No evidence for reduced growth in resident fish species in the era of de-eutrophication in a coastal area in NW Europe

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ARTICLE INFO

ABSTRACT

Coastal areas in north-western Europe have been influenced by elevated nutrient levels starting in the 1960s. Due to efficient measures, both nitrate and phosphate levels decreased since the mid-1980s. The co-occurring declines in nutrient loadings and fish productivity are often presumed to be causally linked. We investigated whether four resident fish species (twaite shad, bull-rout, thick-lipped grey mullet and eelpout), that spend the majority of their life in the vicinity of the coast, differed in growth between the historic eutrophication period compared to the recent lower nutrient-level period. Based on Von Bertalanffy growth models of length at age, and the analysis of annual otolith increments, we investigated the difference in sex-specific growth patterns and related these to temperature, eutrophication level (Chlorophyll *a*), growth window and fish density. In all four species, annual otolith growth rates during the early life stages differed between the two periods, mostly resulting in larger lengths at age in the recent period. All species showed significant correlations between increment size and temperature, explaining the observed period differences. The lack of an effect of total fish biomass provided no evidence for density dependent growth. A correlation with chlorophyll was found in bull-rout, but the relationship was negative, thus not supporting the idea of growth enhanced by high nutrient levels. In conclusion, we found no evidence for reduced growth related to de-eutrophication. Our results indicate that temperature rise due to climate change had a greater impact on growth than reduced food availability due to de-eutrophication. We discuss potential consequences of growth changes for length-based indicators used in management.

1. Introduction

Fish growth is influenced by a variety of environmental factors (Willmer et al., 2005). Abiotic factors such as temperature and oxygen concentration set the physiological boundaries for metabolism and growth (e.g. Pörtner and Knust (2007)), while food intake determines the ingested energy available for metabolism and reproductive or somatic growth (Jobling, 1993). Metabolic rate increases with temperature (Gillooly et al., 2001), consequently, temperature rise may lead to increased food requirements beyond availability (e.g. Teal et al. (2008)).

Food availability can be affected by a suit of factors, as feeding relationships are often complex. Food availability for each individual is determined by prey abundance together with competition (Amundsen et al., 2007). Increased competition for food generally decreases its availability to each individual, so fluctuations in the abundance of competitors may cause variations in growth (Lorenzen and Enberg, 2002). Food production at the bottom of the food chain is steered by nutrient levels. Nutrient enrichment of the environment leads to elevated levels of primary production (Kerr and Ryder, 1992). The evidence for an effect of nutrients cascading onto the next levels, secondary production and beyond, is often not clear in empirical data (Micheli, 1999). Apart from boosting primary production, alternative

effects of nutrient enrichment can also occur, such as changes in phytoplankton composition, altering particle sizes, which may affect food availability for zooplankton and ultimately the trophic levels beyond (Sin et al., 2013).

Pronounced changes in nutrient levels occurred in the international Wadden Sea (van Beusekom et al., 2019), a shallow coastal sea along the Dutch, German and Danish North Sea coast. The Wadden Sea and adjoining coastal areas are regarded as important nursery areas for several fish species, such as plaice *Pleuronectes platessa*, sole *Solea solea* and dab *Limanda limanda* (Bolle et al., 1994; van Beek et al., 1989; van der Veer et al., 2016). Nutrients enter the western Wadden Sea through the Rhine ROFI (Region Of Freshwater Influence), the fresh water plume of the river Rhine in Dutch coastal waters, and through the outflow of lake IJssel. Nutrient levels in the Rhine increased sharply during the 1950s, reaching a maximum during the 1980s (van Bennekom and Wetsteijn, 1990), and declined afterwards due to nutrient reduction methods in waste water treatment and the reduction of nutrient outflow from agriculture (de Jong, 2006). Nutrient levels in the international Wadden Sea (N and P) increased in the 1960–1970s and reached maximum values around the mid-1980s (Loebl et al., 2009; van Beuse-kom et al., 2017) and declined since. This trend in nutrient loading coincided with a peak in total fish biomass in the 1980s, as recorded by a demersal fish survey and fyke net monitoring (Tulp et al., 2008; van der Veer et al., 2015). In the public debate and among fishermen, the declines in nutrient loadings and fish productivity, both in terms of fish density and fish growth, are often presumed to be causally linked (Boddeke and Hagel, 1991). However, the question whether nutrient dynamics can be directly linked to dynamics in the higher trophic levels is unresolved (Philippart et al., 2007; Tulp et al., 2008). While an increase of macrozoobenthos biomass in the Wadden Sea has been linked to an increase in chlorophyll concentrations before the 1980s (Beukema et al., 2002; Beukema and Dekker, 2020), long-term variations in limiting nutrients were only weakly correlated with phytoplankton and macrozoobenthos biomass and more strongly linked to community structures (Philippart et al., 2007).

Interpretation of the relationship between eutrophication levels and processes acting on higher trophic levels is further complicated by the simultaneous increase in sea water temperature (van Aken, 2008) and decrease in nutrient levels since the mid-1980s (van Beusekom et al., 2017). Within the thermal range of a species, growth rate increases with temperature until an optimum and then decreases (e.g. Fonds et al. (1992)). An increase in water temperature may affect both growth rate and the length of the growing season (Teal et al., 2008). In studies focussing on fish growth in relation to food, often aquaculture studies, growth is usually expressed in body mass rather than fish length. However, variation in age-specific length is investigated in many studies and is related to both temperature and food abundance. The latter often in combination with potential density dependence effects. For instance, Lauerburg et al. (2018) related observed changes in the length-at-age of *Merlangius merlangus* in the North Sea to a decline in prey fish abundance. More examples for this relation are provided by Dupont et al. (2020) and Trenkel et al. (2015). For juvenile fish, the relationship between food abundance and fish length has been shown in many studies (Fonds et al., 1992; Freitas et al., 2016; Poiesz et al., 2020a). Reduced growth rates, compared to *ad libitum* laboratory growth rates or maximum growth predicted by bioenergetics modelling, have been observed in juvenile fish, suggesting food limitation (Ciotti et al., 2014; Poiesz et al., 2019; van der Veer et al., 2016), which may be more severe at higher temperatures (Freitas et al., 2012; Teal et al., 2008, 2012).

To examine the effect of de-eutrophication versus temperature on fish growth, we focussed on the Wadden Sea, where changes in temperature and nutrient levels were more pronounced than in offshore areas. We selected resident species, which spend the major part of their lives in or close to the Wadden Sea, so that their juvenile and adult growth patterns are likely to reflect local growing conditions. Based on a large archive of fish otoliths from the Wadden Sea, we compared growth

(length-at-age and otolith growth) during a historic period (1971–1986) of high eutrophication and relatively low temperatures to a recent period (2005–2019) with reduced eutrophication and higher temperatures. The species selection represents resident species with different geographic distributions (Lusitanian and boreal species) and diet. We selected: twaite shad (*Allosa fallax*, Lusitanian-zooplanktivore), bull-rout (*Myoxocephalus scorpius*, boreal-benthivore), thick-lipped grey mullet (*Chelon labrosus*, Lusitanian-phytoplanktivore, hereafter abbreviated to mullet) and eelpout (*Zoarces viviparus*, boreal-benthivore). The effects of decreased nutrients versus increased temperature were compared by examining whether the historic higher nutrient levels resulted in higher growth rates as a consequence of better food conditions, or whether the current increased temperatures led to better growing conditions. As total fish biomass in coastal waters strongly decreased between the two contrasted periods (Tulp et al., 2008), a potential density dependent effect on food conditions and fish growth was also incorporated in the analyses.

