



## Original Article

# Male-biased sexual size dimorphism in the nest building corkscrew wrasse (*Symphodus melops*): implications for a size regulated fishery

Kim Tallaksen Halvorsen<sup>1,2,3\*</sup>, Tonje Knutsen Sjørdalen<sup>1,3</sup>, Caroline Durif<sup>2</sup>, Halvor Knutsen<sup>1,3,4</sup>, Esben Moland Olsen<sup>1,3,4</sup>, Anne Berit Skiftesvik<sup>2</sup>, Torborg Emmerhoff Rustand<sup>5</sup>, Reidun Marie Bjelland<sup>2</sup>, and Leif Asbjørn Vøllestad<sup>3</sup>

<sup>1</sup>Department of Natural Sciences, University of Agder, PO Box 422, 4604 Kristiansand, Norway

<sup>2</sup>Institute of Marine Research, Austevoll Research Station, 5392 Storebø, Norway

<sup>3</sup>Department of Biosciences, Centre for Ecological and Evolutionary Syntheses (CEES), University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

<sup>4</sup>Institute of Marine Research Flødevigen, Nye Flødevigveien 20, 4817 His, Norway

<sup>5</sup>Department of Biology, University of Bergen, PO Box 7803, 5020 Bergen, Norway

\*Corresponding author: tel: +47 40016601; fax: +47 38141699; e-mail: kim.a.halvorsen@uia.no

Halvorsen, K. T.; Sjørdalen, T. K., Durif, C., Knutsen, H., Olsen, E. M.; Skiftesvik, A. B., Rustand, T. E., Bjelland, R. M., and Vøllestad, L. Asbjør. Male-biased sexual size dimorphism in the nest building corkscrew wrasse (*Symphodus melops*): implications for a size regulated fishery. – ICES Journal of Marine Science, 73: 2586–2594.

Received 4 January 2016; revised 5 June 2016; accepted 26 June 2016; advance access publication 31 July 2016.

Size selective harvesting can also be selective on sex in species displaying sexual size dimorphism (SSD). This has potential consequences for mating systems and population dynamics. Here, we assessed spatial variation in SSD and body size in eight Norwegian populations of corkscrew wrasse (*Symphodus melops*), a species where males either mature as nesting or sneaker males. Corkscrew wrasse is increasingly harvested in a size-selective fishery which supplies the Norwegian salmon aquaculture industry with cleaner fish to reduce sea-lice infestations. In our study, mature nesting males had larger body sizes than females and sneaker males, and the size difference was significantly larger in the four northernmost populations. Contrasting life history traits in two of the populations (a southern and a northern), we found that the larger SSD in the north was because of nesting males delaying maturation and growing faster relative to females and sneaker males. Mature northern nesting males also had smaller gonads at smaller sizes relative to their southern counterparts, indicating a trade-off between reproduction and somatic growth in males. Applying the current minimum legal size limit for commercial fishing in Norway (12 cm) would have failed to protect any mature nesting males in five out of the eight populations. Moreover, the findings of more male-biased SSD and female-biased sex ratios in the northern populations imply that there is larger potential for sex-selective harvesting in these populations. To avoid fisheries-induced changes in sex ratios, we advocate for spatially structured management units and to refine the current size-regulations using either sex-specific minimum size limits or a slot limit, also protecting the larger fish and therefore more nesting males.

**Keywords:** aquaculture–environment interactions, corkscrew wrasse, fisheries management, selective harvesting, sexual size dimorphism, *Symphodus melops*.

## Introduction

The strength and form of selection on body size or correlated traits is rarely identical between the sexes and result in sexual size dimorphism (SSD) (Parker, 1992; Andersson, 1994; Fairbairn

*et al.*, 2007). For different reasons, sexual dimorphism is often neglected in assessments and management of commercial fisheries (Hanson *et al.*, 2008; Zhou *et al.*, 2010). This is unfortunate, as size selective harvesting of sexually dimorphic populations is

likely to be sex-selective (Rowe and Hutchings, 2003; Fenberg and Roy, 2008; Kendall and Quinn, 2013). Fisheries induced shifts in sex ratios can affect population productivity if the probability of encountering mates is reduced (Rowe and Hutchings, 2003). In species with parental care, selective removal of the caring sex may have direct consequences for offspring survival (Suski *et al.*, 2003; Sutter *et al.*, 2012). Moreover, sex ratio influence intra-sexual competition and mate choice and therefore the opportunity and strength of sexual selection (Kvarnemo and Ahnesjö, 1996; Clutton-Brock, 2007), so size and sex-selective fishing have potential consequences for the direction and rate of evolutionary change (Rowe and Hutchings, 2003; Hutchings and Rowe, 2008).

