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# Mind the Depth: The Vertical Dimension of a Small-Scale Coastal Fishery Shapes Selection on Species, Size, and Sex in Wrasses

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## Abstract

Small-scale fisheries (SSFs) tend to target shallow waters, but the depth distributions of coastal fish can vary depending on species, size, and sex. This creates a scope for a form of fishing selectivity that has received limited attention but can have considerable implications for monitoring and management of these fisheries. We conducted a case study on the Norwegian wrasse fishery, a developing SSF in which multiple species are caught in shallow waters (mean depth = 4.5 m) to be used as cleaner fish in aquaculture. Several of these wrasses have life histories and behaviors that are sensitive to selective fishing mortality, such as sexual size dimorphism, paternal care, and sex change. An experimental fishery was undertaken over three sampling periods in 2018. Data on catch, length, and sex of wrasses across a depth gradient (0–18 m) were collected and analyzed. We found that depth distributions were species specific and the vertical overlap with the fishery was high for Corkwing Wrasse *Symphodus melops* and Ballan Wrasse *Labrus bergylta*, which were most abundant at depths less than 5 m. Three other wrasse species had invariant or increasing abundance with depth and were therefore less likely to be negatively impacted by this fishery. Body size was positively correlated with depth for these wrasses, and sex ratio became more male biased for the Corkwing Wrasse, the only species that could be visually sexed. This study demonstrates that depth can have strong effects on fishing selectivity at multiple scales and that such knowledge is necessary to develop management strategies that

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**balance fishing mortality sustainably across species, sizes, and sexes. We recommend that management priorities be directed toward the Ballan and Corkwing wrasses—the species having the highest vertical overlap with the fishery. Furthermore, CPUE was strongly affected by seasonality and positively correlated with increasing wave exposure for one of the species. This underscores the general importance of standardizing catch data for several environmental covariates when monitoring species that are affected by SSFs.**

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Small-scale fisheries (SSFs) employ the majority of the world's fishers and are vital for economic and food security in coastal communities (Cohen et al. 2019). The ecosystems sustaining these fisheries are under increasing pressure, and many SSFs are poorly monitored and lightly managed, even in developed countries (Lloret et al. 2018; Damasio et al. 2020). In addition, SSFs are often highly selective, disproportionately targeting specific species, sizes, and sometimes sexes (Lloret et al. 2012; Myers et al. 2014; Emmerson et al. 2017). Depletion of key species or phenotypic diversity within species can have adverse effects on productivity and ecosystem stability—for example, through disrupted mating behavior (Sørdalen et al. 2018) or altered predator–prey dynamics (Selden et al. 2017). Thus, to achieve sustainable SSFs, fishing selectivity must be assessed, monitored, and managed (Lloret et al. 2018).

Fishing selectivity also has a spatial component (Zhou et al. 2010). When habitat preferences differ between species and individuals, those exhibiting the highest spatial overlap with the fishing gear will be captured more often (Alós et al. 2012; Wiig et al. 2013). Small-scale fisheries are typically more intense in shallow waters because they are more accessible to fishers (Tyler et al. 2009; Olsen et al. 2012; Murillo-Posada et al. 2019). Consequently, the selectivity pattern of many SSFs is likely to be strongly depth dependent since the relative abundance of coastal species can change considerably with small changes in depth (Dufour et al. 1995; Bachelier et al. 2014; Jankowski et al. 2015), and some species perform vertical migrations on a daily or seasonal basis or move to deeper waters as they grow larger (Macpherson and Duarte 1991; Olsen et al. 2012; Williams et al. 2019). Similarly, fishing depth may expand or change with time, driven by changes in target species, weather conditions, technology, and fuel costs (Saldaña et al. 2017; Damasio et al. 2020). Variation in the spatiotemporal distribution of fisheries and affected species could also have a considerable impact on the selectivity pattern and catch rates in SSFs. This awareness is important for stock assessments, as catch and length data are often used to monitor temporal changes in stock status within SSFs, but such trends are likely to be biased if depth and other important environmental covariates are not accounted for (Glazer and Butterworth 2002; Bigelow and Maunder 2007; Alonso-Fernández et al. 2019).

To assess depth-dependent fishing selectivity and its implications, detailed knowledge of the vertical distributions of both fish and fisheries is needed, but there are few examples in which such information has been considered for SSFs (but see Tyler et al. 2009; Collins and McBride 2011; Mitchell et al. 2014). This is somewhat surprising given the obvious relevance of this information for managing fisheries on multiple species with different depth distributions (Moore et al. 2016; Gilman et al. 2019). In this context, we undertook a case study on the Norwegian wrasse fishery, a commercially important multispecies SSF for which detailed data on fishing depth and the depth distributions of species were obtained using data loggers fitted to traps. This fishery supplies live wrasses to salmon farms, where they are used as cleaner fish to remove sea lice (Skiftesvik et al. 2013; Halvorsen et al. 2017a). Wrasse fishers predominantly target shallow waters (1–7 m) to avoid inflicting barotrauma on their catch (Halvorsen et al. 2017b), although some of the target species have much wider depth ranges than the depths that are fished (Table 1). Hence, this fishery may have differential impacts on species, sizes, and sexes depending on the species' vertical distributions relative to the fishing depths.

Small-scale commercial wrasse fisheries were first established in Norway and the British Isles in 1988–1990 (Darwall et al. 1992; Skiftesvik et al. 2014). In Norway, this fishery has intensified considerably since 2010, driven by the reduced efficiency of chemotherapeutant-based delousing methods (Rueness et al. 2019). These wrasses are facultative cleaners in the wild, and when deployed in sea-cages with salmon, they feed on sea lice attached to the salmon and can be effective in lowering infestation rates (Bjordal 1991; Skiftesvik et al. 2013). Cleaner fish can therefore reduce the need for chemical or mechanical delousing methods that might have negative impacts for fish in the pens or negative effects on the surrounding ecosystem (Escobar-Lux et al. 2019; Overton et al. 2019; Parsons et al. 2020). On the other hand, there are unresolved challenges surrounding cleaner fish welfare, the possibility for transmission of diseases to both captive and wild fish, and the potential for wrasses to escape and impact the genetic diversity and structure of local populations when imported from distant areas (Faust et al. 2018; Rueness et al. 2019).

TABLE 1. Reported depth range, key life history characteristics, and the total landings (thousands) in the Norwegian wrasse fishery during 2017–2019 (Norwegian Directorate of Fisheries, unpublished data; <https://www.fiskeridir.no/Yrkesfiske/Tall-og-analyse/Fangst-og-kvoter/Fangst-av-leppefisk>). Price per individual is presented with the minimum size limit (cm; in parentheses). For Corkwing Wrasse, the legal minimum size limit decided by the Norwegian Directorate of Fisheries is 12 cm, but the buyers in this region only accept Corkwing Wrasse that are 13 cm or larger. For Ballan and Goldsinny wrasses, the size limit is as specified; for Rock Cook and Cuckoo Wrasse, the legal minimum size limit is 11 cm, but these species are not accepted by buyers on the Skagerrak coastline.

Species	Depth range (m)	Life history characteristics	Norwegian landings (×1,000)			Price (Norwegian kroner) per individual (Skagerrak 2018)
			2017	2018	2019	
Ballan Wrasse <i>Labrus bergylta</i>	0–30 <sup>a,b</sup>	Monandric protogynous hermaphrodite, male parental care, maximum age = 29 <sup>a,c</sup>	2,151	1,879	1,949	30 (>14 cm)
Corkwing Wrasse	Most abundant at depth >5; maximum depth = 18 <sup>b</sup>	Dioecious, male parental care, sneaker males, maximum age = 9 <sup>b,c</sup>	12,102	8,181	8,071	10 (>13 cm)
<i>Symphodus melops</i>						
Goldsinny Wrasse	0–50 <sup>b</sup>	Dioecious, pelagic spawner, maximum age = 20 <sup>b</sup>	12,937	8,040	8,516	14 (>11 cm)
<i>Ctenolabrus rupestris</i>						
Cuckoo Wrasse	2–200 <sup>b</sup>	Diandric protogynous hermaphrodite, male parental care, sneaker males, maximum age = 17 <sup>b</sup>	4	0	13	NA
<i>Labrus mixtus</i>						
Rock Cook	0–40 <sup>b</sup>	Dioecious, spawning behavior not known, maximum age = 10 <sup>b</sup>	623	394	452	NA
<i>Centrolabrus exoletus</i>						
Total			27,818	18,494	19,001	

<sup>a</sup>Dipper et al. 1977.

<sup>b</sup>Sayer and Treasurer 1996.