2. Materials and methods

2.1. Otolith collection

Limited sources were available for otoliths of resident (mainly non-commercial) fish species in the Wadden Sea. The majority of otoliths were obtained from a large otolith archive collected during a fyke survey near the entrance of the western Wadden Sea (Marsdiep, Fig. 1). This ongoing survey has been carried out since 1960. For further survey details see van der Veer et al. (1992). All otoliths of twaite shad, bull-rout, mullet and eelpout available for two periods were selected: 1971–1986 representing the period with strong eutrophication and relatively low temperatures, and 2005–2019 representing the period with lower nutrient levels and higher temperatures. We strived for a representative distribution over sex, age and length in both periods. To supplement underrepresented length or age classes, we added recent period otoliths from a beam trawl survey carried out in the western Wadden Sea in 2009 (for further survey details see Freitas et al. (2016)), and from a fyke survey carried out along the Afsluitdijk (Fig. 1) since 2001 (for further survey details see Winter et al. (2002)). Nevertheless, the number of otoliths available differed between species and periods, with lower numbers in the recent period (Table 1). In these surveys, all fish caught were identified to species level and measured to the cm below. For selected species, subsamples were taken for otolith collection. For each fish in these subsamples, the sagittal otoliths were collected, and the sex and total length (in cm or mm) were recorded.

2.2. Otolith preparation and measurement

Only one otolith of the pair of sagittal otoliths was used in the analysis. For each species, different methods of otolith preparation were first tested using a small set of otoliths, and then the best method was applied to all otoliths from both periods. A detailed description of otolith preparation and increment measurements is presented in Appendix A. Images of the otoliths were acquired with a stereo-microscope and a digital camera. Age determinations and increment measurements were carried out by experienced age readers based on the images.

Measurement of annual otolith increments enables examination of growth in each year of life. The size of the first increment in the otolith corresponds with the fish length at the end of the first year of life, etc. Growth year can be derived from the catch year, the age of the fish and the year of life (increment number). The last complete increment was always deposited in the year before capture. Therefore, growth year = catch year – 1 – age of fish + increment number.

2.3. Environmental data

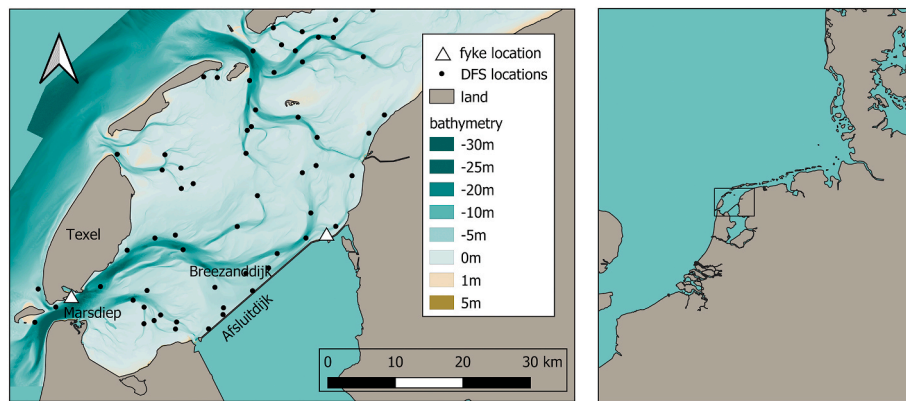As a proxy for nutrient load we used summer (average

Fig. 1. Map of the study area in the western Wadden Sea. Otoliths were obtained from the fyke survey in the Marsdiep, supplemented with otoliths from the fyke survey along the Afsluitdijk and a beam trawl survey throughout the western Wadden Sea. Temperature was measured in the Marsdiep and at Breezanddijk, chlorophyll was measured in the Marsdiep, and total fish biomass estimates were obtained from the annual Demersal Fish Survey (DFS, dots are sample locations).

Table 1
Overview of the number of otoliths, and the age and length range, per species and period.

species	period	age range (y)	length range (cm)	n females	n males	n total
twaite shad	1973–1982	1–8	19–49	148	95	243
	2005–2016	0–8	8–48	51	45	96
bull-rout	1973–1982	0–7	6–27	94	102	196
	2005–2015	0–3	7–22	28	38	66
mullet	1971–1986	4–19	36–67	135	36	171
	2005–2015	2–23	29–71	32	33	65
eelpout	1973–1984	2–8	13–31	88	58	146
	2009–2019	1–7	6–30	24	36	60

May–September) Chlorophyll *a* (hereafter called chlorophyll) concentrations in the Marsdiep from van Beusekom et al. (2017). These data were available for the period 1977–2017 (Fig. 2a).

Summer (average April–September) sea surface water temperature data were obtained from the NIOZ jetty measurements in the Marsdiep, available since 1950 (Fig. 2a, from van Aken (2008)). Daily temperature data were available from the NIOZ jetty for the period 1982–2018 (unpublished data). To reconstruct daily water temperature of the Marsdiep before 1982, daily temperature data of Breezanddijk (Fig. 1) for the period 1955–1989 were used (unpublished data). The temperatures at Marsdiep and Breezanddijk were highly correlated ($R^2 = 0.97$) for the overlapping period (1982–1989) and the slope was close to one. Daily temperatures were used to calculate growth window parameters (see section 2.4).

As a measure for intra-specific competition, potentially causing density dependent growth, we used total fish biomass. Estimates of annual total fish biomass (summed over all species caught) were based on the Demersal Fish Survey, a beam-trawl survey carried out in September each year from 1970 onwards (Fig. 2b). Sampling locations in the western Wadden Sea are shown in Fig. 1, for further survey details see Tulp et al. (2017).

2.4. Growth window

Growth is restricted to a species-specific range of water temperatures. Within this range, growth increases with increasing temperature until a maximum, followed by a decrease with further increasing temperature (Fig. 3). Three temperature parameters were defined:

- Topt: temperature at which growth is maximum;
- Tmin: the (low) temperature at which growth is 10% of maximum growth rate;
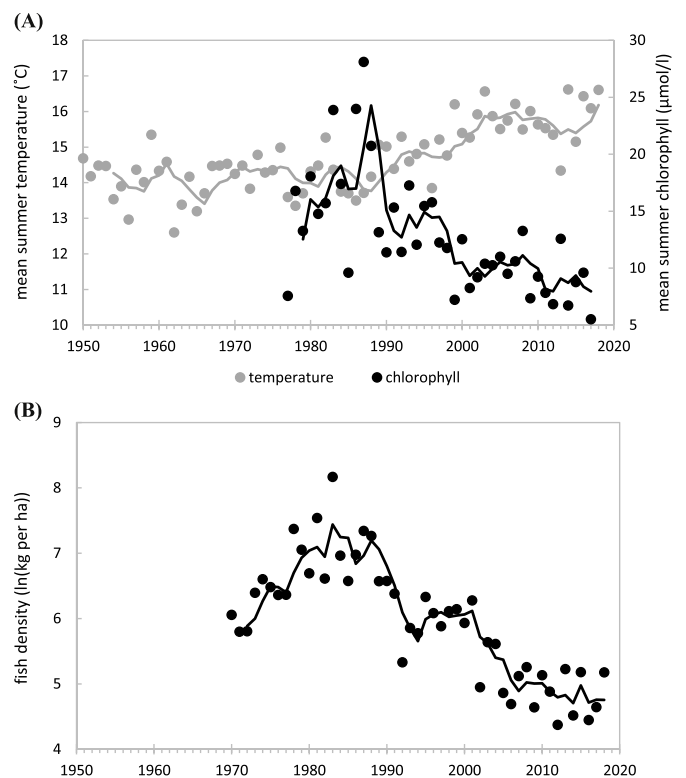

Fig. 2. (a) Long term trends of mean summer chlorophyll (May–Sept, from van Beusekom et al. (2017)) and mean summer temperature (April–Sept, from van Aken (2008)) in the Marsdiep. (b) Long term trends of fish density in the western Wadden Sea, based on the Demersal Fish Survey. Lines represent 3-year running means.

- Tmax, the (high) temperature at which growth is reduced to 10% of maximum growth rate.

Estimates of Tmin, Topt and Tmax (in °C) were derived from the literature for twaite shad, bull-rout and eelpout (Fig. 3). No suitable temperature-related growth data were found for mullet.