In both Scandinavia and on the British Isles, the nest building corkwing wrasse (*Symphodus melops*) is harvested and used as cleaner fish in the salmonid aquaculture industry to reduce lice infestations from the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongates* (Bjordal, 1988; Darwall *et al.*, 1992). Previous studies conducted on the British Isles have found the males, who builds the nests and provide parental care, grow faster, mature later and attain larger sizes than females (Potts, 1974; Darwall *et al.*, 1992; Sayer *et al.*, 1996). In addition, a smaller proportion of males mature as *sneaker males*, which are smaller and mimic the female phenotype to steal fertilizations from the *nesting males* (Potts, 1974; Dipper and Pullin, 1979; Uglem *et al.*, 2000). The wrasse fisheries in Norway and on the British Isles are managed with minimum size limits which therefore may protect nesting males, females and sneaker males unevenly if they differ in body size. During the first wave of wrasse fisheries in Ireland, a reduction of large nesting males and catch per unit effort was observed in a harvested population where nesting males initially were larger than females (Darwall *et al.*, 1992). Given that nesting males provide obligate parental care and are territorial, reducing their frequencies is likely to negatively affect egg survival and the mating system dynamics (Darwall *et al.*, 1992). In Norway, the minimum size limit for corkwing wrasse was raised from 11 to 12 cm in 2015, but fundamental knowledge on size distributions, growth and maturation and sexual dimorphism is lacking from Norwegian waters (Skiftesvik *et al.*, 2014a).

This study seeks to investigate spatial variation and proximate causes of sexual differences in body size in harvested Norwegian corkwing wrasse populations to provide a basis for evaluating whether the current size regulations may promote sex-selective fisheries. First, we assess sexual differences in body size and sex ratios among eight populations distributed along the coastline South Eastern Norway to Hordaland further north on the Western coast. Second, we analyse sex-specific growth and maturation in a selected northern and southern population. Lastly, we evaluate the potential consequences of failing to address this sexual variation in management and propose possible solutions for reducing sex-selective harvesting.

## Material and methods

### Scientific sampling

Scientific sampling of corkwing wrasse was conducted from 11 June 2014 to 4 July 2014 in two main areas: near the field stations of the Norwegian Institute of Marine Research (IMR) in Austevoll, Western Norway and in Arendal on the South-eastern coast (Figure 1). Corkwing wrasse were captured using the same gear types as the commercial fisheries; fyke nets (5 m single

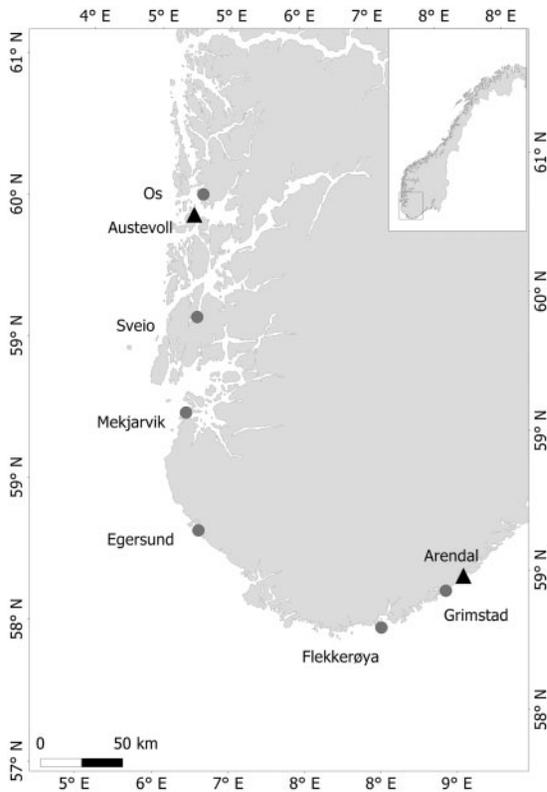
leader, 55 cm diameter entrance ring and leader mesh size of 30 mm) and baited wrasse pots (rectangular prism shaped, 70 cm×40 cm×29 cm, circular entrances (75 mm diameter), two chambers and 15 mm mesh-size), set at 1–7 m depth and hauled every morning. We only included fish sampled in fyke nets when comparing catch per unit effort (CPUE), length and sex ratio data between locations, as pots were not used in the commercial sampling (see below) and the selective properties may differ between the gear types. Fish from both gear types were included when comparing within-population sexual differences in individual growth and age at maturation. Specific sampling sites were selected on the basis of advice from local fishermen (Austevoll) and in areas with documented commercial wrasse fisheries (In Arendal—Gjøsaeter, 2002). Upon capture, total length was measured to the nearest mm and sex and reproductive state (spawning/not spawning) were determined by applying light pressure on the abdomen to check if milt or eggs were extruded from the urogenital papillae (Skiftesvik *et al.*, 2014b). The fish were then released at the site of capture. Certain hauls were selected in which all captured corkwing wrasse were immediately euthanized with an overdose of MS222 and then frozen for analysing age and maturation. The method of euthanizing and handling of live fish in this study was in compliance with Norwegian animal welfare Act (LOV 2009-06-19 nr 97: Lov om dyrevelferd). We strived to minimize handling time and stress imposed on the live animals.