<sup>c</sup>Darwall et al. 1992.

The Ballan Wrasse is the largest in size and the most valued as a cleaner fish, while the Goldsinny and Corkwing wrasses are more abundant and therefore the most economically important species (Table 1). The Rock Cook and Cuckoo Wrasse are only occasionally retained and used in some regions (Rueness et al. 2019). Wrasse species and sizes are kept in tanks onboard the fishing vessel, while smaller specimens are released along with other bycatch species (Halvorsen et al. 2017b). The sustainability of the wrasse fishery has been questioned, particularly due to its selective nature (Darwall et al. 1992; Sayer et al. 1996; Halvorsen et al. 2017a). The fishery reduces abundance and size in Norwegian wrasse populations (Halvorsen et al. 2017a, 2017b), and several of these species display behaviors and life histories that increase their sensitivity to selective fishing mortality (Darwall et al. 1992; Villegas-Rios et al. 2013; Halvorsen et al. 2016; Table 1). For example, males are larger than females, and in three of the species the males also provide obligate parental care (Table 1). In addition, concerns have been raised regarding bycatch of other valued species, such as brown crab *Cancer pagurus*, Atlantic Cod *Gadus morhua*, and European lobster *Homarus gammarus* (Grefsrud et al. 2018:166–174). Since the wrasse fishery also has recently expanded in the southern regions of the UK and in Scotland (Riley et al. 2017; McMurtrie et al. 2019), there is an increasing need for better knowledge of how this fishery impacts target species and bycatch and a need to develop methods for accurate and efficient monitoring of the stocks.

Here, we investigated the vertical distribution of the wrasses and important bycatch species by conducting experimental trap fishing in southern Norway, spanning an extended depth range greater than that normally targeted by fishers in this area. We analyzed depth gradients in CPUE and fish length relative to the target depths of the commercial fishery, which was monitored using data loggers in traps. Sampling was conducted before, during, and late in the fishery, allowing us to examine seasonal variation in these depth gradients. We predicted that the vertical distributions would differ among the wrasse species, as suggested by their depth ranges (Table 1). The Corkwing Wrasse could be visually sexed by fishers, which also allowed us to test whether the sex ratio differed as a function of depth. Lastly, since an earlier study found that wave exposure affects size and CPUE for these wrasses (Skiftesvik et al. 2015), we accounted for this by modeling the average wave height at each sampling location utilizing data on bathymetry and long-term time series of currents and wave height.

## METHODS

### Experimental Fishery

The experimental fishery was conducted on the Skagerak coast in Agder County, southern Norway (Figure 1).

Six local wrasse fishers were contracted to conduct the sampling using the same boats and gear as used in the commercial fishery (Supplementary Information S1 available separately online). They were instructed to choose eight representative sites within the areas that they normally fished, each of which would be visited once per sampling period: June 18–25 (before the fishing season; Figure 2), September 2–9 (during the fishery), and October 22–29 (at the end of the fishing season). Since the first sampling period was conducted outside of the fishing season (opening on July 17, closed on October 31), the fish were released at the catch location. During the second and third sampling periods, wrasses that were caught in the experimental fishery were retained as in the normal fishing procedure if they were larger than the minimum size limit in this fishery (Table 1), and those that were smaller were released immediately at the same site. Permission for experimental fishing was obtained from the Norwegian Directorate of Fisheries (Permit Number 18/9223).

The fishers used two-chamber wrasse traps (OK Marine, Kristiansand, Norway; 70 × 40 × 29 cm; 9-mm-high × 6-mm-wide elliptical entrances; 12-mm mesh size; 12-mm-wide escape openings). Each fisherman used 9 traps/d; three traps (i.e., a set) were linked by a 10-m rope between each trap. The center trap in each set was fitted with a depth–temperature data logger (DST centi-TD; Star-Oddi, Reykjavik, Iceland). Depth and temperature were recorded at 10-min intervals, and the mean depth and temperature for each set were calculated to be used as covariates for statistical analysis (see below). The difference between low and high tide in this area is less than 0.5 m. At each of the eight sites, the fishers were instructed to deploy the sets at the following depth ranges: between 0 and 5 m, between 5 and 10 m, and between 10 and 15 m. Occasionally, traps were set deeper than intended (maximum = 23 m; Supplementary Information S2), and three trap sets that were deeper than 18 m were considered outliers and excluded from further analysis. During the commercial fishery, the traps must be hauled at least once per day, but the set and haul times varied for practical reasons. To reduce variability caused by differences in soak time, the traps were set and hauled between 1000 and 1400 hours. Crushed, raw brown crab was used as bait, as in the commercial fishery. Fishers were instructed and trained ahead of the experiments (including a pilot trial in 2017), provided with standardized equipment for length measurement, and provided with waterproof paper on which to note measurements. In each trap, all wrasses caught were counted and measured for TL (closest 5 mm), while bycatch was identified to species and counted. Data loggers were retrieved shortly after the last sampling period and were calibrated in a saltwater basin following the manufacturer's instructions, and the depth measurements were adjusted accordingly. Daily mean water temperatures

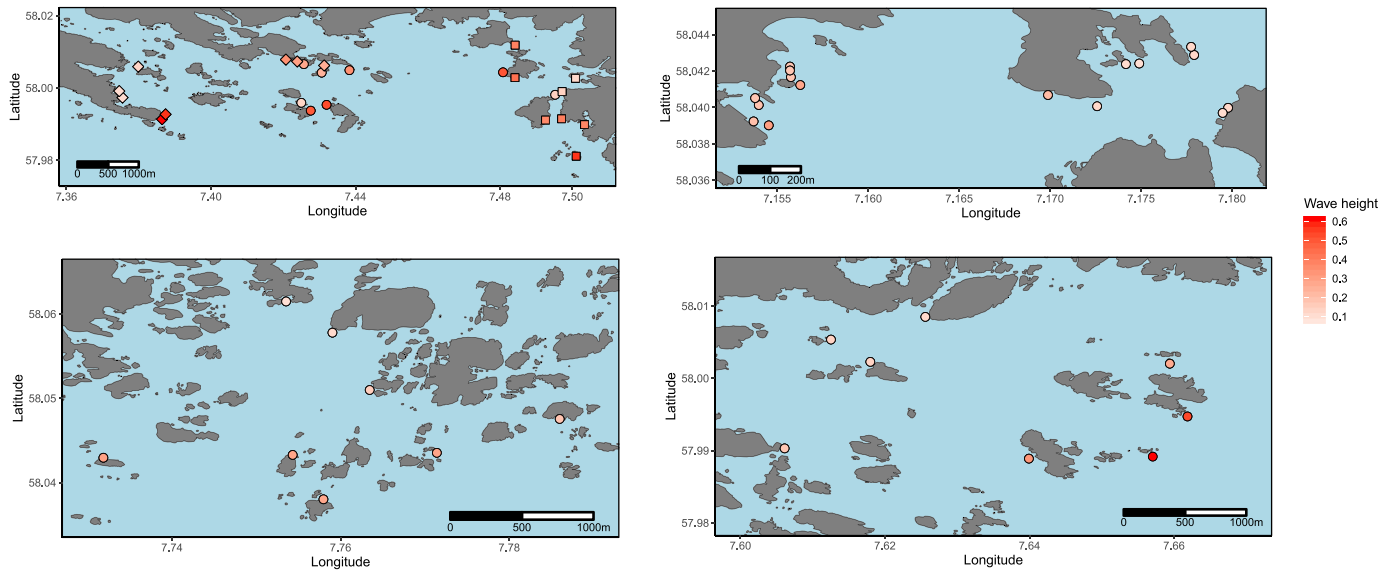


FIGURE 1. Sampling locations in Skagerrak along the Norwegian coast (Agder County). Each fisher ( $n = 6$ ) chose sites within the fishing grounds that they use in the commercial fishery, and traps were set along natural depth gradients. Each site was visited three times in 2018. Different shapes indicate different fishers (in areas with more than one fisher). The fill color reflects the estimated mean wave height at each sampling location.

