
<th>Null deviance</th>
<th>Residual deviance</th>
<th>AIC</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>71.402 on 34 degrees of freedom</td>
<td>71.398 on 33 degrees of freedom</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>

Number of Fisher Scoring iterations: 7
The next thing I was interested to look at was if the winners of the fights were bigger than the losers. A fight has three possible outcomes: win, lose or tie. If a crayfish clearly outpowers its opponent and forces it to withdraw, it is considered as the winner. The crayfish that has to withdraw is considered as the loser. If a fight has no clear winner, it is a tie. Figure 12 shows the number of fights each crayfish was involved in and the size of the winners and losers. To examine if bigger crayfish had a higher probability of winning, I looked at the confidence intervals. I found the confidence intervals using the command `confint(M0)` in R.

\[ M0 = glm(larger\ wins \sim 1). \]

Because the confidence intervals were in logit-units, I had to back-transform them to get the probabilities. To do this, I used the formula: \[ Pr(larger_{wins}) = \frac{1}{(1+e^{-L})} \] where L = the upper and lower confidence interval value. If the confidence limits did not include 0 (= logit(0.5)), then the odds that the larger crayfish win were better than 50:50. The confidence intervals for the probability of winning ranged from 0.4227-0.7727. This means that \( Pr(larger\ wins) \) is not significantly different from 0.5. Bigger crayfish did not have a higher probability of winning. In some cases, the fights ended in a tie. Interestingly, we can see from Table 10 that the probability of a fight ending in a tie was not related to the size.
difference between the contestants (binomial glm p-value = 0.656; see Table 10 for details). In my case, only 4/28 fights ended in a tie.

**Figure 12:** An overview of all the fights and the size of the winners and losers. Gray dots are ties.
Table 10: Summary of a generalized linear model used to test if the probability of a fight ending in a tie was related to the size difference between the contestants.

```
glm(formula = Tieyorno ~ Sizediff, family = binomial, data = fight_df)
```

<table>
<thead>
<tr>
<th>Deviance residuals</th>
<th>Min</th>
<th>1Q</th>
<th>Median</th>
<th>3Q</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-0.691</td>
<td>-0.577</td>
<td>-0.522</td>
<td>-0.489</td>
<td>2.149</td>
</tr>
</tbody>
</table>

| Coefficients: | Estimate | Std. Error | z value | Pr(>|t|) |
|---------------|----------|------------|---------|---------|
| (Intercept)   | -2.211   | 1.125      | -1.96   | 0.050 * |
| Sizediff      | 0.302    | 0.677      | 0.45    | 0.656   |

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

(Dispersion parameter for binomial family taken to be 1)

<table>
<thead>
<tr>
<th>Null deviance</th>
<th>Residual deviance</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.967 on 27 degrees of freedom</td>
<td>22.768 on 26 degrees of freedom</td>
<td>26.768</td>
</tr>
</tbody>
</table>

Number of Fisher Scoring iterations: 4

Temperature and fighting behavior

Because crayfish are more active at higher water temperatures, I wanted to examine if the crayfish were fighting more when the water was warmer. Figure 13 shows a quasi-Poisson regression. According to Table 11, there was no statistically significant relationship between the number of fights and temperature (p-value = 0.943; see Table 11 for details).
Figure 13: A GLM showing the relationship between temperature and the number of fights. Darker dots are multiple overlapping observations. The dotted red lines are prediction bands.
**Table 11:** Summary of a generalized linear model showing the relationship between the number of fights and temperature.

```r
glm(formula = Number_of_fights ~ MedianTemp, family = quasipoisson, data = size_df2)
```

<table>
<thead>
<tr>
<th>Deviance residuals</th>
<th>Min</th>
<th>1Q</th>
<th>Median</th>
<th>3Q</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-1.487</td>
<td>-1.448</td>
<td>-0.097</td>
<td>-0.067</td>
<td>4.284</td>
</tr>
</tbody>
</table>

| Coefficients:      | Estimate | Std. Error | t value | Pr(>|t|) |
|--------------------|----------|------------|---------|---------|
| (Intercept)        | -0.059   | 1.963      | -0.030  | 0.976   |
| MedianTemp         | 0.007    | 0.092      | 0.073   | 0.943   |

(Dispersion parameter for quasipoisson family taken to be 2.217)

<table>
<thead>
<tr>
<th>Null deviance</th>
<th>Residual deviance</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>55.793 on 34 degrees of freedom</td>
<td>55.782 on 33 degrees of freedom</td>
<td>NA</td>
</tr>
</tbody>
</table>

Number of Fisher Scoring iterations: 6

**Light intensity and fighting behavior**

In addition to being more active at higher temperatures, crayfish are nocturnal animals. To see if crayfish fought more during lower light intensities, I used a quasi-Poisson regression (Figure 14). Table 12 shows that the relationship between the number of fights and light intensity was not statistically significant (p-value = 0.201; see Table 12 for details).
**Figure 14:** A GLM showing the relationship between light intensity and the number of fights. Darker dots are multiple overlapping observations. The dotted red lines are prediction bands.
Table 12: Summary of a generalized linear model showing the relationship between the number of fights and light intensity.

```r
glm(formula = Number_of_fights ~ MedianLux, family = quasipoisson, data = size_df2)
```

<table>
<thead>
<tr>
<th>Deviance residuals</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Min</td>
<td>-1.633</td>
<td>-1.258</td>
<td>-0.360</td>
<td>0.226</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.923</td>
</tr>
</tbody>
</table>

Coefficients:

|              | Estimate | Std. Error | t value | Pr(>|t|) |
|--------------|----------|------------|---------|---------|
| (Intercept)  | -2.351e-01| 3.635e-01  | -0.647  | 0.522   |
| MedianLux    | 8.023e-05 | 6.155e-05  | 1.303   | 0.201   |

(Dispersion parameter for quasipoisson family taken to be 2.068)

<table>
<thead>
<tr>
<th>Null deviance</th>
<th>Residual deviance</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>55.793 on 34 degrees of freedom</td>
<td>52.295 on 33 degrees of freedom</td>
<td>NA</td>
</tr>
</tbody>
</table>