### Commercial sampling

We collaborated with commercial wrasse fishermen to obtain additional length and sex ratio data from six locations from 14 May to 2 July (Figure 1). Wrasse was captured with un-baited fyke nets set at 0–7 m depths left over night. A trained researcher joined fishing trips and measured total body length to the nearest 0.5 cm and checked for sex and reproductive state as described before. The total number of corkwing wrasse per haul was noted to calculate the mean catch per unit effort (CPUE) in each location. Fishermen were to keep or release the fish as during a normal fishing operation. The last commercial sample was obtained from a fisherman operating near Egersund. The fish was here sampled at port; hence catch per unit effort data were not available. He used fyke nets as a capture method and was instructed to retain all size classes.

### Determination of age and maturation

Additional data on age and maturation were obtained from a random subsample of the fish in the scientific sampling in Austevoll and Arendal. In the laboratory, gonads were dissected out, blotted dry and weighed to the nearest mg. Gonad wet weight was used as a proxy for reproductive investment and maturity state was determined by macroscopic inspection of the gonads. The mature female gonad is pale or yellow and has clearly visible egg structures, whereas male gonads are opaque and white. Sagittal otoliths were dissected out, cleaned and stored dry. For aging, the otoliths were placed in black multi-celled trays containing 96% ethanol and photographed under a stereo microscope (20×). The otoliths of corkwing wrasse have distinct opaque and translucent growth zones, which makes them easy to read without further processing (Uglem *et al.*, 2000). Thus, age was determined by counting winter annuli independently by two trained readers. Disagreements between readings were infrequent and rare, and if it happened, the photographed otoliths were re-examined by a



**Figure 1.** Corkwing wrasse locations in Southern Norway sampled in scientific surveys (triangles) and during commercial fishing operations (dots).

third reader. No otolith was discarded as unreadable or unresolved.

### Statistical analysis

For statistical analysis, the data were grouped into two datasets; first, we explored spatial variation in SSD and sex ratio across the eight populations. Second, we compared life history traits on aged fish between the southern (Arendal) and northern (Austevoll) population sampled in scientific surveys. For convenience, we hereafter refer to Arendal and Austevoll as the **Southern** and **Northern** population, respectively. All statistical analyses were carried out in R (version 3.2.2, R Core Team, 2015).

For estimating SSD and calculating sex ratios of mature fish, only spawning fish (extruding egg or milt) were included. We used Lovich and Gibbons (1992) method to estimate the size dimorphism index (SDI) for each of the eight populations; the mean of the larger sex divided on the mean of the smallest. The SDI was arbitrarily defined as positive when nesting males were larger than females and negative otherwise. To achieve symmetry around zero, 1 was subtracted from the male-biased SDIs (positive) and added if SDI was female biased (negative) (Lovich and Gibbons, 1992). We tested for significant SDIs using two sided *t*-tests on nesting males and females length, assuming unequal variances.

To compare sexual dimorphism in life history traits between the southern and northern population, sex specific growth trajectories were constructed by fitting the typical parameterization of the von Bertalanffy growth equation to the age and length data:

$$L_t = L_\infty \cdot [1 - e^{-K(t-t_0)}]$$

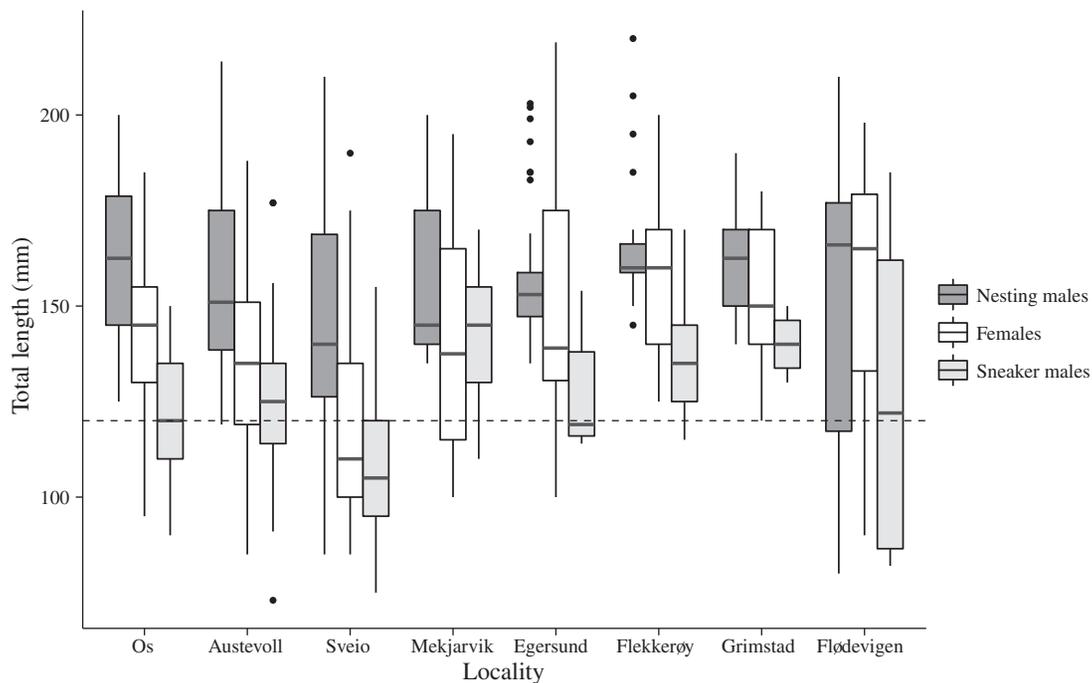
where  $L_t$  is the expected length at age  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  the von Bertalanffy growth parameter and  $t_0$  the age at the hypothetical length 0. Appropriate starting values for the parameters were determined using the R-Package FSA (Ogle, 2016). Estimates and confidence intervals of  $t_0$ ,  $L_\infty$  and  $K$  were obtained by bootstrapping 1000 iterations. Sexual and population differences in growth were assessed by comparing bivariate 95% confidence ellipses surrounding the estimated  $K$  and  $L_\infty$  values (Kimura, 1980). Groups displaying non-overlapping ellipses are considered having significantly different growth parameters (Meekan et al., 2001; Villegas-Ríos et al., 2013). Age differences between groups were tested with Wilcoxon rank sum and age at maturity was assessed by comparing the percentage of mature fish for each cohort. If differences in age at maturity were detected within sexes or male type, we tested for the influence of length on probability of being mature within an age class with logistic regression. Logistic regression models including all age classes were fitted to visualize sex-specific size at maturation and to calculate  $L_{50}$ ; the length at which 50% of the sample is estimated to be mature. Population differences in sex-specific reproductive investment was tested with multiple linear regression models on log transformed gonad wet weight with log total length and population and their interaction as predictor variables. Models were fitted separately for sex and male type and only spawning fish (extruding eggs/sperm when stroked) were included.

