

Catchability and selectivity in a multispecies wrasse fishery in Western Norway

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Abstract

Goldsinny (*Ctenolabrus rupestris*), corkwing (*Symphodus melops*) and ballan wrasse (*Labrus bergylta*) are heavily harvested on the west coast of Norway because of their delousing ability and are supplied to the aquaculture industry as a key tool in controlling salmon lice infestations. Despite rapid development of the fishery in the past decade, knowledge on catchability and selectivity in this multispecies fishery is still limited. This information is essential to ensure sustainable harvesting levels and developing good management strategies for wrasse. In a before-after control-impact (BACI) study, passive integrated transmitter (PIT) tags were used to monitor the fate of individual wrasses before, during and after a period of controlled fishing to quantify species-specific catchability and within-species selectivity in the fishery. Additionally, six indicators were tested for their usefulness in wrasse population monitoring. Logistic regression analysis revealed similar catchability for goldsinny and corkwing (17.5%). Exceptionally low recapture rate of ballan wrasse in the fishery indicates very modest catchability of this species. The wrasse fishery was found to be size- and sex-selective in corkwing. Capture probability was negatively correlated with body size independent of sex and sneaker males entering the fishery (12 cm) had significantly higher catchability (40%) compared with females (25%) and nesting males (17%) of the same size. In goldsinny, the fishery was observed to be sex-selective with significantly higher catchability of territorial males (18%) relative to females (8%). The impact of fishing was successfully detected with three indicators; the proportion of harvestable individuals, proportion of corkwing to goldsinny and catch per unit effort (CPUE) of harvestable individuals. Length- and sex-based indicators did not show any significant effects caused by the fishery. The findings of this study are relevant for improving regulations of the wrasse fishery. The catchabilities found in this study are highly valuable for future stock abundance assessments for the wrasses. Lastly, the observed patterns in selectivity support increasing the minimum size limit for corkwing nesting males to protect immature individuals.

Sammendrag

Bergnebb (*Ctenolabrus rupestris*), grønngylt (*Symphodus melops*) og berggylt (*Labrus bergylta*) fiskes på vest-kysten av Norge til bruk akvakulturindustrien. Leppefiskene er et viktig verktøy for å kontrollere angrep av lakselus. Til tross for rask økning i fangstrater i løpet av det siste tiåret, er kunnskap om fangbarhet og selektivitet i fiskeriet begrenset. Denne informasjonen er essensiell for å sikre bærekraftig høsting og utvikling av gode forvaltningsstrategier for leppefisk. I et før-etter kontroll-påvirkningsstudie (BACI-design) har passivt integrert sender (PIT)-merker blitt brukt for å overvåke skjebnene til individuelle leppefisk av de tre artene, før, under og etter en periode med kontrollert fiske. Dette ble brukt til å kvantifisere artsspesifikk fangbarhet og selektivitet innen hver art i fiskeriet. I tillegg ble seks potensielle indikatorer testet for deres nytte i fremtidig overvåkning av leppefiskbestander. Logistisk regresjonsanalyse viste lik, og generelt lav, fangbarhet for bergnebb og grønngylt (17.5%). Eksepsjonelt lav gjenfangst av berggylt i fiskeriet ga en indikasjon på svært lav fangbarhet for denne arten. Fiskeriet av leppefisk var selektivt på størrelse og kjønn for grønngylt. Fangbarheten var synkende med økende kroppslengde uavhengig av kjønn. Sniker-hanner av høstbar størrelse (12 cm) hadde signifikant høyere fangbarhet (40%) sammenlignet med hunner (25%) og territorielle hanner (17%) av samme størrelse. For bergnebb var fiskeriet selektivt på kjønn med signifikant høyere fangbarhet for hanner (18%) i forhold til hunner (8%). Tre indikatorer viste signifikante effekter av fiskeriet: andel individer større enn minstemål, andel grønngylt til bergnebb og fangst per enhet innsats (catch per unit effort; CPUE) av individer over minstemål. Indikatorer basert på lengde og kjønn viste ingen signifikante effekter av fiskeriet. Resultatene fra dette studiet er svært relevante for videreutvikling av lover og reguleringer i leppefiskfiskeriet. Kunnskap om fangbarhet er verdifullt for fremtidige bestandsmodelleringer av leppefisk. De observerte mønstrene i selektivitet støtter økning av minstemål for territorielle hanner av grønngylt slik at disse beskyttes frem til de er kjønnsmodne.

Preface

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1. Introduction

1.1 Selective fisheries

Fishing is inevitably selective (Law, 2000; Zhou et al., 2010). Selection is defined as a process which produces predictable changes in relative abundance of individuals with different phenotypes. This happens as a result of differential birth and mortality rates associated with individual characteristics (Heino & Godø, 2002). Selective harvesting of fish stocks has persisted for as long as humans have been fishing. Varying economic value as well as temporal and spatial availability of species are important causes of uneven harvesting patterns across marine ecosystems (Zhou et al., 2010). Fishing directly affects the harvested species through elevated mortality rates and by imposing selection. Selection happens within species because of variability in individual characteristics such as body size, sex and behavior (Uusi-Heikkilä, Wolter, Klefoth, & Arlinghaus, 2008; Zhou et al., 2010). In addition, fishing has the potential to affect ecosystem structure and function through alterations of relative species abundances, species interactions and food webs (Zhou et al., 2010).

Fishery-induced selection should be considered together with the species catchability. Catchability is defined as the relationship between the actual abundance of a harvested species and the efficiency of the fishing gear (Arreguín-Sánchez, 1996). In other words, catchability describes the fishing mortality per unit effort (Ellis & Wang, 2007). High catchability consequently means that a large proportion of the available individuals in a population are caught in the fishing gear. Vulnerability to fishery-induced selection can therefore be assumed to increase with catchability as a larger percentage of the population is subjected to the selective forces of the fishery. The interaction between catchability and selectivity thus provides valuable insight for sustainable fisheries management.

Size-selective harvesting is prevalent in marine species of fish. Most commonly, fisheries tend to target larger individuals (Fenberg & Roy, 2008). Over time, selectivity for larger size can lead to overall decline in body-size, reduced age at maturation and slower growth. The negative effects of a size-selective fishery can be exacerbated because of loss of the disproportionately higher reproductive output of older and larger individuals (Hixon, Johnson, & Sogard, 2014). Larger mothers have been found to produce more, bigger and higher quality eggs (Barneche, Robertson, White, & Marshall, 2018). Size-selective fisheries oppose the natural selection for large size and old age (Berkeley, Hixon, Larson, & Love, 2004).

In sexually dimorphic species, size-selective harvesting can result in sex-selectivity solely based on length differences between the sexes (Fenberg & Roy, 2008; Stubberud et al., 2019). Sexual size dimorphism (SSD) is a phenomenon where body size is significantly different between the two sexes of the same species. It occurs because sexual and natural selection affects the two sexes differently, their costs and benefits related to larger size are not the same (Parker, 1992). Sex-selective harvesting can also be caused by spatial and/or temporal differences in distribution or by unique sex-specific behaviors (Hanson, Gravel, Graham, Shoji, & Cooke, 2008). Expected effects of sex-selective harvesting depends on which sex is targeted, in combination with a range of other factors including the life history traits of the species. The response of a species to sex-selective harvesting is thus challenging to predict.

In general, phenotypic changes in fish stocks in response to harvesting are well documented (Law, 2000). Changes to phenotype can also happen as a result of plasticity (change along a reaction norm) or be caused by factors unrelated to fisheries such as environmental change. In order for evolutionary change to occur, the variations in phenotype need to have a genetic basis (Fenberg & Roy, 2008). The degree of heritability and the strength of selection will determine the rate of evolutionary change. Considering selectivity in management of fisheries is increasingly important with degree of heritability of the traits selected on. Fishery-induced evolution can lead to cascading effects in local communities and ecosystems, affecting species interactions and food webs (Kuparinen & Merilä, 2007).

Separating effects of intense exploitation from size-selective harvesting can be difficult, as all age-classes experience elevated mortality from high fishing pressure (Fenberg & Roy, 2008). Overfishing, harvesting a stock above the maximum sustainable yield, generally decreases abundance and yield in the long-term and can have profound ecological consequences (FAO, 2018). In 2015, 33% of the worlds marine fish stocks were declared overfished (FAO, 2018). Even moderate levels of exploitation alter the age-structure in a population, and results in age-truncation (loss of older age groups; Berkeley et al., 2004). A species ability to withstand high fishing pressure depends on life history traits like growth, maximum body size and size at maturity (Heino & Godø, 2002). In this paper, the species-specific catchability and intraspecific (within species) selectivity of the wrasse fishery in Western Norway is studied in a unique before-after control-impact study.

1.2 The wrasses

1.2.1 Distribution and ecology

The wrasses (family *Labridae*) are an abundant group of fish along the Norwegian coast with important roles within the coastal ecosystem. They are opportunistic mesopredators who mainly feed on crustaceans and mollusks (Costello, 1991; Deady & Fives, 1995; Dipper, Bridges, & Menz, 1977; Hilledén, 1978b) and act as prey for larger predators such as gadoids, eel (*Anguilla anguilla* Linnaeus, 1758) and sea birds (Hilledén, 1978b; Salvanes & Nordeide, 1993). There are six species of wrasse present in Norwegian waters (Figure 1): corkwing (*Symphodus melops* Linnaeus, 1758), goldsinny (*Ctenolabrus rupestris* Linnaeus, 1758), ballan (*Labrus berggylta* Ascanius, 1767), rock cook (*Ctenolabrus exoletus* Linnaeus, 1758), cuckoo (*Labrus mixtus* Linnaeus 1758) and the less abundant scale-rayed wrasse (*Acantholabrus palloni* Risso, 1810; Espeland et al., 2010). All of these species have complex behaviors and life history traits, including territoriality and SSD (Costello, 1991). With exception of the scale-rayed wrasse, all named species are harvested for their delousing ability and supplied to the Norwegian salmon aquaculture industry (Rueness et al., 2019; Skiftesvik et al., 2014).

The wrasses are generally found in shallow areas with rocky bottom and algal cover (Costello, 1991; Sayer, Gibson, & Atkinson, 1993). Although they share similar habitats, there are species and size-specific spatial patterns (Skiftesvik, Durif, Bjelland, & Browman, 2015). Factors determining wrasse abundance include access to suitable habitats, degree of exposure and food availability. Corkwing are found in sheltered areas, goldsinny and ballan are found in areas with intermediate exposure and rock cook are found in exposed areas. Additionally, smaller individuals of all species tend to occupy more sheltered areas (Skiftesvik et al., 2015). Goldsinny are limited by the availability of suitable refuge, small caves or crevices in between rocks, where they seek shelter (Sayer et al., 1993).

1.2.2 Life history and reproduction

Goldsinny, corkwing and ballan collectively make up more than 90% of harvested wild wrasse (Rueness et al., 2019), and these three species will be the main focus of this thesis. Variations in maximum size, growth-rate and life span among these three species are substantial. Goldsinny is the smallest species with a maximum length of approximately 20 cm and maximum age of 20 years (Sayer, Gibson, & Atkinson, 1995). Corkwing grow faster, they reach a maximum size of 24 cm and are not found to be older than 8 years. Finally,

ballan is the largest species of wrasse in Norway with a maximum length of 60 cm and can live up to 25 years (Costello, 1991). All species display male territoriality and the wrasse density in an area will be limited by the amount of suitable territories along with a combination of interspecific and intraspecific competition for space. Territory and home range size is species dependent, smallest for goldsinny with territories reported up to 2m² (Hilldén, 1981; Sjølander, Larson, & Engstrom, 1972), somewhat bigger for corkwing, up to 10m² (Skiftesvik et al., 2014). Ballan wrasse have the largest reported territories of the wrasses and can defend an area of 2-300 m² (Sjølander et al., 1972). However, outside of the spawning season the home ranges of ballan wrasse have been found to be much larger, up to 91 000 m² (Villegas-Ríos et al., 2013).

Male territoriality is common among species of bony fish with parental care provided by the male. The most frequently occurring types of parental care in teleosts are guarding and nest-building (Blumer, 1979). This behavior is found in both corkwing and ballan wrasse (Darwall, Costello, Donnelly, & Lysaght, 1992). The male ballan wrasse shares his defended territory with a small harem of females (Sjølander et al., 1972). The females clear their own spawning sites within the territory, while the male constantly patrols the area and protects the eggs from predation (Sjølander et al., 1972). On the other hand, the male corkwings can be separated into two categories based on their mating strategy, nesting males and sneaker males. Nesting males build and maintain a nest within defended territories during the spawning season (Potts, 1985). These males are larger and brightly colored in blue, green and orange (Potts, 1974). During spawning, the female deposits her eggs in the nests. Sneaker males, or accessory males, have a female phenotype and perform sneak fertilization when females spawn with a nesting male (Dipper & Pullin, 1979). After spawning the nesting male exhibits parental care by protecting and fanning the fertilized eggs in the nest (Potts, 1985). Benthic eggs limit the dispersal of these wrasses to the pelagic larval stage (Darwall et al., 1992). Despite male territoriality in goldsinny, this is the only species of wrasse with pelagic eggs along the Norwegian coast (Hilldén, 1981). Sneaker males also occur in this species, and they join the spawning as it happens in mid-water (Hilldén, 1981). The territorial behavior of male wrasses can affect their vulnerability to fishing compared to females.

SSD is pronounced in corkwing, where males grow faster and have a larger size-at-age than females (Halvorsen et al., 2016; Sayer, Gibson, & Atkinson, 1996). Size differences are less pronounced in goldsinny, but males are generally found to be significantly longer than females (Olsen, Halvorsen, Larsen, & Kuparinen, 2018; Treasurer, 1994). Ballan wrasse has a more extreme form of SSD, namely protogynous hermaphroditism. This means that

individuals mature first as females and sequentially develop into males induced by body size in combination with other factors such as sex ratio, conspecific behavior and season (Muncaster, Norberg, & Andersson, 2013). Consequently, the size-selective nature of the wrasse fishery can potentially be sex-selective in all species. Large differences in maximum body size, growth rate and degree of SSD strengthens the need to evaluate the selective pressures separately for each species.

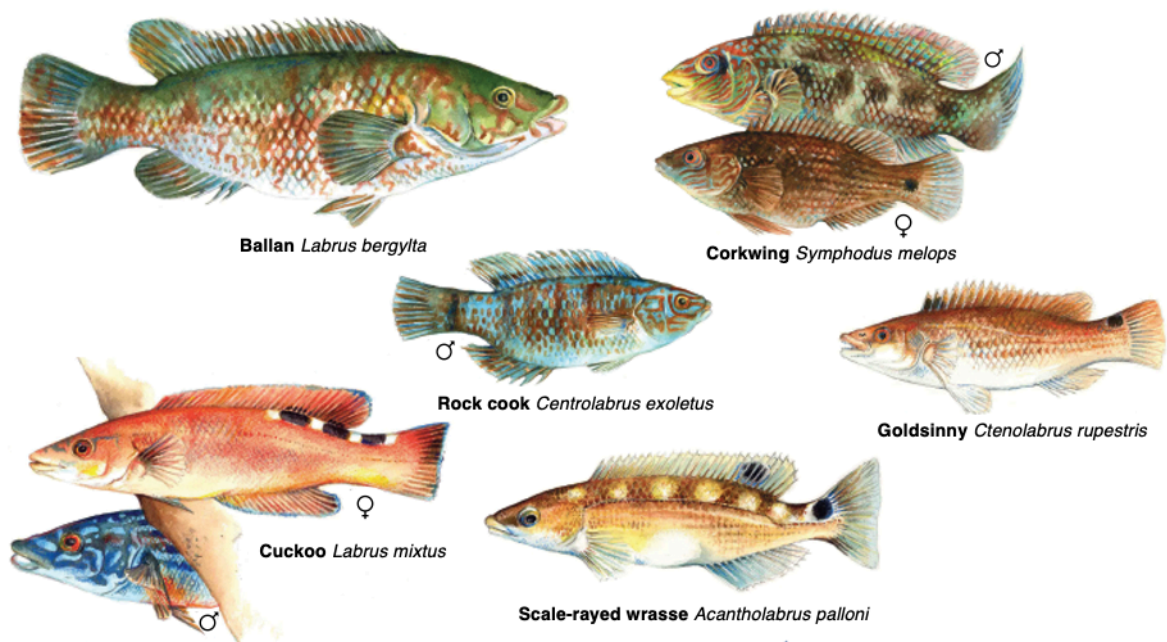


Figure 1: The wrasses of Norway. Upper left: ballan wrasse. Upper right: corkwing wrasse, the larger male in the back and the female in the front. Center: a male rock cook wrasse, females are similar but less blue. Bottom left: cuckoo wrasse, the blue male in the back and the red female in the front. Bottom right: goldsinny wrasse. Bottom center: the rarer scale-rayed wrasse. Illustration by Stein Mortensen. Modified with permission.