Number of Fisher Scoring iterations: 6

Size and residence time

Although bigger crayfish did not fight more than smaller crayfish, I was curious to see if bigger crayfish stayed for a longer time in the trap than smaller crayfish. Figure 15 shows the regression produced by a GLM. In this case, there was a statistically significant relationship between size and residence time, suggesting that bigger crayfish do stay longer than smaller crayfish (p-value = 0.002334; see Table 13 for details).
Figure 15: A GLM showing the relationship between size & residence time. Darker dots are multiple overlapping observations. The dotted red lines are prediction bands.
**Crayfish activity pattern**

A main goal of this project was to study when crayfish are most active. Figure 16 shows the crayfish activity in the open traps. The activity seems to be pretty even across the whole day, except for a peak at around 11-12 pm. However, this sudden increase in crayfish activity could be a result of an artifact caused by the graph ending at 12 pm. Therefore, caution should be used when interpreting the results from Figure 16. For the 12 mm and 21 mm traps, the activity is highest during the night, with a peak at around 12-1 (Figure 17). From 5 am to 5 pm the activity is fairly low before it increases again during the evening at around 6 pm. The results from Figure 16 and 17 suggest that crayfish are more active during the night than during the day.
Figure 16: Number of crayfish arriving and leaving for every hour of the day across all deployments in the open traps. Darker dots are multiple overlapping observations. The dotted lines are mean values.
**Figure 17**: Number of crayfish arriving for every hour of the day in the 12 mm and 21 mm traps. Darker dots are multiple overlapping observations. The dotted lines are mean values.

**Crayfish activity, temperature & light intensity**

I was also interested to look at the relationship between crayfish activity and temperature, light intensity, and trap type. I ran a generalized additive model (GAM) with trap type, temperature, and light as the fixed effects while adding smoother terms for temperature and light. There was a significant difference between the open trap and 12/21 mm traps, but no significant difference between 12 mm and 21 mm (see Table 14 for details).
Table 14: Summary of a generalized additive model used to see if there was a difference in number of crayfish arriving between the different trap types.

Family: poisson
Link function: log
Formula:
Numberofcrayfisharriving ~ Mesh + s(median.temp) + s(sqrt(sqrt(median.Lux)))

| Parametric coefficients: | Estimate | Std. Error | z value | Pr(>|z|) |
|-------------------------|----------|------------|---------|----------|
| (Intercept)             | -1.017   | 0.110      | -9.261  | <2e-16 ***|
| Mesh21mm                | -0.146   | 0.150      | -0.972  | 0.331    |
| Meshopen                | 0.331    | 0.123      | 14.965  | <2e-16 ***|

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

Approximate significance of smooth terms:

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<th></th>
<th>edf</th>
<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
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<td>s(median.temp)</td>
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<td>89.12</td>
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<tr>
<td>s(sqrt(sqrt(median.Lux)))</td>
<td>6.175</td>
<td>7.205</td>
<td>94.860</td>
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Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

R-sq.(adj)        Deviance explained | UBRE | Scale est. | n
0.391             46.3%          | 0.248 | 1           | 582

According to Figure 18, there seems to be an activity optimum at around 22.5°C. There is also a sharp decline in activity at around 10000 lux. In addition, the figure shows that the activity is about \( e^{1.84} = 6.3 \) times higher in the open traps compared to the 12 mm and 21 mm traps. I transformed the light intensity using a fourth root transformation. The reason why I chose to use a fourth root transformation is that square roots and fourth roots handle zeros better than log. In my case, fourth root seemed to perform even better than square root.
Figure 18: The top left and right graphs show the spline smoother terms for the activity pattern at different temperatures and light intensities, respectively. The lower left graph shows the difference in activity between different trap types. The graphs are predictions from a GAM.

I also wanted to test if crayfish activity is determined by an interaction of temperature and light. To do this, I used a similar GAM as before but including an interaction term between light intensity and temperature (Figure 19, Table 15). We can see from the figure that the crayfish activity increases with increasing temperature up to about 19°C, irrespective of light intensity. When the temperature exceeds 19°C, the crayfish become more active at lower light intensities and less active at higher light intensities. It also seems like the activity decreases irrespectively of light intensity when the temperature exceeds about 23°C.
Figure 19: Predicted crayfish activity in the open traps as a function of temperature and light. The figure is a prediction from a GAM, allowing for an interaction between temperature and light intensity.
### Table 15: Summary of a generalized additive model with an interaction term between light intensity and temperature.

- **Family:** poisson
- **Link function:** log
- **Formula:**
  
  Number of crayfish arriving ~ Mesh + te(median.temp, sqrt(sqrt(median.Lux)))

| Parametric coefficients: | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|----------|
| (Intercept)              | -1.059   | 0.110      | -9.587  | <2e-16 *** |
| Mesh21mm                 | -0.136   | 0.150      | -0.907  | 0.364    |
| Meshopen                 | 1.874    | 0.124      | 15.126  | <2e-16 *** |

---

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

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<th>edf</th>
<th>Ref.df</th>
<th>Chi.sq</th>
<th>p-value</th>
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</thead>
<tbody>
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<td>te(median.temp, sqrt(sqrt(median.Lux)))</td>
<td>17.52</td>
<td>19.630</td>
<td>192.800</td>
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Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 1

<table>
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<tr>
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<th>Deviance explained</th>
<th>UBRE</th>
<th>Scale est.</th>
<th>n</th>
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</thead>
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<tr>
<td>0.411</td>
<td>48.4%</td>
<td>0.223</td>
<td>1</td>
<td>582</td>
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**Daytime recording bias**

A problem with the activity data was that there were more daytime recordings than nighttime recordings. The reason for this was that the batteries used to power the LEDs were too small. As a result, they died before the night began, making it impossible to see anything in the dark. This happened whenever I deployed the traps in the morning or in the afternoon. Figure 20 shows the daytime bias of the recordings.
Figure 20: The figure shows the daytime bias of the recordings for different trap types. Horizontal dotted lines represent the total number of recordings. The solid lines represent the part of the recordings that could be used for video analysis.
Discussion