### Results

In the combined commercial and scientific fyke net sampling, 1806 out of 3367 corkwing wrasse were classified as spawning and included for assessing spatial variation in SSD. Nesting males were significantly larger than females in six populations and the minimum legal size limit would not have protected any spawning nesting males in five of the populations (Figure 2). A spatial pattern emerged, with the four northernmost populations displaying the most male-biased sexual SDI and had the lowest proportions of nesting males (11–15% of spawning fish) (Table 1). In addition, the mean body size was lower while the catch per unit effort (CPUE) was higher in the northern populations. Nesting males were generally more common than sneaker males, with the relative proportion of nesting males to sneaker males ranging from 49% to 86% (Table 1).

For life history analyses, we determined age and maturity for 403 fish (Northern  $n=239$  and Southern  $n=164$ , Figure 3). Mean and maximum age was twice as high in the northern population (mean = 3.05, range: 1–8) compared with the southern population (mean = 1.49, range: 1–4) (Wilcoxon rank sum test,  $W=4497.5$ ,  $p < 0.001$ ). Moreover, nesting males were on an average younger than females in both populations (Wilcoxon rank sum test, **Southern:**  $W=1922$ ,  $p < 0.001$ , **Northern:**  $W=3354$ ,  $p < 0.001$ ) (Figure 3).

Growth rates were faster for both males and females in the southern population compared with the northern population (Table 2 and Figure 4). Further, nesting males grew significantly faster than females in the northern population, indicated by non-overlapping 95% confidence ellipses around the growth model parameter estimates (Table 2 and Figure 4). In the southern population the growth rate of females and nesting males did not differ significantly. Growth models were not fitted for sneaker males, because of low sample sizes, nevertheless they corresponded to the smallest individuals in each age class in both populations (Figure 4). In the northern



**Figure 2.** Sex specific length distribution of spawning corkwing wrasse sampled in eight locations in Southern Norway ( $n = 1807$ ), arranged (left to right) in the order they appear along the coastline from North West (Os) to South East (Arendal). Centre line is the median value and the upper and lower edge of box represent the 25th and 75th percentiles, respectively. The vertical lines correspond to the highest value within the range that is 1.5 times the distance between the 25th and 75th percentiles, and filled dots are any individuals outside this range. Dashed horizontal line refers to the minimum legal landing size (120 mm).

**Table 1.** Sampling summary of corkwing wrasse captured with fyke nets in southern Norway in 2014

Region	Location	Fyke net hauls	CPUE (range)	$n$ (spawners)	Mean length (s.d.) of spawners	SDI	Sex proportion of spawners (% nesting males–sneaker males–females)
South	<b>Arendal</b>	76	3.5 (0–18)	267 (94)	152.0 (34.0)	−0.01	40–9–51
South	Grimstad	26	4.5 (0–22)	118 (89)	155.5 (17.3)	<b>0.06**</b>	27–4–69
South	Flekkerøy	15	9.3 (0–40)	139 (127)	156.1 (20.3)	<b>0.06*</b>	16–15–69
South	Egersund	NA	NA	101 (88)	152.6 (24.7)	0.06	43–8–49
North	Mekjarvik	9	21.3 (0–69)	192 (144)	141.3 (26.1)	<b>0.14***</b>	15–6–79
North	Sveio	45	26.5 (0–228)	1193 (470)	121.1 (25.1)	<b>0.25***</b>	14–17–69
North	Os	25	19.5 (1–83)	488 (240)	136.5 (22.2)	<b>0.15***</b>	11–9–80
North	<b>Austevoll</b>	60	14.5 (0–73)	869 (554)	141.2 (22.1)	<b>0.16***</b>	15–15–70

Both spawning and non-spawning fish was used in estimating mean catch per unit effort (CPUE). The two locations in bold are the northern and southern population compared for sexual dimorphism in life history traits. Values in bold indicates significant sexual sized dimorphism index (SDI— $t$ -test of difference in mean length between nesting males and females). The level of significance is indicated by asterisks:

\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

population, all 1-year-old fish would have been protected by the size limit while 35% ( $n = 104$ ) would have been harvestable in their second year, of which 36 were nesting males and 2 were females. In the southern population, 12% would have reached the size limit during the first year (only nesting males), whereas all 2-year-old fish would have been harvestable.

