

Sex-dependent natural survival and catchability in corkwing wrasse (*Symphodus melops*)

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Abstract

Corkwing wrasse (*Symphodus melops*) are along with three other temperate species of wrasse extensively harvested along the Norwegian coast due to their ability to restrict sea-lice infections in commercial fish farming. Concerns from the scientific community have been raised regarding the wrasse fisheries long-term sustainability and its effects on natural populations. Corkwing, which is one of the most exploited wrasse species in Norway display complex life history characteristics including nest building and parental care of eggs by territorial males, female choice, and primary males which expresses sneaker behaviour. Although much research on corkwing have been done, knowledge regarding their natural survival pattern is still lacking.

Based on 4 years of mark-recapture data collected from a marine protected area (MPA), I used capture-mark-recapture (CMR) models to investigate the natural survival pattern of corkwing. A total of 3820 individuals were tagged over 10 sampling occasions and 567 individuals were recaptured. I used a time-dependant Cormac Jolly Seber-model (CJS) to estimate monthly apparent survival and capture probability for territorial males, females and sneaker males (apparent and not the true survival is estimated from the CJS-model due to an unknown factor of migration). My results show a seasonal trend in corkwings natural survival pattern with high survival rates over the winter, decreasing rates in the spring (spawning period) and even lower rates during the summer (main feeding period). Intra-sexual differences were also found where territorial males had an overall lower survival rate compared to females and sneakers. The largest difference was during the summer, suggesting an elevated mortality cost for territorial males through increased predation risk in relation to movement and feeding post spawning. Territorial males were also estimated to have a lower apparent survival during the spawning period, likely due to a mortality cost through male-male competition. The capture probability of corkwing was found to be low with minor intra-sexual and seasonal differences. The overall low estimates suggests that the study population is large and dense.

The wrasse fishery is size- and sex-selective and tend to target large territorial males at higher rates. The selective harvest is likely to impact natural populations through altered sex-ratios and removal of high-quality males. Further research regarding fishery-induced impacts, implementing seasonal and intra-sexual differences in survival pattern, is therefore needed.

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This thesis is written as a contributing part in a larger project organized and funded by the Institute of Marine Research (IMR) in order to study the Norwegian wrasses. The aim for the project was to study population dynamics and life history strategies. I am very grateful to have been a part of this project.

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1 Introduction

Anthropogenic activities impose increasing pressure on populations of wild animals and ecosystems world-wide. Monitoring population dynamics of key species is therefore important to set management goals and conservation measures to ensure future sustainability. Population dynamics describes the abundance with gains and losses to a population over time and takes into account demographic parameters such as recruitment (births), mortality (deaths) and migration (Ranta et al., 2005).

A natural population of animals is complex and consists of individuals of different sizes, ages, sexes and morphologies. Survival is likely to be dependant of physical and behavioural variations between such groups (Lebreton et al., 1992). Much intra-specific variation which in turn can affect survival is connected to reproduction and reproductive behaviour. Sexually selected traits provide a mating advantage to the bearer, but also comes with an underlying viability cost through natural selection (Promislow et al., 1992). Mating competition often result in higher rates of natural mortality which is the case for a large variety of mammal taxa where natural mortality is male-biased much due to male-male competition (Promislow, 1992, Shuster and Wade, 2019). Female survival often depends on reproductive investment, and this cost of reproduction is suggested as the main factor leading to the observed female-biased mortality for monogamous mammal taxa (Promislow, 1992). Elevated rates of mortality in the largest sex for sexual dimorphic species is evident but not always the case. From a comparative study on 28 passerine birds with larger sexual dimorphic males with brighter colouration, 21 of the examined species showed that female mortality was higher than male (Promislow et al., 1992). Males however, had a mortality rate positively correlated with sexual size dimorphism, which suggest a cost from male-male competition. Sexual dimorphism in coloration may also increase mortality by greater attraction from predators to more colourful individuals (Godin and McDonough, 2003). Other traits connected to reproduction and reproductive behaviour that may cause variation in survival between sexes is parental care and protection of territories. From a comparative study of 37 species of western Palearctic birds, it was shown that parental care of eggs and juveniles had a direct mortality cost for the provider, and that feeding and defence was more costly than nest building and incubation of eggs (Owens and Bennett, 1994). Complex life histories are evident in the

marine environment as well as the terrestrial (Parker, 1992). Fish can have extraordinary and diverse mating systems (Wheeler, 1969, Wootton, 2012). One family of fish in which complex mating systems are evident are the wrasses (*Labridae*). Reproduction involving nest building, holding of territories and parental care of eggs and juveniles are not uncommon for the wrasses (Darwall et al., 1992).

Fish behaviour and life history is strongly influenced by seasonal environmental changes (Wootton, 2012). Usual adaptations for coastal fish occupying high latitude are feeding and reproduction associated with distinct time-periods (McBride et al., 2015, Houston et al., 2007, Villegas-Ríos et al., 2014). A trade off in the use of acquired energy between structural growth and energy storage to increase winter survival is also evident (Giacomini and Shuter, 2013). Fish behaviour is largely influenced by their life-history strategy, especially when it comes to energy allocation and reproductive strategy (McBride et al., 2015). A variety of pelagic fish species such as the Atlantic blue fin tuna (*Thunnus thynnus*), the Norwegian spring-spawning herring (*Clupea harengus*) and the Atlantic cod (*Gadus morhua*) undergo long migrations for reproductive or feeding purposes (Block et al., 2001, Holst et al., 2002, Rose, 1993). Meanwhile, many coastal species of fish are sedentary with a relatively small home range in which both feeding and reproduction occur (Botsford et al., 2009, March et al., 2010, Kramer and Chapman, 1999). Seasonal patterns in feeding, movement, reproduction and predation can affect the survival of a species.

One sedentary species of marine fish which display sexual dimorphism in both size and colouration is the corkwing wrasse (*Symphodus melops*) (hereafter: corkwing) (Halvorsen et al., 2021, Potts, 1974, Uglem et al., 2000). Much research is done on this species (Halvorsen et al., 2016a, Halvorsen et al., 2016b, Uglem and Rosenqvist, 2002, Darwall et al., 1992), however, information regarding their survival pattern is lacking. The reproduction biology of corkwing is quite complex and involve nest building, lekking behaviour and parental care of eggs by large territorial males (Figure 1) (Halvorsen et al., 2020, Karaszkiwicz, 2020). In addition to the territorial males some smaller males expresses sneaker behaviour, mimicking females in order to steal fertilisations. The sneaker male strategy appears to be fixed throughout the lifespan of an individual (Halvorsen et al., 2016a, Uglem et al., 2000). Most males develop into secondary (territorial nesting) males while a smaller proportion develop to be primary (sneakers) males (Potts, 1974, Uglem et al., 2000). Corkwing spawn between May and July and the highest proportion of spawning fish is observed to be from June to early July

(Skiftesvik et al., 2014b). Females can lay several clutches of eggs during the spawning period and territorial males can guard and nurture several clutches (Potts, 1985). During spawning, territorial males are fiercely chasing away all intruders except for receptive females (Potts 1974), and males of both morph have been observed with flesh wounds and missing scales, presumably caused by aggressive encounters with other males (Halvorsen et al., 2016b, Karaszkiwicz, 2020). Following the spawning period is the main feeding period which are shown to peak during July (Deady and Fives, 1995). The growth rate of corkwing in general is higher for smaller individuals compared to larger, and it is overall higher during spring and summer (Krosshavn Vik, 2019). Territorial males grow faster and tend to mature a year later than females and sneaker males (Halvorsen et al., 2016a, Uglem et al., 2000, Krosshavn Vik, 2019).



Figure 1: Picture of the different sexes and male strategies in corkwing wrasse. Top: territorial male, middle: Female and bottom: sneaker male. Photo: Tonje K. Sordalen.

Since the late 1980s, corkwing (along with three other wrasse species) have been the target for a small-scale fishery (Skiftesvik et al., 2014a). They are used as cleaner fish to control sea lice infections by the ectoparasite copepod *Lepeophtheirus salmonis* in open-pen fish farming of Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Costello and

Bjordal, 1990, Treasurer, 1994, Skiftesvik et al., 2013, Leclercq et al., 2014). Of the four wrasse species used as cleaner fish, corkwing along with goldsinny (*Ctenolabrus rupestris*) is the most numerous and therefore the most economically important (Halvorsen et al., 2020). The estimated use of wild caught wrasse in Norway surpassed 18 million fish in 2020, of which more than eight million was corkwing (Norwegian Directorate of fisheries; <https://www.fiskeridir.no/Yrkesfiske/Tall-og-analyse/Fangst-og-kvoter/Fangst/Fangst-av-leppefisk>).

Concerns have been raised regarding the current fishing pressure and its long-term sustainability (Espeland et al., 2010, Skiftesvik et al., 2014a, Halvorsen et al., 2016a, Halvorsen et al., 2017). The peak of the commercial demand for cleaner fish coincides with the spawning season of corkwing wrasse, and the fishery is size-selective (Halvorsen et al., 2016b). A recent study from the Skagerrak coast of Norway found that local populations of wrasse showed signs of depletion (Halvorsen et al., 2017). The study showed that corkwing had a higher catch per unit effort in three out of four marine protected areas (MPAs) compared to surrounding fished areas, and that individuals over the commercial size limit were larger and older inside the protected areas. Continuous fishing pressure in the same areas may also affect the population structure and disrupt mating behaviour (Skiftesvik et al., 2014b, Darwall et al., 1992). More knowledge on the survival pattern for the corkwing is therefore needed.

The objective for this thesis is to explore the natural survival pattern of corkwing. Based on 4 years of capture-mark-recapture (CMR) data from a marine protected area (MPA), I use CMR-modelling to detect seasonal and intra-sexual patterns in both apparent survival and capture probability in fyke-nets, one of the gear types used in the commercial fishery. Based on corkwing's complex reproductive behaviour it is logical to expect that their survival during the spawning is sex-dependant. I hypothesise that territorial males have lower survival rates in comparison to females and sneakers due to their active role with nest building, competition and parental care. Post spawning in the main feeding period it is also likely that survival rates are low due to increased movement in the search for food. Because territorial males invest much energy during the spawning period it is plausible that they compensate by taking greater risks when searching for food, leading to increased predation risk.