In my study, bigger crayfish did not have a higher chance of winning. This is contrary to findings from other studies (Goessmann et al. 2000, Sato & Nagayama 2012). Bigger crayfish won 17/28 fights, while smaller crayfish only won 7/28. These observations suggest that bigger crayfish should win more often. However, the difference was not statistically significant. Body size plays a central role in the structure of dominance hierarchies in Astacus astacus. Bigger crayfish are usually the most dominant with the highest ranks. Interestingly, my results showed that bigger crayfish did not fight more than smaller crayfish. This might reflect the theory that by establishing dominance, crayfish decrease the time needed for fighting, so that they can spend more energy on collecting resources (Goessmann et al. 2000). Furthermore, there was a positive correlation between body size and residence time in the open traps. Larger crayfish could thus feed at the bait for a longer time than smaller crayfish. Another interesting finding in this study was that the probability of a fight ending in a tie was not related to the size difference between the contestants. This could indicate that fighting behavior is not only influenced by body size but by other factors as well.

Although difficult to test, it is possible that personality is a contributing factor. Animal personality is usually defined as the presence of consistent between-individual differences in the expression of individual behavioral traits (Dall et al. 2004, Sih et al. 2004, Briffa & Weiss 2010, Schuett et al. 2010, Van Oers & Mueller 2010). Personality is known to affect many things, including aggression, exploration, foraging and sexual behavior (Kralj-Fišer & Schuett 2014). The presence of personality differences may affect how animal populations respond to change. It is important to study and learn more about personality differences, as they can have significant evolutionary and ecological consequences (Dall et al. 2004). Personality can be influenced by neurotransmitters. There is a link between serotonin and aggressiveness. Higher serotonin levels are associated with increased aggressiveness and a higher motivation to fight (Tricarico & Gherardi 2006). Furthermore, there is evidence that boldness is related to aggressiveness, and that bolder crayfish are more aggressive (Pintor et al. 2008). Bolder crayfish are often the ones that are dominant too (Aquiloni et al. 2012). In addition, crayfish with previous winning experience became bolder and had a higher chance of winning subsequent agonistic encounters (Daws et al. 2002, Goessmann et al. 2000).

Many crustaceans display increased agonistic behavior in response to increased temperature and lower light intensities (Hoffman et al. 1975, Van der Meeren 1993). Based on this, I
expected to see more crayfish fights at higher temperatures and at lower light intensities. However, neither temperature nor light intensity had a statistically significant effect on the number of fights. This could be due to the low sample size in this study. In addition, the LEDs were draining the battery quicker than expected. The built-in light sensor of the LEDs was supposed to turn on the IR-light only when the light level was below a certain threshold. However, for some reason, the lights were turned on too early in the day. Because of this, the batteries died too quickly, making it impossible to see anything at night. As a result, only a few successful nighttime recordings were made. The sample size during nighttime recordings was therefore much smaller than during daytime (see Figure 20). This could explain why I could not find any effect from light intensity on the number of fights. The relatively short sampling period might also be an explanation that we did not see an influence of temperature on fighting activity. Because the summer of 2018 was abnormally warm, water temperatures were fairly high throughout the whole sampling period. This made it difficult to capture the full effects of a wider temperature range on fighting behavior.

The results from my activity data showed that crayfish activity was highest during the night. All three trap types displayed a peak in activity at around 11 pm to 1 am. My findings support the view that *Astacus astacus* is nocturnal (Musil 2010). The daytime activity was higher in the open traps compared to the 12/21 mm traps. This could be explained by the easier access to food in the open traps. An advantage of using open traps to measure activity is the possibility to count the number of crayfish leaving. By looking at both arrivals and exits, one gets a more accurate measurement than by just looking at arrivals alone. It should be mentioned that the battery problem mentioned earlier also applies to the activity data. As a consequence of this, there might be a larger uncertainty in the night measurements.

I also assessed the relationship between temperature, light intensity and crayfish activity in this study. It is evident that crayfish activity is affected by temperature and light intensity (Styrishave et al. 2013, Westin & Gydemo 1988, Peay 2000, Zimmerman 2012). The findings in this study confirm that *Astacus astacus* is a nocturnal species of crayfish that is more active at higher temperatures. My results seemed to indicate an activity optimum at around 22.5°C. This is within the optimal thermal range of *Astacus astacus*, which is believed to be around 16-24°C (Renai et al. 2007). There was also a sharp decline in activity above approximately 10000 lux (Figure 18, Table 14). If we look at Figure 19, there is an interactive effect where a certain temperature is needed for the animals to be active, but daytime light conditions will suppress activity once it is warm enough. When the temperature exceeds a certain limit, the
activity decreases. This is true for many other aquatic invertebrates as well, such as starfish (Peck et al. 2008). The reason for this is likely that too high temperatures cause disturbances in metabolism and other physiological processes, which are crucial in maintaining normal behavior and function (Yamaguchi 1974). It could also be that there might not be enough data in the colder and sunny side to make good predictions for the interaction between light and temperature in the colder range. A relationship between light intensity and activity is also found in many other crustaceans, such as lobster and crabs (Hammond & Naylor 1977, Strachan et al. 1999). The choice of being nocturnal or diurnal is largely affected by the activity pattern of their predators, as well as other environmental factors (Powers & Bliss 1983). As for temperature, many lobsters and crabs are more active at higher water temperatures (Moland et al. 2011, Mat et al. 2017).

Furthermore, it looks like bigger size allows crayfish to stay longer with the food. This could indicate that size is linked to dominance. However, I was not able to find a relationship between size and the probability of winning a fight. This implies that fighting behavior and dominance are not only influenced by size, but by other factors as well. Although I could not find any effect from temperature and light intensity on fighting behavior, it does not necessarily mean that no relationship exists. Failing to reject a null hypothesis means that you do not have enough statistical power in your data to disprove the null hypothesis. It does not prove that the null hypothesis is true. A source of error in this study is the relatively small sample size. A small sample size is often associated with low statistical power. Low statistical power reduces the chance of detecting a true effect. It also reduces the likelihood that a statistically significant result reflects a true effect (Button et al. 2013). With high statistical power, the chance of drawing the right conclusions increases. As a result, the reliability and credibility of a study will be dependent on its statistical power.