1.3 The wrasse fishery

In the late 1980's, a cleaning symbiosis between the wrasses and Atlantic salmon (*Salmo salar* Linnaeus, 1758) was described by Bjordal (1988). Ectoparasitic salmon lice (*Lepeophtherius salmonis* Krøyer, 1873 and *Caligus elongatus* Nordmann, 1832) attach to the skin of salmon and rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792), where they cause damage and stress to the fish (Costello, 2006). The discovery by Bjordal marked the beginning of harvesting wild wrasse for delousing in salmon aquaculture (Espeland et al., 2010). During the late 2000's, salmon lice developed resistance the most common chemical

pesticide used (Besnier et al., 2014), and the demand for wild-caught wrasse substantially increased (Skiftesvik, et al., 2014). Controlling salmon lice infestations remains one of the main challenges of the salmon aquaculture industry (Aaen, Helgesen, Bakke, Kaur, & Horsberg, 2015; Overton et al., 2019).

Recent advances in delousing technology, especially mechanical and thermal treatments, are now largely replacing the use of chemical pesticides in Norwegian salmon farming (Overton et al., 2019). However, salmon farms are still dependent on cleaner fish for delousing and about 50 million cleaner fish (including common lump sucker *Cyclopterus lumpus* Linnaeus, 1758 and several wrasse species) were reported supplied to the industry in 2018 (Rueness et al., 2019). Although the production of cleaner fish is steadily increasing, wild caught individuals still represented 37 % of the reported use in 2018 (Rueness et al., 2019). The extensive use of wrasse as cleaner fish has led to transportation of wrasses from southern Norway and Sweden to western and northern Norway as the locally caught wrasse cannot meet the high demands (Rueness et al., 2019; Skiftesvik et al., 2014).

Prior to discovery of their delousing abilities, the wrasses were not commercially harvested and knowledge about species distributions and biology were limited (Costello, 1991). The wrasse fishery is therefore relatively young, only existing for a few decades. The rapid development with high catch rates has caused several authors to raise concerns about the sustainability of the fishery (Darwall et al., 1992; Espeland et al., 2010; Halvorsen et al., 2017; Halvorsen et al., 2016; Skiftesvik et al., 2015). The Norwegian wrasse landings peaked in 2017 with 27 million harvested individual wrasses (Rueness et al., 2019). Since 2017 there has been a yearly landing cap of 18 million wrasse nationwide, with 10 million allocated to the Western coast of Norway. Currently, the fishery is managed with a seasonal closure (open from mid-July to mid-October) and species-specific minimum size limits; 11 cm for goldsinny, rock cook and cuckoo, 12 cm for corkwing and 14 cm for ballan wrasse (Norwegian Directorate of Fisheries, 2020). These minimum size limits contribute to a size-selective fishery for wrasses.

Currently, well-suited indicators for monitoring wrasses have yet to be established. Monitoring the state of fisheries and detecting changes in population structure is essential to avoid overfishing. Low degree of dispersal combined with territorial behavior and limited horizontal movement (Aasen, 2019) restricts population connectivity for wrasses. In fact, recent discoveries have confirmed that the wrasses are genetically structured into small, local populations along the coast (Jansson et al., 2017; Knutsen et al., 2013). This makes abundance monitoring over larger areas challenging and complicates management of the

fishery. Depletion of local populations can occur even though high catches are maintained as fishermen often change fishing grounds (Halvorsen et al., 2017).

1.4 Aims and objectives

The primary aim of this study is to estimate relative catchabilities of the three main wrasse species harvested in the fishery. Quantifying catchability for wrasses in the multispecies fishery has not previously been done. Catchability is a key parameter in stock assessments for fisheries management and will be highly valuable when modelling population developments of the wrasses in response to fishing. Second, this study aims to describe selectivity on size and sex within each species. For corkwing, the selectivity on age will also be evaluated by using scales for ageing. Knowledge on selectivity within the species is valuable to better adapt fishery regulations and to ensure sustainable harvesting of the wrasses. A third objective is to investigate the short-term effects on the wrasse community composition after a period of intense fishing. Finally, six indicators and their abilities to detect population responses of wrasse to fishing are tested and evaluated for their potential use in monitoring.

2. Methods

2.1 Study area

Data collection was carried out in Austevoll municipality on the Western coast of Norway. The study was done in an area designated for research on wrasse, where all fishing for wrasse has been prohibited by law since 2017 (Figure 2; Norwegian Directorate of Fisheries, 2020). The two islands selected within the protected area, Bleikjo and Saltkjerholmane, are separate from each other by 270 m and a maximum depth of about 25 m. The smallest island, Bleikjo, was chosen for the experimental fishery and will hereby be named fished area. Saltkjerholmane will be referred to as the control area (Figure 2). Both islands were divided into approximately equally sized zones with mean shoreline of 79.8 m in the fished area (4 zones) and 141.3 m in the control area (12 zones; as described in Aasen, 2019).

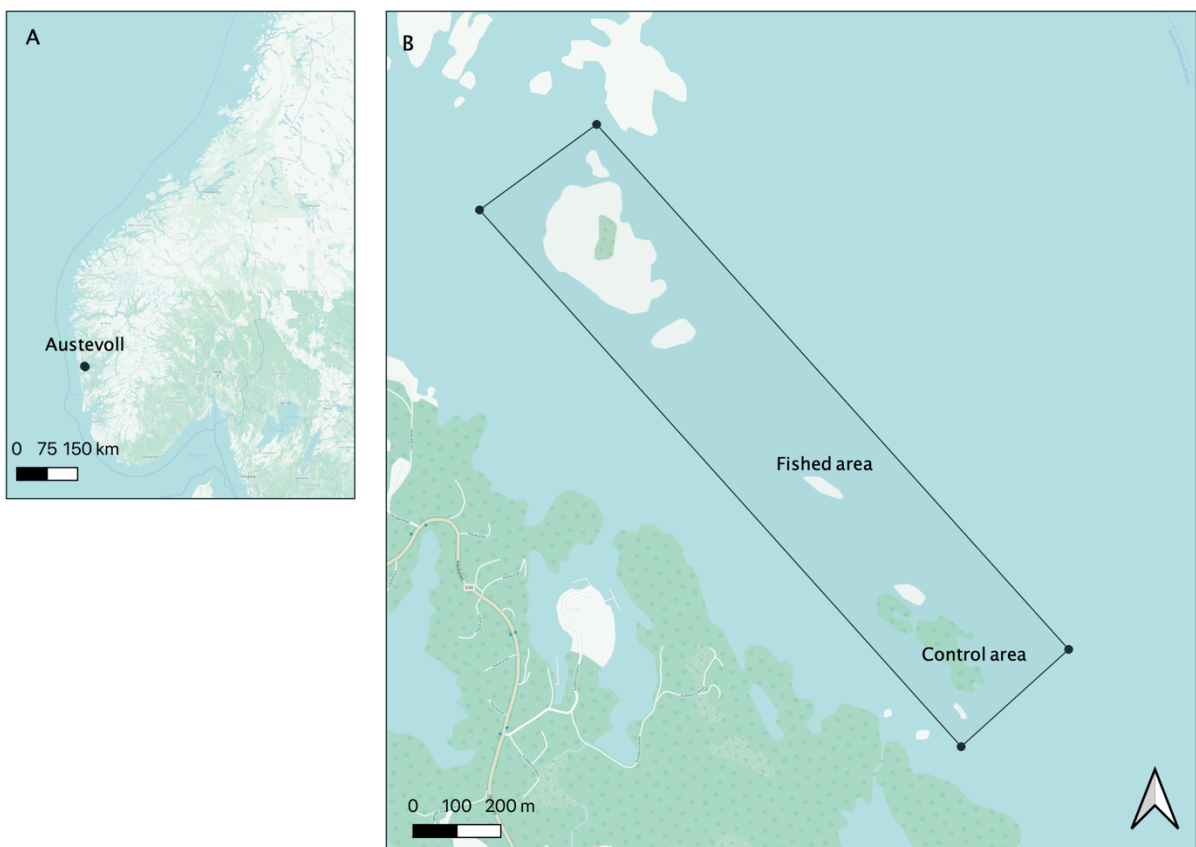


Figure 2: Map showing the study area in Western Norway (A) and the protected research area, (B; boxed area). The two islands are indicated on the map (B), the fished area in the center and the control area in the bottom right corner. Maps created by Kaya Asdal.

2.2 Data collection

2.2.1 Fish sampling

Since protection of the area in 2017, tagging of wrasse has been done in seven sampling periods (Table 1). 2017 had one tagging period in August-September, while 2018 and 2019 each had three tagging periods (May, July and September in both years). In August 2019 an experimental fishery was conducted in the fished area (prior to the final tagging period in September). Unbaited fyke nets (7.8 m single leader, 70 cm entrance ring, and leader mesh size of 11 mm) were used for sampling in the tagging periods. Eight fyke nets were placed out per day for six days. The fyke nets were put out the afternoon and left overnight, resulting in soak times between 15-20 hours. Placement of fyke nets alternated between even- and odd-numbered zones. Each zone (n=16) was sampled every other day, in total 3 times per period. The fyke nets were placed perpendicular to the shoreline, with the leader net extending approximately to the surface. Theoretically, all individuals that move along the bottom will be guided into the chambers by following the leader net.

All catch was determined to species level and measured for total length to the nearest mm. In addition, information on sex (based on sexual products extruded when light pressure was applied to abdomen; female, male or sneaker) was collected for the wrasses. Sneakers have a female phenotype and were only distinguishable in the mating season when sexual products were extruded. When no sexual products were present, sex was determined by phenotype for corkwing and goldsinny wrasse. Corkwing nesting males are brightly colored in blue, orange and green, while females are mostly brown or yellowish and have a dark urogenital papilla (Potts, 1974). Goldsinny males are distinguishable from females by red coloration on the abdomen (Hilldén, 1981). Ballan wrasse cannot be sexed based on phenotype. All catch was gently released at the same location as capture.

2.2.2 PIT-tagging

The fate of individual wrasse was monitored using Passive Integrated Transponder (PIT) tags. These are small glass-encapsulated transponders commonly used in mark-recapture studies of fish and other animals (Gibbons & Andrews, 2004). The use of PIT-tags is well-documented for wrasse and has previously been used to estimate fishing mortality in corkwing (Halvorsen et al., 2017). For this study, half duplex PIT tags were used (12.0 mm × 2.12 mm, Oregon RFID). All wrasses in the catch were scanned to check for presence of a PIT-tag from earlier tagging periods. Previously tagged individuals were treated as described

above and individual PIT-tag ID numbers were noted. Individuals of corkwing, ballan and goldsinny wrasse >100 mm that were not previously tagged, were injected with a PIT-tag in the body cavity using a needle fitted to a tag injector. Prior to tagging, the fish were anesthetized in 50-100 mg l⁻¹ tricaine methanesulfonate (MS-222) in 8-10 l of seawater until loss of equilibrium. This occurred, depending on size and species, after 1 – 3 minutes. The tag injector was cleaned in 96% ethanol between each tag injection and the needle was replaced after tagging approximately 20-40 individuals.

Following the tagging, scales were collected from corkwing in the fished area during period 6 and 7 by using a set of tweezers while the fish were still anesthetized. Scales were collected to investigate age-selectivity in the experimental fishery. The scales were dried and stored in Eppendorf tubes until further processing. All sedated individuals were left in a bucket of seawater to fully recover from the anesthetics before gentle release at the location of capture. FOTS ID: 15307.

2.2.3 Experimental fishery

The experimental fishery was performed in the fished area from the 7th to the 15th of August 2019. Pots (rectangular prism shaped, 70 × 40 × 28 cm, 11 mm mesh size, two 60 × 90 mm elliptical entrances and two chambers, 12 × 70 mm escape gaps) baited with shrimp (*Pandalus borealis* Krøyer, 1838), the most common bait for wrasse fishing in the area obtained from a local source, were used to replicate the local fishery. In contrast to the fyke nets, the fish need to be attracted to the bait and actively enter the pots. Four pots were placed randomly in each zone (n=4) per haul, total 16 pots per haul and overall total of 240 pots (15 hauls; distribution shown in Figure 3). The pots had a soak time between 3-20 hours. Two hauls were performed daily (soak time of about 3 hours for daytime and 12-20 hours for overnight), with exception of days 4, 5 and 9 when only one haul could be performed (soak time overnight 12-20 hours). The pots were put at depths between 1 – 7 m, corresponding to the depths fished in the commercial fishery for wrasse (to avoid problems with decompression when hauling the pots; Halvorsen, Sjørdalen, Larsen, Rafoss, & Skiftesvik, 2020; Halvorsen et al., 2017).

Goldsinny, corkwing and ballan wrasse were determined into three size categories, 1 [<100 mm], 2 [100 mm – species specific minimum size limit] and 3 [$>$ species specific minimum size limit], and sex (based on phenotype as described above, only for goldsinny and corkwing). The wrasses in category 1 were too small have a PIT-tag. Wrasses in size categories 2 and 3 were scanned for presence of a PIT-tag and if present the ID number was

recorded. Individuals in category 2 were below the minimum size limit and thus not harvested. All individuals belonging to size category 3 were removed from the island and kept at the IMR station in Austevoll. Remaining catch was determined to species level, sex (when possible) and measured for total length to the nearest mm, and finally released gently at the site of capture along with the undersized wrasses.

Table 1: Overview of sampling periods and effort throughout the study period. Sampling dates for each tagging period and the experimental fishery. During tagging periods, sampling effort was evenly distributed in both areas and the number of fyke nets is relative to the number of zones in each area, 4 in the fished area and 12 in the control. During the experimental fishery, no activity took place in the control.

Period	Date	Activity	Gear	Sampling effort	
				Fished	Control
1	02.08.2017 – 08.09.2017	Tagging	Fyke nets, unbaited	20	72
2	11.05.2018 – 18.05.2018	Tagging	Fyke nets, unbaited	8	24
3	02.07.2018 – 09.07.2018	Tagging	Fyke nets, unbaited	8	24
4	04.09.2018 – 11.09.2018	Tagging	Fyke nets, unbaited	8	24
5	16.05.2019 – 23.05.2019	Tagging	Fyke nets, unbaited	12	36
6	09.07.2019 – 14.07.2017	Tagging	Fyke nets, unbaited	12	36
Fishery	07.08.2019 – 15.08.2019	Harvesting	Pots, baited	240	-
7	03.09.2019 – 08.09.2019	Tagging	Fyke nets, unbaited	12	36

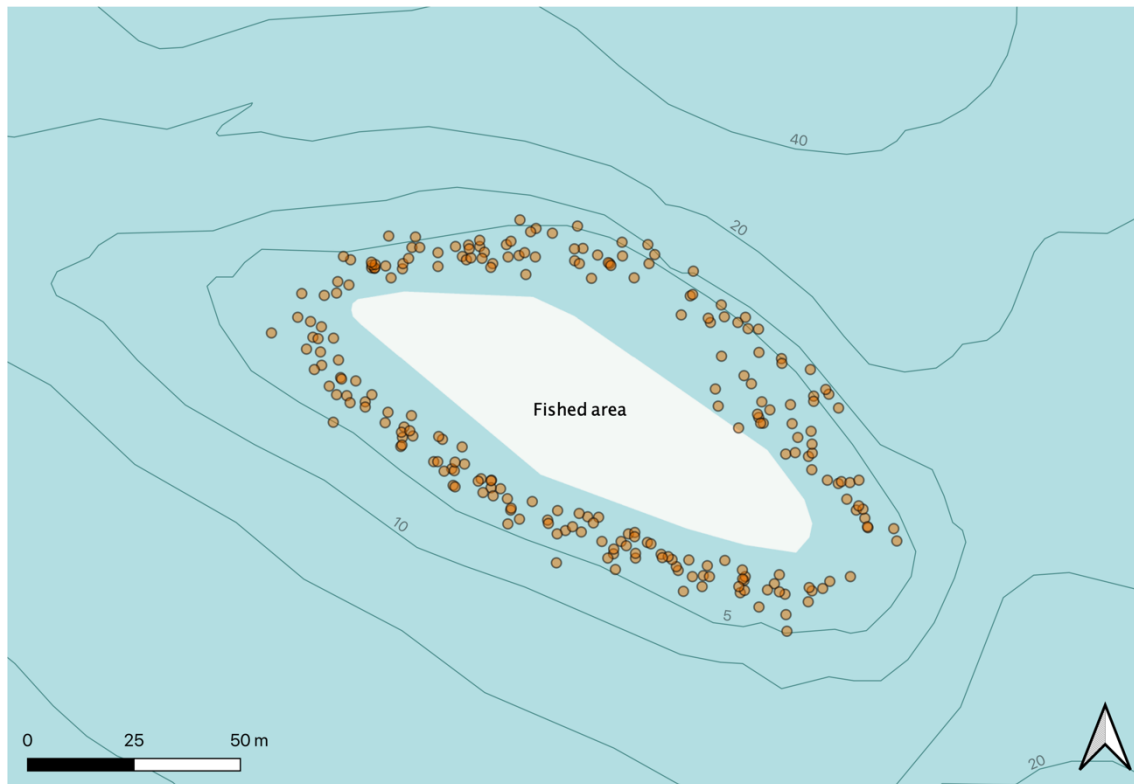


Figure 3: Spatial distribution of fishing effort during the experimental fishery in August 2019. Each orange dot represents one pot ($n=240$). Numbers along the contour lines indicate depth in m. Map created by Kaya Asdal.