The populations also differed in sex-specific age at maturation. Whereas sneaker males matured in their first year in both populations, nesting males delayed maturation relative to females in the northern population (Figure 3). Here, females were found to mature in their second year, but only 26% of the 2-year-old nesting males were mature. The probability of being mature at age 2 years increased with size for the males (glm,  $Z_{45} = 2.87$ ,  $p = 0.003$ ). In

the southern population, 10% nesting males and 23% females were mature in their first year and all except for one nesting male was found to be mature at age 2 years. There were no significant effects of body size on the probability of being mature in their first year for either nesting males ( $Z_{84} = 0.294$ ,  $p = 0.769$ ) or females ( $Z_{28} = 1.83$ ,  $p = 0.07$ ). The size at maturation was consequently more sexually dimorphic in the northern population (Figure 5). In the northern population, only 3% ( $n = 33$ ) of the mature nesting males were below the minimum size limit ( $L_{50} = 136.6$ , s.e. = 2.2), compared with 44% ( $n = 109$ ) of the females ( $L_{50} = 87.6$ , s.e. = 1.4) and 57% ( $n = 28$ ) of the sneaker males (all mature). In the southern population, the minimum size limit would have protected 33% ( $n = 24$ ) of the mature

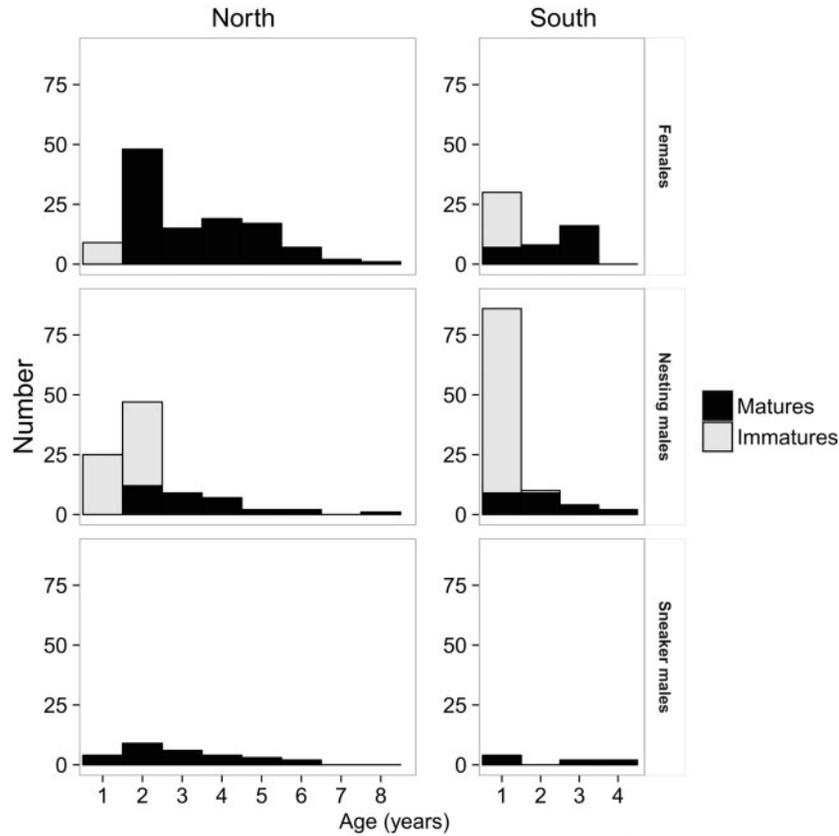


Figure 3. Stacked age histogram of immature and mature corkwing wrasse sampled in the northern and southern population.

