
Habitat niche differentiation of
Ballan wrasse (*Labrus bergylta*) and Corkwing wrasse
(*Symphodus melops*) revealed by acoustic telemetry:
Implication for an urban restoration project



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Cover photo: Corkwing wrasse, by Knut Wiik Vollset

Abstract

Anthropogenic changes to natural habitats impact species behavior and habitat use, changing ecological interactions and ecosystem dynamics. Human influenced ecosystems can be found all along the Norwegian coast, where the Bergen city centre fjord is a good case. This urban fjord has been repurposed as a harbour for hundreds of years, with high and increasing boat and human activities, resulting in a highly polluted seabed of Store Lungegårdsvannet of heavy metals (PCB7 and PAH16) and organic pollutants. This is considered threatening with negative influences on both the marine ecosystem and human health. Therefore, Store Lungegårdsvannet is in an ongoing state of garbage removal and following a restoration planned for 2023, including that a proportion of the seafloor is going to be covered by sand sediments to reduce the effect of polluted marine substrate. Wrasses are an abundant fish family inhabiting the Norwegian coast and they are often used as bioindicator species for evaluating anthropogenic impacts. In order to use wrasse as a bioindicator for the effects of seafloor restoration, however, we need to understand their spatiotemporal habitat use. At a local scale, the different wrasse species are expected to use the habitat in slightly different ways, also known as habitat niche partitioning. A consequence of fine scale niche partitioning is that different species of wrasse may respond differently to anthropogenic changes and habitat restoration. To investigate possible differences in behaviour of two wrasse species, 34 individuals of ballan wrasse (*Labrus bergylta*) and corkwing wrasse (*Symphodus melops*) in Store Lungegårdsvannet (Bergen, Norway) were implanted with acoustic tags in June 2021 and July 2022. These tags were instrumented with sensors for measuring temperature and depth, providing information on wrasse behaviour for over a year. Results from this study revealed that (1) ballan wrasse inhabited deeper depths than corkwing wrasse, that (2) the experienced temperatures of the two species were similar despite differences in depth use, that (3) changes in behaviour when temperature decreased during winter was clearly present for both species, by moving to deeper waters and that (4) ballan wrasse started activity earlier than corkwing wrasse during summer and later in autumn. The results support existence of habitat niche differentiation for ballan wrasse and corkwing wrasse, making them differently impacted by habitat disturbance from a restoration process.

1. Introduction

As humans increasingly explore and exploit the sea, a consequence is the impact on marine habitats. The urban encroachment upon coastal ecosystems continues to increase due to a rising demand for space and food with a growing human population (Bulleri & Chapman, 2010; Waltham et al., 2020). Anthropogenic changes may alter pristine habitats by impacts from artificial infrastructures, pollution, introduced species, and seafloor alterations resulting in loss of biodiversity and habitat heterogeneity (Airoldi et al., 2021). These changes to coastal ecosystems in urban fjords may alter species behavior and their habitat use, changing ecological interactions and ecosystem dynamics (Airoldi et al., 2021).

Human influenced ecosystems can be found all along the European coast, often around cities or in major harbours and ports (Todd et al., 2019). In the second largest city of Norway, Bergen, the urban fjord has been repurposed as a harbour for hundreds of years, with high and increasing boat activities from both the shipping industry and tourism (Harris, 2010; McArthur & Osland, 2013). The city centre fjord is also highly influenced by human activities such as littering and habitat disturbance, resulting in a highly polluted seabed with heavy metals (PCB7 and PAH16) and persistent organic pollutants (Bergen Kommune, 2022). This contamination is considered degrading with negative influences on both the marine ecosystem and on human health (Bergen Kommune, 2022). Because of this pollution, parts of the urban fjord such as Store Lungegårdsvannet are undergoing garbage removal in preparation for a restoration project planned for 2023 (Bergen Kommune, 2022). This restoration process will entail that a proportion of the seafloor be covered by clean sand sediments to reduce the effect of polluted marine substrate (Bergen Kommune, 2022).

Physical restoration may biologically impact species, where changes in the environment can alter the behaviour of fishes (Airoldi et al., 2021). One of the most abundant species in fjords around Bergen are wrasse. This fish family inhabiting the Norwegian coast is often used as a bioindicator species for evaluating anthropogenic impacts by, for instance, revealing biological effects of contaminants from a liver comparative analysis or biochemical and bioaccumulation approaches for investigating marine pollution (Broeg et al., 2008; Tomasello et al., 2012). Wrasse has an important role in the ecosystem as both an important consumer, preying on small invertebrates, and a prey species for many larger fish and birds (Skiftesvik et al., 2015). This group of fishes are also a common and classic fjord species, which, if understood, facilitates knowledge about behavior of human influenced coastal species (Skiftesvik et al., 2015). In order to use wrasse as a bioindicator for the effects of seafloor restoration, we need to understand their spatiotemporal habitat use (Lapointe et al., 2013).

Although the geographical distribution of many of the most common wrasse species in Norway is similar, the different species of wrasse are expected to use the habitat in slightly different ways, termed habitat niche partitioning (Halvorsen et al., 2020; MacArthur, 1958). Habitat niche partitioning is a mechanism of coexistence between similar species that inhabit the same space, avoiding competition against one another by partitioning available resources within the habitat (MacArthur, 1958). Several studies have revealed the nature of habitat niche partitioning for organisms such as warblers, plants, and reef fishes (Brandl et al., 2020; MacArthur, 1958; Queenborough et al., 2007)(MacArthur, 1958). A consequence of this fine scale niche partitioning is that different species of wrasse may respond differently to

anthropogenic impacts and to the process and outcome of habitat restoration. Two abundant wrasse species in the coastal waters of Norway are ballan wrasse (*Labrus bergylta*) and corkwing wrasse (*Symphodus melops*), which seems to be inhabiting slightly different habitats, from a study looking at wrasse distribution and habitat preferences (Skiftesvik et al., 2015). Comparing the fine scale behaviour of these two species could give insights into how the species use and potentially partition the available habitat. This knowledge could further be used in the context of a restoration by establishing behaviours and habitat use throughout a year for the two species that could be influenced by sand covering (Brownscombe et al., 2022).

There is some, but limited research available on behavioral differences between ballan wrasse and corkwing wrasse, which, if further studied, would be relevant to determine how restoration impacts the two species (Halvorsen et al., 2021; Rodrigues et al., 2015; Skiftesvik et al., 2015; Villegas-Ríos et al., 2013). Ballan wrasse has a life history strategy of growing big, living long, and mature late, whilst corkwing wrasse are a smaller fish, living shorter but maturing earlier (Blanco Gonzalez & de Boer, 2017). This would make ballan wrasse a species that is expected to use more of the water column, feed more actively, hibernate for a shorter period during winter, and wake up earlier to utilize more of the day to feed. Physical changes from a restoration would therefore differently impact the two species with diverse life history strategies. Previous studies have found that ballan wrasse inhabits greater depths than corkwing wrasse, meaning they would be more vulnerable to actions affecting deeper areas (Halvorsen et al., 2020, 2021; Moen & Svensen, 2020; Rodrigues et al., 2015). The effect of sea temperature on depth use has been studied for ballan wrasse, however, studies on corkwing wrasse and temperature differences between the two species are poorly studied (Freitas et al., 2021). Additionally, previous research on the behavior of the two species during winter indicates hibernation, but research on this topic is deficient and scarce (Halvorsen et al., 2021; Mattingsdal et al., 2018; Sayer & Reader, 1996). Knowledge on time of hibernation is important in knowing when the two species is most vulnerable to changes from the restoration, by covering the seafloor with sand. Another aspect that is of relevance to seabed restoration is at what time the different species come out of their shelter in the morning (here defined as wake-up time). Wake-up time for the two species is also a behaviour that is not well studied but determines when activities would make the fish most active and reactive. A previous study stated that further studies using acoustic telemetry would be useful to obtain more detailed insights into home-range and habitat use of wrasse species, for instance in revealing the location and duration of winter hibernation (Halvorsen et al., 2021). To access information on benefits or disadvantages of a restoration process, acoustic telemetry is a commonly used method and enables details on fish movement, behaviour, and physiology across different temporal and spatial scales (Brownscombe et al., 2022).

The aim of this study was to compare the behaviour of two species of wrasse, *Labrus bergylta* and *Symphodus melops*, in an urban marine ecosystem with an ongoing and planned restoration by capping polluted sediments with ~30 cm clean sand. This is done by observing the species' behaviour using acoustic telemetry, giving information about depth use, temperature, hibernation behaviour, and diurnal activity of the two species over the course of more than a year. I hypothesized that habitat niche differentiation exists for ballan wrasse and corkwing wrasse. To reveal if this is the case, four hypotheses were investigated:

1. Ballan wrasse inhabits deeper depths than corkwing wrasse over a year.
2. Ballan wrasse and corkwing wrasse experiences different temperatures over a year.
3. Ballan wrasse hibernate for a shorter time period than corkwing wrasse.
4. Ballan wrasse wakes up earlier than corkwing wrasse during summer.

Comparative analysis of behaviour is a strong tool to further discuss how the two species may be differentially impacted by restoration in the city centre fjord of Bergen. The results from this study could actively be used by the local municipality to guide present restoration and plan future restoration activity in Store Lungegårdsvannet and other areas of the urban fjord. This is done by providing insight into when the two species of wrasse are most vulnerable to disturbance by sea floor covering, and by revealing possible differences in behaviour. Information on these differences is important for understanding their ecology and planning of a successful restoration.

2. Materials and Methods

2.1 Study area

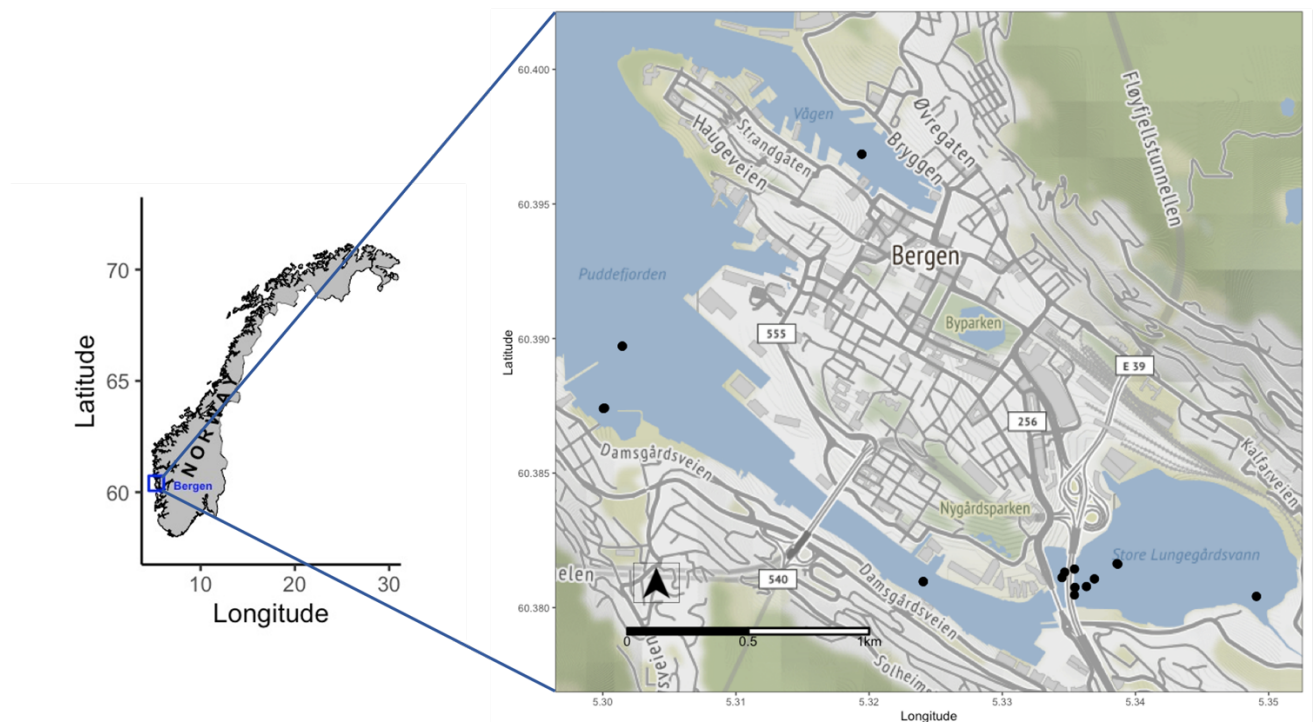


Figure 1: Map of study area, circled black dots (●) indicate where receivers were stationed in Store Lungegårdsvann, Puddefjorden and Vågen, Norway.

This study was conducted in Store Lungegårdsvannet and the city centre fjord (Puddefjorden and Vågen) of Bergen, Norway (Figure 1) in the period May 2021 – November 2022. Store Lungegårdsvannet covers an area of 0,45 km², has a maximum depth at 26 m, and a ground sill at 3 m. The urban ocean surrounding Bergen city is inhabited by several important habitat types such as kelp beds, rocky shores, and sandy bottoms, which support ecosystems in this fjord. There are various fish species that live here, such as species from the wrasse family, cod family and salmonids. In addition, multiple other organisms depend on these ecosystems including birds and crustaceans (Skiftesvik et al., 2015).