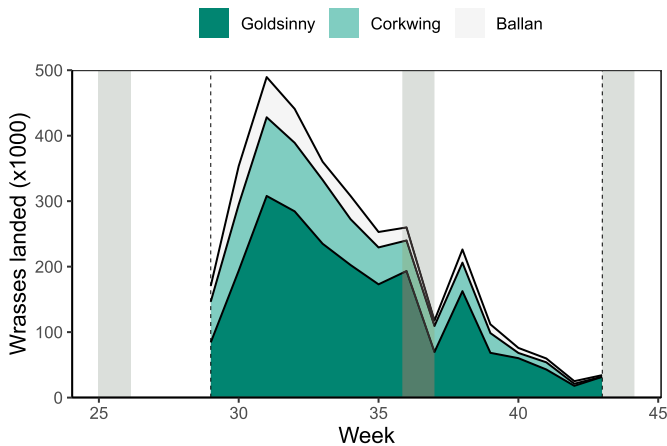


FIGURE 2. Seasonal patterns in weekly landings in the wrasse fishery conducted in Skagerrak (Agder County, Norway) during 2018 (official landings data from the Norwegian Directorate of Fisheries). Vertical shaded columns indicate the weeks when experimental fishing was carried out, with six fishers targeting an expanded depth range.

in the experimental fishery ranged between  $7^{\circ}\text{C}$  and  $15^{\circ}\text{C}$  during June 18–25, with up to a  $3^{\circ}\text{C}$  difference between the deepest and shallowest depths. There were no depth gradients in the following periods: for September 1–9, the temperature was stable at around  $17.5^{\circ}\text{C}$ ; and for October 22–29, the temperature steadily declined from  $13.5^{\circ}\text{C}$  to  $11.5^{\circ}\text{C}$  (Supplementary Information S3).

### Commercial Fishery

The data loggers remained in the fisher's traps between sampling periods so that data on the seasonal variation in

fishing depth could be collected. The mean fishing depth of traps set in the commercial fishery was 4.5 m, with 75% of the traps being set shallower than 5.6 m and only 0.4% of the traps being set deeper than 10 m. The fishery in Agder County opened on July 17, and weekly landings peaked at the beginning of August at almost 500,000 individuals, followed by a relatively steady decline (Figure 2). The second period in the experimental fishery was carried out halfway into the fishing season, but the majority of wrasse had already been fished at this point. Goldsinny Wrasse made up between 50% and 90% of the catches. The proportion of Corkwing and Ballan wrasses became smaller toward the end of the season.

### Wave Exposure Index

The Norwegian coastline is heterogeneous, with numerous islands and skerries, resulting in spatially fine-scale variation in wave exposure. Wrasse fishers operate across the full range from inshore sheltered areas to the outermost islands that are exposed to the open sea. The relative abundances of wrasse species and sizes appear to differ between sheltered and exposed habitats (Skiftesvik et al. 2015). To be able to test and account for the effects of exposure on variation in species abundance and body size, we developed a wave exposure model operating on the highest resolution bathymetric data available ( $50 \times 50$  m). Bathymetry data were collected from the online data source Geonorge (<https://data.geonorge.no/sosi/dybdedata>), which is hosted by the Norwegian Mapping Authority. In the absence of a dynamic coastal wave model with such a high resolution, we applied fetch data, wind statistics, and

offshore swell data to generate a statistical measure of the long-term averaged wave height (significant wave height) for each fishing site according to the equations in Norsk Standard (2009), the Norwegian standard for localizing marine fish farms. The fetch at each site was calculated for 36 sectors. The wind observations were sorted into 12 cardinal directions and based on more than 10 years of measurements from Lindesnes Lighthouse, situated west of the study area (data provided by the Norwegian Meteorological Institute; <http://eklima.met.no>). The infinite fetch sectors were tuned toward an offshore significant wave height corresponding to a long-term value provided by the operational wave forecasting system at the Norwegian Meteorological Institute (wave model WAM-4 km; e.g., Carrasco and Gusdal 2014).

### Statistical Analysis

*Fishing depth during the regular fishery.*—To test for a temporal trend in fishing depth during the commercial fishery, a simple linear model was applied to the individual trap depth measurements (pooled from all six fishers), with days from the start of the fishery as the predictor variable. Based on information from interviews with the fishers prior to the study, fishing depth was predicted to deepen as the season progressed.

*Wrasse CPUE in the experimental fishery.*—Standardized CPUE was estimated to assess abundance along gradients in depth and wave exposure for the five wrasse species. The sampling unit was a set (i.e., the three linked traps), and species-specific generalized linear mixed-effect models (GLMMs) with a negative binomial distribution were fitted using the R package *glmmTMB* (Brooks et al. 2017). Generalized linear mixed-effect models are widely applied to spatiotemporal catch and length data in fisheries; this flexible modeling framework allows for assessing and accounting for the effects of environmental covariates and random effects and provides standardized CPUE and length estimates (Maunder and Punt 2004; Thorson and Minto 2015; Alonso-Fernández et al. 2019). The following model structure, defined a priori, was applied:

$$\text{Catch} \sim \beta_0 + \beta_1(\text{soak time}) + \beta_2(\text{wave exposure}) + \beta_3(\text{depth}) + \beta_4(\text{period}) + \beta_5(\text{depth} \times \text{period}).$$

The covariates of primary interest were depth and wave exposure. A linear effect of soak time was assumed because all traps were set overnight and hauled at specific times, which was confirmed by model validation (there were no nonlinear patterns in residuals versus fitted values for soak time). Furthermore, a depth  $\times$  period interaction effect was included, as the first sampling period was conducted during the spawning period, when males of all species are highly territorial, whereas some of the species form feeding shoals after spawning (Potts 1974; Costello

1991; Darwall et al. 1992). Due to a lack of overlapping temperature intervals among sampling periods, temperature was not included as a covariate since it could not be disentangled from seasonality in the models (Supplementary Information S3). Random effects were used to account for the remaining spatiotemporal variability, including day (24 groups) and the eight areas for each of the six fishers (48 groups). Day accounted for shared daily conditions in weather, temperature, current, moon phase, etc., that could potentially affect catchability, while the fisher area random effect handled variation that was attributed to site-specific conditions, such as habitat quality and past fishing activity. A simple, two-step model selection process was carried out using pairwise comparisons of Akaike's information criterion (AIC) scores, and the model with the lowest AIC value was chosen. If the AIC difference ( $\Delta\text{AIC}$ ) was less than 2, the model with fewer estimated parameters was chosen in favor of the more complex model (Burnham and Anderson 2002). First, models with and without the depth  $\times$  period interaction effect were compared. Second, since the visual inspection of residual versus fitted values revealed indications of a higher spread in residuals during period 1 relative to the other two periods, we tested whether allowing for heterogeneous variance between periods improved the fit (AIC) of the model. The underlying statistical assumptions (homogeneity of variance, normal distribution of residuals) in all models were assessed by graphical inspection of residuals plotted against fitted values and covariates. For mixed-effects models, continuous covariates were standardized with a mean of zero and an SD of 1, and *P*-values were estimated using the Kenward-Roger approximation (Bolker et al. 2009) implemented in the R package *sjPlot* (Lüdtke 2018). All statistical analyses were performed in R version 3.5.1 (R Core Team 2018).

*Wrasse length.*—To analyze depth gradients in body size, linear mixed-effects models with the restricted maximum likelihood estimation procedure were fitted using the *lmer* function in the R package *lme4*. The initial mixed model structure was the same as for catch but without the random effect for sampling day. Length data were modeled assuming homogeneous variance among the sampling periods—an assumption that was supported by assessment of the spread of residuals between sampling periods. Model selection and validation were otherwise conducted as described above for wrasse CPUE.

*Corkwing Wrasse sex ratio.*—A GLMM (Bernoulli distribution) was applied to estimate the probability of a Corkwing Wrasse being a male, with the same model structure as for length data except that the soak time effect was excluded because it was not assumed to influence the sex ratio. To reduce the likelihood of individuals being wrongly sexed, only Corkwing Wrasse larger than 12 cm were included in the analysis, which corresponds to

the size at maturity, when secondary sexual characteristics become more visible and sex determination is straightforward (Potts 1974; Halvorsen et al. 2016). Model selection was carried out as described above.

*Bycatch species.*—The sample sizes for European lobster, brown crab, and Atlantic Cod were considerably lower than those for the wrasses (Supplementary Information S4), with zero catches being the most frequent observation. Bycatch was therefore modeled as presence–absence data (Bernoulli distribution) using generalized linear models without random effects (GLMMs had higher AIC values than generalized linear models; data not shown). As for the wrasse models, models with and without a depth  $\times$  period interaction were compared by using AIC.

## RESULTS

Overall, 1,350 traps were sampled during the experimental fishery, trapping more than 15,000 individuals belonging to 28 species of fish and crustaceans (Supplementary Information S4). Wrasse constituted 94.6% of the catch by number, and Goldsinny Wrasse alone constituted 69% of the catch. Our three focal bycatch species (European lobster, brown crab, and Atlantic Cod) together constituted 3.6% of the catch by number. At the opening of the fishery (July 17; Figure 3), the mean fishing depth was 3.33 m (SE = 0.18; linear model), which increased significantly as the season progressed ( $\beta_{day} = 0.05$ , SE = 0.01;  $t = 7.52$ ,  $P < 0.001$ ).

