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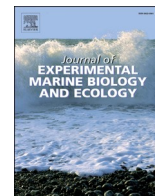
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A rockling's choice: The trade-off between thermal preference and physical structure in the five bearded rockling, *Ciliata mustela*

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ABSTRACT

Changes in the environment can alter the suitability of habitats for organisms. In marine systems, fish species have their own specific requirements in terms of temperature and other habitat features. Behavioral responses such as thermoregulatory behavior in ectothermic species allow mobile organisms to respond to detrimental changes and search for more suitable habitats. However, for many species, limited information exists on the ecological requirements to help explain species abundance in a changing habitat. An example of a quickly changing habitat is the Wadden Sea, where five bearded rockling (*Ciliata mustela*) abundance has increased, unlike other Wadden Sea species. The increasing abundance of rockling has coincided with increasing average sea water temperatures and the recovery of mussel and Pacific oyster beds. Warming waters and increased structural habitat may have provided rockling with a more desirable habitat. Therefore, to better understand why rockling abundance is increasing within a changing Wadden Sea, a water temperature preference chamber was used to determine rockling's preferred temperature range. In addition, rockling's affinity for structural habitat and the trade-off between preferred temperature was examined by following their response to the systematic removal of artificial physical structures within the preferred temperature conditions. The preferred temperature range of rockling was found to be 10.4–15.7 °C. Following structure removals, rockling repeatedly moved away from their chosen temperatures to adjacent compartments with different temperatures but containing physical structure, indicating that the presence of physical structure was more important than preferred temperature until 18.6 °C. These novel findings provide insight and experimental support for the hypothesis explaining rockling's increase in the Wadden Sea: 1) mean annual temperatures have been steadily increasing towards rockling's preferred thermal range and 2) increasing mussel and Pacific oyster beds are plausibly providing structural habitat, an important habitat requirement for rockling. When fish display a strong association with physical structure it is necessary to link physiological and habitat preferences to better understand climate change related responses.

1. Introduction

Habitat selection is the process when an individual species preferentially chooses and occupies a certain spatial area characterized by specific physical and (a)biotic factors such as temperature, food availability, structure, and predators (Morris, 2003). Within a habitat not all factors are optimal so inherent trade-offs between factors can exist. For example, an association with physical structure (i.e. sheltering) can provide predation protection at the costs of reduced foraging time (Krause et al., 1998; Ruxton et al., 2000). Because marine fishes are

ectothermic, the surrounding water temperature (i.e. thermal habitat) controls their body temperature and the rate of physiological processes (Huey and Kingsolver, 1989; Pawson et al., 2000). Water temperature is therefore a major driver determining fish distribution and ability to thrive/survive in a habitat (Pörtner and Peck, 2010; Deutsch et al., 2015). The chosen habitat not only influences the physiological capabilities of an individual fish (e.g. through metabolism and growth rate), but ultimately the habitat constitutes the potential for the species' ecological performance (e.g. survival; Huey, 1991).

Increasing mean global ocean temperatures (IPCC, 2022) have

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contributed to changes in marine environments such as loss of biodiversity and shifting animal ranges (Perry et al., 2005). In particular, throughout 2001–2021, mean annual water temperature measurements at a fixed location in the western Dutch Wadden Sea, increased by >1.0 °C (range = 10.3–12.5 °C; van Leeuwen et al., 2021, 2022) resulting in changes to community structure (Tulp et al., 2008, 2017; Teal et al., 2008; Freitas et al., 2012; van der Veer et al., 2015). For example, warming water temperatures have been postulated to underlie the offshore shift of juvenile plaice (*Pleuronectes platessa*) and therefore a less suitable Wadden Sea habitat for older year classes (> 0 group) of plaice (Teal et al., 2012; Cardoso et al., 2016). In contrast, water temperature is a critical positive contributor to the abundance of sea bass (*Dicentrarchus labrax*) in the Wadden Sea with a general increase in fish abundance with increased water temperatures (Cardoso et al., 2015). Other species may be similarly driven by changes in sea water temperature and research on species' preferred temperature range may guide our insights into changing population abundances, especially in a fast-warming ecosystem such as the Wadden Sea.

Species' preferences for particular water temperature(s) are taken to indicate near optimal circumstances for growth, survival, and reproduction (e.g., Pedersen and Jobling, 1989; Imsland et al., 1996, 2006; Jonassen et al., 1999; Björnsson et al., 2001). Aquaculture studies have produced in-depth knowledge of the preferred temperatures of commercially important species (e.g. European sea bass (*Dicentrarchus labrax*); Pawson et al., 2000; Ayala et al., 2001; Person-Le Ruyet et al., 2004). However, for a majority of fish species in the Wadden Sea, many of which are non-commercially yet ecologically important, this type of information is not known. One example of an ecologically important Wadden Sea species is the five-bearded rockling (*Ciliata mustela*) (hereafter rockling), found throughout the Northeast Atlantic in intertidal, rocky habitats with larger rockling also found in mud, sand, and gravel habitats (Demir et al., 1985; Heessen et al., 2015; Camphuysen and Henderson, 2017). In their ecosystems, rockling are an important and high-energy prey source (Camphuysen and Henderson, 2017) for nesting birds (Wheeler, 1969), seals (*Phoca vitulina*, *Halichoerus grypus*); Kavanagh et al., 2010; Aarts et al., 2019), and likely for other fish. Interestingly, the abundance of rockling, a resident Wadden Sea species, has continually increased in the western Dutch Wadden Sea since 1990 (Tulp et al., 2022), while other fish species have declined (van der Veer et al., 2015; Tulp et al., 2017; Tulp et al., 2022). The increasing abundance of rockling coincided with increasing average and maximum sea water temperatures (Van Aken, 2003; Van Aken, 2008; van Aken, 2010; van Leeuwen et al., 2021, 2022), and the recovery of inter- and subtidal mussel (*Mytilus edulis*) and Pacific oyster (*Crassostrea gigas*) beds, which plausibly provide structural habitat (van der Meer et al., 2019; Troost et al., 2022).

