

Sea temperature effects on depth use and habitat selection in a marine fish community

Carla Freitas^{1,2}  | David Villegas-Ríos^{3,4}  | Even Moland^{1,5}  | Esben Moland Olsen^{1,5} 

¹Institute of Marine Research, Flødevigen, His, Norway

²Marine and Environmental Sciences Center (MARE), Funchal, Madeira, Portugal

³Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Department of Ecology and Marine Resources, Esporles, Balearic Islands, Spain

⁴Instituto de Investigaciones Marinas (CSIC), Department of Ecology and Marine Resources, Vigo, Pontevedra, Spain

⁵Centre for Coastal Research (CCR), Department of Natural Sciences, University of Agder, Kristiansand, Norway

Correspondence

Carla Freitas
Email: carla@hi.no

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Abstract

1. Understanding the responses of aquatic animals to temperature variability is essential to predict impacts of future climate change and to inform conservation and management. Most ectotherms such as fish are expected to adjust their behaviour to avoid extreme temperatures and minimize acute changes in body temperature. In coastal Skagerrak, Norway, sea surface temperature (SST) ranges seasonally from 0 to over 20°C, representing a challenge to the fish community which includes cold-, cool- and warm-water affinity species.
2. By acoustically tracking 111 individuals of Atlantic cod *Gadus morhua*, pollack *Pollachius pollachius* and ballan wrasse *Labrus bergylta* in 2015–2018, we examined how coexisting species within a fish community adjusted their behaviour (i.e. vertical distribution in the water column and habitat selection) to cope with the thermal variation.
3. Mixed-effect models showed that thermal preference was a main driver of behaviour and habitat use of the fish community in a southern Norwegian fjord. Cod used colder waters, compared with pollack and ballan wrasse. Increases in SST during summer were associated with the use of deeper, colder waters by cod, especially by larger individuals, and conversely with the occupancy of shallower areas by pollack and ballan wrasse. During winter, when SST dropped and the thermal stratification reversed, pollack and ballan wrasse moved to deeper, relatively warmer areas, while cod selected shallower, colder habitats. Although habitat selection was affected by temperature, species-specific habitat selection was observed even when temperature was similar throughout habitats.
4. This study shows how cohabiting fish species respond to thermal heterogeneity, suggesting that (a) temperature regulates the access to the different depths and habitats and (b) behavioural plasticity may be an important factor for coping with temperature variability and potentially for adaptation to climate change.

KEYWORDS

acoustic telemetry, biologging, habitat use, resource selection functions, Vemco VPS

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1 | INTRODUCTION

Temperature is a main determinant of the distribution and behaviour of organisms. By directly impacting the thermal environment, climate change has increased the need to understand how species respond to temperature variability (Pacifiçi et al., 2015; Sinclair et al., 2016). Changes in climate are expected to alter existing environments and create novel ones, which may lead to local loss of organisms and their associated function in the ecosystem (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). It has been suggested that behavioural responses, such as shifts in activity in space and time, may enable species to cope with thermally stressful environments, allowing them to maintain their functional roles in the ecosystem despite changed temperature (Fey et al., 2019; Wolff et al., 2020).

Marine ecosystems provide fewer microclimates compared with terrestrial ecosystems, making marine animals, in particular ectotherms, more vulnerable to warming (Pinsky et al., 2019). However, behavioural thermoregulation is possible in the ocean. Some shark species, for example, undertake diel vertical migrations between deep cold waters, where temperature is favourable, and shallow feeding areas, which are less favourable thermally (Sims et al., 2006; Vaudo et al., 2016). Conversely, tunas and sea turtles, forage at depth and use warmer surface waters to thermoregulate (Freitas et al., 2019; Holland et al., 1992). Other organisms, such as American lobster *Homarus americanus*, seek optimal thermal habitats by moving seasonally in relation to water temperature (Jury & Watson, 2013).

In the absence of other constraints, it is expected that ectotherms will seek suitable thermal conditions within their available habitat. However, the use of thermal refuges during unfavourable temperature conditions may be challenging if such behavioural thermoregulation is depriving species from vital resources. For instance, moving deeper can allow marine species to avoid hot surface temperatures but may limit their access to prime foraging habitats (Freitas et al., 2016). Shifting to deeper areas may also expose species to hypoxia, as oxygen availability typically decreases with depth (Deutsch et al., 2015). Furthermore, it is expected that changes in ocean temperature will pose significant risk to species that exhibit strong behavioural preferences for specific habitat types while generalist species are assumed to be less vulnerable (Matis et al., 2018).

While thermal conditions are expected to directly constrain species distribution, changes in thermal conditions may also allow for species coexistence through thermal resource partitioning. More specifically, thermal preferences may enable species to coexist because the thermal regime will dictate when a particular habitat is available to each species (e.g. Attrill & Power, 2004; Crowder et al., 1981). High-latitude marine ecosystems offer a unique opportunity to understand the patterns of resource use by species with different thermal affinity. For instance, sea surface temperature along the Norwegian Skagerrak coast ranges annually between 0°C and more than 20°C. Skagerrak is also characterized by temperature stratification inversions during winter (i.e. cool water lies above warmer water). Such inversions, typical for subpolar regions, form

when the relatively warmer surface water of summer is trapped by the cooler, fresher conditions that exist during winter (Sprintall et al., 2019). Although sea temperature in Skagerrak has increased ~1°C in the last decades, seasonal oscillations and inversions in sea temperature are natural phenomena (Albretsen et al., 2012). Seasonal oscillation may, however, become even more pronounced in the future, given a predicted rise of 2–4°C in sea surface temperature in this region by the end of the century (Dye et al., 2013; Gröger et al., 2019). Large seasonal variations in sea temperature in Skagerrak likely represent a challenge to the local fish community, which includes cold-, cool- and warm-water affinity species, such as Atlantic cod *Gadus morhua*, pollack *Pollachius pollachius* and ballan wrasse *Labrus bergylta*, respectively.

Cod is a cold-water species distributed in the northern areas of the North Atlantic. Their optimal temperature for growth ranges between 9 and 15°C (Björnsson & Steinarsson, 2002; Björnsson et al., 2007; Lafrance et al., 2005). Pollack occurs further south in the Atlantic, from Portugal to northern Norway and shows maximum growth at temperatures between 12 and 18°C (Person-Le Ruyet et al., 2006; Suquet et al., 1996). Finally, ballan wrasse is the most warm-water-adapted species, occurring from Morocco up to southern Norway (Sayer & Treasurer, 1996). Juveniles (~15 g) grow faster at temperatures above 16°C (Cavrois-Rogacki et al., 2019), whereas larger individuals (~300 g) also show increased physiological performance when temperature increases from 0 to 25°C, with low metabolic rates and inactivity at low temperatures, that is, 5–10°C (Yuen et al., 2019). In coastal Skagerrak, cod typically avoids shallow waters when temperatures rises above 16°C and instead choose deeper waters that are up to 5°C cooler (Freitas et al., 2015, 2016).