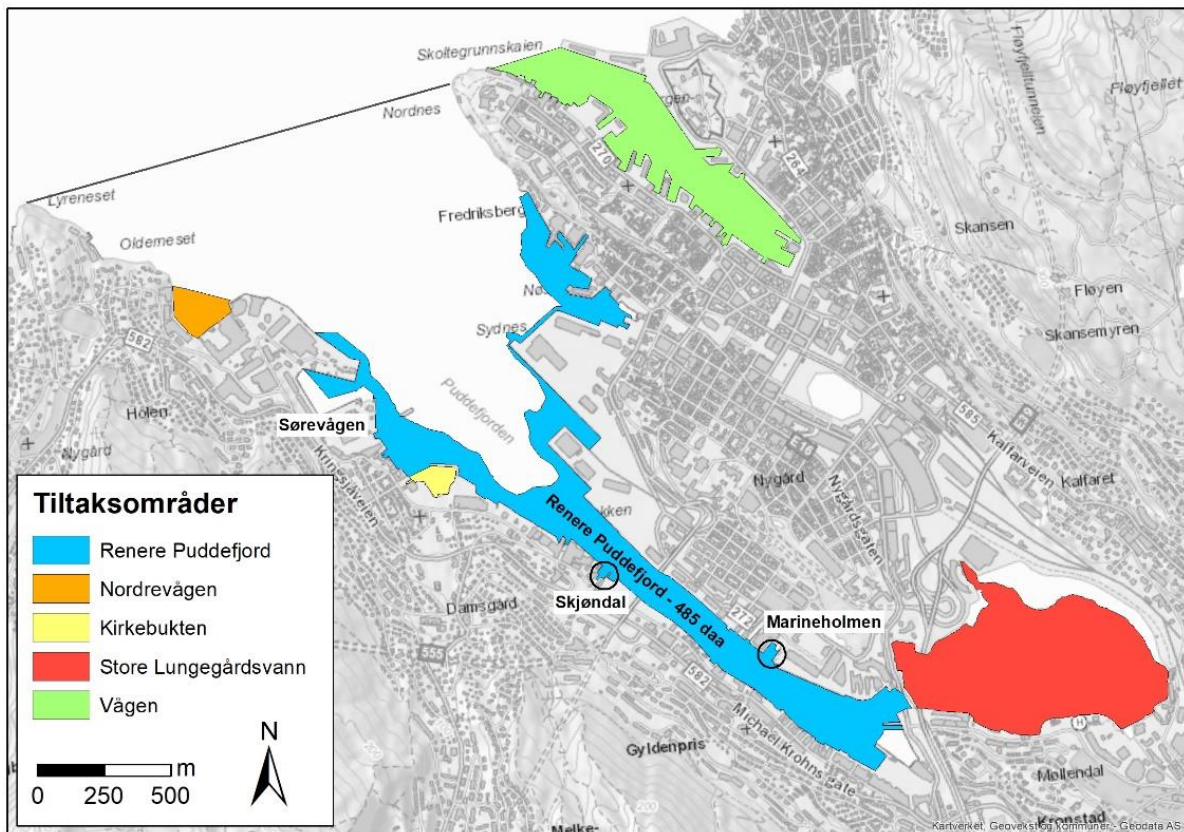


Figure 2: Overview of areas in the Bergen city center fjord. Bergen commune has responsibility for Renere Puddefjord (cleaner Puddefjorden), Store Lungegårdsvann and Vågen. Garbage removal has been performed for Nordrevågen, Søreivågen, Marineholmen and Skjøndal according to permission from state administrators in Vestland».

The seabed of Store Lungegårdsvannet is highly polluted by heavy metals (PCB7 and PAH16) and organic pollutants, which are considered toxic with negative influences on both the marine ecosystem and human health (Bergen Kommune, 2022). Store Lungegårdsvannet is therefore in an ongoing state of garbage removal and is following a restoration planned for Store Lungegårdsvannet in 2023 by capping polluted sediments with ~30 cm clean sand (Bergen Kommune, 2022). In 2018, inner Puddefjorden was restored, leaving outer Puddefjorden unrestored and Vågen planned for a restoration program to be initiated in 2025 (Figure 2) (Bergen Kommune, 2022).

2.2 Acoustic transmitters and receivers

Acoustic transmitters were used as tags in this study: with a length of 23.2 mm, a diameter of 7.3 mm, a weight of 2.7 g in air and a weight of 1.8 g in water (2LP7-DT, Thelma Biotel AS, Trondheim, Norway). These tags produce sound at 139 dB with a frequency of 69 kHz in intervals between 60 and 120 sec. The tags were equipped with temperature and depth sensors both having their own unique IDs, meaning each tag originally had two ID numbers linked to its data sampling. Signals were then recorded and interpreted by the acoustic receivers: logging ID, timestamps, depth (0-51m) and temperature (0-25 °C). Receivers were used to capture spatial variation and function by registering these factors from an acoustic transmitter when it is within range.

To gather data, 13 hydroacoustic receivers (TBR 700L, Thelma Biotel AS, Trondheim, Norway) were submerged to the bottom at depths from 6.2 m – 38.1 m in and around Store Lungegårdsvannet (*Figure 1*), mounted to the bottom on concrete blocks and recovered by an ROV. Array deployment was done prior to sampling and tagging of the fish. These passive acoustic receivers are battery-operated and were powered for about 16 months. Therefore, batteries were changed, and data downloaded for all the receivers in May 2022. Data was also downloaded in November 2022 in order to increase the amount of data for this specific study.

2.3 Sampling and tagging

In total, 34 individuals of wrasse species (13 corkwing wrasse, 21 ballan wrasse) were caught using wrasse cages stationed in and around Store Lungegårdsvannet. These cages were checked daily, and wrasse species > 200 mm (total length) were internally tagged with acoustic transmitters between 15.06.2021 – 24.06.2021 ($n = 24$) and 13.07.2022 – 29.07.2022 ($n = 10$) in the city centre of Bergen. The total length of the individuals ranged from 200 – 430 mm (mean = 244 ± 59), with an average of 215 ± 14 mm for corkwing wrasse and 258 ± 62 mm for ballan wrasse. All wrasse were visually inspected to ensure enough room for insertion of the tag into the fish's abdominal cavity.

Prior to tagging, the fish were anaesthetised in well oxygenated baths (50L) with 1.5-2.0 mL Aquí S per 10 L water until loss of movement and orientation (mean anaesthetic time: 6.6 min) (Wargo Rub et al., 2014). After close observation of the fish, length measurements (total length) were taken and additional information such as species, damage, temperature, and any comments were noted.

The tagging procedure was done in a V-shaped foam cradle (for smaller individuals) and in a polyvinyl chloride tagging tube (for bigger individuals). To maintain stable anaesthesia and respiration, medicated water (0.75 – 1.00 mL Aquí S per 10L) was pumped continuously over the gills using a silicone tube positioned in the mouth of the fish. For insertion of the tag into the abdominal cavity, a sterile surgical scalpel was used to make a small incision (8-10 mm) on the side of linea alba (posterior to the pectoral fins and anterior to the pelvic fins). After insertion, 1-2 interrupted sutures (Ethicon Vicryl 4-0 polyglactin suture with FS-2 19 mm 3/8c swaged on needle) were made to close the incision (mean surgery time: 3.6 min).

Lastly, the fish were stationed in well oxygenated recovery tanks (50 L, for 3-10 min) to verify normal behaviour and equilibrium orientation before release into the same site or close to capture site at day. During the period of tagging, the water temperature was between 12.5 – 18 °C. The procedure was completed according to all welfare regulations and with permission granted from Norwegian National Animal Research Authority (FOTS ID: 27466).

2.4 Data analysis

Acoustic tracking data from the receivers were then analysed in the statistical program R-studio version 1.4.1717 (R Core Team 2021). Generalized additive models were fitted to understand the depth and temperature use of the two species over the course of > 1 year of tracking and secondly, depth plots were made to extract time of hibernation for each individual.

Before starting analysis of the data, raw data were organized and cleaned to improve data quality. First, relevant data on wrasse from the project were filtered using the *tidyverse* package (Wickham et al. 2019). False detections and any data following the death of an animal were then identified and removed using tools from the *dplyr* package (Wickham et al. 2023). Four individuals died sometime during the study period, and the detections after time of death were removed. To identify death of an individual, depth-detection figures were used. Repeated detections at the same depth across several days indicated that the fish was dead (*Appendix 1, Figure 16*). However, it is important to take into consideration that this could also indicate that the tag was ejected (Smircich & Kelly, 2014). In addition, four individuals showed unusual and unlikely depth behaviour, these detections were also removed from the data (*Appendix 1, Figure 17*)

To analyse the data, models were made and interpreted by visualisation of model predictions. Visualisations of the data were produced with the *ggplot2* package (Wickham 2016), and models illustrated with the *gratia* package (Simpson 2022). The R script including the main code for making figures used in this project can be found in *Appendix 2*. Generalised additive models (GAMs) were used to analyse the data and assembled with *mgcv* package (Wood 2017). Lastly, the Akaike Information Criterion (AIC) was used for model comparison (Akaike 1974). For depth and temperature, three candidate models were tested against each other to choose the best fitted models.

For the study site (Bergen city centre fjord), maps showing where the study was conducted were made using the packages *maps*, *mapdata* and *ggmap* (Kahle & Wickman 2013). In addition, global radiation, precipitation, and wind speed data from the Florida weather station in Bergen (60.3837, 5.3318) were used to test the influence of abiotic factors during the period of the study (Geofysisk institutt, 2023).

2.4.1 Hypothesis 1: Species differences in depth use

To analyse depth use of the two species, the depth detection data were fitted to a generalized additive model (GAM) to investigate potential spatiotemporal relationships between the depth use of the two species (*Model 1.1*). For this model, depth detections were included as the response variable, whereas time of day (denoted as hour) and day of year were included as explanatory variables. Factors fish ID and receiver were also included as random effects, whereas length was included as a fixed effect. For each of the temporal variables (hour and day of year), a smoother (denoted as s ()) was added to fit non-linear patterns over time, as well as “by = species” to fit the smoothers by each species as an interaction (Pedersen et al., 2019). A smoother was also added to the random effects (fish_ID and receiver) to take nestedness and repeated measurements into consideration. Furthermore, k (the level of

wiggleness) was modified to all smoothers involved and bs (smoothing base) was set to account for splines ("cc" for cubic splines and "re" for random effects). Lastly, family was set to Gamma (link="log") due to non-zero positive measurements in depth.

Model 1.1

$$\begin{aligned} \text{depth} \sim & s(\text{hour}, \text{bs} = \text{"cc"}, k = 4, \text{by} = \text{species}) + \\ & s(\text{day_of_year}, \text{bs} = \text{"cc"}, k = 20, \text{by} = \text{species}) + \\ & s(\text{fish_ID}, \text{bs} = \text{"re"}, k = 34) + s(\text{receiver}, \text{bs} = \text{"re"}) + \text{length}, \\ & \text{family} = \text{Gamma}(\text{link} = \text{"log"}) \end{aligned}$$

Abiotic factors (precipitation and wind speed) were also included in a GAM to test for any effect on the depth use for the two species (*Model 1.2*). The same procedures done for *Model 1.1* were repeated for this model. Because this model tested for abiotic factors retrieved from 2021, the day of year was restricted to year 2021 (denoted as day_of_year_2021). For this model, precipitation and wind speed were included as linear effects.

Model 1.2

$$\begin{aligned} \text{depth} \sim & s(\text{hour}, \text{bs} = \text{"cc"}, k = 4, \text{by} = \text{species}) + \\ & s(\text{day_of_year_2021}, \text{bs} = \text{"cc"}, k = 20, \text{by} = \text{species}) + \\ & s(\text{fish_ID}, \text{bs} = \text{"re"}, k = 23) + s(\text{receiver}, \text{bs} = \text{"re"}) + \\ & \text{length} + \text{precipitation} + \text{windspeed}, \\ & \text{family} = \text{Gamma}(\text{link} = \text{"log"}) \end{aligned}$$

2.4.2 Hypothesis 2: Species differences in experienced temperature

To analyse temperature experienced by the two species, the temperature detection data were fitted to a generalized additive model to investigate potential spatiotemporal relationships between temperature of the two species (*Model 2.1*). For this model, temperature detections were included as the response variable, whilst time of day and day of year were included as explanatory variables. Factors fish ID and receiver were also included as random effects, whereas length was included as a fixed effect. For each of the temporal variables (hour and day of year), a smoother was added to fit non-linear patterns over time, as well as "by = species" to fit the smoothers by each species. A smoother was also added to the random effects (fish_ID and receiver) to take nestedness and repeated measurements into consideration. Furthermore, k (the level of wiggleness) was modified to all smoothers involved and bs (smoothing base) was set to account for splines. Lastly, family was set to Gamma (link="log") due to non-zero positive measurements in temperature in the dataset.

Model 2.1

$$\begin{aligned} \text{temperature} \sim & s(\text{hour}, \text{bs} = \text{"cc"}, k = 4, \text{by} = \text{species}) + \\ & s(\text{day_of_year}, \text{bs} = \text{"cc"}, k = 20, \text{by} = \text{species}) + \\ & s(\text{fish_ID}, \text{bs} = \text{"re"}, k = 34) + s(\text{receiver}, \text{bs} = \text{"re"}) + \text{length}, \\ & \text{family} = \text{Gamma}(\text{link} = \text{"log"}) \end{aligned}$$

2.4.3 Hypothesis 3: Species differences in hibernation

To reveal possible hibernation processes, depth detection by each individual throughout a year was plotted to look for a hibernation indicating pattern. The pattern that indicated a hibernation process was established to be downwards migration of a fish to deeper water, followed by continuous positioning at this depth over several days (*Appendix 1, Figure 15*). Death indications of an individual has a similar pattern but can be distinguished by depth detections at nearly the same depth over time, in contrast to some fluctuating detections (and often followed by upwards migration) for hibernation. These depth detection plots were used to further determine start time, end time, and duration for existing hibernation processes. Additionally, three linear models (lm) were made to investigate differences in start time, end time and duration of hibernation for the two species (*Model 3.1, Model 3.2, Model 3.3*). For all three models the summary function was used to evaluate the hypothesis.

Model 3.1

lm (hibernation_start_time ~ species)

Model 3.2

lm (hibernation_end_time ~ species)

Model 3.3

lm (hibernation_duration ~ species)

2.4.4 Hypothesis 4: Species differences in wake-up time

Analysis of individuals' wake-up time was conducted by looking at when (hour) each fish started their daily activity. Times of the first detection for each individual per day (wake-up time) was plotted as points and a line was fitted. This was done to see average wake-up time for each species over some months (June – November), to test for possible differences in daily rhythms. The reason why these months were chosen for this research question, was because a linear pattern inverse correlating with solar radiation was expected to be seen for wake-up time from June to November. Lastly, a linear mixed effect model (lmer) was made to investigate any differences between wake-up time for the two species by day of year (June-November) with fish ID as a random effect (*Model 4.1*). For this model, p-values was used to evaluate the hypothesis.

Model 4.1

lmer (wake_up_time ~ species × day_of_year + (1|fish_ID))

3. Results

Description of tagged wrasse

In total, there were 2 268 661 detections during the study (1 473 335 in 2021 and 795 326 in 2022), provided by the 34 tagged wrasse. Mean detection time for all individuals was six months, equally distributed between the two species (glm: $P = 0.229$, $Z = 1.204$). However, individual differences in detection time varied from a one month to 13 months. Four of the 34 individuals were inferred to have died sometime during the period of study (ID= 4281, 4285, 4351 and 4355), resulting in a one-year minimum mortality rate of 11.76%. Furthermore, unlikely depth behavior was found for four individuals (ID = 4283, 4311, 4341, 4369). Out of these eight individuals, where some detections were excluded, two were ballan wrasse and six were corkwing wrasse. The final sample after removal of both dead and unlikely detections included 1 598 076 detections.

3.1 Hypothesis 1: Species differences in depth use

The two species occupied relatively similar average depths for most months, with an exception during winter (*Figure 3*). For winter months (November – March), ballan wrasse (smoother significance = $P < 0.001$, $F = 3023.9$) were found deeper than corkwing wrasse (smoother significance = $P < 0.001$, $F = 837.2$) (*Figure 3*). Furthermore, ballan wrasse showed a greater depth range than corkwing wrasse during a year (*Figure 3*).