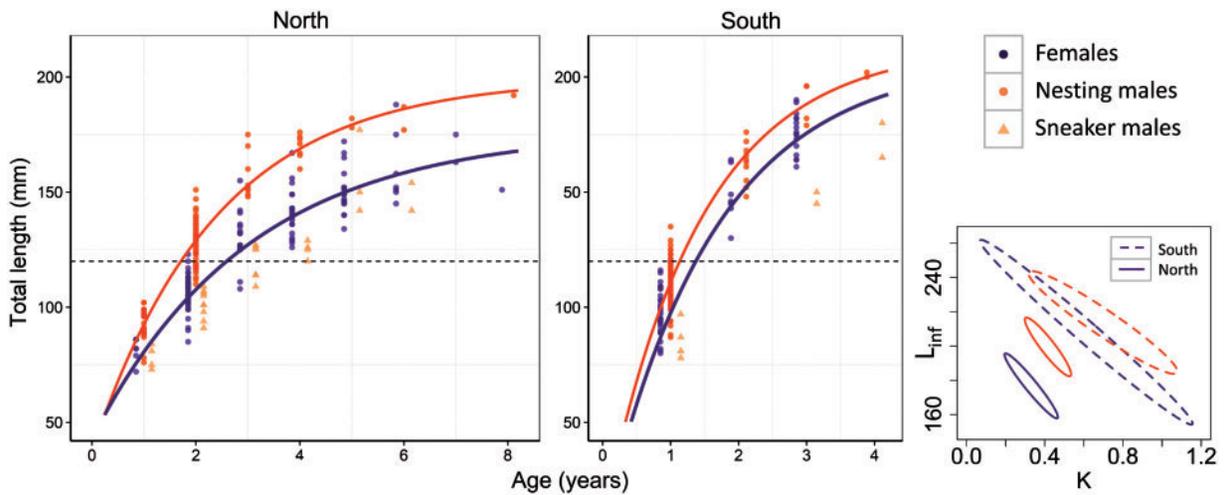


Figure 4. Sex-specific Von Bertalanffy growth curves fitted to length-at-age data of corkwing wrasse in the northern (left) and southern population (centre) sampled in Southern Norway. Length-at-age values for individual sneaker males are included (triangles). Dashed horizontal line corresponds to the legal size limit at 120 mm. The right panel displays 95% confidence intervals around  $K$  and  $L_{\infty}$ .

nesting males ( $L_{50} = 139.2$ ,  $s.e. = 5.7$ ), 23% ( $n = 31$ ) of the mature females ( $L_{50} = 109.9$ ,  $s.e. = 4.6$ ) and half of the sneaker males ( $n = 8$ , all sneaker males mature).

The relationship between gonad weight and body size was similar for sneaker males and females in the two populations, but the smaller nesting males in the southern population had relatively larger gonads than in the northern population; a difference that

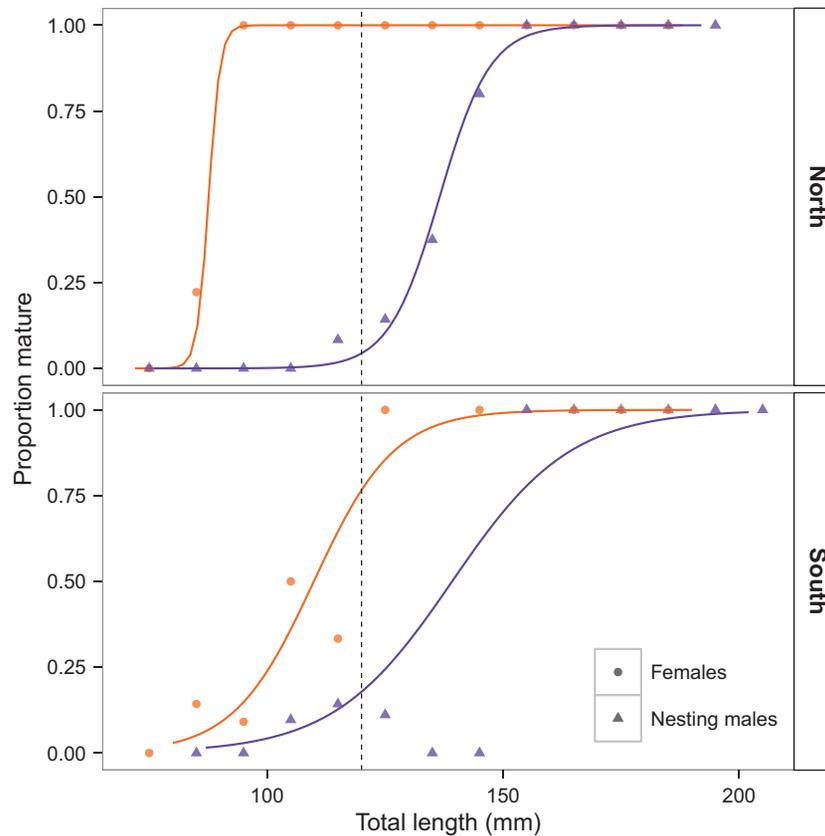
diminished with increasing body size (significant population  $\times$  log length interaction; Figure 6 and Table 3).

### Discussion

This study demonstrates male-biased SSD in corkwing wrasse, which was significant in six out of eight populations in Southern Norway. A clear spatial pattern emerged, with the four

**Table 2.** Parameter estimates from the von Bertalanffy growth models of corkwing wrasse from two populations in Norway

Population	Sex	$L_{inf}$	Confidence interval		K	Confidence interval	
			2.5%	97.5%		2.5%	97.5%
Southern	Nesting males	215.46	195.32	246.97	0.71	0.42	1.03
	Females	217.20	183.45	300.47	0.62	0.26	1.04
Northern	Nesting males	199.75	187.09	214.56	0.42	0.33	0.52
	Females	177.68	164.96	197.85	0.33	0.22	0.43