2 Materials and methods

2.1 Study area

The study was conducted around a small island called Saltskjærholmane which lies in an experimental marine protected area (MPA). The MPA is located near the field station of Institute of Marine Research in Austevoll, outside of Bergen in Western Norway. The MPA consisted of three small islands (Figure 2) where no commercial wrasse fishing has been permitted since 2016.

The shoreline at low tide at Saltskjærholmane is 141 m long with a distance of 80 m to the nearest island Bleikjo. The maximum depth between the two islands is 25 m (Aasen, 2019). The habitats surrounding the island is mostly hardbottom covered by a large variety of macroalgae, which is a suitable for corkwing wrasse (Skiftesvik et al., 2014a, Lythgoe and Lythgoe, 1991). The dominant ecotype is kelp forests of sugar kelp (*Saccharina latissima*), Oarweed (*Laminaria digitate*) and tangle (*Laminaria hyperborea*) (Aasen, 2019). Thread algae habitats were predominant in the most sheltered areas at Saltskjærholmene (Aasen, 2019). Usually, corkwing is found at water depths less than 5 m, although they can occur down to 15-18 m (Uglem et al., 2000, Sayer et al., 1994, Halvorsen et al., 2020). It has been observed seasonal variation in depth distribution where they inhabit shallower waters in the summer and move to deeper waters towards winter (Skiftesvik et al., 2014a, Halvorsen et al., 2020). Between the islands and the surrounding areas there is limited habitat connectivity, and in addition with the distances and depths it functions as natural barriers. A study of wrasse movement conducted in the same MPA found no movement of corkwing wrasse larger than 10 cm between the islands (Aasen, 2019). Since then, a few individuals have been observed to move between the closest islands, but in conclusion the corkwing population on Saltskjærholmane is presumably closed with little-to-no emigration of larger fish.

In the ecosystem, corkwing functions as intermediate predators which prey on a variety of invertebrate taxa (Skiftesvik et al., 2014b, Helfman et al., 2009). They are in turn preyed upon by piscivorous birds and other fish (Dehnhard et al., 2021, Espeland et al., 2010, Svåsand et al., 2000, Nedreaas et al., 2008).

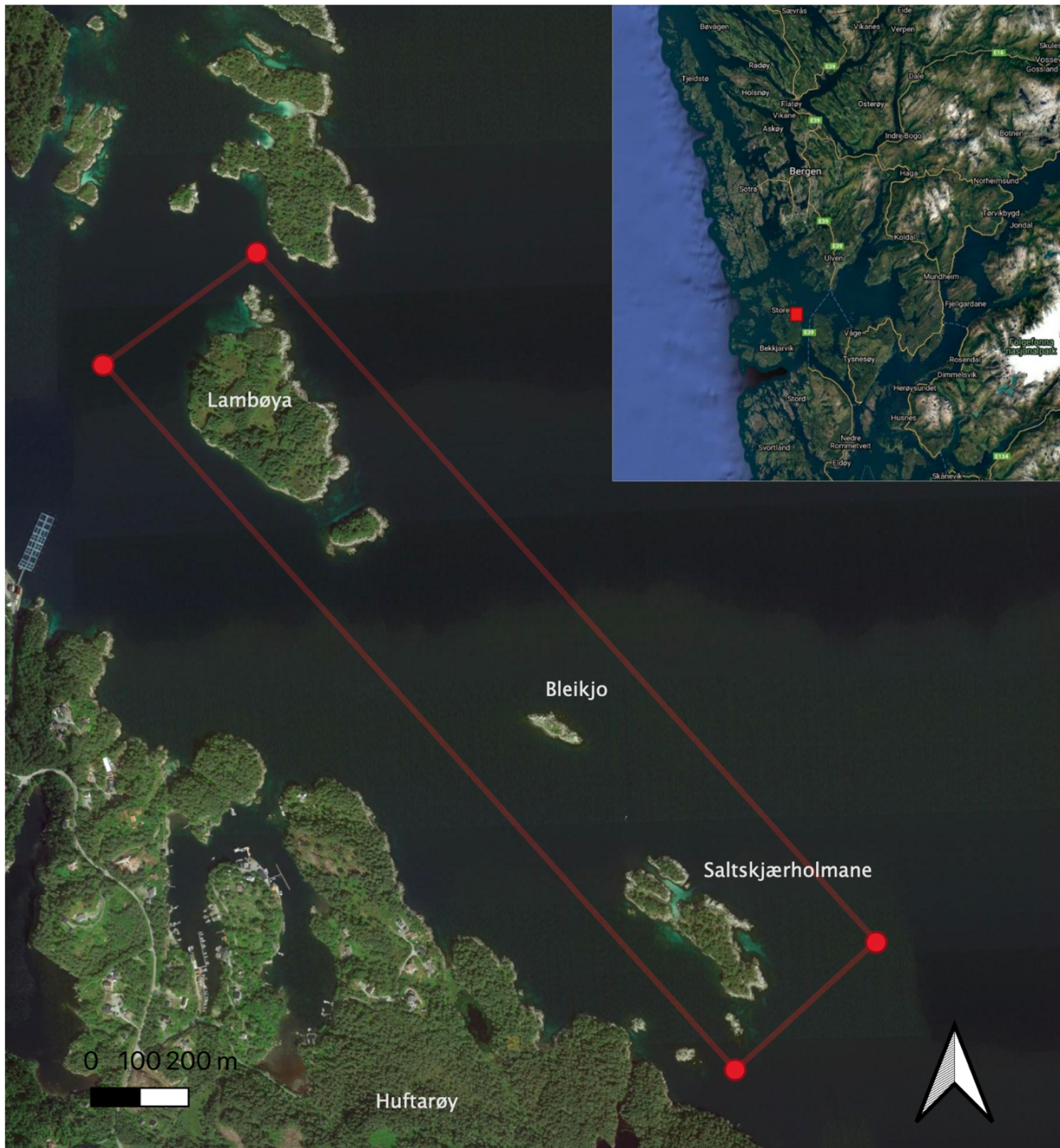


Figure 2: Map showing the location of the study area. The red dots mark the coordinates which surrounds the marine protected area (MPA). The map was generated using QGIS and the QuickMap Services plugin (QGIS Development Team, 2009).

2.2 Estimation of natural mortality in wild fish populations

Natural mortality (M) is any loss to a population except for human harvesting, such as predation, disease or old age (Simpfendorfer, 2005, Wootton, 2012). In general, it is of fundamental ecological importance to understand the mechanisms that shapes fluctuations in abundance. Meanwhile, in the context of assessment of commercial stocks, it is in addition of economic importance as it is used for deciding on management measures and estimating sustainable exploitation levels (e.g., through catch quotas). Given its importance, natural mortality is however quite methodically challenging to estimate and require a substantial amount of data (Simpfendorfer, 2005). When assessing an exploited population, its necessary to differentiate between removal of individuals from human harvesting and death from natural causes. For exploited fish stocks, the total mortality (Z) is the sum of natural mortality (M) and fishing mortality (F) (Beverton and Holt, 2012). One important point to make is that when total mortality is estimated for an unexploited group or population, the estimates are actually of natural mortality since the fishing mortality in that scenario equals zero (Vetter, 1988, Beverton and Holt, 2012). In other words, mortality estimates of a population in a natural state is of natural mortality.

Several methods have been created to estimate natural mortality (Vetter, 1988, Simpfendorfer, 2005). Two widely used methods are catch curve analysis and capture-mark-recapture (CMR) analysis (also referred to as mark-recapture or capture-recapture) (Wootton, 2012). These are examples of direct methods (applied to the actual population in question) and are recognised to give the most precise estimates. Catch curve analysis assumes that a decrease in observed number of individuals across the population age-structure is the result of mortality. Because the CMR-analysis is the model being used in this thesis, I will further explain that in more detail. CMR use multinominal tools for estimating demographic rates such as survival and capture probability for a given population. Natural mortality is not estimated directly, but survival estimates (S) can be converted into mortality estimates by using Ricker's equation: $S = e^{-Z}$ (Ricker, 1975, Wootton, 2012, Simpfendorfer, 2005).

For CMR-analysis there is a variety of different model frameworks which require different study designs (Lebreton et al., 1992), but since the question in focus is on an open population with live-recapture, I narrow the focus in this section to that. The live-recapture model was

first developed by Cormack (1964), Jolly (1965) and Seber (1965), and is (as the name states) based on live recaptures of marked individuals.

The general idea is that animals are captured or observed over a series of occasions, and on each occasion every unmarked individual are given a unique mark. After the first occasion, both marked and unmarked animals are caught. Their identities are recorded, and unmarked animals are marked. The caught animals are released back into their environment after each occasion. After conducting a study, each individual gets a capture history with length depending on the number of capture occasions. A capture history consists of a binary string of 1s and 0s where 1 indicate (re)capture and 0 indicate that the animal is not observed. To illustrate, if we have a 3-occasion study, one possible capture history could be 101. This tells us that the animal was captured and marked at occasion 1, not observed in occasion 2 and recaptured in occasion 3. The length between capture occasions do not have to be equal, but they should reflect what the researcher is trying to detect. For instance, if the objective is to study annual survival, the occasions would naturally be one year apart. They may also be shorter, for instance by season or month, depending on the organism in question and what the aim for the study is.

The Cormack-Jolly-Seber model (CJS), which I use in this thesis, give estimates of apparent survival (ϕ), and capture probability (p). Due to uncertainty of the fate of some marked animals the survival estimates from this model is apparent and not the true survival. If an animal is not recaptured it is not known if it died, emigrated out from the study area or is present but not captured (Figure 3).

Apparent survival is defined as the probability that a marked individual in the study population at sampling period i survives and remains in the population to period $i+1$. In other words, ϕ_i relates to the survival between period i and $i+1$. Capture probability (or catchability) is defined as the probability that a marked individual, present in the study population at sampling period i , is captured.