2.3 Scale-analysis and age-determination of corkwing wrasse

The use of scales has been evaluated as a successful method to determine age for corkwing wrasse (Vik, 2019). All available scales (1-6 scales per individual) were cleaned, dried and mounted between two microscopy slides. Individual scales were photographed with an IS 1000 microscope camera using the software IS capture and magnification 7,50x.

Age-readings were done in the software ImageJ (Rueden et al., 2017). The scales have alternating translucent and opaque zones. The broad translucent zones are deposited during the growth period every spring-summer and the narrow opaque zones are deposited during the winter when virtually no growth is happening (Boughamou, Derbal, & Kara, 2014; Vik, 2019). Each opaque zone visible on the scale was counted as one year. Quality of scales was noted from 0 to 3, where 0 was unreadable, 1 was somewhat uncertain, 2 was moderate certainty and 3 was high certainty. Only scales with quality 2 and 3 were used for further analyses. Two readers analyzed the scales independently, and the two individual readings were compared. Age reading was done without knowledge of fish characteristics apart from period of sampling (May or July), as this will influence the length of the final growth zone. Scales given a different age by the two readers were re-examined and an age was agreed upon with help from a third and more experienced reader.

Age was plotted against length for nesting males, females and sneaker males separately. Length-age plots were used to draw conclusions about sex-specific growth rates.

2.4 Statistical analysis

Statistical analyses were performed in the R software, version 3.6.1 (R Core Team, 2019). Plots were made to visualize the results using the ggplot2 (Wickham, 2016) and cowplot (Wilke, 2019) packages. Population size estimates were created using the FSA package (Ogle, 2013; Ogle, Wheeler, & Dinno, 2020). Generalized linear models with negative binomial distribution for CPUE was analyzed by means of the glm.nb () in the MASS package (Venables & Ripley, 2002).

2.4.1 Population size estimates

Population sizes were estimated separately per period (2019 only), area and species (goldsinny and corkwing). Within each period the days were grouped into pairs (day1+2, 3+4, 5+6) because the zones were sampled every other day. The pairs therefore represented one sample from all zones. Each tagged fish was seen in a given pair of days (1) or not (0) which

was combined to create a unique capture history per individual. The islands were assumed to be closed populations due to their separation from each other by water ~25 m deep and no natural mortality was assumed due to the short time span of the periods.

2.4.2 Catchability

Interspecific catchability was analyzed using logistic regression (by means of the glm-function) with logit link. The response variable was captured in experimental fishery (1,0). A tagged individual was either captured in the experimental fishery and given the value 1 or not captured in the fishery and given the value 0. PIT-tagged individuals from all tagging periods in the fished area were included in the analysis. Explanatory variables were species (factor) and year last observed (factor). Year was included to look at differences in survival between the species. The natural mortality rate will affect the populations, thus individuals that were tagged in previous years are less likely to still be present in the area.

To study intraspecific selectivity goldsinny and corkwing were analyzed separately. Due to insufficient sample size of ballan wrasse, this species could not be analyzed. The response variable captured (1,0) was the same as for interspecific catchability in all binomial glms(). First, binomial glms() were fitted to investigate selectivity on sex within each species. These models included year last observed (factor) and sex (factor). In corkwing the males were split into two categories, nesting males and sneaker males, resulting in three categories (including female) for this species. Only one goldsinny sneaker male was observed in the fished area, therefore selectivity on this male category in goldsinny could not be analyzed.

To look at selectivity on length, the datasets were reduced to individuals observed in 2019. Only observations done in 2019 had a length measurement reflecting the true length of the fish during the experimental fishery. Explanatory variables were sex (factor), length at last observation (in mm, continuous) and period last observed (factor). Finally, the selectivity on age in corkwing was examined in two alternative ways. The dataset for this analysis was reduced to only individuals with age determined from scale-readings. First, age, as a continuous explanatory variable, was added to the model, along with sex (factor) and period (factor). As an alternative, age was converted to a two-level factor where the first level (2-) contained individuals of age 1 – 2 and the second level (3+) contained ages 3 – 6.

2.4.3 Indicators

Six indicators were tested for their ability to detect a population response to intense fishing on a wrasse community. All indicators were tested on the fyke net data from tagging periods July and September, before and after the fishery, respectively. The indicators were tested only on individuals larger than minimum size limit and separately for each species. Two indicators, proportion of harvestable size and CPUE, were also tested on all species combined. The length-based indicators should not be combined for all species due to the species great differences in maximum length. Similarly, the proportion of males should remain species-specific, because the sex ratios differ among the tested species. For all models two explanatory variables were included: treatment (fished and control) and period (before (6) and after (7) the experimental fishery). The indicator was considered successful of detecting an effect of the fishery when the interaction term (treatment \times period) was significant ($p < 0.05$).

Table 2: Overview of indicators. The indicator is described along with the statistical test, a detailed description of the response variable and comments.

Indicator	Test	Response variable	Comment
Proportion of individuals larger than minimum size	Binomial glm	Harvestable size (1,0). Individuals of harvestable size were given the value 1 and smaller individuals were given the value 0.	
Proportion of males	Binomial glm	Male (1,0). Males were given the value 1 and females were given the value 0. For corkwing 1 was only given to nesting males, and sneakers were combined with females and given the value 0.	Only individuals larger than minimum size. Not applicable to ballan wrasse. (Halvorsen et al., 2017)
Proportion of corkwing to goldsinny	Binomial glm	Corkwing (1,0). Corkwing were given the value 1 and goldsinny were given the value 0.	Only individuals larger than minimum size. (Skiftesvik et al., 2015)
Mean length of harvestable individuals	F-test	Mean length (mm) of individuals larger than minimum	Only individuals larger than minimum size.
$L_{\max 5\%}$	F-test	Mean length of 5% largest individuals	Not possible for ballan wrasse due to low sample size (Miethe, Reeht, & Dobby, 2019)
CPUE	Negative binomial glm	Number of individuals larger than minimum per fyke net	Only individuals larger than minimum size.

2.4.4 Model selection

For all parts of the analyses, model selection was performed using Akaike's Information Criterion (AIC). The model with the lowest AIC was selected unless a model with fewer estimated parameters and $\Delta AIC < 2$ existed, in this case the latter was considered the most parsimonious model and therefore selected (Burnham & Anderson, 2004).

3. Results

3.1 Fish sampling and tagging periods

A total of seven tagging periods were completed between August 2017 and September 2019, resulting in 1627 and 4492 individual wrasses tagged in the fished area and the control area, respectively (Table 3). Mean CPUE throughout all tagging periods is shown per species in appendix (Figure A.1). Throughout the study period 13.5% of corkwing were recaptured once and 2.2% were recaptured more than once. 8.8% of goldsinny were recaptured once and 1.4% more than once. The maximum number of recaptures of an individual of both corkwing and goldsinny were five times. Finally, 4.5% of ballan wrasse were recaptured once or more with a maximum of six recaptures of the same individual. Daily temperature in the study area between May and September in 2019 is shown in appendix (Figure A.2). The mean temperatures in the tagging periods at 5 m depth were 9.34 °C, 14.06 °C and 16.24 °C in May, July and September 2019 respectively.

Table 3: Number of fish captured, and individuals PIT-tagged (in parenthesis) per area and year. Tagged individuals are only represented once, in the year of tagging.

Fished area				
	2017	2018	2019	Total
Ballan	11 (11)	14 (14)	35 (31)	60 (56)
Corkwing	189 (131)	367 (302)	723 (546)	1279 (979)
Goldsinny	213 (118)	358 (218)	360 (256)	931 (592)
				2270 (1627)
Control area				
	2017	2018	2019	Total
Ballan	46 (46)	104 (95)	102 (91)	252 (232)
Corkwing	754 (553)	1326 (930)	1595 (1093)	3675 (2576)
Goldsinny	614 (407)	904 (514)	1064 (763)	2582 (1684)
				6509 (4492)

The control and the fished area showed similar trends in estimated population size for goldsinny and corkwing wrasse (Table 4). Both species increased in abundance between July and September, with goldsinny experiencing greater population growth than corkwing. However, note the wide 95% confidence intervals. These estimates were based on tagged individuals and therefore reflects the population of individuals > 100 mm. Unfortunately, due to low number of recaps it was not possible to estimate population size for only individuals larger than the minimum size limit.

Prior to the experimental fishery a total of 47 ballan, 842 corkwing and 498 goldsinny were tagged in the fished area. Of wrasse sampled in 2019, overall mean lengths in both areas prior to the fishery were 107 mm for goldsinny, 132 mm for corkwing and 182 mm for ballan (Figure 4). A detailed overview of sample sizes per area, species and sex is given in Table 5 along with mean lengths and degree of protection within each category.

Table 4: The table shows estimated population sizes in each sampling period during 2019 with 95% confidence intervals per area, species and period. R = number of recaptures within period.

Species	Area	May (95%)	R	July (95%)	R	September (95%)	R
Corkwing	Fished	4106 (1682 – 10147)	3	1659 (786 – 3794)	5	1880 (770 – 4645)	3
	Control	9735 (3987 – 24057)	3	6044 (1839 – 11789)	1	7203 (4263 – 13003)	12
Goldsinny	Fished		0	1066 (325 – 2080)	1	1649 (602 – 3983)	2
	Control		0	4510 (1645 – 10892)	2	7909 (3938 – 17290)	6

Table 5: Summary of the number of sampled wrasses before and after the fishery in 2019 by area, species and sex (S – sneaker males, F – females and M – nesting/territorial males). Before fishery includes both tagging periods in May and July, while after fishery is the tagging period in September. N indicates sample size within each category. Mean length is given per sex with standard deviation (sd). The proportion of individuals protected, smaller than minimum size limit, within the category is given in percent (%<MSL). Multiple observations (recaptures) are included.

	Species	Sex	Before fishery			After fishery		
			N	Mean length ± sd	% <MSL	N	Mean length ± sd	% <MSL
Fished area	Ballan		27	181.9 ± 58	19	9	119.4 ± 18	78
	Goldsinny	S	1	94.0	100	-		
		F	87	104.9 ± 12	69	75	104.2 ± 12	73
		M	107	109.0 ± 9	50	102	106.9 ± 9	64
	Corkwing	S	39	124.7 ± 16	44	2	118.5 ± 13	50
		F	245	136.9 ± 23	22	120	109.0 ± 23	70
M		236	133.2 ± 40	38	122	115.4 ± 26	81	
Control area	Ballan		62	181.6 ± 74	27	45	145.9 ± 60	67
	Goldsinny	S	3	97.0 ± 22	67	-		
		F	222	106.8 ± 11	64	200	106.2 ± 12	62
		M	322	106.3 ± 9	66	363	109.2 ± 9	55
	Corkwing	S	63	121.8 ± 17	43	3	131.3 ± 13	33
		F	424	134.8 ± 22	23	522	108.7 ± 25	69
M		257	125.0 ± 35	39	394	113.3 ± 22	83	

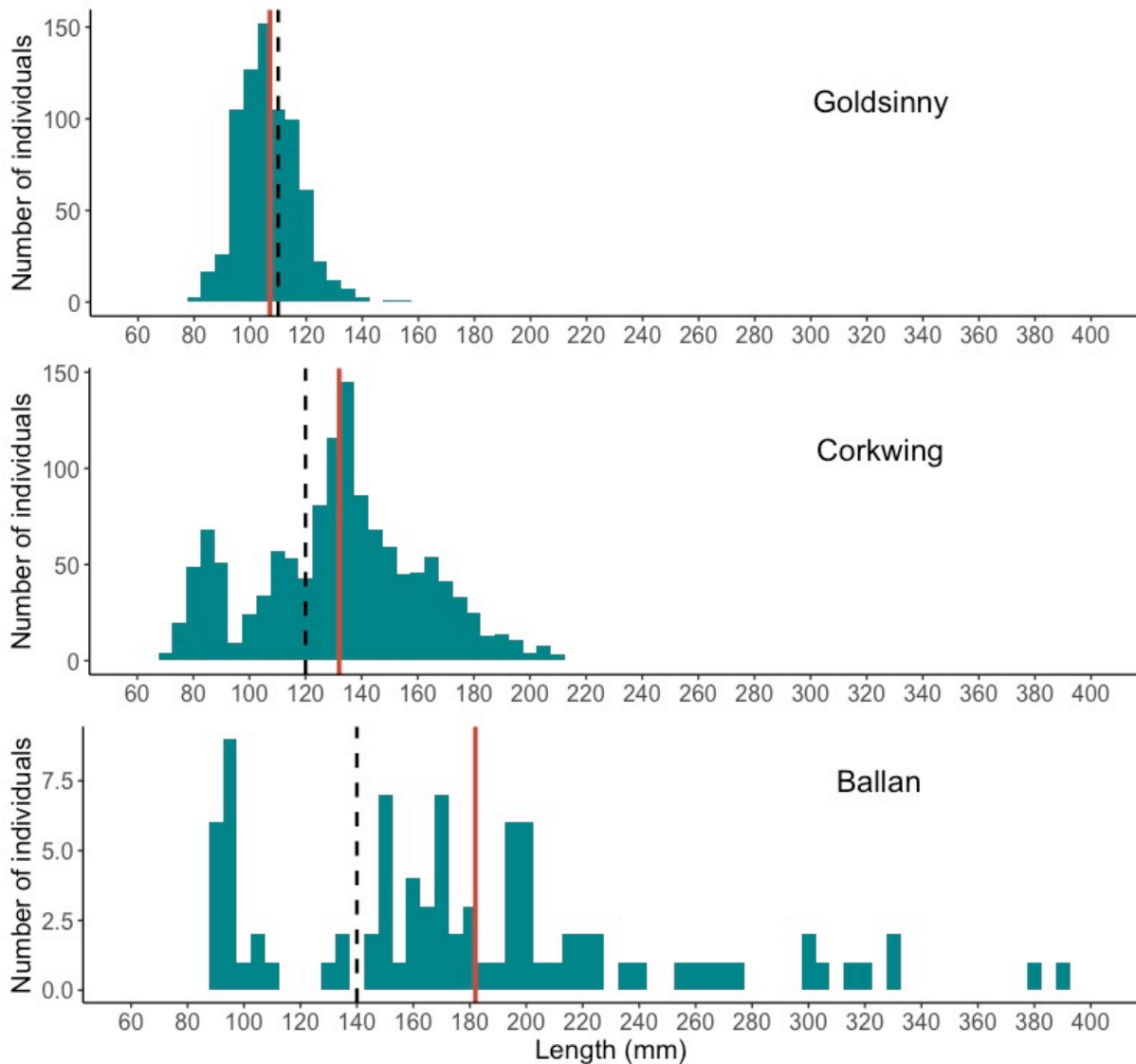


Figure 4: Length distributions of goldsinny (top panel), corkwing (middle panel) and ballan (bottom panel) from tagging periods prior to the experimental fishery in 2019 (May and July) and both areas combined. Species-specific minimum size limits are displayed with dashed black lines (110 mm for goldsinny, 120 mm for corkwing and 140 mm for ballan) and mean lengths of each species are displayed with solid red lines (107 mm for goldsinny, 132 mm for corkwing and 182 mm for ballan). Note the differences in the y-axis.

3.2 Experimental fishery

Total catch of target species, ballan, corkwing and goldsinny wrasse, during the experimental fishery was 2645 individuals, whereof 983 (37%) were above their minimum size limit and harvested. Tagged individuals made up 7.3% (193 individuals) of the total catch and 16.7% (164 individuals) of the harvest. The species composition of harvested individuals was 58% goldsinny, 40% corkwing and 2% ballan wrasse (Table 6). The overall mean CPUE of the three target species in the fishery was 11.02 ± 8.5 (ind/pot, Table 6) and the proportion

of harvestable individuals decreased from above 50% (days 1-2) to below 30% (days 7-9; Figure 5). The two other labrids, rock cook and cuckoo wrasse, were the most abundant species in the bycatch with 189 and 52 individuals, respectively (appendix, Table A.1).

Table 6: Number of individuals of each species captured and harvested in the experimental fishery. Number in parenthesis is tagged individuals in the given category. Tagged individuals below minimum size limit were counted once even though they were captured multiple times.