Video filming techniques are versatile techniques that have a wide range of use. There are many examples in the literature of how they can be used to estimate density and abundance (Willis & Babcock 2000, Stobart et al. 2015), monitor biodiversity (Mallett & Pelletier 2014), study movement patterns (Smith et al. 1993), and measure size (Cappo et al. 2003). This project has demonstrated how such filming techniques can be performed with the use of relatively simple, inexpensive, homemade equipment. The total cost of one rig was approximately 10000 NOK (see Materials list in Appendix C for more details). In comparison, a professional rig would cost about 35000 NOK (Haggit et al. 2014). Another advantage of my system is the modular design. The modular design allows for easy
customization and high flexibility. It also makes it simple to perform changes that could improve the performance of the system. By further improving the system, it would make it possible to measure and document more about the interactions between individuals of the same species, and even between species.

Unlike the many laboratory studies published, this study examines behavior out in the field. The advantage of field experiments is that they provide a more realistic view of how crayfish behave in their natural environment. A main aim of this project was to look at fighting behavior. I specifically chose to look at fighting during foraging. There is some evidence that crayfish fight more for shelter than food. Moreover, fights for shelter are often longer and more intense than fights over food resources (Bergman & Moore 2003). This raises the question if I missed the most important fighting arena. A future study could be to examine fighting behavior in conjunction with shelter availability instead of food availability.

Understanding behavioral and ecological patterns are crucial when trying to conserve endangered species. Video techniques are useful tools that provide the opportunity of studying animals without having to perform laboratory experiments. The use of remote camera traps has enabled us to learn more about rare species that are otherwise difficult to study. Such rare species include the African golden cat (Bahaa-El-Dinet al. 2015) and the Sumatran tiger (Pusparini et al. 2017). By gaining knowledge about rare, endangered species, it is possible to initiate conservation actions to prevent them from going extinct. Camera traps have helped in conserving many species, such as the giant armadillo (Desbiez & Kluyber 2013) and the Javan rhino (Gokkon 2018). In addition, camera traps have helped in spreading information and increasing the awareness of endangered animals around the world. Conservation organizations, such as World Wildlife Fund, are now actively using camera trap footage as a part of their campaigns to save threatened or endangered species (WWF).
Conclusion

The results from this study show that crayfish activity is positively correlated with temperature and negatively correlated with light intensity. There was a clear tendency of higher activity during the night than during the day for all trap types. These findings demonstrate the nocturnal activity pattern of Astacus astacus. Crayfish activity increased with increasing temperature up to about 22.5°C. A further increase in temperature caused a decrease in activity. This shows that there is a temperature optimum, at which the activity is highest. Temperature and light intensity had no significant effect on fighting frequency. Bigger crayfish did not fight more than smaller crayfish. There was no correlation between size and odds of winning. The lack of correlation between size and odds of winning in this study implies that crayfish fighting behavior is influenced by personality. Personality is a growing field of interest in science. Researchers are becoming more aware of the importance of personality in animal behavior. More research is needed to investigate the impact of personality on crayfish behavior.
References


Microevolution of the noble crayfish (Astacus astacus) in the Southern Balkan Peninsula. BMC Evolutionary Biology. 17, 1-19.


Appendices

Appendix A

**R-code:**

### Data preparation

install.packages("tidyverse", "readxl", "AER", "gam", "lme4")
library(tidyverse)
library(readxl)
library(lubridate)
library(MASS)
library(AER)
library(gam)
library(tidyverse)
library(lme4)

# Environmental variable
env_df = read_excel("env.xlsx", range = cell_cols("A:C"))

env_df_Day = env_df %>%
  mutate(Onlyday = date(Date)) %>%
  group_by(Onlyday) %>%
  summarise(TempMean = mean(TempC, na.rm = TRUE),
            MaxLight = max(IntensityLux, na.rm = TRUE),
            MeanLight = mean(IntensityLux, na.rm = TRUE)) %>%
  ungroup()

env_df_Day2 = env_df %>%
  mutate(Onlyday = date(Date)) %>%
  group_by(Onlyday)

env_df_Hour2 = env_df %>%
  mutate(Onlyday = date(Date),
```r
Onlyhour = hour(Date) %>%
group_by(Onlyday, Onlyhour) %>%
ungroup()

env_df2 = env_df_Day %>%
  left_join(env_df_Hour)

# Field data
files <- dir(pattern = "*.gender.xlsx")

readddder = function(x) {read_excel(path = x)}

field_df <- data_frame(filename = files) %>%
  mutate(file_contents = map(filename, readddder)) %>%
  unnest() %>%
  separate(filename, c("Day", "Month", "Year", "Mesh", "Camera", "Time", "out" ), sep = "-") %>%
  select(-"out") %>%
  separate(Time, c("Hour", "Minute"), sep = -2) %>%
  unite(Time, c(Hour, Minute), sep = ":") %>%
  unite(Date2, c(Year, Month, Day), sep = "-") %>%
  unite(Date, c(Date2, Time), sep = " ") %>%
  mutate(Date = ymd_hm(Date)) %>%
  mutate(Onlyday = date(Date),
         Onlyhour = hour(Date))

# Fight data
files <- dir(pattern = "*.fight.xlsx")

readddder = function(x) {read_excel(path = x, na = "NA")}
```

63
fight_df <- data_frame(filename = files) %>%
  mutate(file_contents = map(filename, readddder)) %>%
  unnest() %>%
  separate(filename, c("Day", "Month", "Year", "Mesh", "Camera", "Time", "out" ), sep = "-") %>%
  select(-"out") %>%
  separate(Time, c("Hour", "Minute"), sep = -2) %>%
  unite(Time, c(Hour, Minute), sep = ":") %>%
  unite(Date2, c(Year, Month, Day), sep = "-") %>%
  unite(Date, c(Date2, Time), sep = " ") %>%
  mutate(Date = ymd_hm(Date)) %>%
  mutate(Onlyday = date(Date),
         Onlyhour = hour(Date))

names(fight_df) <- c("Date", "Mesh", "Camera", "Fight_number", "Win_size", "Lose_size",
                    "Sizediff", "Tieyorno", "MeanTemp", "MeanLux", "Onlyday", "Onlyhour")