An indiscriminate diet based more on availability than selectivity (Badsha and Sainsbury, 1978) suggests rockling utilize physical structure for predatory opportunistic feeding and in addition for their own predation protection (i.e. sheltering). On-going Wadden Sea field experiments found rockling abundances up to five times higher on artificial and natural structure than on bare sediment, control sites (Mulder et al., 2020; Watson et al., 2023; Dickson et al., 2023). In addition, displacement experiments, in tide-pools with varying degrees of rocky substrate, found 45% of displaced rockling returned to "home" tide-pools indicating high site fidelity (Gibson, 1967). These factors suggest rockling would associate with physical structure despite the potential costs of suboptimal temperatures, as found in other species (Vaudo and Heithaus, 2013; Matis et al., 2018; Chrétien et al., 2021).

In this study, the preferred temperature range of rockling was examined and analyzed in the context of a trade-off with an artificial physical structure. We used a circular water temperature preference chamber to 1) expose rockling to a temperature gradient and determine its preferred temperature range in a setting where physical structures were omnipresent and 2) follow the rockling's response to systematic removal of physical structures within the rockling's chosen temperature

conditions. This approach provides novel insight into rockling's preferred temperature range in addition to testing the influence exerted by physical structures on rockling's thermoregulatory behavior. Therefore, we predicted rockling would behaviorally select for physical structure in all non-preferred temperatures over its preferred temperature(s) without physical structure.

2. Materials and methods

2.1. Five bearded rockling

Rockling were collected in fall 2020 and spring 2021 by local fishermen in the Wadden Sea (near Kornwerderzand at the Afsluitdijk and Texel, Netherlands). The fish were housed at Wageningen Marine Research, IJmuiden and held in a 2×2 m rounded square tank at 10 °C and salinity of 28 g/kg. A layer of coarse sand and aquarium gravel were present in the tank in addition to variously sized circular PVC (polyvinyl chloride) tubes to provide physical structural habitat. The fish were acclimatized to 16 ± 0.1 °C, by increasing the temperature 1.5 °C per day. The acclimation temperature was chosen based on the median value of rockling occurrence (8–24 °C; Moreira et al., 1992). The rockling were fed pellet food (BioMar INICIO PLUS, 1.1 mm) on a daily basis to visually observed satiation. We worked with well-fed individuals because temperature preference is found to decrease with decreased feeding (Brett et al., 1969; Jobling, 1994). Thus overfeeding the fish reduced interactive effects of feeding level on temperature preference and reduced complicating factors in the analysis of results. Following the acclimation period of four weeks, the rockling were sorted into experimental groups.

Rockling were first weighed and then separated into three size classes (small: 20–40 g, medium: 50–70 g, and large: 75–100 g). Experimental fish lengths ranged from ~15 to 25 cm corresponding to mature 1–3(4) year age-groups (Badsha and Sainsbury, 1978; Smietana, 1992). Due to an overabundance of medium sized fish, it was not feasible to create experimental groups ($N = 6$) with even size class distributions. Therefore, six experimental groups were created, four groups consisting of one small, one medium, and one large fish, one group of two medium and one small fish, and one group of two medium fish. The abundance of medium sized experimental fish, corresponding to the 2 year age-group, are commonly caught in the Dutch Wadden Sea (Heessen et al., 2015) and therefore should be viewed as representative of the study area and not an overrepresentation of a specific size class. Fish within each size range were randomly selected, separated into experimental groups, and placed into separate aquaria (50 × 30 cm). The experimental group aquaria were maintained at 16 ± 0.5 °C and salinity of 28 ± 1.2 g/kg with daily excess feeding (1 g) for the duration of the experiments.

2.2. Preference chamber

A circular temperature preference chamber was used to determine rockling temperature preference. The preference chamber used in this experiment is an adapted design from Myrick et al. (2004) and was successfully used in previous studies (Schram et al., 2013; Post et al., 2017). The preference chamber, constructed of sand-colored polypropylene, consists of a middle section and 3 circular rings: mixing channel, swimming channel, and effluent channel (Fig. 1). Water flows into the mixing channel at eight locations. Round holes in the walls of each ring allows water entering the mixing channel to travel into the swimming channel and subsequently the effluent channel before entering the water drains within the central section (Fig. 1). Water then flows into five separate water storage tanks (60 L) located beneath the chamber, where it is heated or cooled to the desired temperature(s), and recycled to the mixing channel thus creating a closed system. The water storage tanks were heavily aerated to mix the heated and cooled water and to minimize the risk of gas supersaturation while heating the water. The chamber allows constant water flow, ensuring the creation of a