Species	Captured		Harvested	
	N (tagged)	CPUE mean \pm sd	N (tagged)	CPUE mean \pm sd
Ballan	28 (1)	0.12 \pm 0.4	19 (1)	0.08 \pm 0.3
Goldsinny	1608 (70)	6.70 \pm 6.7	570 (55)	2.38 \pm 2.5
Corkwing	1009 (122)	4.20 \pm 3.8	394 (108)	1.64 \pm 2.1
Total	2645 (193)	11.02 \pm 8.5	983 (164)	4.10 \pm 3.7

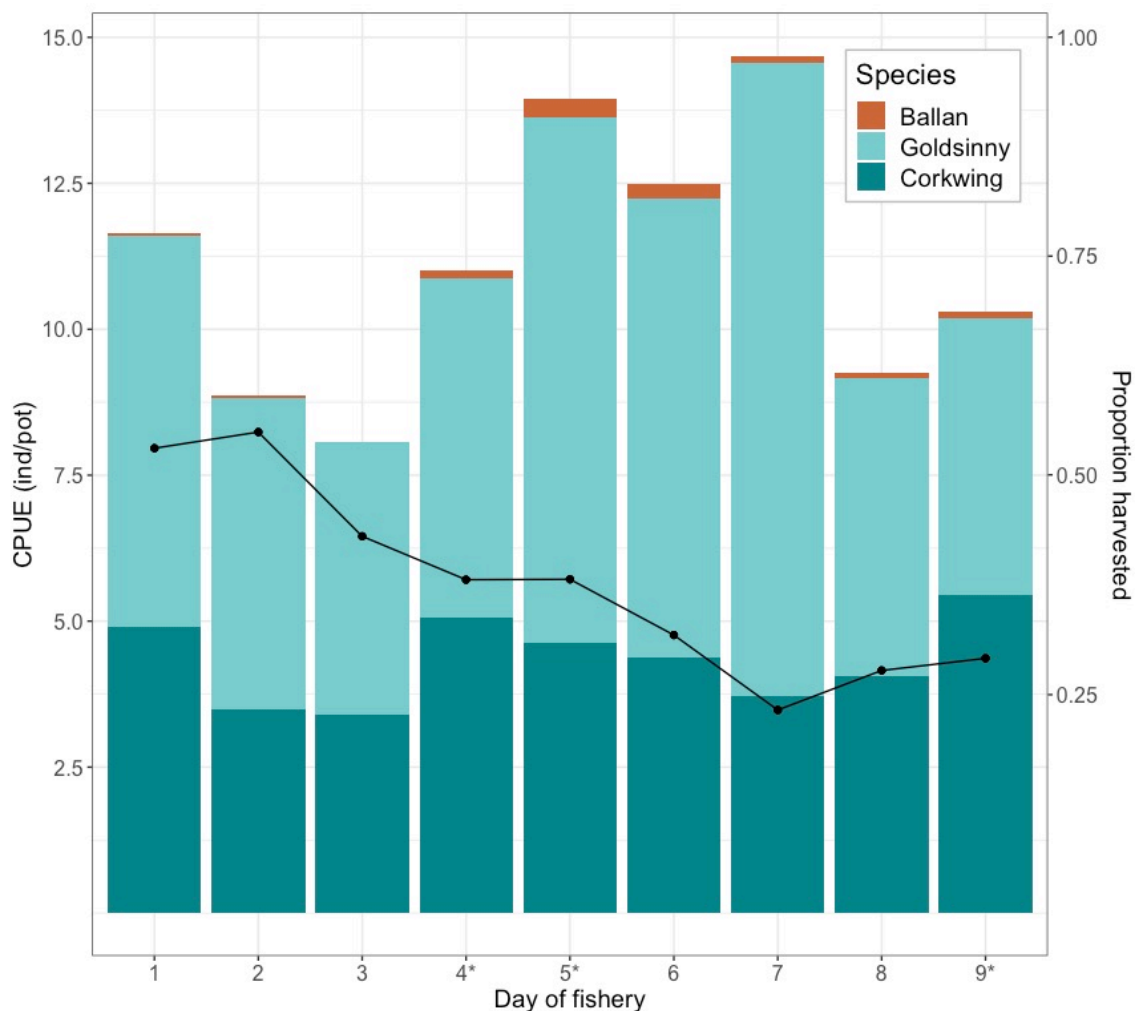


Figure 5: CPUE (individuals per pot; average of overnight and daytime hauls) of captured individuals per species during the experimental fishery. The black line shows proportion of catch harvested throughout the period. *Days 4, 5 and 9 had only one haul (pots set overnight).

3.3 Interspecific catchability

All individuals of corkwing and goldsinny tagged before the experimental fishery (N=1339, 844 and 495 respectively) were used to analyze interspecific catchability of wrasses. Only one previously tagged ballan wrasse (tagged in May 2018) was captured in the experimental fishery, and this species was therefore not included in the analysis.

The model with the lowest AIC had an interaction effect between year last observed and species. However, the model with additive effect of the two explanatory variables were within 2 units in AIC value ($\Delta AIC = 1.57$) and had fewer estimated parameters, thus this was the chosen model (Table 7). The species term was not significant (Table 8) suggesting that there was no difference between the catchability for goldsinny and corkwing. Both species showed a significant increase in catchability with year last observed, i.e. the more recently an individual was observed, the more likely it was to be caught in the fishery (Table 8). Predictions from the model show that goldsinny and corkwing tagged in 2019 had an overall catchability of 17.5%.

Table 7: Model selection of logistic regression on interspecific capture probability. The table gives an overview of model structure, number of estimated parameters, AIC values and ΔAIC , which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	ΔAIC
Captured (0,1) ~			
Year \times Species	6	1091.06	0.00
Year + Species	4	1092.63	1.57

Table 8: Model coefficients for the chosen model for interspecific catchability. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Species goldsinny and Year 2019.

Coefficients	Estimates	Standard error	z value	Pr(> z)
(Intercept)	-1.48	0.17	-8.98	< 0.001
Year 2017	-0.84	0.25	-3.31	< 0.001
Year 2018	-0.31	0.17	-1.83	0.07
Species corkwing	-0.09	0.17	-0.52	0.61

3.4 Intraspecific catchability

3.4.1 Goldsinny

All goldsinny observed in the fished area prior to the experimental fishery (n=495) were included in the analysis. The model with the lowest AIC score had an additive effect of year and sex. However, the model with only sex as the explanatory variable was the most parsimonious model with an AIC score within 2 units of the best model ($\Delta AIC = 1.50$) and fewer estimated parameters (Table 9). The latter, most parsimonious model was used to estimate catchability for male and female goldsinny. According to the model, males had a significantly higher catchability (0.18 ± 0.02) in the wrasse fishery compared with females (0.08 ± 0.02 ; Table 10).

Table 9: Model selection of logistic regression on sex-specific capture probability in goldsinny. The table gives an overview of model structure, number of estimated parameters, AIC values and ΔAIC , which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	ΔAIC
Captured (0,1) ~			
Year \times Sex	6	400.24	3.77
Year + Sex	4	396.47	0.00
Year	3	404.59	8.12
Sex	2	397.96	1.50

Table 10: Model coefficients for the chosen model for sex-specific catchability in goldsinny. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Sex male.

Coefficients	Estimates	Std.error	z value	Pr(> z)
(Intercept)	-1.55	0.15	-10.51	< 0.001
Sex female	-0.90	0.32	-2.84	< 0.01

The dataset was reduced to all goldsinny observed in the fished area in May and July 2019 (n=142) to analyze selectivity on length. The model with the lowest AIC score had only sex as the explanatory variable (appendix, Table A.2). This model estimated a significantly higher catchability for males (0.25 ± 0.05) compared with females (0.11 ± 0.04 ; appendix, Table A.3). However, as the effect of length was not significant, the model based on all individuals from all years was chosen as the primary model.

3.4.2 Corkwing

All corkwing tagged in the fished area prior to the experimental fishery (n=844) were included in the analysis for effects of sex and year last observed on the probability of capture. The model with the lowest AIC score had year and sex as additive effects. This model was chosen for statistical inference (Table 11). Nesting males had significantly lower catchability than females and sneaker males in all years. In addition, the estimated probability of capture increased with year last observed (Table 12). Predictions of the model are shown in Figure 6.

Table 11: Model selection of logistic regression on capture probability. The table gives an overview of model structure, number of estimated parameters, AIC values and Δ AIC, which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	Δ AIC
Captured (0,1) ~			
Year \times Sex	9	671.94	5.71
Year + Sex	5	666.23	0.00
Year	3	686.46	20.23
Sex	3	673.28	7.05

Table 12: Model coefficients for the chosen model for sex-specific catchability in corkwing. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Year 2019 and Sex nesting male.

Coefficients	Estimates	Std.error	z value	Pr(> z)
(Intercept)	-2.31	0.23	-10.13	<0.001
Year 2017	-1.13	0.42	-2.72	<0.01
Year 2018	0.06	0.22	0.29	0.77
Sex female	0.83	0.23	3.54	<0.001
Sex sneaker male	1.81	0.40	4.47	<0.001

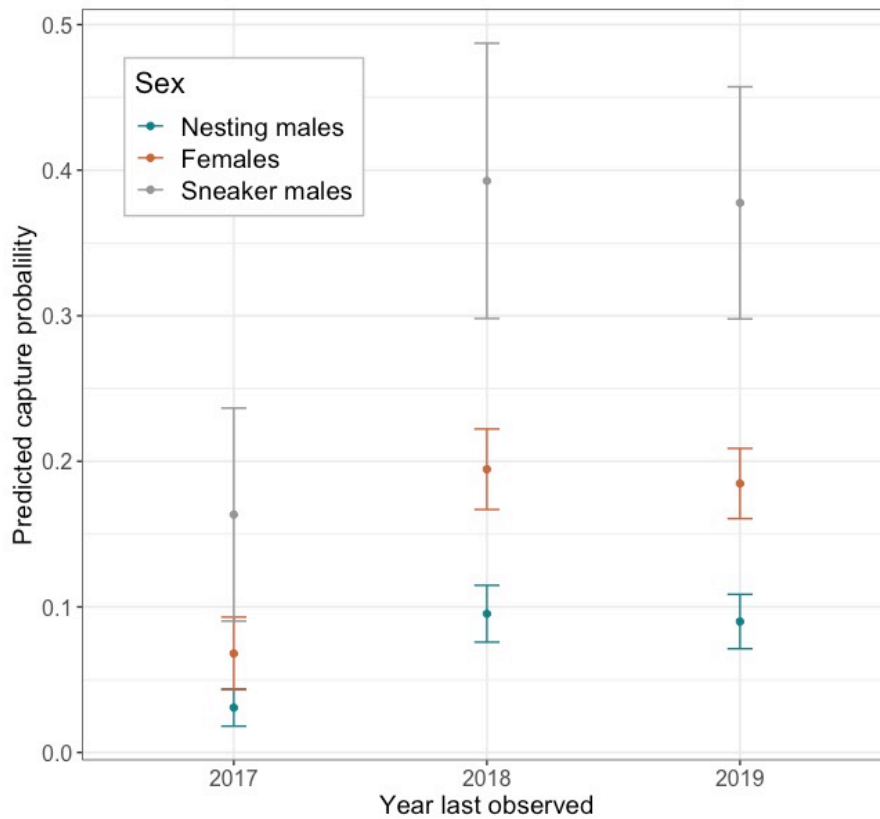


Figure 6: Model predictions from the chosen model of sex-specific catchability in corkwing. The predicted catchability with error bars indicating standard error of the estimate are presented per year and sex. Predicted catchability for nesting male is given in blue, female in orange and sneaker male in gray.

Further, the effect of length on catchability was tested by reducing the dataset to only include individuals last observed in 2019 (May and July; n=399). The model with the lowest AIC had sex and length as additive effects, this model was chosen for statistical inference (Table 13). Estimates from the model show a significantly higher catchability for sneaker males compared with nesting males. All sexes also displayed decreasing catchability with increasing length (Table 14). Predictions from the model are shown in Figure 7.

Table 13: Model selection of logistic regression on length- and sex- specific capture probability in corkwing. The table gives an overview of model structure, number of estimated parameters, AIC values and Δ AIC, which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	Δ AIC
Captured (0,1) ~			
Sex + Length \times Period	6	341.47	0.17
Sex + Period + Length	5	341.46	0.16
Sex \times Length + Period	7	344.00	2.70
Sex \times Length	6	343.97	2.67
Sex \times Period	6	348.20	6.90
Sex + Length	4	341.30	0.00
Sex + Period	4	346.46	5.16
Length \times Period	4	346.05	4.75
Length + Period	3	345.56	4.26
Sex	3	349.80	8.50
Length	2	343.92	2.62
Period	2	362.61	21.31

Table 14: Model coefficients for the chosen model for length- and sex-specific catchability in corkwing. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Sex nesting male.

Coefficients	Estimates	Std.error	z value	Pr(> z)
(Intercept)	0.99	1.09	0.91	0.37
Sex female	0.55	0.37	1.49	0.14
Sex sneaker	1.26	0.49	2.57	<0.05
Length	-0.02	0.01	-3.09	<0.01

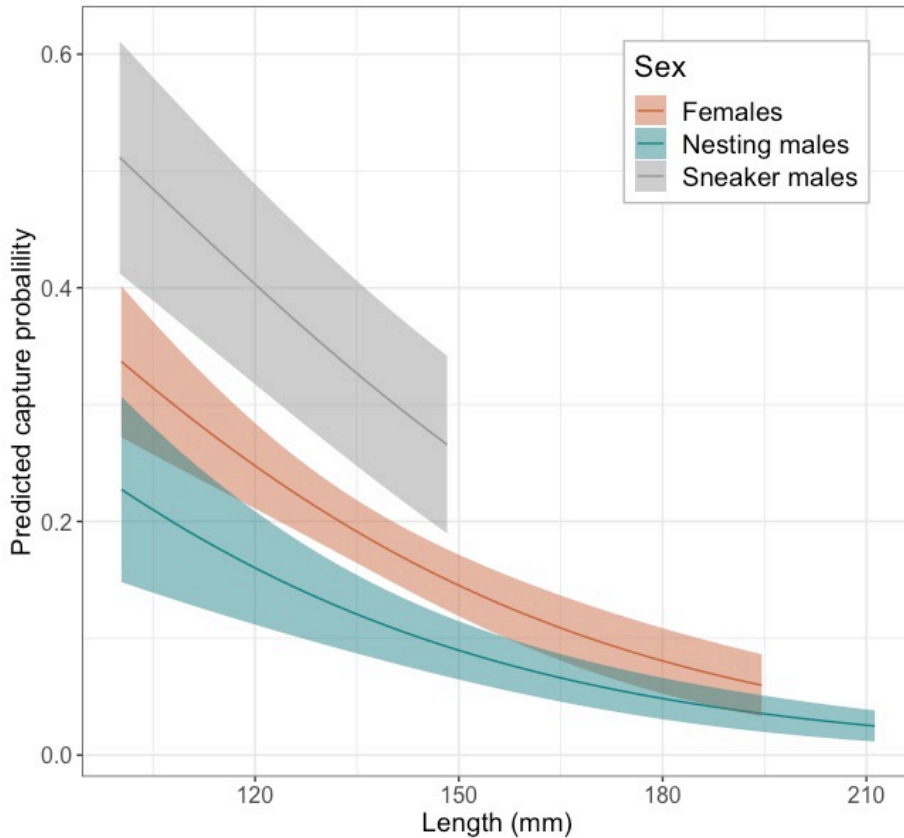


Figure 7: Model predictions from the chosen model of length- and sex-specific catchability in corkwing, only individuals observed in 2019. The predicted catchability (line) with standard error of the estimate (shaded area) are plotted against length and displayed per sex. Predicted catchability for nesting males is given in blue, female in orange and sneaker male in grey.

3.4.3 Scale analysis and age-length relationships in corkwing

In total, 920 scales from 328 individual corkwing were analyzed. 310 scales (34%) were of insufficient quality to provide a reliable age-estimate and were therefore discarded (appendix, Table A.4). Age was successfully determined for 279 individuals, and the remaining 49 individuals (15%) were excluded from the analysis. An overview of number of individuals, mean length and age per period and sex is given in appendix (Table A.5).

The mean lengths of all sexes were significantly smaller in July (mean = 136.64) compared to in May (mean = 146.83; $t = 3.69$, $df = 321.17$, $p < 0.001$). Nesting males (mean = 155) were significantly longer than females (mean = 134; Linear model; Tukey's test: $df=276$, $t=7.29$, $p < 0.0001$) and sneaker males (mean = 120; Linear model; Tukey's test: $df=276$, $t=6.67$, $p < 0.0001$). Nesting males (mean = 2.67) were significantly younger than females (mean = 3.27; Linear model; Tukey's test: $df=276$, $t = -4.55$, $p < 0.0001$), but not

significantly different in mean age from sneaker males (mean = 3.04; Linear model; Tukey's test: $df=276$, $t = -1.58$, $p = 0.25$). Only one individual of age 1 was observed, a nesting male sampled in period 7 with length 101 mm. There was a clear sex-specific age-length relationship (Figure 8). Nesting males showed fast initial growth from age 1 – 3, with a reduction in growth from age 4 – 5. Females and sneaker males showed a more linear relationship between length and age across all ages, with no clear leveling off (Figure 8).

Most individuals were of age 2 and 3, independent of sex (Figure 9). There were clear sex-related differences in age of reaching harvestable size (120 mm). 90% of nesting males were larger than minimum size limit at age 2, while only 2.6% of the females and none of the sneaker males were available to the fishery at this age. Sneaker males did not reach harvestable size until age 3 (Figures 8 and 9).