Species-specific growth windows were quantified by calculating temperature sums within the thermal growth range. Contrary to mean summer temperature, these growth window parameters take into account species-specific temperature preferences. Temperature sums were calculated for three periods within the growth range as:
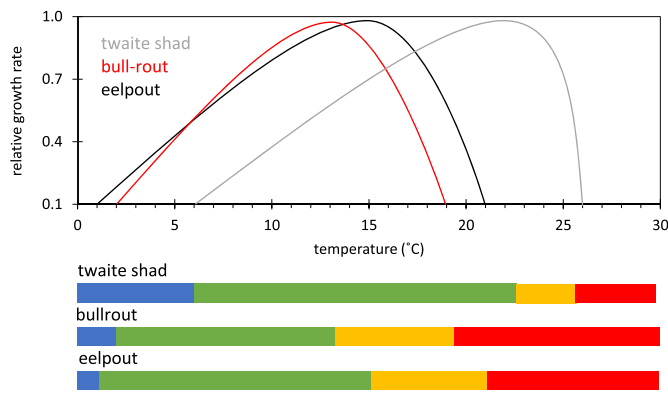
Fig. 3. Illustration of the thermal growth range for twaite shad derived from La Mesa et al. (2015), and for bull-rout and eelpout derived from Fonds et al. (1989). The coloured bars indicate the range below Tmin (blue), between Tmin and Topt (green), between Topt and Tmax (yellow) and above Tmax (red).

$$\sum_{i=1}^{n} (daily\ temperature - Tmin),$$ where n depends on the period:

- Temperature sum between Tmin and Tmax (*temp.sum1*), n = all days of the year for which temperature was above Tmin and below Tmax.
- Temperature sum between Tmin and Topt (*temp.sum2*), n = all days of the year for which temperature was above Tmin and below Topt.
- Temperature sum between Tmin and Tmax in the period January–June (*temp.sum3*), n = all days in the period January–June for which temperature was above Tmin and below Tmax.

The first period (*temp.sum1*) covers the full temperature range in which growth rate is at least 10% of maximum growth rate. The second and third period (*temp.sum2* and *temp.sum3*) were added to examine the effect of temperature sum under the assumption that prey availability limits growth at the end of the growing season (Poiesz et al., 2019; Teal et al., 2008).

2.5. Data analyses

The data were analysed using two different approaches: fish length at age growth curves and annual otolith increments. Growth curves integrate growth conditions throughout the fish's lifetime, while the analysis of annual otolith increments provides information for each year of life and allows comparison to year-specific environmental conditions.

2.5.1. Fish length at age
A von Bertalanffy growth model (VBGM) was fitted to length at age data: $L = Linf(1 - e^{-k(a-t0)})$, where a is age (in years), k is the growth coefficient, $t0$ is a value used to calculate size at age 0, and *Linf* (in cm) is the asymptotic size. VBGM parameters were analysed using the FSA library in R (http://derekogle.com/fishR/examples/oldFishRVignettes/VonBertalanffy.pdf). All potential models with either common or separate *Linf's*, *k's* and *t0's* (for sexes or periods) were fitted. The best fitting model was chosen based on AIC (Appendix B). The model with the fewest predictor variables among the AIC ranked models was selected. A more complicated model was only selected if the model was improved by more than 2.0. Firstly, differences in growth parameters between sexes were tested. Subsequently, period differences were tested for females and males separately.

2.5.2. Annual otolith increments
Otolith growth was analysed using the lme4 library in R for fitting Linear Mixed-Effects Models (Bates et al., 2015). Increment size was related to the increment number (*inc.nr* as factor) and various explanatory variables. Each fish aged 2 years or older contributed more than

one observation of increment size. To account for repeated measurements within individual fish, *fish-ID* was included in the models as random intercept. The analyses were limited to the first five increments, because the number of observations past the fifth increment was small in all species except mullet.

First, differences between sexes (*sex* as factor) and periods (*period* as factor) were examined. Subsequently, correlations between increment size and year-specific environmental conditions were analysed. The latter was split into two time periods, because of limited availability of chlorophyll and fish biomass data. For the full time series, increment size was analysed in relation to *inc.nr*, *sex*, *temperature* and the three growth window parameters described in section 2.4 (*temp.sum1*, *temp.sum2* and *temp.sum3*). For the period for which these data were available, 1977–2017, *chlorophyll* and *fish biomass* were included in the models, besides the previous variables. Interactions between increment size and all other explanatory variables were included, to allow different responses in different increments.

Collinearity between explanatory variables occurred and variables were omitted if variance inflation factors (VIFs) exceeded 5 (Appendix B). VIFs were calculated using the corvif function developed by Zuur et al. (2009). After eliminating collinear variables, backward model selection was applied based on AIC and Chi-square testing, using the drop1 function in lme4. Thus, the model with the lowest AIC was selected, or a model with a higher AIC if fewer predictor variables resulted in an ΔAIC of less than 2.0 (Appendix B). The maximum likelihood (ML) method was applied during model selection. The selected models were refitted with the restricted maximum likelihood (REML) method for optimal parameter estimation (Zuur et al., 2009).

3. Results

3.1. Otolith samples

To evaluate whether the samples collected in both periods were representative for the specific periods, the length-frequency distributions of the Marsdiep fyke catches (Fig. 4a) were visually compared to those of the sampled fish (Fig. 4b). For the recent period, size ranges in the samples and the catches were similar. For the historic period, smaller individuals were underrepresented in the samples, especially in twaite shad.

3.2. Length at age growth curves

The growth curves of twaite shad were significantly different between males and females (Table B1). Both *Linf* and *t0* differed, with females reaching a *Linf* of 48.0 and males of 42.5 cm (Table 2). Comparison of periods for males and females separately resulted in significant differences. For males both *Linf* and *k* were different, with higher *Linf* and lower *k* in the recent period compared to the historic period. Females showed similar *Linf* and *t0* in both periods, but a lower *k* in the recent period (Table 2, Fig. 5).

In bull-rout growth curves differed by sex, with higher *Linf* (28.3 vs 19.9 cm) and lower *k* in females. Growth curves did not differ between the two periods, for either sex (Table 2, Fig. 5). Because in the recent period older individuals were lacking, we repeated the analyses for ages that were represented in both periods, which yielded the same result as the total dataset.

Growth curves of mullet showed no significant sex difference. Growth rates differed significantly between periods, with higher growth rates in the recent period (Table 2, Fig. 5). For both sexes, the difference in growth rates was due to a higher *Linf* in the recent period (females historic: 80.8, females recent: 83.6, males historic: 59.4, males recent: 67.2).