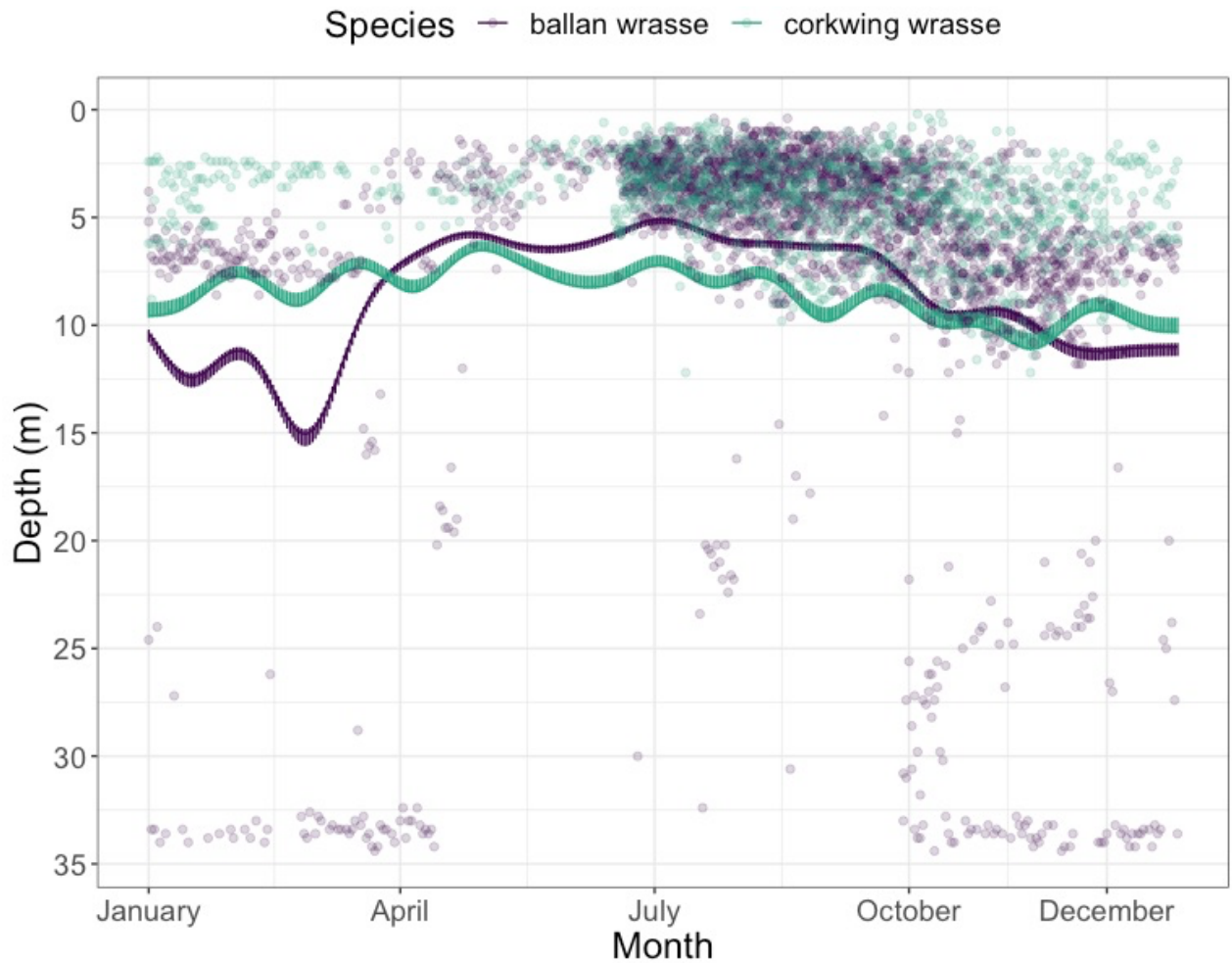


Figure 3: Smooth GAM showing average depth (m) use from all individuals of ballan wrasse (purple) and corkwing wrasse (green) over a year. Upper limit of the line represents the maximum depth and lower limit represents the minimum depth of the individuals. Points represent a selected individual depth detection from each day of the year.

The individual random variation was assessed to be normally distributed according to the qqplot and varied from -0.5 to 0.5 indicating a large between individual variation in average depth (smoother significance = $P < 0.001$, $F = 31341$) (Appendix 1, Figure 19E). Receiver random variation was less normally distributed varying from -0.5 to 1 random effect (smoother significance = $P < 0.001$, $F = 666122$) (Appendix 1, Figure 19F). This random effect was included to account for that wrasse can inhabit different depths at different locations (receivers). Standardized length did not have a significant effect ($P = 0.071$), but average total length was 215 ± 14 mm for corkwing wrasse and 258 ± 62 mm for ballan wrasse (t.test, $H_0: \mu_1 = \mu_2$, $P = 0.006$).

The model including abiotic factors (1.2) revealed no significant effect for precipitation ($P = 0.580$) or wind speed ($P = 0.789$) looking at depth use over a year (2021). The Akaike Information Criterion was also lower for a model including abiotic factors (Model 1.2, AIC: 1 769 640) compared to the model without (Model 1.1, AIC: 2 009 360). There was a difference for ballan wrasse (smoother significance = $P < 0.001$, $F = 770.7$) and corkwing wrasse (smoother significance = $P < 0.001$, $F = 9215.4$) in depth by hour. Ballan wrasse was found shallower at night (10 PM-7 AM) and deeper during day (8 AM-9PM). As a contrast, corkwing wrasse was

found deeper at night (8 PM-6 AM) and shallower during day (7 AM-7PM) (Appendix 1, *Figure 19A and Figure 19B*).

In late July, individual trajectories for ballan wrasse showed active movements in the water column during daytime and less activity in shallower waters at night-time (*Figure 4*, ID 4331 and 4335). Corkwing wrasse seemed to follow the same pattern but at shallower depths (*Figure 4*, ID 4363 and 4371). In early November, the two species showed less activity than in July and were detected at deeper depths at night (*Figure 5*, ID 4337, 4353, 4365, 4367, and 4373).

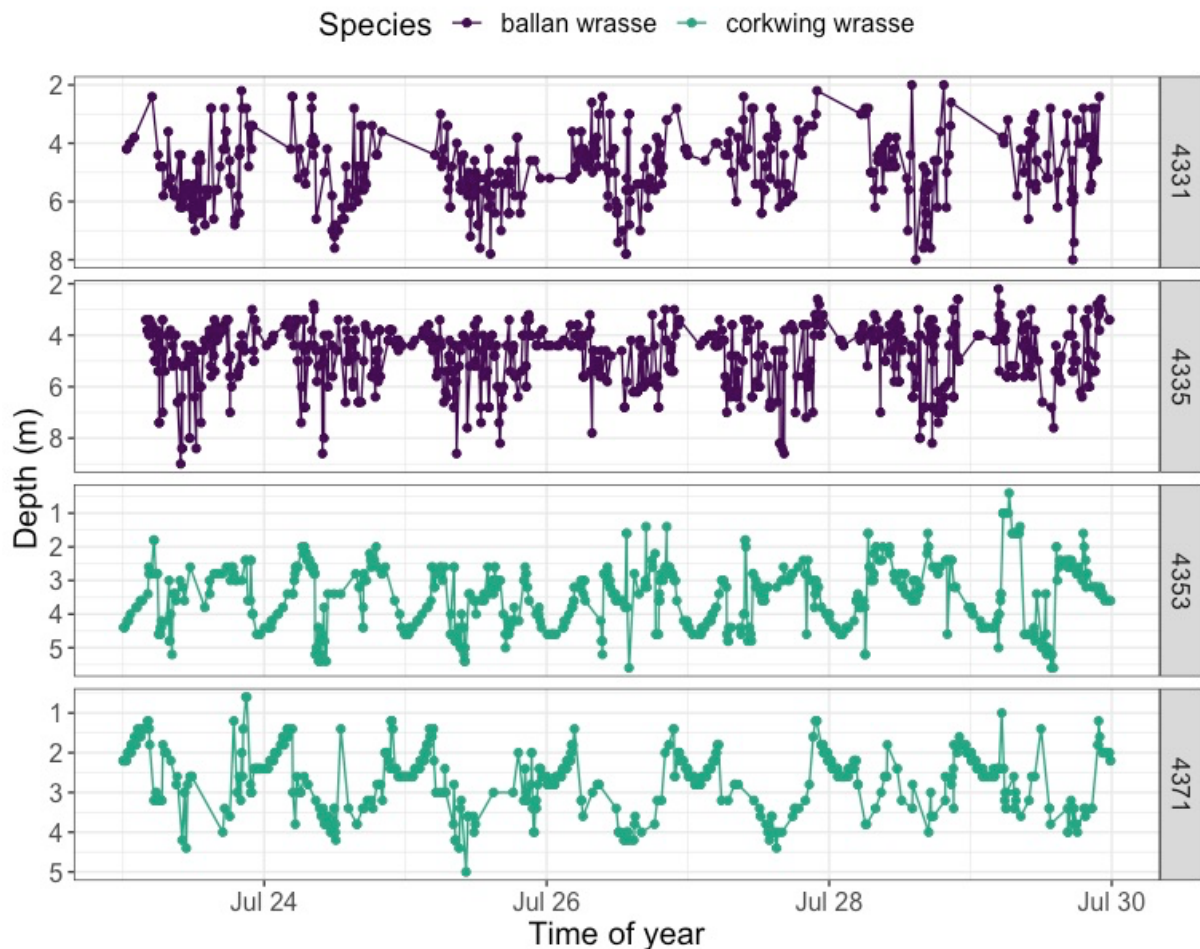


Figure 4: Individual depth (m) use for ID 4331 and 4335 of ballan wrasse (purple) and ID 4353 and 4371 of corkwing wrasse (green) in late July, showing diel depth rhythms.

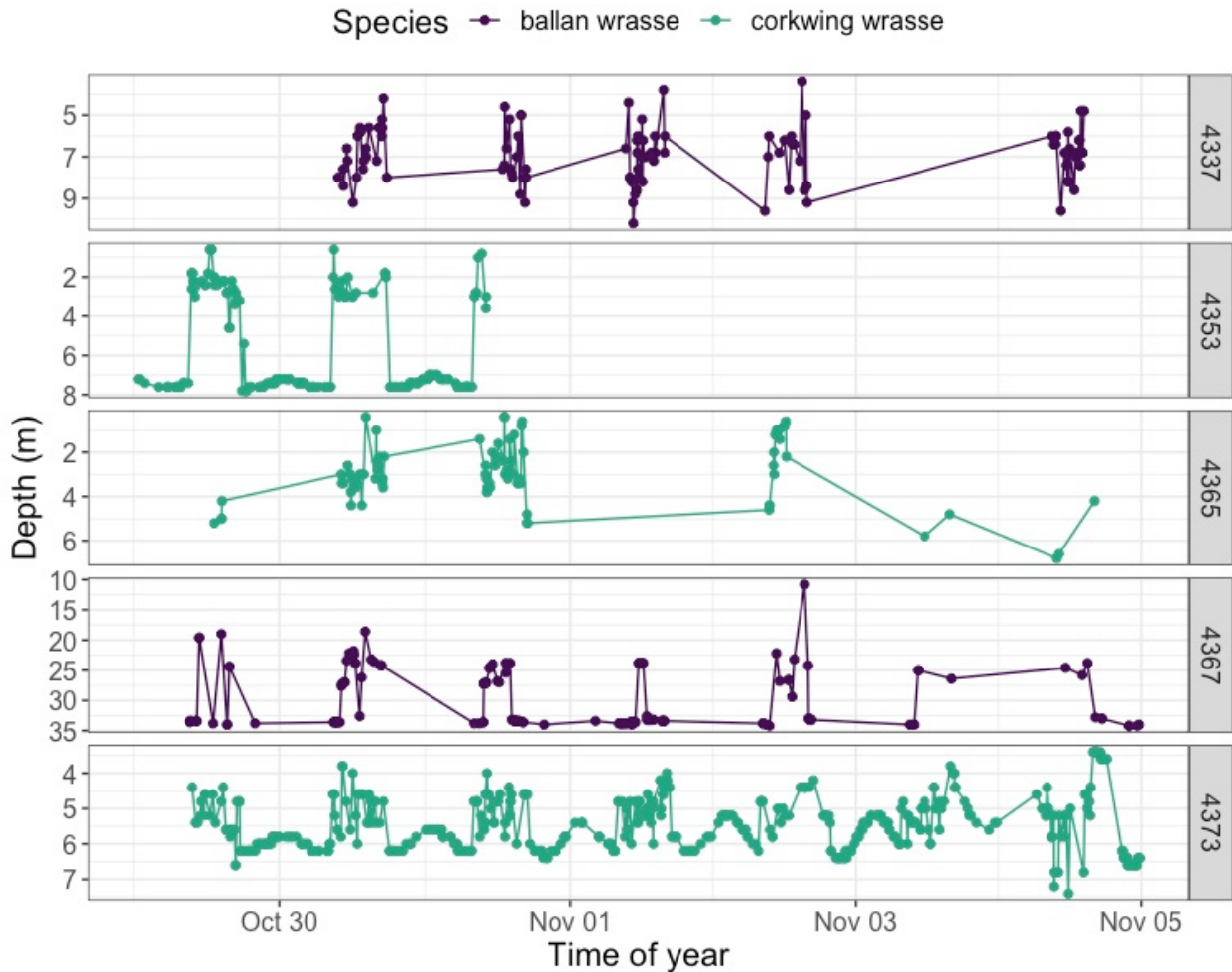


Figure 5: Individual depth (m) use for ID 4337 and 4367 of ballan wrasse (purple) and ID 4353, 4365 and 4373 of corkwing wrasse (green) in early November, showing diel depth rhythms.

3.2 Hypothesis 2: Species differences in experienced temperature

Ballan wrasse (smoother significance = $P < 0.001$, $F = 47439$) and corkwing wrasse (smoother significance = $P < 0.001$, $F = 73274$) experienced small differences in average temperature over a year (Figure 5). During colder months (December (day 340) – May (day 121)) the two species experienced temperatures from ca. 5-10°C. Temperature experienced in warmer months (Late May (day 140) - November (day 310)) ranged from ca. 10-19°C, including some outliers at <5°C (Figure 6).