In this study, we used acoustic telemetry to track co-occurring cod, pollack and ballan wrasse in coastal Skagerrak. We analysed the intraspecific and interspecific variation in behaviour of these ecologically important demersal predators over a period of 3 years to understand how coexisting species with contrasting thermal affinity cope with the striking seasonal oscillations in water temperature. We hypothesized that (a) species with contrasting thermal tolerance will display different strategies (i.e. habitat selection and vertical distribution in the water column) to cope with the thermal variation and (b) within a species, individual traits such as body size will influence their behavioural plasticity to temperature change.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in a marine-protected area (MPA) located in the Tvedestrand fjord on the Norwegian Skagerrak coast (Figure 1). The MPA, established in 2012, is closed to all fishing activities and this qualifies as a no-take marine reserve where fish behaviour can be studied in the absence of any disturbance from fishing gear. The MPA comprises waters ranging from 0 to 90 m

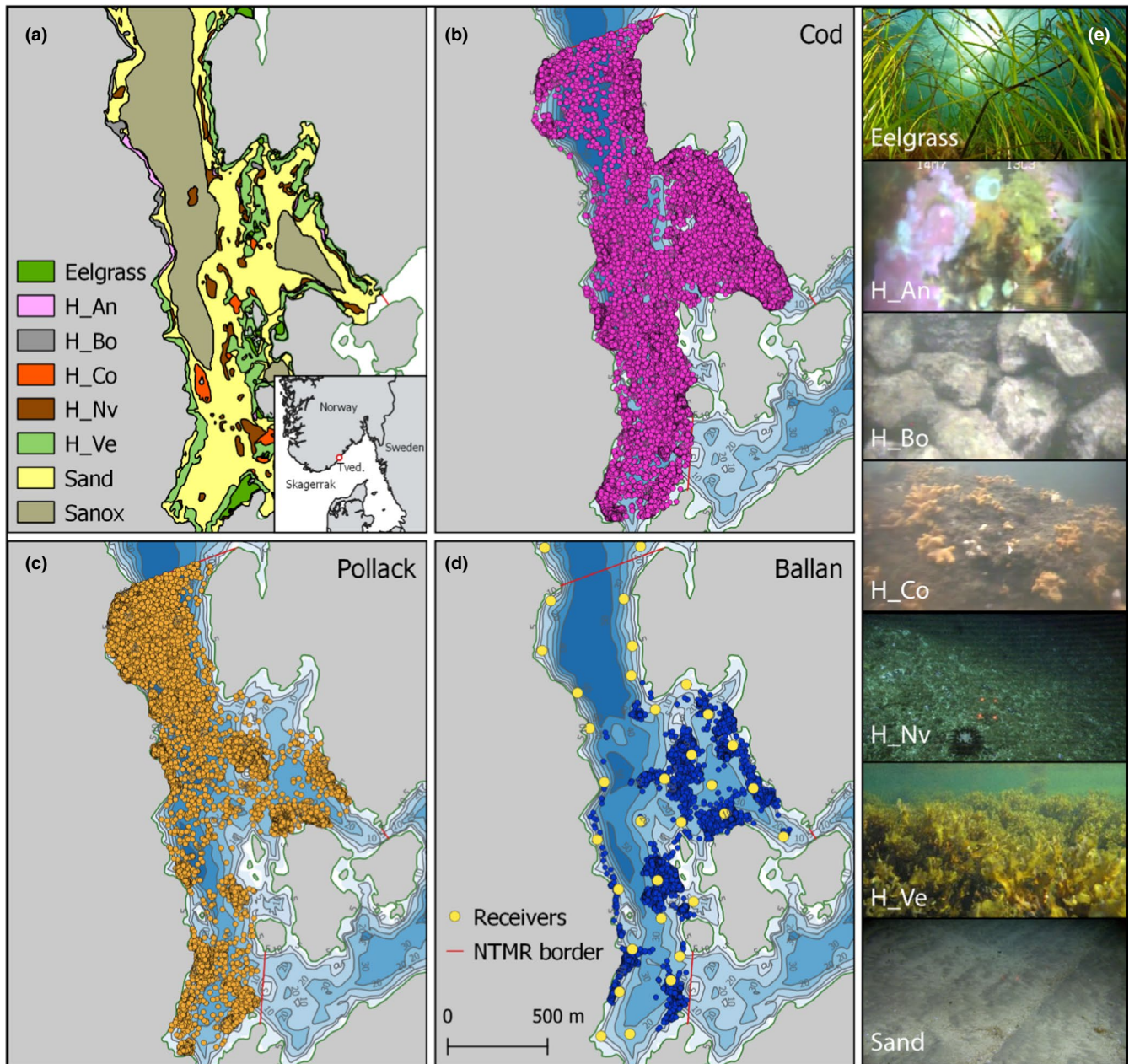


FIGURE 1 Maps of the study area in Tvedestrand (Tved.), Norway, showing the habitat map (a) and filtered locations obtained from cod (b), pollack (c) and ballan wrasse (d). Panel d shows also the network of acoustic receivers and borders of the no-take marine reserve (NTMR). Pictures in panel e show the following habitats: eelgrass; H_An, rock wall with anemones; H_Bo, boulders; H_Co, Hard substrate with corals; H_Nv, non-vegetated hard substrate; H_Ve, Vegetated hard substrate and; Sand, oxygenated soft substrate. Soft anoxic substrate not shown

depth. Seafloor habitats were mapped in 2013 using video surveys (Freitas et al., 2016). The following eight habitat types are found in the study area (Figure 1): Eelgrass (soft substrate covered by eelgrass *Zostera marina*; present at depths 0–6 m); Vegetated hard substrate (hard substrate covered by macroalgae; present at depths 0–17 m depth approximately); Non-vegetated hard substrate (hard substrate with no macroalgae; present below 17 m depth approximately); Coral rocky substrate (uneven hard substrate covered by soft corals and patchy macroalgae); Anemone rocky wall (steep rock wall covered by anemones and other invertebrates); Boulders

(bare boulders; present in the steep western margin of the fjord); Sand (soft, oxygenated substrate) and Soft anoxic substrate. Sea temperature in the study area was monitored using temperature loggers deployed at six different depths: 1, 5, 10, 15, 20 and 33 m. Temperatures at 1–20 m were recorded using Hobo UA-002-6 loggers, which registered temperature each hour. Temperature at 33 m was recorded using a Vemco V13T-1x sensor, logging temperature each 500–700 s. All temperature records were later averaged daily. Temperature at 1 m depth is hereafter referred to as sea surface temperature.

2.2 | Fish telemetry

A total of 111 fish (75 cod, 19 pollack and 17 ballan wrasse) were tagged in 2015–2017, using either Vemco transmitters V9P or V13P, equipped with pressure sensors (Table 1). Transmitters were set to transmit a signal every 110–250 s, with a random interval to reduce code collision. Tagging procedures have been described elsewhere (Olsen et al., 2012; Villegas-Ríos et al., 2017). A Vemco positioning system (VPS) was used to obtain information on fish depth and horizontal location (Figure 1). The VPS system was composed of (a) 33 acoustic receivers (Vemco VR2W, 69 kHz), used to record data transmitted by the tagged fish; (b) 33 synchronization tags, 'Synctags' (Vemco V16-4x), moored along with each receiver to correct for clock drift between receivers and (c) four reference tags (three Vemco V13-1x and one Vemco V13T-1x) placed within the receiver grid to measure system performance during location estimation. Earlier performance tests indicated that the median location error of the VPS array was 1.8–4.4 m (Freitas et al., 2016). Two datasets were obtained from this telemetry system: (a) detection data (fish ID, detection time, depth) downloaded from the receivers and (b) fish location data (fish ID, detection time, depth, latitude, longitude, horizontal position error) provided by Vemco after post-processing of the detection data. Horizontal position error (HPE) is a relative, unitless estimate of how sensitive a calculated position is to errors in its inputs (Smith, 2013). Locations with the highest HPE values were removed from the dataset (7.7% of the locations), based on a trade-off between accuracy and quantity, as described in Freitas et al. (2016). Locations outside the study area (i.e. the no-take marine reserve; Figure 1) were also removed from the dataset. Data were inspected for individual fate, namely death and dispersal, following the method described in Villegas-Ríos et al. (2020). Data obtained after natural mortality events, characterized by stabilized vertical and horizontal movements, were removed from the datasets.