There were clear species-specific patterns in CPUE–depth gradients over the sampled depth range (0–18 m). Ballan and Corkwing wrasses were most abundant at less than 5-m depth and therefore showed the strongest overlap with the fishing depth in the commercial fishery (Tables 2, 3; Figures 4, 5). This had a strong effect on catch composition: for example, the Corkwing Wrasse CPUE at 0.5 m was twice as high as the CPUE in traps set only 5 m deeper (Figure 4). The Goldsinny Wrasse was more evenly distributed with depth, while CPUE increased with depth for Cuckoo Wrasse and Rock Cook, with the former showing the steepest gradient. There were also strong seasonal effects on CPUE, with the pooled CPUE for wrasses being four to six times higher in September and October compared to June (Figure 4; Table 3). A general trend of wrasses having a shallower depth distribution in June was also detected, with a gradual shift toward deeper waters in September and October (Figure 4), as supported by significant depth  $\times$  period interaction effects for all wrasses except the Cuckoo Wrasse (Table 3). Ballan Wrasse CPUE was positively correlated with wave exposure, while no such effects were detected for the other four wrasses (Table 3).

All wrasses showed a positive correlation between depth and length (Table 4; Figure 6). This effect was strongest for the Ballan Wrasse, as the model estimated an

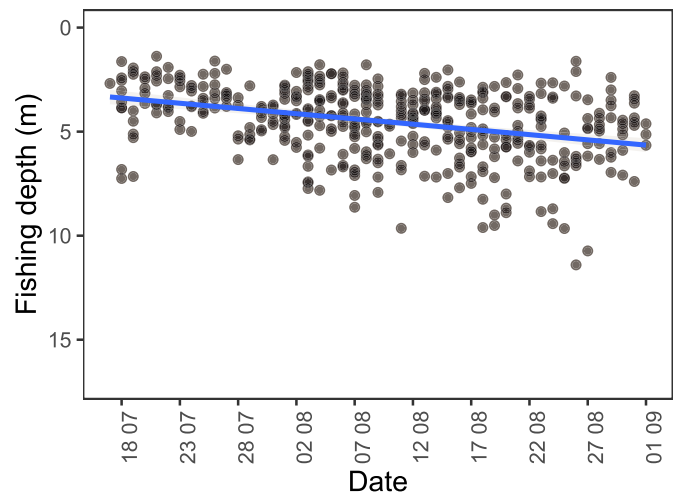


FIGURE 3. Fishing depth in the commercial wrasse fishery conducted in Skagerrak (Agder County, Norway) during 2018. The six fishers kept depth loggers in the traps from the opening of the fishery (July 17) until the second sampling period (September 2). A regression line is fitted to the data and depicts the temporal development in mean target depth.

approximately 20% increase in length from 0.5- to 18.0-m depth in the first fishing period (length difference = 6.2 cm). Ballan Wrasse that were caught in June (during spawning) were also larger than those caught later in the season (e.g., estimated 19% larger in June versus October at 0.5-m depth; Table 4). Seasonal effects on length for the other wrasse species were small but significant (Table 4). Length was not affected by the degree of wave exposure. For Corkwing Wrasse, sex ratios became increasingly male biased with depth (Table 5; Figure 7) and gradually became more female biased later in the season (Table 5).

The probability of catching Atlantic Cod and European lobster increased with depth, although there was no significant trend for brown crab (Table 6; Figure 8). Catches of European lobster were highest in September (during the wrasse fishery); for Atlantic Cod, catches were highest in June and declined throughout the season; and catches of brown crab were highest in October (Table 6). High wave exposure was positively related to Atlantic Cod catches but did not affect the probability of catching European lobster or brown crab (Table 6).

## DISCUSSION

This case study demonstrates that the vertical dimension of a multispecies SSF is an important factor shaping selectivity, as even small changes in fishing depth (<5 m) had a large effect on species composition, size, and sex ratio. Furthermore, the effects of season and wave exposure on catch rates and length were strongly species specific. Consequently, both the spatial and temporal

TABLE 2. Model selection for wrasse CPUE, wrasse length, probability of a Corkwing Wrasse being male, and bycatch presence in the Norwegian wrasse fishery (GLMM = generalized linear mixed-effect model; LMM = linear mixed-effects model; GLM = generalized linear model). Akaike's information criterion (AIC) was compared for models with and without a depth  $\times$  period interaction effect. Shaded cells indicate the final model structure; when the AIC difference ( $\Delta$ AIC) was less than 2, the model without an interaction effect was selected. For wrasse CPUE models, a second step was conducted in which the optimal model from step 1 was compared with a model allowing for heterogeneous variance between sampling periods. See Methods text for further details on selection criteria.

Model	Species	AIC, depth $\times$ period	$\Delta$ AIC, depth + period	$\Delta$ AIC, heterogeneous variance
Wrasse CPUE (negative binomial GLMM)	Ballan Wrasse	1,250	45.2	-15.3
	Corkwing Wrasse	1,387	3.3	-6.3
	Cuckoo Wrasse	1,489	-2.7	-5.0
	Goldsinny Wrasse	1,592	10.8	-10.1
	Rock Cook	3,354	3.6	-9.7
Wrasse length (LMM)	Ballan Wrasse	6,710	-2.4	
	Corkwing Wrasse	13,549	2.4	
	Cuckoo Wrasse	9,534	-3.7	
	Goldsinny Wrasse	82,140	22.8	
	Rock Cook	5,741	-0.6	
Corkwing Wrasse male (Bernoulli GLMM)	Corkwing Wrasse	1,801	-2.2	
Bycatch presence (Bernoulli GLM)	European lobster	306	-0.3	
	Atlantic Cod	531	0.6	
	Brown crab	556	-3.3	

distributions of the fishery have considerable effects on catch composition and the relative impact on affected species. Therefore, it is clearly important to standardize trap survey data for depth, season, and wave exposure. Beyond the specific implications for management of the developing wrasse fisheries in northern Europe, this study illustrates the general necessity of assessing and accounting for spatial distributions of both fish and fisheries when designing surveys and management strategies for SSFs.

### Fishing Depth and Implications for Fishing Selectivity on Species, Size, and Sex

Selective fishing practices are among the main concerns about SSFs (Lloret et al. 2018; Sordalen et al. 2018). Restrictions on gear design and setting minimum and maximum size limits are some of the management measures that deal directly with selectivity and are commonly applied in SSFs (Lloret et al. 2012; Erisman et al. 2017; Sordalen et al. 2018). However, as shown here, selectivity can also be strongly dependent on the spatiotemporal dynamics of the fishery and this information should therefore be incorporated in monitoring, assessment, and management strategies for this and similar SSFs.

The wrasse fishery targets shallow waters (<6 m), and the species displaying the strongest vertical overlap with the fishing gear also have life histories and behaviors thought to be sensitive to fishing, such as sequential hermaphroditism (Ballan Wrasse), male parental care (Ballan and Corkwing wrasses), and alternative male life history pathways (Corkwing Wrasse). The Goldsinny Wrasse showed little change in relative abundance with depth; therefore, deeper waters provide a refuge from fishing. However, we cannot exclude the possibility that shallow-water fishing has already affected the depth distribution of this species, especially considering that Goldsinny Wrasse display very strong site fidelity (Hilldén 1984; Sayer 1999), have a long life span (up to 20 years; Table 1), and make up the highest proportion of the wrasse landings in this area (Figure 2). The CPUE increased with depth for the two noncommercial wrasses (Cuckoo Wrasse and Rock Cook) as well as for Atlantic Cod and European lobster. This suggests that the wrasse fishery has a limited negative impact on bycatch species.

The general pattern of increasing fish length with depth observed here demonstrates that fishing depth affects size selectivity on wrasses. Positive depth–body size correlations



TABLE 3. Generalized linear mixed-effect model summaries for wrasse CPUE models, showing estimated incident rate ratios ( $\beta$ ; exponentiated model coefficients), SEs, and  $P$ -values for the five wrasse species (bold italics denote significance). The intraclass correlation coefficient (ICC) is provided for random effects. Data are from 450 sets (3 traps/set). Continuous covariates were standardized (stn) with a mean of zero and an SD of 1.