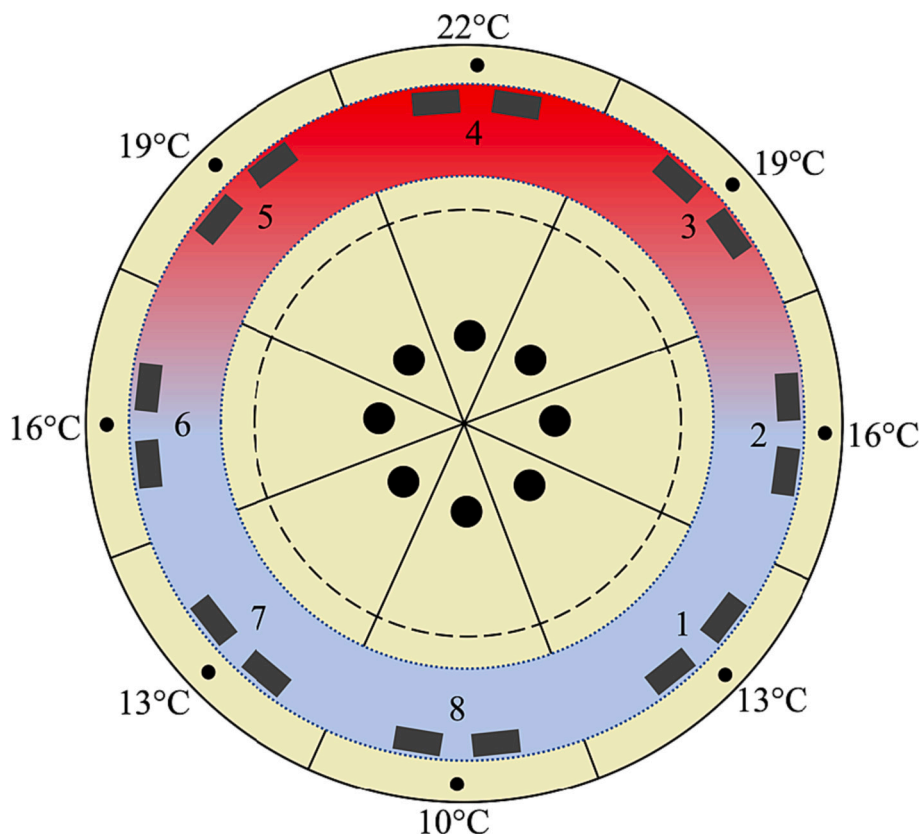


Fig. 1. Schematic presentation of preference chamber with physical structures (dark gray rectangles), compartment numbers, and main elements including water inflows (small black circles), mixing channel (outermost ring), swimming channel (color gradient ring), effluent channel (inner ring), and central section with water drains (large black circles).

temperature gradient of five different temperatures between the eight equally sized compartments (Fig. 1). The dimensions of the preference chamber are presented in Table 1 and a more detailed description can be found in Schram et al. (2013). Natural North Sea seawater (with a salinity of 34 g/kg) was diluted to the desired salinity of 28 g/kg and used within the preference chamber for all experiments. Four video cameras were positioned over the chamber to ensure recording of the experimental distribution of fish without disturbance. The lighting scheme was held at a 12 h light:12 h dark cycle with dim light (5 lx; Lutron LX-107, sensitivity = ± 0.05%), providing increased contrast in the chamber for improved recording quality.

Physical structures, consisting of two identical gray-colored, square shaped, PVC structures (Table 1) were attached in each compartment with 1.5 mm white, polyester, braided cord (Fig. 1). The physical structures were secured to allow small horizontal movement while

remaining in their respective compartment.

2.3. Experimental protocol

A total of six experimental trials were conducted with each temperature preference and physical structure experiment performed over the course of 47 h (Fig. 2). Six hours before the start of the experiment, one chosen experimental group of fish ($N = 2$ or 3) was fed to visually observed satiation (~1 g) to ensure a well-fed status. At $T = 0$ h, the experimental acclimation began by transferring one group of fish ($N = 2$ or 3) to the preference chamber; maintained at a uniform temperature of 16 °C and a salinity of 28 PSU and matching the aquaria conditions. Each fish was placed into a randomly assigned compartment within the preference chamber swimming channel. Fish then were allowed to acclimate to the preference chamber until $T = 14$ h. For the period $T = 14$ to 15 h, the distribution of fish within the preference chamber was video recorded (Fig. 2). The recording period was termed the “non-gradient observation” because of the absence of a temperature gradient and it served to determine any non-random preference for regions of the chamber resulting from non-temperature related factors. Additionally, the recording period served to substantiate rockling’s affinity for physical structure. Upon completion of the non-gradient observation ($T = 15$ h), the heating and cooling units (JUMO eTRON M, sensitivity = ± 0.1 °C) were turned on to establish the temperature gradient (10–13–16–19–22 °C) within the preference chamber (Fig. 2).

A stable temperature gradient occurred by $T = 17.5$ h and from $T = 18$ to 19 h, the distribution of fish within the chamber were recorded and termed the “short-term preference observation” (Fig. 2). The temperature gradient was maintained within the chamber until the termination of the experiment (i.e. $T = 47$ h). When fish are exposed to a temperature gradient, fish will distribute according to their short-term preference

Table 1
Dimensions and settings of the preference chamber and physical structures.

Parameter	Value	Unit
Preference chamber		
Diameter	190.0	cm
Width mixing channel	9.5	cm
Width swimming channel	19.0	cm
Width effluent channel	9.5	cm
Surface area swimming channel	0.91	m ²
Water height swimming channel	13.5	cm
Total water volume swimming channel	122.5	L
Total water volume preference chamber	472.0	L
Average flow rate per section	8.39	L/min
Physical structure		
Width	6.5	cm
Length	10.0	cm