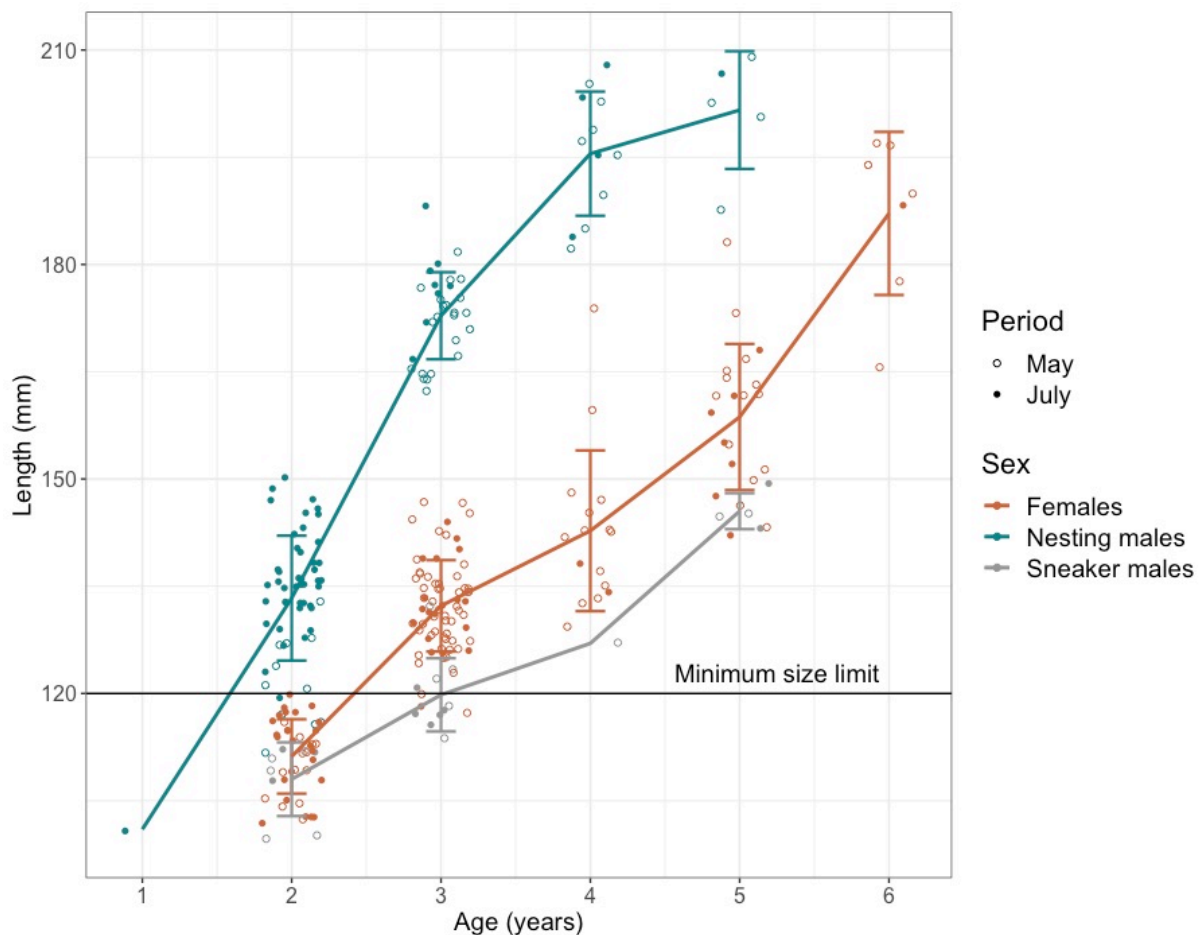


Figure 8: Age-length relationship for corkwing wrasse. Individuals tagged in May are indicated with open circles while individuals tagged in July have filled circles. Nesting males are shown in blue, females in orange and sneakers in grey. The points have been spread out using the jitter function to avoid overlapping. Age-length relationship is drawn as a line through the mean length at age for each sex/male category. Standard deviation of the mean is displayed as error bars.

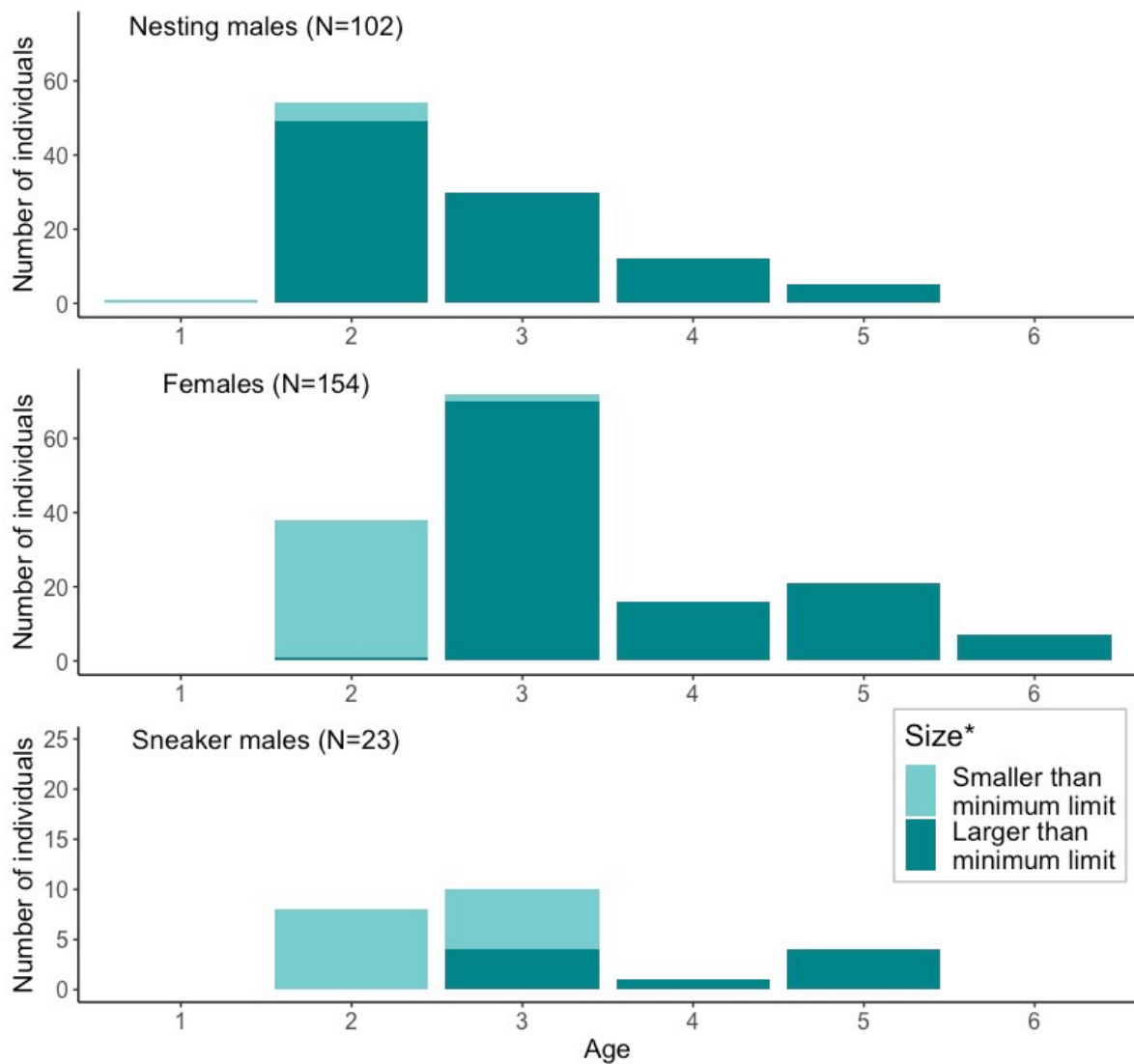


Figure 9: Age-distribution of corkwing per sex/male category, divided into size classes below or above minimum size limit. Lighter colored area represents individuals smaller than harvestable size while darker color are individuals available to the fishery. Number in parenthesis indicates sample size. *Size is size at sampling (May or July).

All corkwing with a reliable age-estimate (n=279) were included in the analysis of effects of age on catchability in the experimental fishery. Age was analyzed in two different ways, as a numeric variable (continuous) and as a factor variable. The first factor level consisted of individuals aged 1 and 2 years (2 –), while the second factor level consisted of all individuals aged 3 years and older (3 +). Splitting age into a factor variable with two levels was built on arguments that this appears to be a threshold age where corkwing have high growth, reach sexual maturity and become available to the fishery.

The model with the lowest AIC score included sex and age (factor) as explanatory variables with an additive effect (Table 15). Inferring from the chosen model, age-group 1–2 had significantly higher catchability than the 3+ age-group (Table 16). The reoccurring pattern in sex-determined catchability is also seen here, with nesting males having significantly lower catchability compared with females and sneaker males (Figure 10).

Table 15: Model selection of logistic regression on age- and sex-specific capture probability in corkwing. The table gives an overview of model structure, number of estimated parameters, AIC values and Δ AIC, which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	Δ AIC
Captured (0,1) ~			
Period + Sex \times Age (factor)	7	241.26	0.58
Period + Sex \times Age (continuous)	7	247.11	6.44
Period \times Sex + Age (factor)	7	244.74	4.07
Period \times Sex + Age (continuous)	7	247.30	6.63
Period + Sex + Age (factor)	5	241.49	0.82
Period + Sex + Age (continuous)	5	243.94	3.27
Period \times Sex	6	245.79	5.12
Period + Sex	4	242.41	1.74
Period \times Age(factor)	4	250.30	9.63
Period \times Age (continuous)	4	251.87	11.20
Period + Age(factor)	3	252.73	12.06
Period + Age (continuous)	3	253.76	13.09
Sex \times Age (factor)	6	240.73	0.06
Sex \times Age (continuous)	6	247.24	6.57
Sex + Age (factor)	4	240.67	0.00
Sex + Age (continuous)	4	244.30	3.63
Period	2	251.77	11.10
Age (factor)	2	251.25	10.58
Age (continuous)	2	253.15	12.48
Sex	3	243.52	2.85

Table 16: Model coefficients for the chosen model for age- and sex-specific catchability in corkwing. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Age(factor) 1–2 and Sex nesting male.

Coefficients	Estimates	Std.error	z value	Pr(> z)
(Intercept)	-2.02	0.37	-5.49	< 0.001
Sex female	1.07	0.43	2.50	< 0.05
Sex sneaker	2.08	0.57	3.65	< 0.001
Age(factor) 3+	-0.78	0.35	-2.21	< 0.05

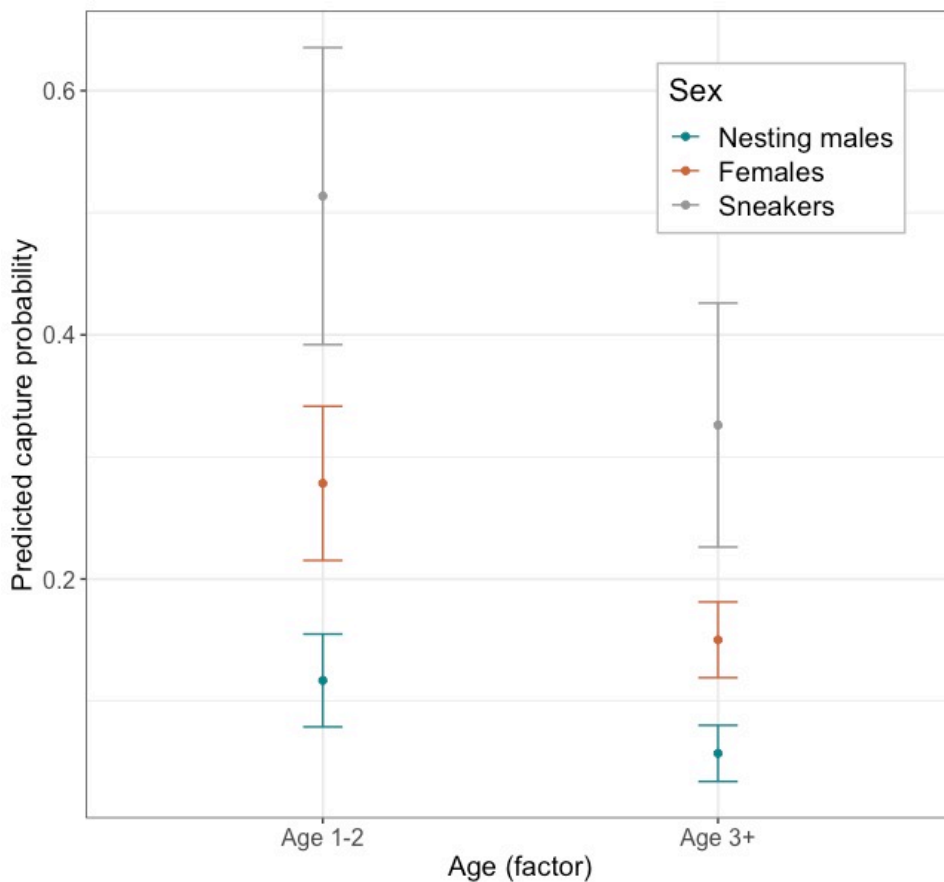


Figure 10: Model predictions from the chosen model of age- and sex-specific catchability in corkwing. The predicted catchability is presented with error bars for standard error of the estimate are p displayed per sex and age-category. Predicted catchability for nesting males is given in blue, female in orange and sneaker male in grey.

3.5 Indicators

The proportion of harvestable individuals revealed significant interactions between treatment and period in two of the tests, all species combined (Logistic regression; Wald's test: $\beta = -0.50$, $\text{std.error} = 0.18$, $z = -2.86$, $p < 0.01$) and goldsinny (Logistic regression; Wald's test: $\beta = -0.83$, $\text{std.error} = 0.29$, $z = -2.83$, $p < 0.01$). The proportion of harvestable individuals was significantly larger in the fished area prior to the fishery. Both areas show a significant decline in proportion of harvestable individuals when all species are combined, however the reduction in the fished area is much greater than in the control (Figure 11 A). For goldsinny, there was a significantly larger proportion of harvestable individuals in the fished area compared to the control area prior to the fishery. After the fishery, there was a significant increase in the control paired with a significant decrease in the fished area (Figure 11 B).

Proportion of males in the catch didn't not reveal any significant interaction for neither goldsinny ($\beta = -0.61$, $\text{std.error} = 0.49$, $z = -1.25$, $p = 0.21$) nor corkwing ($\beta = 0.41$, $\text{std.error} = 0.38$, $z = 1.07$, $p = 0.28$). Proportion of males in the catch was not applicable for ballan wrasse, because for most individuals of this species the sex was not known.

The proportion of corkwing to goldsinny also showed a slightly significant interaction between treatment and period ($\beta = -0.62$, $\text{std.error} = 0.30$, $z = -2.09$, $p < 0.05$). Before the fishery there was a significantly larger proportion of corkwing in the fished area compared with the control. The amount of corkwing to goldsinny decrease in both areas, however the decrease is stronger in in the fished area in after the fishery (Figure 11 C).

There were no significant differences in mean lengths for any of the species in the two areas. The interaction between treatment and period was thus also not significant, goldsinny ($F(1,434) = 0.143$, $p = 0.71$), corkwing ($F(1,586) = 0.05$, $p = 0.82$) and ballan ($F(1,43) = 0.49$, $p = 0.49$).

$L_{\text{max}5\%}$ was tested on goldsinny and corkwing without detecting significant effects of the fishery. This indicator could not be applied to ballan wrasse due to low sample size of this species. The mean length of the 5% longest goldsinny were barely significantly different between the treatments ($F(1,57) = 4.07$, $p < 0.05$) and the periods ($F(1,57) = 6.28$, $p < 0.05$), however the interaction was not significant ($F(1,57) = 1.82$, $p = 0.18$). In corkwing, there were clearly significant differences between treatments ($F(1,87) = 40.46$, $p < 0.001$) and periods ($F(1,87) = 17.49$, $p < 0.001$), however no significant interaction ($F(1,87) = 0.09$, $p = 0.77$).

The final indicator, CPUE of harvestable individuals revealed significant interaction between treatment and period for all species combined ($\beta=-1.11$, $\text{std.error}=0.37$, $z=-2.96$, $p<0.01$) and corkwing ($\beta=-1.31$, $\text{std.error}=0.48$, $z=-2.72$, $p<0.01$). For all species combined, there is a significant decline in the harvested population and a small, but significant increase in the CPUE for the control population (Figure 11 D). CPUE of corkwing above minimum size limit was significantly larger in the fished area compared with the control prior to the fishery. However, following the fishery the CPUE of harvestable individuals was similar in both areas (Figure 11 E).

All results from indicator analysis are summarized in Table 17, model predictions from models with significant interactions are visualized in Figure 11 and details of all statistical models are presented in appendix (Tables A.6, A.7 and A.8).

Table 17: The table shows interaction terms between treatment (fished/control) and period (pre-/post-fishery) for all tested indicators. For indicators tested with generalized linear models, the estimates, standard error, z-value and corresponding p-value are given. For indicators tested with F-test, the degrees of freedom (Df) are given for the interaction term and residuals respectively, along with F-value and corresponding p-value. The results are given per species and significant interactions are indicated in bold.

