REVIEW

Changes in functioning of the largest coastal North Sea flatfish nursery, the Wadden Sea, over the past half century

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ABSTRACT: The international Wadden Sea is an important flatfish nursery. Information from the Dutch Wadden Sea indicates that the flatfish nursery function of the area has been affected during the last decades. Increased seawater temperature has affected settling, habitat suitability for and growth performance of the various flatfish species. Settling of plaice, flounder and to a lesser extent sole larvae occurs earlier nowadays. In the 1960s, 0-, I-, II- and III-group plaice were present, but since 2000, II-group has disappeared and densities of I-group have decreased. For juvenile flounder, II-group almost disappeared, and for dab, a decline in densities of all age groups was observed from the 1990s onwards. Summer temperatures exceed the optimum for the cold-water species (plaice, flounder and dab) with increasing frequency, level and duration. Only for 0-group sole, the period with optimal growth conditions has become longer and has resulted in increased growth. Mortality rates in 0-group plaice have increased, coinciding with an increase in water temperatures and an increase in the abundance of predators. The decrease in density of juvenile plaice and dab in the Wadden Sea has not affected recruitment to North Sea stocks, suggesting that other areas have taken over part of the nursery function. The predicted increase in seawater temperature in the next decades will continue to improve the conditions for sole. The temperature tolerance of plaice and dab and to a lesser extent flounder will further reduce their scope for growth and may ultimately result in their disappearance from the Wadden Sea.

KEY WORDS: Wadden Sea · Nursery function · Juvenile flatfish · Long-term trends · Climate change · Species composition · Growth · Mortality

1. INTRODUCTION

The temperate North Sea harbours an important and abundant group of flatfish species, each of which is characterised by a specific life cycle, habitat requirements and distribution (Heessen et al. 2015). The juvenile stages of a number of these species, such as plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, sole *Solea solea*, brill *Scophthalmus rhombus*, turbot *Scophthalmus maximus* and to

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a lesser extent dab *Limanda limanda*, concentrate in relatively shallow coastal nursery areas around the North Sea. The international Wadden Sea and its coastal zone (water depth <10 m), bordering the western coast of Denmark and the northern coasts of Germany and The Netherlands, has historically been the largest juvenile flatfish nursery in the North Sea (Zijlstra 1972, van Beek et al. 1989).

The use of coastal areas as nursery grounds was already observed during the first investigations in Danish (Petersen 1895, Johansen 1913) and Dutch waters (Redeke 1905). The first quantitative inventory in the western Dutch Wadden Sea in 1961–1964 (Creutzberg & Fonds 1971) found numerous juvenile plaice, flounder, sole and dab in the subtidal and deeper parts (Fonds 1983). Both the annual Demersal Fish Survey (DFS) carried out from the early 1970s onwards (Zijlstra 1972) and the bycatch data of the shrimp *Crangon crangon* fishery confirmed these observations. An analysis of the first decades of the annual DFS concluded that the Wadden Sea was an important nursery area for plaice and sole contributing substantially to annual recruitment and that abundance indices of 0-group plaice and I-group sole were correlated with recruitment rates to the North Sea fishery stocks (Rauck & Zijlstra 1978, van Beek et al. 1989).

Worldwide, coastal ecosystems are critical transition zones between freshwater and marine environments (Beck et al. 2001, Levin et al. 2001). For centuries, such areas have suffered from anthropogenic disturbance including fisheries, port activities, eutrophication and land reclamation. Such activities have caused major structural and functional changes (Jackson et al. 2001, Lotze 2005, Lotze et al. 2006). The Wadden Sea has also experienced major ecosystem changes (for an overview, see Kloepper et al. 2017).

In the western Dutch Wadden Sea, sea surface temperature (SST) measurements from 1947 onwards show that annual means varied around 10°C until 1982, but thereafter increased to about 12°C in recent years. This increase occurred for all seasons at an average rate of about 1°C per 20–25 yr (van Aken 2008a, Royal Netherlands Institute for Sea Research [NIOZ] unpubl.). Increases in SST are not restricted to the Wadden Sea and occur in the whole Dutch coastal zone (van Aken 2010). In the 1980s, eutrophication doubled the nutrient concentrations in the western Dutch Wadden Sea (van der Veer et al. 1989, van Raaphorst & de Jonge 2004), resulting in a period of increased chlorophyll concentrations and primary production (Philippart et al. 2007). Since the 1990s,

annual planktonic primary production has decreased and recently stabilized (Jacobs et al. 2020). The increased chlorophyll concentrations and planktonic primary production resulted in a doubling of the macrozoobenthic biomass in the intertidal areas (Beukema & Dekker 2020). During the subsequent period of de-eutrophication, reduced primary production did not cause a decrease in macrozoobenthic biomass (Beukema & Dekker 2020).

Predation pressure by top predators has also increased strongly since the 1990s as a result of an increased abundance of cormorants *Phalacrocorax carbo*, harbour seals *Phoca vitulina* and grey seals *Halichoerus grypus* (for references see van der Veer et al. 2015a). Commercial shrimp fisheries, an important source of bycatch-induced fish mortality in the Wadden Sea, also increased strongly during the last decades (van der Hammen et al. 2015, van der Veer et al. 2015a). In the western part of the Wadden Sea, catches of both pelagic and demersal fish showed a 10-fold decrease from the late 1970s before stabilizing in the late 1990s (Tulp et al. 2008, van der Veer et al. 2015a). Densities of scavengers and benthic predators such as shore crabs increased strongly since the early 2000s (Tulp et al. 2012), simultaneously with the recovery of mussel beds (van der Meer et al. 2019).