Predictor	Ballan Wrasse			Corkwing Wrasse			Goldsinny Wrasse			Cuckoo Wrasse			Rock Cook		
	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$
Intercept	0.93	0.15	0.643	0.17	0.3	<0.001	5.1	0.11	<0.001	0.85	0.11	0.148	0.22	0.3	<0.001
Soak time (stn)	1.16	0.06	<b>0.014</b>	1.23	0.06	<0.001	1.01	0.04	0.887	1.06	0.05	0.271	1.08	0.09	0.388
Wave exposure (stn)	1.21	0.07	<b>0.008</b>	0.89	0.11	0.279	0.97	0.04	0.398	0.98	0.06	0.775	1.06	0.13	0.662
Depth (stn)	0.5	0.14	<0.001	0.18	0.3	<0.001	0.94	0.07	0.335	2.28	0.05	<0.001	0.41	0.32	<b>0.005</b>
Period 2	1.54	0.17	<b>0.011</b>	25.5	0.3	<0.001	7.65	0.14	<0.001	3.17	0.13	<0.001	11.08	0.29	<0.001
Period 3	1.07	0.18	0.72	9.75	0.3	<0.001	4.87	0.14	<0.001	1.26	0.15	0.139	2.29	0.34	<b>0.013</b>
Depth: period 2	1.52	0.16	<b>0.008</b>	2.59	0.31	<b>0.002</b>	1.08	0.08	0.346				3.73	0.33	<0.001
Depth: period 3	1.36	0.18	0.087	2.67	0.32	<b>0.002</b>	1.25	0.09	<b>0.013</b>				7.99	0.38	<0.001
Random effects															
ICC <sub>Fisher area</sub>	0.10			0.29			0.05			0.08			0.27		
ICC <sub>Fishing day</sub>	0.02			0.00			0.10			0.02			0.00		

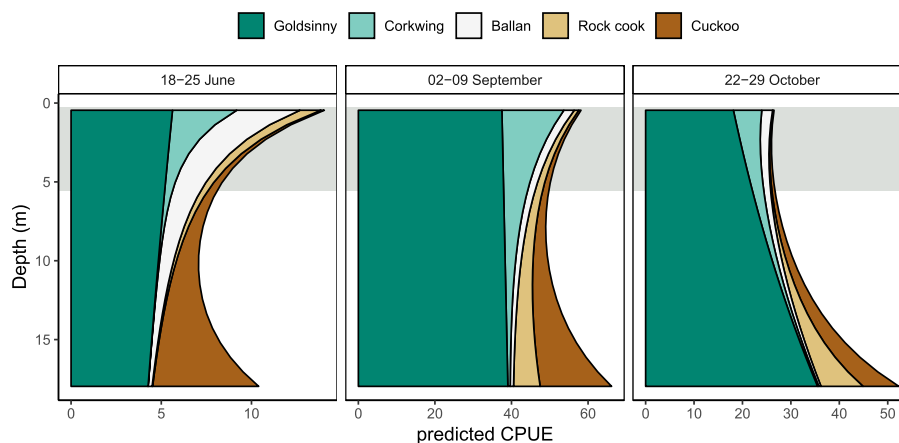


FIGURE 4. Seasonal depth gradients in species composition from the experimental wrasse fishery. Standardized CPUE was estimated with a generalized linear model for each species, which was combined and visualized along a depth gradient ( $y$ ). Note that the range on the  $x$ -axis (CPUE = fish/sampling unit [i.e., a set of three traps]) differs between the three periods. Seventy-five percent of the traps in the commercial fishery were set shallower than 5.58 m, indicated by the shaded area.

have been observed for many demersal fish species (Macpherson and Duarte 1991; Mitchell et al. 2014; Williams et al. 2019). For the wrasses, it is possible that this relationship has been shaped by past fishing concentrated in shallow waters for the three commercially important wrasses. The Ballan Wrasse, which is the most sought-after species, showed the steepest depth gradient. However, the noncommercial wrasses (Cuckoo Wrasse and Rock Cook) also showed an increase in body size with depth, although not as steep as those for the other species. This suggests that a gradual ontogenetic habitat shift for wrasses is plausible and may have contributed to the observed patterns. For Corkwing Wrasse, the latter explanation is supported by a tag recovery study conducted in western Norway, where recapture probability in the trap fishery in shallow waters was negatively correlated with body size (Halvorsen et al. 2017b). It is possible that the largest individuals tagged during the spawning season moved to deeper water for feeding later in the season, thus avoiding the fishery. A study on the Hogfish *Lachnolaimus maximus*, a labrid subjected to an SSF in the Gulf of Mexico, found that populations in shallow waters were smaller and younger than those found deeper and further offshore (Collins and McBride 2011). Similar to the wrasses in Norway, fishing pressure on Hogfish is presumably highest in shallow waters, so deeper offshore waters were suggested to act as refuges for larger, older, and faster-growing individuals. Lower fishing mortality for large and reproductively important individuals can be beneficial for productivity (Froese 2004; Hixon et al. 2014). On the other hand, if shallow-water fisheries let fewer fish survive to reach the size at maturity, then negative effects on recruitment and yield—and ultimately productivity—can be expected (Froese

2004; Kindsvater et al. 2017). Whether this is an issue for the wrasse fishery depends on the size-dependent mortality associated with capture and discard, which has yet to be investigated. For example, it is possible that predation occurs inside the traps or by sea birds or larger fish when catch is thrown back into the sea (Raby et al. 2014; Uhlmann and Broadhurst 2015).

A recurrent concern for wrasse fisheries has been the possibility of depletion of large males in the species with male parental care (Darwall et al. 1992; Halvorsen et al. 2016, 2017b; Kindsvater et al., in press). In nesting fish species, larval production can be reduced if the numbers and sizes of nests are being reduced or if smaller males are less effective in providing parental care (Suski and Ridgway 2007; Sutter et al. 2012). For Corkwing Wrasse, fishing may cause female-biased sex ratios, since males have higher catchability in traps and mature later than females (Halvorsen et al. 2016, 2017b). We found that the Corkwing Wrasse sex ratio became slightly more male biased with increasing depth. Since males tend to be larger than females, this might reflect the overall pattern of increasing body size with depth. Thus, the fact that fishing is restricted to shallow waters may to some extent relax sex selectivity in the fishery. This probably also applies for Ballan Wrasse, which had the steepest depth-length relationship. Ballan Wrasse cannot be sexed by visual inspection, but sex change occurs at a length between 34 and 40 cm (Muncaster et al. 2013), so the proportion of males probably increases with depth for this species. For protogynous hermaphrodites, such as the Ballan Wrasse, size-selective harvesting can be particularly harmful, depending on the plasticity in the size at which sex change occurs (Alonzo and Mangel 2005; Kindsvater et al. 2017; Sato et al. 2018).