Indicators	Species	Result				
Binomial glm		Estimate (β)	Std.error	z-value	Pr(> z)	
Proportion of individuals larger than minimum size limit	All species	-0.50	0.18	-2.86	< 0.01	
	Goldsinny	-0.83	0.29	-2.83	< 0.01	
	Corkwing	-0.12	0.24	-0.53	0.60	
	Ballan	-0.81	1.08	-0.75	0.45	
Proportion of males in catch	Goldsinny	-0.61	0.49	-1.25	0.21	
	Corkwing	-0.41	0.38	1.07	0.28	
Proportion of corkwing to goldsinny	Corkwing, goldsinny	-0.62	0.30	-2.09	< 0.05	
F-test		Df		F-value	Pr(>F)	
Mean length of individuals larger than minimum size limit	Goldsinny	1, 434		0.14	0.71	
	Corkwing	1, 586		0.05	0.82	
	Ballan	1, 43		0.49	0.49	
Lmax5% - mean length of the 5% largest individuals in the catch	Goldsinny	1, 57		1.82	0.18	
	Corkwing	1, 87		0.09	0.77	
Negative binomial glm		Estimate (β)	Std.error	z-value	Pr(> z)	
CPUE – number of individuals larger than minimum size limit per fyke net	All species	-1.11	0.37	-2.96	< 0.01	
	Goldsinny	-0.68	0.43	-1.58	0.12	
	Corkwing	-1.31	0.48	-2.72	< 0.01	
	Ballan	-1.17	0.92	-1.27	0.20	

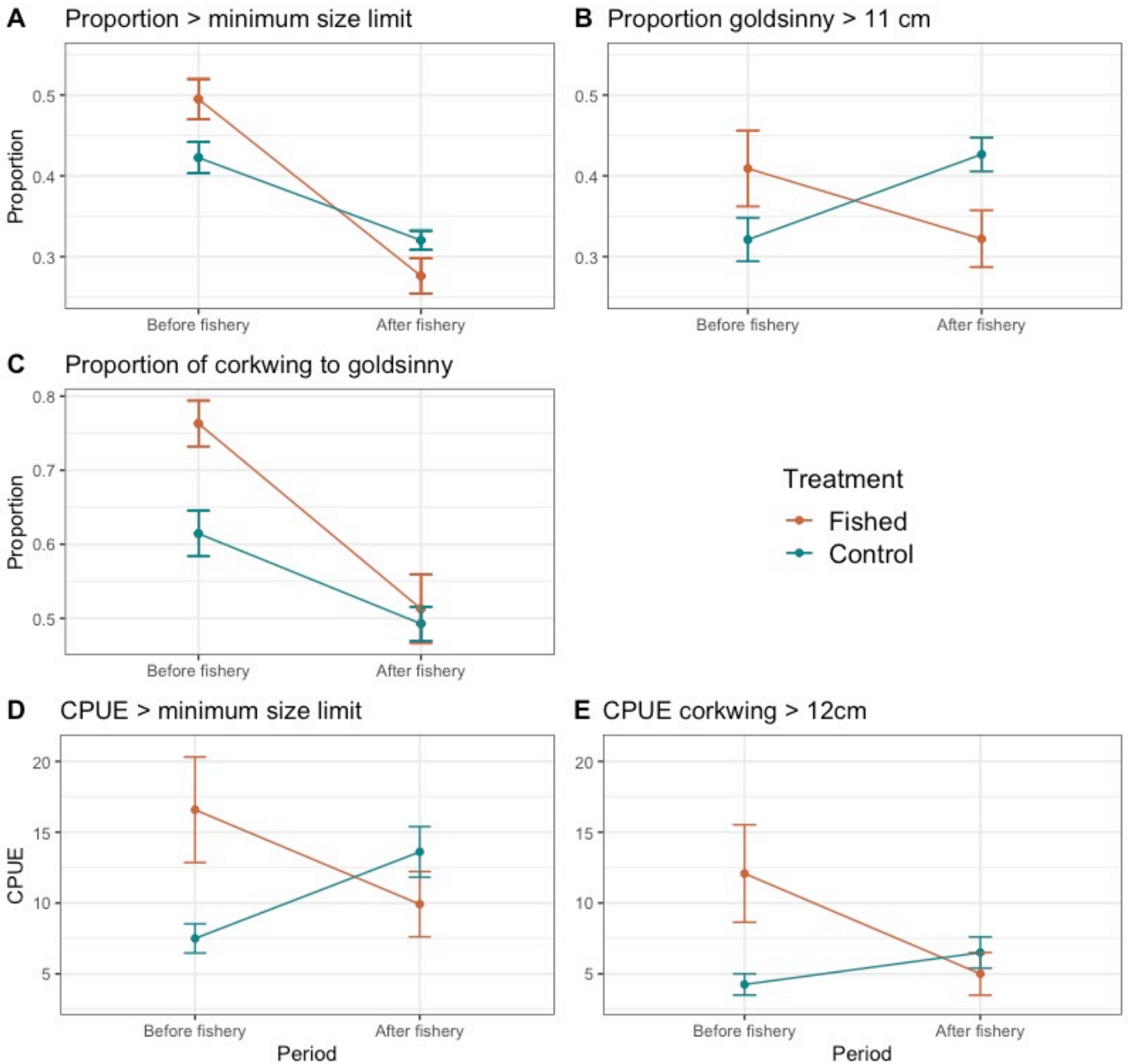


Figure 11: Model predictions of indicators with significant interaction term $Treatment \times Period$. Treatments are fished and control, visible in orange and blue respectively. Periods are before fishery (July) and after fishery (September) in 2019. Panel A: shows interaction between treatment and period for the proportion of harvestable individuals of all species. Panel B: shows interaction between treatment and period for the proportion of harvestable individuals of goldsinny. Panel C: shows interaction between treatment and period for the proportion of corkwing to goldsinny (only individuals of harvestable size). Panel D: shows interaction between treatment and period for the CPUE (ind/fyke) of harvestable individuals of all species. Panel E: shows interaction between treatment and period for the CPUE (ind/fyke) of harvestable individuals of corkwing.

4. Discussion

This before-after control-impact study was designed to quantify catchability and selectivity in three wrasse species, goldsinny, corkwing and ballan, harvested in Western Norway. Realistic estimates of catchability coefficients and selectivity within the species are highly valuable in stock assessments and for guiding management of the fishery. Estimated catchability for corkwing and goldsinny was generally low (17.5%), which could imply that the wrasses are somewhat naturally protected against fishing. This study found patterns of size- and sex-selectivity in the wrasses consistent with previous studies. The size- and sex-selective nature of the fishery has potential to destabilize social structures and cause fishery-induced changes to the populations. Biological explanations of the observed patterns in catchability and selectivity in the wrasses are discussed in context with the implications for fisheries-management. Finally, catch-based indicators showed potential for further development of large-scale wrasse monitoring. Indicators based on length and sex-ratios were not significant.

4.1 Wrasse catchability

Surprisingly, the overall catchability in the wrasse fishery was generally low (17.5%) and this study did not discover any differences in catchability for goldsinny and corkwing. The catchability of ballan wrasse appears to be very low, with only one tagged individual harvested in the experimental fishery. Although the sample size of ballan wrasse was considerably smaller than for the other two species, the findings still give an indication of lower catchability in ballan relative to corkwing and goldsinny. Goldsinny and corkwing wrasse have many similar traits presumably contributing to the observed similarities in catchability. These two species have similar diets (Deady & Fives, 1995; Fjøsne & Gjørseter, 1996; Hilledén, 1978b; Sayer et al., 1996) and are present in the study area throughout the season in relatively high densities. In addition, goldsinny and corkwing both have restricted spatial movement (Aasen, 2019).

Although territories in both goldsinny and corkwing are relatively small, 2m² and 10m² respectively (Hilledén, 1981; Skiftesvik et al., 2014), the territory size may not reflect actual home range size outside of the spawning season. This is supported by findings of mean horizontal movement of 42 m (maximum 386 m) in goldsinny and 121 m (maximum 592 m)

in corkwing (Aasen, 2019; Halvorsen et al., 2020). In ballan wrasse, the reported territory sizes during the spawning period are much smaller than the reported home range sizes outside of the spawning period, 2-300 m² versus 91 000 m², respectively (Sjølander et al., 1972; Villegas-Ríos et al., 2013). However, the very limited size of the fished area in this study may restrict possibilities for horizontal movement in both species (Aasen, 2019) and could potentially mask differences in catchability related to movement patterns.

Goldsinny and corkwing wrasse overlap in dietary preferences and this could result in equal attraction to the bait in the fishing gear. The two wrasse species both display opportunistic feeding behavior and mainly consume crustaceans and mollusks (Deady & Fives, 1995; Fjøsne & Gjøsøter, 1996; Hilledén, 1978b; Sayer et al., 1996). High overlap in diet could imply that these two species compete for the same resources. On the other hand, dietary overlap need not imply competition if the prey species are abundant (Fjøsne & Gjøsøter, 1996). Studies directly comparing the dietary overlap and potential food competition between the species are not available.

4.2 Size-selectivity in the wrasse fishery

In this study, corkwing wrasse displayed a significant decrease in catchability with increasing length independent of sex, which is consistent with previous studies (Halvorsen et al., 2017). As discussed above, dietary preferences may affect attraction towards the bait in the fishing gear. In corkwing dietary preference is length-dependent, changing gradually from crustacean-dominated to a mollusk-dominated diet as body length increases (Deady & Fives, 1995). Other explanations for the observed pattern of size-selectivity in corkwing wrasse include altered spatial distribution after the spawning period or higher natural mortality of larger individuals.

Smaller corkwing primarily feed on crustaceans while older and larger individuals mainly feed on mollusks (Deady & Fives, 1995). The shift to a mollusk-dominated diet has been found to occur when individuals reach ~15 cm (Deady & Fives, 1995) and correspond well to the reduced capture probabilities of individuals >15 cm observed in this study (Appendix, Figure A.3). The majority of fishermen on the western coast of Norway use crustacean bait, mostly shrimp and some crab (Halvorsen et al., 2017). It is possible that the higher catchability of smaller individuals of corkwing is caused by their preference for this bait (Halvorsen et al., 2017).

Spatial distribution of wrasses is size-dependent and larger individuals are found in more exposed areas (Skiftesvik et al., 2015). Additionally, horizontal movement increases with increasing length in corkwing (Aasen, 2019). It could therefore be hypothesized that larger corkwing move to nearby and/or deeper areas post-spawning (Halvorsen et al., 2017). Preferable nesting areas may not be optimal foraging grounds for larger fish, thus resulting in altered spatial distributions after the spawning period has ended. This could potentially explain the pattern of size-selectivity observed in corkwing in this study.

The mean length of corkwing decreased throughout the season in this study (Table 5). As the smallest individuals of corkwing have higher growth rates (Vik, 2019), individuals in their first year are more likely to be retained in the fyke net further out in the season as they become too large to escape through the mesh. In addition, the small and immature males are chased away from the shallow nesting areas during the spawning period by aggressive and territorial nesting males (Potts, 1974). Tagging periods in May and July are just prior to and at the end of the spawning period, respectively. Thus, as tagging effort is concentrated from 1 – 7 m depth, fewer immatures may be present in the catch as these are forced towards deeper and presumably sub-optimal areas during the spawning period (Potts, 1985).

Although recruitment appears to be the main factor contributing to reduced mean length, the observed seasonal pattern could also be connected to loss of longer individuals. Reduced catchability of older and larger corkwing could be caused by increased natural mortality rates post-spawning (Skiftesvik et al., 2014). Spawning is energetically costly and could affect vulnerability to predation or susceptibility to parasites and disease (Harkestad, 2011).

Contrary to corkwing, no size-selectivity was observed in goldsinny in this study. Following the diet hypothesis, this corresponds to findings of no length-dependent shifts in diet of goldsinny (Hilldén, 1978b). Additionally, the mean length of goldsinny showed a more stable trend throughout the season (Table 5). Growth rates in goldsinny are slower than in corkwing along with overall shorter total length (Costello, 1991), presumably causing the less pronounced recruitment-effect on mean length in goldsinny.

4.3 Sex-selectivity in the wrasse fishery

The sex-selective nature of the fishery operated differently in the two species. The fishery was observed to be male selective in goldsinny, whereas it was sneaker selective in corkwing. Sex-selective fishing can be caused by a range of different mechanisms, including

sex-related differences in growth rates, behavior or movement patterns (Biro & Sampson, 2015). Sex-selective harvesting can alter sex-ratios in a population and negatively impact sexual selection and recruitment (Kendall & Quinn, 2013; Sørtdalen, Halvorsen, Vøllestad, Moland, & Olsen, 2020).

In goldsinny, males grow faster and to larger maximum lengths than females (Olsen et al., 2018), thus potentially requiring higher energy input. Capture probability can be positively correlated with growth rate and activity level (Biro & Post, 2008; Biro & Sampson, 2015). This can cause sex-selectivity in species where these processes are sex-specific (Myers et al., 2014). The observed differences in catchability in male and female goldsinny in this study, could be explained by these differences in growth rates.

Contrary to goldsinny, the significant difference in catchability between male strategies in corkwing is likely caused by other factors than growth rate. In corkwing, the sneaker males have the slowest growth rate and the highest capture probability while the faster growing nesting males have the lowest capture probability. Knowledge on corkwing sneaker males is limited and largely confined to studies conducted during the spawning period when these males can be distinguished from females. The reported proportion of sneakers in corkwing vary from 20% (Dipper & Pullin, 1979) to 5% (Sayer et al., 1996). In this study, sneakers made up 19,6% (n=29) of all males tagged in 2019 prior to the fishery. Notably, the sample size of sneakers in this study is small compared with nesting males and females and the results should therefore be interpreted with caution.

The two male types have very distinct behaviors, which may influence their catchability in the fishery. The nesting male's aggressive behavior towards other males could limit the amount of nesting males entering the pots. Trapping mechanisms of pots and fyke nets are different and fyke nets are considered to be less selective (Halvorsen et al., 2017). When sampling with fyke nets, individuals are guided along the leader net and enter the long chamber without being able to easily see if there are other individuals inside. The pots, however, are much smaller and attract fish by the presence of bait. Other individuals caught in the pot will presumably be visible to a larger extent, compared to in a fyke net, for approaching individuals. More specifically, if one large nesting male is already present smaller males may avoid the fishing gear because of their inferior status. Aggressive behavior between two nesting males occurred in fyke nets, the smaller male was typically found with injuries assumedly caused by the larger male (pers. obs; Halvorsen et al., 2017). Behavioral patterns in corkwing are mainly studied during the spawning period, and it is likely that the territoriality of nesting males is more relaxed outside of the mating season. As the fishery is

limited to the post-spawning period it is difficult to evaluate to which degree these sex-specific behaviors may contribute to the observed differences in catchability. However, selective harvesting of either of the male types can potentially destabilize the elaborate social structures in corkwing wrasse (Darwall et al., 1992).

4.4 Responses to harvesting and fishing intensity

Through the removal of males of both species, fishing frees up territories. The experimental fishery in this study was only conducted down to 7 m depth, to mimic the commercial fishing for wrasse. Wrasse are however distributed deeper, and populations may be replenished by individuals from the deep when new territories become available. Goldsinny is found down to 50 m depth (Sayer et al., 1993) in contrast to corkwing and ballan wrasse, who are only abundant in the top 10 m (Halvorsen et al., 2020). The replenishment of individuals from deeper areas will thus likely be more limited for these latter species. Vertical movement by goldsinny has potential to shift the relative species composition. Population size estimates in this study revealed slightly higher densities of corkwing compared with goldsinny in both the fished and control area prior to the fishery (Table 4). Goldsinny generally have smaller home ranges than corkwing (Hilldén, 1981; Skiftesvik et al., 2014), meaning a similar sized area could theoretically support more goldsinny males than corkwing. However, as the corkwing density appears higher, this species may have a competitive advantage in the specific habitat of the study area. Nevertheless, due to limited knowledge on competition for space between goldsinny and corkwing, it is difficult to predict how this would affect the densities of each species in the following season.

Throughout the experimental fishery in this study the proportion of harvestable individuals clearly decreases (Figure 5). This indicates a depletion of the harvestable part of the population, suggesting that if replenishment from other areas occurs, it likely does not happen as an immediate response or is not strong enough to fully replace all size-classes. Replenishment through horizontal movement from nearby islands is presumably very limited as only one individual, a female corkwing, tagged in the control area was harvested in the fished area. Horizontal movement in this study is likely restricted because the islands are separated by 270 m with depths down to 25m. Depth preference of corkwing, maximum of 10 m (Halvorsen et al., 2020), naturally limits migration between the islands for this species. Although goldsinny is distributed deeper than 25 m, very restricted horizontal movement (Aasen, 2019; Halvorsen et al., 2020) presumably limits migration between the islands in the

study area. However, in areas with higher connectivity along shallow areas potential replenishment from nearby populations should not be overlooked.

Although the proportion of harvestable individuals clearly decreased throughout the experimental fishery in this study, the total CPUE remained high (Table 6). Consequently, the proportion of undersized individuals in the catch increased. Tagged individuals below the minimum size limit were recaptured multiple times, with a maximum of six times for corkwing and two times for goldsinny. It is also likely that many individuals too small to be tagged (< 100 mm) were caught multiple times during the fishery. Survival of these released, undersized individuals is likely high as indicated by multiple recaptures of the same individuals.