The combined impact of these major changes in the Wadden Sea ecosystem on the flatfish nursery function is unclear. For the flatfish nursery function of the Wadden Sea, 2 aspects are important: (1) the local hydrodynamic and morphodynamic conditions in the coastal zone and tidal inlets that provide connectivity for the drifting pelagic larval stage in the North Sea with the areas in the Wadden Sea used by the subsequent juvenile life stage, and (2) the provision of essential demersal habitats for juveniles which ultimately contribute to the recruitment to the North Sea fish stocks. The connectivity between larval habitat in the North Sea and demersal habitat for juveniles in the coastal area has been described by van der Veer et al. (1998), Bolle et al. (2009), Hufnagl et al. (2013) and Tiessen et al. (2014).

This paper addresses the importance of the Wadden Sea in providing essential demersal habitat for juveniles and its contribution to recruitment to the North Sea fish stocks. The focus is on the boreal (cold-water) species plaice, flounder and dab and on the Lusitanian (warm-water) species sole (Fonds 1983). First, the species-specific physiological performance of the various flatfish species is described. Next, based on the changes in the Wadden Sea over the last 50 yr, expectations on the impact on the flatfish nursery functioning of the area are formulated

and reviewed. This paper focusses on the western part of the Wadden Sea, is based on both published and unpublished data and elaborates on previous studies presenting aspects of the flatfish nursery function of the Wadden Sea (van der Veer & Bergman 1987a, Bergman et al. 1988, Lozán et al. 1994).

2. FLATFISH PHYSIOLOGICAL PERFORMANCE

Poikilothermic marine organisms are affected differently by physical factors, depending on their species-specific physiological preferences and tolerance (for an overview, see Willmer et al. 2000). Within the full range of physical factors, water temperature is the controlling factor regulating and dictating metabolism; salinity is a masking factor loading metabolism and thereby creating sub-optimal conditions; and oxygen conditions are a limiting factor constraining maximum possible metabolic scope (Fry 1971, Neill et al. 1994).

The Wadden Sea is a dynamic area with abiotic conditions varying spatially and temporally at a scale ranging from, respectively, tidal gully to tidal basin and tide to year (e.g. van Aken 2008a,b). In the Wadden Sea, water temperature is among the most important factors controlling and regulating metabolism and hence growth (e.g. see Fonds et al. 1992). At present, profound salinity gradients occur only in the few remaining open estuarine basins, the Ems Dol-

lard and the Elbe. Oxygen deficiencies including sediment black spots occurred in the 1990s especially in the German part of the Wadden Sea (Neira & Rackemann 1996, Böttcher et al. 1998), but during the last decades, this phenomenon has not been reported.

For many flatfish species and life stages, basic information about the effect of various factors on metabolism is scarce, and most available information deals with the impact of temperature as a controlling factor. Some experimental studies addressed the effect of temperature in combination with salinity as a masking factor (Fonds et al. 1992, Augley et al. 2008), or in combination with oxygen as a limiting factor (Pörtner & Knust 2007). The sensitivity for environmental factors is often species- and size-specific with a well-defined tolerance range. From the juvenile stage onwards, flatfish may also be able to avoid unfavourable masking and limiting conditions in the field by active migration.

Thermal tolerance ranges are determined by the combined impact of the rate-enhancing influence of temperature on enzyme function ultimately reflected in growth and the increasing destructive effects, especially structural damage (Willmer et al. 2000). As a consequence, physiological performance (such as growth) increases with temperature until a maximum rate is reached (at the optimum temperature), followed by an abrupt decrease to zero. Within the tolerance range, a temperature preference range can be defined where growth rates exceed a certain minimum (Fig. 1). Temperature tolerance and optimum are often determined under experimental laboratory conditions.

Experimental data indicate that the temperature tolerance of plaice eggs and larvae ranges from 2°C to at least an optimal temperature of 10°C (Ryland et al. 1975), similar to that for flounder larvae (Hiddink 1997). For dab, no experimental data are available, but in the North Sea, developing larvae were found within a temperature range of 4 to 10°C (Malzahn et al. 2007). For sole eggs and larvae, the temperature tolerance ranges from 10°C to at least 19 and 22°C, respectively (Fonds 1979). For all species, the upper temperature tolerance limits of the eggs and larvae are unclear. For juvenile flatfish, more detailed information is available (Fig. 2). 0-group sole has the largest temperature tolerance
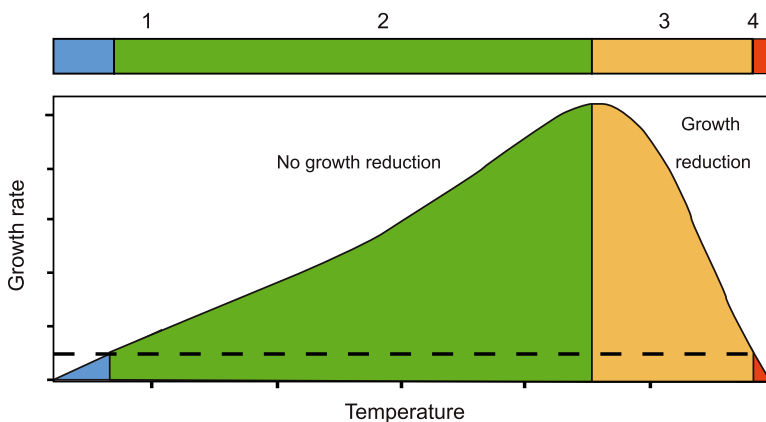

Fig. 1. Flatfish thermal tolerance range. Dashed line indicates selected minimum growth rate (here 10% of the maximum growth rate). Blue: lower temperature range with growth rates <10% of the maximum growth rate at the optimal temperature; green: range of temperatures with increasing growth rates until maximum growth at the optimal temperature; orange: range of temperatures above optimal temperature with decreasing growth rates until 10% of the maximum growth rate; red: temperatures above which growth becomes <10% of the maximum growth. The green and orange area define the preference range within the tolerance range