2.3 | Data analysis

2.3.1 | Thermal habitat and temperature use

Temperature profiles were generated from the available daily temperature data at 1, 5, 10, 15, 20 and 33 m, using linear interpolation in between measurements. Temperature at >33 m was assumed to be the same as at 33 m depth. Based on the analysis of the temperature

profiles (Figure 2), four seasons were defined: winter (January–March), spring (April and May), summer (June–September) and fall (October–December). Winter was defined as the months when surface temperature was typically colder than deeper water masses. Conversely, summer was defined as the months when surface layers were warmer than deeper water masses (Figure 2).

Average depth used by each fish during day and night was calculated using the detection data. For a given day, average depth during the day was calculated as the average of all depths recorded between sunrise and sunset (i.e. when solar elevation was $\geq 0^\circ$). Average depth during the night was calculated as the average of all depths recorded from sunset in the previous day to sunrise of that day. Note that repeated depths records (i.e. the same depth record received simultaneously by multiple receivers) were removed from the dataset before calculating mean depths. Temperatures at mean daily depths were later calculated by linear interpolation of temperatures recorded by temperature loggers.

2.3.2 | Vertical distribution relative to sea temperature

Generalized additive mixed-effect models (GAMMs) were used to test whether depth use was affected by sea surface temperature and fish body length. Separate models were fitted for each species during the day and night and took the following form:

$$\text{Depth}_{ij} = \alpha + f(\text{T1m}_j) + \beta \text{Len} + f(\text{T1m}_j, \text{Len}) + \alpha_i + \varepsilon_{ij}.$$

Depth_{ij} denotes the average depth used during daytime or nighttime by individual i at day j . T1m_j is the average sea surface temperature at day j , modelled as a smooth function (penalized regression splines, with 4 knots). Len_i is the fish body length, modelled as a linear term, with slope β . The term $f(\text{T1m}_j, \text{Len})$ tests for an interaction between temperature and body length. The random intercept α_i allows for a random variation around the intercept α and is assumed to be normally distributed with mean 0 and variance σ_i^2 . The term ε_{ij} is independently normally distributed noise. An autoregressive process of order 1, corAR1 (see Zuur et al., 2009), was added to the random structure of the model to take temporal autocorrelation into account. Model selection was performed based on the Akaike information criterion, AIC (Table S1). Model validation took place by inspecting residual distributions and also residuals against fitted values and covariates, as recommended by Zuur and Ieno (2016).

TABLE 1 Summary data for the 111 fish acoustically tracked in Tvedstrand fjord from May 2015 to April 2018. Selected VPS locations refer to the number of VPS locations used in the analyses (10 best VPS locations per day; see Section 2.3.3)

Species	Number of individuals	Body length, cm: min–max ($M \pm SD$)	Days tracked: min–max ($M \pm SD$)	Number of detections	Number of VPS locations	Selected VPS locations
Cod	75	34–74 (48 ± 9)	29–884 (265 ± 176)	12,698,625	830,134	126,874
Pollack	19	35–52 (40 ± 5)	52–670 (311 ± 175)	4,373,925	328,920	40,710
Ballan wrasse	17	26–42 (35 ± 5)	57–702 (389 ± 222)	2,576,268	139,128	32,107
Total	111		29–884 (292 ± 187)	19,648,818	1,298,182	199,691

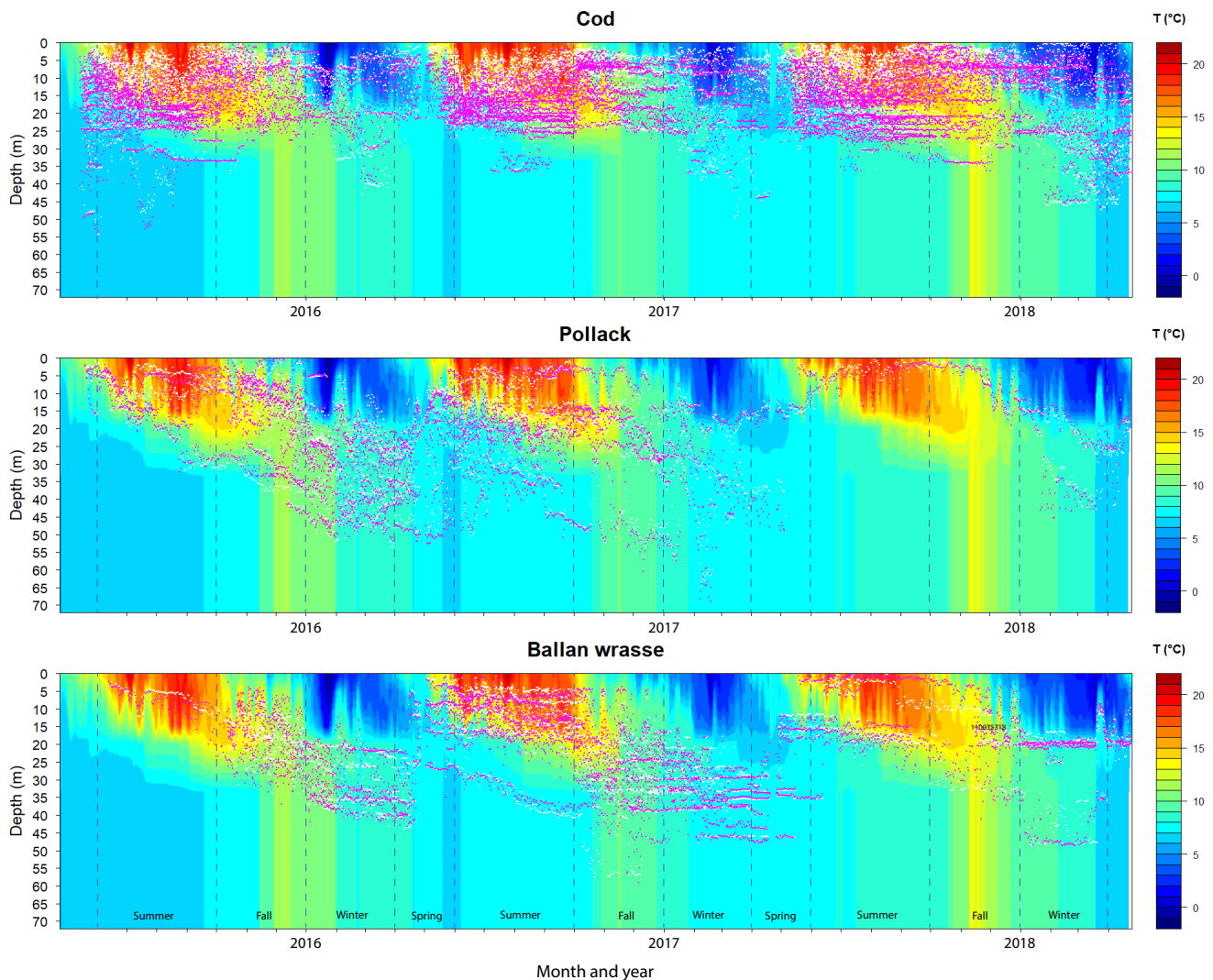


FIGURE 2 Water temperature recorded in Tvedestrand between April 2015 and April 2018, and average depth used by cod ($N = 75$), pollack ($N = 19$) and ballan wrasses ($N = 17$) during the day (magenta dots) and night (white dots). Dashed vertical lines delineate seasons: summer, fall, winter and spring. Temperatures below 33 m were assumed to be equal to the 33 m measurements (see Section 2.3.1)