Water temperature can affect catch rates of wrasses as activity levels in wrasse are temperature-dependent, with very reduced activity below 8-9 °C (Skog, Mikkelsen, & Bjordal, 1994). A threshold for catching wrasse in pots occurs when temperature is below 10-11 °C, due to reduced foraging activity and low attraction to bait in water below this temperature (Skog et al., 1994). The water temperature throughout the experimental fishery was well above this threshold, with mean temperature of 17,8 °C at 5 m depth (measured at the IMR research station in Austevoll; Appendix, Figure A.2), and low catchability is presumably not restricted by water temperature in the fished area.

Fishing intensity in this study was high compared to what is believed to be normal fishing practices (Halvorsen et al., 2017). It can therefore be argued that the lack of dramatic results in this study is not likely caused by insufficient fishing effort or unfavorable environmental conditions. It is more likely that the relatively small impact of the fishery can be attributed to the low catchability of all species (Halvorsen et al., 2020).

4.5 Past-fisheries selection

In the years prior to protection the wrasse fishery intensified. Fishery-induced selection may have already taken place and affected the structure of the wrasse populations. The study area has probably been heavily harvested for almost a decade prior to protection in 2017. Through 2014 the minimum size limit for corkwing wrasse was 11 cm (as opposed to 12 cm since 2015; Halvorsen et al., 2017). It is possible that the years of heavy harvesting has led to age-truncation in corkwing. Halvorsen et al (2016) found both corkwing nesting males and females in western Norway to have a maximum age of 8 years in a study conducted in 2014. Contrary to the study by Halvorsen et al. (2016), this study did not find nesting males

older than age 5 and females older than age 6. Given the observed age-length relationships in corkwing wrasse, the majority of corkwing wrasse in the study area have not been available to the fishery prior to the experimental fishery in 2019.

The older individuals remaining in the population are presumably those who have survived for several fishing seasons. These individuals likely possess traits that cause them to avoid entering the fishing gear or which reduce vulnerability to fishing (Halvorsen et al., 2017). Given that these traits are heritable, these individuals would have a selective advantage. Older and larger individuals are often more successful in reproducing, with more and higher quality offspring (Barneche, White, & Marshall, 2018). It could therefore be assumed that these individuals, capable of escaping harvest, potentially are larger contributors to the next generations, thus contributing to the spread of these “avoidance traits” in the population (Arlinghaus et al., 2017).

Behavioral traits were not assessed in this study but can be subject to fishery-induced selection (Uusi-Heikkilä et al., 2008). Fishing with passive gears is expected to result in directional selection towards more timid behavioral types (Arlinghaus et al., 2017). The wrasses have elaborate social structures and it seems likely that there are also individual variations in behavior which could be altered by selective fishing. No studies exist on variations in personality or behavioral traits in relation to harvesting in the three wrasse species in this study.

Wrasses in the study area did not show increasing trends in CPUE throughout the protected period (Appendix, Figure A.1). The observed catchability for wrasses in this study was relatively low suggesting that the population sizes were not necessarily restrained by fishing. This could suggest that the study area was at its carrying capacity for wrasse, likely caused by limited space or available resources. On the other hand, wrasse populations may be controlled by predators. Large gadoids in the catch (most commonly pollock; *Pollachius pollachius*, Linnaeus 1758) were often found with tagged wrasses in their stomachs (pers. obs). Top-down control of mesopredators does occur in areas with high piscivore abundance, however studies along the Swedish coast have shown that bottom-up mechanisms are more important in determining abundance of intermediate predators such as the wrasses (Bergström et al., 2016).

4.6 Degree of protection and age of availability to the fishery

There are disparities between the age at maturity and the age of availability to the fishery between the sexes and male types in corkwing wrasse. Sneaker males mature in their first year, females in their second year and the majority of nesting males are not sexually mature until their third year (Dipper & Pullin, 1979; Halvorsen et al., 2016). Large differences in growth rates, however, cause the nesting males to reach harvestable size already at age 2 while the females and sneaker males don't reach harvestable size until age 3. Consequently, nesting males is the only sex available to the fishery prior to sexual maturation. These immature male corkwings have about twice as high catchability in their second year compared to when they have reached maturity in their third year. Higher catchability prior to sexual maturity can increase the strength of fishery-induced selection on the nesting males by removing certain individuals before they can reproduce.

Unfortunately, no data on age-distribution was available for goldsinny wrasse in this study as successful aging is not possible without retrieving otoliths. Other studies have documented the age-length relationship for goldsinny wrasse and found that this species reaches harvestable size of 110 mm at age 4-5 in Norway (Skiftesvik et al., 2014) and age 3 in Sweden (Hilldén, 1978a). Goldsinny become sexually mature at age 2 (Costello, 1991), allowing at least two spawning seasons before they become available to the fishery. Presumably, the minimum size limits already established for this species provides protection to a relatively large proportion of sexually mature individuals along with a more even protection of the sexes (Table 5).

Ballan wrasse has been considered more vulnerable to size-selective fishing because of its life history as a protogynous hermaphrodite with relatively high site-fidelity (Villegas-Ríos et al., 2013). Higher vulnerability to fishing in protogynous species relative to gonochoristic species may occur if the males are selectively removed, as it can cause sperm limitation (Alonzo & Mangel, 2004). The current minimum size limit of 14 cm does not protect sexually mature individuals of either sex. Ballan wrasse reach 14 cm in total length already at age 3, whereas females typically spawn for the first time between 6 and 9 years of age (Dipper & Pullin, 1979). The variation in age of maturity for males is much greater and individuals undergoing sex-inversion can be between 5 and 20 years old (Dipper & Pullin, 1979). For these reasons, ballan wrasse has been of special concern. Nevertheless, the finding of exceptionally low catchability for ballan wrasse in this study could imply lower vulnerability to fishing of this species.

4.7 Evaluation of indicators

A great variety of indicators have been developed to detect changes caused by fishing (reviewed in Rochet & Trenkel 2003). Characteristics of a good indicator include meaningfulness and behaving in a predictable way, enabling the development of reference points or threshold values. It should also be easily measurable and able to detect changes exclusively caused by fishing (Rochet & Trenkel, 2003). The suitability of an indicator depends largely on the fishery selectivity and life history traits, thus requiring individual assessments for each species. Of the indicators tested in this study, only three demonstrated a significant interaction between treatment and period. These significant indicators were evaluated as promising for use in monitoring wrasse. Due to the limited extent of the study in both space and time, all indicators would need further testing and development before implementation in monitoring programs.

Overexploitation and size-selective harvesting commonly result in truncated age-distributions (Fenberg & Roy, 2008). Thus, without replenishment of individuals from deeper or adjacent areas, the proportion of individuals available to the fishery would be expected to decrease with increasing fishing pressure. In this study, significant reduction in proportion of harvestable individuals after the experimental fishery was detected on all species combined and on goldsinny alone. The proportion of harvestable individuals is influenced by recruitment. A challenge with this indicator would be separating the effects of recruitment from the effects of fishing. Recording discarded fish in addition to catch is also more time consuming for fishermen and is one of the drawbacks of this indicator along with sensitivity to recruitment.

Significant reduction in CPUE of harvestable individuals over time also could suggest overharvesting and depletion of local populations similarly to the proportion of harvestable individuals. In this study, a significant decrease in CPUE of harvestable individuals was observed for all species combined and corkwing separately. Reporting fishing effort along with the catch is relatively simple for the fishermen and does not require much extra time.

The proportion of corkwing to goldsinny as an indicator was proposed by Skiftesvik et al (2015), based on the ability of goldsinny to colonize a wider range of habitats compared with corkwing. Given that the catchability for goldsinny and corkwing remains similar (as found in this study, Table 8) over consecutive seasons of fishing, a decrease in the proportion of corkwing could indicate reduction in abundance of this species. On the other hand, the ratio of corkwing to goldsinny will be influenced by the local conditions and using this indicator over very large areas may not allow detection of change to smaller, local communities. A

great benefit of this indicator is that it can be calculated solely based on catch data from the fishery and thus can be applied without the need to collect more data.

Traditionally, length-based indicators such as mean length of the catch has been used as an indicator along with length at maturity as a reference point (Rochet & Trenkel, 2003). Despite its widespread use in fisheries monitoring, mean length has been criticized for being overly sensitive to recruitment (Miethe et al., 2019). Corkwing grow fast, especially younger fish (Vik, 2019), and many individuals will become available to the fishery during the harvesting season. In fact, both the fished and the control area in this study had reductions in mean length of corkwing after the fishery. Naturally, recruitment contributes to reduce mean length in a population. This reduction can be mistaken as a change in the length distribution, although unrelated to harvesting, and can result in erroneous conclusions about the effects of harvesting on the monitored population (Rochet & Trenkel, 2003).

To minimize the influence of recruitment and evaluate the presence of large individuals, the mean length of the 5% longest individuals ($L_{\max 5\%}$) can function as an alternative indicator along with appropriate reference points (Miethe et al., 2019). No significant change in mean length of the longest 5% of individuals was evident in either corkwing or goldsinny in this study. The reduced catchability with increasing length in corkwing could protect the larger individuals and contribute to the lack of detectable changes in $L_{\max 5\%}$ in this species.

Despite the discovery of sex-selective harvesting in both corkwing and goldsinny in this study, none of the species had significant changes to the sex ratio associated with harvesting. This is consistent with other studies, where sex-ratios in both corkwing and goldsinny wrasse were similar in marine protected areas and harvested control areas on the southern coast of Norway (Halvorsen et al., 2017). The sex-selectivity in the fishery operates differently within the two species, male goldsinny have the highest catchability while corkwing nesting males has the lowest. The corkwing sneaker males have the highest catchability in the fishery, however males of this type are indistinguishable from females outside of the spawning period without examining the gonads (Dipper & Pullin, 1979). Designing an indicator to detect changes the proportion of sneaker males is thus very challenging. The different sex-selectivity in the two species found in this study underlines the less intuitive nature of an indicator based on sex ratio. Expected effects of fishing would have to be derived based on observed patterns of selectivity within each species, complicating the use of such an indicator. In addition, this indicator is also more time consuming to measure and more error prone, as determining sex for wrasses requires training and skill. This

increases the risk of flawed estimates and drawing incorrect conclusions. Sex-ratio is therefore evaluated to be an unsuitable indicator for wrasse monitoring through catches reported by fishermen. However, monitoring sex-ratios over time in scientific surveys could yield insight to the long-term effects of sex-selective harvesting of wrasses.

Grouping the three wrasse species together can be problematic, as it may mask species-specific effects of fishing. On the other hand, grouping all species is a simple way of monitoring the wrasse community as a whole and could be sufficient to detect fishery-induced changes to the wrasse community. Great benefits of both the proportion of harvested individuals and CPUE of harvestable individuals, are their simplicity and predictable direction of change in response to fishing. Along with geographic location of fishing, by for example GPS-tracking of fishing vessels, these two indicators could be developed to become powerful tools in wrasse monitoring.

The relative species abundance changes throughout the season and over short distances (Skiftesvik et al., 2015). Consequently, the development of reference points for is challenging. Environmental factors such as temperature can also alter catchability through controlling wrasse activity levels (Skog et al., 1994). Developing reference points may consequently be challenging for this indicator and would have to be controlled for both spatial and temporal factors which influence capture probability.

4.8 Implications for stock assessment and management

Catchability is a key parameter in estimating both fishing mortality and abundance, both important in stock assessments for fisheries management (Arreguín-Sánchez, 1996). The catchabilities found in this study will contribute to higher certainty in future modelling of population responses of wrasses to harvesting. The low catchability is positive from a management perspective as the wrasses vulnerability to fishing presumably is lower than previously thought. This is also reflected in the limited observable effects of the fishery on the tested indicators in this study.

Time-varying catchability is well-documented in a range of marine species (Wilberg, Thorson, Linton, & Berkson, 2010) and a seasonal pattern in catchability is evident in the wrasses when comparing to previous studies. Current management regulations with a closure of the fishery during the spawning season appears to be a successful measure in reducing the vulnerability of corkwing wrasse to harvesting. This is supported by the finding of overall higher catchability, especially for nesting males, during fishing in early summer (Halvorsen et

al., 2017) compared to in the late summer (this study). Overall catchability of corkwing at ~40%, independent of sex, was higher when fishing was initiated in June (Halvorsen et al., 2017), compared with the finding of overall catchability of ~20% when fishing was initiated in August (this study). The study by Halvorsen et al. (2017) was carried out in 2014, prior to the legislation protecting the wrasses in their peak spawning period. Similar timing of spawning and behaviors in goldsinny and ballan wrasse, suggests that these species assumedly also benefit from protection in the spawning period.

Restricting fishing to the post-spawning period appears especially important for corkwing nesting males. Fishing mortality of intermediate sized nesting males (125 – 155 mm) in June and July 2014 was between 44 and 76 % (Halvorsen et al., 2017) which is substantially different from fishing mortality of ~20% in August 2019 of similar sized males (120 – 150 mm) found in this study (Figure A.1 Appendix). This seasonal change in catchability, especially for the nesting males, could potentially be related to altered behavior (i.e. moving deeper to forage) or higher natural mortality after the mating season as discussed above.

To reduce the potential fishing-induced selection on nesting males in corkwing wrasse, the minimum size limit should be increased to protect a larger proportion of immature individuals. A sex-specific minimum size-limit for nesting males could be an alternative, as these males are relatively easy to distinguish from females based on phenotype (Halvorsen et al., 2016). The findings of this study would suggest that 15 cm could be suited as a minimum size limit for corkwing nesting males, as this would protect the majority of individuals in their second year.

The Institute of Marine Research recommends the implementation of species-specific maximum limits in addition to the minimum size limits already in place (Skiftesvik & Halvorsen, 2019). The suggested maximum limits for goldsinny and corkwing are 14 cm and 17 cm, respectively. Modelling approaches to compare the effects of minimum size limits to harvesting slots (protecting both small and very large individuals) have indicated that harvesting slots may be a more optimal management strategy when the objectives include other goals than just optimizing biomass of the catch (Ahrens, Allen, Walters, & Arlinghaus, 2020). The wrasses are sold per individual regardless of size, thus optimizing numbers of individuals in the catch would be preferred rather than optimizing biomass. Implementing a maximum size limit to create a slot size would consequently not have large negative effects on profits for the fishermen (Halvorsen et al., 2016).

For goldsinny in this study, the benefits of the proposed slot size would likely be limited as only a very small proportion of individuals were larger than 14 cm (Figure 4). Despite this, due to the local structure of goldsinny populations and their varying size distributions over short distances (Olsen et al., 2018), other populations may benefit to a larger degree. A maximum limit could counter selection for slower growth, which may occur with removal of the largest individuals in the population.

In corkwing, the proposed maximum size limit of 17 cm would assumedly have protected a larger proportion of individuals. However, catchability decreases with size for all sexes and individuals above 17 cm are captured at an exceptionally low rate (Figure 7 and Appendix, Figure A.3). Given that this model reflects the true catchability for corkwing, the implementation of an upper size limit might seem unnecessary as the species appears to encounter the fishing gear at a lower rate as size increases. However, the underlying reasons for the low catchability of longer individuals are largely unknown and could be because of higher natural mortality. Female reproductive output and quality of offspring increases disproportionately with body size, and these larger mothers are likely to be essential contributors in replenishing future populations (Barneche et al., 2018). Larger nesting males have bigger nests and initiate nest building earlier in the season. This could suggest higher reproductive success through room for more eggs in a bigger nest and an extended spawning season (Uglem & Rosenqvist, 2002). The loss of these larger individuals (both females and nesting males) could therefore have large and unforeseen effects on reproductive output in the population. A maximum size limit for corkwing could be beneficial to protect potentially few remaining large individuals (Halvorsen et al., 2017).

5. Concluding remarks and future directions

To conclude, this study found generally low catchability of goldsinny and corkwing wrasse. Ballan wrasse appears naturally protected through low recapture probability in the fishery. Catchability is a key parameter in stock assessments and the findings of this study can greatly improve modelling approaches to evaluate wrasse population responses to harvesting on a larger scale. The overall low catchability for wrasses is good news as it could imply that these populations are less vulnerable to fishery-induced selection and local depletion. The wrasse fishery was observed to be size- and sex-selective in corkwing and sex-selective in goldsinny. The underlying mechanisms of the observed selectivity patterns are unknown. Further studies are needed to evaluate whether the reduced catchability with size in corkwing is a result of higher mortality of large individuals or naturally lower catchability related to other factors. As a precaution, implementation of a maximum size limit is recommended in combination with the current minimum size limit in corkwing. In addition, it is recommended to increase the minimum length for corkwing nesting males so that the sexes are equally protected until sexually mature. Finally, catch-based indicators appear to be promising for wrasse monitoring. Further development of indicators and reference points should account for both spatial and temporal variation to ensure sustainable harvesting of wrasses.