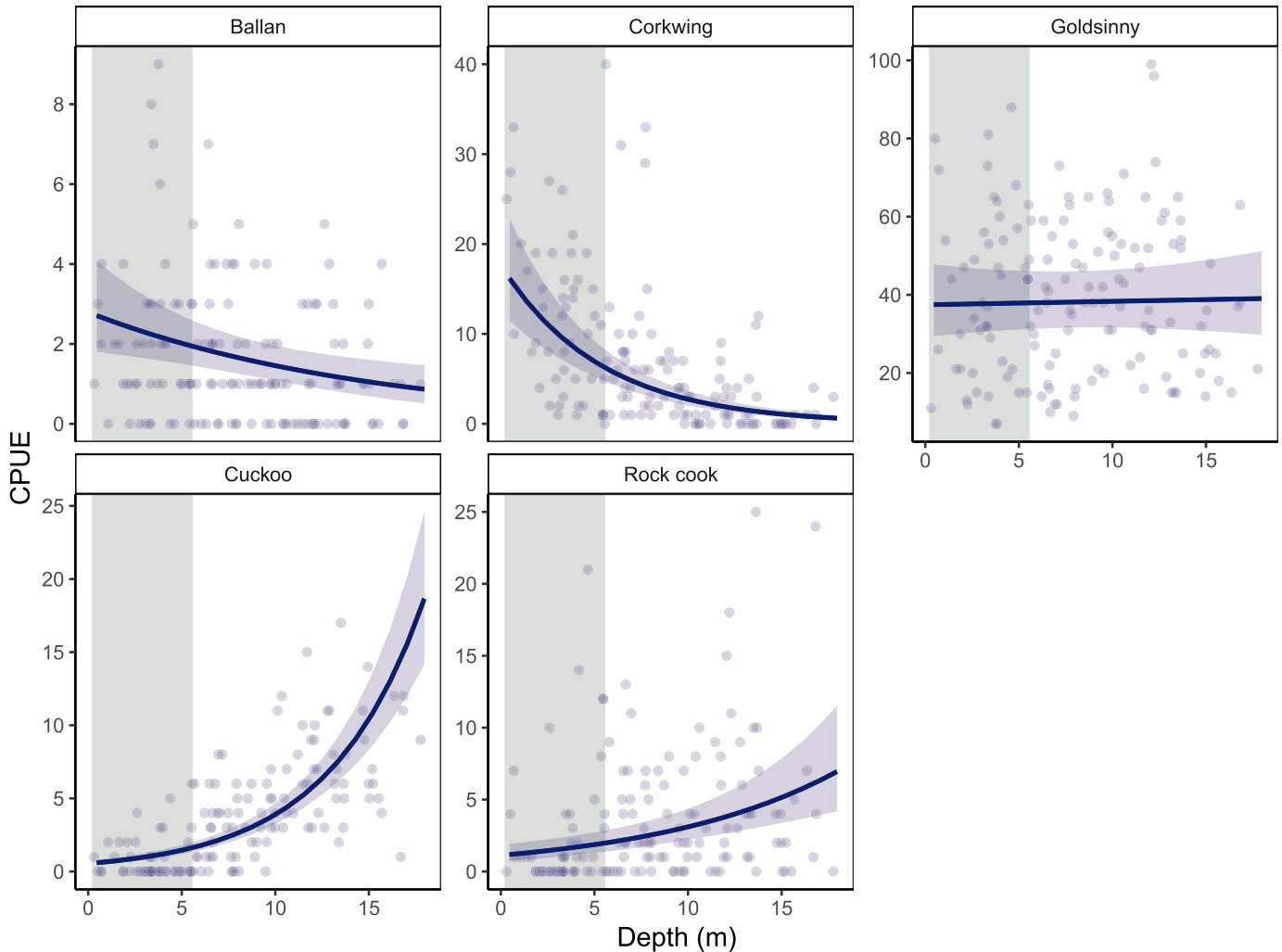


FIGURE 5. Catch as a function of depth for the five wrasse species caught during the experimental fishery in September (e.g., coinciding with the commercial fishery); points (CPUE) are the observed numbers per sampling unit (i.e., a set of three traps), and solid lines are model predictions standardized for soak time and wave exposure, with 95% CIs. The vertical shaded area indicates the depth fished in the commercial fishery (75th percentile of traps).

Although the data reported here clearly demonstrate how selectivity can be modified as a function of fishing depth, it is important to keep in mind that these changes are only relative to—and superimposed on—the true selectivity of the fishery, which is still unknown for these wrasses. Capture probability in traps can vary with species, size, and sex (Dalzell 1996; Frusher and Hoenig 2001; Bacheler et al. 2013; Tuda et al. 2016). For example, even though Ballan and Corkwing wrasses are more likely to encounter traps in their immediate surroundings, catchability is also affected by the motivation and ability to enter and escape traps and by morphology, physiology, and behavior. Traps are generally regarded to be relatively unselective on body size, but the mesh size and the shape and size of escape openings and entrances can restrict

catches of the smallest and largest fish, typically creating a dome-shaped selectivity pattern (Arreguín-Sánchez 1996; Robichaud et al. 2000; Langlois et al. 2015). Very large Ballan Wrasse (>40 cm) are unable to pass through the entrances used in these traps, and the compulsory escape opening permits Goldsinny Wrasse smaller than the minimum size limit (11 cm) to escape from the trap (Jørgensen et al. 2017). Mark-recapture data would be necessary to directly estimate selectivity and catchability (Arreguín-Sánchez 1996; Myers et al. 2014).

It was not possible to prevent or monitor commercial fishing intensity on the sites between sampling periods since other fishers were also operating in the area. If fishing reduces densities in shallow waters, it might motivate fish from deeper water to move up, thereby increasing

TABLE 4. Summaries for linear mixed models predicting length, showing estimated TL (mm;  $\beta$ ), SEs, and  $P$ -values for the five wrasse species (bold italics denote significance). The intra-class correlation coefficient (ICC) is provided for the *Fisher area* random effect. Data are from 450 sets (3 traps/set). Continuous covariates were standardized (stn) with a mean of zero and an SD of 1.

Predictor	Ballan Wrasse			Corkwing Wrasse			Goldsinny Wrasse			Cuckoo Wrasse			Rock Cook		
	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$
Intercept	266.76	5.2	< <b>0.001</b>	168.87	5.82	< <b>0.001</b>	112.25	0.88	< <b>0.001</b>	224.2	3.19	< <b>0.001</b>	129.75	1.91	< <b>0.001</b>
Soak time (stn)	3.74	2.37	0.116	0.59	0.81	0.465	1.11	0.17	< <b>0.001</b>	0.96	1.41	0.497	-0.18	0.61	0.767
Wave exposure (stn)	-2.58	3.41	0.451	2.02	1.22	0.103	0.03	0.45	0.943	0.95	1.74	0.588	0.47	0.73	0.526
Depth (stn)	15.54	2.7	< <b>0.001</b>	14.37	4.96	<b>0.004</b>	2.52	0.5	< <b>0.001</b>	3.52	1.55	<b>0.023</b>	1.56	0.58	<b>0.007</b>
Period 2	-42.33	5.53	< <b>0.001</b>	-22.04	5.82	< <b>0.001</b>	-1.7	0.52	<b>0.001</b>	-7.91	3.2	<b>0.014</b>	1.94	2.01	0.336
Period 3	-45.63	6.13	< <b>0.001</b>	-15.79	5.93	<b>0.008</b>	-0.24	0.55	0.66	12.45	3.71	<b>0.001</b>	1.58	2.28	0.488
Depth: period 2				-12.55	5.04	<b>0.013</b>	-0.08	0.53	0.888						
Depth: period 3				-11.32	5.17	<b>0.029</b>	-1.7	0.56	<b>0.003</b>						
Random effects															
ICC <i>Fisher area</i>	0.12			0.08			0.13			0.06			0.08		