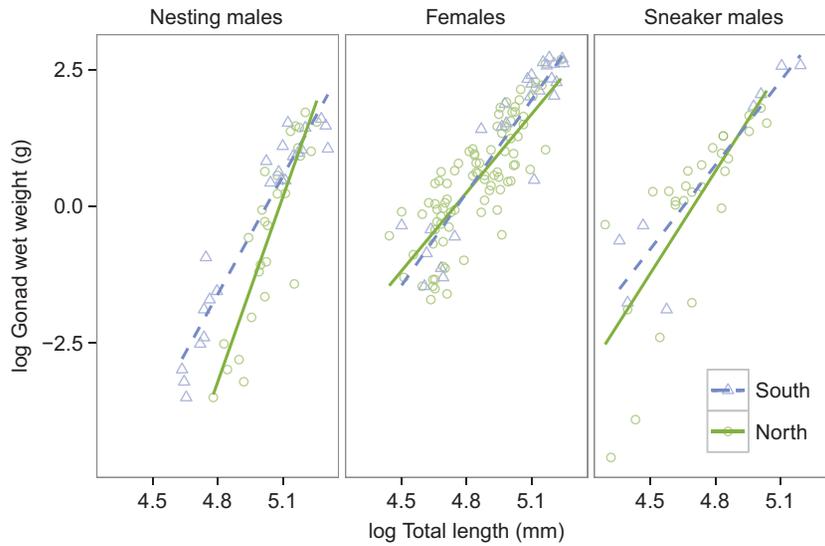


**Figure 5.** The proportion of mature nesting males and females and different body lengths (mm) in the northern and southern populations. Lines show logistic regression model predictions for maturation probability as a function of body length (mm). Sneaker males were mature at all sizes. Dashed vertical line indicates the minimum legal landing size (120 mm).

northernmost populations displaying more male-biased SSDs, lower proportions of nesting males, smaller body sizes and higher catch per unit effort (CPUE). The proximate cause of the SSD in a northern population was found to be higher growth rates and delayed maturation of nesting males relative to females. Sneaker males were smaller and matured earlier than both nesting males and females in both populations. We discuss the possible causes for spatial variation in SSD and the implications for management and sustainability of the fisheries of corkwing wrasse in Norway.

The latitudinal pattern of greater sexual dimorphism in age at maturation in the northern population is not reflected at larger spatial scales in previous studies of corkwing wrasse. In Southern England nesting males was found to mature later (third year) than sneaker males (first year) and females (second year) (Dipper and Pullin, 1979), similar to we detected in the northern population. On the contrary, both nesting males and sneaker males

matured in their first year in western Sweden (Uglem *et al.*, 2000). Intraspecific variation in male-biased SSD in other fish species has been proposed to be result of sex-specific plastic responses to the strength of sexual selection (Lengkeek *et al.*, 2008; Walker and McCormick, 2009). The nesting males of corkwing wrasse are fiercely territorial during the nesting season and larger individuals tend to win aggressive confrontations (Potts, 1974, 1985). Thus, the intensity of male–male competition and sexual selection on body size is likely to increase with population density. The densities of the four northern populations was probably higher, as indicated by higher CPUE, which therefore offer a plausible explanation of the more pronounced SSD. Moreover, the smaller nesting males in the northern population had smaller gonads relative to those in the southern. Since no population differences were detected for females and sneaker males, it appears likely that smaller nesting males in the north trade off sperm



**Figure 6.** Linear regression of log transformed gonad weight (g) on log transformed total length (mm) of mature corkwing wrasse in the southern and northern population fitted separately for each sex and male type.

**Table 3.** Summary of the linear models between log transformed gonad wet weight and log total length of corkwing wrasse, fitted separately for mature females, nesting males and sneaker males

	Explanatory variable	Estimate	s.e.	t value	p value
Females multiple $R^2=0.75$					
	Intercept	-22.68	1.77	-12.81	<0.001
	Log length	4.78	0.36	13.09	<0.001
	Population (south)	-4.22	3.13	-1.35	0.18
	Log length:Population	0.88	0.63	1.39	0.17
Nesting males multiple $R^2= 0.85$					
	Intercept	-57.21	5.23	-10.94	<0.001
	Log length	11.25	1.04	10.85	<0.001
	Population (south)	21.10	6.06	3.48	0.001
	Log length: Population	-4.06	1.20	-3.37	0.002
Sneaker males multiple $R^2= 0.66$					
	Intercept	-26.81	4.24	-6.33	<0.001
	Log length	5.70	0.90	6.35	<0.001
	Population (south)	2.98	6.75	0.44	0.66
	Log length: Population	-0.58	1.42	-0.41	0.69

The Northern population (Austevoll) is considered the reference level.

volume for somatic growth to attain larger body size and increase their competitiveness. The northern populations had also consistently smaller mean body sizes than the southern, which possibly is related to gradually decreasing summer temperatures from South-Eastern Skagerrak to further north on the Western Coast (Sætre, 2007). Moreover, the presumably higher density in the northern populations could also contribute to lower growth rates and smaller body size, as density and growth tend to be inversely correlated (Lorenzen and Enberg, 2002). It is possible that the north-south differences in SSD and body size have a genetic basis, because an on-going population genetic study has found large genetic differences between populations on each side of the Jæren sand banks (Enrique Blanco, pers. comm.), which also separates the northern and southern populations in the current study.