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Appendix

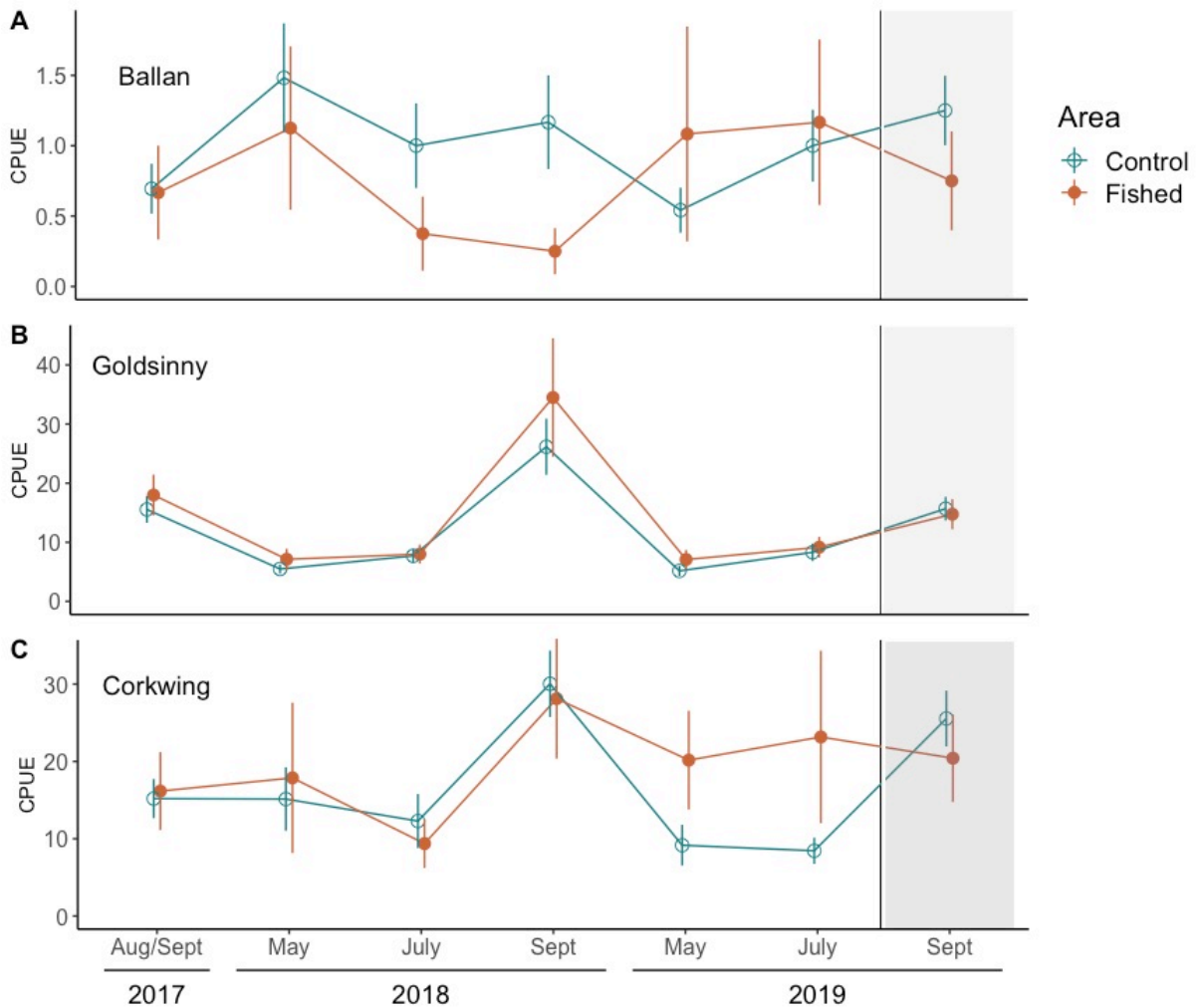


Figure A.1: Mean CPUE (ind/fyke net) per tagging period shown as month and year. Fished area displayed in orange with filled circles and control area in blue with open circles. Panel A shows CPUE of ballan wrasse. Panel B shows CPUE for goldsinny. Panel C shows CPUE for corkwing. Error bars indicate standard error of the mean. Grey area marks the tagging period after the experimental fishery.

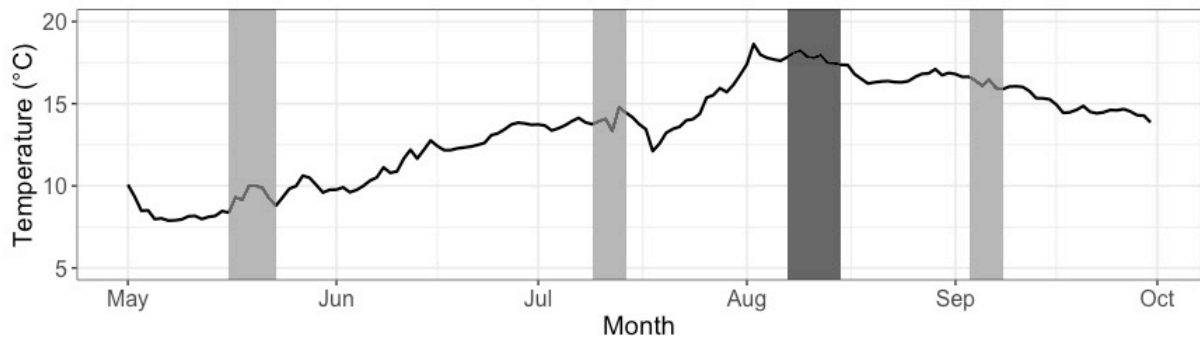


Figure A.2: Daily temperature (in °C) at 5 m depth throughout the study period in 2019, measured at the IMR research station in Austevoll (data obtained from Anne Berit Skiftesvik). Light grey areas indicate tagging periods while the dark grey area indicates the period of experimental fishery.

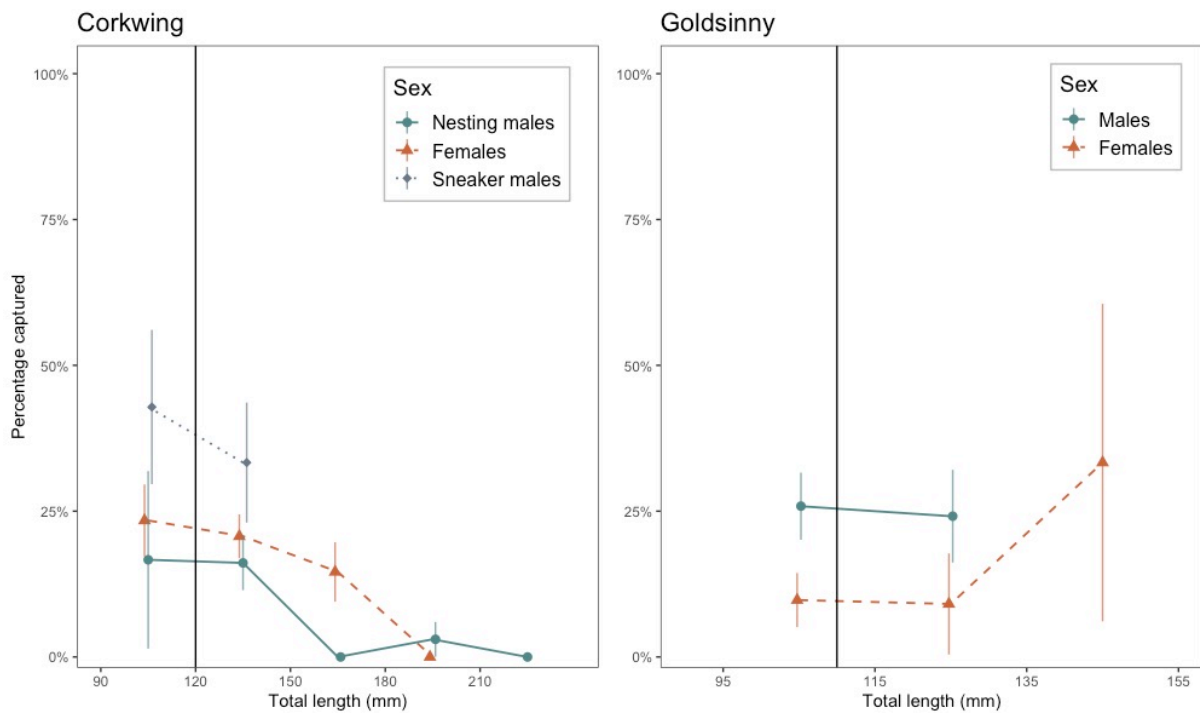


Figure A.3: Percentage of individuals tagged in 2019 that were captured in the experimental fishery per size categories. Categories for corkwing are 90-120, 120-150, 150-180, 180-210 and >210 mm. Categories for goldsinny are 95-115, 115-135 and >135 mm. The black vertical lines illustrate species specific minimum size limits, all individuals on the right side of the line (larger than minimum) were harvested.

Table A.1: Overview of by-catch in experimental fishery. Table shows total number of individuals caught (N) per species, in order of highest occurrence to lowest.

Species	N
Rock cook wrasse (<i>Centrolabrus exoletus</i> , Linnaeus 1758)	189
Cuckoo wrasse (<i>Labrus mixtus</i> , Linnaeus 1758)	52
Fivebeard rockling (<i>Ciliata mustella</i> , Linnaeus 1758)	51
Longspined bullhead (<i>Taurulus bubalis</i> , Euphrasen, 1786)	44
Black goby (<i>Gobius niger</i> , Linnaeus 1758)	14
Rock gunnel (<i>Pholis gunnellus</i> , Linnaeus 1758)	8
Shanny (<i>Lipophrys pholis</i> , Linnaeus 1758)	2
Shore rockling (<i>Gaidropsarus mediterraneus</i> , Linnaeus 1758)	1
Poor cod (<i>Trisopterus minutus</i> , Linnaeus 1758)	1

Table A.2: Model selection of logistic regression on length- and sex- specific capture probability in goldsinny. The table gives an overview of model structure, number of estimated parameters, AIC values and Δ AIC, which is the difference in AIC between the given model and the model with the lowest AIC. The model chosen for statistical inference is indicated in bold.

Model structure	Parameters	AIC	Δ AIC
Captured (0,1) ~			
Sex + Period + Length	4	142.79	2.49
Sex \times Length + Period	5	144.79	4.49
Sex \times Period + Length	5	144.39	4.09
Sex \times Length	4	143.10	2.80
Sex + Length	3	141.10	0.80
Sex \times Period	4	143.73	3.43
Sex + Period	3	142.12	1.82
Length \times Period	4	147.31	7.01
Length + Period	3	145.54	5.24
Sex	2	140.30	0.00
Length	2	143.84	3.54
Period	2	144.81	4.51

Table A.3: Model coefficients for the chosen model for sex-specific catchability in goldsinny. Response variable is captured (0,1). The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference level is Period 5/May and Sex male.

Coefficients	Estimates	Std.error	z value	Pr(> z)
(Intercept)	-2.10	0.43	-4.86	< 0.001
Sex female	-1.02	0.50	-2.04	< 0.05

Table A.4: *Quality of scales and number of scales in each category.*

Quality	Meaning	Number of scales
3	High certainty	209
2	Moderate certainty	401
1	Uncertain	87
0	Unreadable	223
Total		920

Table A.5: *Overview of corkwing used in age-length analysis. The table shows number of individuals per period and per sex with associated mean length and standard deviation (sd) per category. Number of individuals in parenthesis indicated number of individuals with reliable age-estimate, these were included in the analysis of age-length relationship and age-specific selectivity. Mean age along with range is given for all individuals with reliable age estimates within each group.*

Period (Month)	Sex	N (N in age analysis)	Mean length (mm) \pm SD	Mean age (range)
5 (May)	Female	115 (100)	141.02 \pm 21.26	3.5 (2 – 6)
	Nesting male	53 (45)	166.79 \pm 28.36	3.1 (2 – 5)
	Sneaker male	17 (13)	123.94 \pm 15.41	3 (2 – 5)
	Total	185 (158)	146.83 \pm 26.69	
6 (July)	Female	65 (54)	127.02 \pm 18.2	2.9 (2 – 6)
	Nesting male	66 (57)	148.26 \pm 23.82	2.3 (1 – 5)
	Sneaker male	12 (10)	124.83 \pm 14.81	3.1 (2 – 5)
	Total	143 (121)	136.64 \pm 23.30	

Table A.6: Model coefficients for indicators analyzed with logistic regression. Response variables are written in bold. The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference levels are Treatment fished and Period post-fishery. Pre-fishery is the tagging period in July and post-fishery is the tagging period in September.

	Model coefficients	Estimate (β)	Std.error	z value	Pr ($> z $)
Proportion harvestable (0,1)					
All species	(Intercept)	-0.96	0.11	-8.95	< 0.001
	Control	0.21	0.12	1.75	0.08
	Pre-fishery	0.94	0.15	6.43	< 0.001
	Control:Pre-fishery	-0.50	0.18	-2.86	< 0.01
Goldsinny	(Intercept)	-0.74	0.16	-4.63	< 0.001
	Control	0.45	0.18	2.47	< 0.05
	Pre-fishery	0.38	0.25	1.50	0.14
	Control:Pre-fishery	-0.83	0.29	-2.83	< 0.01
Corkwing	(Intercept)	-1.13	0.15	-7.58	< 0.001
	Control	0.05	0.17	0.30	0.76
	Pre-fishery	1.21	0.19	6.35	< 0.001
	Control:Pre-fishery	-0.12	0.24	-0.53	0.60
Ballan	(Intercept)	-1.25	0.80	-1.56	0.12
	Control	0.56	0.86	0.65	0.52
	Pre-fishery	1.84	0.98	1.88	0.06
	Control:Pre-fishery	-0.81	1.08	-0.75	0.45
Proportion males (0,1)					
Goldsinny	(Intercept)	0.62	0.28	2.22	< 0.05
	Control	0.16	0.31	0.52	0.61
	Pre-fishery	-0.02	0.42	-0.05	0.96
	Control:Pre-fishery	-0.61	0.49	-1.25	0.21
Corkwing	(Intercept)	- 0.48	0.27	-1.79	0.07
	Control	- 0.41	0.30	-1.36	0.17
	Pre-fishery	0.77	0.31	2.44	< 0.05
	Control:Pre-fishery	0.41	0.38	1.07	0.28
Proportion corkwing to goldsinny (0,1)					
	(Intercept)	0.05	0.19	0.28	0.78
	Control	-0.08	0.21	-0.39	0.70
	Pre-fishery	1.12	0.25	4.45	< 0.001
	Control:Pre-fishery	-0.62	0.30	-2.09	< 0.05

Table A.7: Model coefficients for indicators analyzed with F-test. Response variables are written in bold, mean length of individuals larger than minimum size limit and $L_{max5\%}$, mean length of the 5% longest individuals. The table shows source, degrees of freedom, sum of squares, mean squares, F-value and associated p-value. Significant model coefficients are marked in bold.

	Source	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Mean length						
Goldsinny	Treatment	1	100	99.83	2.13	0.15
	Period	1	2	2.25	0.05	0.83
	Treatment:Period	1	7	6.72	0.14	0.71
	Residuals	434	20390	46.98		
Corkwing	Treatment	1	547	546.8	1.66	0.20
	Period	1	781	780.6	2.38	0.12
	Treatment:Period	1	16	16.3	0.05	0.82
	Residuals	586	192587	328.6		
Ballan	Treatment	1	3958	3958	0.81	0.37
	Period	1	4310	4310	0.89	0.35
	Treatment:Period	1	2397	2397	0.49	0.49
	Residuals	43	209111	4863		
Lmax5%						
Goldsinny	Treatment	1	138.2	138.24	4.07	< 0.05
	Period	1	213.0	213.01	6.28	< 0.05
	Treatment:Period	1	61.6	61.58	1.82	0.18
	Residuals	57	1934.4	33.94		
Corkwing	Treatment	1	4036	4036	40.46	< 0.001
	Period	1	1744	1744	17.49	< 0.001
	Treatment:Period	1	9	9	0.09	0.77
	Residuals	87	8678	100		

Table A.8: Model coefficients for indicators analyzed with generalized linear models (negative binomial distribution). Response variable is CPUE, mean number for individuals larger than minimum size limit per fyke net. The table shows model coefficients, estimates, standard error of the estimate, z-value and associated p-value. Significant model coefficients are marked in bold. Reference levels are Treatment fished and Period post-fishery. Pre-fishery is the tagging period in July and post-fishery is the tagging period in September.

	Model coefficients	Estimate (β)	Std.error	z value	Pr ($> z $)
CPUE (individuals larger than minimum)					
All species	(Intercept)	2.29	0.23	9.89	< 0.001
	Control	0.32	0.27	1.19	0.24
	Pre-fishery	0.51	0.32	1.59	0.11
	Control: Pre-fishery	-1.11	0.37	-2.96	< 0.01
Goldsinny	(Intercept)	1.56	0.26	5.98	< 0.001
	Control	0.34	0.30	1.15	0.25
	Pre-fishery	-0.24	0.37	-0.63	0.53
	Control: Pre-fishery	-0.68	0.43	-1.58	0.12
Corkwing	(Intercept)	1.61	0.30	5.34	< 0.001
	Control	0.26	0.35	0.76	0.45
	Pre-fishery	0.88	0.41	2.13	< 0.05
	Control: Pre-fishery	-1.31	0.48	-2.72	< 0.01
Ballan	(Intercept)	-1.79	0.74	-2.43	< 0.05
	Control	0.92	0.79	1.16	0.25
	Pre-fishery	1.50	0.84	1.80	0.07
	Control: Pre-fishery	-1.17	0.92	-1.27	0.20