

## Sex- and size-selective harvesting of corkwing wrasse (*Symphodus melops*)—a cleaner fish used in salmonid aquaculture

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Fishery-induced changes in sex ratios can have negative effects on reproductive rates and affect sexual selection and evolutionary trajectories. Here, we investigate sex- and size-selectivity of the fishery for corkwing wrasse (*Symphodus melops*) in Western Norway. The males that build and guard nests (nesting males) grow faster than females and sneaker males. Corkwing wrasse were tagged ( $n = 1057$ ) during (May–June) and after (July) the spawning period in 2014 within a no-take site and in a nearby site open for fishing. We monitored the fishery within and nearby the tagging sites from June to October and sampled recaptures on all commercial fishing trips. Fishing mortality was higher for nesting males than for females (open site; tagged *during spawning*: 36% vs. 29%; *after spawning*: 49% vs. 36%) and was found to be caused by nesting males having higher capture probabilities than females, independently of body size. The fishing mortality of sneaker males did not differ from nesting males, but the sample of sneaker males in the study was small. The probability of being retained by fishers once captured depended on size, but not on sex. The small no-take site reduced fishing mortality, and the sex- and size-selectivity was similar to the open site. By demonstrating the capture process to be male-selective in a commercial fishery, our study highlights the importance of assessing sex-selectivity in similar fisheries. If detected, management measures protecting the sexes more equally should be implemented, such as slot-size limits and marine-protected areas large enough to account for sexual differences in spatial behaviour.

**Keywords:** aquaculture-environment interactions, marine-protected areas, selective fisheries, sex-selective harvesting, Western Norway.

### Introduction

Fisheries often selectively target large individuals (Fenberg and Roy, 2008; Zhou *et al.*, 2010; Gwinn *et al.*, 2015). Many commercial fisheries are regulated with minimum size limits or gear modifications to limit exploitation on immature fish. In addition, large fish tend to be higher valued and targeted, especially in recreational fisheries (Lewin *et al.*, 2006). In species with sexual size dimorphism, the larger sex may therefore be harvested at higher

rates than the smaller (Rijnsdorp *et al.*, 2010; Kendall and Quinn, 2013). Moreover, passive fishing gears (e.g. gillnets, pots, hook and line, fyke nets) can select against fast growth and active and risk-taking behaviours (Uusi-Heikkilä *et al.*, 2008; Biro and Sampson, 2015; Arlinghaus *et al.*, 2016). Thus, sex-selective harvesting may happen independently of body size if other traits that affect capture probability differ between sexes. Fishery-induced changes in sex-ratios may have consequences for reproductive

output and sexual selection (Fenberg and Roy, 2008; Rowe and Hutchings, 2003; Kendall and Quinn, 2013). Quantifying sex-selectivity is therefore necessary in order to understand how populations will respond to fishing and to design optimal management strategies.

In this study, we used tag-recovery data to estimate sex-selectivity in the commercial fishery for corkwing wrasse (*Symphodus melops*) in Western Norway. Together with other wrasse species, the corkwing wrasse is increasingly harvested in Scandinavia and the British Isles to be deployed as cleaner fish in salmonid aquaculture net pens, where salmon lice (*Lepeophtheirus salmonis*) infestations can be a major issue (Darwall et al., 1992; Skiftesvik et al., 2014a; Halvorsen et al., 2016). Corkwing wrasse is found in shallow, rocky coastal habitats from North Africa to Norway and may attain a total length of 28 cm and a maximum age of 9 years (Quignard and Pras, 1986; Darwall et al., 1992; Sayer and Treasurer, 1996). Most males develop as colourful nest-building males, growing faster and maturing later than females (Potts, 1974; Halvorsen et al., 2016). A small proportion of males adopt an alternative sneaker strategy. These males are indistinguishable from females in appearance and perform sneak fertilizations during pair spawning between a nesting male and female (K.T. Halvorsen, pers. obs.). The sneaker strategy appears to be fixed throughout their lifespan, and sneaker males grow more slowly and mature earlier than the nesting males (Uglem et al., 2000; Halvorsen et al., 2016). The wrasse fishery is conducted with baited pots or fyke nets set at shallow reefs or rocky shorelines. In Norway, it is managed by a spring closure (lasting until 17 June in the year of study) to restrict fishing during the main spawning period, which has been shown to peak in June (Skiftesvik et al., 2014b). In addition, a minimum legal size is enforced, which was 11 cm in 2014 when this study was conducted, but increased to 12 cm in 2015. The undersized wrasses are released alive on site of capture. The wrasse fishery in Norway could therefore be expected to be sex-selective for two reasons; first, the higher growth rates of nesting males means they reach the minimum size limit before females and sneaker males (Halvorsen et al., 2016). Second, the sexes may have differential capture probabilities in passive gears. Size-selective gear will catch sexes at different rates if they differ in body size. Moreover, the higher growth rates of nesting males imply higher feeding intensity, which can increase attraction to baited traps (Biro and Sampson, 2015). In addition, other sexual behaviour differences can affect capture probability. For instance, males are investing in nesting and territory defence and feed less than females during the spawning period (Potts, 1974; Deady and Fives, 1995). Combined, the two independent selective processes of size regulations and gear selectivity interact to produce either stronger or weaker overall sex selectivity.