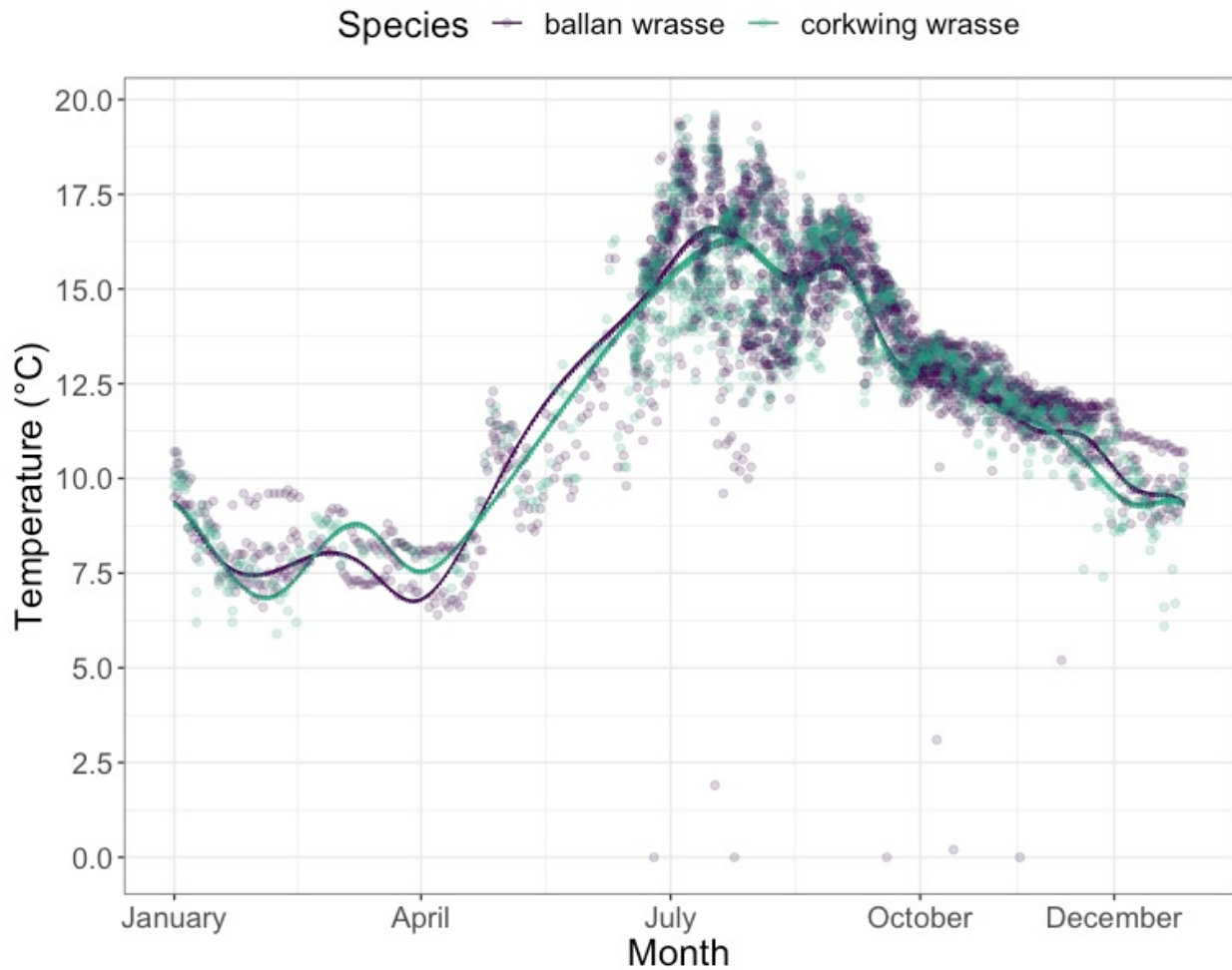


Figure 6: Smooth GAM showing average temperature (°C) experienced by all individuals of ballan wrasse (purple) and corkwing wrasse (green) over a year. Upper limit of the line represents the maximum depth and lower limit represents the minimum depth of the individuals. Points represent a selected individual depth detection from each day of the year.

Temperature for the two species by hour was also similar based on the interaction term in the model. This interaction revealed similar smoother patterns for ballan wrasse (smoother significance = $P < 0.001$, $F = 1336$) and corkwing wrasse (smoother significance = $P < 0.001$, $F = 617$) in temperature use by hour (*Figure 20A and Figure 20B*). Fish ID and receiver were included as random effects in the model. The individual variation was slightly normally distributed varying from -0.1 to 0.2 random effect with some individuals detected at cooler temperatures and some at higher temperatures (smoother significance = $P < 0.001$, $F = 49912$) (*Appendix 1, Figure 20E*). Receiver variation was also slightly normally distributed varying from -0.2 to 0.1 random effect (smoother significance = $P < 0.001$, $F = 537117$) (*Figure 20F*). Standardized length did not have a significant effect ($P = 0.129$).

3.3 Hypothesis 3: Species differences in hibernation

Clear changes in depth behaviour when temperature decreased during winter occurred for many wrasse, both for ballan wrasse and corkwing wrasse. Here, distinct movements to deeper waters were observed and are referred to as hibernation (*Figure 7*). Six individuals stopped being detected during hibernation, clearly illustrated by movements to deeper waters followed by an end of detections after a while (ID= 4277, 4304, 4305, 4331, 4335 and 4343) (*Appendix 1, Figure 18*). In addition, five individuals provided no detections in winter months (inferred hibernation period) with one that reappeared in summer months (ID = 4337, 4345, 4365, 4371 and 4373).

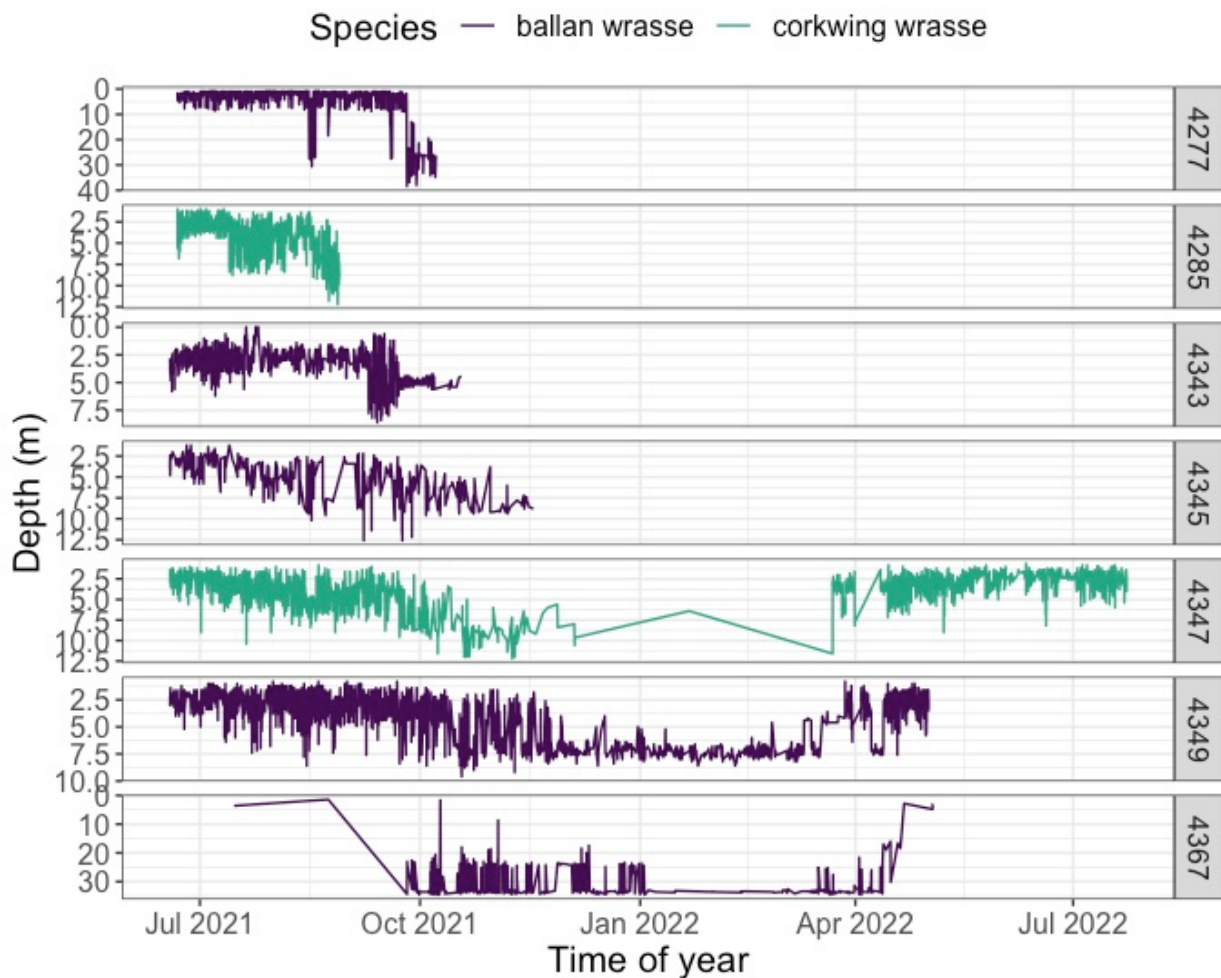


Figure 7: Individuals (ID) depth (m) detection plots for ballan wrasse (purple) and corkwing wrasse (green) over a year showing hibernation processes.

Over the course of the study period (May 2021 – November 2022), ballan wrasse and corkwing wrasse were detected by nearly all and mainly at similar receivers, but at different quantities (*figure 8*). When looking at positions of detections during hibernation, ballan wrasse were observed in Store Lungegårdsvannet, Vågen, and mostly in Puddefjorden (*figure 9*). Corkwing wrasse on the other hand, were observed to hibernate mostly in Store Lungegårdsvannet (*figure 9*).

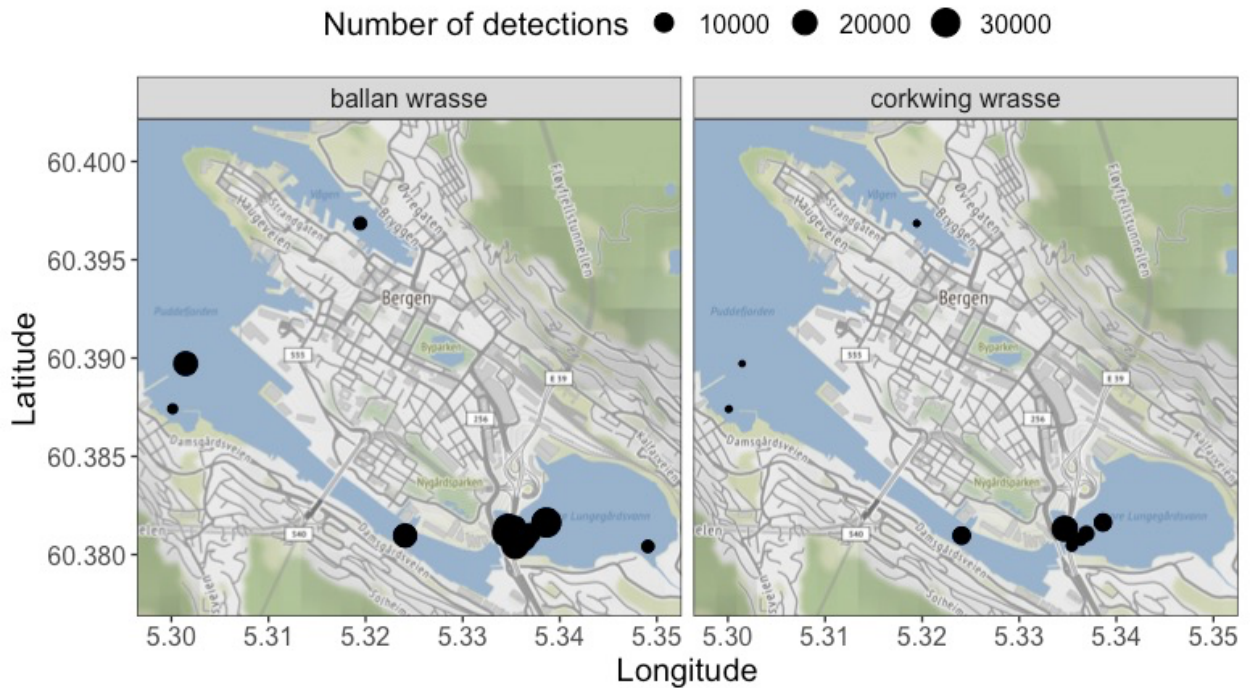


Figure 8: Position of receivers (●) where fish were detected during the study period (May 2021 – November 2022) for ballan wrasse and corkwing wrasse. The size of the black dots shows number of detections.

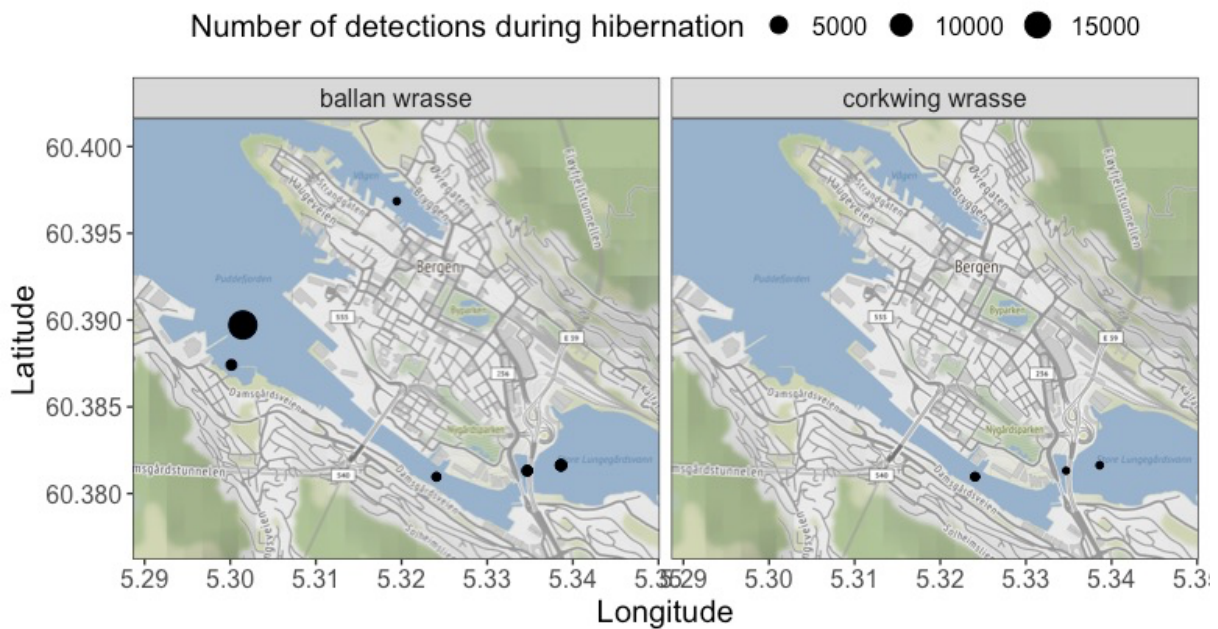


Figure 9: Position of receivers (●) where fish were detected during hibernation for ballan wrasse and corkwing wrasse. The size of the black dots shows number of detections.

For analysis, there were available data on hibernation start time from 18 individuals, where 13 were ballan wrasse and 5 corkwing wrasse (*Figure 10*). Due to lack of detections for some individuals during hibernation, hibernation end time was absent for six individuals. This provides in total hibernation duration for 12 individuals (9 ballan wrasse, 3 corkwing wrasse) (*Figure 11*).