Fig. 2. Thermal tolerance range for 0-group sole, flounder, dab and plaice. Temperature tolerance range (combined blue, green, orange and red bar), optimal temperature (maximum of green bar), and temperature preference range (green + orange bar) for various flatfish species and age groups. Temperature preference range is defined as the temperature range with growth rates >10% of maximum rate at optimal temperature (see Fig. 1 for more detail). For references, see Section 2. Data from Freitas et al. (2010)
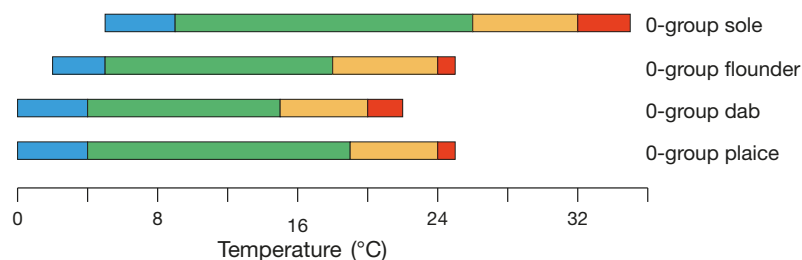
range including the highest temperatures (4–35°C) (Lefrançois & Claireaux 2003); 0-group dab has the narrowest and lowest range (0–22°C) (Fonds & Rijnsdorp 1988); 0-group plaice (0–25°C) and flounder (2–25°C) are intermediate in extent and level of temperature tolerance (Fonds et al. 1992). The optimum temperature varies from 15°C in juvenile dab, 18°C in juvenile flounder, 19°C in juvenile plaice to 26°C in juvenile sole (Fig. 2). Overall, flatfish eggs and larvae have narrower temperature tolerance ranges than juveniles (see also Dahlke et al. 2020).

3. WADDEN SEA ECOSYSTEM CHANGES AND EXPECTED IMPACT ON FLATFISH NURSERY FUNCTIONING

Based on the observed changes in the Wadden Sea ecosystem, expectations about potential impacts on the flatfish nursery function of the area are formulated. With respect to the effect of climate change, we build on the study of climate effects on fish populations by Rijnsdorp et al. (2009).

3.1. Expectation 1: Coastal warming advances larval flatfish immigration

Egg development rates are species-specific and are determined by a variety of factors including in particular seawater temperature. Egg development rates are inversely related to seawater temperature (e.g. Pauly & Pullin 1988). Larval stage duration is also inversely related to seawater temperature (e.g. Bolle et al. 2009). From hatching onwards, feeding starts and larval stage duration also depends on food abundance, whereby food limitation increases development time. Consequently, larval development depends on the interplay between temperature and food conditions. Field studies of drifting plaice larvae in the Southern Bight of the North Sea observed an inverse relationship between larval stage duration and seawater temperature, albeit less strong than

expected based on experimental data (van der Veer et al. 2009). Warming of the Dutch coastal zone is expected to accelerate egg and larval development and to advance the timing of flatfish immigration in spring.

3.2. Expectation 2: Effect of increased seawater temperature on spatial distribution and growth potential is species-specific

Temperature preference and tolerance differ between flatfish species, with ranges varying from 20°C for dab to 30°C for sole (Fig. 2). Temperature optima also differ, from 15°C for juvenile dab, 18°C for juvenile flounder, 19°C for juvenile plaice to 26°C for juvenile sole (Fig. 2). In the western Dutch Wadden Sea, mean summer seawater temperatures in the Marsdiep tidal inlet already exceeded the optimum temperature for the 0-group dab in the late 1940s (Fig. 3). For the 0-group flounder and plaice, mean summer temperatures are still within their respective tolerance ranges but have reached or even exceeded their optimum temperature in the last decades. For 0-group sole, mean summer seawater temperatures are still below their optimum temperature. Shallower waters, such as intertidal areas, will warm up even more and will experience even larger fluctuations and maximum water temperatures (van der Veer & Bergman 1986, Frölicher & Laufkötter 2018). For cold-water species, the water temperature in the Wadden Sea increasingly exceeds their temperature optimum and preference.

3.3. Expectation 3: Increased top predator abundance and fisheries have increased flatfish mortality

Juvenile flatfish are prey to a wide range of predators such as larger fish, seals and piscivorous birds. Various fish species in the Wadden Sea (including flatfish) consume juveniles, both in the intertidal and
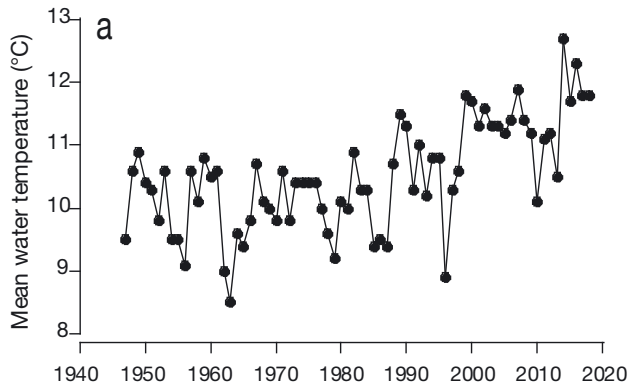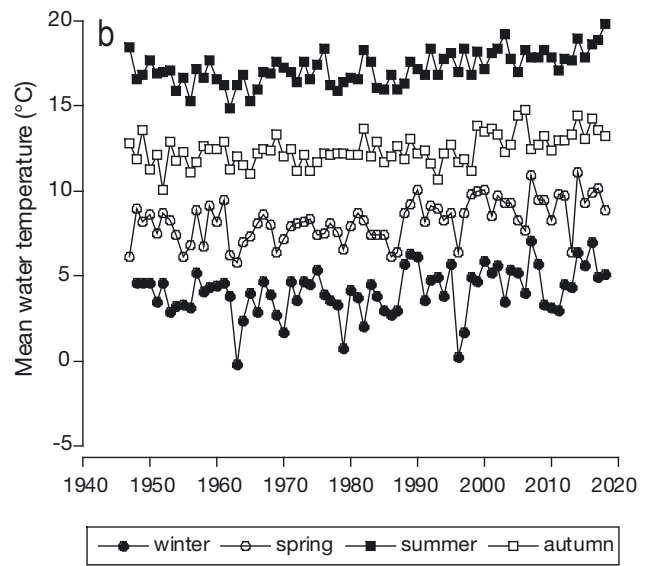
Fig. 3. Water temperature in the Marsdiep inlet at the Royal Netherlands Institute for Sea Research (NIOZ) jetty (1.5 m below surface) for the period 1947–2020. (a) Mean annual water temperature. (b) Mean winter (December–February), spring (March–May), summer (June–August) and autumn (September–November) water temperature. Data from NIOZ (van Aken 2008a, S. van Leeuwen unpubl.)