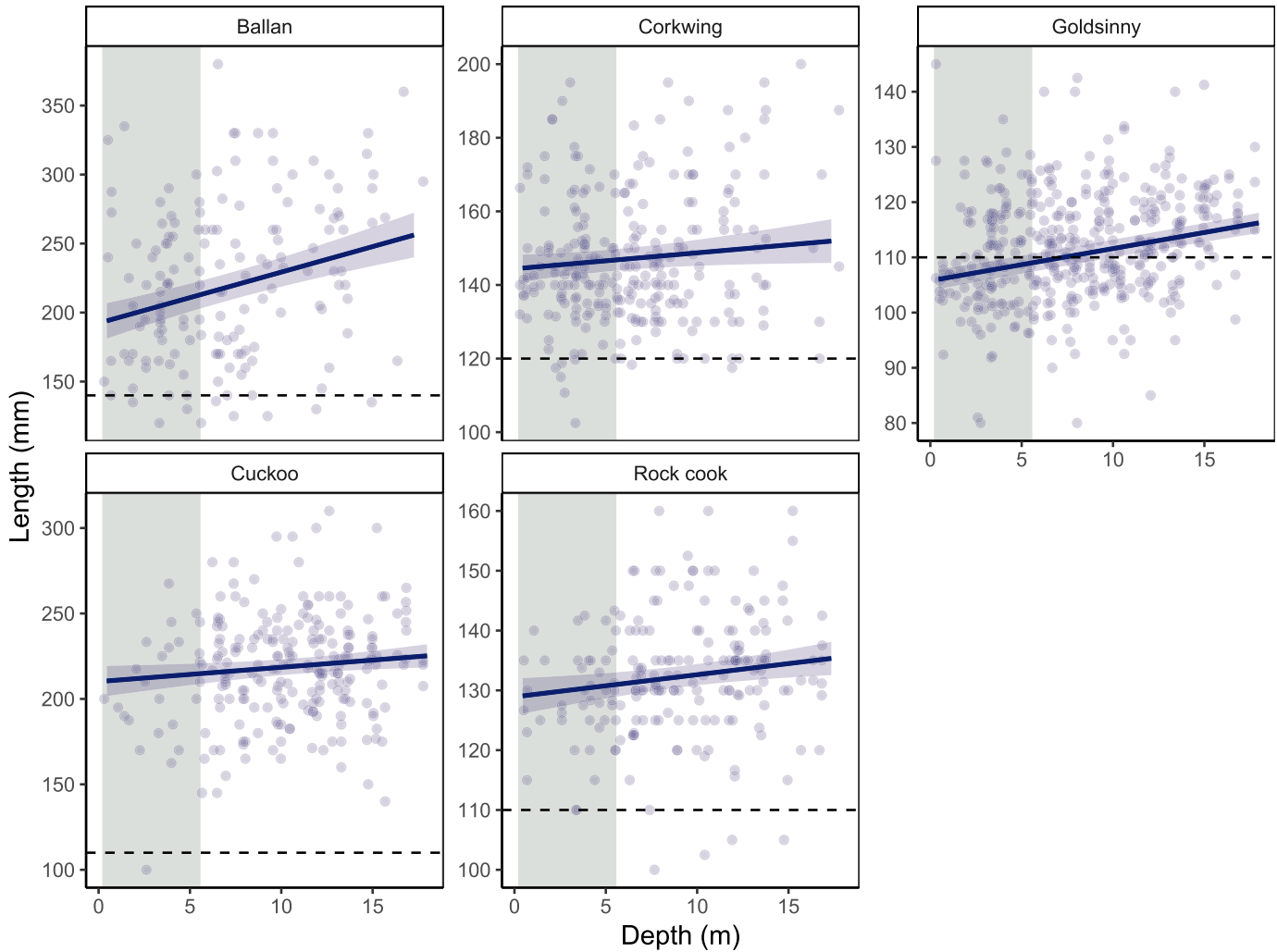


FIGURE 6. Total length (mm) as a function of depth for the five wrasse species caught during the experimental fishery in September; points are observed mean length per sampling unit (i.e., a set of three traps), and solid lines are model predictions standardized for soak time and wave exposure, with 95% CIs. The vertical shaded area indicates the depth fished in the commercial fishery (75th percentile of traps).

TABLE 5. Summary for the generalized linear model predicting the probability of a Corkwing Wrasse being a male, showing estimates ( $\beta$ ; log odds), SEs, and  $P$ -values (bold italics denote significance). The intra-class correlation coefficient (ICC) is provided for the *Fisher area* random effect. Data are from 450 sets (3 traps/set). Continuous covariates were standardized (stn) with a mean of zero and an SD of 1.

Predictor	$\beta$	SE	$P$
Intercept	1.03	0.25	<b>&lt;0.001</b>
Wave exposure (stn)	-0.06	0.09	0.498
Depth (stn)	0.22	0.08	<b>0.003</b>
Period 2	-1.23	0.25	<b>&lt;0.001</b>
Period 3	-0.82	0.26	<b>0.002</b>
Random effects			
ICC <sub><i>Fisher area</i></sub>	0.05		

their vulnerability to capture the next time the fisher visits. However, we suspect that density-dependent vertical displacement would be slow during the relatively short fishing season since these wrasses, particularly the Goldsinny Wrasse, display very strong site fidelity over several years (Hilldén 1984; Sayer 1999; Halvorsen et al. 2017b; Mucientes et al. 2019).

**Effects of Season and Wave Exposure**

For wrasses, CPUE was generally lowest in June and highest in September, corresponding to the coldest and warmest of the sampling months, respectively, which might reflect increasing activity and catchability with temperature for these wrasses (Costello 1991; Darwall et al. 1992). There were also seasonal differences in length, most notably for the Ballan Wrasse, which was considerably

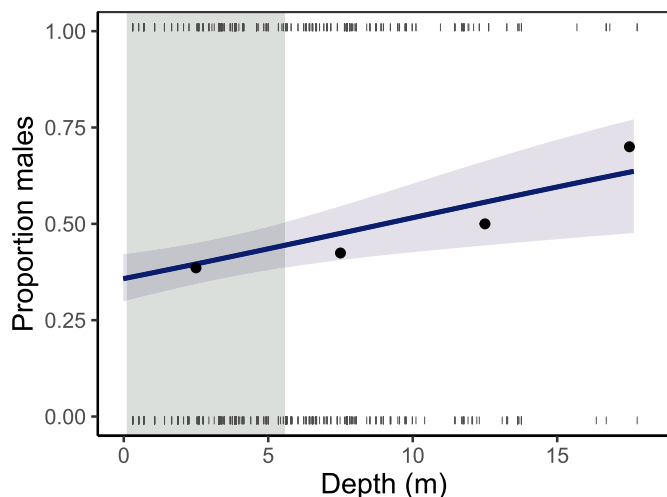


FIGURE 7. Proportion of Corkwing Wrasse that were male as a function of depth during the experimental fishery in September; points are the observed proportion male at different depth intervals, individual observations are shown as small vertical dashes in the rug plot (female:  $y = 0$ ; male:  $y = 1$ ), and the solid line represents the predicted proportion male standardized for soak time and wave exposure, with the 95% CI. The vertical shaded area indicates the depth fished in the regular commercial fishery (75th percentile of traps).

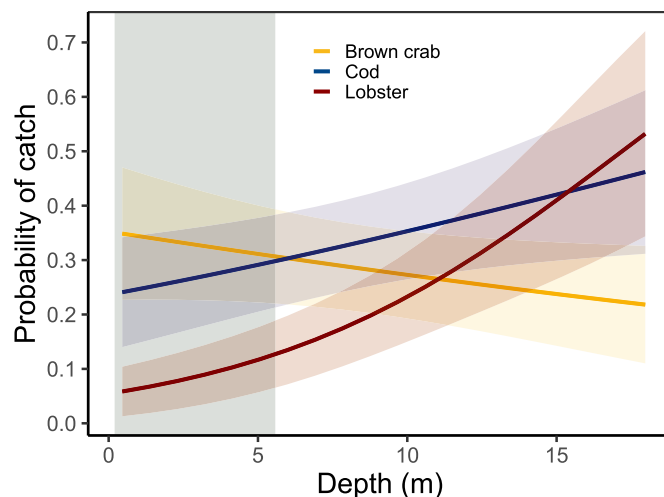


FIGURE 8. Probability of presence of selected bycatch species (brown crab, Atlantic Cod, and European lobster) as a function of depth during the experimental wrasse fishery in September. Solid lines are model predictions standardized for soak time and wave exposure, with 95% CIs. The vertical shaded area indicates the depth fished in the regular commercial fishery (75th percentile of traps).

TABLE 6. Summaries for generalized linear models predicting the presence of bycatch species (European lobster, Atlantic Cod, and brown crab), showing estimates ( $\beta$ ; log odds), SEs, and  $P$ -values (bold italics denote significance). Data are from 450 sets (3 traps/set). Continuous covariates were standardized (stn) with a mean of zero and an SD of 1.

Predictor	European lobster			Atlantic Cod			Brown crab		
	$\beta$	SE	$P$	$\beta$	SE	$P$	$\beta$	SE	$P$
Intercept	-3.19	0.38	<b>&lt;0.001</b>	-0.37	0.16	<b>0.022</b>	-1.02	0.18	<b>&lt;0.001</b>
Soak time (stn)	-0.17	0.14	0.225	0.10	0.11	0.332	-0.24	0.10	<b>0.021</b>
Wave exposure (stn)	0.18	0.14	0.203	0.27	0.10	<b>0.010</b>	0.15	0.10	0.137
Depth (stn)	0.70	0.16	<b>&lt;0.001</b>	0.24	0.11	<b>0.025</b>	-0.16	0.11	0.140
Period 2	1.55	0.43	<b>&lt;0.001</b>	-0.52	0.25	<b>0.035</b>	0.01	0.26	0.980
Period 3	1.16	0.45	<b>0.009</b>	-1.20	0.28	<b>&lt;0.001</b>	0.70	0.25	<b>0.005</b>

larger in June during the spawning period. This aligns with previous studies on Corkwing Wrasse, for which a larger mean length was observed in May–June than in July–September (Darwall et al. 1992; Halvorsen et al. 2017b). The fact that the fishers revisited the same sites in each sampling period makes it reasonable to assume that the differences in CPUE and length between sampling periods primarily reflect seasonal variation in size-dependent catchability. However, the areas were open to the fishery between sampling periods, and fishing might have left a footprint of size-selective fishing at these sites (Pita and Freire 2011; Halvorsen et al. 2017a). In addition, growth and natural mortality over the season may contribute to the temporal patterns observed: 17 weeks

separated the first and the last sampling periods. The wrasses also had a slightly shallower distribution in June, which might reflect different optimal depths for spawning and feeding.