Models were fitted in the R software (R Core Team, 2018) using the package `MGCv`, function `gamm` (Wood, 2006).

2.3.3 | Habitat selection

Bottom habitat type was extracted for each fish VPS position using QGIS software. To investigate whether fish were close to the bottom or in the water column, bottom depth was also extracted for each position, using 5 m resolution bathymetry data available from the Institute of Marine Research. Resource selection functions (RSFs) were used to quantify habitat selection by the study species. An RSF estimates the probability of that animal using a certain resource proportional to the availability of that resource in the environment (Boyce & McDonald, 1999; Johnson et al., 2006; Manly et al., 2002). We estimated RSFs using a use-availability design and used logistic regression to compare the habitat selected by fish (VPS locations,

coded as '1') to what was theoretically available (random locations, coded as '0')—see Johnson et al. (2006). An RSF above 1 denotes selection (i.e. disproportional use relative to availability), whereas an RSF below 1 denotes avoidance; an RSF equal to 1 denotes proportional use relative to availability. The number of locations obtained per day for each fish varied from 1 to 327 ($M \pm SD = 55.6 \pm 56.4$), distributed generally through 1–3 habitats. To decrease pseudo-replication of data, improve temporal independency and decrease unbalanced observations between days, we selected 10 positions per day for each fish, by retaining the best 10 positions (i.e. with the lowest HPE). Hence, the resulting dataset used for further analysis of habitat selection and use had a maximum of 10 locations per day for each fish ($M \pm SD = 8.6 \pm 2.9$). To represent availability, we drew random points from the area detectable by our array of receivers, using the same number of points as in the sample of used locations ($n = 199,691$, see Section 3) and extracted habitat type for these positions. Following the recommendations in McDonald (2013), RSFs

were estimated from the logistic regression coefficients, using an exponential link:

$$w(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n).$$

In the equation, $w(x)$ is the RSF and β_1 to β_n represent the coefficients for the variable X_1 to X_n . To account for differences in sampling intensity and random variation between individuals, random intercepts for each individual were added to the logistic model. Telemetry location data are often autocorrelated, which does not influence estimates of model coefficients but can deflate standard errors (Fieberg et al., 2010; Schielzeth et al., 2020). To minimize temporal autocorrelation, we added Julian day, nested within individual, to the random-effects structure. We fitted 12 RSFs, representing different combinations of seasons and species. Models were fitted using the function `glmer()` of the R package `LME4` (Bates et al., 2015).

2.3.4 | Habitat use

Following Lele et al. (2013), a habitat use distribution can be used to quantify the probability that a used habitat unit is of type x , that is, $p(x)$. Considering only the set of used locations, we quantified p for the most common habitats in the study area (eelgrass, vegetated hard substrate, non-vegetated hard substrate and sand), using GAMMs, with a binomial link:

$$\text{Logit}(p_{ij}) = \alpha + f(\text{T1m}_i) + \beta_1 \text{Diel}_j + \beta_2 \text{Len}_i + \beta_3 \text{Diel}_j \times \text{Len}_i + \alpha_i + \varepsilon_{ij}.$$

In this model, p_{ij} denotes the probability that a used habitat unit is of type x . Surface temperature (T1m), diel period, that is, day or night (Diel) and fish body length (Len) were included as explanatory variables. The interaction Diel \times Len was used to investigate whether diel changes in the probability of using habitat x were dependent on fish body size. Individual ID was used as random-effect variable (α_i) to account for individual variability. An autocorrelation structure of type AR1 was used to account for temporal autocorrelation. Model selection was performed based on the AIC (Table S2). Models were fitted using the function `bam()` of the R package `MGCv` (Wood et al., 2015).

3 | RESULTS

Individual cod, pollack and ballan wrasse were tracked for 29–884 days ($M \pm SD$: 292 ± 187), between May 2015 and April 2018 (Table 1). A total of 19,648,818 detections and 1,298,182 VPS locations were obtained. From these, 199,691 VPS locations were selected and further used in the habitat analyses.

3.1 | Thermal habitat and temperature use

High thermal heterogeneity was observed in Tvedstrand fjord, both temporally (throughout the year) and spatially (vertically in the water

column). Sea temperature ranged between -1.2 and 21.2°C at 1 m depth and between 6.1 and 13.5°C at 33 m depth. During summer, surface layers surpassed 15°C , whereas in winter they remained below 5°C (Figure 2). During the transition seasons (spring and fall), no vertical thermal gradients were observed, that is, water temperature was nearly homogeneous throughout the water column (Figure 2).

Overall, cod and pollack used similar temperature ranges, between 0 and 19.3°C , while ballan wrasse used temperatures from 4.6°C to 19.4°C . During spring and autumn, when water temperatures were similar throughout the water column, no substantial differences in temperature use were found between species (Figure 3). During summer (June–September), cod and pollack showed affinity to colder waters, using median temperatures 2.5°C colder than ballan wrasses. In winter (January–March), cod used colder waters compared with both pollack and ballan wrasse (Figure 3). Note that the latter two species used similar median winter temperatures, but pollack sometimes explored colder areas (Figure 3).

3.2 | Depth use relative to sea temperature

Cod, pollack and ballan wrasse were detected from surface to a maximum of 62, 75 and 76 m depth, respectively. The largest mean depth during the day or night was 54, 69 and 76 m for cod, pollack and ballan wrasse, respectively (Figure 2). A significant relationship was found between the vertical distribution of each species and sea surface temperature (Figures 2 and 4; Table 2). Responses to temperature were, however, contrasting between species. Pollack and ballan wrasse occupied shallower waters when sea surface temperature increased, moving to deeper (warmer) water layers when surface temperature decreased in winter (Figures 2 and 4). This pattern was particularly evident for ballan wrasse. Cod, in opposite, constrained themselves to deeper (colder) waters when surface temperature increased in summer, occupying shallower areas when surface temperature dropped (Figures 2 and 4). In winter, in particular when sea surface temperature fell under 5°C , cod moved again to deeper (warmer) areas. Body size had a significant effect on the vertical position of cod relative to temperature during the night, with larger individuals located in deeper, colder areas when surface temperature increased (Figure 4; Table 2). No relationship was found between depth use and body size for pollack and ballan wrasse (Table 2).