in the subtidal (Fig. 4). Seals in the Wadden Sea feed predominantly on juvenile flatfish, resulting in substantial mortality (Aarts et al. 2019). Cormorants are important fish-eating birds in the Wadden Sea, and flatfish comprise a large part of their diet. Based on otoliths in regurgitated pellets, the average contribution of flatfish in the diet was estimated at 73% in numbers and 79% in mass (Leopold et al. 1998). Bycatch mortality from shrimp fisheries is also substantial (Glorius et al. 2015). The increase in populations of seals (since the 1990s) and fish-eating birds (since the 1970s), as well as bycatch mortality (since the 1970s) will have increased flatfish mortality in the area.
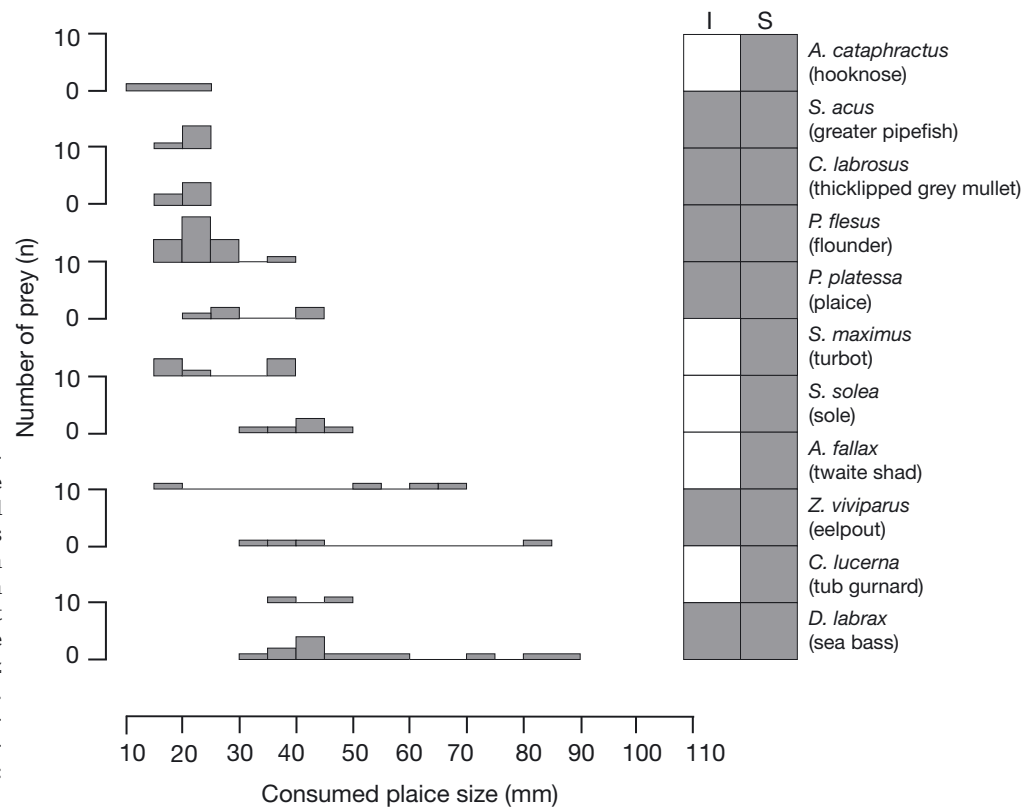

Fig. 4. Size-frequency distribution of 0-group plaice consumed in the intertidal and the subtidal by various fish species in the western Dutch Wadden Sea. Data based on stomach content analysis of NIOZ fyke catches 2011–2018 (Poiesz et al. 2020, NIOZ unpubl). Indicated is predator distribution: I: intertidal; S: subtidal. Grey: present; white: absent

3.4. Expectation 4: Year-class strength of cold-water species will decrease in response to increased seawater temperatures offshore

Year-class strength and ultimate recruitment in fish are primarily determined by mortality processes operating during the pre-juvenile stage of the life history (Leggett & DeBlois 1994), and flatfish are no exception (Brander & Houghton 1982, van der Veer et al. 2015b). Interannual variability in year-class strength is generated during the pelagic egg and larval stage, probably by variations in the hydrodynamic circulation (Bolle et al. 2009) and in mortality rates of eggs and larvae (Harding et al. 1978, van der Veer et al. 2000a). For most species, the underlying mechanisms are unclear. Settling plaice larvae in the western Wadden Sea originate mainly from the spawning location in the Southern Bight of the North Sea (Talbot 1977, Bolle et al. 2009), and year-class strength is inversely related to seawater temperature during egg and larval development (Brander & Houghton 1982, van der Veer 1986, Fox et al. 2000). Year-class strength of plaice may therefore decrease in response to the increase in seawater temperature in the coastal zone (van Aken 2010), and this may also hold for other cold-water species.