Corkwing wrasse started hibernation in advance of ballan wrasse and exhibited a slightly later end of hibernation (*Figure 10*). However, there was not a significant difference in hibernation start time ($P=0.098$, $t=-1.757$) or hibernation end time ($P=0.691$, $t=-0.409$) between the two species. Hibernation duration was not significantly different for ballan wrasse and corkwing wrasse ($P=0.846$, $t=-0.199$). Therefore, hibernation duration seemed to be similar for the two species (*Figure 11*).

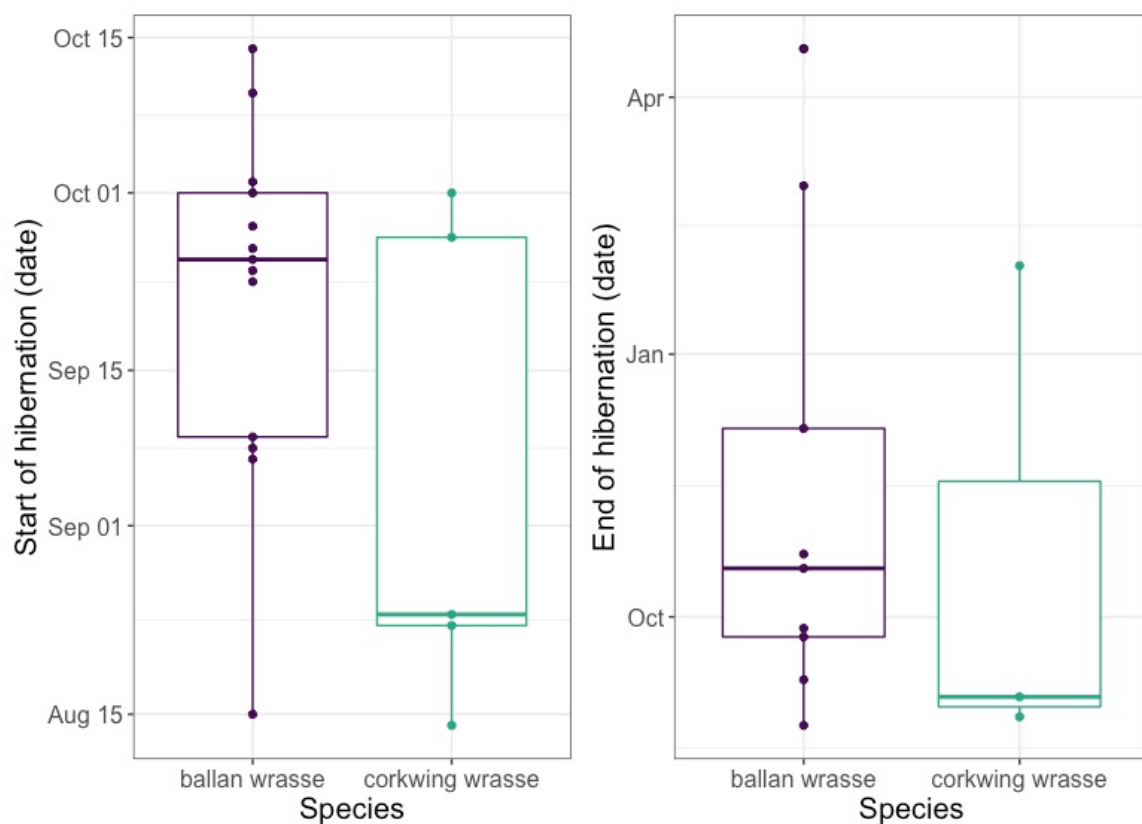


Figure 10: Boxplots showing start and end time of hibernation (date) by species.

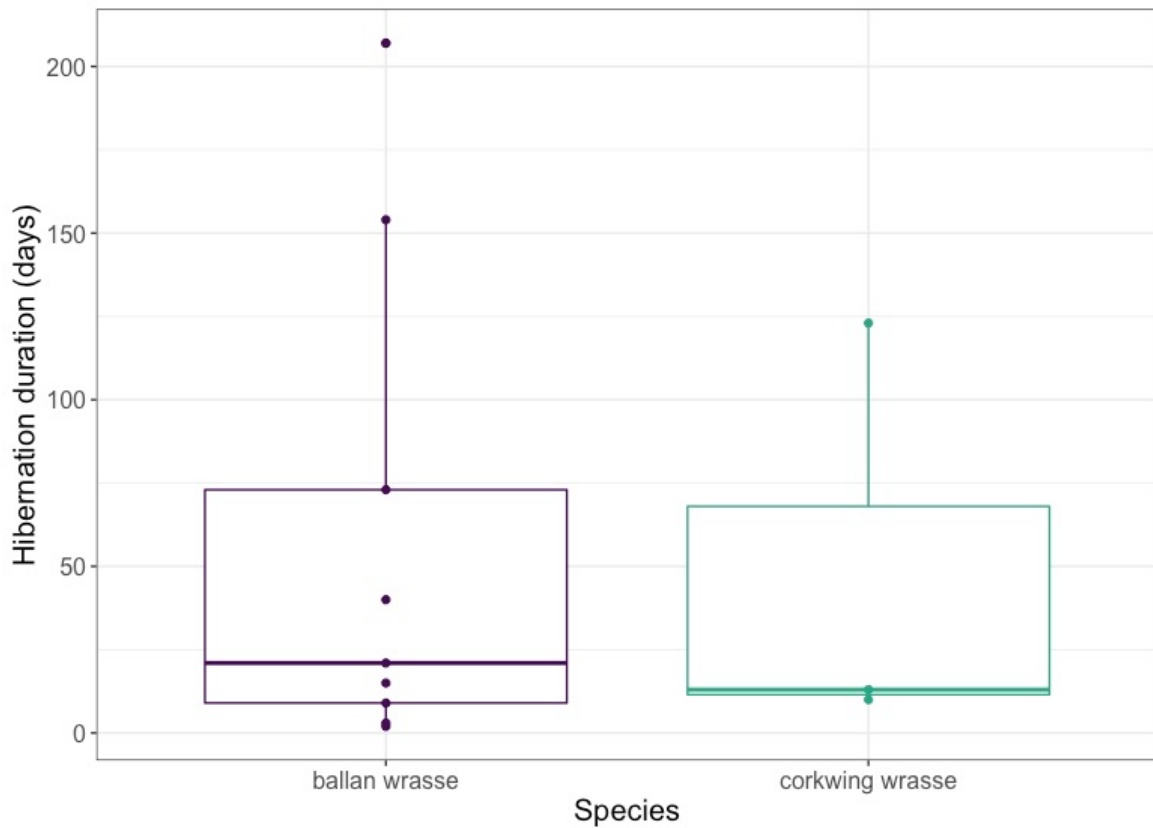


Figure 11: Boxplots showing duration of hibernation (days) for ballan wrasse (purple) and corkwing wrasse (green).

3.4 Hypothesis 4: Species differences in wake-up time

Ballan wrasse appeared to have their first detection of the day (wake-up time) earlier than corkwing wrasse from June 02. to August 09. (summer), whilst corkwing wrasse woke up earlier from August 14. to November 06. (autumn). In between, from August 09. to August 14., species wake-up time overlapped (Figure 12). Ballan wrasse and corkwing wrasse had an increasing trend in wake-up time, meaning a later wake-up time over the year (June – November), where the slope was steeper for ballan wrasse (Figure 12). Wake-up time was significantly different for the two species ($P= 0.001$, $t= 3.362$) and by day of year ($P < 0.001$, $t= 15.660$).

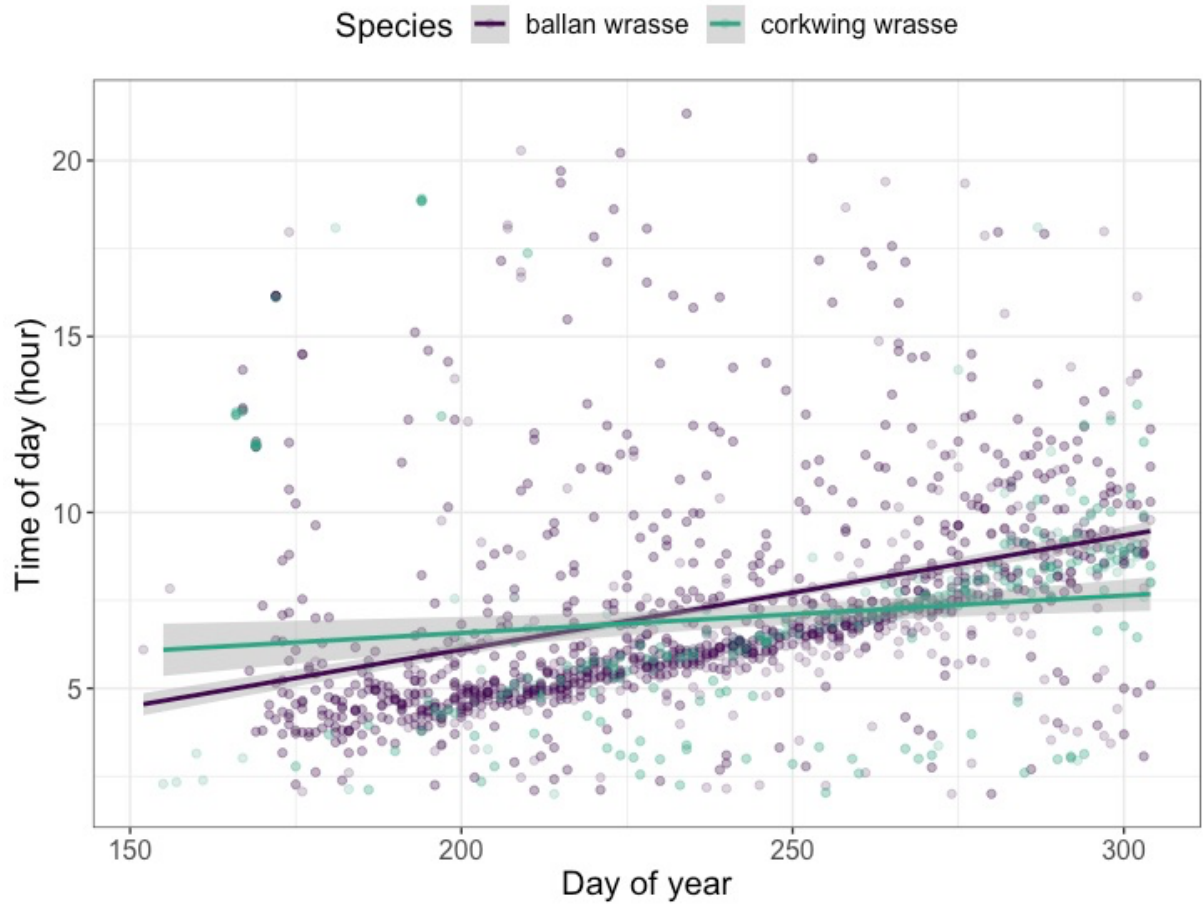


Figure 12: Time (hour) of the first detection of the day for ballan wrasse (purple) and corkwing wrasse (green) over a year (day 150=May 31). Grey area along the curves represents the 95 % confidence interval.

4. Discussion

In this study, the behaviour of ballan wrasse (*Labrus bergylta*) and corkwing wrasse (*Symphodus melops*) was investigated in an urban marine ecosystem with an ongoing and planned restoration by capping polluted sediments with ~30 cm clean sand. The aim of this study was to reveal possible behavioural differences between the two species. I showed that (1) ballan wrasse inhabited deeper depths than corkwing wrasse, that (2) the experienced temperatures of the two species were similar despite differences in depth use, that (3) changes in behaviour when temperature decreased during winter was clearly present for both species, where the two species seemed to hibernate at the same time, and that (4) ballan wrasse started activity earlier than corkwing wrasse during summer and later in autumn. The results support existence of habitat niche differentiation for ballan wrasse and corkwing wrasse, making them differently vulnerable by changes from a restoration process. Additionally, the results reveal how these differences must be considered when designing a restoration project, and how wrasse potentially may be used as bioindicator for pollutants.

4.1 Hypothesis 1: Species differences in depth use

Differences observed between the two species were that ballan wrasse showed a greater depth range than corkwing wrasse during a year, whereas ballan wrasse were found at deeper depths than were corkwing wrasse. This supports the hypothesis of habitat niche differentiation, where these differences promote coexistence of the two species (Davis & Wing, 2012). Here, the two similar fish species living in the same ecosystem seem to partition their behaviour by occupying different depths, resulting in species being limited by different factors such as temperature, predators, and food (MacArthur, 1958). Species that inhabit the same ecological niche can coexist without directly competing with another, by partitioning the available resources within the habitat, even though the species could potentially have a larger realised niche in the absence of the other (MacArthur, 1958). A way to test if this is habitat niche partitioning rather than habitat preference would be an experimental study looking at the depth use of corkwing wrasse in the absence of ballan wrasse (Schoener, 1983). Several previous studies on depth positions for ballan wrasse and corkwing wrasse complement the findings in this present study, where ballan wrasse was found at deeper depths than corkwing wrasse (Halvorsen et al., 2020, 2021; Moen & Svensen, 2020; Rodrigues et al., 2015). Additionally, a study by Rodrigues identified differences in both depth and diet composition for three wrasse species. Here, *S. melops* occurred at shallower depths due to different feeding, explained by interspecific competition (Rodrigues et al., 2015). The differences in depth use revealed in this present study could also be explained by differences in diet composition for ballan wrasse and corkwing wrasse. Another study comparing the diet of these two species found that molluscs and crustaceans were the major prey for ballan wrasse, whereas corkwing wrasse exploited the same food categories but with different emphasis (Deady & Fives, 1995a). Corkwing wrasse are also known to feed on molluscs, hydroids, bryozoans, worms, and various crustaceans, making their diet more varied than ballan wrasse (Quignard & Pras 1986). Together, these detected differences in depth, combined with data about diet for ballan wrasse and corkwing wrasse, support the hypothesis of habitat niche differentiation, making the two species with contrasting behaviour differently impacted by the expected habitat changes from a restoration.