# Sizedata
files <- dir(pattern = "*size.xlsx")

readddder = function(x){read_excel(path = x)}

size_df <- data_frame(filename = files) %>%
  mutate(file_contents = map(filename, readddder)) %>%
  unnest() %>%
  separate(filename, c("Day", "Month", "Year", "Mesh", "Camera", "Time", "out" ), sep = "-") %>%
  select(-"out") %>%
  separate(Time, c("Hour", "Minute"), sep = -2) %>%
  unite(Time, c(Hour, Minute), sep = ":") %>%
  unite(Date2, c(Year, Month, Day), sep = "-") %>%
  unite(Date, c(Date2, Time), sep = " ") %>%
  mutate(Date = ymd_hm(Date)) %>%
mutate(Onlyday = date(Date),
        Onlyhour = hour(Date))

names(size_df) <- c("Date", "Mesh", "Camera", "Crayfish_number", "Arrival_time",
"Residence_time", "Size", "Number_of_fights", "MeanTemp", "MeanLux", "HourLux",
"Onlyday", "Onlyhour")

# Arrivaldata
files <- dir(pattern = "*arrivals.xlsx")

readddder = function(x){read_excel(path = x, na = "NA")}

arrivals_df <- data_frame(filename = files) %>%
  mutate(file_contents = map(filename, readddder)) %>%
  unnest() %>%
  separate(filename, c("Day", "Month", "Year", "Mesh", "Camera", "Time", "out" ), sep = "-") %>%
  select(-"out") %>%
  separate(Time, c("Hour", "Minute"), sep = -2) %>%
  unite(Time, c(Hour, Minute), sep = ":") %>%
  unite(Date2, c(Year,Month,Day), sep = "-") %>%
  unite(Date, c(Date2, Time), sep = ") %>%
  mutate(Date = ymd_hm(Date)) %>%
  mutate(Onlyday = date(Date),
         Onlyhour = hour(Date),
         Starttime = hour(Starttime),
         Endtime = hour(Endtime))

arrivals_df2 = arrivals_df %>%
  rowwise() %>%
  mutate(meantemp2 = (TempA + TempB + TempC)/3,
         meanlux2 = (LuxA + LuxB + LuxC)/3)
### Sex distribution

gender <- table(field_df$Gender, fill = field_df$Mesh)
barplot(gender, main = "Crayfish sex distribution", xlab = "Day", ylab = "Number",
legend=c("Female", "Male"),
    col=c("red", "blue"), ylim = c(0,200))

t2 = glmer(Gender01 ~ Mesh + (1|Date), data = df, family = binomial)
summary(t2)
plot(t2)
hist(resid(t2))
plot(resid(t2))

### Size distribution

d <- read.table("field_df.txt", header=TRUE, sep="\t")
library(lattice)
 bwplot(Length ~ Gender | Mesh, data= d, main="Crayfish length distribution for different trap types", xlab="Trap type", ylab="Length (cm)")

dat <- read.table("field_df.txt", header=TRUE, sep="\t")
average <- tapply(dat$Length, dat$Gender, mean)
print(average)
with(dat, t.test(Length[Gender=="female"], Length[Gender=="male"])

lm(Length ~ Gender*Mesh, data = field_df)

### Size change during summer

d <- read.table("field_df.txt", header=TRUE)
summary(d)

d$Onlyday <- as.Date(d$Onlyday)
d$Julianday <- as.numeric(format(d$Onlyday, "%j"))

summary(m <- lm(Length ~ Julianday, data=d))
plot(Length ~ Onlyday, data=d, xlab="Date", ylab="Length (cm)", ylim=c(6, 12), pch=19, col=gray(0.4))

t <- 170:250
p <- as.data.frame(predict(m, newdata=data.frame(Julianday=t), type = "response", se.fit=TRUE))

x <- as.Date(as.Date("2018-01-01") + t)

lines(fit ~ x, type="l", data=p, lwd=3, col="blue")
lines(fit + se.fit ~ x, data=p, lty=2, col="red")
lines(fit - se.fit ~ x, data=p, lty=2, col="red")

summary(m3 <- lm(Length ~ Onlyday * Gender, data = field_df))
summary(m2 <- lm(Length ~ Onlyday + Gender, data = field_df))
summary(m1 <- lm(Length ~ Onlyday, data = field_df))
anova(m1, m2, m3)

###Size & number of fights

cor1 <- select(size_df, Size, MeanTemp, HourLux, Residence_time, Arrival_time)
cor(cor1)

size1 <- glm(Number_of_fights ~ Size + MeanTemp + HourLux + Arrival_time + offset(log(Residence_time)), family=quasipoisson, data=size_df)
size2 <- glm(Number_of_fights ~ Size * MeanTemp + HourLux + Arrival_time + offset(log(Residence_time)), family=quasipoisson, data=size_df)
size3 <- glm(Number_of_fights ~ Size * HourLux + MeanTemp + Arrival_time + offset(log(Residence_time)), family=quasipoisson, data=size_df)
size4 <- glm(Number_of_fights ~ Size * Arrival_time + MeanTemp + HourLux + offset(log(Residence_time)), family=quasipoisson, data=size_df)
size5 <- glm(Number_of_fights ~ Size + MeanTemp * HourLux + Arrival_time + offset(log(Residence_time)), family=quasipoisson, data=size_df)
size6 <- glm(Number_of_fights ~ Size + MeanTemp * Arrival_time + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size7 <- glm(Number_of_fights ~ Size + MeanTemp + HourLux * Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size8 <- glm(Number_of_fights ~ Size + MeanTemp + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size9 <- glm(Number_of_fights ~ Size + MeanTemp + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size10 <- glm(Number_of_fights ~ Size * MeanTemp + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size11 <- glm(Number_of_fights ~ Size * MeanTemp + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size12 <- glm(Number_of_fights ~ Size + MeanTemp + Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size13 <- glm(Number_of_fights ~ Size * MeanTemp + Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size14 <- glm(Number_of_fights ~ Size + MeanTemp * Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size15 <- glm(Number_of_fights ~ Size * Arrival_time + MeanTemp +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size16 <- glm(Number_of_fights ~ Size + HourLux + Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size17 <- glm(Number_of_fights ~ Size * HourLux + Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size18 <- glm(Number_of_fights ~ Size + HourLux * Arrival_time +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
size19 <- glm(Number_of_fights ~ Size * Arrival_time + HourLux +
offset(log(Residence_time)), family=quasipoisson, data=size_df)
anova(size1, size2, size3, size4, size5, size6, size7)
anova(size8, size9, size10, size11)
anova(size12, size13, size14, size15)
anova(size16, size17, size18, size19)
size20 <- glm(Number_of_fights ~ Size + HourLux + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