Eelpout showed a sex-specific difference in growth curves characterised by a higher *Linf* for females (27.4 vs 24.8). Females did not show different growth rates in the two periods, whereas males had lower *Linf*
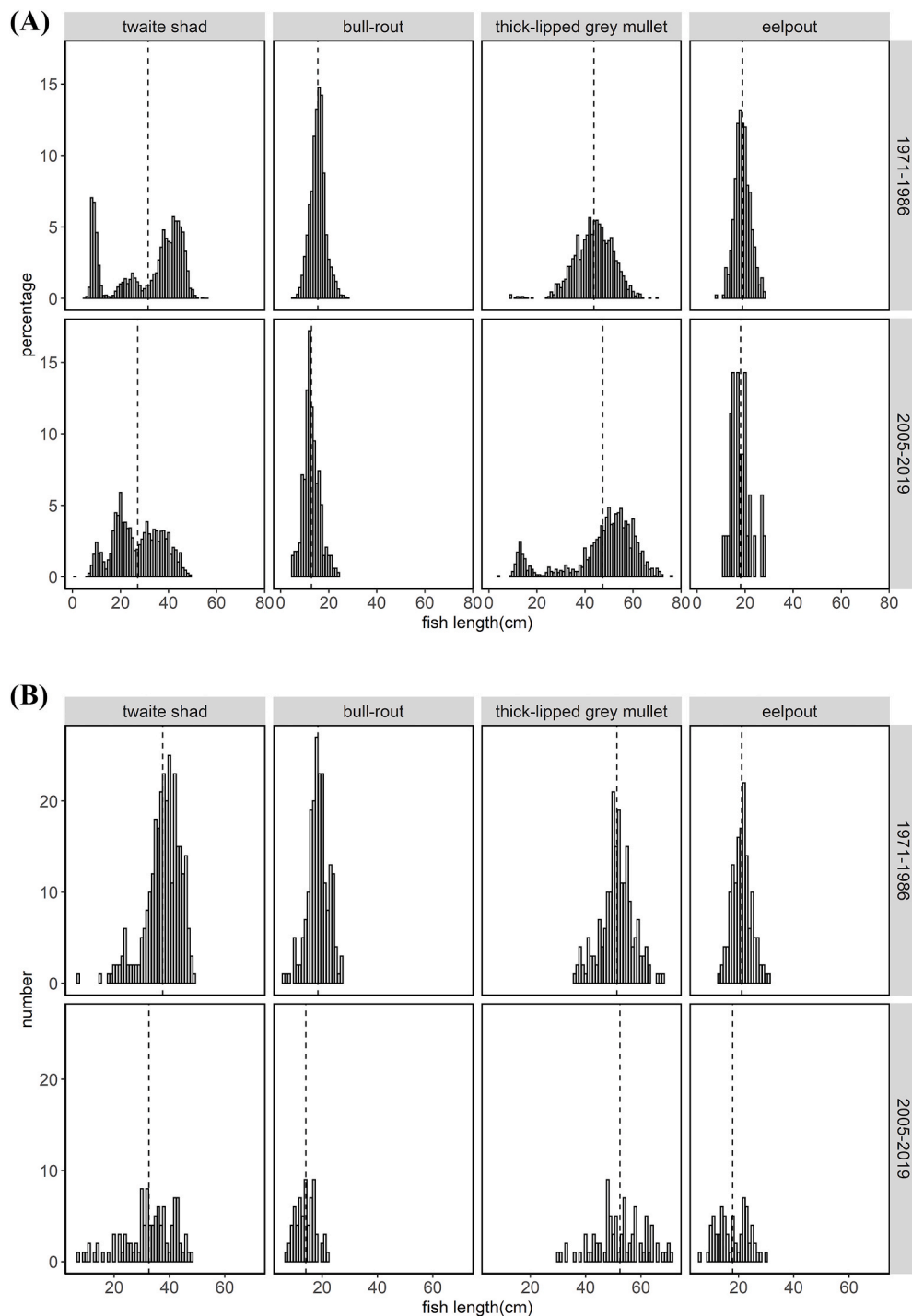
Fig. 4. Length-frequency relationships for the four species per period in the fyke catches (a) and selected otoliths (b). Dotted lines indicate mean lengths.

and higher *k* in the historic period as compared to the recent period (Table 2, Fig. 5). When the growth comparison was limited to the overlapping age range, male growth curves differed in *Linf* and *t0*.

3.3. Annual otolith increments

Differences in increment size were observed between the two periods. The interaction between *period* and increment number (*inc.nr*) was significant in all species, indicating different effects in different years of life (Table 3). In all species except eelpout, the first increment was largest. Also, in all species except eelpout, the first increment was larger in the recent period than in the historic period. In eelpout, the second,

third and fourth increment were larger in the recent period than in the historic period. The second increment of twaite shad and bull-rout showed an inversed pattern compared to the first increment: lower growth rates in the recent period compared to the historic period (Fig. 6).

Increment size differed between sexes for bull-rout and eelpout, with smaller increments in males than in females. No sex differences in increment size were found for twaite shad or mullet (Table 3). This corresponds with the sex differences observed in fish length at age (section 3.2) for all species except twaite shad.

All species showed correlations between increment size and *temperature*, or temperature related growth window parameters (*temp.sum1* or

Table 2
Von Bertalanffy growth parameters *Linf*, *k* and *t0*, per species and comparison.

		twaite shad			bull-rout			mullet			eelpout		
		Linf	*K*	*t0*	*Linf*	*k*	*t0*	*Linf*	*k*	*t0*	*Linf*	*k*	*t0*
sex difference	females	48.0		−0.31	28.3	0.38					27.4		
	males	42.5		−0.98	19.9	0.61					24.8		
	no difference		0.36				−0.92	76.0	0.08	−5.16		0.50	−0.24
period difference for females	historic		0.35					80.8					
	recent		0.32					83.6					
	no difference	48.1		−0.48	28.0	0.40	−0.87		0.06	−6.65	27.7	0.50	−0.14
period difference for males	historic	39.9	0.44					59.4			22.6	0.59	
	recent	47.4	0.29					67.2			29.5	0.39	
	no difference			−0.93	20.1	0.58	−1.00		0.15	−1.55			−0.31

temp.sum3). In all species the interaction between increment number (*inc.nr*) and one of the temperature parameters was significant, indicating that the effect of temperature differed between years of life (Table 4). In twaite shad, temperature sum between Tmin and Tmax (*temp.sum1*) had the largest effect on otolith growth (Table 4): a positive effect on the size of the first increment and a negative effect on the size of the second increment (Fig. 7). In bull-rout, both *temperature* and temperature sum between Tmin and Tmax (*temp.sum1*) had an effect on otolith growth (Table 4): *temperature* had a positive effect on the size of the first increment and a negative effect on the size of the second increment (Fig. 7), while *temp.sum1* had a positive effect on the size of both increments. Growth window parameters were not available for mullet, but *temperature* was positively correlated with the size of the first increment (Table 4, Fig. 7). In eelpout, increment size showed a negative correlation with *temperature* in the first increment and a positive correlation in following increments (Table 4, Fig. 7).

Examination of the effect of *chlorophyll* and *fish biomass* on increment size was limited to the period 1977–2017 due to data availability. A correlation with *chlorophyll* was found in bull-rout: growth decreased with an increase in *chlorophyll* (Table 5, Fig. 7). No correlations with *fish biomass* were found. *Chlorophyll* and *fish biomass* were to some extent collinear (Fig. 2), but only in eelpout, one of these variables needed to be removed because of VIF-values higher than 5 (Table B4).

4. Discussion

4.1. Species characteristics relevant for growth

The degree to which the four resident species selected in this study actually stay within the Wadden Sea throughout their life is unknown. Mullet is generally described as a year-round inhabitant of coastal waters; they leave the Wadden Sea to coastal waters in October and return in May/June (Schepers, 1975). The distribution of bull-rout is also typically coastal, although they occur in low densities further offshore (Heessen et al., 2015). Eelpouts are described as characteristic inhabitants of the Wadden Sea, particularly found in the vicinity of mussel beds. Twaite shad have a coastal distribution in summer but the degree to which they venture further offshore in winter, outside the area under influence of the (de)eutrophication, is less clear (Heessen et al., 2015). Of the four species, eelpout is likely to be most strongly bound year-round to the Wadden Sea.

The species in this study differ in their geographic distribution. According to a biogeographic classification of North Sea fish (Engelhard et al., 2011), twaite shad and mullet are southern species for which the North Sea is in the northern part of their distribution range (Lusitanian species), while eelpout and bull-rout are northern species for which the North Sea is in the southern part of their distribution range (boreal species). These differences in geographic distribution are reflected by differences in temperature preference.