An important aspect to take into consideration for this study is the significant size difference between the two species, where the average total length was 215 ± 14 mm for corkwing wrasse and 258 ± 62 mm for ballan wrasse. This contrast between the length of the two species could have an influence on the depth results due to collinearity between species and size, challenging interpretations of the underlying mechanisms for depth use. Previous research on depth behaviour of wrasse species found that depth distributions were species specific, and that body size (length) was positively correlated with depth (Halvorsen et al., 2020). Hence, the different depth use shown in this present study could also be explained by size differences between sampled ballan wrasse and corkwing wrasse. Previous data from the north-eastern Atlantic and the Mediterranean showed that corkwing wrasse has a maximum standard length of 280 mm (male), whilst ballan wrasse has a maximum total length of 659 mm (male) (Quignard & Pras 1986, IGFA 2001). Accordingly, growth by ballan wrasse could possibly be a way to avoid competition with corkwing wrasse that are limited in their growth. Looking at this from an ultimate perspective, the two species has adapted to different life history strategies where ballan wrasse benefits from growing bigger and spawning later (reach maturity after 6-9 years) whilst the smaller corkwing wrasse benefits from spawning at an earlier age (mature after 1-3 years) (Blanco Gonzalez & de Boer, 2017; Darwall et al., 1992)

Depth use by hour for the two species showed dissimilar patterns where ballan wrasse was detected shallower at night and deeper in the day. As a contrast, corkwing wrasse was found deeper at night and shallower during daytime. Again, this supports the hypothesis of habitat niche differentiation where the two species inhabit different habitats at different times to avoid interspecific competition (Davis & Wing, 2012). The behaviour of ballan wrasse might coincide with diel vertical movement to shallower, warmer water at night to benefit from several factors (Brierley, 2014). A typical influencing factor is foraging opportunities, where fish migrate to shallower waters at night by following their prey. However, ballan wrasse does mainly not feed upon vertically moving prey and are known to rest at night (Deady & Fives, 1995a; Leclercq et al., 2018; Speers-Roesch et al., 2018; Villegas-Ríos et al., 2013). Avoiding predators that hunt by sight is a probable reason as the species are mainly predated by bigger fish such as cod that feed more actively during day (Løkkeborg, 1998; Norin et al., 2021). In this case, their diel vertical movement might have been triggered by changes in light intensity where declining illumination at dusk triggered ascent and increasing illumination at dawn triggered decent to hide from predators (Mehner, 2012). Corkwing wrasse on the other hand showed the opposite depth use by hour. This could also be explained by an ultimate cause where corkwing wrasse has a life history strategy of living shorter but spawning at an earlier age. Ballan wrasse can live up to 29 years, whilst corkwing wrasse lives up to 9 years (Blanco Gonzalez & de Boer, 2017). Here corkwing wrasse, in order to grow faster, seems to take more risk during daytime to feed in the shallower predation risk waters and move to deeper waters at night to rest. However, even though there is deficient research on diurnal activity for corkwing wrasse, these results revealed that their daily depth use differed from ballan wrasse. This again supports dissimilar habitat niche for the two species, resulting in different impacts from changes of a restoration.

Individual trajectories for ballan wrasse showed active movements in the water column during daytime and less activity in shallower waters at night in July. Corkwing wrasse seemed to follow the same pattern but at shallower depths. These results deviate from the results in the depth by hour model, suggesting that individual variation is present. Fish ID and receiver were

included as random effects in the model, and some effects were detected. These random effects are essential to take into consideration, to exclude that the observed differences between the species is in fact explained by interspecific differences and not for instance individual differences. The individual variation was normally distributed with some effects, where individuals were detected at both shallower depths and deeper depths. This is because there were some individual variations between each fish as depth detections varied from 0.6 – 7 m for one individual (ID=4355) and from 0.8 – 39.4 m for another (ID=4277). However, these contrasting depth ranges were detected by a corkwing wrasse and a ballan wrasse, respectively. In this study, corkwing wrasse was detected from 0.2 – 12.4 m, and ballan wrasse from 0.2 – 39.4 m. Therefore, even though effects from individual variation was present, the depth differences are also explained by species variation. Variation was additionally detected for the receivers as they were placed at different depths from 6.2 – 38.1 m, but this is just a spatial aspect not necessarily influencing the depth use of the fish. To summarize, the differences obtained from the data is affected by individual variation, but additionally explained by species variation.

Surprisingly, abiotic factors such as wind speed and precipitation showed no significant effect on depth use for the two species over a year. A previous study on habitat preferences for five wrasse species indicated that wave exposure (caused by for example strong wind speed) affected the vertical distribution of the fish, due to food and shelter availability being influenced by wave exposure (Skiftesvik et al., 2015). In addition, wind speed can create turbulence in the water, mixing different layers of the water column and changing the temperature, oxygen level and nutrient levels. These factors may influence the depth position of fish, making wind speed an important factor to take into consideration. The reason why wind speed showed no effect in this study, is probably because species as a factor showed a stronger effect on depth use. Precipitation was also important to include as it may have influenced the vertical gradient of salinity which could have an effect on the depth position of the fish (Royer, 1979). Here, the same reasoning as for wind speed could explain the missing effect from precipitation on depth use in this study. Therefore, abiotic factors seem to have had a significantly smaller effect on the depth positions of ballan wrasse and corkwing wrasse compared to interspecific differences.

4.2 Hypothesis 2: Species differences in experienced temperature

Interestingly, ballan wrasse and corkwing wrasse experienced only small differences in average temperature during most months and, when comparing their average temperature use over the course of a year, temperature was nearly the same for both species. Even though depth use differed between the species, temperature experienced seemed to remain similar. This similarity is likely to be explained by the relatively small depth range the fish were detected at within Store Lungegårdsvannet and the Bergen city centre fjord (Puddefjorden). Even though small differences might be important, the magnitude was simply not very large. Because the depth detections varied from 0.2 - 39.4 m and the temperatures were the same, a thermocline was not evident as a driver of the fishes' behaviour. This still supports the hypothesis of niche differentiation for ballan wrasse and corkwing wrasse, where similar temperatures in the water column makes it possible for the two species to be at different depths but at the same time fall within or close to their thermal optima to facilitate metabolic

rates needed for foraging and growth (Peat et al., 2016). A previous study looking at physiological performance of ballan wrasse at different temperatures revealed increased aerobic scope in temperatures from 5 to 25°C, and low metabolic rates and inactivity at low temperatures (5–10°C) (Yuen et al., 2019). Research on temperature range for corkwing wrasse is limited, but a decrease in corkwing activity at low temperatures has been described (Deady & Fives, 1995b). For this present study, the two species experienced temperatures from ca. 5-10°C during colder months (December – May), indicating months with less activity. In addition, temperatures experienced during warmer months (late May – November) ranged from ca. 10 - 19 °C, indicating greater activity than for previous months. However, previous studies have found interspecific differences in metabolic rates of several fish species, leaving a potential for dissimilarities in metabolic rates of ballan wrasse and corkwing wrasse (Jerde et al., 2019; Killen et al., 2016). Even though they experienced the same temperatures, metabolic rates could be different resulting in different growth and foraging for the two species which again supports the hypothesis of niche differentiation.

As for depth use, Fish ID and the receiver detecting the fish were also included as random effects in the temperature model, and some effects were detected. Here, the individual variation varied with some individuals detected at lower temperatures and some at higher temperatures. This is because there was some individual variation between each fish as temperature experienced varied from 12.7 – 15 °C for one individual (ID=4369) and 0 – 20.3 °C for another (ID=4357). Regarding temperature, the individual variation is more variable, in contrast to species variation where the species experienced the same temperatures over the year. Meaning that there are individual differences in temperature experienced. Variation was also present for the receivers as they were placed at different depths from 6.2 m – 38.1 m, but this is again just a spatial aspect.

4.3 Hypothesis 3: Species differences in hibernation

The results revealed clear evidence of changes in behaviour when temperature decreased during winter for both ballan wrasse and corkwing wrasse, also suggested to be hibernation in this study. Revealing possible hibernation processes for these two species are advantageous when looking at when ballan wrasse and corkwing wrasse are vulnerable to changes by for example restoration. The reason why the results showed clear changes in behaviour was because several wrasse depth patterns during a year expressed migration to depth at the beginning of winter months together with continuous detections at deeper waters for the ensuing winter months. A previous study also showed hibernation in wrasse species, which was defined by low oxygen consumption rates during the winter by the western Atlantic wrasse, cunner (*Tautoglabrus adspersus*) (Curran, 1992). In addition, several studies conducted on wrasse indicates hibernation for ballan wrasse and corkwing wrasse, a behaviour that is common among labroid fishes in the north (Halvorsen et al., 2021; Mattingsdal et al., 2018; Sayer & Reader, 1996). Another study investigating behavioural patterns for three wrasse species revealed that foraging and resting showed a marked seasonality in the three wrasses where less activity was observed in winter months when temperature dropped (Rodrigues et al., 2015). My results, together with previous research indicate hibernation for wrasse species, both by migrating to deeper waters (from my result) and low activity (previous research) documented during winter. As mentioned, this is

important knowledge about the two species prior to restoration, as sand covering may especially impact the fish in an already vulnerable state.

Both species showed a deeper depth use in winter months, which is likely to be explained by migration to warmer deeper waters during winter to benefit from the temperature when resting (Speers-Roesch et al., 2018). In addition, ballan wrasse was observed to have a deeper average depth use than corkwing wrasse during winter months, when these fish are shown to migrate to deeper water when surface water becomes cold (winter hibernation). A previous study looking at sea temperature effects on depth use revealed a particular evident pattern for ballan wrasse that moved to deeper (warmer) water layers when surface temperature decreased in winter (Freitas et al., 2021). In addition, a study looking at physiological performance of ballan wrasse revealed low metabolic rates and inactivity at low temperatures (5–10°C) (Yuen et al., 2019). Research on physiological performance of corkwing wrasse is limited, but a decrease in activity at cool temperatures has been described. In this prior study, feeding intensity of corkwing wrasse was influenced by the seawater temperature and non-feeding fish were recorded between November and March (Deady & Fives, 1995b). These challenging physiological changes together with a hibernation process can cause even more competition between the two species and may explain why ballan wrasse was especially observed at deeper waters than corkwing wrasse during winter months. In colder waters with less food, resulting in decreasing metabolic rates to preserve energy, winter hibernation is a common life history strategy for survival (Curran, 1992). By occupying different depth during hibernation, the two species avoid competition for space when vulnerable, again supporting habitat niche differentiation.

The study revealed no differences in time or duration of hibernation between the two species. Because of their different life history strategies, a difference in time of hibernation would be expected, where corkwing wrasse started hibernation in advance of ballan wrasse or exhibited hibernation over a longer period. Given that corkwing wrasse is a smaller sized species than ballan wrasse, starting hibernation in advance would be beneficial (Quignard & Pras 1986, IGFA 2001). Looking at this from an ultimate perspective, differences could be explained by ballan wrasse having a life history strategy of growing bigger and living longer, whilst the smaller corkwing wrasse has a life history strategy more limited in growth but compensates by maturing earlier (Darwall et al., 1992). Although start time, end time, and duration of hibernation for the two species was not significantly different, the amount of data on hibernation for ballan wrasse and corkwing wrasse in this study was limited. Further studies on this topic would be useful to obtain more detailed insights into hibernation of wrasse species, for instance in revealing possible differences of winter hibernation that could be applicable for ballan wrasse and corkwing wrasse, causing different periods of vulnerability.

For this project, six individuals stopped being detected during hibernation and five individuals provided no detections during winter months (inferred hibernation period), leaving available data on hibernation start time for 18 individuals (13 ballan wrasse and 5 corkwing wrasse), hibernation end time and duration for 12 individuals (9 ballan wrasse and 3 corkwing wrasse). The reason why this number of individuals stopped being detected during or starting hibernation (in winter months) may be due to migration out of the receiver's detection range. Ballan wrasse detected during hibernation, were observed to be in Store Lungegårdsvannet, Vågen, and mostly in Puddefjorden, resulting in a possibility for migration further out of the

receivers' ranges in Puddefjorden. Corkwing wrasse on the other hand, were observed to hibernate mostly in Store Lungegårdsvannet. Wrasses are especially known to hide both under/between rocks (Leclercq et al., 2018; Rodrigues et al., 2015; Villegas-Ríos et al., 2013), which makes it difficult for the receivers to detect the transmitters. In addition, it is important to note that there is limited hibernation data on corkwing wrasse compared to ballan wrasse producing a more reliable result for ballan wrasse. Moreover, the tags that we used had a power output of 139 dB, relatively low power with a smaller detection range than larger tags that are available for larger fishes. This makes it hard to make conclusions to the results, and further research on this topic would be necessary to reveal hibernation processes.

4.4 Hypothesis 4: Species differences in wake-up time

The two species differed in diel activity patterns where ballan wrasse started activity earlier than corkwing wrasse during summer (June – August) and corkwing wrasse started their daily activity earlier in autumn (August – November). These interspecific differences in wake-up time also supports the hypothesis of niche differentiation for ballan wrasse and corkwing wrasse. Here, the bigger ballan wrasse, in need to forage, seems to start their diel activity earlier during summer when the conditions for foraging are optimal (Yuen et al., 2019). A previous study on growth of corkwing wrasse revealed that periods of increased corkwing growth occurred mostly in autumn (Sayer et al., 1996). Spawning is also an essential factor to account for regarding wake-up time for these first summer months since spawning occurs in spring for both species, with a peak in May for ballan wrasse and a peak in June for corkwing wrasse in Norway (Halvorsen et al., 2017; Muncaster et al., 2010). It is therefore important to take into consideration that these results may have been influenced by sex differences given that males are known to perform parental care for nests during spawning season, potentially influencing their behaviour and therefore wake-up time (Halvorsen et al., 2017). However, these differences in diel behaviour contribute to coexistence where ballan wrasse and corkwing wrasse inhabits different diel rhythms in order to achieve a stable equilibrium, again supporting niche differentiation (MacArthur, 1958). Consequently, changes from a restoration would differentially impact the two species with various diel rhythms.

Ballan wrasse and corkwing wrasse had an increasing trend in wake-up time, meaning a later wake-up time during the year (June – November), where the slope was steeper for ballan wrasse. These observed increasing patterns in wake-up time from June to November is most likely connected to a decrease in light from summer to winter, influencing the time when they start activity (*Appendix 1, Figure 21*).

4.5 Methodological issues and limitations

When working with acoustic telemetry, applied to a fish habitat study, there are some key challenges and considerations that should not be overlooked (Brownscombe et al., 2022). Firstly, there is a risk using acoustic telemetry by interfering with the fish during catching, anesthesia, surgery, and release as these processes may influence the fish by stress and reduced fitness. In addition, tagging of fish may alter their behaviour (Cooke et al., 2010), but there are several studies that reveal insignificant effects on the behaviour of tagged fish (Hondorp et al., 2015; Hubbard et al., 2020). Hence, the behaviour of the tagged wrasse in this study is to be expected of the behaviour of non-tagged wrasse.

Secondly, another important aspect to take into consideration, is the bias that can arise with the small number of individuals studied ($n=34$), relatively to the population size. This may cause biases in the data, especially since a particular sampling technique was used (traps with bait) that targets a specific behavioural type such as foraging (Brownscombe et al., 2022). It is also important to find a balance between removing a large amount of the data and including false detections that contributes to inaccurate information. For this study, 13 corkwing wrasse and 21 ballan wrasse were studied. In addition, 6 corkwing wrasse and 2 ballan wrasse died, which means that there was in total full data on 7 corkwing wrasse and 19 ballan wrasse creating skewness and more reliable data for ballan wrasse than corkwing wrasse. Furthermore, unusual observations were detected in the tails (winter months), which is most likely to be explained by a small amount of data from this period because of resting and little activity giving few detections by the receivers.