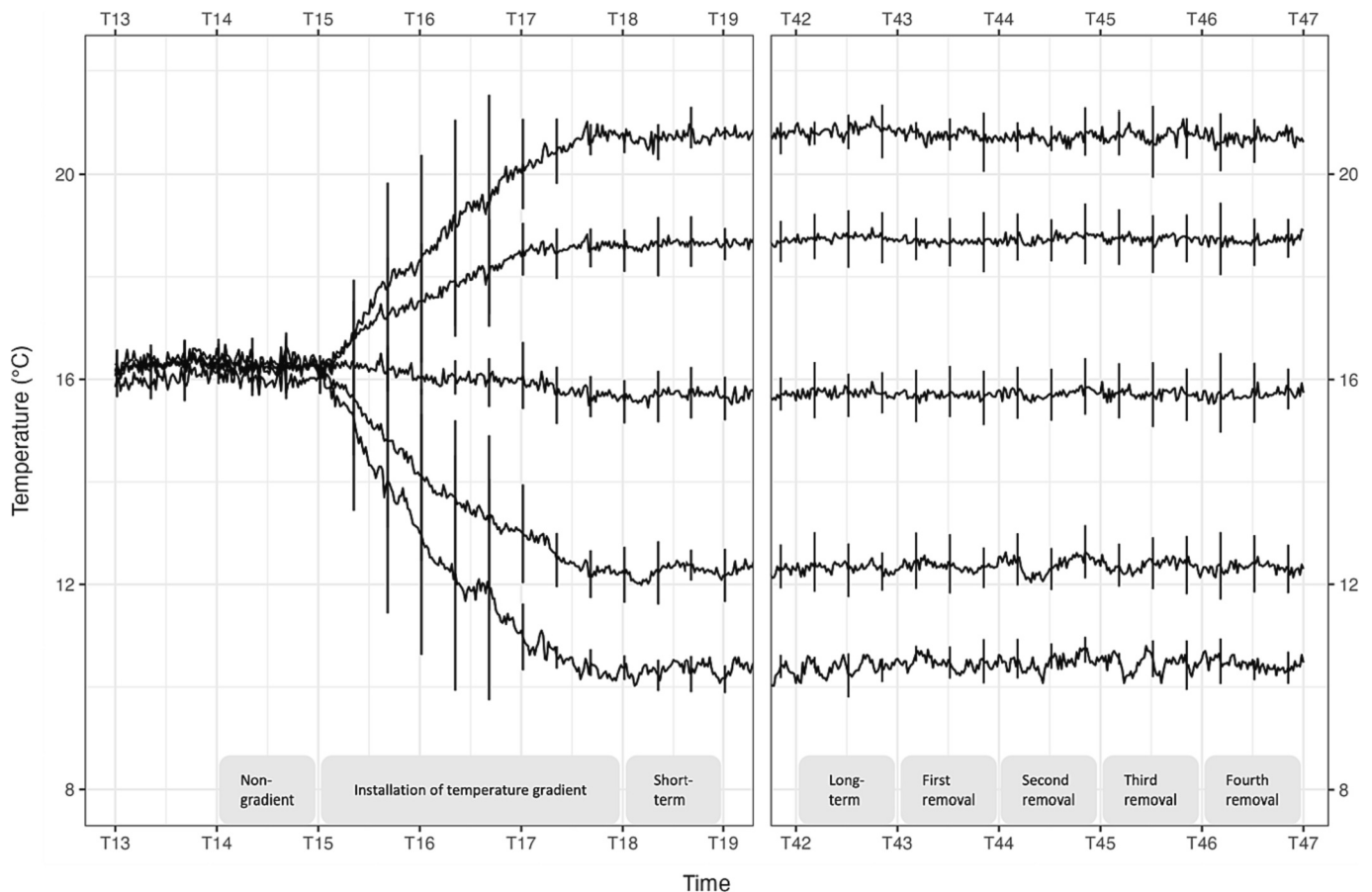


Fig. 2. Water temperature in the preference chamber during preference tests (mean \pm SD, $n = 4$). Please note the time break in the x-axis.

which is influenced by the previous thermal environment (i.e. acclimation temperature in this study; Reynolds and Casterlin, 1979). After some time (~ 24 h), fish will acclimate to the gradient and will move towards their long-term preferred temperature, independent of the previous thermal environment (Reynolds and Casterlin, 1979). The ensuing recording period, “long-term preference observation”, occurred 24 h later from $T = 42$ to 43 h (Fig. 2). Until this point in the experiment, two physical structures were present in each compartment.

Following the long-term preference observation, structures were removed from the compartment in which the fish were present and in case all fish were not within the same compartment, then structures were removed from the coldest compartment containing a single fish. The physical structures within the lowest temperature compartment were then removed from the swimming channel and the “first structure removal observation” recording took place from $T = 43$ to 44 h. Visual observation again determined the lowest temperature compartment containing at least one fish, physical structures were removed, and the “second structure removal observation” occurred from $T = 44$ to 45 h. The same observation and physical structure removal process continued from $T = 45$ to 46 h and $T = 46$ to 47 h comprising the “third and fourth structure removal observations”, respectively. The experiment concluded following completion of the fourth structure removal observation at $T = 47$ h (Fig. 2). Physical structures were removed from both matching temperature compartments during their respective removals.

Water was continuously recycled and measured in the preference chamber’s closed loop system to ensure consistent conditions throughout the entire experiment. Dissolved oxygen concentration (WTW Multi 3430®), oxygen saturation (WTW FDO925®), pH (WTW ph-electrode sentix®), and salinity (WTW Cond 315i, sensor tetracon 325®) were measured and remained stable in each mixing channel

compartment prior to the acclimation period and following the temperature preference observations (Supplemental Table 1). These measurements did not occur following the physical structural removal observations to minimize disturbance but were completed following the conclusion of the experiment ($T = 47$ h). Water temperature was automatically measured and recorded (Votcraft K204®) every minute in each effluent channel compartment for the entirety of the experiments (Fig. 2). Ammonium (NH_4) was also measured (JBL ProAquaTest) prior to all acclimation periods to ensure safe levels (<0.05 mg/L).

2.4. Data acquisition

For each experimental trial, the distribution of fish over the eight compartments (Fig. 1) was measured in one-hour video recordings during each observational period: non-gradient, short-term preference, long-term preference, first-fourth structure removals. The number of fish in each compartment were counted at twelve time points corresponding to the start and every fifth minute of the recorded hour for the non-gradient, short-term preference, and long-term preference observations. Fish were similarly counted for each of the four structure removal observations, however, at only three time points corresponding to the fiftieth, fifty-fifth, and sixtieth minute of the hourlong video recording. The reduced counting frequency was chosen to allow the fish to redistribute and acclimate following the physical structure removal. In the case of a fish being located within two compartments, the compartment containing the head of fish was counted (following protocol in Schram et al., 2013). Although uncommon, if a fish was in the act of swimming at a specific time point, the fish was visually followed in the recording until movement ceased for 10 s and then the corresponding compartment was counted.

Additionally, the association of rockling with physical structure was measured at each time point by counting the location of rockling inside (and in contact with) or outside structure (i.e. no contact). Furthermore, rockling behavior was classified into four categories (Table 2) and measured at each time point of non-gradient, short-term, and long-term preference observations.

2.5. Data analysis

Video recordings provided the distribution of fish within each compartment and therefore a measure of compartmental usage during each observational period. Compartmental usage was statistically analyzed using pcTEMP (Dye, 2023) developed following the methods of Aebischer et al. (1993) and Schram et al. (2013).