In this study, we tested whether fishing mortality on corkwing wrasse differs between sexes and male types and also investigated the combined effect of sex and body size on capture probability and on the probability of being retained once captured. A secondary objective was to assess whether a small marine-protected area (MPA) would reduce fishing mortality and whether sex and size selectivity differed relative to that in the open site. MPAs can maintain natural sex ratios, size and age structure (Pillans et al., 2005; Claudet et al., 2010; Baskett and Barnett, 2015), but a recent study has highlighted the possibility of MPAs inducing selection for individuals with small home ranges which are more likely to stay within the protected area (Villegas-Ríos et al., 2016). Thus, if

spatial behaviour differences between sexes or size classes exist, a relatively small MPA may protect these groups differently. We tagged corkwing wrasse with passive integrated transponder (PIT) tags during and after the spawning period in a small protected site and a nearby open site with a wrasse fishery representative for the area located in a semi-enclosed bay. The fate of tagged fish in the fishery was determined by recording recaptures on all commercial fishing trips occurring within the bay over a three month period. We then decomposed size- and sex-selectivity in two separate analyses, estimating (i) the probability of being captured and (ii) the probability of retention given captured. This allowed for testing for sex-selectivity adjusting for body size and evaluating how these different processes affect the overall selectivity of the fishery.

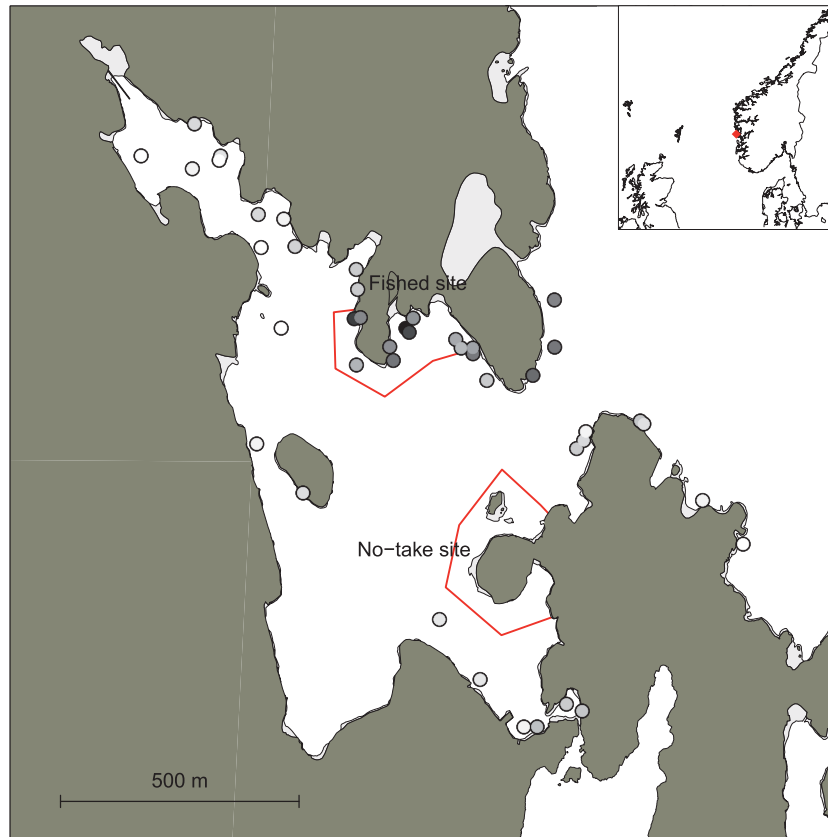
## Material and methods

### Study area

The study was carried out on the Huftarøy Island in Austevoll municipality, western Norway (Figure 1). There are several salmon farms on the archipelago, mainly using locally caught wrasse for delousing. Based on consultation with local fishers, the Storebø bay was selected as study area representative of the wrasse fisheries. The bay is a semi-sheltered basin with a maximum depth of 40 m and some freshwater discharge into the southern and northern parts. The local fishing community agreed to inform us whenever traps were set inside the bay or up to 1 km outside the bay inlet. In addition to the commercial fishery, corkwing wrasses were sampled for tagging at two sites within the bay: i) a temporary no-take zone of approximately 600-m coastline, defined in agreement with the local fishers and (ii) a similar-sized study site on the opposite side of the bay with no restriction on fishing activity (Figure 1).

### PIT tagging

PIT tags were used to monitor the fate of individual corkwing wrasse in their natural environment in the bay. PIT tags are small glass-encapsulated passive transponders inserted into the body cavity or muscle tissue and are well proven and widely used as an identification method for studies of fishes (Prentice et al., 1990; Gibbons and Andrews, 2004; Bolland et al., 2009). We used half duplex PIT tags (12.0 mm × 2.12 mm, Oregon RFID) inserted in the body cavity with a needle fitted to a tag injector. Individuals measuring <95 mm in total length were not tagged. The fish were first anaesthetized in a solution 50–100 mg l<sup>-1</sup> tricaine methane-sulfonate (MS-222) in volume of 8–10 l of seawater. As sea temperature varied throughout the season, we determined the dosage used each sampling day based on a target time of 1–3 minutes until loss of equilibrium of the fish. Post tagging, the fish was allowed to completely recover before release (2–5 minutes). The injector needles were cleaned and disinfected in 96% ethanol or replaced between each tagging operation. We carried out a pilot experiment to assess post-tagging survival under controlled conditions the year prior to the field study. To this end, 51 randomly sampled corkwing wrasse were length measured, tagged as described above, and held in a 5 × 5 m fish pen with artificial shelters in the sea for 59 days (6 June to 4 August 2013). No tag-loss or mortality was evident by the end of the period. The method of capture, tagging and handling of live fish in this study was approved by the Norwegian Animal Research Authority (Application ID: 6428).