Lastly, acoustic interference caused by sources like wind, tides and bypassing boats (especially relevant in this urban ocean) influence the range of receivers (Mathies et al., 2014). Disturbance was therefore considered while constructing the receiver array, and receivers were mostly placed in more sheltered and undisturbed areas in Store Lungegårdsvannet and Puddefjorden. However, it is difficult to steer clear of disturbance on the range of the receivers, especially when working in a human impacted fjord, influencing part of the results when working with acoustic telemetry.

4.6 Future considerations and improvements

In order to maximize the outcome of future studies, there are a few things that could be considered. Firstly, by including more species or/and individuals would be interesting, to look at a broader group of species and to get results closer to reality by increasing the number of individuals studied. In addition, by looking at the same individuals for a longer time period, potentially with fewer pings per hour or larger battery for transmitters, resulting in more data to analyse and interpret. Secondly, it could have been relevant to look at diet compositions as well, for comparison of the two species in accordance with depth use. This is difficult to include because acoustic telemetry builds upon studying living animals, but taking stable isotopes samples from the individuals could be a way of reconstructing diet information (Peterson & Fry, 2003). Lastly, another important factor that would have been ideally to include is sex, to exclude gender differences such as different behaviours (males perform parental care for nests during spawning season (Halvorsen et al., 2017)).

4.7 Management implications

These two species are occasionally treated as the same species by fisheries management, but with possible interspecific differences, revealed in the results, they might be differentially impacted by physical restoration (Blanco Gonzalez & de Boer, 2017). This accounts for different measures regarding restoration because any changes that are favourable for one of the two species would potentially disturb a balanced ecosystem. A previous study revealed that undergoing restoration efforts for local species could be informed by detailed characterization of niche partitioning (Raby et al., 2020). Furthermore, research on species living in urban ecosystems are important for understanding anthropogenic influences and to predict the outcome of anthropogenic changes.

The results also revealed that ballan wrasse and corkwing wrasse were detected by nearly all receivers stationed in Store Lungegårdsvannet, inner Puddefjorden, outer Puddefjorden and Vågen, which is a contrast to previous studies stating stationarity and a small home range in wrasse species (Villegas-Ríos et al., 2013). This could influence the effect and success of the restoration process in Store Lungegårdsvannet by wrasse species moving in and out of Store Lungegårdsvannet. Consequently, bringing pollutants from outer Puddefjorden and Vågen (not restored) into inner Puddefjorden (restored) and Store Lungegårdsvannet (soon to be restored) (Bergen Kommune, 2022). Hence, the spatial use of these species needs to be considered when interpreting data from studies using them as bioindicators for pollutants.

The clear existence of changes in behaviour for ballan wrasse and corkwing wrasse during winter, revealed in this study, is also important to take into consideration when planning restoration. Knowledge on time of winter hibernation provides important management information on when wrasses are most vulnerable to changes. Here they spend their time on the bottom resting, and a by covering the seafloor with masses could fatally influence the wrasse. A paper on applications of telemetry to fish habitat science and management, stated that the robust data that telemetry enables to provide should have an increasing role in fish habitat decision making. This information on habitat use is essential to assess how potential anthropogenic changes may affect established ecosystems (Brownscombe et al., 2022). In addition, this study also revealed that multispecies acoustic telemetry approaches has been effective in evaluating fish habitat restoration (Brownscombe et al., 2022).

5. Conclusion

The aim of this study was to understand the behavior of ballan wrasse (*Labrus bergylta*) and corkwing wrasse (*Symphodus melops*) in an urban marine ecosystem with an ongoing and planned restoration, possibly revealing habitat differentiation for the two species. This study discovered that ballan wrasse inhabited deeper depths than corkwing wrasse, especially during winter months. However, the experienced temperatures of the two species were similar despite differences in depth use. Additionally, clear changes in behavior when temperature decreased during winter was present for both species suggesting hibernation. During hibernation, sand covering may especially impact the fish in an already vulnerable state. Therefore, avoidance of restoration during winter would be advisable. Additionally, the two species showed less activity at night-time, suggesting that the action of sand covering should not take place at this time. Interspecific differences in behavior revealed in this study support existence of habitat niche differentiation for ballan wrasse and corkwing wrasse, making them differentially impacted by changes from a restoration process. In conclusion, this type of study will be beneficial by providing knowledge prior to restoration. However, further research on the behavior of ballan wrasse and corkwing wrasse would be useful for this restoration project, by looking at the species behavior post restoration in comparison to these results and evaluate whether there have been changes to the behavior following the changes made to their habitats in the urban fjord.

6. References

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7. Appendices

Appendix 1.

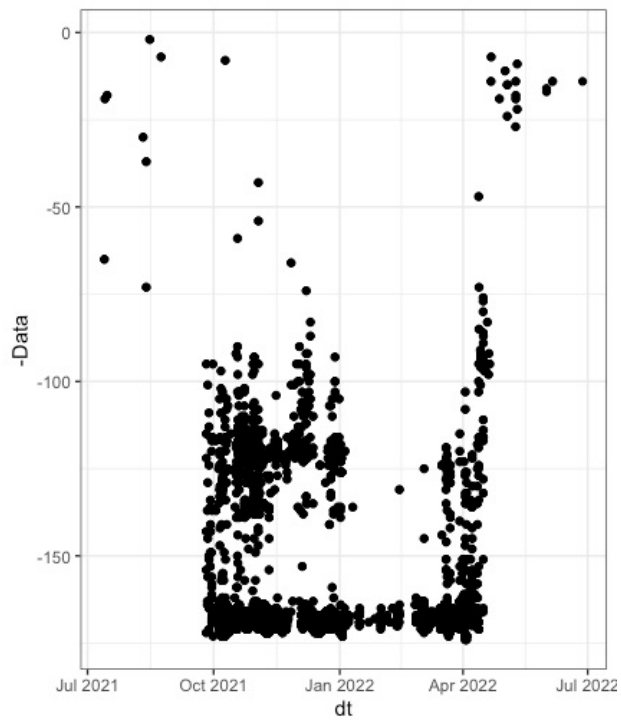


Figure 15: Depth detection plot (ID=4367) showing indication of hibernation (October-March)

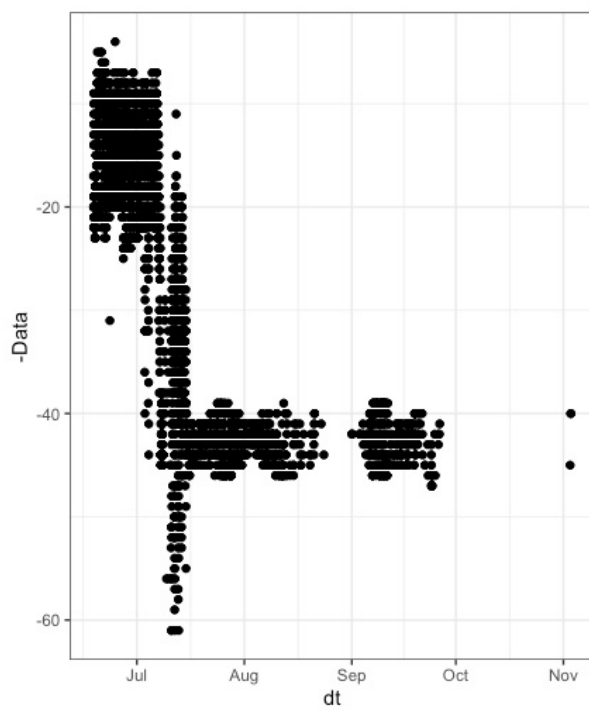


Figure 16: Depth detection plot (ID=4351) showing indication of death (mid-July)

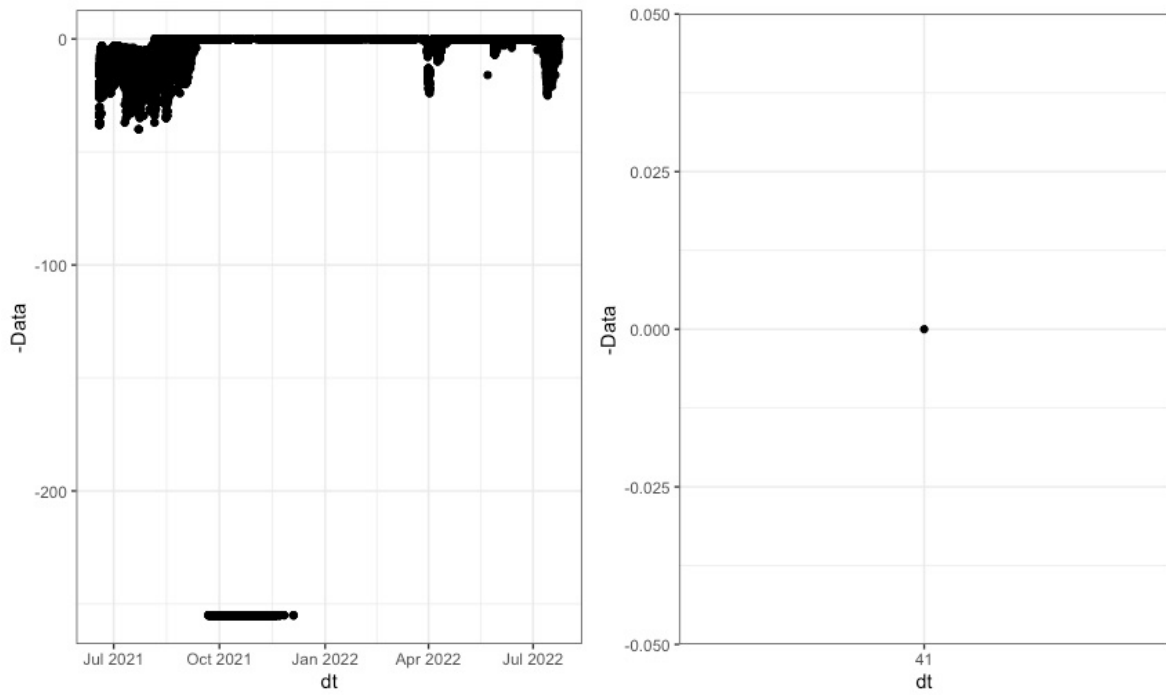


Figure 17: Depth detection plot showing unusual detections, where ID=4341 (left) is detected at two depths at the same time and ID=4283 (right) has only one detection at an unlikely depth.

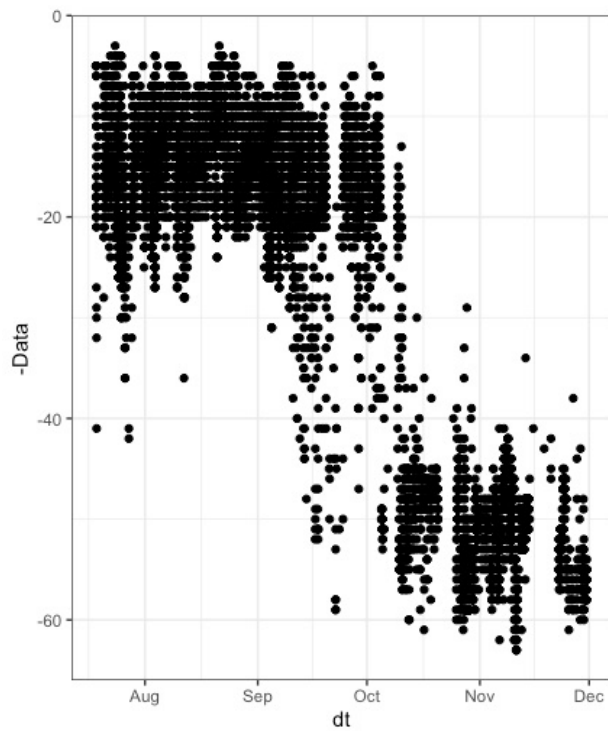


Figure 18: Depth detection plot (oid=4305) indicating disappearance during hibernation.

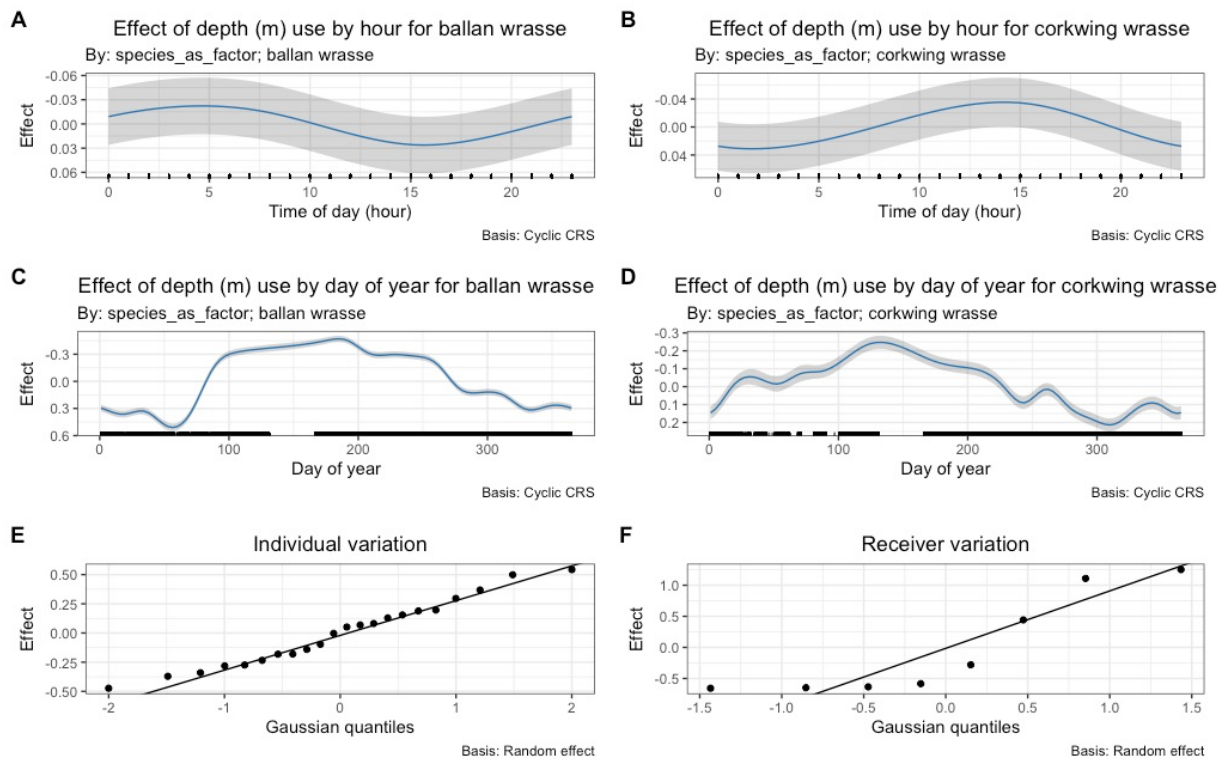


Figure 19: Smooth GAM output on depth use for ballan wrasse by hour (A) and corkwing wrasse by hour (B) (0=12:00 am) and over a year (1=1. January) for ballan wrasse (C) and corkwing wrasse (D). Including factors: fish ID (E) and receiver (F) as random effects. Grey area along the curves represents the 95 % confidence interval.