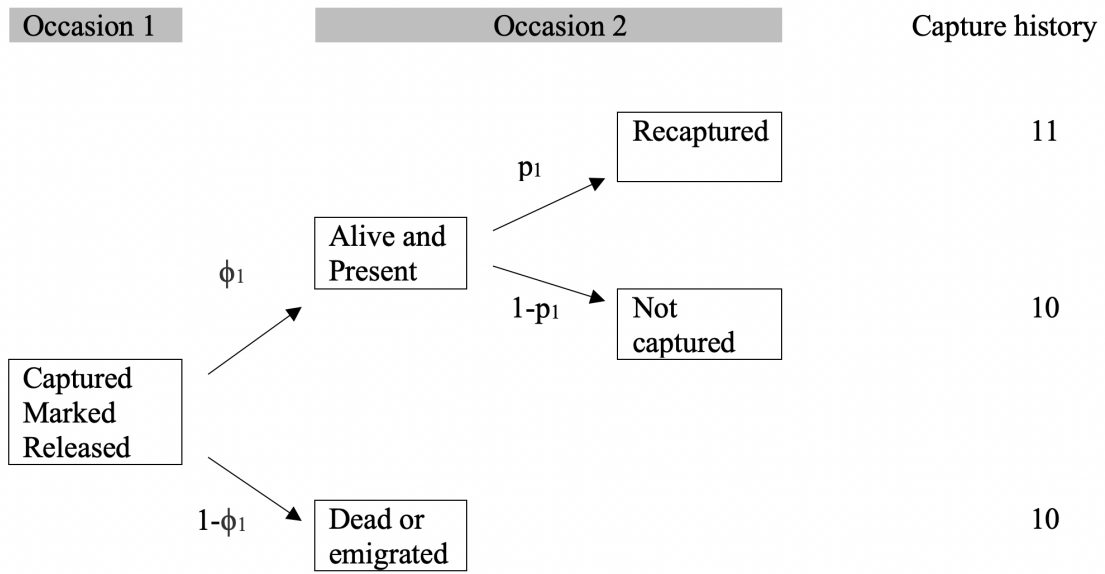


Figure 3: Illustration of the potential fates of a marked individual between two sampling occasions. To the right is the belonging capture histories to each fate. Notice there is two possible ways an individual can get the capture history 10.

2.3 Data collection

The data analysed in this thesis was collected during 10 periods over 4 years by the Institute of marine research (IMR) (Table 1). As part of a team of three, I contributed to the last two periods. The first sampling period differed from the subsequent in duration and effort and was carried out over three shorter sessions (between 8. August and 9. September 2017).

Subsequent samplings were conducted 3 times each year and lasted 6-8 days. Additionally, from 2018 the fishing intensity on Saltskjærholmane increased because previous sampling effort was split between another islands. The fishing periods of the annual survey were distributed over the seasons starting in spring (early May), summer (late June - early July) and fall (late August – early September).

Table 1: Overview over the periods for the standardized fyke-net survey. Sown are the dates and type of activity.

Sampling period	Date	Activity
1	08.08 – 09.09 / 2017	Tagging (3 shorter sessions)
2	10.05 – 18.05 / 2018	Tagging
3	02.07 – 09.07 / 2018	Tagging
4	04.09 – 11.09 / 2018	Tagging
5	14.05 – 23.05 / 2019	Tagging
6	09.07 – 14.07 / 2019	Tagging
7	03.09 – 08.09 / 2019	Tagging
8	04.05 – 09.05 / 2020	Tagging
9	27.06 – 02.07 / 2020	Tagging
10	26.08 – 31.08 / 2020	Tagging

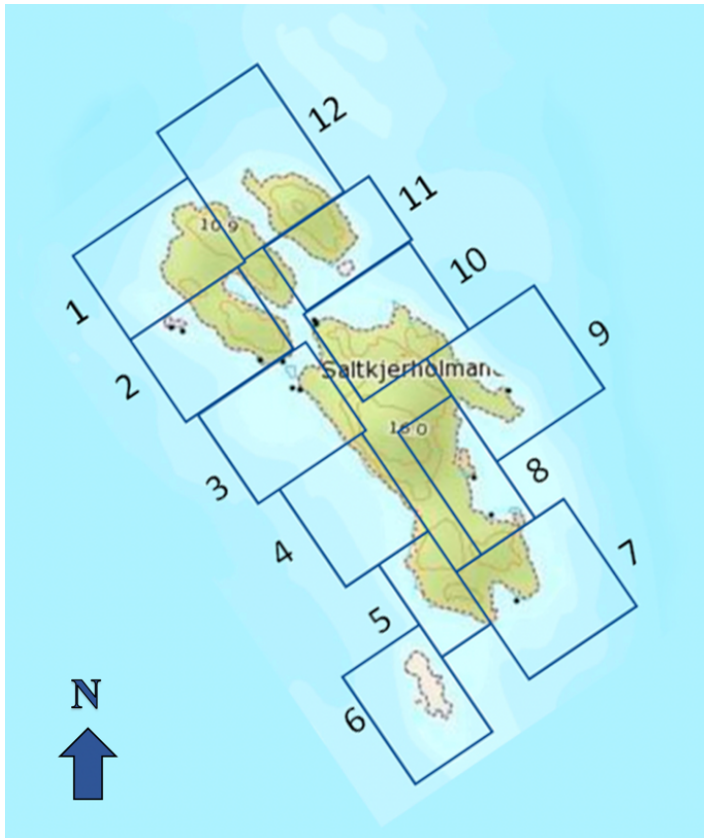


Figure 4: Illustrating map showing Saltkjærholmane divided into 12 zones of similar size.

The project was performed as a standardized mark-recapture survey. Un-baited fyke-nets were used to catch our target-species (7.8 m leader net, 70 cm diameter entrance ring, 11 mm mesh size). To ensure similar sampling effort, Saltkjærholmane was divided into different zones of similar size (Figure 4). To mark and identify individuals we used PIT-tags (passive integrated transponders) which is inserted into the abdominal cavity. Every PIT-tag has a unique 6-digit number which allows us to recognise each marked individual by using a scanner (BioMark HPR). We used glass-encapsuled half duplex PIT-tags (12.0 mm x 2.12 mm, RFID solutions). The use of PIT-tags is a well-tested method and have little effect on the fish's survival (Halvorsen et al., 2016b, Peterson et al., 1994, Achord et al., 1996, Gries and Letcher, 2002). To measure temperature and depth, a datalogger (Star-Oddi; DST centi-TD) was attached to each fyke-net. It was mounted at the trap site on top of the first capture ring (70 cm above the seabed) and temperature was recorded every 15 minutes. A handheld GPS (Garmin GPSMAP78 s) was used to record the position of every fyke-net.

This experiment was approved by the Norwegian Food Safety Authority (FOTS-id: 23108) (https://www.mattilsynet.no/dyr_og_dyrehold/dyrevelferd/forsoksdyr/forsoksdyrsoknader/felt_forsok_leppefisk_merkinggjenfangst_forsok_202022.38237).

The fyke-nets were placed on the seafloor at a depth of 1-10 m, and with the leader net towards the shoreline to lead passing fish down into the trap. Eight fyke-nets were placed in different zones to passively fish overnight (soak-time between 12-24 hours). To avoid fishing in adjacent zones we varied between sampling in odd and even number zones from day to day. Each sampling day the eight fyke-nets were hauled one at the time, and the catch were put in a tub with seawater and kelp (for stress relief) and further processed individually. Although in this thesis the main focus is on the corkwing, several other wrasse species was examined during the survey. All the wrasses were identified to species, counted and measured for total length to nearest mm. The gender and reproductive state were also determined visually (when possible). For corkwing, we differentiated between females, territorial males and sneaker males, by examining the presence of eggs or running sperm. Accurate gender determination was therefore only possible during the spawning season (May-July).

Our size limit for PIT-marking was 100 mm, therefore all wrasse larger than the size limit were scanned for a PIT-tag, to detect if it was previously marked (recaptured). If a mark was detected, they were measured as described above before it was released at the catch site. For wrasse caught for the first time, with no detectable PIT-tag, a scale sample, fin sample and a photo were taken, in addition to the measurements described above. Before tagging, the fish was sedated using 50-100mg L⁻¹ Finquel (Ethyl-3-aminobenzoate methanesulfonate – MS-222) diluted in 4-6 L of seawater. After 1-2 minutes in the sedation tub when loss of equilibrium occurred, the PIT-tag was injected with a hypodermic needle into the fish abdominal cavity (Figure 5). The fin sample, scale sample and the photo were taken while the fish was sedated. After a few minutes' recovery time in normal seawater the fish was released at the catch site. The needle was sterilized in 96% ethanol between each marking and changed regularly.

For bycatch (e.g., Crustaceans and non-target fish species), species and sex (when possible) were determined. Total length was also measured before it was released at the catch site along with the wrasse. Bycatch that could potentially harm the wrasse were released immediately after hauling the fyke nets.



Figure 5: Picture illustrating how the fish was tagged. Bottom right is the device used for measuring body length. Photo: Ovin M. Holm.

2.4 Data analysis

The data was analysed in R (version 3.6.3; R Development Core Team, 2020). To analyse apparent survival and catchability I used the package RMark (Laake, 2013) which is an interface version in R of the program MARK (White and Burnham, 1999). Data from each sampling occasion were joined and converted into a long matrix to make it readable for RMark. The long matrix was structured such that each row contained information from each individual corkwing. Each row contained a pit number, binary capture history ($n=10$) and whether it was a female, territorial male or a sneaker. Recaptured sneakers which first was determined as females were corrected in the dataset. The time intervals were discretized and specified as 8.3 months between the fall- and spring-occasions, 1.7 months between spring and summer, and 2.0 months between summer and fall (Figure 6).

Because the objective was to investigate if there were time-dependant differences in survival and capture probability, I used a standard CJS-model (Cormack, 1964, Jolly, 1965, Seber, 1965) with time-specific parameters (apparent survival ϕ_t and catchability p_t) (Figure 6). By specifying the time-intervals in the model to months, the survival estimates from the analysis in RMark will be on a monthly scale.