**Figure 1.** Study area, tagging sites (within lines) and distribution of commercial fishing activity in the Storebø bay July–August 2014. The circles represent the approximate centre position of each pot chain (7–22 pots linked) hauled by fishermen during the commercial fishery. The number of tagged corkwing captured per pot in the fishery is indicated by the white-black gradient fill in the circles (black= 1.5 recaptures per pot, white = 0 recaptures). A total of 820 pots of 43 pot chains were set and 280 recaptures of tagged fish were recorded.

### Data collection

Corkwing wrasse were tagged in two sampling periods during the summer of 2014 (period 1: 20 May to 26 June; period 2: 18 to 22 July). The first period coincided with the reproductive season, while the second sampling was conducted after the reproductive season (see Results). We considered it important to compare fishing mortality and capture probability for fish tagged both during and after spawning due to the large sexual differences in behaviour during the nesting period (Potts, 1974), which is likely to influence the vulnerability to the passive gears used for sampling. During the spawning period, nesting males are occupied by nest building and territory defence, whereas females and sneaker males may move freely between nests. Thus, the experimental design with tagging both before and after the spawning period provided an opportunity to investigate this potential source of sampling bias and whether it affected the estimates of capture probability in the fishery. A drawback of sampling after spawning was that sneaker males could not be distinguished from females.

Sampling during the first period was conducted in three shorter sub-sessions (May 20–24; June 9–12 and 21–26). When analysing fishing mortality, these sessions were pooled since the commercial fishing did not happen to occur in the area before July 2. In order to reduce selectivity in our own sampling, we used both baited wrasse pots and un-baited fyke nets. In the first period, the sampling effort was slightly higher in the fished site

(fished site: 25 fyke nets and 49 pots; no-take site: 20 fyke nets and 42 pots), while the effort was identical the second period (18 pots and 18 fyke nets per site) (Table 1). To be captured in pots, the fish have to be attracted to the bait and actively enter the gear, whereas fyke nets are set perpendicular to the shoreline to create a physical barrier leading passing fish into the collecting chamber (gear descriptions/pots/rectangular prism shaped,  $70 \times 40 \times 29$  cm, 15-mm mesh size, two 75-mm diameter entrances and two chambers, fyke nets: 5-m single leader, 55-cm diameter entrance and leader mesh size of 30 mm). The gear was randomly placed within the two study sites at 1- to 7-m depth with 10- to 30-m spacing between each trap and left over night and hauled the following day (soak time: 12–24 hours). Corkwing wrasse were measured for total length (to the nearest mm) and checked for reproductive state by applying gentle pressure on the abdomen and examining the sexual products (egg/sperm). A fish was classified as spawning (reproductively active) if any eggs or milt was extruded. Nesting males could easily be distinguished from females and sneaker males based on coloration, whereas the sex of sneaker males and females could only be determined during the spawning season by stripping as described above. All sneaker males ( $n=19$ ) observed more than once within the first tagging period extruded milt at every encounter, proving high accuracy of this sexing method during the spawning season. In the second tagging period, we could not distinguish sneaker males and

**Table 1.** Summary of the number of tagged corkwing wrasse, the mean body size, number of fish captured and fishing mortality in the Storebø bay summer 2014.

Site	Sex	Sampling period 1 (20.5–26.6)				Sampling period 2 (18.7–22.7)			
		n	Total length mm (SD)	Captured (retained)	Fishing mortality (%)	n	Total length mm (SD)	Captured (retained)	Fishing mortality (%)
Fished	Nesting males	74	140.9 (24.8)	28 (27)	36	63	118.7 (22.2)	40 (31)	49
	Females	308	135.9 (20.1)	94 (89)	29	78	126.2 (19.2)	33 (28)	36
	Sneaker males	41	122.8 (14.7)	17 (16)	39	1	99.0	1 (0)	0
	Total	423	135.5 (21.0)	139 (132)	31	142	122.7 (20.9)	74 (58)	41
No-take	Nesting males	105	141.0 (26.6)	12 (12)	11	62	124.0 (22.1)	11 (9)	15
	Females	189	130.9 (18.7)	6 (5)	3	108	125.5 (18.5)	9 (5)	5
	Sneaker males	26	129.0 (15.2)	1 (1)	4	2	115.5 (12.0)	1 (1)	50
	Total	320	134.1 (21.9)	19 (18)	6	172	124.8 (19.8)	21 (15)	9
	Grand total	743	134.9 (21.4)	158 (150)	20	314	123.9 (20.3)	95 (73)	24

females, but individuals of female appearance were classified as females, which were much more common than sneaker males in the first period (Table 1). This implies that the majority of sneaker males first encountered in period 2 have been sexed as females, since only 6 out of 22 sneaker males had running milt when recaptured in period 2 (being tagged and sexed in period 1). After checking each individual for the presence of PIT tag, new encounters were tagged as described before and gently released at the site of capture.