3.3 | Habitat selection

RSFs, used to compare selected habitats relative to habitat availability, revealed interspecific and seasonal differences in habitat selection (Figure 5). Of the three species, cod used the widest range of habitats. During spring and fall, when there were no vertical temperature constrains (i.e. temperatures were homogeneous throughout the water column), cod selected eelgrass and hard bottom habitats (i.e. anemone rock walls, coral rock substrates, vegetated and

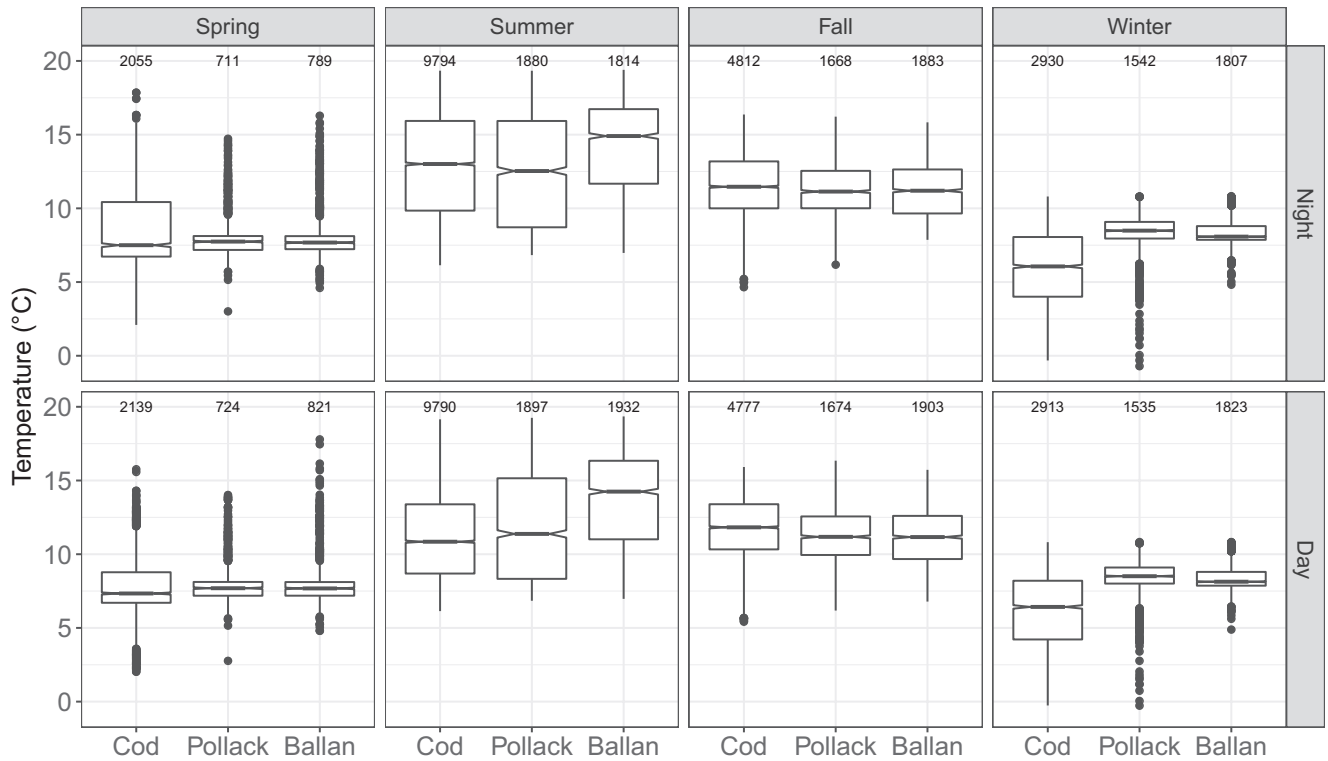


FIGURE 3 Temperature use by cod, pollack and ballan wrasse in Tvedestrand fjord, Norway. Data are shown by season and diel period. Number of daily observations is given above each box. Boxes show the median, as well as the first and third quartiles (the 25th and 75th percentiles). Notches give a rough 95% confidence interval for comparing medians—see McGill et al. (1978). Black dots are extreme values that extend outside one and a half times the interquartile range

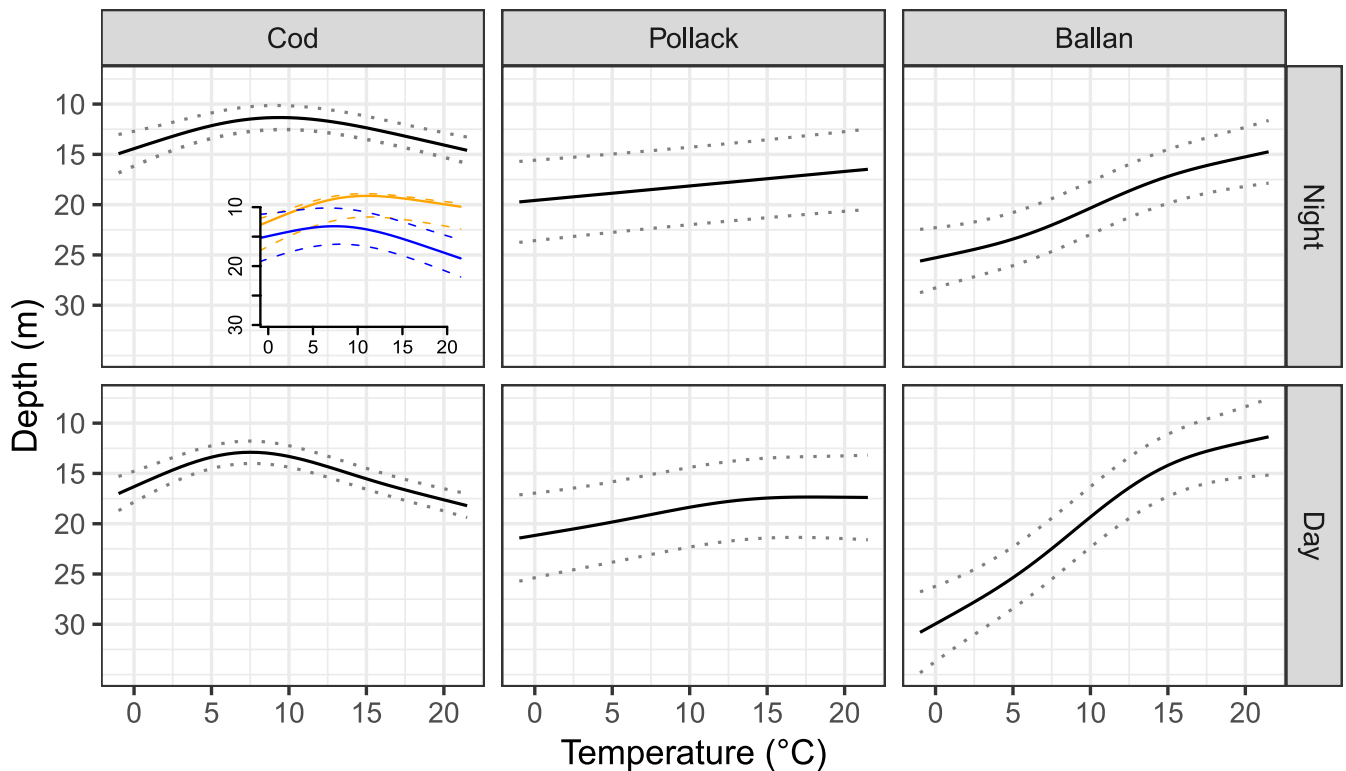


FIGURE 4 Average depth used by cod, pollack and ballan wrasse during the day and night as a function of sea surface temperature, as predicted from GAMMs. Solid lines are estimated mean effects and dashed lines are 95% confidence intervals. Body size was found to have a significant effect on depth use by cod during the night, as illustrated in the inset