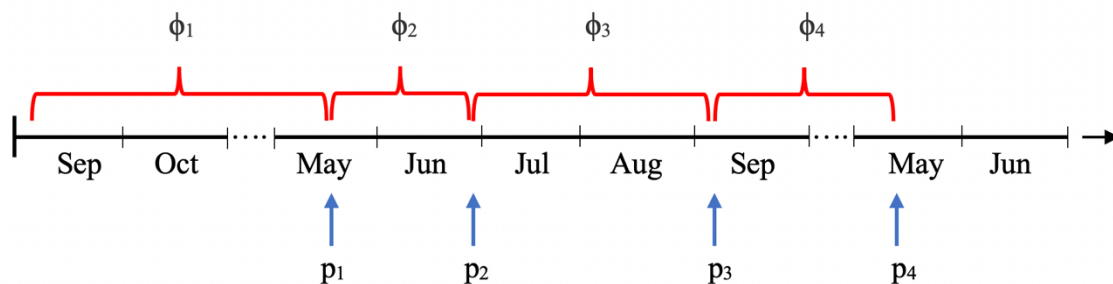


Figure 6: Show the parameterisation in the CJS-model for the first 4 time-intervals between the 5 first capture occasions in my model. ϕ_1 is the apparent survival between occasion 1 and 2, and p_1 is the capture probability at occasion 2.

The covariates used to build model structures was time and sex (including female, territorial male and sneaker male). In addition, I grouped the time variable into a seasonal variable to use as a potential covariate for the survival estimates. Different candidate model structures were formed to test which hypotheses was best supported by the data. Akaike's information criterion (AIC) was used to rate the best supported candidate models (Akaike, 1974). The

most parsimonious model was chosen based on the lowest AICc-value (Akaike's information criterion corrected for small sample sizes). The highest ranked (most parsimonious) candidate model was chosen if the difference to second best in AICc-units was more than 2. For visualisation of the data, I used the package ggplot2 in R (Villanueva et al., 2016).

The CJS-method is open for emigration and immigration of individuals to and from the population, hence the apparent and not the true survival is estimated. Estimates of apparent survival have an unknown component of migration and is the product of the probabilities of true survival and the study area fidelity (Lebreton et al., 1992). The apparent survival is therefore lower than the true survival unless the study area fidelity equals one (Schaub and Royle, 2014). Corkwing are known to be sedentary and move within a small area (Halvorsen et al., 2021, Aasen, 2019). Their narrow home range suggest low levels of migration and high site fidelity. Consequently, in this case it is likely that the estimates of apparent survival from this thesis is actually closer to the true survival of corkwing wrasse.

To analyse differences in length between sexes and male morphs, I used a standard linear regression model in R. Two separate models were made, one for all the catches, and one for catches over 100 mm. Territorial males were set at intercept in both models.

3 Results

3.1 Data overview

From the 4 year-long mark recapture survey on Saltskjærholmane, 6123 corkwings were captured (Table 2). A total number of 3820 corkwings were tagged (> 100 mm) and a total of 567 was recaptured over the 10 sampling occasions. The number of caught individuals varied quite a bit between the 10 sampling occasions. Overall, the sampling occasions from September in addition to the last July-occasion stood out with the highest number of caught individuals. There was no trend in recapture rate over time, as could have been expected. Recapture rate varied between 11.3% and 25.1% and had a mean value of 15.2%.

Table 2: Total number of caught and processed corkwing over the 10 sampling occasions. Shown are the total captures of all sizes, total captures over the size limit for tagging (>100mm), tagged individuals from each occasion, recaptured individuals from pervious occasion(s) and recapture rate in %. For total captures over the size limit, recaptures from within the sampling period are excluded. Recapture rate was determined by the number of recaptures in relation to total number of captures of individuals larger than 100 mm (after the indicial occasion).

Sampling occasion (year_month)	Total captures (All sizes)	Total captures (> 100 mm)	Tagged individuals	Recaptured individuals	Recapture rate (in %)
2017_09	917	654	654	-	-
2018_05	418	319	283	36	11.3%
2018_07	295	197	164	33	16.8%
2018_09	721	508	445	63	12.4%
2019_05	360	350	279	71	20.3%
2019_07	303	191	143	48	25.1%
2019_09	919	521	455	66	12.7%
2020_05	272	238	195	43	18.1%
2020_07	1018	721	620	101	14.0%
2020_09	900	688	582	106	15.4%
<i>Total</i>	6123	4387	3820	567	15.2% (mean)

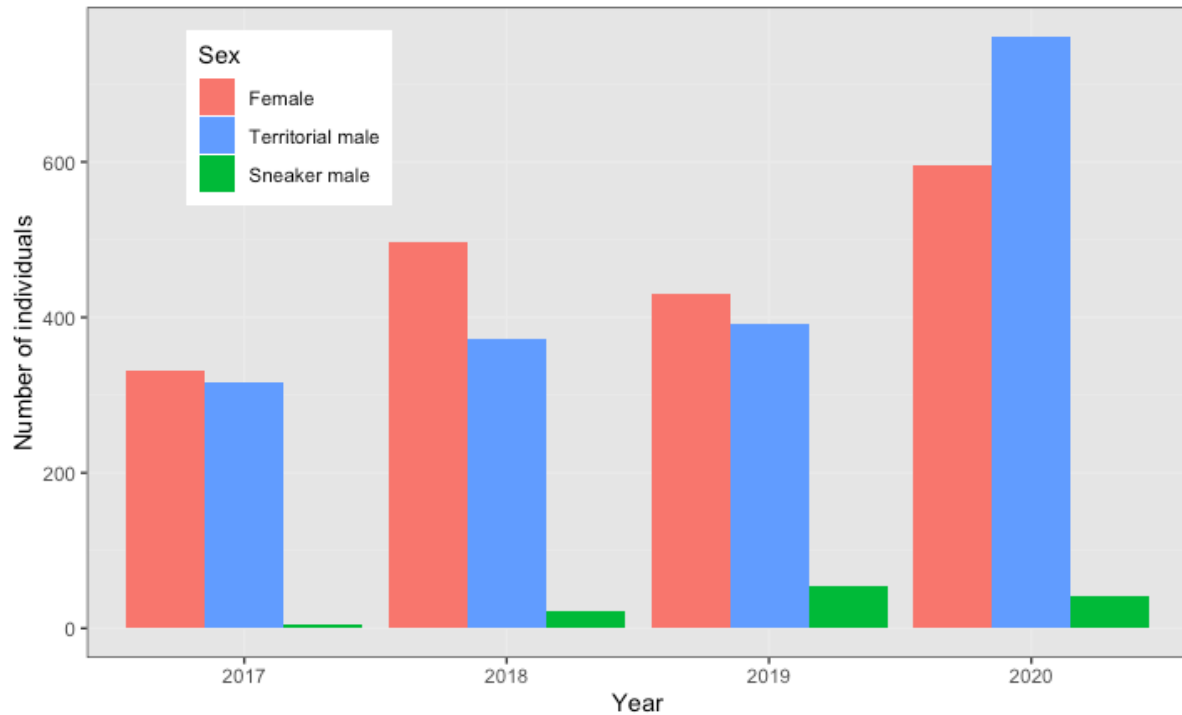


Figure 7: Number of territorial males, sneaker males and females of corkwing wrasse (> 100 mm) tagged during the period 2017 to 2020.

The majority of the tagged corkwing was either territorial male morph (n=1855, 48.7%) or females (n= 1842, 48.2%), while a much smaller proportion was sneaker males (123, 3.2%). In 2017, 2018 and 2019 it was caught slightly more females than territorial males while in 2020 the territorial male morph was most numerous (Figure 7).

3.2 Length analysis

The body length of the captured corkwing span from 65 mm (min) to 215 mm (max) with a mean of 120.2 mm. The majority of caught corkwing from the fyke-nets was over the size limit for tagging (Figure 8). Also note that there is quite a lot of fish just under the size limit, and that the fyke-nets used in this survey is size selective and do not capture the smallest individuals. Length distributions for captured corkwing from each sampling year are found in appendix A.

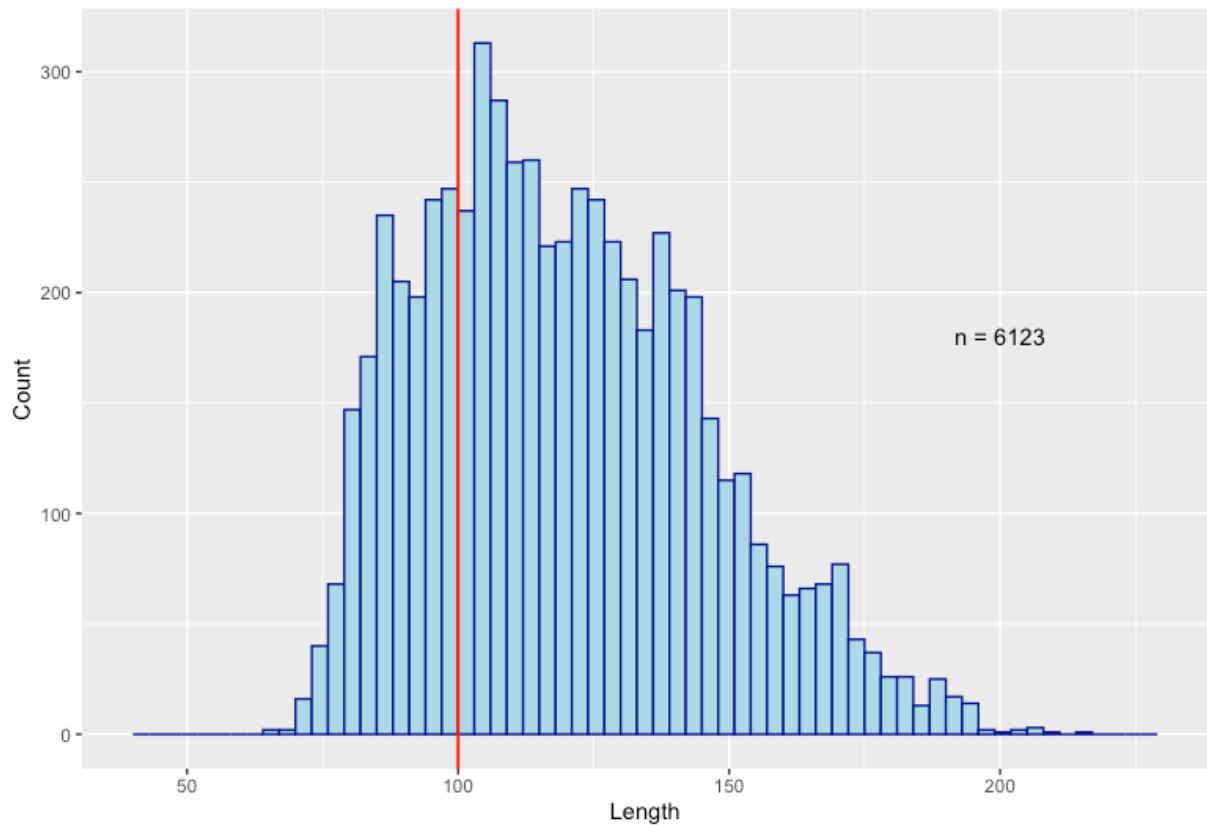


Figure 8: Length distribution for the 6123 caught corkwings from Saltskjærholmane. The red vertical line highlights the size limit for tagging (100 mm).