Wave exposure had limited influence on CPUE and length except for Ballan Wrasse, which exhibited a positive correlation between CPUE and the estimated mean wave height. This is in contrast with a study conducted in western Norway, which reported that the Rock Cook was most abundant at exposed sites, the Ballan and Goldsinny wrasses were most abundant at sites with intermediate exposure, and the Corkwing Wrasse preferred sheltered areas (Skiftesvik et al. 2015). Furthermore, the same study found a clear size effect, with smaller wrasses (>11 cm)

being relatively more abundant at sheltered sites. Exposure was qualitatively assigned in the earlier study, while the current study used a model-derived estimate of mean wave height as a quantitative exposure index, and sampling spanned both highly sheltered areas and sites that were exposed to the open sea. Thus, the seeming inconsistency between these studies could be an artifact of different methodology or could reflect broader-scale adaptations to different environments. Skagerrak has a relatively open coastline, with short distances between exposed and sheltered areas, while western Norway is more heterogeneous, with wide and deep fjords. The species composition among wrasses is also very different, with the Corkwing Wrasse and Rock Cook having a much higher relative abundance in western Norway compared to along the Norwegian coast of Skagerrak (Skiftesvik et al. 2014, 2015; Halvorsen et al. 2017a; present study).

In the commercial fishery, the fishing depth gradually increased as the season progressed, possibly reflecting that fishers target deeper waters to optimize catch value, since the wrasses were generally found deeper later in the fishing season. We did not assess the horizontal behavior of fishers, but anecdotally they informed us that in order to catch more Ballan Wrasse, they tended to fish at more exposed locations when weather conditions allowed it.

### Implications for Survey Design and Management

The finding that wrasse catch rates and lengths are highly sensitive to environmental, spatial, and temporal variability has considerable implications for survey design and assessment of wrasse and analogous fisheries. Like many SSFs, this fishery can be regarded as data limited. Stock assessment models suitable for such situations have received increasing attention in recent years; however, good models cannot substitute for poor data (Dowling et al. 2019). If environmental factors affect catchability and selectivity but are not accounted for, the resulting bias in CPUE and size distributions can lead to inappropriate management decisions—for example, if abundance is overestimated and quotas are set too high (Bigelow and Maunder 2007; Bentley 2015; Maunder and Piner 2015). Standardization of length data for environmental covariates is also clearly necessary, especially relative to depth and season. This is important because length-based models are increasingly being proposed to assess data-limited stocks (Cope and Punt 2009; Froese et al. 2018; Rudd and Thorson 2018). For the Norwegian wrasse fishery, a formal stock assessment has yet to be conducted, although there have been efforts to establish a time series of relative abundance based on raw CPUE (daily catch/number of gears hauled) from a fishery-dependent survey established in 2011. However, those data showed very high and unexplained variance, probably because the relevant covariates for standardization were

not available (Skiftesvik et al. 2019). In addition, the fishing gear used was not consistent in space and time, introducing bias of unknown direction and magnitude. When preliminary results from the present study were available in late 2018, the survey was revised and redesigned. Sampling gear was standardized and the methodology reported here was adopted, enabling researchers to standardize CPUE for depth and other covariates in a GLMM framework. This will hopefully serve as a solid foundation for implementing stock assessment models for the Norwegian wrasse fishery in the coming years, and the approach can easily be applied to other countries in which similar wrasse fisheries are conducted. We propose that better collection and utilization of environmental covariates would be beneficial for many SSFs in which traps or similar gear are used and fishery-dependent CPUE data are collected for the purpose of assessing abundance trends, such as in the Norwegian lobster fishery (Kleiven et al. 2017) and the coastal reference fleet (Bjørkan 2011).

To mitigate the risks of a negative impact from the wrasse fishery, several management regulations have recently been implemented in Norway, most notably an extension of the spawning season closure and individual transferable quotas. However, the quotas are not species specific and have been arbitrarily set based on a precautionary approach due to the lack of reliable data on wrasse abundance, selectivity, and the impact on bycatch species. Given the higher degree of overlap between the fishery and the Ballan and Corkwing wrasses, we suggest that these species should be given higher priority in management decisions. Managing selectivity can be an option to reduce the risk of overfishing on the more vulnerable species. For example, most traps used in Norway today have elliptical entrances (height = 90 mm; width = 60 mm), but new regulations state that their diameter must be a maximum of 60 mm (circular openings; regulations in effect from January 1, 2021) to prevent Ballan Wrasse larger than 28 cm from entering the trap. Compared to Ballan Wrasse, the Corkwing Wrasse has a life history suggesting higher resilience to fishing, all else being equal. The Corkwing Wrasse does not change sex and has a considerably shorter life span than the Ballan Wrasse (maximum = 4 years at Skagerrak, 8 years in western Norway; Halvorsen et al. 2016). There are species-specific minimum size limits for wrasses in Norway (Table 1); individuals below the size limit must be released immediately in shallow water. For Corkwing Wrasse, the size limit is set to 12 cm, but this does not allow males to attain maturity before reaching harvestable size. Raising the minimum size limit or implementing a slot size limit, which also protects large males, might reduce the effect of fishing on Corkwing Wrasse (Halvorsen et al. 2016; Kindsvater et al., in press).

Slot size limits have already been implemented for Ballan Wrasse in Sweden (15–30 cm; Rueness et al. 2019) and for Ballan Wrasse (18–28 cm), Corkwing Wrasse (14–22 cm), and Goldsinny Wrasse and Rock Cook (12–18 cm) in the Southern District of the Inshore Fisheries and Conservation Authority in England (IFCA 2020). In Scotland, new mandatory regulations, which include slot size limits for all species, have been proposed and are under consideration (Scottish Government 2020). Slot size limits have gained increased attention in fisheries science (Gwinn et al. 2015; Sjørdalen et al. 2018; Ahrens et al. 2020), and wrasses are good candidate species for further empirical and theoretical work on the effectiveness of slot size limits in preserving the phenotypic diversity and reproductive potential of targeted species while maintaining economically viable fisheries.

As for many SSFs, the wrasse fishery targets multiple species, and changes in management must therefore be carefully planned to avoid the situation in which solving one problem causes another. For example, implementing measures aimed at reducing impacts on one species (e.g., gear design, size limits, and seasonal closures) may cause changes in fishing behavior and shift effort toward other species or size-groups, with negative consequences. In this regard, knowledge of spatial and temporal variation in the distribution and catchability of affected species, combined with effective monitoring of fishing behavior, is valuable for developing and adjusting management strategies for the wrasse fisheries in Norway and elsewhere. Furthermore, knowledge on the spatial distribution of wrasses can be useful for implementing spatial management measures, such as marine protected areas (MPAs). Small MPAs have a higher abundance of wrasses compared to nearby open areas (Halvorsen et al. 2017a). Our study indicates that to design MPAs specifically with the purpose of protecting vulnerable wrasses (Ballan and Corkwing wrasses), hard-bottom, shallow (<10 m) areas with moderate to high wave exposure should be prioritized.

### Conclusions and Future Directions

This case study illustrates that the vertical dimension of an SSF can shape selectivity patterns and highlights the importance of standardizing catch and length data from such fisheries with precise environmental covariates. The contrasting depth distribution among affected species clearly indicates that vulnerability to fishing is species specific in the wrasse fishery, and resources and efforts in future studies can therefore be better allocated and focused to have higher relevance for management and conservation. Specifically, for the wrasse fishery, formal stock assessments are warranted given the wrasses' high socioeconomic importance, which would allow managers

to adjust regulations to the natural population dynamics of these species. Stock assessments require time series of relative abundance and/or size structure, and this study has identified key covariates for standardization of such data.

Further studies on selectivity and fishing mortality in the wrasse fishery are still needed, especially studies that examine vertical movements and how depth-selective fishing interacts with this process. This is particularly relevant for the Goldsinny Wrasse, which has similar density within and below the target depths of the fishery. Studies that are conducted along depth gradients inside and outside of protected areas, as has been done on coral reefs (Tyler et al. 2009; Goetze et al. 2011), would also be valuable to assess how fishing affects densities at different depths and whether such gradients remain stable over time.


Data loggers and GPS are efficient and relatively cheap methods of providing detailed spatial data from an SSF. Tracking temporal trends in fisher behavior and understanding the underlying drivers are important in order to monitor and manage SSFs, especially since environmental conditions and technology are changing constantly and the changes are increasingly rapid (Salas and Gaertner 2004; Saldaña et al. 2017; Damasio et al. 2020). Recent technological advances and reduced costs of vessel tracking systems now allow for fleet-scale monitoring (Mendo et al. 2019). Beginning in 2020, all wrasse fishing boats in Norway must install automated identification system equipment, which continuously collects positional data. This will provide an excellent opportunity to study temporal and spatial trends and patterns in fisher behavior. Furthermore, the availability of automated identification system data can provide quantitative measures of fishing effort and can be scaled to estimate fishing mortality directly (e.g., tagging studies) or indirectly (comparisons of fished and protected areas).

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## SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.