size21 <- glm(Number_of_fights ~ Size * HourLux + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

anova(size20, size21)

size22 <- glm(Number_of_fights ~ Size + MeanTemp + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

size23 <- glm(Number_of_fights ~ Size * MeanTemp + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

anova(size22, size23)

size24 <- glm(Number_of_fights ~ Size + Arrival_time + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

size25 <- glm(Number_of_fights ~ Size * Arrival_time + offset(log(Residence_time)),
family=quasipoisson, data=size_df)

anova(size24, size25)

anova(size5, size8, size12, size16, size20, size22, size24)

d <- read.table("size_df.txt", header=TRUE, sep="\t")

dim(d)

summary(d)

summary(m1 <- glm(Number_of_fights ~ Size + offset(log(Residence_time)),
family=quasipoisson, data=d))

z <- seq(1, 6.5, 0.1)
pred.data <- data.frame(Size=z, Residence_time=60)
pred.fights <- predict(m1, newdata=pred.data, type="link", se.fit=TRUE)

plot(I(Number_of_fights / (Residence_time / 60)) ~ Size, data=d,
ylim=c(0, 10), xlab="Body size (cm²)", ylab="Fights per hour", main="Body size & number of fights")

lines(exp(fit) ~ z, type="l", data=pred.fights, lwd=3, col="blue")
lines(exp(fit + 1.96 * se.fit) ~ z, data=pred.fights, lty=2, col="red")
lines(exp(fit - 1.96 * se.fit) ~ z, data=pred.fights, lty=2, col="red")

d$did.fight <- (d$Number_of_fights > 0)
summary(m2 <- glm(did.fight ~ Size, family=binomial, data=d))

###Are winners bigger or not?

d <- read.table("fight_df.txt", header=TRUE, sep = "\t")
summary(d)

x0 <- rep(1, nrow(d))
y0 <- d$Lose_size
x1 <- rep(2, nrow(d))
y1 <- d$Win_size

tie <- d$Tieyorno

plot(c(0.7, 2.3), c(0.5, 6.5), type="n", xlab="", ylab="Size (cm²)", main = "Size of winners and losers", axes=FALSE)
points(y0 ~ x0, cex=1.2, pch=19, col=c("black", "gray")[tie])
points(y1 ~ x1, cex=1.2, pch=19, col=c("black", "gray")[tie])
arrows(x0, y0, x1, y1, length=0, col=c("black", "gray")[tie])

axis(1, at=c(1, 2), labels=c("Loser", "Winner"))
axis(2)

###Do bigger crayfish have a higher probability of winning a fight?

d <- read.table("fight_df.txt", header=TRUE)
summary(d)
d$larger.wins <- with(d, (Win_size > Lose_size) & (Tieyorno == "n"))

d$abs.size.diff <- with(d, abs(Win_size - Lose_size))

summary(m1 <- glm(larger.wins ~ abs.size.diff, family=binomial, data=d))

m0 <- glm(larger.wins ~ 1, family=binomial, data=d)
summary(m0)

confint(m0)

1 / (1 + exp(-coef(m0)[1]))

###Size difference & tie
sizediff2 <- glm(Tieyorno ~ Sizediff, family = binomial, data = fight_df)
summary(sizediff2)

###Temperature & number of fights
size_df3 <- read.table("size_df.txt", header=TRUE, sep="\t")
size_df2 <- as.data.frame(size_df3)
sm <- glm(Residence_time ~ MedianTemp, family=poisson, data=size_df2)
dispersontest(sm, trafo=0)

d <- read.table("size_df.txt", header=TRUE, sep="\t")

str(d)
summary(d)

summary(m1 <- glm(Number_of_fights ~ MedianTemp, data=d, family=quasipoisson))
z <- seq(1, 25, by = 0.1)
pred.data <- data.frame(MedianTemp = z)
pred.fights <- predict(m1, newdata=pred.data, type="response", se.fit=TRUE)

plot(Number_of_fights ~ MedianTemp, data=d, xaxt="n",
     ylim=c(0, 10), xlim=c(15, 25), pch = 19, col=rgb(0,0,0,0.3), xlab="Temperature (°C)",
     ylab="Number of fights", main="Temperature & number of fights")
axis(1, at = 15:25)

lines(fit ~ z, type="l", data=pred.fights, lwd=3, col="blue")
lines(fit + se.fit ~ z, data=pred.fights, lty=2, col="red")
lines(fit - se.fit ~ z, data=pred.fights, lty=2, col="red")

### Temperature & light intensity
lum <- glm(Number_of_fights ~ MedianLux, family=poisson, data=size_df2)
dispersiontest(lum, trafo=0)

d <- read.table("size_df.txt", header=TRUE, sep="\t")

str(d)

summary(d)

summary(m1 <- glm(Number_of_fights ~ MedianLux, data=d,
                   family=quasipoisson))

z <- seq(0, 10000, by = 0.1)
pred.data <- data.frame(MedianLux = z)
pred.fights <- predict(m1, newdata=pred.data, type="response", se.fit=TRUE)

plot(Number_of_fights ~ MedianLux, data=d, pch = 19, col=rgb(0,0,0,0.3),
     ylim=c(0, 10), xlim=c(0, 10000), xlab="Light intensity (lux)",
     ylab="Number of fights", main="Temperature & number of fights")
axis(1, at = 0:10000)
xlim=c(0, 10000), xlab="Light intensity (lux)", ylab="Number of fights", main="Light intensity & number of fights")

lines(fit ~ z, type="l", data=pred.fights, lwd=3, col="blue")
lines(fit + se.fit ~ z, data=pred.fights, lty=2, col="red")
lines(fit - se.fit ~ z, data=pred.fights, lty=2, col="red")