Commercial fishing activity in and around the bay was monitored from 17 June (the opening date of fishing in 2014) to 31 October 2014 in agreement with the local fishers who allowed researchers on-board for detecting recaptures. The study area and the surrounding coastline can be visually assessed from the facilities of the Institute of Marine Research and was daily surveyed by boat or by binoculars from the shoreline to ensure that all fishing activity was accounted for. The fishers used pots of the same type used in the scientific sampling baited with 2–3 prawns (*Pandalus borealis*) or crushed edible crab (*Cancer pagurus*). The pots were linked in chains of 7–23 and set on 1- to 7-m depth with approximately 5- to 10-m spacing between each pot. Upon capture, the catch was emptied in a container with running sea water for being sorted on size. Wrasse that were to be retained were transferred to a holding tank, while by-catch, and wrasse below the size limit were discarded close to shore. A PIT-tag reader with an external antenna attached was used to detect any tagged fish present by continuously passing the antenna through the container where the catch of each pot was placed. We were able to infer whether an individual was discarded or retained by scanning the container with the remaining fish before release. In addition, the holding tank was thoroughly scanned after the end of each fishing trip to confirm the individuals being retained. The scanner stores time and tag number for each observation, and we noted exact position for each recapture and the start and end point of each pot chain. This method for tag detection allowed for minimal interference with normal work procedure for the fishers.

### Data analysis

First, we compared the mean body size between sexes, sites and sampling periods. Within each period, we used linear models to test for sex differences in body size (total length) independently for each study site (i.e. including an interaction effect between sex

and site in the model). Due to low sample size, sneaker males were not included in the model for period 2. Linear models were also used to compare body size between the two periods, independently of site and separately for nesting males and females. In all models, a likelihood ratio test (LRT) was applied to compare the goodness-of-fit of the model including interactions against a reduced model with additive effects and to select the model for statistical inference. Wald's tests were used to assess significance between factor levels.

Second, we estimated sex- and site-specific fishing mortality as the proportion of tagged fish harvested (captured and retained) in the commercial fishery at any point later in the study. Although all retained fish were kept alive to be transported to salmon farms, we adhere to the term *fishing mortality* since the fish can be regarded as dead from the perspective of the natural population. We tested for differences in fishing mortality between sexes (nesting males, females and sneaker males) and the two sites (fished or no-take) using logistic regression with *harvested* (0,1) as the response variable. Even though no commercial fishing took place within the no-take site during the study, some individuals dispersed out in the bay and were subsequently recaptured (Table 1, Figure 1). The two sampling periods were analysed separately, since the behaviour during spawning, when males are territorial and guard nests, is likely to influence the selectivity in the sampling and as well in the commercial fishery. Individuals were assigned to the period they were first encountered (tagged), thus disregarding that some were recaptured in the second period. Moreover, sneaker males were excluded in the models for the second period, when only three of the tagged fish could be classified as sneaker males. As before, an LRT was used to test whether an interaction was supported in the model. A significant interaction would indicate that sex-specific fishing mortality differs between the no-take site and the fished site.

Lastly, since fishing mortality has two components, the probability of being captured in the fishing gear and the probability to be retained once captured, we conducted separate analyses of these two sources of selectivity. Capture probability was modelled with similar logistic regression models as with fishing mortality, but with body size (total length) included as a trait in addition to sex to test for sexual differences in capture probability independent of body size. We ignored that some individuals were captured and discarded more than once. The starting models included the

three covariates (sex, body size and site) with interactions and were compared against six reduced candidate models. We used the Akaike Information Criterion corrected for small sample size ( $AIC_c$ ) for selecting the optimal model, and if the difference in  $AIC_c$  between two models were less than two units, the model with less estimated parameters was selected for statistical inference (Burnham and Anderson, 2002). Logistic regression was also used to model the probability of being retained once captured with sex and body size as covariates, including fish from both sites and periods. Since the fish were not measured for length when captured in the fishery, the length at time of tagging was used. As with capture probability,  $AIC_c$  was used for model selection. To facilitate interpretation of the capture probability and retention probability models, the length variable was scaled and mean centred with  $SD$  of one. All statistical analyses were carried out with the software R, version 3.2.2 (R Core Team 2015).

## Results

A total of 1057 corkwing wrasse (fished site = 565, no-take site = 492) were tagged during the two sampling periods (Table 1). Of these, 260 were recaptured at least once in the scientific sampling. Those recaptured in the second period had on average increased their total length with 5.5 mm (range, 0–23 mm) since being measured and tagged in the first period. The first sampling period coincided with the spawning season, with the percentage of fish releasing eggs or milt when stripped being 75% at the start of the period (20–24 May), dropping to 45% towards the end (21–26 June; data not shown). In comparison, only 3% released eggs or milt in the second period (of these, only one nesting male), indicating the spawning season had, or was close to have ended.