Compartmental usage was determined by first counting the total number of fish within each compartment. The total fish count in each compartment was then divided by the grand total of counts (# fish per experimental group x # time points = total count) producing a set of eight fractions (i.e. components), summing to 1, and referred to as a composition. To break the unit sum constraint on a composition, log transformation was performed on the set of ratios consisting of one particular component as the denominator by which all other components were divided (Aitchison, 1986). The chosen denominator does not affect the results of the analyses (Aebischer et al., 1993) and the calculated set of log ratios describes the compartmental usage. Then the log ratios describing compartmental usage were divided by the availability of each temperature zone to correct for abundance differences in temperature zones (Fig. 1 and equation below).

$$L = \left(\ln \left(\frac{\text{use } 10^\circ\text{C}}{\text{use } 16^\circ\text{C}} \right) - \ln \left(\frac{1/8}{1/4} \right), \ln \left(\frac{\text{use } 13^\circ\text{C}}{\text{use } 16^\circ\text{C}} \right) - \ln \left(\frac{1/4}{1/4} \right), \dots, \ln \left(\frac{\text{use } 22^\circ\text{C}}{\text{use } 16^\circ\text{C}} \right) - \ln \left(\frac{1/8}{1/4} \right) \right)$$

To assess evidence of preference (deviation from random use) within the preference chamber during each observational phase: 1) a matrix was created of the log-ratios (i.e. a vector (L) for each experimental group and observational phase) of compartmental usage. 2) The generalized likelihood ratio statistic ($\Lambda = |R_1|/|R_2|$) was calculated by comparing a model without preference (M_2) against a model with preference (M_1). Each model has a corresponding residual matrix calculated from the log-ratio matrix; R_2 is the residual matrix of raw sums of squares and cross products and R_1 is the matrix of mean-corrected sums of squares and cross products. 3) A p value, providing evidence for or against random use, was obtained by performing a chi-square test χ^2 using the value $= -N \times \ln(\Lambda)$, N = number of matrix rows. Additionally, the matrix of log-ratios was analyzed using MANOVA to assess evidence for preference differences between observational

Table 2
Rockling behavioral criteria and classification.

Classification	Criteria
Single fish separate compartment	One fish alone within a compartment Either inside or outside structure
Single fish same compartment	One fish within a compartment containing either: 1. Another individual fish Either inside or outside structure 2. Two fish within one of the compartment structures (i.e. Classification - "Two fish single structure")
Two fish single structure	Two fish within one of the compartment structures
Three fish single structure	Three fish within one of the compartment structures

phases.

Following evidence for non-random compartmental usage, compartments/associated temperature (during temperature gradient and structure removal observations) were ranked from least to most preferred. Temperature preference ranking was accomplished by computing a cross-table with pairwise differences between matching log-ratios (e.g. $\ln \left(\frac{\text{use } 10^\circ\text{C}}{\text{use } 16^\circ\text{C}} \right) - \ln \left(\frac{1/8}{1/4} \right)$). The ranking of preferred temperature was performed separately for each temperature gradient phase (short and -long term) and structure removal observation (first, second, third, and fourth). The count of positive values in each row indicated the level of preference with 0 being the least preferred temperature and the greatest positive value the most preferred. After ranking, the mean/standard error ratio (with $N = 6$ replicates per observational phase ranking) was computed for each matrix element, yielding a t-value. The data were examined for normality using the Shapiro-Wilk test ($\alpha = 0.05$), and the statistical significance of pairwise temperature zone comparisons was determined (i.e. temperature preference).

3. Results

3.1. Physical structure preference and baseline behavior

Rockling were located within or in direct contact with the physical structures, 93%, 100%, and 100% of the time during the non-gradient, short-term preference and long-term preference observations, respectively. Based on this study's classification of behavior (Table 2), rockling did not display any behavioral differences between the three observational periods (non-gradient, short-term preference, and long-term

preference; repeated measures ANOVA ($N = 353$, $F(2, 6) = 0.039$, $p = .96$; Fig. 3). Rockling were commonly located in separate compartments or within the same compartment with no more than two fish per structure. Although less common, rockling did group together within one structure (i.e. Table 3 - Three fish single structure).

3.2. Temperature preference

Rockling were evenly distributed throughout the preference chamber during the non-gradient observation, indicating rockling displayed no preference (deviation from random use) for certain preference chamber compartment(s) ($\chi^2(4, N = 6) = 6.06$, $p = .19$). Rockling distribution deviated from random use during the presence of the temperature gradient in both short-term ($\chi^2(4, N = 6) = 23.7$, $p \leq .001$) and long-term ($\chi^2(4, N = 6) = 229.1$, $p \leq .001$) observations. Evidence for significant distributional differences between observational phases (MANOVA ($F(8, 24) = 2.92$, $p = .02$) allowed observational phase specific temperatures to be ranked from least to most preferred and tested for statistical significance.

Despite rockling's temperature ranking indicating preference for intermediate temperatures during short term exposure (short-term preference observation) to a temperature gradient, the preference was only statistically significant between 12.3 and 20.7 °C compartments (t-statistic ($N = 6$), $p = .01$) and 15.7 and 20.7 °C compartments (t-statistic ($N = 6$), $p = .04$). The results suggest rockling equally preferred all (10.4–18.6 °C) but the highest temperature (20.7 °C) on short time scales (Table 3). Longer term exposure (long-term preference observation) narrowed rockling's preference with significant differences found between 12.3 and the two highest temperatures (20.7 and 18.6 °C (t-