Table 3: Linear regression models testing length-differences between sexes and male strategy for corkwing wrasse. Two separate analysis were made, one for the total catch (all sizes) and one for individuals larger than 100 mm. For both analysis, territorial males were set as intercept and compared to females and sneakers. This analysis is based on data collected during the spring and summer capture occasions for all years pooled (when sneakers can be differentiated from females).

		<i>Estimate</i>	<i>Std. Error</i>	<i>t-value</i>	<i>Pr(> t)</i>
<i>(All sizes)</i>	(Intercept)	123.39	0.78	158.60	< 0.001
	Female	0.26	1.09	0.24	0.81
	Sneaker	-7.43	2.24	-3.31	< 0.001
<i>(> 100 mm)</i>	(Intercept)	139.71	0.77	181.06	< 0.001
	Female	-9.16	1.05	-8.71	< 0.001
	Sneaker	-18.81	2.09	-8.99	< 0.001

Both the linear regression models showed that sneakers were significantly smaller than both territorial males and females (Table 3). Only data from the capture occasions in spring and summer were used (when females can be differentiated from sneakers). When comparing sexes and male strategies of all sizes, territorial males and females was not significantly

different. However, when running the model for individuals over 100 mm, the length-difference between territorial males and females became significant. For individuals over 100 mm territorial males had a mean length of 139.7 mm while females had a mean length of 130.6 mm (Figure 9). Sneaker males had a mean length of 120.9 mm.

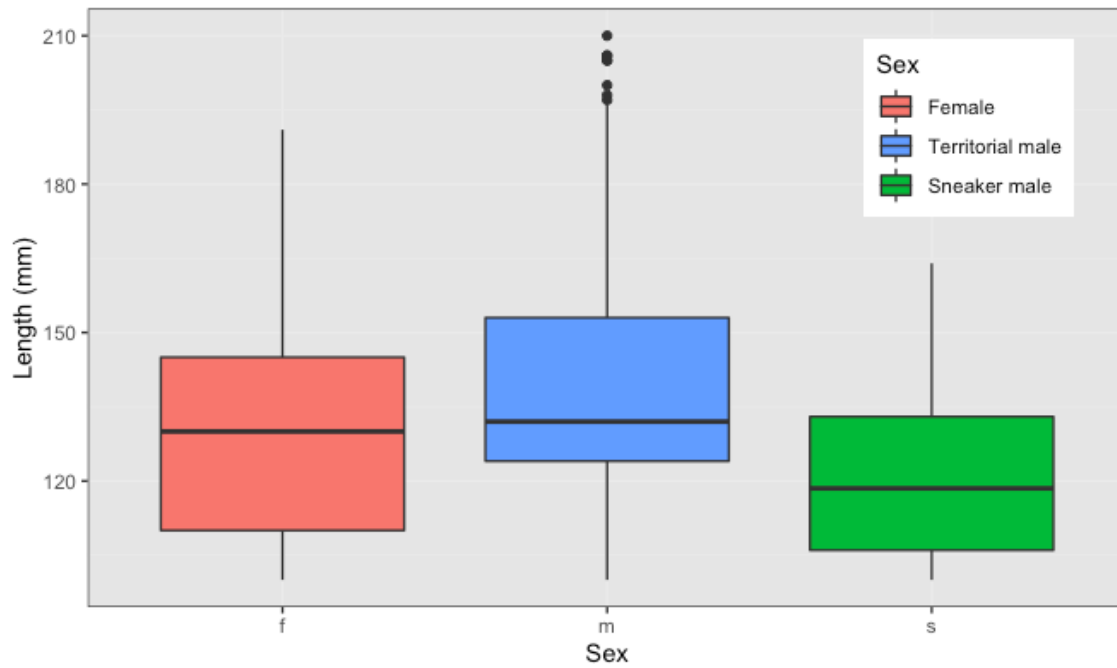


Figure 9: Boxplots showing the length distribution of tagged corkwing (> 100 mm) for females, territorial males and sneaker males. This is based on data collected during the spring and summer capture occasions for all years pooled (when sneakers can be differentiated from females). The upper and the lower edges of the boxes represent the 25th and 75th percentiles, while the vertical lines extend to the highest value maximum 1.5 times the distance between the 25th and 75th percentiles. Black dots represent outliers.

3.3 CMR-analysis

I used a standard CJS-model with time-specific parameters to estimate the apparent survival and capture probability for corkwing wrasse. In total, 24 candidate models were tested to find the most parsimonious representation of the obtained CMR-data (Table 4). The best model with lowest AICc-value ($(\Delta AIC_c$ vs second ranked model = 5.54) showed that apparent survival (Φ) varied by season with an additive effect of sex and that the capture probability (p) varied by a time and sex interaction. Real and beta estimates for apparent survival and capture probability are found in appendix B (table A and B).

Table 4: List of the 10 highest ranked candidate CJS models fitted to the obtained CMR-data for corkwing wrasse. The models are ranked by Akaike's information criterion corrected for small sample sizes (AICc). The most parsimonious model is indicated in bold. Shown are the model rank, model structure for apparent survival (Φ) and capture probability (p), number of parameters (n_{par}), AICc, difference to the best fit model (ΔAIC_c), model weight and the deviance.

<i>Rank</i>	<i>Model structure</i>	<i>n_{par}</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>Weight</i>	<i>Deviance</i>
1	Phi(~season + sex) p(~time * sex)	32	4251.26	0.00	0.93	358.55
2	Phi(~season * sex) p(~time * sex)	36	4256.80	5.54	0.06	355.93
3	Phi(~time + sex) p(~time * sex)	38	4260.70	9.43	0.01	355.74
4	Phi(~season + sex) p(~time + sex)	16	4265.52	14.26	0.00	405.24
5	Phi(~season + sex) p(~time)	14	4267.66	16.39	0.00	411.41
6	Phi(~sex) p(~time * sex)	32	4267.72	16.46	0.00	379.08
7	Phi(~time + sex) p(~time)	20	4267.91	16.65	0.00	399.55
8	Phi(~season * sex) p(~time + sex)	20	4268.20	16.94	0.00	399.84
9	Phi(~season * sex) p(~time)	18	4270.27	19.01	0.00	405.96
10	Phi(~time) p(~time * sex)	36	4279.96	28.70	0.00	379.10

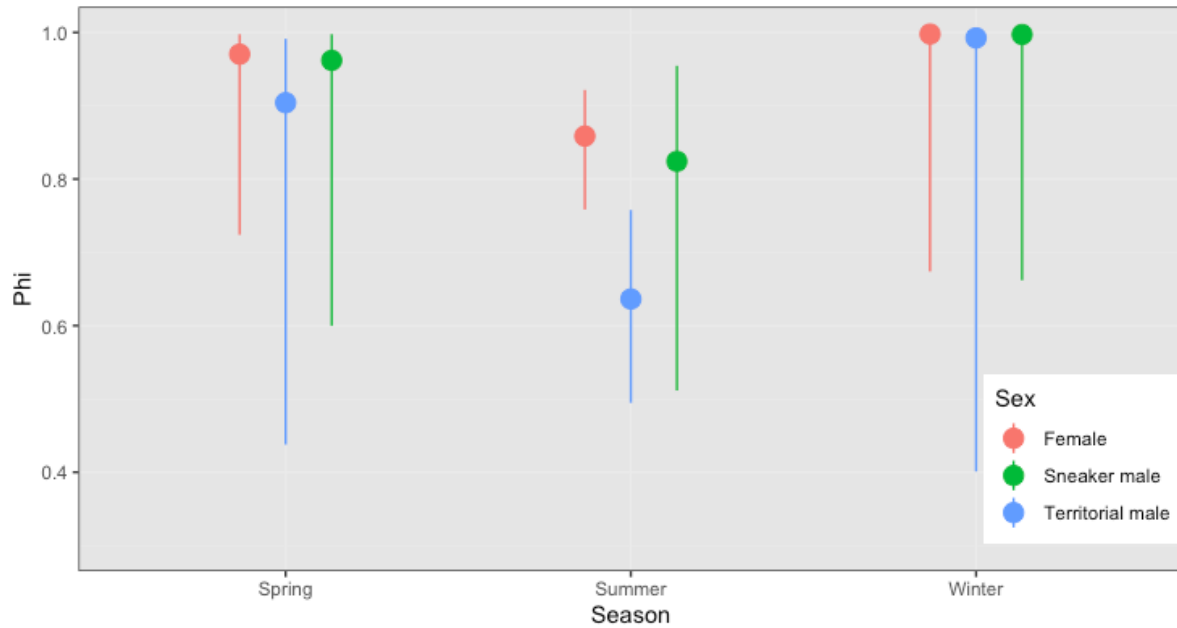


Figure 10: Estimated apparent monthly survival probability (Phi) for territorial male, sneaker male and female corksing wrasse during different seasons. The confidence intervals are asymmetrical and shown as lines.

The estimated apparent survival was lower during the summer interval (early July to early September) compared to winter and spring (Figure 10). The highest survival estimates were during winter (early September to mid-May) and there was a slightly decrease in the spring towards summer (mid-May to early July). There was also a significant variation between the sexes and male strategies. The territorial males were estimated to have an overall lower survival probability compared to females and sneakers. The difference was greatest over the summer where territorial males had an estimated monthly survival probability of 0.66 while females had 0.86 and sneakers 0.82. During the winter (early September to mid-May) the apparent survival was high and similar for the females and the two male strategies. The confidence intervals were wide, especially for the spring and winter estimates for territorial male.