Temperature may affect growth rate and the duration of the growth period. Both effects have been included in our study. Temperature may also affect the timing of spawning and therefore the start of the growing season in the first year of life (Teal et al., 2008). The timing of spawning for most of the selected species is generally in spring, varying between January–March for bull-rout (Luksenburg et al., 2004), January–April for mullet (Hickling, 1970; Leyzer, 2006), mid-May to mid-July for twaite shad (Maitland and Hatton-Ellis, 2003). The exception amongst the investigated species is the live bearing eelpout: fertilization takes place in August and early September. The embryos stay inside their mothers body where they suckle from ovarian follicles (Skov et al., 2010). The young are released, as fully developed 4 cm fish, between December and March. The late mating season of eelpout is reflected by the fact that the length of the first increment is smaller than the second. Information on potential shifts in the timing of spawning/mating (and hence repercussions on length of the first growing season) is unavailable for the species we studied.

To what extent potential growth rates are realised under different environmental conditions might be species-specific, related to differences in diet, life history characteristics or habitat choice. Twaite shad and mullet are pelagic species, whereas bull-rout and eelpout are benthic species. Mullet mainly grazes algae from the seafloor or hard substrate, while eelpout and bull-rout predominantly feed on epibenthic crustaceans, and twaite shad feeds on zooplankton, epibenthic crustaceans and small fish (Aprahamian, 1989; Poiesz et al., 2020b). So, of the four species, mullet has the shortest foodweb link with primary production and nutrients.

4.2. Differences in growth between sexes and regions

As in most fish species, sex differences in growth occurred for twaite shad, bull-rout and eelpout, with a larger length at age for females than males. At the level of separate otolith increments, sex differences were found in eelpout and particularly in bull-rout, with females having larger increments.

Only for bull-rout, a comparison of sex-specific growth rates can be made with published literature (Luksenburg and Pedersen, 2002), although this study was carried out at quite a different latitude in northern Norway. The growth rates reported for Norwegian bull-rout were lower than we observed in the western Wadden Sea, characterised by a lower *Linf*, higher *t0*, and comparable *k* estimates (Fig. 8). Published records on growth of eelpout in the German Wadden Sea (Ulleweit, 1995) are for combined sexes. The sexes-combined growth curve for the German Wadden Sea was slightly higher than the curve we estimated for females. The growth curve for the Baltic (Ulleweit et al., 1998), however, differed greatly from those for the Wadden Sea, characterised by a much higher *Linf* (Fig. 8). The lack of a sex difference in growth rate in mullet is in accordance with earlier findings (Richter, 1995). Compared to Northern Ireland at a similar latitude, in our study growth curves were much higher, characterised by a much higher *Linf* and a much lower *t0*, but a slightly lower *k* (Fig. 8). Lower growth rates in the Irish Sea as compared to the southern North Sea occurs in more species (Thorsen et al., 2010).

For fish, Bergmann's rule, which states that the body size should increase with increasing latitude (Lindsey, 1966), is not self-evident
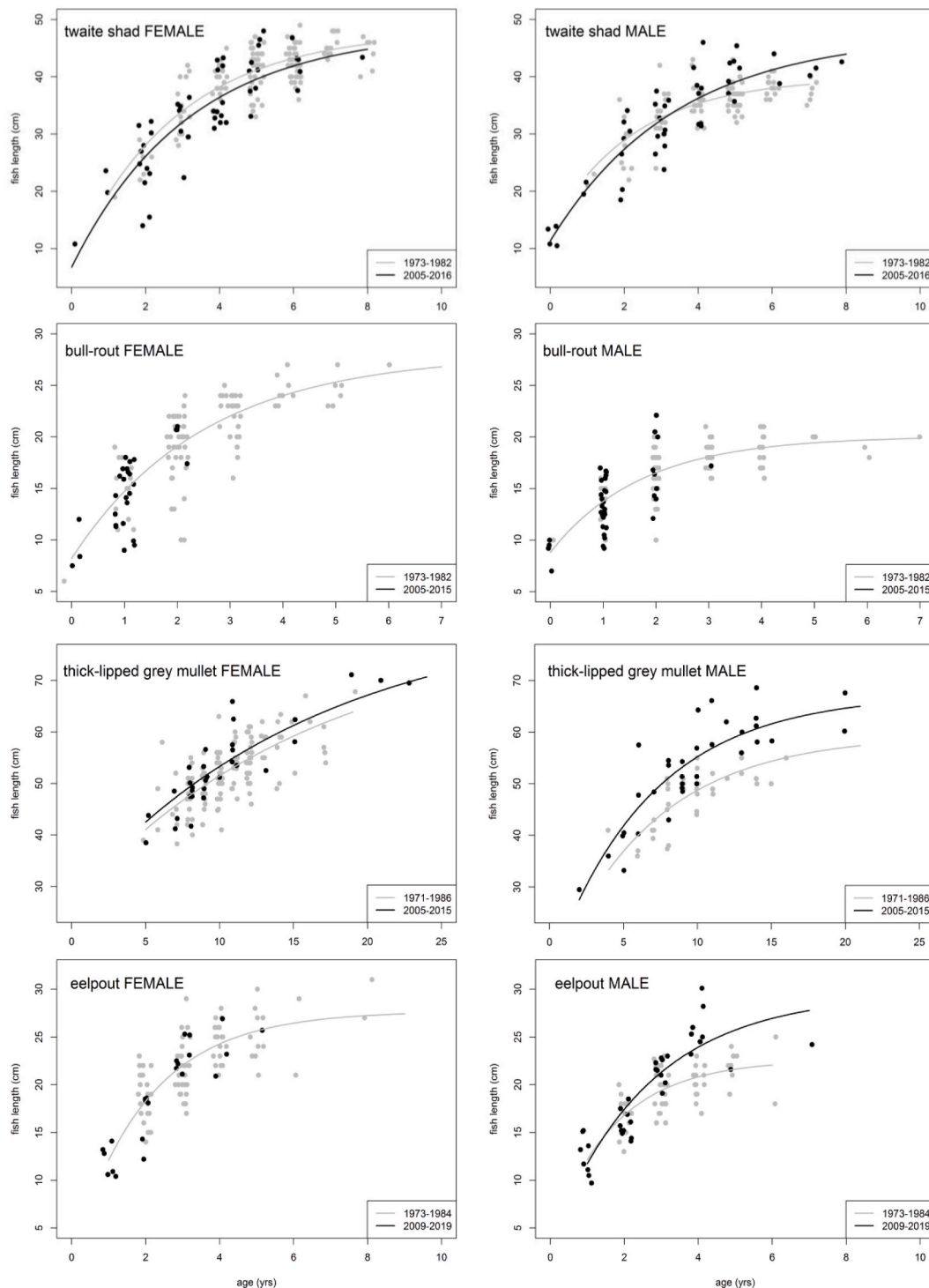
Fig. 5. Age-length relationships of female and male twaite shad, mullet, bull-rout and eelpout in the two periods. A combined fitted line is presented if the difference between periods was insignificant. The exact periods differed slightly between species depending on data availability.

(Saunders and Tarling, 2018). As latitude increases, fish species are confronted with longer winters and shorter growing seasons which may result in smaller sizes. Comparison of growth curves not only showed latitudinal, but also regional differences in growth rates, which may be related to differences in food situation and environmental regimes (e.g. salinity, oxygen saturation, tidal conditions).