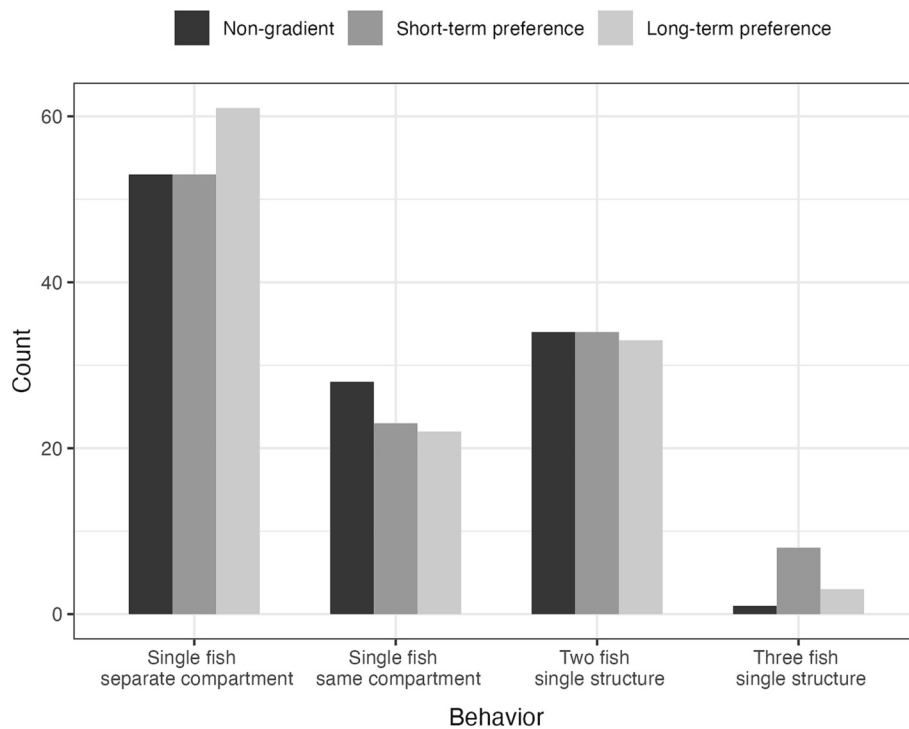


Fig. 3. Rockling behavior throughout the non-gradient, short-term preference, and long-term preference observations.

Table 3

Rockling's short-term and long-term thermal preference (mean (SD)) ranking. Ranking numbers sequentially decrease from the most preferred temperature (number 4) to the least preferred temperature (number 0). Different subscript letters to ranking numbers indicates significant differences (t-statistics, $p < .05$).

Temperature (°C)	Short-term	Long-term
20.7 (0.4)	0 ^a	0 ^a
18.6 (0.5)	1 ^{ab}	1 ^a
15.7 (0.5)	3 ^b	2 ^{ab}
12.3 (0.5)	4 ^b	4 ^b
10.4 (0.3)	2 ^{ab}	3 ^{ab}

statistic(s) ($N = 6$), $p \leq .001$, $p = .003$, respectively). The results indicate rockling's long-term preference is within the range of 10.4–15.7 °C (Table 3).

3.3. Trade-off between temperature and structure

Physical structures were systematically removed from the preference chamber compartments to determine the influence of structure on rockling temperature selection. The presence of physical structure supersedes rockling's mean long-term preference for 12.3 °C, although this outcome is restricted to temperatures of 18.6 °C or less (Fig. 4). Structure was either first removed in the 10.4 (Fig. 4, bottom panel) or 12.3 °C (Fig. 4, top panel) compartments following the conclusion of the long-term preference observation. Following the removal of structure in the 10.4 °C compartment, rockling significantly preferred the 12.3–15.7 °C compartments (t-statistic(s) ($N = 6$), $p \leq .05$) with structure over the lowest temperature (10.4 °C) without structure and the highest temperature compartment (20.7 °C) with structure (Fig. 4, bottom panel; Table 3). When structure was removed in the 12.3 °C compartments, the rockling's preference significantly changed to the 10.4 °C compartment (t-statistic(s) ($N = 6$), $p \leq .05$) containing structure over all other compartments (Fig. 4, top panel; Table 3). In the absence of structure in both 10.4 and 12.3 °C compartments, rockling significantly preferred 15.7 °C with structure (t-statistic(s) ($N = 6$), $p \leq .05$; Fig. 4). After structures in

the 15.7 °C compartments were removed, rockling significantly preferred the 18.6 °C compartments with structure and the 12.3–15.7 °C compartments without structures (t-statistic(s) ($N = 6$), $p \leq .05$; Fig. 4) over the highest (20.7 °C) temperature with structure and lowest (10.4 °C) temperature without structure. Rockling followed the presence of structure into higher than preferred 18.6 °C water, however rockling were also found in 12.3 and 15.7 °C waters without structure. Once the 18.6 °C structures were removed, rockling were scarcely found associated with the remaining structure in 20.7 °C and were significantly distributed throughout all compartments (Fig. 4; t-statistic(s) ($N = 6$), $p \geq .05$).

4. Discussion

4.1. Temperature preference and acclimation temperature

When exposed to a water temperature gradient within an experimental circular chamber, rockling exhibited thermoregulatory behavior by largely selecting for compartments with water temperature of 12.3 °C, resulting in a calculated preferred thermal range of 10.4–15.7 °C. Additionally, the short-term thermal range of rockling was found to be 10.4–18.6 °C when acclimated at 16 °C. Unlike the long-term preference, the short-term temperature preference, customarily measured within 2 h of exposure to a temperature gradient (Reynolds and Casterlin, 1979), is commonly influenced by the acclimation temperature (i.e. thermal history). On short time scales, fish acclimated to temperatures higher than their species-specific preferred temperature(s) generally select temperatures lower than their acclimation temperature (Cherry et al., 1977; Neill, 1979; Hofmann and Fischer, 2002). This general pattern partially matches our finding of rockling short-term preference for temperatures lower (but also higher) than the acclimation temperature. Rockling display a wide, short-term thermal range when acclimated to the median temperature of their distributional range. Further investigation using higher, sub-optimal acclimation temperatures could provide insight into rockling's ability to tolerate rising temperatures and marine heat waves (Frölicher and Laufkötter, 2018). Upon establishment of the temperature gradient, rockling