The nesting males were larger than females (Linear model; Wald's test:  $\beta = -7.52$ ,  $t = -4.04$ ,  $p < 0.0001$ ) and sneaker males (Linear model; Wald's test:  $\beta = 16.28$ ,  $t = -5.39$ ,  $p < 0.0001$ ) in the first period, while nesting males and females were of similar size in the second period (Linear model; Wald's test:  $\beta = 4.39$ ,  $t = 2.35$ ,  $p = 0.063$ ). There were no significant interactions between site and sex in either period (LRT: period 1:  $df = 5$ ,  $\chi^2 = 5.08$ ; period 2:  $df = 4$ ,  $\chi^2 = 1.64$ ,  $p = 0.20$ ). Both nesting males and females were considerably smaller in the second period than in the first (Linear model; Wald's test: nesting males:  $\beta = -22.23$ ,  $t = 5.31$ ,  $p < 0.0001$ ; females:  $\beta = -7.41$ ,  $t = 1.70$ ,  $p < 0.0001$ ). The females were also smaller in the no-take site relative to the fished site (Linear model; Wald's test:  $\beta = -3.78$ ,  $t = -2.48$ ,  $p = 0.013$ ), whereas nesting males were of similar size in the two sites (Linear model; Wald's test:  $\beta = 2.27$ ,  $t = 0.80$ ,  $p = 0.42$ ). The interaction between site and period was not significant for neither nesting males (LRT:  $df = 4$ ,  $\chi^2 = 0.83$ ,  $p = 0.36$ ) nor females (LRT:  $df = 4$ ,  $\chi^2 = 1.59$ ,  $p = 0.21$ ).

The commercial fisheries involved four fishermen who set a total of 820 pots in and around the Storebø bay from 2 July to 26 August. Scientific personnel participated on all fishing trips. Fishing intensity was highest after the second sampling period (710 pots). A total of 280 fisheries recaptures were recorded of 253 uniquely tagged wrasses. A total of 223 recaptures were retained and sold to salmon farms (Table 1). The majority (238) of the fisheries recaptures were caught after the second sampling, thus including recaptures of fish tagged in both sampling periods. Moreover, most recaptures were caught within or close to the fished site (Figure 1). One nesting male that had been tagged in the no-take site was recaptured in the fished site. Mean time

between tagging and harvesting was 45.6 days (range, 6–98) for those tagged in period 1, while 8.8 days (range, 3–39) for those tagged in period 2.

The overall fishing mortality was higher in the fished site relative to the no-take site in both periods (period 1: fished, 36%; no-take, 6%; period 2: fished, 42%; no-take 9%, Logistic regression; Wald's test: period 1:  $\beta = -2.14$ ,  $z = -7.91$ ,  $p < 0.0001$ ; period 2:  $\beta = -2.07$ ,  $z = -6.26$ ,  $p < 0.0001$ ). For modelling fishing mortality, the interaction between sex and site was not significant in either period (LRT: period 1:  $df = 4$ ,  $\chi^2 = 4.67$ ,  $p = 0.097$ ; period 2:  $df = 3$ ,  $\chi^2 = 1.11$ ,  $p = 0.29$ ). Adjusted for site, fishing mortality was significantly higher for nesting males than for females in both tagging periods (Logistic regression; Wald's test: period 1:  $\beta = -0.62$ ,  $z = -2.608$ ,  $p = 0.009$ ; period 2:  $\beta = -0.74$ ,  $z = -2.498$ ,  $p = 0.013$ , Table 1). There were no differences in fishing mortality between nesting and sneaker males in the first period when the sneaker males could be distinguished from females (Logistic regression; Wald's test:  $\beta = -0.18$ ,  $z = -0.510$ ,  $p = 0.61$ , Table 1).

For capture probability for fish tagged in the first period, the model with interaction between sex and length and an additive effect of site had marginally better  $AIC_c$  score as the model without interactions between the same factors. However, the latter model was considered the most parsimonious as fewer parameters were estimated (Table 2). Applying this model, nesting males had, adjusted of body size, higher capture probability than females but not sneaker males (Table 3, Figure 2). Regardless of sex, the capture probability decreased with increasing body size (Table 3, Figure 2). For those tagged in the second period, the model with interaction effect between sex and body size and additive effects of site was supported (Table 2). Female capture probability declined with body size as in the first period, while for nesting males, intermediate-sized fish had the highest capture probability (Table 3, Figure 2).

When hauling the pots, the fishers sorted the catch on size consecutively by eye or sometimes (when in doubt) by using a length measure drawn on the sorting board. Two of the fishers occasionally used 130 mm as their size limit because of the demand from the salmon farms. In total, the fishers retained 87% of the tagged corkwing and all fish larger than 123 mm at the time of tagging. Moreover, 43% of the fish below the minimum size limit (110 mm) at the time of tagging ( $n = 79$ ) were retained. Model selection of retention probability favoured the model with only body size as predictor, although the more complex model with an interaction between sex and length had only slightly lower  $AIC_c$  score (Table 2). The probability of being retained was strongly dependent on body size (Table 3, Figure 3).