4.3. Changes in growth in relation to changes in the environment

Comparison of length at age growth curves and otolith increments between a historic period (with high eutrophication and relatively low temperatures) and a recent period (with reduced eutrophication and higher temperatures) generally showed higher growth rates in the recent period. Growth curves of four of the eight species-sex combinations were higher in the recent period as compared to the historic period (twaite shad males, mullet both sexes, eelpout males). In female eelpout and in

Table 3

Increment size in relation to increment number (*inc.nr*), *period* (historic or recent) and *sex*. ANOVA table of the selected model per species (for model selection see Table B2). *Fish-ID* was included in all models as random intercept.

species	n obs.	n fish	fixed terms	df	F-value
twaite shad	1366	332	factor(*inc.nr*)	4	3008.4
			factor(*period*)	1	2.2
			factor(*inc.nr*):factor(*period*)	4	55.9
bull-rout	573	253	factor(*inc.nr*)	4	424.4
			factor(*period*)	1	11.7
			factor(*sex*)	1	37.3
			factor(*inc.nr*):factor(*period*)	2	6.0
mullet	1175	236	factor(*inc.nr*)	4	866.3
			factor(*period*)	1	21.4
			factor(*inc.nr*):factor(*period*)	4	11.9
eelpout	636	206	factor(*inc.nr*)	4	255.0
			factor(*period*)	1	13.3
			factor(*sex*)	1	4.4
			factor(*inc.nr*):factor(*period*)	4	6.3
			factor(*inc.nr*):factor(*sex*)	4	2.8

bull-rout (both sexes) no difference was found, while female twaite shad showed the reverse pattern. Otolith increments were larger in the recent period compared to the historic period in twaite shad, bull-rout and

mullet during the first year of life, and in eelpout during the second to fourth year of life. In twaite shad and bull-rout, the increased growth during the first year of life was compensated by lower growth rates during the second year of life. The observed differences in otolith growth were limited to the earlier years of life. Growth changes are better detectable in this stage than at later stages, simply because growth rates are highest in young fish (Barneche and Allen, 2018). The generally higher growth rates we found in the recent period do not provide evidence for the hypothesis that the historic higher nutrient loadings resulted in higher growth rates.

All four species showed significant correlations between otolith growth and temperature or temperature sum. Furthermore, the differences between the periods showed corresponding correlations with temperature (sum): a positive correlation for the first increment of twaite shad, bull-rout and thick-lipped grey, and for the second and third increment of eelpout; a negative correlation for the second increment of twaite shad and bull-rout. Although correlative, these results provide a strong indication that the differences in growth rates between periods were caused by temperature changes.

The negative correlation between growth and temperature sum that was observed for twaite shad in the second year of life is surprising, as this is a Lusitanian species with a relatively high optimum temperature for growth. Thermal growth range estimates for twaite shad were
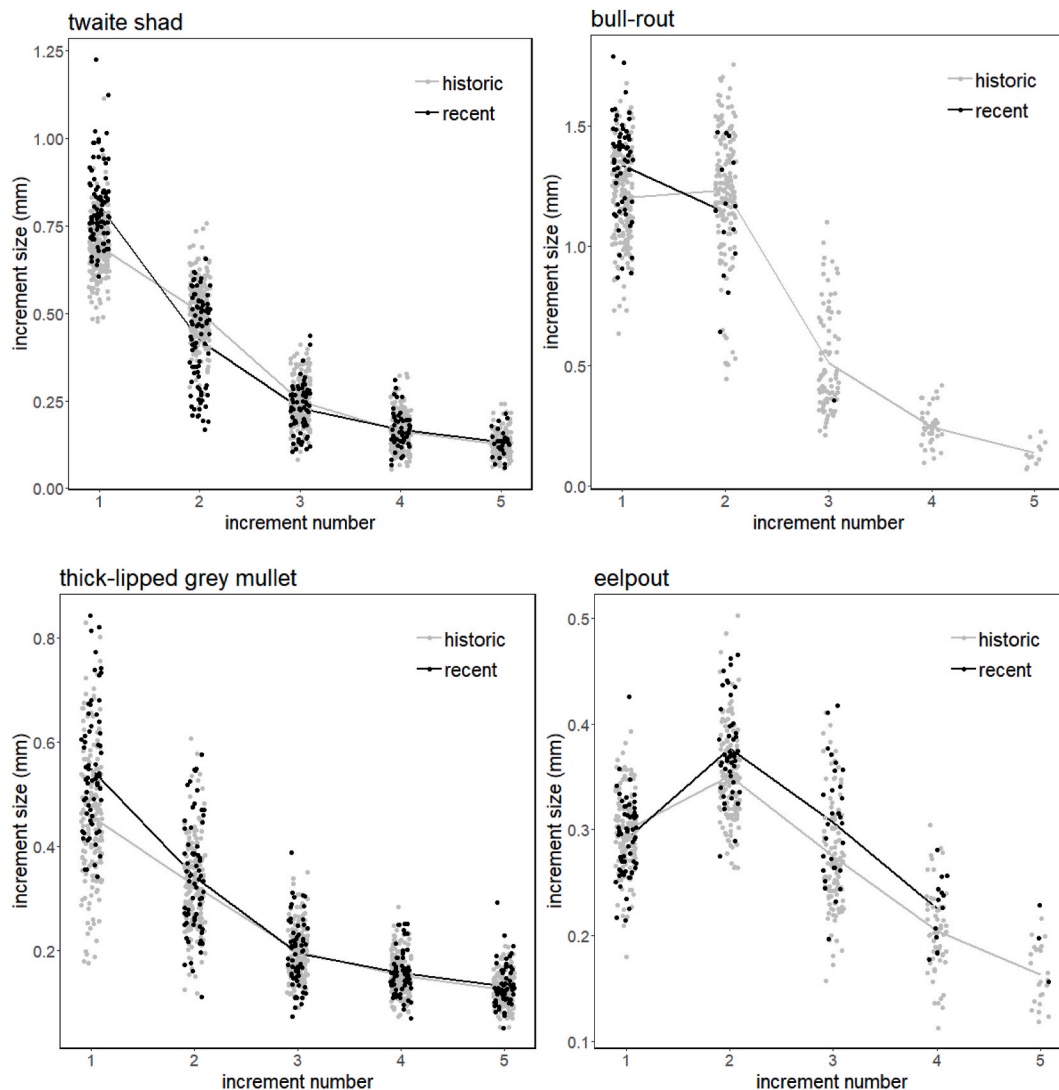

Fig. 6. Annual otolith increments of twaite shad, bull-rout, mullet and eelpout in the two periods (both sexes combined per species). The line represents the model prediction (Table 3).

Table 4
Increment size in relation to increment number (*inc.nr*), *sex*, *temperature* and three growth window temperature sums: between Tmin and Tmax (*temp.sum1*), between Tmin and Topt (*temp.sum2*), and in the first half of the year (*temp.sum3*). ANOVA table of the selected model per species (for model selection see Table B3). *Fish-ID* was included in all models as random intercept.

species	n obs.	n fish	fixed terms	df	F-value
twaite shad	1366	332	factor(*inc.nr*)	4	3038.9
			temp.sum1	1	9.4
			temp.sum3	1	3.7
			factor(*inc.nr*):*temp.sum1*	4	49.2
			factor(*inc.nr*):*temp.sum3*	4	8.0
bull-rout	573	253	factor(*inc.nr*)	4	445.0
			factor(*sex*)	1	28.9
			temperature	1	11.4
			temp.sum1	1	14.5
			factor(*inc.nr*):factor(*sex*)	4	3.0
			factor(*inc.nr*):*temperature*	4	2.8
mullet [1]	1175	236	factor(*inc.nr*)	4	850.7
			temperature	1	15.7
			factor(*inc.nr*):*temperature*	4	7.7
eelpout	636	206	factor(*inc.nr*)	4	254.6
			factor(*sex*)	1	4.4
			temperature	1	9.4
			factor(*inc.nr*):factor(*sex*)	4	2.8
			factor(*inc.nr*):*temperature*	4	6.8

[1] Growth window parameters not available for mullet.

obtained from a Mediterranean study (La Mesa et al., 2015), and this range may be lower at higher latitudes. Differences in thermal range occur within species, due to acclimation or permanent population differences (Pörtner and Peck, 2010). Consequently, our calculation of temperature sum within the growing season may not be representative for the Wadden Sea. Nevertheless, temperature sum and temperature (not dependent on thermal range estimates) had a similar effect on growth. Our results for twaite shad clearly indicate that the relationship between growth and water temperature changes with increasing fish age or size. Changes in thermal tolerance related to life stage or size have previously been reported in other species (Daufresne et al., 2009; Pörtner and Peck, 2010; Teal et al., 2012).