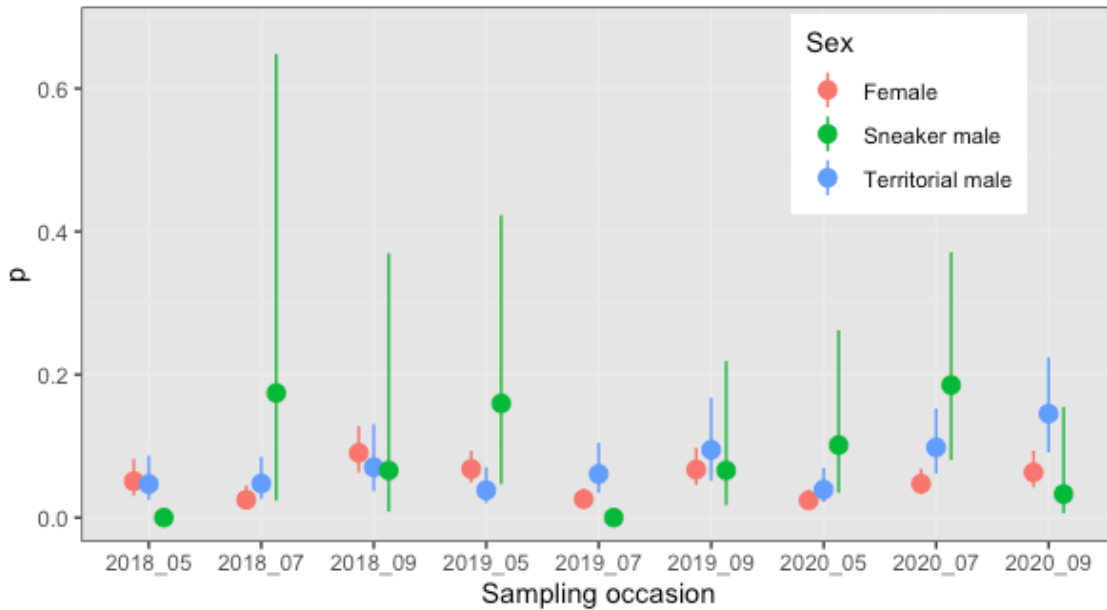


Figure 11: Estimated capture probabilities (p) for territorial male, sneaker male and female corksling wrasse from each sampling occasion after the first in the survey. p for sneaker in 2018_05 and 2019_07 was not estimable. The confidence intervals are asymmetrical and shown as lines.

The estimated capture probabilities (or catchability) were low in all capture occasions with the highest estimated value of 0.17 (Figure 11). When comparing the sex and male strategies, sneaker males stood out with either the highest or the lowest catchability estimates in comparison to females and territorial males. Note that the catchability for sneaker males in 2018_05 and 2019_07 was not estimable, likely due to insufficient data. From the capture occasions in May and July, sneaker males were estimated to have higher catchability than the territorial males and females. For each of the capture occasions in September sneaker males had lower capture probability compared to territorial males and females. Territorial males and females had overall more similar estimated catchability. However, territorial males had higher catchability compared to females in each capture occasion from July. In two out of the three occasions in May, females had higher estimated catchability than territorial males. The last capture occasion in May (2020_05) differed where the territorial males was estimated to have a slightly higher catchability than females. From the capture occasions in September, Territorial males had higher catchability than females in the last two (2019_09 and 2020_09) but not in the first (2018_09). For both territorial males and females there was a tendency for higher catchability in the September occasions. The confidence intervals for the estimates for territorial males and females was narrow. The estimates for sneakers had much wider confidence intervals.

4 Discussion

In this study I estimated the apparent survival and capture probability of corkwing wrasse. The main findings were that the survival varied throughout the yearly cycle with a high rate during winter and lower rates during spring and summer. The lowest survival rates were detected in the main feeding period between early July and early September. I also found intra-sexual differences in survival where territorial males had an overall lower survival compared to females and sneakers. The biggest difference was during spring (mid-May to early July) and summer (early July to early September) which suggests that nest building and nest defence in the spring and increased predation risk in the summer reduces survival for territorial males. The estimated capture probability was overall low for corkwing wrasse with minor intra-sexual and seasonal trends. These main findings are discussed further in the next sections based on what we know regarding corkwings ecology. Lastly, I discuss the implications for sustainable management of the corkwing wrasse.

4.1 Survival

From the most parsimonious model from the CMR analysis (Model 1 from Table 4) it was estimated that the apparent survival of corkwing varied between sex and male strategy and by season. The overall trend was that survival rate was high during winter, a decrease in the spring and lowest over the summer. These findings are likely to be a result of both biotic and abiotic factors related to seasonal fluctuations. Predators are more active and abundant during the spring and summer months due to food availability and metabolic rate (Wootton, 2012). Corkwing along with other wrasses is an important prey-organisms for gadoid fishes and piscivorous seabirds (Dehnhard et al., 2021). Several of the piscivorous birds migrate south during the fall and winter and return in the spring. One of these is the great cormorant (*Phalacrocorax carbo*) which is known to heavily predate on wrasse in the North sea and Skagerrak coast (Dehnhard et al., 2021). Another factor that may explain the estimated decrease in survival during the spring and summer is their reproduction and weakening of individuals after spawning. Corkwing wrasse have an intricate reproduction behaviour with lekking, parental care and nest building which take place from May to July (Skiftesvik et al., 2014b). A decrease in survival due to a cost through reproduction is shown for several animal taxa (Hutchings et al., 1999, Promislow, 1992, Owens and Bennett, 1994). It is likely that the

estimated variations in seasonal apparent survival for corkwing wrasse is a combination between a cost through reproduction and fluctuations in predation rate. The high apparent survival during the winter support that the decrease during the spring and summer is due to a reproductive cost. High winter survival can also be explained by the fact that corkwing is less active during that time-period and therefore less exposed to predation from larger fish and sea birds. Metabolic rate, food consumption and activity levels are generally lower during cold periods (Deady and Fives, 1995), which also applies to the predators.

The reproductive behaviour of the corkwing wrasse may also explain the intra-sexual differences in survival rate for corkwing. Territorial males stood out with a lower apparent survival in comparison to females and sneakers during spring (spawning period) and summer (post spawning / main feeding period). During the spawning season the territorial males are highly active and known to construct and maintain nest (Potts, 1974). All sizes of the territorial male morph is shown to have the potential to reproduce as nest building territorial males when intra-sexual competition is absent (Uglem and Rosenqvist, 2002). However, limited availability of nest sites results in competition and aggression between rival males (Potts, 1985). They guard and defend their territory from rival males (of both morphs) and this competition is likely to come with a viability cost through energy loss and increased predation risk. Territorial males also spend much energy in building and maintaining the nest (Potts, 1985). Another factor which may explain lower rates of survival for territorial males are food consumption and movement connected to food search. The feeding intensity of corkwing wrasse is shown to coincide closely with changes in sea water temperature throughout the yearly cycle (Deady and Fives, 1995). The study showed low rates of feeding intensity from November to March followed by an increase in April with a peak in July. The feeding intensity of males was significantly lower between April and July compared to females (Deady and Fives, 1995). Territorial males usually stay in close proximity to the constructed nest while sneakers and females move more freely during spawning (Halvorsen et al., 2016b). They spend much time building, defending and maintaining their nest, which means that less time and energy can be used in food search. It is therefore likely that territorial males spend less time feeding during spawning season compared to females and sneakers. Low energy input for territorial males during the spawning season is likely to be a contributing factor to their lower survival rate. However, it may also explain the even lower survival rate estimated for territorial male post spawning in the summer. A decrease in food consumption during spawning means that territorial males to a larger extent need to search for

food afterward. That relates to more activity and movement which in turn increases the risk of predation.

The time-dependant CJS-method which in this thesis was used to estimate the apparent survival gave estimates on a monthly scale. However, it might be more intuitive to determine the likelihood of surviving from one year to the next. Because the estimates are probabilities of survival, we can take the estimates raised to the power of the monthly time-interval (over which the estimates are) and multiply them together. The annual apparent survival of territorial males is 0.32 (calculations are found in Appendix B). This means that the probability of surviving from one year to the next for a territorial male morph is as low as 32%. For females the annual apparent survival is 0.69 (69%), while for sneaker males it is 0.62 (62%). Females and sneakers have approximately twice as big a chance as the territorial males to survive from one year to the next. A previous study on corkwing from the same study area found that the population had a relatively young age structure (Krosshavn Vik, 2019). Few individuals get old, and this supports the relatively low annual survival for corkwing found here.

4.2 Capture probability

Capture probability (or catchability) is estimated independent of survival and defined in the CJS model framework as the probability that a marked individual, present in the study population in the sampling period is captured. Catchability is known to vary by a variety of factors such as abundance, population size, fishing gear, fishing intensity, behaviour and environmental conditions (Arreguín-Sánchez, 1996). Catchability is usually related to abundance, and if abundance levels change over time, so does the catchability (Maunder et al., 2006). For corkwing wrasse caught in fyke-nets (one of the gear-types used in the commercial fishery), there was an overall low catchability from all the sampling occasions, with minor seasonal trends. Low catchability can be a consequence of rapid migration or that a relatively small proportion of the population is marked. Based on what we know regarding corkwings' limited movement (Aasen, 2019, Halvorsen et al., 2021), the low catchability shown here is not likely to be caused by emigration. It is however more likely to be a consequence of a low percentage of tagged fish in relation to the whole population. This indicates that the population is dense and that a relatively small proportion of the population was tagged. If a large number of fish is available for capturing, the probability of catching one

given individual goes down. Catchability have been found to decrease with increasing density (VanDeValk et al., 2005, Chittleborough, 1970). There was a small seasonal trend for a higher catchability for females and territorial males in the occasions from September. One possible explanation for this is increased movement connected to food search when food supply is decreasing. Hungry fish usually have higher catchability, and the catchability increase when the food supply is low (VanDeValk et al., 2005, Chittleborough, 1970).