TABLE 2 Parameter estimates for generalized additive mixed models (GAMMs) used to model the mean depth used during day and night (response variables) by cod, pollack and ballan wrasse in Tvedestrand, Norway. Explanatory variables were surface temperature (T1m), fitted as a smooth term, body size (Len), fitted as a linear term, as well as the interaction between these [ti(T1m, Len)]

Response	Species	Smooth term	EDF	F	p value	Linear term	β	SE	t
Mean depth at day	Cod	s(T1m)	2.94	53.27	<0.001				
	Pollack	s(T1m)	2.20	8.46	<0.001				
	Ballan	s(T1m)	2.74	81.77	<0.001	Intercept	25.90	10.17	2.55
		ti(T1m, Len)	4.37	4.98	<0.001	Len	-0.18	0.29	-0.61
Mean depth at night	Cod	s(T1m)	2.82	16.85	<0.001	Intercept	6.11	3.03	2.02
		ti(T1m, Len)	1.00	5.59	0.018	Len	0.13	0.06	2.11
	Pollack	s(T1m)	1.00	8.02	0.005				
	Ballan	s(T1m)	2.51	38.04	<0.001				

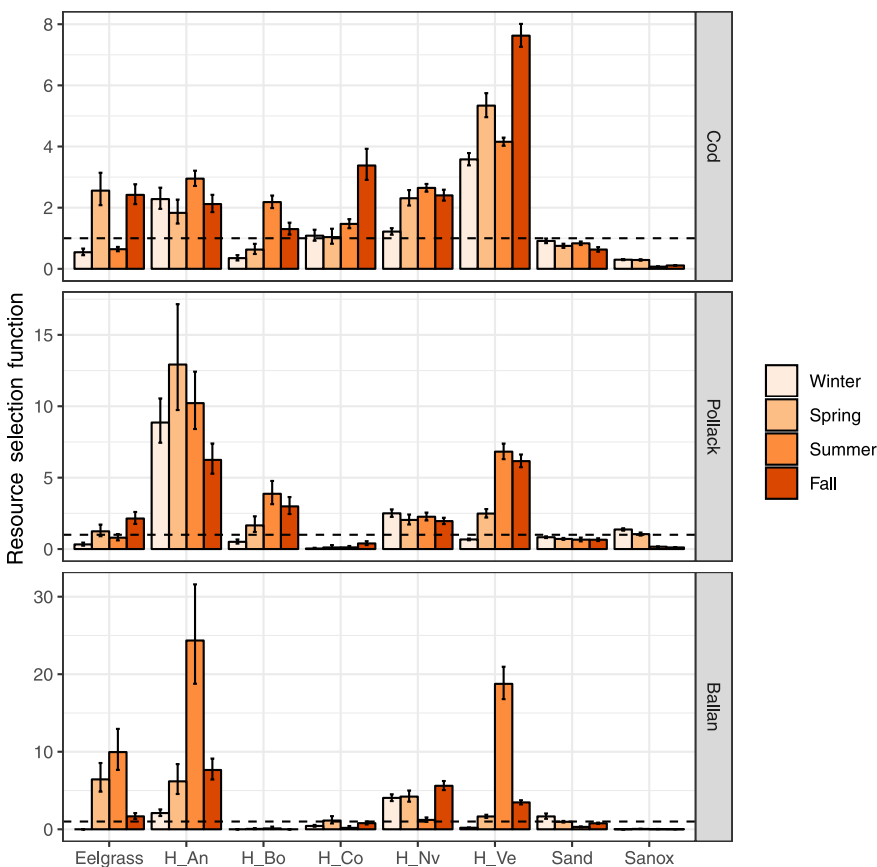


FIGURE 5 Resource selection functions (RSFs, with 95% confidence intervals) for cod, pollack and ballan wrasse in coastal Skagerrak in different seasons. RSFs provide the probability of using a habitat relative to its availability. RSFs above 1 denote selection (disproportional use relative to availability); below 1 denote avoidance and equal to 1 denote proportional use relative to availability. Note different ranges in the y-axis. H_An, rock wall with anemones; H_Bo, boulders; H_Co, Hard substrate with corals; H_Nv, non-vegetated hard substrate; H_Ve, Vegetated hard substrate; Sanox, Soft anoxic substrate

non-vegetated hard substrate), avoiding sand and anoxic habitats. In summer, cod decreased the preference for eelgrass and vegetated hard habitats located in shallower areas. In contrast, ballan wrasse showed a preference for eelgrass during spring and summer months when temperatures were higher in the shallows. Both pollack and ballan wrasse exhibited a high preference for rocky walls with anemones year-round, especially during summer. In addition, pollack selected boulders, as well as vegetated and non-vegetated hard substrates, avoiding eelgrass, hard bottom with corals and sand. All species avoided anoxic habitats, except pollack which selected areas above anoxic fjord bottom during spring (Figures 2 and 5). This does not imply that pollack was necessarily located in anoxic layers, as

this species swam on average $26.4 (\pm 3.8)$ m above the seafloor when detected over anoxic habitats (Figure 6).

3.4 | Habitat use

For all three species, habitat use was clearly associated with sea surface temperature (Figure 7; Table S3). Furthermore, habitat use by cod was significantly affected by diel period and individual body size (Table S3). Cod showed a higher probability of using eelgrass and vegetated hard substrate, available in shallow areas, when sea surface temperature was between 5 and 15°C, using deeper

FIGURE 6 Mean (\pm SE) vertical position of tagged cod, pollack and ballan wrasse relative to bottom depth as a function of habitat type in Tvedestrand fjord. Number of individuals in each habitat is provided for each species. Fish positions below sea bottom may arise from inaccuracies on bottom bathymetry and/or on fish depth and location data. Abbreviations see Figure 5