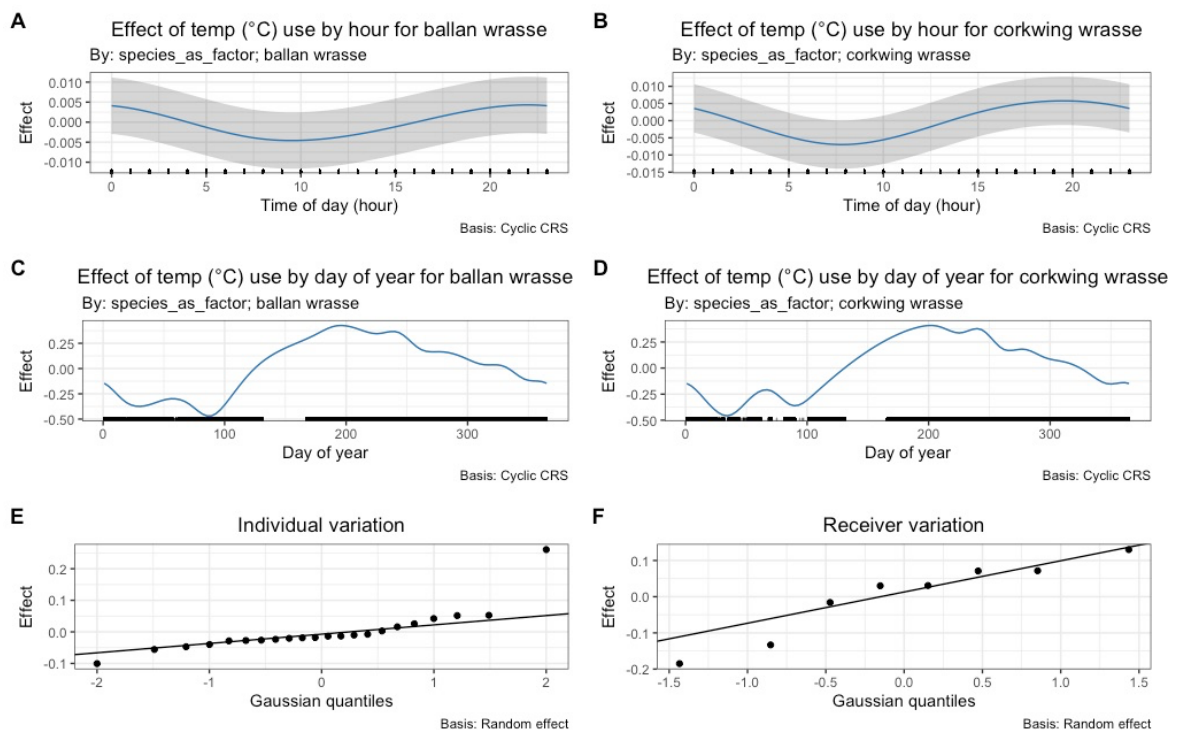


Figure 20: Smooth GAM output on temperature experienced for ballan wrasse by hour (A) and corkwing wrasse by hour (B) (0=12:00 am) and over a year (1=1. January) for ballan wrasse (C) and corkwing wrasse (D). Including factors: fish ID (E) and receiver (F) as random effects. Grey area along the curves represents the 95 % confidence interval.

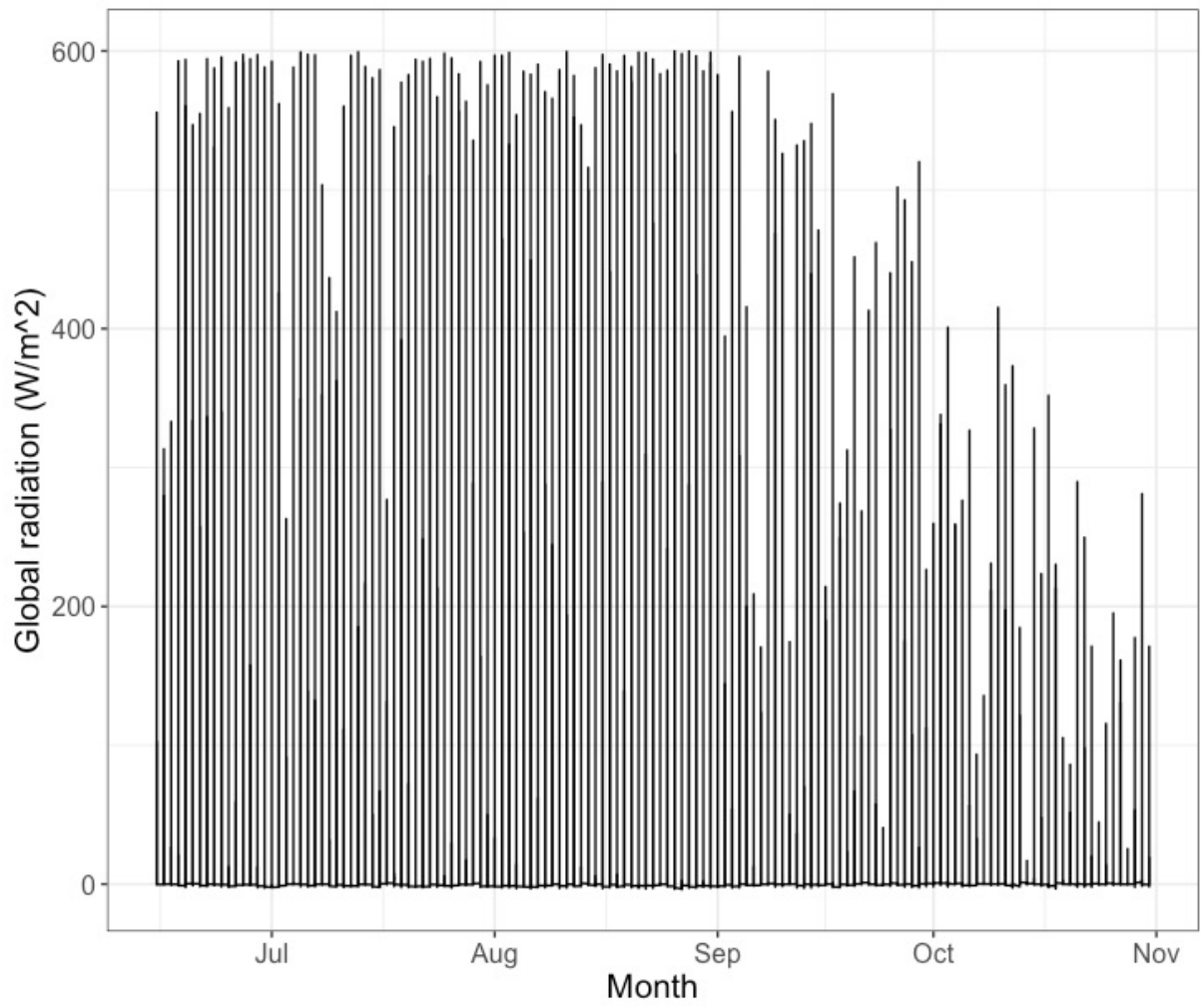


Figure 21: Global radiation (W/m^2) from late June to November at Florida meteo station in Bergen.

Appendix 2

This appendix include the main code for making my figures, not including the code for filtering and creating data frames.

```
##### Reading in data #####

boats_data <- readRDS("boats.RDS")
wrasse_data <- boats_data |>
  filter(species %in% c("ballan wrasse", "corkwing wrasse"))

id_details <- read_excel("wrasse_individuals_details.xlsx")

wrasse_data <- merge(wrasse_data, id_details, by = "id")

##### Figure 1 #####
#### Norway map

norway <- map_data(database="worldHires", regions="Norway", resolution=0, type="n")

map_norway <- ggplot() +
  coord_quickmap(xlim=c(5, 30), ylim=c(57.5, 72.5)) +
  geom_polygon(data=norway, aes(x=long, y=lat, group=group), fill="grey", colour="black",
lwd=0.2) +
  annotate("text", x=11, y=63, label="N O R W A Y", fontface=2, colour="black", size=5,
angle=65) +
  geom_point(aes(x=5.3, y=60.4), shape = 22, size=5, colour="blue", stroke=1.5,) +
  theme_classic(base_size=20) +
  labs(x="Longitude", y="Latitude") +
  annotate("text", x=9.2, y=60.3, label="Bergen", fontface=2, colour="blue", size=3)

#### Bergen map

wrasse_data_map <- wrasse_data |>
  distinct(Receiver, lat, lon)

bergen_map_background <- get_map(location = bergen_bbox, source = "google", maptype =
"terrain", zoom = 14)

bergen_map <- ggmap(bergen_map_background) +
  geom_point(data = wrasse_data_map, mapping = aes(x = lon, y = lat), size = 3) +
  labs(y = "Latitude", x = "Longitude")
  ylim(c(60.378, 60.401)) +
  xlim(c(5.299, 5.35)) +
  scale_colour_grey(end = 0.5)
```

Figure 3

```
ggplot(aes(day_of_year, depth, colour=species))+  
geom_line()+  
scale_x_continuous(breaks = c(1, 90, 180, 270, 340), labels = c("January", "April", "July",  
"October", "December")) +  
scale_y_reverse(n.breaks=10) +  
theme(text = element_text(size = 17)) +  
theme(legend.position = "top") +  
scale_color_viridis_d(end = 0.6) +  
labs(y="Depth (m)", x="Month", colour="Species") +  
geom_point(data=wrasse_data |>  
  group_by(id, date |>  
    slice_sample(n=1),  
  aes(day_of_year, depth, colour=species),  
  alpha=0.2)
```

Figure 4

```
wrasse_data |>  
filter(id == c(4331, 4335, 4353, 4371)) |>  
filter(week == 30) |>  
ggplot(aes(day_of_year, depth, colour = species)) +  
geom_point() +  
geom_line() +  
scale_y_reverse() +  
labs(y="Depth (m)", x="Time of year", colour="Species") +  
scale_color_viridis_d(end = 0.6) +  
facet_grid(rows = vars(id), scales="free") +  
theme(legend.position = "top") +  
theme(text = element_text(size = 15))
```

Figure 5

```
wrasse_data |>  
filter(id == c(4337, 4367, 4365, 4373, 4353)) |>  
filter(week == 44) |>  
ggplot(aes(day_of_year, depth, colour = species)) +  
geom_point() +  
geom_line() +  
scale_y_reverse() +  
labs(y="Depth (m)", x="Time of year", colour="Species") +  
scale_color_viridis_d(end = 0.6) +  
facet_grid(rows = vars(oid), scales="free") +  
theme(legend.position = "top") +  
theme(text = element_text(size = 15))
```

```
##### Figure 6 #####
```

```
ggplot(aes(day_of_year, temperature, colour=species))+  
  geom_line()+  
  scale_x_continuous(breaks = c(1, 90, 180, 270, 340), labels = c("January", "April", "July",  
"October", "December")) +  
  scale_y_continuous(n.breaks=10) +  
  labs(y="Temperature (°C)", x="Month", colour="Species") +  
  theme(text = element_text(size = 17)) +  
  theme(legend.position = "top") +  
  scale_color_viridis_d(end = 0.6) +  
  geom_point(data=wrasse_data |>  
    group_by(id, day_of_year |>  
      slice_sample(n=1),  
    aes(day_of_year, temperature, colour=species),  
    alpha=0.2)
```

```
##### Figure 7 #####
```

```
wrasse_data |>  
  filter(id==c(4277, 4285, 4343, 4345, 4367, 4347, 4349)) |>  
  ggplot(aes(day_of_year, depth)) +  
  geom_line(aes(colour =species)) +  
  scale_y_reverse() +  
  scale_color_viridis_d(end = 0.6) +  
  facet_grid(rows = vars(id), scales = "free") +  
  labs(x = "Time of year", y = "Depth (m)", colour = "Species") +  
  theme(legend.position = "top") +  
  theme(text = element_text(size = 15))
```

```
##### Figure 8 #####
```

```
bergen_map_detections <- ggmap(bergen_map_background) +  
  geom_point(data = wrasse_data, mapping = aes(x=lon, y=lat, size = n)) +  
  facet_wrap(~species) +  
  ylim(c(60.378, 60.401)) +  
  xlim(c(5.299, 5.35)) +  
  labs(y = "Latitude", x = "Longitude", size = "Number of detections") +  
  theme(legend.position = "top") +  
  theme(text = element_text(size = 15))
```

```
##### Figure 9 #####
```

```
wrasse_data_hibernation_detections <- wrasse_data |>  
  filter(dti>hibernation_start_time) |>  
  filter(dti<hibernation_end_time) |>  
  group_by(id, species, lon, lat) |>
```

```
count()
```

```
bergen_map_detections_hibernation<- ggmap(bergen_map_background) +  
  geom_point(data = wrasse_data_hibernation_detections, mapping = aes(x=lon, y=lat, size =  
n)) + facet_wrap(~species) +  
  ylim(c(60.378, 60.401)) +  
  xlim(c(5.299, 5.35)) +  
  labs(y = "Latitude", x = "Longitude", size = "Number of detections during hibernation") +  
  theme(legend.position = "top") +  
  theme(text = element_text(size = 15))
```

```
##### Figure 10 #####
```

```
start_time <- id_details |>  
  filter(hibernation_start_time) |>  
  ggplot(aes(species, hibernation_start_time, colour = species)) +  
  geom_boxplot() +  
  geom_point() +  
  scale_color_viridis_d(end = 0.6) +  
  labs(x = "Species", y = "Start of hibernation (date)") +  
  theme(legend.position = "none") +  
  theme(text = element_text(size = 15))
```

```
end_time <- id_details |>  
  filter(hibernation_end_time) |>  
  ggplot(aes(species, hibernation_end_time, colour = species)) +  
  geom_boxplot() +  
  geom_point() +  
  scale_color_viridis_d(end = 0.6) +  
  labs(x = "Species", y = "End of hibernation (date)") +  
  theme(legend.position = "none") +  
  theme(text = element_text(size = 15))
```

```
grid.arrange(start_time, end_time, nrow=1)
```

```
##### Figure 11 #####
```

```
id_details |>  
  filter(hibernation_duration) |>  
  ggplot(aes(species, hibernation_duration, colour = species)) +  
  geom_boxplot() +  
  geom_point() +  
  scale_color_viridis_d(end = 0.6) +  
  labs(x = "Species", y = "Hibernation duration (days)") +  
  theme(legend.position = "none") +  
  theme(text = element_text(size = 15))
```



```
##### Figure 12 #####
```

```
wake_up <- wrasse_data |>  
  ggplot(mapping = aes(day_of_year, hour, colour=species))+  
  geom_point(alpha=0.2) +  
  geom_smooth(method = "lm") +  
  scale_color_viridis_d(end = 0.6) +  
  labs(x = "Day of year", y = "Time of day (hour)", colour = "Species") +  
  theme(legend.position = "top") +  
  theme(text = element_text(size = 15))
```