In bull-rout and eelpout, the thermal growth range estimates were considered to be appropriate as they were obtained from a study in the Wadden Sea (Fonds et al., 1989). Although eelpout is classified as a boreal species (Engelhard et al., 2011), it showed positive correlations between growth and temperature. Pörtner and Knust (2007) examined physical mechanisms underlying thermal tolerance in eelpout in the German Wadden Sea. They showed that both growth and abundance decrease above the temperature at which oxygen limitation starts (pejus temperature). With increasing maximum summer temperatures, they observed a decrease in abundance and linked this to heat-induced mortality. They argue that temperature rise would primarily affect large eelpout, as thermal sensitivity increases with size. This could be expressed by a reduction of the relative abundance of large eelpout, but that is not evident in our data (Fig. 4a). Although eelpout is not a true migratory species, they may be able to escape oxygen limitation in parts of the Wadden Sea by small scale movements towards pockets of water of lower salinity and thus higher oxygen saturation (van Beek, 2001). Such areas of lower salinity are more likely to occur in our near-shore (fyke) monitoring than in the study area of Pörtner and Knust (2007). With regard to growth, they showed that their pejus temperature estimate corresponds with the optimum temperature for growth as estimated by Fonds et al. (1989) based on laboratory observations. However, our field observations of growth achieved during the second and third year of life showed increased growth rates with an increase of temperature. Apparently, the advantage of temperature rise in the period before optimum temperature outweighs the disadvantage in the period beyond optimum temperature. In contrast to the second and third year, the relation between growth and temperature is negative in the

first year. This is likely due to the late mating season of eelpout, limiting the first growing season to the second half of the year, in which temperature is more likely to exceed optimum temperature.

Based on the simultaneous decline in fish biomass and nutrient loadings in the Wadden Sea, a positive relationship between fish productivity and nutrient loadings has been suggested (Boddeke and Hagel, 1991). We examined fish growth in relation to summer Chlorophyll *a* (as proxy for nutrient load). Of the four species examined, only bull-rout showed a correlation, but this correlation was negative and therefore does not support the hypothesis that growth rates increase with increased nutrient loadings. We cannot exclude the possibility that negative effects of reduced nutrient loadings in the recent period were overruled by positive effects of increased temperature. Furthermore, de-eutrophication may lead to reduced fish densities thus alleviating density-dependent growth reduction. However, the lack of a correlation between total fish biomass and growth indicates that density dependent growth is likely not playing a role in the growth of the investigated species in the Wadden Sea. Year-specific estimates of total fish biomass were based on the Demersal Fish Survey, as it is the only long-term survey covering the entire western Wadden Sea. This survey may not provide the best proxy for density dependent food competition in twaite shad or mullet, because these pelagic species are underrepresented in this beam-trawl survey.

The decrease in total fish biomass in the Wadden Sea since the 1980s is mainly due to a decrease of non-resident species, which only use the Wadden Sea as nursery area (Tulp et al., 2017). For plaice it has been shown that the decrease in density in the Wadden Sea and coastal waters was caused by an offshore shift in the distribution of juveniles (van Keeken et al., 2007). This may also be the case for other species, such as dab (unpublished data). In an attempt to separate the effect of temperature and nutrient levels on spatial distributional patterns of juvenile plaice, Stottrup et al. (2017) compared densities along the Danish coast to the Dogger Bank, representing a contrast in nutrient loadings but less so in temperature. The strong decline in the coastal areas of age groups 1 to 3 was not observed in the Doggerbank area and was therefore explained by the contrasted pattern in nutrient loadings. However, salinity and to some extent temperature differed between the Doggerbank and coastal area. As temperature preferences and growth potential differ at different salinities (Akimova et al., 2016; Imsland et al., 2001), the salinity-temperature interaction may be confounding in this study (Boeuf and Payan, 2001). Further, the young plaice in this study spent only the first year(s) of their lives in coastal waters, migrating to deeper waters thereafter.

Changes in growth have been observed in many fish species. Long-term growth changes have mostly been linked to (1) global warming, either positively or negatively (Baudron et al., 2014; Cheung et al., 2013; Lyashevska et al., 2020; Matta et al., 2018; Thresher et al., 2007; van der Sleen et al., 2018; Vieira et al., 2020), (2) density-dependent processes, including changes in density related to fishing intensity (Bolle et al., 2004; Denechaud et al., 2020; Jansen and Burns, 2015; van der Sleen et al., 2018; Vieira et al., 2020), (3) phenotypic or evolutionary changes due to size-selective fishing (Hunter et al., 2016; Rijnsdorp and van Leeuwen, 1996; Swain et al., 2007), and (4) eutrophication (Boddeke and Hagel, 1991; Rijnsdorp and van Leeuwen, 1996). In this study we examined growth changes in four resident fish species in the Wadden Sea. Potential effects of de-eutrophication on growth were expected to be most pronounced in these resident species, who spend their whole life in shallow coastal areas where nutrient levels changed markedly. Our results, however, clearly indicate that temperature rise due to climate change had a greater impact on growth than reduced food availability due to de-eutrophication. For future research, we recommend to further tease apart the potential effects of food and temperature on growth by comparing achieved growth to maximum growth under ambient temperatures, as predicted by DEB (Dynamic Energy Budget (Kooijman, 2010)) modelling.
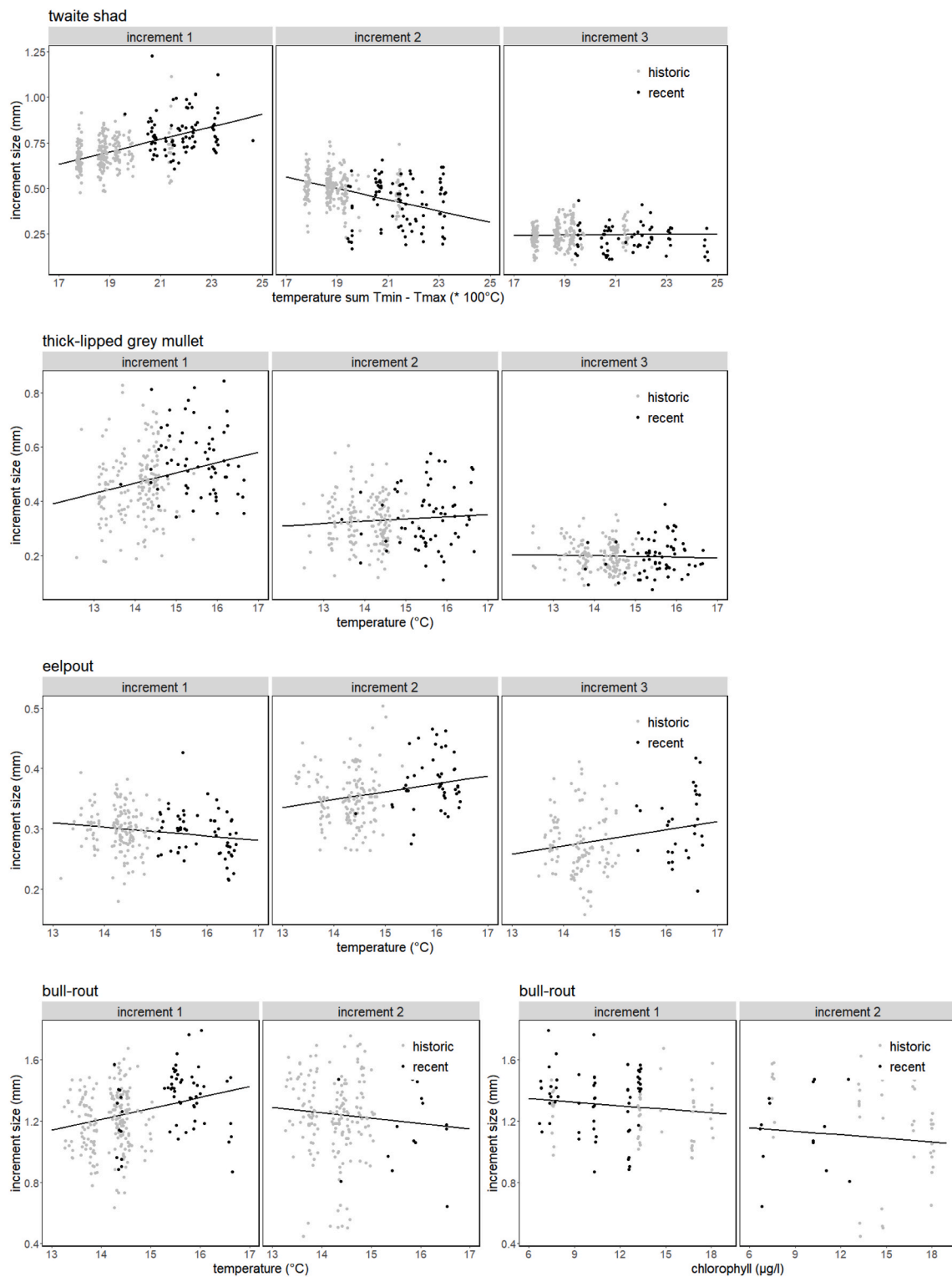
Fig. 7. Primary correlations between otolith increment size and environmental conditions.