The overall recapture rate was relatively low (mean = 15.2%) which concede with the low values of estimated catchability. However, not in line with my expectations was that the frequency between captured and recaptured fish varied over the occasions with no clear trend. I expected the frequency to increase over time as more fish is tagged from each occasion. Variations in number of captured and recaptured individuals can be affected by a number of factors such as fishing intensity, differences in year and age classes or seasonal variations in weather, temperature and predation. One plausible explanation for the varying recapture rate is that individuals under the size limit for tagging is rapidly growing and become available. Based on the length distribution we can see that a large proportion of the population have a length just under 100 mm, and therefore constantly supply the part of the population which is available for tagging between occasions.

4.3 Implications for sustainable management of the corkwing wrasse

Catchability is closely linked to the gear-type and its efficiency (Arreguín-Sánchez, 1996). In the commercial wrasse fishery the two gear-types used is fyke nets and baited pots (Halvorsen et al., 2017). The fyke nets used in this survey is similar to the ones used in the fishery. By comparing catch per unit effort (CUPE) between fyke nets and baited pots for corkwing, fyke nets have been showed to be more effective with 72% higher relative mean observed CUPE (Halvorsen et al., 2017). The low estimated catchability (this study) may show that natural populations of corkwing is not as exposed or vulnerable to over-exploitation as first believed. However, due to their sedentary behaviour, intensive fishing in the same area may cause depletion.

Depletion of corkwing (and the other wrasses) from fishing may also have wider ecosystem consequences through altered predator prey dynamics (Selden et al., 2017). Either as bottom-

up effects as a reduced food source for large piscivores, or as top-down effects on mesograzers (Dehnhard et al., 2021, Kraufvelin et al., 2020). The Cormorant (*Phalacrocorax carbo*) which prey on wrasses have been estimated to consume 110% of the amount of human catches (Dehnhard et al., 2021). Concerns for the cormorant regarding their resource competition with the fishery have been raised (Dehnhard et al., 2021).

Another concern is that the fishery is sex and size selective which have consequences regarding populations structure, sex ratios and reproduction (Halvorsen et al., 2016b). From studies comparing fished areas with no-take areas it is shown that individuals over the commercial size limit were larger and older in the protected areas (Halvorsen et al., 2017) and that territorial males are subject to higher fishing mortality than females and sneakers (Halvorsen et al., 2016b, Darwall et al., 1992). The wrasse fishery partly overlaps with the spawning season and main feeding period of corkwing. As territorial males have higher fishing mortality in addition to lower rates of natural survival during this period, extensive fishing may have implications for sex-ratios, social structure and disrupt reproductive behaviour (Sørdalen et al., 2018). Removal of large territorial males may have direct negative consequences for off-spring survival due to parental care. Male-male competition and mate choice will be reduced which in turn can alter sexual selection (Kvarnemo and Ahnesjö, 1996). In the absence of large territorial males, it is shown that females spawn with smaller low-quality males (Uglem and Rosenqvist, 2002). Constant reshuffling of social ranks as a result of extensive size selective fishing can prolong the intervals between egg-batch releases due to increased time used by females to evaluate male quality. Removal of large males will reduce the scope of female choice and the females may resort to mate with males of nonpreferred genotypes or phenotypes.

In the context of studying population dynamics and size selective fishing mortality of exploited fish populations with obligate male parental care, Kindsvater et al. (2020) estimated the natural mortality of corkwing (based on estimates of total mortality from catch curve analysis). This was based on published data by Halvorsen et al. (2016a) in addition to unpublished data collected in 2017. Natural mortality (M) was assumed to be constant (after age 1) and estimated to be similar for territorial males and females ($M = 0.54$) and lower for sneakers ($M = 0.40$) (Kindsvater et al., 2020). By using a simulation approach, they studied the effects of slot limit (min and max capture size limit) as a conservation measure over different rates of fishing mortality. They found that the natural mortality for corkwing was

high enough so that very few individuals in the model survived beyond the maximum size limit (max slot limit, 170 mm), especially under strong fishing mortality (Kindsvater et al., 2020). A maximum slot limit was found to increase care capacity by decreasing the capture of large males, while the minimum limit was sufficient to protect female egg-production such that recruitment to the adult population was not affected. However, the author pointed out that these results may be an oversimplification of reality because stock-recruitment relationships vary according to inter-annual fluctuations in the environment. Increasing rates of fishing mortality was found to decrease the spawning potential (availability of care) through removal of the largest males, and fishing had a stronger negative effect on larval supply under the assumption of an effect from care capacity depending on male size or larval production (Kindsvater et al., 2020).

The survival pattern for corkwing found in this thesis may indicate that the natural mortality estimates used by Kindsvater et al. (2020) are underestimated for territorial males. To better compare the estimates of natural mortality found by Kindsvater et al. (2020), we can convert them into survival rates using Ricker's equation: $S = e^{-Z}$ (Ricker, 1975, Wootton, 2012). Note that for an unexploited population of fish, total mortality (Z) equals natural mortality (M) when fishing mortality (F) equals zero. The estimated natural mortality translates to survival rate $e^{-0.57} = 0.56$ for territorial males and females and $e^{-0.40} = 0.67$ for sneaker males. In comparison, my estimates of annual apparent survival, females and sneaker males are quite similar to the catch curve estimates. However, the estimates of annual apparent survival for territorial males (0.32) differ. Although, catch curves and CMR analysis is regarded as two of the most precise approaches to estimate natural mortality, this highlights the importance of getting good estimates. Rerunning the models from Kindsvater et al. (2020) with a higher natural mortality rate for territorial males is likely to alter the results in a way that increased fishing mortality to a larger extent have the potential to harm populations and its sustainability.

4.4 Possible errors and future research

Capture-mark-recapture analysis are conducted under certain assumptions, and violations of these can potentially alter the results. For the standard CJS-model used in this thesis there are four assumptions (Cooch, 2008). Firstly, the assumption that every tagged animal in the population have the same probability of being recaptured, and secondly, that every tagged

animal has the same probability of surviving from one occasion to the next. As these two assumptions is never actually met but instead usually highlights basis of why we conduct recapture studies in the first place, these assumptions are addressed by dividing the population into groups (e.g., sex or size-classes). The assumptions become instead that individuals within these groups have the same probability of being recaptured and survive to the next occasion. Potential errors can occur when failing to acknowledge factors which causes variation when grouping the population. Size is usually a cause of much variation in survival and catchability. An evident pattern for fish is that juvenile and smaller stages have lower survival than larger stages (Wootton, 2012). However, in my case, the objective was to determine intra-sexual and seasonal variations for the adult part of the population, so I would argue that these assumptions are met for the purpose of this study. Meanwhile, if comparing my results to other populations with deviating sex-ratios or size distribution, it might be useful to have in mind. Thirdly, is the assumption that tags are neither lost or overlooked and are recorded correctly. This rises the potential for human error in handling of catch, tagging procedure and recording of data. Tag-loss is a potential cause of error in CMR studies. The use of passive integrated transponders (PIT) to tag individuals is well-tested and are proven to have little effect on the fish's survival with minimal chance of tag-loss (Halvorsen et al., 2016b, Peterson et al., 1994, Achord et al., 1996, Gries and Letcher, 2002). Lastly, is the assumption that all samples are instantaneous and recaptured animals are released immediately. In reality they are short periods, and given the time scale this study operating on, I would argue that this assumption is met.

Another topic worth mentioning is whether or not the study area had been protected long enough for the corkwing population to be in a natural state in terms of sex-ratio and social-structures. No wrasse fishing has been permitted in the study area since 2016. Based on the captured individuals from each year we see that the sex-ratio is stable over the four years of sampling. Additionally, the length distribution from each year is stable with the majority of the population larger than 100 mm (Appendix A). Presence of numerous large individuals over the 4 years and stable sex-ratios would imply that the populations was in a natural state during the study.

For future research of corkwing, it would be interesting to conduct similar CMR-studies in commercially fished areas to compare with my results. It would be interesting to investigate how fishing pressure affect natural survival. As this study is conducted in a relatively small

and restricted area surrounding an island, conducting similar studies in open areas with more habitat connectivity would be interesting. To study potential differences in survival and catchability, but also size-distribution and sex-ratios connected to habitat characteristics.

5 Conclusion

Firstly, I found that corkwing wrasse had a seasonal survival pattern with high rates over winter, decreasing rates during spring (during spawning) and lowest rates in the summer (main feeding period). This pattern is likely to be a consequence of seasonal fluctuations in predation risk with more active predators during the spring and summer months.

Secondly, there was intra-sexual variations in apparent survival with the biggest differences during spawning season and main feeding period. Corkwing males of the territorial morph was found to have lower survival rates compared to females and sneakers in both periods with the lowest apparent survival in the main feeding period. Lower apparent survival for territorial males during spawning suggests that their active reproductive role with nest building, parental care and competition comes with a mortality cost. In the summer, territorial males were found to have even lower survival rates. To explain this, I suggest an elevated predation risk connected to increased food search. Territorial males spend more energy and feed less during spawning compared to females and sneakers, and this is likely to be accounted for by increased movement and greater risk-taking in the search for food after the spawning period. I also argue that the estimates of apparent survival for corkwing is close to the true survival due to their sedentary behaviour which implies little-to-no emigration.

Lastly, the catchability of corkwing was overall low with minor intra-sexual variations and seasonal patterns, suggesting that the population was large and that a small proportion was tagged.

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Appendix A

This appendix contains length distribution of captured corkwing (All sizes) for each sampling year (2017-2020). Note that the fyke-nets used do not capture the smallest individuals. Overall minimum length was 65 mm.