###Residence time & number of fights

d <- read.table("size_df.txt", header=TRUE, sep="\t")
str(d)
summary(d)
summary(m1 <- glm(Residence_time ~ Size, data=d, family=Gamma(link = "inverse")))

z <- seq(1, 7, by = 0.1)
pred.data <- data.frame(Size = z)
pred.fights <- predict(m1, newdata=pred.data, type="response", se.fit=TRUE)

plot(Residence_time ~ Size, data=d, xlab="Size (cm)", ylab="Residence time (min)", main="Size & Residence time")

lines(fit ~ z, type="l", data=pred.fights, lwd=3, col="blue")
lines(fit + se.fit ~ z, data=pred.fights, lty=2, col="red")
lines(fit - se.fit ~ z, data=pred.fights, lty=2, col="red")

###Crayfish activity open traps

d <- read.table("arrivals_df.txt", header=TRUE, sep="\t")

dim(d)
summary(d)

d$net.arrival <- with(d, Numberofcrayfisharriving - Numberofcrayfishleaving)
d1 <- subset(d, Mesh == "open")

mean.arrival <- aggregate(NumberOfcrayfisharriving ~ Starttime, data=d1, mean)
mean.leave <- aggregate(NumberOfcrayfishleaving ~ Starttime, data=d1, mean)
mean.net <- aggregate(net.arrival ~ Starttime, data=d1, mean)

plot(NumberOfcrayfisharriving ~ Starttime, data=d1, pch=19, col=gray(0.1, 0.1))
lines(NumberOfcrayfisharriving ~ Starttime, data=mean.arrival, lwd=3, col=2)

plot(NumberOfcrayfisharriving ~ factor(Starttime), data=d1, xlab="")
lines(NumberOfcrayfisharriving ~ I(Starttime+1), data=mean.arrival, lwd=3, col=2)

plot(NumberOfcrayfisharriving ~ Starttime, data=d1, pch=19, xlab="Start time",
ylab="Number of crayfish arrivals and departures", main="Crayfish activity open traps",
       col=rgb(1, 0, 0, 0.1), ylim=c(-10, 10))
lines(NumberOfcrayfisharriving ~ Starttime, data=mean.arrival, lwd=3, col="red")
points(-NumberOfcrayfishleaving ~ Starttime, data=d1,
           pch=19, col=rgb(0,0, 1, 0.1))
lines(-NumberOfcrayfishleaving ~ Starttime, data=mean.leave, lwd=3, col="blue")
abline(v=seq(0, 23, 6), lty=2, col=gray(0.5, 0.5))
abline(h=0, lty=2, col=gray(0.5, 0.5))
legend("bottomright", c("arriving", "leaving"), lwd=3, col=c("red", "blue"))

plot(net.arrival ~ Starttime, data=d1, pch=19, col=gray(0.1, 0.1))
lines(net.arrival ~ Starttime, data=mean.net, lwd=3, col=2)

###Crayfish activity 12mm & 21mm traps

d <- read.table("arrivals_df.txt", header=TRUE, sep="\t")

dim(d)
summary(d)
with(d, table(Mesh, is.na(Numberofcrayfishleaving)))

d1 <- subset(d, Mesh == "open")
d1$net.arrival <- with(d1, Numberofcrayfisharriving - Numberofcrayfishleaving)

mean.arrival <- aggregate(Numberofcrayfisharriving ~ Starttime, data=d1, mean)
mean.leave <- aggregate(Numberofcrayfishleaving ~ Starttime, data=d1, mean)
mean.net <- aggregate(net.arrival ~ Starttime, data=d1, mean)

plot(Numberofcrayfisharriving ~ factor(Starttime), data=d1, xlab="")
lines(Numberofcrayfisharriving ~ I(Starttime+1), data=mean.arrival, lwd=3, col=2)

plot(net.arrival ~ Starttime, data=d1, pch=19, col=gray(0.1, 0.1))
lines(net.arrival ~ Starttime, data=mean.net, lwd=3, col=2)

plot(Numberofcrayfisharriving ~ Starttime, data=d1, pch=19, col=rgb(1, 0, 0, 0.1), ylim=c(-10, 10))
lines(Numberofcrayfisharriving ~ Starttime, data=mean.arrival, lwd=3, col="red")
points(-Numberofcrayfishleaving ~ Starttime, data=d1, pch=19, col=rgb(0,0, 1, 0.1))
lines(-Numberofcrayfishleaving ~ Starttime, data=mean.leave, lwd=3, col="blue")
abline(v=seq(0, 23, 6), lty=2, col=gray(0.5, 0.5))
abline(h=0, lty=2, col=gray(0.5, 0.5))

d2 <- subset(d, Mesh != "open")
d2$Mesh <- factor(d2$Mesh)

mean.arrival.12mm <- aggregate(Numberofcrayfisharriving ~ Starttime, data=subset(d2, Mesh == "12mm"), mean)
mean.arrival.21mm <- aggregate(Numberofcrayfisharriving ~ Starttime, data=subset(d2, Mesh == "21mm"), mean)
plot(Numeroofcrayfisharriving ~ Starttime, data=d2, pch=19, xlab="Start time", ylab="Number of crayfish arriving", main="Crayfish activity 12 mm & 21 mm traps", col=c(rgb(1, 0, 0, 0.1), rgb(0, 0, 1, 0.1))[Mesh])
lines(Numeroofcrayfisharriving ~ Starttime, data=mean.arrival.12mm, lwd=3, col="Green")
lines(Numeroofcrayfisharriving ~ Starttime, data=mean.arrival.21mm, lwd=3, col="Brown")
abline(v=seq(0, 23, 6), lty=2, col=gray(0.5, 0.5))
legend("topright", c("12mm", "21mm"), lwd=3, col=c("green", "brown"))