## Discussion

Our study has demonstrated male-selective harvesting of a commercially important species with male parental care, the corkwing wrasse. Independently of body size, nesting males had higher vulnerability to being captured in a baited pot fishery. Several possible factors could drive the higher capture probability of nesting males. First, their higher growth rates imply higher feed demand which can result in higher motivation for entering baited pots. Myers *et al.*, (2014) also proposed higher growth and feeding rates as an explanation for finding females (who grows faster) more prone to angling in a walleye (*Sander vitreus*) fishery. Second, higher growth rates can be correlated with more active and risk-taking behaviour that may increase their vulnerability to

**Table 2.** Model selection of logistic regression on capture probability (fish captured in the fishery) and retention probability once captured.

Period 1				Period 2			
Model structure	P	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model structure	P	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
<b>Capture probability</b>							
Sex × length × site	12	659.5	4.67	Sex × length × site	8	314.39	5.18
Sex × length + site	7	654.83	0	Sex × length + site	<b>5</b>	<b>309.21</b>	<b>0</b>
Sex + length × site	6	655.52	0.69	Sex + length × site	5	314.7	5.49
Sex × site	6	681.19	26.36	Sex × site	4	317.02	7.81
Sex + length + site	<b>5</b>	<b>654.84</b>	<b>0.01</b>	Sex + length + site	4	312.64	3.43
Length × site	4	659.79	4.96	Length × site	4	320.44	11.23
Sex + site	4	681.11	26.28	Sex + site	3	314.97	5.76
Length + site	3	659.48	4.65	Length + site	3	318.39	9.18
<b>Retention probability (both periods)</b>							
Sex × length	6	180.5	0				
Sex + length	4	184.51	4.01				
Sex	3	283.96	103.46				
Length	<b>2</b>	<b>180.63</b>	<b>0.13</b>				

For capture probability models were fitted separately for the two sampling periods. The table gives model structure, the number of estimated parameters ( $P$ ) the  $\Delta AIC_c$  score and the difference between the specified model and the model with the lowest AICc score. The model with the lowest AICc score is used for statistical inferences (in bold), or in the case when  $\Delta AIC_c$  is less than two units between two models, the model with fewer parameters is considered the most parsimonious.

**Table 3.** Summary of the selected logistic regression models on capture probability and retention probability once captured.

Period 1						Period 2					
Variable	$\beta$	SE	Odds ratio	z-value	p	Variable	$\beta$	SE	Odds ratio	z-value	p
<b>Capture probability</b>											
Intercept	-0.09	0.22	0.91	-0.42	0.67	Intercept	0.57	0.26	1.77	2.19	0.03
Sex (Females)	-0.72	0.24	0.49	-2.97	0.003	Sex (females)	-1.15	0.33	0.32	-3.46	0.0005
Sex (Sneaker males)	-0.54	0.37	0.58	-1.45	0.15	Length	-0.01	0.20	0.99	-0.05	0.96
Length	-0.56	0.11	0.97	-5.07	<0.0001	Site (no-take)	-2.15	0.30	0.12	-7.11	<0.0001
Site (No-take)	-2.28	0.27	0.10	-8.45	<0.0001	Sex (females) × length	-0.77	0.34	0.46	-2.26	0.02
<b>Retention probability (both periods)</b>											
Intercept	2.96	0.41	19.25	7.21	<0.0001						
Length	2.82	0.43	16.83	6.60	<0.0001						

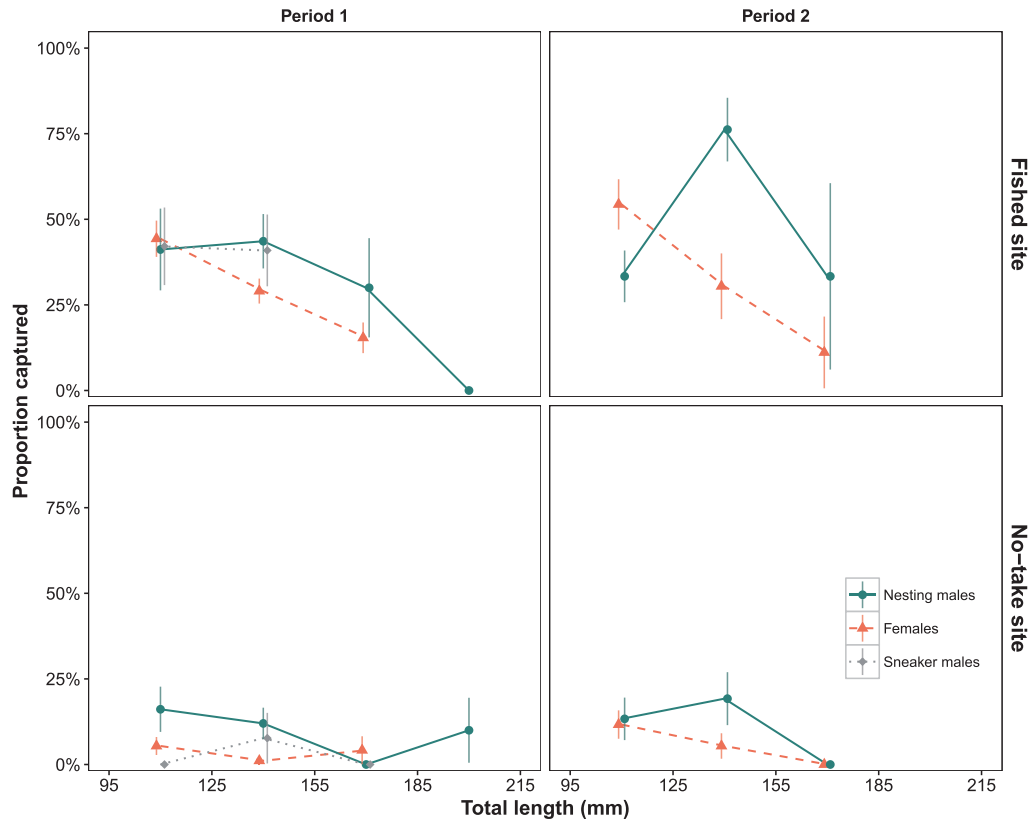
Nesting males and the fished site are considered as reference levels. The length variable is scaled and centred in both analyses.