The growth analyses showed the minimum size limit (12 cm) to be sex-divisive towards the age classes first entering the fisheries, especially in the northern population. These ages were also clearly the most abundant in our catches, indicating a strong potential for size-selective fishing to alter the relative frequencies of nesting males, sneaker males and females. Nesting males

represented only 15% or less of the spawning fish in the four northern populations with the strongest SSD; implying male-biased harvesting is more likely where the proportion of nesting males is lowest. The Norwegian wrasse fishery first intensified in 2009 and has increased substantially since then (Skiftesvik et al., 2014a, b), so it is plausible that the sex ratios reported in this studied have already been shifted by fishing. In a study conducted prior to commercialization of the fisheries in Os (one of the northern sites in this study) during 1997–1999, nesting males constituted 34–39% of the spawning population (Skiftesvik et al., 2014b), which is substantially higher than what we found in the same areas (Os 11% and Austevoll 15%). Pre-fishing data are not available from the more southern populations, but an on-going study finds no differences in sex ratios between two MPAs established in 2006 and the corresponding fished sites (Halvorsen, unpublished). This is consistent with the absence of SSD in the southern population, translating into less opportunity for fisheries induced changes in sex ratios. With the exception of Sveio, the size limit protected less than half of the mature females. Thus, with the current regulations, fishing during the spawning season

may both reduce the egg production and remove the males that guard them. As a conservation measure, fishing is now prohibited until 11 July (2016) and if the main spawning period occurs prior to the opening date, this may allow some nesting males and females to breed at least once before being harvestable. Although previous surveys has found the highest proportions of spawning fish in June and July, a lower proportion of spawners were also present in August (in Arendal) and September (in Os) (Hanssen, 2014; Skiftesvik *et al.*, 2014b). Moreover, nesting males guard and fan the eggs for 11–16 days after spawning (Potts, 1974), and could therefore be vulnerable for a prolonged period after males extrude milt, which is used as an indicator for spawning in the mentioned surveys.

If size-selective fishing reduces the proportion and density of nesting males, this may reduce competition over territories and could therefore weaken the strength of sexual selection on male body size. In addition, sexual selection arising from female choice is also expected to weaken when sex ratios become more female-biased and densities are lowered (Kvarnemo and Ahnesjö, 1996; Kokko and Rankin, 2006; Székely *et al.*, 2014). The combination of size-selective harvesting and sexual selection on body size may produce stronger selection for smaller body size than if reproductive success is independent of body size (Hutchings and Rowe, 2008). In addition, fishing may also induce selection on the mechanism determining the probability of maturing as sneaker male if the relative proportion of sneaker males increases and in that way alters the relative fitness of the two male tactics. Whether selective harvesting can affect sexual selection and fitness of male tactics directly and indirectly are interesting questions that can be addressed in future studies using corkwing wrasse as a model.

On the basis of the clear differences in SSD and body size between northern and southern populations, we suggest to manage these regions separately and to reevaluate the size limits. To reduce the potential of sex selective harvesting in the northern populations, raising the minimum size limit further has limited effect, as the sexual size differences are maintained as body size increase. Alternatively, sex-specific minimum size limit with basis in the male and female size at maturation is a possible and feasible solution. The distinct colouration of nesting males makes it easy for fishermen to distinguish them from females and sneaker males. Another, and perhaps better, option is to use slot limits; a combination of a maximum size and minimum size limit (Gwinn *et al.*, 2015). The faster growth of males implies that they would reach a maximum size limit at a younger age than females. In addition, protecting large and more fecund individuals of both sexes can benefit recruitment and reduce the risk of evolutionary downsizing (Conover and Munch, 2002; Birkeland and Dayton, 2005). The economic consequences of implementing a slot limit are likely to be small as wrasses are sold per individual and not per weight. In the southern populations, a slot size limit is probably less needed because of weaker SSD and shorter longevity which then would protect large individuals near the end of their natural life span. Increasing the size limit so the 1-year-old fish is fully protected and ensuring that the opening date is protecting the population during the nesting season appears to be a better solution. Ideally, growth and maturation data from more locations combined with the information on spatial genetic structure would be beneficial for determining the appropriate distribution of spatial management units and the specific size regulations.

In conclusion, this study has demonstrated spatial variation in sexual dimorphism and life history traits in corkwing wrasse in Norway. There was a particularly strong mismatch between sexual dimorphism and management practices in the northernmost populations in our sampling. To reduce the risk associated with sex-selective harvesting, we suggest spatially structured management regulations with sex-specific size limits or slot-limits reflecting the regional sex-specific growth and maturation patterns.

## Acknowledgements

We are indebted to Torkel Larsen and Emma Matland for skilful assistance during field work and are thankful for the patience and helpfulness from the collaborating fishermen. Suggestions from two anonymous referees improved the quality of this article. This study received financial support from Norwegian research council (project PROMAR—201917), from UiA through funding from the Ministry of Education and Research and by the Öresund-Kattegat-Skagerrak Interreg project, MarGen.

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Handling editor: Jonathan Grabowski