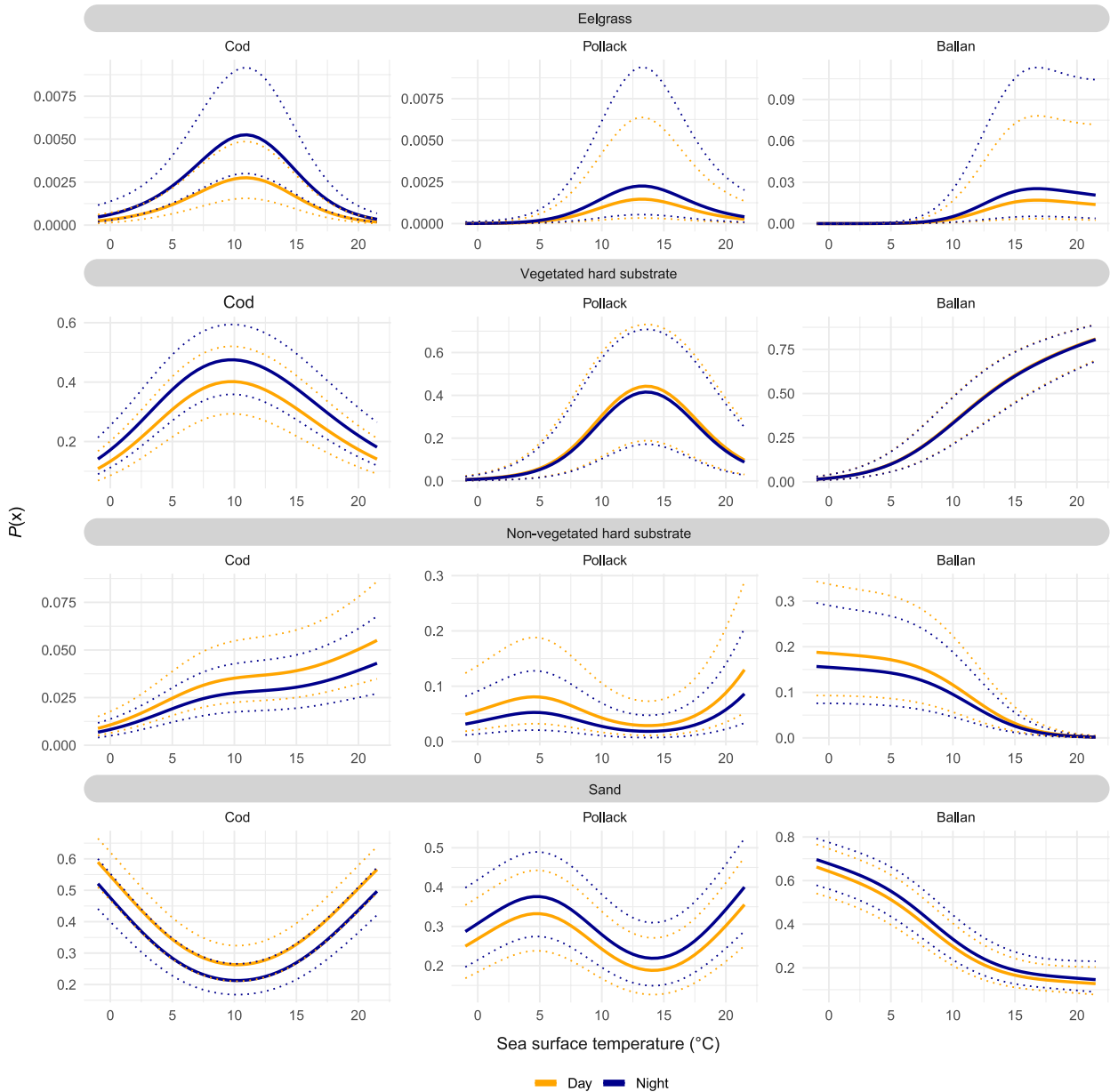
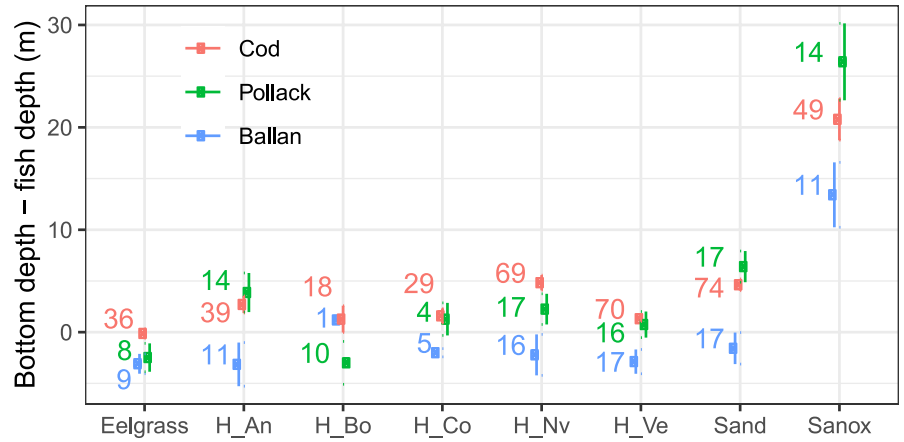


FIGURE 7 Probability that a used habitat unit is of type x , $p(x)$, during the day and night, as a function of sea surface temperature, as predicted from GAMMs for cod, pollack and ballan wrasse in Tvedestrand. Habitat types are provided at the top of each panel row. Solid lines are estimated mean effects and dashed lines are 95% confidence intervals

habitats (sand and non-vegetated hard substrate and sand) otherwise (Figure 7). The probability of using the habitats eelgrass and vegetated hard substrate increased slightly at night for this species, in particular for small individuals as indicated by the significant negative interaction between diel period and body length (Table S3). In contrast to cod, ballan wrasse showed a marked tendency to use shallow habitats (eelgrass and vegetated hard substrate) as sea surface temperature increased while using deeper habitats (non-vegetated hard substrate and sand) when surface temperature decreased (Figure 7). Pollack showed an intermediate behaviour, presenting a higher probability of using shallow habitats when surface temperature was between ~ 10 and 18°C , moving to deeper areas when surface temperature decreased under $\sim 10^{\circ}\text{C}$ or above $\sim 18^{\circ}\text{C}$. Despite statistical significance (possibly resulting from a large sample size; Table S3), the effect of diel period on pollack and ballan wrasse habitat use may be of limited biological significance, as indicated by their similar means and overlapping confidence intervals (Figure 7). Body size differences in habitat use were also less clear for pollack and ballan wrasse compared with cod (Table S3).

4 | DISCUSSION

4.1 | Behavioural responses to temperature

This study highlights the importance of sea temperature in shaping the habitat selection and depth use by a fish community in a high-latitude marine ecosystem. Species with warmer water affinity (pollack and ballan wrasse) used shallow habitats when surface temperature increased in summer, shifting to deeper, warmer areas when surface waters cooled during winter, while cod behaved oppositely.

Ballan wrasse used the warmest water layers available throughout the year. This warm-water affinity was not unexpected, given its southern distribution range and relatively high optimal temperature for growth ($>16^{\circ}\text{C}$; Cavrois-Rogacki et al., 2019; Yuen et al., 2019). Ballan wrasse showed a preference to rock walls with anemones, as well as to eelgrass and vegetated hard bottoms. Indeed, steep rock walls are typically where subsistence and recreational fishers in south Norway would historically (and presently) target ballan wrasse using rod and line (Scott, 1908). Ballan wrasse feed on invertebrates, such as Gastropoda, Decapoda, Echinodermata and Bivalvia (Figueiredo et al., 2005). High prey availability in shallow habitats, coupled with a high physiological performance in warm waters, likely provides thriving conditions for growth for this species during the summer months. Ballan wrasse selected hard non-vegetated and sandy bottoms in winter, which probably are less profitable in terms of food, but more thermally favourable.