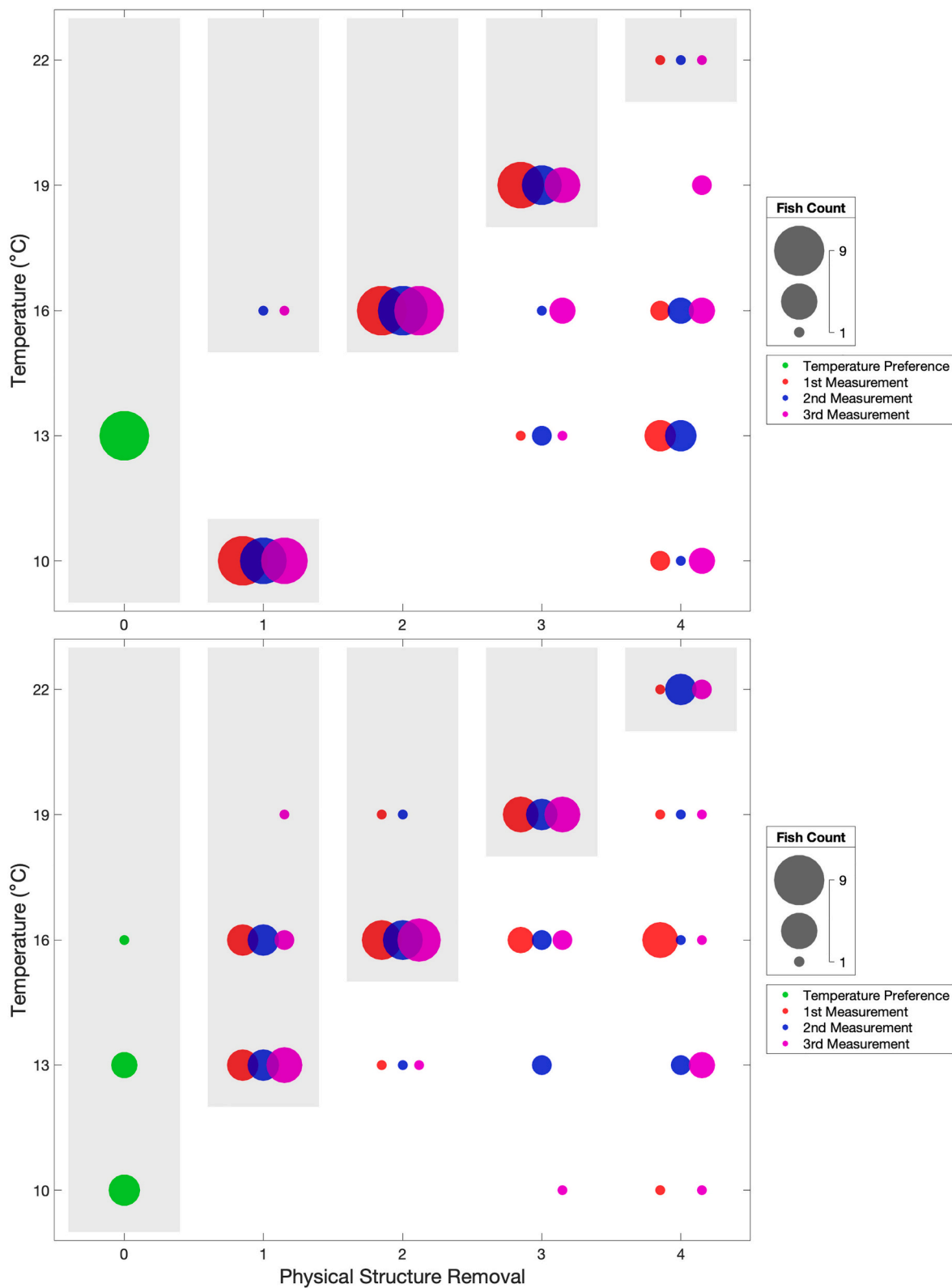


Fig. 4. Trade-off between preferences for temperature and physical structure. Thermal preferences of five bearded rockling observed 50, 55, and 60 min (1st, 2nd, 3rd measurements, respectively) following removal of physical structures (gray regions). Structures were removed from the compartment(s) in which the fish were present and in case all fish were not within the same compartment, then structures were removed from the coldest compartment containing a single fish. Structure first removed in 12.3 °C compartments (top panel) and 10.4 °C compartment (bottom panel).

displayed thermoregulatory behavior moving to previously unused compartments. This behavior provided evidence for the effectiveness of our experiments in determining temperature preferences and in addition for the effectiveness of studying the trade-off between physical structure and temperature.

4.2. Trade-off between temperature and physical structure

Rockling's strong affinity for physical structure, indicated by rockling being located within or in contact with structure over 97 % of the time allowed the trade-off between temperature and structure to be tested. Following structure removals, rockling repeatedly moved away from their preferred temperature to adjacent compartments containing physical structure. Rockling first chose colder temperatures with structures and subsequently warmer temperatures with structure; it is unknown whether rockling would continue seeking colder temperatures with physical structure because the preference chamber was restricted to one compartment colder than the preference we found for rockling. Rockling went to any compartment when the remaining structures were only present in the preference chamber's highest temperatures. These choices indicated a behavioral trade-off where rockling no longer selected for structures in these higher temperatures. Interestingly, upon departing from structure, many rockling did not return to the 12.3 °C compartments, but were evenly distributed throughout all compartments. Greater insight into these findings may be found by extending the experiment to include a longer observational period following the final structure removal. Our results support previous findings in which the presence of physical structure influenced the chosen thermal environment of other fish species (Bevelhimer, 1996; Matis et al., 2018; Nay et al., 2020). Various ecological benefits are associated with physical structure (e.g., providing shelter, spawning location, protection against predation, and ambush for attacking prey; Smokorowski and Pratt, 2007) and the demonstrated role of physical structure on thermoregulatory behavior should be considered when assessing habitat use, selection, and availability for fish species displaying a natural dependence on structure.

4.3. Other relevant factors affecting the trade-off

Other factors prompt fish species to occupy non-optimal (i.e. outside preferred temperatures) habitats: parturition state (Wallman and Bennett, 2006), predator abundance (Vaudou and Heithaus, 2013; Nay et al., 2021), grouping behavior (Cooper et al., 2018; Nay et al., 2021), personality (Rey et al., 2015; Cerqueira et al., 2016), and food availability (Freitas et al., 2016). Thermal preferences can differ depending on personality type with the more aggressive, proactive fish preferring higher temperatures as compared to the more shy, reactive fish (Rey et al., 2015; Cerqueira et al., 2016). The effect of personality was not explicitly tested on rockling preferred temperature. Therefore, we cannot discount the role personality may have played, however, no visual indication of personality driven behavior(s) (e.g. larger fish forcing smaller fish from physical structure) occurred during the video analysis. Throughout all experiments, regardless of experimental group and observational phase, rockling were found at various times to be either independent of one another (i.e. within separate compartments and/or opposite sides of the preference chamber) or in close proximity (i.e. sharing physical structure; Fig. 3). From our observations of rockling's solitary, social, and non-assertive behaviors, we do not expect personality to play a major interfering role in our experimental design. Nevertheless, personality-driven behavior would be an interesting element to account for in a targeted study. Clearly many factors influence habitat selection and trade-offs exist between these factors and physiological performance. Previous studies and the work presented here provide a quality basis for further exploring such trade-offs.