4. CHANGES IN WADDEN SEA NURSERY FUNCTIONING

4.1. Expectation 1: Coastal warming advances larval flatfish immigration

Recent information about larval supply to the Wadden Sea is not available; however, the patterns in abundance of settling and just-settled flatfishes provide an indication of both timing and abundance of larval supply (van der Veer 1986). Such data are available for the Balgzand intertidal area located in the western Wadden Sea for plaice, flounder and sole from 1979 to 2019 with less frequent observations in recent years.

Larval immigration at Balgzand, as indicated by the time of maximum (= peak) abundance, starts with plaice, followed by flounder and finally by sole (Fig. 5). In the 1980s, peak abundance of plaice occurred at the end of April, followed by flounder at the end of May and sole at the end of June. Over time, peak abundance for plaice and flounder has shifted and in recent years occurred about 1 mo earlier for plaice and 1.5 mo earlier for flounder. For sole, a similar shift occurred before 2000, but the time of peak abundance has been stable since then. The data are in line with the expectation that the recent warming of the Dutch coastal zone has advanced larval flatfish immigration in spring, especially of the cold-water species.

4.2. Expectation 2: Effect of increased seawater temperature on spatial distribution and growth potential is species-specific

4.2.1. Spatial distribution

Settling flatfish larvae have species-specific habitat and sediment preferences (Gibson & Robb 2000). Newly settled flatfish larvae have been observed in most of the Wadden Sea habitats, especially in intertidal and subtidal areas (Kuipers 1977, Zijlstra et al. 1982, van der Veer & Witte 1993, Freitas et al. 2016). Plaice larvae settle on a wide range of sediment types in intertidal and subtidal areas between March and mid-May (Kuipers 1977, Zijlstra et al. 1982, van der Veer & Witte 1993, Jager et al. 1995). Flounder larvae settle in relatively muddy areas at low salinities, or in fresh water in rivers or canals (Berghahn 1984, van der Veer et al. 1991, Jager et al. 1995). Settlement of sole larvae occurs more widely in coastal areas, and within the Wadden Sea mainly in sandy and muddy habitats (Rijnsdorp et al. 1992), with a preference for finer sediments (Post et al. 2017). Dab larvae settle mainly in coastal waters in the North Sea, and the size range of 0-group dab observed within the Wadden Sea indicates that they migrate into the Wadden Sea after settlement (Bolle et al. 1994). This means that habitat use within the Wadden Sea differs among species, with juvenile plaice and flounder using both intertidal and subtidal areas, and sole and dab concentrating mainly in subtidal areas.

Juvenile flatfish spatial distribution patterns have changed over time. Until the 1990s, various age groups of plaice and flounder could be found in intertidal areas (van der Veer et al. 2011). Subsequently, the densities of I- and II-group plaice in intertidal areas decreased, and from 2000 onwards only 0-group was observed. A similar pattern, though less pronounced, was observed for juvenile flounder in the intertidal areas (van der Veer et al. 2011). Simultaneously with the strong decreases in I- and II-group plaice in intertidal areas, increased numbers were observed in subtidal areas and tidal channels (Freitas et al. 2016) and also in deeper waters outside the Wadden Sea (van Keeken et al. 2007). Inside the
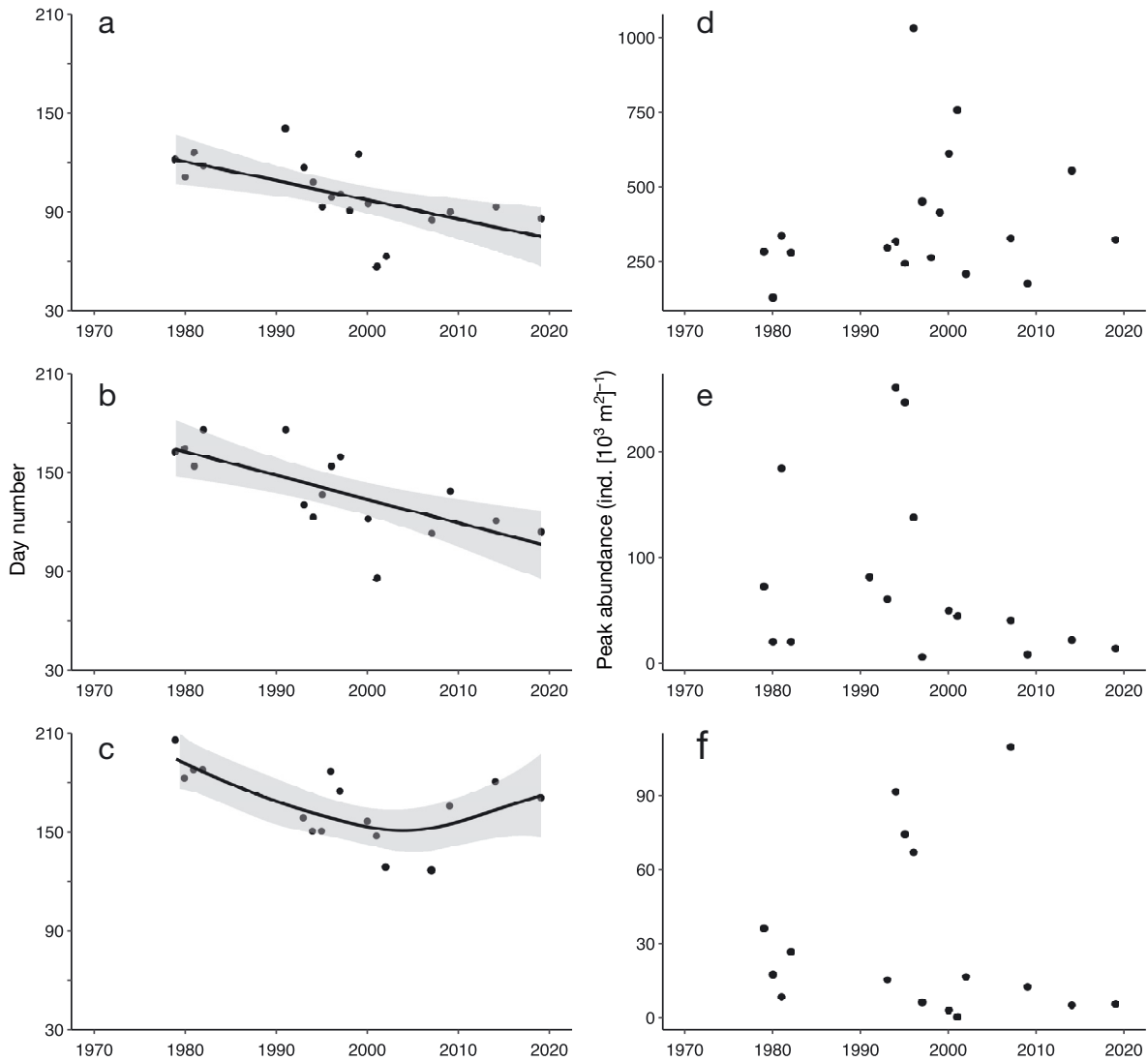
Fig. 5. Immigrating flatfish (plaice *Pleuronectes platessa*, flounder *Platichthys flesus* and sole *Solea solea*) larvae (just-settled individuals ≤15 mm) at Balgzand as a proxy for larval immigration. Interannual pattern in time of peak abundance of just-settled 0-group (a) plaice, (b) flounder and (c) sole in spring. Generalized additive model (GAM) with 95% confidence interval; plaice $R^2_{adj} = 0.34$; $p < 0.05$; flounder $R^2_{adj} = 0.43$; $p < 0.05$; sole $R^2_{adj} = 0.49$; $p < 0.05$. Pattern in year-class strength of (d) plaice, (e) flounder and (f) sole, as indicated by peak density during settlement. Data from the compilation in Jung et al. (2017) and H. van der Veer & J. Witte (unpubl.) For more information, see van der Veer (1986) and Section 4.1