Pollack also showed preference for warmer winter conditions compared with cod, occupying deep, warmer water layers. Similar to ballan wrasse, the species moved to shallower waters when surface temperature increased in summer. However, during the peak

summer surface heat events, pollack did not venture into as warm areas as ballan wrasse. Laboratory experiments have shown that pollack has maximum growth at temperatures ranging from 9 to 12 – 18°C , followed by a decrease from 18°C , with no growth at 21°C (Person-Le Ruyet et al., 2006; Suquet et al., 1996). Thermal preference reported in this study for pollack in their natural habitat seems to conform with the suitable temperatures for growth reported in the mentioned laboratory studies. Pollack showed a strong selection for both vegetated and non-vegetated habitats, but no specific preference for eelgrass. Pollack has a piscivorous diet (Høines & Bergstad, 1999), contrasting with wrasses that prey mainly on invertebrates. Although both species use similar depth layers during most of the year, they probably explore different niches in terms of food resources.

Cod selected colder-water conditions compared with the other two species, and used significantly deeper waters when sea surface temperature increased in summer, avoiding water layers with temperature above 16°C . Similar temperature-associated changes in depth use were previously reported for cod in Skagerrak (Freitas et al., 2015, 2016) and in the Gulf of Maine (Conroy et al., 2018). Cod has optimal growth and physiological performance at temperatures between 9 and 15°C (Björnsson & Steinarsson, 2002; Björnsson et al., 2007; Lafrance et al., 2005), which may explain the observed temperature preference in their natural habitat. Despite a low-temperature affinity, cod avoided waters below 5°C , and were altogether absent from the surface during the coldest period in winter, as previously reported from another area of southern Norway (Freitas et al., 2015). Also, Björnsson and Steinarsson (2002) found that growth rate of cod decreases when temperatures drop below 5°C . Note that spawning activity may also explain the use of deeper waters in winter (Meager et al., 2012).

Body size had a significant effect on the behavioural responses to temperature in cod. Larger cod were more sensitive to increases in surface temperature, occupying deeper, colder waters at night compared with smaller individuals, similar to patterns reported for cod in a nearby study area in Skagerrak (Freitas et al., 2015). Preference of larger individuals for colder waters is in agreement with laboratory experiments, showing that optimal temperature for physiological performance in fish generally decreases with body size (Pörtner et al., 2008; Pörtner & Farrell, 2008). For Atlantic cod in particular, temperature preference in captivity and optimal temperature for growth decrease with increased body size (Björnsson et al., 2007; Lafrance et al., 2005). We did not find body-size effects on depth use during the day. Cod were generally located deeper during daytime and it might be that temperature was favourable at daytime depths, regardless of body size. Alternatively, it might be that deeper waters were poorer in oxygen and thus unfavourable. Contrary to our expectations, we did not find a significant effect of body size on the behavioural responses to temperature for pollack and ballan wrasse. Note that the sample size and range of body sizes included in the study were not as broad for these two species as it was for cod.

4.2 | Niche overlap and climate change implications

Ecological niche theory predicts that sympatric species, especially when closely related or sharing similar morphological traits, may show segregation in spatiotemporal habitat utilization or diet to avoid competition (Pianka, 1981; Schoener, 1974). It has been suggested that thermal resource partitioning may allow species coexistence, because the thermal regime will dictate when a particular habitat is available to each species (e.g. Attrill & Power, 2004; Crowder et al., 1981). In a review study, Paterson and Blouin-Demers (2017) pointed out that there is still insufficient evidence to conclude unequivocally that thermal resource partitioning allows species coexistence. However, recent research suggests that physiological trait differences drive differential responses to winter conditions (reduced temperature and light) ultimately promoting the coexistence of species in freshwater systems (McMeans et al., 2020). Our study further suggests that thermal preference facilitates coexistence of species, but emphasizes the role of water column use, as well as habitat selection as a likely driver of species performance throughout the year. Spatial and temporal segregation may be particularly important for species with similar diet requirements. Cod in Skagerrak feed on both benthic invertebrates and fish (Hop et al., 1992) and may therefore overlap their diet with both ballan wrasse that feeds on invertebrates (Figueiredo et al., 2005) and pollack that has a piscivorous diet (Høines & Bergstad, 1999). On the other hand, cod, pollack and ballan wrasse showed species-specific habitat selection during spring and fall when thermal conditions were similar throughout habitats, indicative of habitat and diet specialization.

Recent studies have suggested that behavioural plasticity may enable terrestrial mammal species to cope with unsuitable environmental conditions, allowing them to maintain their functional role in the ecosystems as climate changes (Abernathy et al., 2019; Buchholz et al., 2019; Wolff et al., 2020). In this study, both warm-water and cold-water affinity species showed the capacity to adjust their behaviour in space and time to cope with the seasonal thermal heterogeneity of the ecosystem. This may allow these fish species to cope with future changes in temperature, such as earlier summer warming or longer duration of cold or warm periods. These results support a growing consensus that behavioural traits are important determinants of the resilience of animal species to a rapidly changing global climate and that behavioural responses of animals to climate change need to be integrated in predictive models of species susceptibility to this threat to biodiversity (Buchholz et al., 2019). The use of thermal refuges by individuals may however deprive fish from other vital needs, such as prime feeding habitats. Our study demonstrated that shallow habitats, such as eelgrass meadows and vegetated hard substrates have become inaccessible for cod during summer, as previously reported by Freitas et al. (2016), and to a lesser degree for pollack during the warmest periods. Eelgrass and other vegetated habitats are more favourable in terms of prey compared with non-vegetated substrates (Persson et al., 2012). Temporary exclusion

of cod and pollack from such habitats during summer may be detrimental for individual fitness. In fact, there is evidence that cod in coastal Skagerrak has lower somatic growth during late summer (Gjosaeter & Danielssen, 2011), opposite to what is found in more northern latitudes. Furthermore, cod in the Baltic appears to present poorer condition during the summer, as indicated by stable isotope analyses (Ljungberg et al., 2019). The limiting effect of sea temperature on habitat use of cold-water species is likely to become increasingly apparent as climate changes. Sea temperature has increased globally in the last decades (Cheng et al., 2019; IPCC, 2013), including in Skagerrak where surface temperature has increased ~1°C in the last decades (Albretsen et al., 2012). Further temperature increases are projected for the future, with rises between 2 and 4°C being predicted by the end of the century in the Skagerrak and shallow southern North Sea (Dye et al., 2013; Gröger et al., 2019). Future increases in summer temperature in Skagerrak may intensify the trade-offs between favourable temperature and optimal feeding areas for cod and pollack, likely to affect growth rates and condition. At the same time, warmer-water species such as ballan wrasses are expected to thrive. In fact, fish communities in shallow nursery areas in Skagerrak have shifted in the last decades towards novel assemblages dominated by warm-water species in association with increased sea temperature (Barceló et al., 2016). As pointed out by Buchholz et al. (2019), further research is needed to better understand the fitness trade-offs of behavioural responses to environmental change. We suggest that future work would in addition benefit from looking at individual-level responses to environmental change, as these may be key to understand individual fitness and eventually how populations adapt to new environments.

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AUTHORS' CONTRIBUTIONS

C.F., D.V.-R., E.M. and E.M.O. designed the study and collected the data; C.F. analysed the data and led the writing of the manuscript; all co-authors contributed substantially to the interpretation of the data and writing of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.37pvmcvk6> (Freitas et al., 2021).

ORCID

Carla Freitas  <https://orcid.org/0000-0002-5676-0514>

David Villegas-Ríos  <https://orcid.org/0000-0001-5660-5322>

Even Moland  <https://orcid.org/0000-0002-6521-2659>

Esben Moland Olsen  <https://orcid.org/0000-0003-3807-7524>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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