###Contour plot

d <- read.table("arrivals_df.txt", header=TRUE, sep="\t")

d <- subset(d, !is.na(Numeroofcrayfisharriving))

dim(d)

length(unique(d$Date))

D$Date <- as.Date(strptime(d$Date, "%Y-%m-%d %H:%M:%S"))

D$Time <- as.POSIXct(D$Date) + (60 * 60) * D$Starttime

summary(d)

plot(Starttime ~ Time, data=d, pch=19, col=Mesh)
plot(Date ~ Time, data=d, pch=19, col=Mesh)
plot(d[, c(9, 11, 13, 15, 19)])
plot(d[, c(10, 12, 14, 16, 20)])
plot(sqrt(d[, c(10, 12, 14, 16, 20)]))
plot(sqrt(sqrt(d[, c(10, 12, 14, 16, 20)])))
plot(log10(d[, c(10, 12, 14, 16, 20)]))

summary(d$median.Lux)

max(d$median.Lux, na.rm=TRUE)

max(d$median.temp, na.rm = TRUE)
\[ d \text{median.temp} \leftarrow \text{apply}(d[, c(9, 11, 13)], 1, \text{median}) \]
\[ d \text{median.Lux} \leftarrow \text{apply}(d[, c(10, 12, 14)], 1, \text{median}) \]

\[
\text{plot(} \text{median.temp \sim Time, data=d, pch=19, ylim=c(15, 25))} \\
\text{points(} \text{TempA \sim Time, data=d, col=2)} \\
\text{points(} \text{TempB \sim Time, data=d, col=3)} \\
\text{points(} \text{TempC \sim Time, data=d, col=4)} \\
\]

\[
\text{plot(} \text{median.Lux \sim Starttime, data=d, pch=19, ylim=c(0,50000))} \\
\text{points(} \text{LuxA \sim Starttime, data=d, col=2)} \\
\text{points(} \text{LuxB \sim Starttime, data=d, col=3)} \\
\text{points(} \text{LuxC \sim Starttime, data=d, col=4)} \\
\]

\[
\text{summary(} m1 \leftarrow \text{gam(} \text{Numberofcrayfisharriving \sim Mesh + median.temp + sqrt(sqrt(median.Lux))),} \\
\text{family=quasipoisson, data=d)} \\
\]

\text{library(mgcv)}

\[
\text{summary(} m2 \leftarrow \text{gam(} \text{Numberofcrayfisharriving \sim Mesh + s(median.temp) + s(sqrt(sqrt(median.Lux))),} \\
\text{family=poisson, data=d)} \\
\]

\text{par(mfrow=c(2,2))} \\
\text{plot(m2)} \\
\text{termplot(m2)} \\

\[
\text{summary(} m3 \leftarrow \text{gam(} \text{Numberofcrayfisharriving \sim Mesh + s(median.temp) + s(sqrt(sqrt(median.Lux))) + ti(median.temp, sqrt(sqrt(median.Lux))),} \\
\text{family=poisson, data=d)} \\
\]
summary(m4 <- gam(Numberofcrayfisharriving ~ Mesh + te(median.temp, sqrt(sqrt(median.Lux))),
               family=poisson, data=d))

  t <- seq(15, 25, 0.1)
  L <- seq(0, 12, 0.1)^4

  temp.lux <- expand.grid(median.temp=t, median.Lux=L)
  pred.data <- data.frame(Mesh="open", temp.lux)

  pred.data$pred.arrival <- predict(m4, newdata=pred.data, type="response")

  pred.matrix <- matrix(pred.data$pred.arrival, nrow=length(t))
  contour(t, L, pred.matrix, levels=0:12, labcex = 1.2,
          xlab="Temperature (C)", ylab="Light intensity (Lux)",
          main="Predicted crayfish arrival per hour in open traps")

  ###NA-values distribution
  plot(aggregate(!is.na(Numberofcrayfisharriving) ~ Starttime, FUN=mean, data=d), ylim=c(0, 1), type="b")

  ###Daytime recording bias
  arrivals_df3 = arrivals_df2 %>% mutate(recordingyesno =
          ifelse(is.na(Numberofcrayfisharriving), 0, 1))

  arrivals_df4 = arrivals_df3 %>% group_by(Starttime, Mesh) %>% summarise(numrec =
                           sum(recordingyesno))

  arrivals_df5 = arrivals_df4 %>% group_by(Mesh) %>% summarise( maxrec = max(numrec))

  arrivals_df4 %>% ggplot(aes(x = Starttime, y = numrec, color = Mesh)) + geom_line() +

                   ...

geom_hline(aes(yintercept = maxrec, color = Mesh), linetype = "dashed", data = arrivals_df5) + scale_y_continuous("Number of recordings", breaks = c(1,2,3,4,5,6,7,8,9,10,11,12)) + scale_x_continuous("Time in day") + ggtitle("Number of recordings for different times of the day") + labs(color='Trap type') + theme(plot.title = element_text(hjust=0.5))

theme_set(theme_bw())
theme_update(text = element_text(size=12), panel.grid.major = element_blank(), panel.grid.minor = element_blank(), strip.background = element_blank())
Appendix B

**STL files:**

Camera plates
LED attachment plate

LED attachment cylinder
## Appendix C

### Materials list:

<table>
<thead>
<tr>
<th>Item</th>
<th>Quantity</th>
<th>Distributor</th>
<th>Price per unit (NOK)</th>
<th>Price per rig (NOK)</th>
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<td>Blue Robotics 3” Cast Acrylic Tube with O-Ring Flange, Transparent Dome End Cap and Aluminum End Cap</td>
<td>3</td>
<td><a href="http://www.jmrobotics.no">http://www.jmrobotics.no</a></td>
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<td>USB cable</td>
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Appendix D

Camera assembly
LED assembly
LED and associated components inside aluminum tube
Camera and LED assembly illustration

To wire two batteries in parallel, solder the black (-) wires together and the red (+) together.
LED wiring diagram