Wadden Sea, settlement of 0-group plaice still occurs in intertidal areas, but they move quickly to deeper subtidal areas and tidal channels (Freitas et al. 2016). It is not clear whether a similar shift in distribution to deeper waters has also occurred for flounder and sole (van der Veer et al. 1991, 2001).

The age composition of juvenile flatfish in the Dutch Wadden Sea has also changed over time. In the 1960s, 0-, I-, II- and III-group plaice were observed (Fonds 1983). In the early 1980s, III-group disappeared from the Wadden Sea. From the mid-1980s onwards, densities of I- and II-group plaice also decreased (van der Veer et al. 2011; Fig. 6). Since 2000, II-group has disappeared and densities of I-group have been low (Fig. 6). For dab, a decline in all age groups was observed from the 1990s onwards (Tulp et al. 2008; Fig. 6). For flounder, the time series is shorter and does not reveal any clear change in the past 15 yr. For sole, a decrease in the density of I-group occurred since the 1990s, but the pattern is less clear than for plaice and dab (Fig. 6).

The changes in juvenile flatfish distribution patterns and age composition in the Wadden Sea are species-specific, and in line with the expectation.
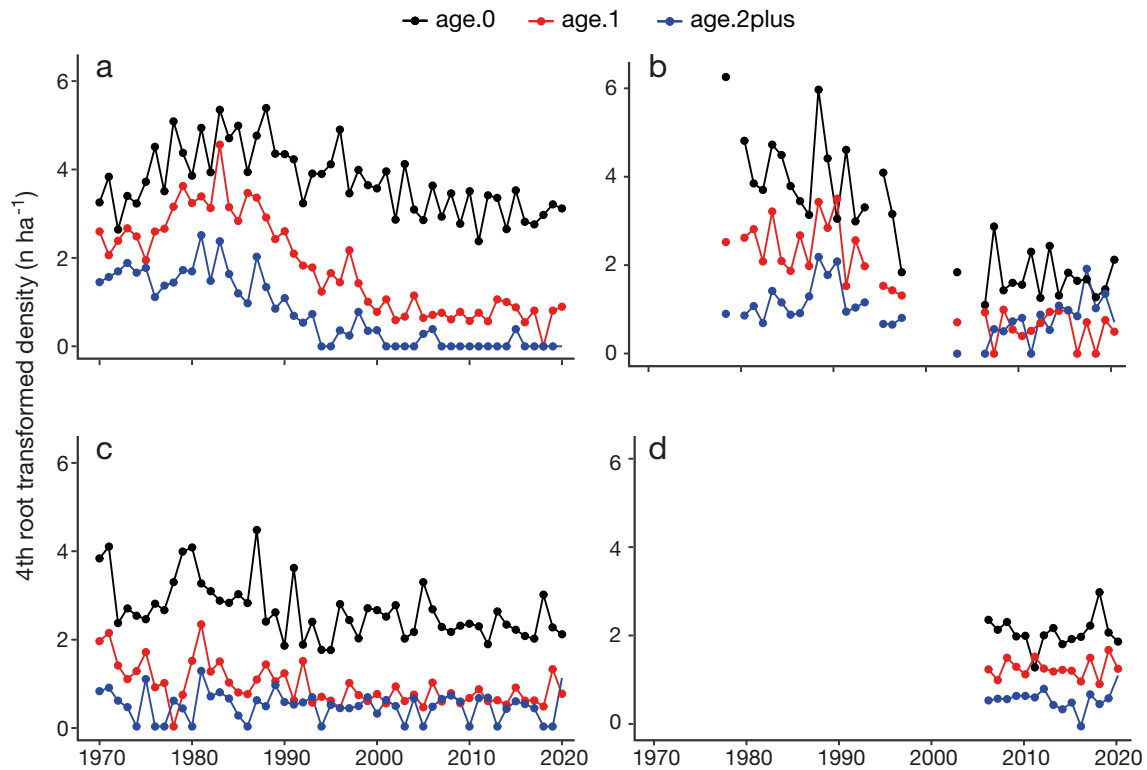
Fig. 6. Mean catch (fourth root transformed density of different age groups of juvenile (a) plaice, (b) dab, (c) sole and (d) flounder in the Demersal Fish Survey in the subtidal areas of the Dutch Wadden Sea in autumn. Data: Wageningen Marine Research (unpubl.). Missing years for dab and flounder are due to missing age data

The disappearance of the cold-water species with their low temperature preference and tolerance suggests a relationship with the increased seawater temperatures in the Wadden Sea.