4.4. Fish size

The experimental fish sizes were appropriate given this study's interest in rockling's temperature preference and affinity to structure. Five bearded rockling spawn in winter and post larvae transform to pelagic juveniles at lengths of 2 cm (Demir et al., 1985). The pelagic rockling juveniles reside within the water column and undergo a color transformation to silver colored abdomen and sides and mottled green back in addition to developing longer fins (Demir et al., 1985). In late spring to summer, the pelagic rockling undergo another color and morphological transformation to resemble adult rockling, adopt demersal life, and migrate into estuaries. The size at which the pelagic to demersal transformation occurs is largely unknown (Heessen et al., 2015). Individuals measuring 3 cm lengths have been reported in demersal trawl surveys (Heessen et al., 2015) however, the first arrivals (0+ age group) of northern rockling (*Ciliata septentrionalis*) into British estuaries were 6–8 cm in length, indicating considerable growth occurs within the first summer (Claridge and Gardner, 1977). Wadden Sea five bearded rockling also exhibit considerable first year growth reaching lengths of 13–14 cm (Smietana, 1992), ~65–85% of their commonly found lengths (17–20 cm; Cohen et al., 1990). The experimental range (15–25 cm) adequately represents rockling's demersal stage and the lack of potentially smaller demersal size classes is not expected to influence the results.

Size dependent differences in thermal optima are commonly found. For example, optimal growth temperatures differed by 1.3 °C in two size classes (130 and 370 g) of juvenile spotted wolffish (*Anarhichas minor*; Imsland et al., 2006). Similarly, preferred temperatures differed by 2.8 °C in small and large (10–20 and 20–30 cm) burbot (*Lota lota*; Hofmann and Fischer, 2002). Evidence for size-dependent optima generally occurs on greater size scales than the experimentally tested rockling so it is unlikely that size dependency strongly influenced the results. Jobling (1994) defined the long-term preference as a range rather than a specific temperature so any size-dependent variation within the experimentally tested rockling is likely captured within the preferred long-term range. In addition, thermal size dependence may not be as apparent in rockling as with other fishes such as the Atlantic cod (Lafrance et al., 2005); which is capable of growing to much larger sizes (200 cm; Cohen et al., 1990) as compared to rockling's maximum length of 25 cm (Cohen et al., 1990; Munk and Nielsen, 2005).

Rockling abundance has increased in the western Dutch Wadden Sea since 1990 (Tulp et al., 2022) which coincides with an increase in Wadden Sea mussel and Pacific oyster beds (van der Meer et al., 2019; Troost et al., 2022). It is plausible that the increased presence of mussel and oyster beds, serving as physical structure, have provided rockling with greater availability of beneficial habitat. The results from this study provide empirical evidence to support experimental field research regarding physical structure serving as important habitat for certain fish species (e.g. Santos et al., 2008).

4.5. Climate change

Throughout 2001–2021, mean annual water temperature measurements have increased by >1.0 °C (range = 10.3–12.5 °C; van Leeuwen et al., 2021, 2022) towards rockling's mean preferred temperature of 12.3 °C. Since physiological performance is considered near optimal at preferred temperatures, increasing western Dutch Wadden Sea water temperature may be providing a more suitable habitat for the rockling where it is able to benefit through enhanced growth, reproduction, and survival. However, rockling may already be threatened by peak summer temperatures (August 2001–2021 monthly mean (SD) = 19.4 (1.4) °C) and extreme temperature events (2001–2021 daily range = -1.5–24.1 °C) exceeding the temperature range when rockling abandoned physical structure (above 18.6 °C; Fig. 4).

Bolle et al. (2021) found that increasing water temperature had a greater effect on the growth of four resident Wadden Sea fish species

(twaite shad (*Alosa fallax*), bullrout (*Notesthes robusta*), thick-lipped gray mullet (*Chelon labrosus*), eelpout (*Zoarces viviparus*)) than reduced food availability from de-eutrophication. The Wadden Sea supports a high biomass and commercial fishery of brown shrimp, *Crangon crangon*, a main prey of rockling (Camphuysen and Henderson, 2017). Respondek et al. (2022) found fishing pressure on brown shrimp has greatly increased, yet it remains unclear to what extent shrimp in preferred size-classes are less available to predators, such as rockling (Tulp et al., 2016).

Additionally, changes in western Dutch Wadden Sea brown shrimp settlement, density, and body sizes were linked to increasing water temperatures by Penning et al. (2021). The influence of increasing water temperatures on Wadden Sea fish species and their food sources is evident and warrants further investigation. Rockling is an ecologically important yet relatively unstudied fish species with increasing abundance in the Wadden Sea that could serve as a model species to better understand community change in the Wadden Sea.

When fish display a strong association with physical structure (Bevelhimer, 1996; Matis et al., 2018; Nay et al., 2020), predicting species geographical distributions under climate change scenarios cannot be based solely on water temperature regimes. For instance, future warming water temperatures could be less of a driving factor in fish distribution than the availability and developments in physical structure. However, somehow the energetic costs associated with living in non-optimal temperatures (e.g. Freitas et al., 2016) have to be accounted for when maintaining an association with physical structure. Therefore, linking physiological and behavioral studies to current and predicted future environmental conditions is needed for determining climate change-related ecological responses for species with specific habitat requirements (Horodysky et al., 2015).

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CRediT authorship contribution statement

Bass Dye: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Ingrid Tulp:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Anieke van Leeuwen:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Ewout Blom:** Conceptualization, Methodology, Resources, Writing – review & editing. **Edward Schram:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code that support the findings of this study are available at https://github.com/bassdye/Dye_et_al_2023_rockling

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2023.151959>.

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