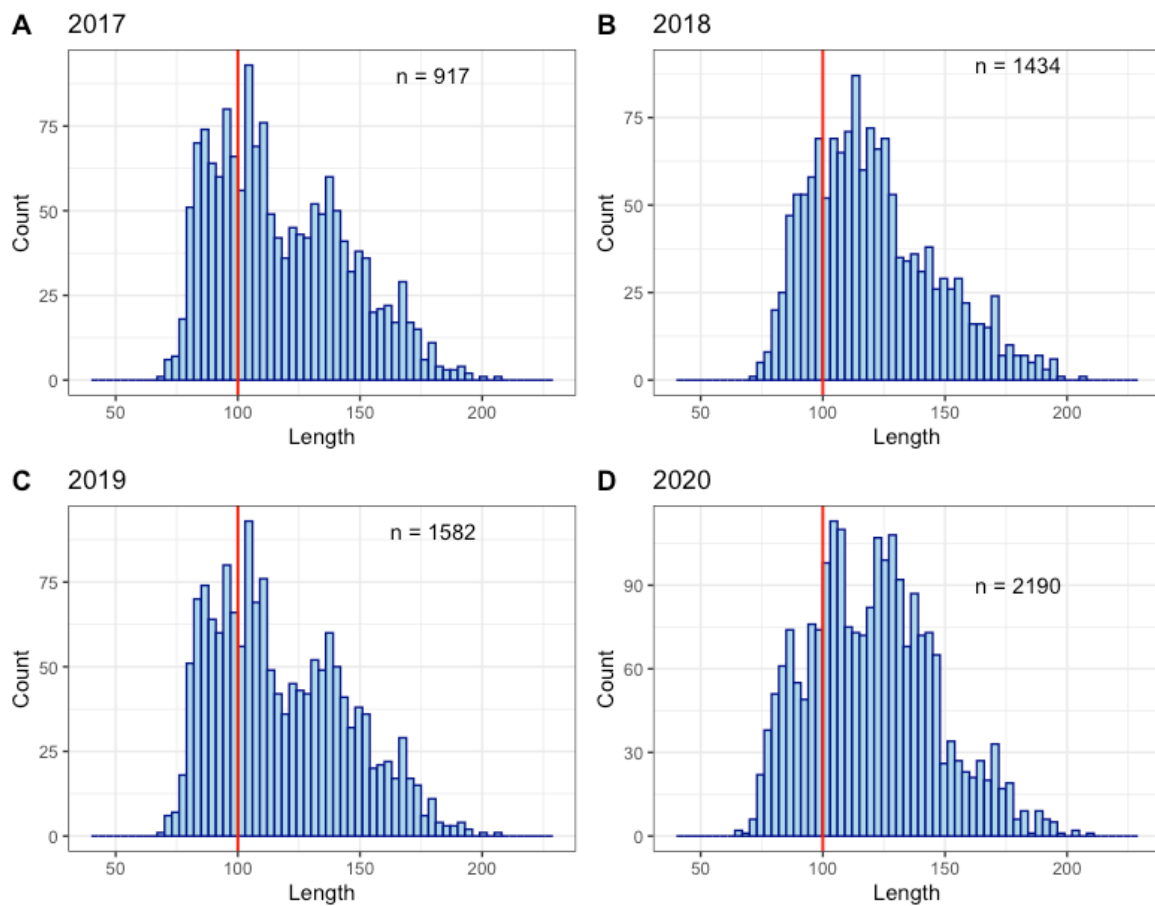


Figure A: Length distributions for the captured corkwing wrasse from Saltskjærholmane from each sampling year. The red vertical lines highlight the size limit for tagging (100 mm).

Appendix B

This appendix contains the estimates from the most parsimonious candidate model (Model 1 in Table 4) from the capture-mark-recapture (CMR) analysis. A standard Cormac-Jolly-Seber (CJS) model with time-specific parameters was used. Real and beta estimates of apparent survival (Φ) and capture probability (p) of corkwing wrasse presented in table A and B.

The estimates of apparent survival are on a monthly scale and are the probability of surviving a month in the time-interval between the capture occasions. The time intervals were discretised to be 8,3 months between early September and mid-May (winter), 1.7 months between mid-May to early July (spring) and 2.0 months between early July and early September (summer).

Additionally, calculations of annual apparent survival for territorial males, females and sneakers are presented.

Table A: Real estimates of apparent survival and capture probability for corkwing wrasse. f = female, m = territorial male, s = sneaker male, se = standard error, lcl = lower 95% confidence interval, ucl = upper 95% confidence interval.

<i>Parameter</i>	<i>Effect</i>	<i>estimate</i>	<i>se</i>	<i>lcl</i>	<i>ucl</i>
Phi	Winter f	0.998	0.006	0.674	1.000
	Spring f	0.970	0,037	0.724	0.998
	Summer f	0.859	0.041	0.758	0.922
	Winter m	0.993	0.020	0.401	1.000
	Spring m	0.904	0.110	0.438	0.991
	Summer m	0.636	0.069	0.495	0.758
	Winter s	0.997	0.007	0.662	1.000
	Spring s	0.962	0.053	0.600	0.998
	Summer s	0.824	0.111	0.512	0.954
p	2018_05 f	0.051	0.013	0.031	0.082
	2018_07 f	0.025	0.008	0.014	0.045
	2018_09 f	0.091	0.016	0.063	0.128
	2019_05 f	0.068	0.011	0.049	0.094
	2019_07 f	0.026	0.006	0.016	0.041
	2019_09 f	0.067	0.013	0.046	0.098
	2020_05 f	0.024	0.006	0.015	0.039
	2020_07 f	0.047	0.009	0.033	0.068
	2020_09 f	0.063	0.013	0.042	0.094
	2018_05 m	0.047	0.015	0.025	0.087
	2018_07 m	0.048	0.014	0.026	0.085
	2018_09 m	0.071	0.023	0.037	0.130
	2019_05 m	0.038	0.012	0.021	0.070
	2019_07 m	0.061	0.017	0.035	0.105
	2019_09 m	0.095	0.029	0.052	0.167
	2020_05 m	0.039	0.012	0.022	0.069
	2020_07 m	0.098	0.023	0.062	0.153
	2020_09 m	0.145	0.034	0.091	0.224
	2018_05 s	0.000	0.001	0.000	1.000
	2018_07 s	0.174	0.159	0.024	0.648
	2018_09 s	0.066	0.067	0.008	0.370
2019_05 s	0.160	0.092	0.047	0.423	
2019_07 s	0.000	0.000	0.000	0.000	
2019_09 s	0.066	0.043	0.018	0.219	
2020_05 s	0.101	0.053	0.035	0.262	
2020_07 s	0.185	0.073	0.081	0.371	
2020_09 s	0.033	0.027	0.006	0.155	

Table B: Beta estimates (logit scale) from the most parsimonious model (Model 1 in Table 4). f = female, m = territorial male, s = sneaker male, se = standard error, lcl = lower 95% confidence interval, ucl = upper 95% confidence interval.

<i>Parameter</i>	<i>Effect</i>	<i>estimate</i>	<i>se</i>	<i>lcl</i>	<i>ucl</i>
Phi	(Intercept) Season: Winter	6.137	2.761	0.726	11.548
	Sex: f				
	Season: Spring	-2.648	3.549	-9.605	4.308
	Season: Summer	-4.333	2.785	-9.791	1.125
	Sex: m	-1.244	0.297	-1.826	-0.662
p	Sex: s	-0.259	0.739	-1.707	1.189
	(Intercept) time8	-2.925	0.262	-3.439	-2.411
	Sex: f				
	time9.5	-0.740	0.406	-1.537	0.056
	time11.3	0.618	0.329	-0.027	1.263
	time19.3	0.308	0.308	-0.296	0.912
	time20.8	-0.703	0.353	-1.396	-0.010
	time22.6	0.294	0.333	-0.359	0.947
	time30.6	-0.778	0.360	-1.484	-0.073
	time32.1	-0.075	0.326	-0.714	0.565
	time33.9	0.230	0.339	-0.434	0.895
	Sex: m	-0.087	0.402	-0.875	0.702
	Sex: s	-10.378	318.893	-635.409	614.653
	time9.5: Sex: m	0.758	0.580	-0.379	1.895
	time11.3: Sex: m	-0.184	0.573	-1.308	0.939
	time19.3: Sex: m	-0.518	0.509	-1.517	0.480
	time20.8: Sex: m	0.980	0.537	-0.072	2.032
	time22.6: Sex: m	0.462	0.565	-0.646	1.570
	time30.6: Sex: m	0.591	0.529	-0.445	1.627
	time32.1: Sex: m	0.869	0.498	-0.108	1.846
	time33.9: Sex: m	1.010	0.534	-0.036	2.056
	time9.5: Sex: s	12.488	318.895	-612.547	637.522
	time11.3: Sex: s	10.034	318.895	-615.001	635.068
	time19.3: Sex: s	11.334	318.894	-613.698	636.366
	time20.8: Sex: s	-7.410	1034.478	-2034.987	2020.166
	time22.6: Sex: s	10.360	318.894	-614.672	635.393
	time30.6: Sex: s	11.899	318.894	-613.133	636.931
	time32.1: Sex: s	11.897	318.894	-613.135	636.928
	time33.9: Sex: s	9.693	318.895	-615.340	634.727

Calculations of annual apparent survival for corkwing wrasse:

The estimates of apparent survival (Table A) are probabilities of survival on a monthly scale. To calculate the annual apparent survival, we first need to find the survival over the whole time-intervals. We do this by taking the monthly estimates raised to the power of the monthly time-interval. Further, we multiply them together to find the annual probabilities of apparent survival.

Territorial males:

Apparent survival over the time-interval between the seasonal capture occasions:

$$0.993 ^ 8.3 = 0.9433 \text{ (Probability of survival over winter)}$$

$$0.904 ^ 1.7 = 0.8423 \text{ (Probability of survival over spring)}$$

$$0.636 ^ 2.0 = 0.4044 \text{ (Probability of survival over summer)}$$

Annual apparent survival probability:

$$0.9433 * 0.8423 * 0.4044 = 0.3213 \approx \underline{\underline{0.32}}$$

Females:

Apparent survival over the time-interval between the seasonal capture occasions:

$$0.998 ^ 8.3 = 0.9835 \text{ (Probability of survival over winter)}$$

$$0.970 ^ 1.7 = 0.9495 \text{ (Probability of survival over spring)}$$

$$0.857 ^ 2.0 = 0.7344 \text{ (Probability of survival over summer)}$$

Annual apparent survival probability:

$$0.9835 * 0.9495 * 0.7344 = 0.6858 \approx \underline{\underline{0.69}}$$

Sneaker males:

Apparent survival over the time-interval between the seasonal capture occasions:

$$0.997 ^ 8.3 = 0.9753 \text{ (Probability of survival over winter)}$$

$$0.962 ^ 1.7 = 0.9363 \text{ (Probability of survival over spring)}$$

$$0.824 ^ 2.0 = 0.6790 \text{ (Probability of survival over summer)}$$

Annual apparent survival probability:

$$0.9753 * 0.9363 * 0.6790 = 0.6200 \approx \underline{\underline{0.62}}$$