4.4. Consequences of change in growth for management

Changes in growth patterns may have consequences for length-based indicators that are used within several European management strategies aiming at a Good Environmental Status (GES). The large fish indicator (LFI) is used in the OSPAR (Convention for the Protection of the Marine Environment of the North East Atlantic) Ecological Quality Objective (EcoQO) for the demersal fish communities in the North Sea, and within

the Marine Strategy Framework Directive (MSDF). The LFI is defined as the proportion of total fish biomass of a defined set of species exceeding a specified threshold length (Greenstreet et al., 2011). This includes all species quantitatively sampled well in surveys, also non-commercial species. Shifts in especially *Linf* can have large consequences with regard to the LFI. As changes in fish growth can be caused by different mechanisms, for management purposes it is important to investigate which is the predominant cause. Apart from the goals defined for

Table 5

Increment size in relation to increment number (*inc.nr*), *sex*, *chlorophyll*, *fish biomass*, *temperature* and three growth window temperature sums: between Tmin and Tmax (*temp.sum1*), between Tmin and Topt (*temp.sum2*), and in the first half of the year(*temp.sum3*). ANOVA table of the selected model per species (for model selection see Table B4). *Fish-ID* was included in all models as random intercept. Analysis limited to 1977–2017 due to availability *chlorophyll* and *fish biomass* data.

species	n obs.	n fish	fixed terms	df	F-value
twaite shad	566	197	factor(*inc.nr*)	4	1198.0
			temp.sum1	1	0.2
			temp.sum3	1	3.3
			factor(*inc.nr*):*temp.sum1*	4	7.3
			factor(*inc.nr*):*temp.sum3*	4	5.6
bull-rout	190	124	factor(*inc.nr*)	4	73.2
			factor(*sex*)	1	6.6
			chlorophyll	1	29.0
			temperature	1	0.1
			temp.sum1	1	5.9
			factor(*inc.nr*):*temperature*	3	5.2
mullet [1]	407	93	factor(*inc.nr*)	4	374.8
eelpout	179	88	factor(*inc.nr*)	4	107.3
			factor(*sex*)	1	8.0
			temp.sum3	1	8.1

[1] Growth window parameters not available for mullet.

length-based indicators, there is also a goal to reduce human-induced eutrophication levels (descriptor 5 in the GES). Potentially, a growth reduction due to de-eutrophication can end up in a conflict between these two goals.

For commercially harvested species, the European Common Fisheries Policy sets rules for conserving fish stocks, including regulations on minimum landing size. In our set of four species only thick-lipped mullet is commercially harvested, but shifts in growth patterns are also apparent in other commercial species (e.g. Vieira et al. (2020)). Changes in growth may undermine the effectiveness of harvesting rules (Brown et al., 2012).

Other European management strategies relevant for the Wadden Sea, such as the Water Framework Directive and the Habitats Directive, implement only limited fish indicators, none of which are based on fish length.

Ethics

This study was performed in accordance with Dutch law on animal experiments. Otolith collections during recent years were conducted under approval of the Centrale Commissie Dierproeven (approval numbers AVD4010020171304 and AVD8020020174165).

Data availability

Data will be made available on request.

CRediT authorship contribution statement

Loes J. Bolle: Conceptualization, Methodology, Validation, Data curation, Formal analysis, Writing – original draft, Project administration. **Ruben Hoek:** Methodology, Investigation. **Ineke Pennock:** Methodology, Investigation. **Suzanne S.H. Poiesz:** Investigation, Writing – review & editing. **Justus E.E. van Beusekom:** Investigation, Writing – review & editing. **Henk W. van der Veer:** Conceptualization, Writing – review & editing. **Johannes IJ. Witte:** Investigation. **Ingrid Tulp:** Conceptualization, Formal analysis, Writing – original draft, Visualization, Project administration, Funding acquisition.

Declaration of competing interest

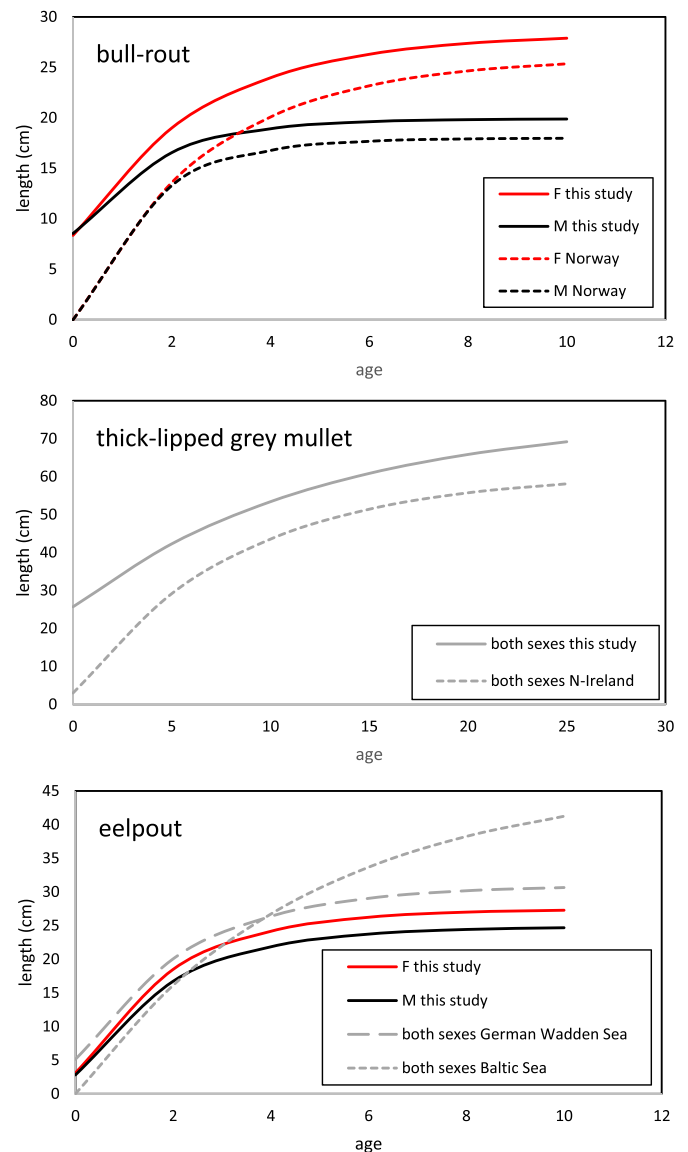The authors declare that they have no known competing financial

Fig. 8. Comparison of von Bertalanffy growth parameters with the literature (Luksenburg and Pedersen, 2002; Richter, 1995; Ulleweit, 1995; Ulleweit et al., 1998).

interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2021.105364.

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