passive gears (Biro and Post, 2008; Biro and Sampson, 2015). Moreover, behavioural traits positively related to the intensity of parental care and the aggression of nest-tending males have been shown to be correlated with increasing vulnerability to angling in largemouth bass (*Micropterus salmoides*) (Sutter et al., 2012). Sexual differences in life history traits, physiology and behaviour are widespread in fishes, but often ignored (Hanson et al., 2008). Thus, the findings presented here underscore the need for more investigations of the extent, underlying mechanisms and implications of sex-selective harvesting in commercial and recreational fisheries.

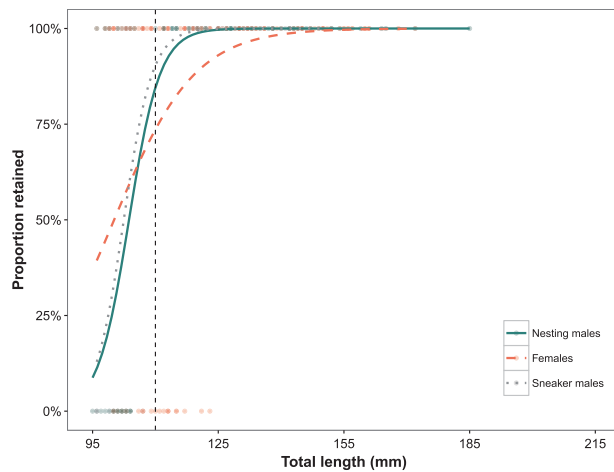
In the light of the growth rate hypothesis, the similar pattern of size-dependent capture probability for sneaker males and nesting males was unexpected, given that sneaker males grow even slower than females (Halvorsen et al., 2016). However, too few sneaker males were tagged to draw any firm conclusion. Moreover, since we were unable to distinguish sneaker males from females outside the spawning season the differences in capture probability between nesting males and females in the second period must be interpreted with caution. Nevertheless, the main pattern was highest capture probability for intermediate-sized

nesting males. Most of the commercial fishing happened after spawning, so the finding of higher capture probability of nesting males is most likely unrelated to reproductive behaviour.

There was a notable shift in body size towards smaller fish in the second period, which was most evident for nesting males. During the nesting period, the males are fiercely chasing away all conspecifics except for receptive females (Potts, 1974), and this activity may force immature fish away from the shallow depths where nesting occur (Potts, 1985). Both we and the commercial fishers targeted depths of 1–7 m to avoid problems with inflated swim bladders when hauling the gear from deeper waters. A size-dependent shift in depth preference during and outside the spawning period could therefore lead to different selectivity on body size. This may also explain the negative correlation between body size and capture probability for those tagged in the first period. However, finding the same pattern for females and large nesting males tagged after spawning suggests that other factors may also be of importance. For instance, dietary preferences may change with body size and sex and therefore affect attraction to baited gear. In our study system, the commercial fishers used exclusively crustacean bait (prawn and crushed edible crab).



**Figure 2.** The proportion of corkwing wrasse captured in the corkwing wrasse fisheries in Austevoll 2013 in four size categories (95–124, 125–154, 155–184, 185–214 mm). The data are aggregated in to tagging period and site. Error bars show SE around the observed proportions.



**Figure 3.** The probability of being retained once captured in the corkwing wrasse fishery as a function of total length at tagging. The vertical dashed line refers to the official minimum size limit (110 mm).

The diet of smaller corkwing has been found to consist of predominately small crustaceans, while *bivalvia* is the main prey group for fish larger than 15 cm (Deady and Fives, 1995). Thus, crustacean bait may attract smaller corkwing wrasse more strongly. Alternatively, larger (and older) fish must have survived previous years of selective fishing in the area, so those remaining

may possess traits that are less vulnerable to capture. Lastly, despite the relatively short time between tagging and capture in the fisheries, there is a possibility that some large individuals dies or move larger distances after the spawning period. During the first period, nesting males and sneaker males were often observed with flesh wounds and missing several scales, presumably caused by aggressive encounters with other males. The spawning behaviour and nest building and guarding may also increase the risk to predation. Natural mortality could also explain the finding of lower fishing mortality for those tagged in the first period relative to the second, since the time from tagging to fisheries capture was generally longer in the first period and therefore increasing the probability of dying from natural causes before being fished. Future tagging studies investigating spatial and depth behaviour and multi-year capture–recapture data for estimating natural mortality would be useful for understanding why the larger corkwing wrasse have low encounter rates after spawning.