4.2.2. Growth

The species-specific temperature preference and tolerance ranges (see Fig. 1 for explanation) can be applied to the temperature conditions in the Wadden Sea to determine the seasonal growth windows for the various species. Daily seawater temperature measurements from the NIOZ jetty in the Marsdiep tidal inlet in the western Wadden Sea are available from 1982 onwards, and were reconstructed for the period 1956–1982. Specifically, SST data were taken from 2 stations in the western Dutch Wadden Sea: the NIOZ jetty and Breezanddijk. Daily SST measurements were available from 1957 to 1989 for Breezanddijk (https://waterinfo.rws.nl) and from 1982 to present for the NIOZ jetty (NIOZ unpubl.). Data for the period 1982–1989 were used to determine the linear relationship between daily SST at Breezanddijk and daily SST at the NIOZ jetty:

$SST_{Marsdiep} = 0.91 \times SST_{Breezanddijk} + 1.47$ ($R^2 = 0.96$; p < 0.001). This relationship was used to reconstruct daily SST for the period 1956–1982 for the NIOZ jetty.

Classification of daily water temperatures for preference and tolerance of the 0-groups of the various flatfish species during the growing season (1 April to 30 September) shows that in spring the temperatures are within the tolerance limits of all flatfish species, and do not restrict growth in any year (Fig. 7a). In summer, the number of days with temperatures within the respective preference ranges and below the optimum temperatures (green in Fig. 7) decreased for 0-group plaice and dab, especially in the last decades. For 0-group flounder, there was no trend. For 0-group sole, a warm-water species, temperatures were at the low end of the preference range in spring and autumn (blue), and below the optimum in summer (green).

For 0-group plaice and flounder, water temperatures during the growing season remain within their respective tolerance ranges, but they exceed the optimum during parts of the summer. For 0-group dab, water temperatures in summer exceed the tolerance range (red). The growth conditions during the growing season improved over the years for 0-group
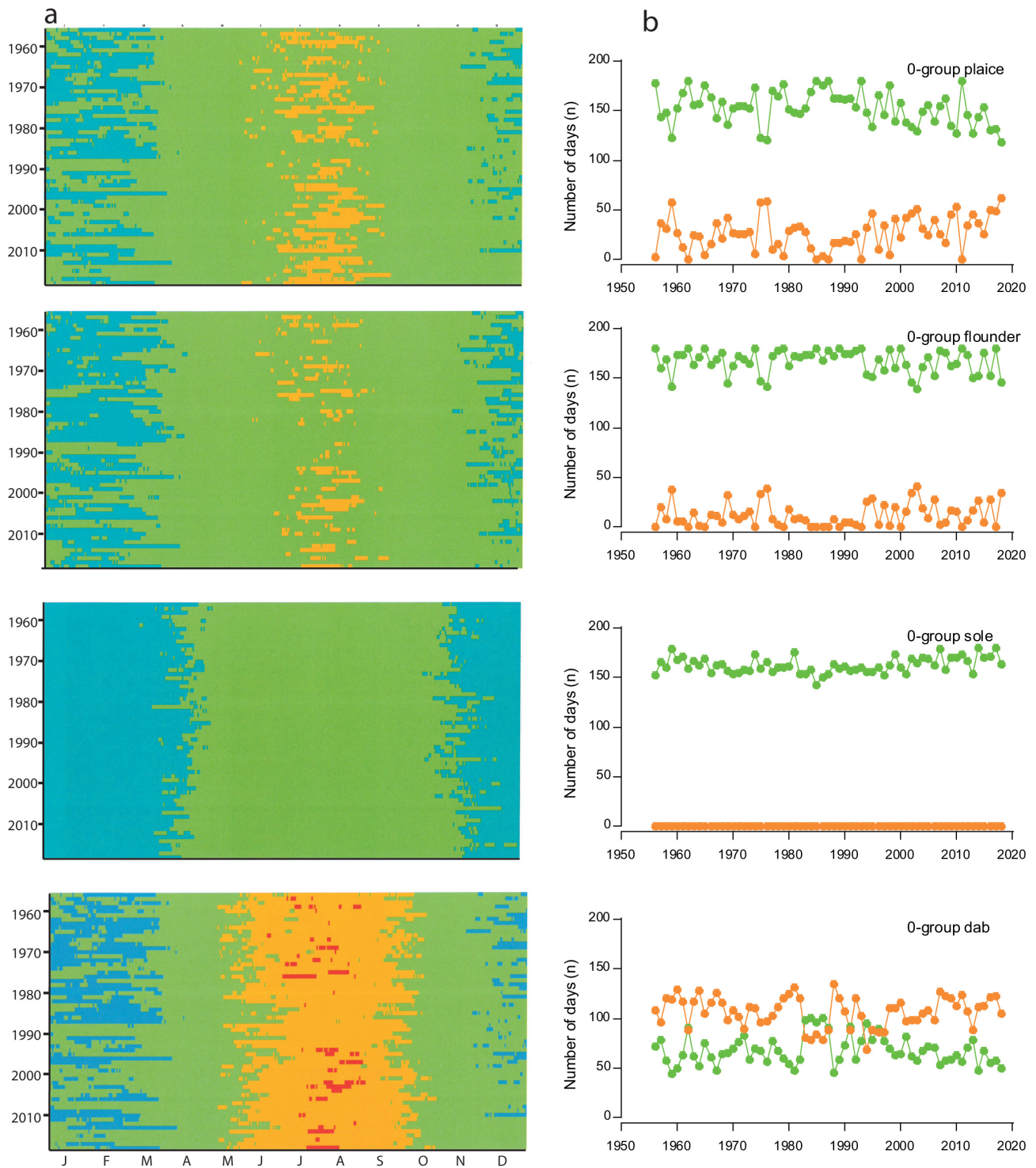
Fig. 7. Classification of daily water temperature conditions for 0-group flatfish growth in the western Wadden Sea between 1956 and 2018, based on daily water temperature measurements in the Marsdiep. (a) Daily classification according to species-specific tolerance range from 1956 to 2018 for the 4 species. Blue: low temperatures less than 10% maximum growth; green: growth rates >10% maximum growth until maximum growth at the optimal temperature; orange: growth range of temperatures above optimal temperature until 10% maximum growth; red: high temperatures <10% maximum growth. (b) Number of green and orange days during the growing season (1 April to 30 September) for the 4 species. For more explanation, see Fig. 1