Fishing mortality was similar to capture probability, since the fishers retained the majority (87%) of the captured corkwing, including a number of that was below the size limit at the time of tagging. This does not necessary reflect the fishers retaining under-sized fish, but is most likely caused by fish growing to reach harvestable size during the time between tagging and capture. The survival of discarded fish was probably high, as the fishers released the catch at shallow depths, and the fish was kept in running water at any time. However, we occasionally observed some of the discarded fish being eaten by seagulls. Intermediate-sized nesting males (125–155 mm) had the highest fishing

mortality (Fished site, period 1: 44%; period 2: 76%) and is comparable to annual fishing mortality (>60%) estimated for large ( $\geq 45$  cm) coastal Atlantic cod (*Gadus morhua*) in Southern Norway (Fernández-Chacón *et al.*, 2015). Increased adult mortality in general selects for maturing at younger ages and potentially smaller size (Stearns 1992). Thus, the corkwing fishery may induce selection for nesting males maturing at smaller size, as the size class experiencing the highest fishing mortality correspond to the size at maturation for nesting males ( $L_{50} = 136.6$ ; Halvorsen *et al.*, 2016). On the other hand, since capture probability was found to decrease with body size, this may counter such selective pressures as those growing fast may be less prone to capture once a large body size is attained, under the premise that the low capture probability for large individuals we observed was not caused by higher natural mortality or effects of past fisheries selection.

Sex-selective fishing mortality has the potential to alter sex ratios and therefore have consequences for sexual selection and population productivity. If fishing reduces the density of nesting males, this may relax competition over nesting territories and consequently weaken sexual selection for large male body size. In a fisheries-induced evolution perspective, modelling has demonstrated that the evolutionary rate of reduction in body size may accelerate if fishing erodes phenotypic variation in traits under sexual selection (e.g. body size) (Hutchings and Rowe, 2008). Fishing can also affect the relative fitness between nesting males and sneaker males (Darwall *et al.*, 1992). Although we did not detect differences in fishing mortality between nesting males and sneaker males, sneaker males mature 1–2 years earlier than nesting males and grow slower, so the ratio of male types on the spawning ground can be expected to be altered by fishing (Halvorsen *et al.*, 2016). In turn, a higher proportion of sneaker males could have consequences for mating system dynamics as studies of the closely related *Symphodus ocellatus* have shown that the number of sneaker males present affects the willingness of nesting males and females to spawn and the probability of the male deserting the nest (Alonzo and Warner, 1999, 2000; Alonzo and Heckman, 2010).

The horizontal movements of corkwing wrasse appear to be limited, as only one individual was found to have moved between the two sites and the number of recaptures was substantially lower in pot chains set farther away from the tagging sites. Managing species with high site-fidelity is challenging, since fishing may deplete populations with limited potential of being replenished from nearby areas with lower exploitation rates (Gunderson *et al.*, 2008; Wilson *et al.*, 2010). It is also difficult to set catch quotas and monitor trends in the fishery based on landing statistics, as fishers may constantly move from depleted areas to lesser exploited sites and therefore maintain high catch per unit effort. We have shown that fish tagged in the no-take site had significantly lower fishing mortality despite the small size of the MPA, but sex-selectivity was similar to the open site. Thus, to ensure equal protection for sexes, an MPA size should be larger than the home range of both sexes and male types, and studies on spatial behaviour are therefore needed. As a measure to protect a declining European lobster (*Homarus gammarus*) population, a network of nine MPAs has been established in the Hardangerfjord in Western Norway, effective from October 2016. These are fully protecting wrasse from commercial fishing since passive gear such as fyke nets, pots and gillnets are prohibited. However, five of these MPAs are only protecting 1–4 km of a

coastline with little complexity in terms of islands, reefs and skerries. Thus, a comparable sex-bias in protection as found for the MPA in this study may be anticipated in the smaller MPAs. On the Skagerrak coast farther south, a total of 10 MPAs with similar gear regulations have been established from 2006 to 2016. The effects of protection on sex-ratio, age and size structure of wrasses are currently being investigated in four MPA and control pairs in Skagerrak.

Another possibility for reducing sex- and size selectivity is to change the length-based management regulations. A sex-specific minimum size limit reflecting the differences in growth and size at maturation, or a slot limit, protecting both small and large fish of both sexes has previously been proposed (Halvorsen *et al.*, 2016). One may argue, as we have shown that capture probability appears to decrease with body size, that large fish are ‘naturally’ protected with less need for a maximum limit. However, as already pointed out, we do not know whether the absence of observations of larger fish in the fishery is due to effects of past harvest selection, natural mortality or size-dependent behaviour changes. Furthermore, protecting the larger fish will have small economic consequences, as the fish are sold per individual regardless of body size (Halvorsen *et al.*, 2016).

To conclude, we show that trap fisheries can be sex-selective, in this case harvesting corkwing wrasse males at higher rates than females. This selectivity was primarily caused by nesting males having higher capture probability, but not due to larger body size. The present study highlights the importance of investigating and recognizing sexual differences in life history traits and behaviour to better understand how populations may respond to fishing. MPAs, in combination with sex-specific size limits or a slot-size limit, appear to be a promising solution of reducing the risk associated with sex-selective harvesting.

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