Table 1. Maximum densities, mortality rates of 0-group flatfish for various Wadden Sea nursery areas and years — Nordstrander Bay, Germany (54° 28′ N, 8° 47′ E); Dollard, The Netherlands (53° 17′ N, 7° 07′ E); Balgzand, The Netherlands (52° 54′ N, 4° 91′ E). t_{max}: time (d) of maximum observed density from 1 January; D_{max}: maximum observed density; M: mean daily instantaneous mortality rate based on the slope of the regression of densities over time; M_t: total stage mortality (M × number of days from peak numbers until 30 September). For more information, see Beverton & Iles (1992). Empty cells: years with insufficient data

Location	Year	t_{max}	D_{max} (ind. $[10^3\,m^2]^{-1}$)	M (d^{-1})	Days until 30 Sept	M_t	Reference
0-group plaice							
Nordstrander	1981	145	70	0.002	125	0.250	Berghahn (1986) in: Iles & Beverton (1991)
Bay	1982	154	105	0.013	116	1.508	Berghahn (1986) in: Iles & Beverton (1991)
	Mean	150	88	0.008		0.879	
Dollard	1992	113	46	0.011	157	1.727	Jager et al. (1995)
	Mean	113	46	0.011		1.727	
Balgzand	1973	129	500	0.010	141	1.410	Kuipers (1977) in: Iles & Beverton (1991)
	1975	122	137		148		Zijlstra et al. (1982) in: Iles & Beverton (1991)
	1976	126	191	0.009	144	1.296	Zijlstra et al. (1982) in: Iles & Beverton (1991)
	1977	88	202	0.007	182	1.274	Zijlstra et al. (1982) in: Iles & Beverton (1991)
	1978	129	519	0.009	141	1.269	Zijlstra et al. (1982) in: Iles & Beverton (1991)
	1979	121	320	0.008	149	1.192	Zijlstra et al. (1982) in: Iles & Beverton (1991)
	1980	113	164		157		van der Veer (1986) in: Iles & Beverton (1991)
	1981	126	360	0.025	144	3.600	van der Veer (1986) in: Iles & Beverton (1991)
	1982	118	297	0.014	152	2.128	van der Veer (1986) in: Iles & Beverton (1991)
	1993	117	370	0.034	153	5.202	van der Veer et al. (2000b)
	1994	108	375	0.030	162	4.860	van der Veer et al. (2000b)
	1995	94	244	0.029	176	5.104	van der Veer et al. (2000b)
	1996	98	1282	0.021	172	3.612	van der Veer et al. (2000b)
	1997	100	453	0.031	170	5.270	van der Veer et al. (2000b)
	1998	91	262	0.026	179	4.654	van der Veer et al. (2000b)
	1999	83	312	0.022	187	4.114	van der Veer et al. (2000b)
	2000	94	674				H. van der Veer & J. Witte (unpubl.)
	2001	125	760				H. van der Veer & J. Witte (unpubl.)
	2002	63	324				H. van der Veer & J. Witte (unpubl.)
	2007	85	379				H. van der Veer & J. Witte (unpubl.)
	2009	90	216				H. van der Veer & J. Witte (unpubl.)
	2014	93	582				H. van der Veer & J. Witte (unpubl.)
	2019	87	379				H. van der Veer & J. Witte (unpubl.)
	Mean	104	404	0.020	166	3.213	
0-group flounder							
Balgzand	1979	162	89	0.023	108	2.484	van der Veer et al. (1991)
	1980	163	28	0.071	107	7.597	van der Veer et al. (1991)
	1981	153	227	0.089	117	10.413	van der Veer et al. (1991)
	1982	158	23	0.043	112	4.816	van der Veer et al. (1991)
	1993	130	88	0.034	140	4.760	H. van der Veer & J. Witte (unpubl.)
	1994	122	305	0.050	148	7.400	H. van der Veer & J. Witte (unpubl.)
	1995	136	399	0.050	134	6.700	H. van der Veer & J. Witte (unpubl.)
	1996	153	229	0.054	117	6.318	H. van der Veer & J. Witte (unpubl.)
	1997	146	9	0.039	124	4.836	H. van der Veer & J. Witte (unpubl.)
	1998						
	1999						
	2000	122	80	0.055	148	8.140	H. van der Veer & J. Witte (unpubl.)
	2001	157	51	0.022	113	2.486	H. van der Veer & J. Witte (unpubl.)
	2002						
	2007	113	51	0.035	157	5.495	H. van der Veer & J. Witte (unpubl.)
	2009	139	13	0.006	131	0.786	H. van der Veer & J. Witte (unpubl.)
	2014	121	36	0.016	149	2.384	H. van der Veer & J. Witte (unpubl.)
	Mean	141	116	0.042	129	5.330	
Dollard	1992	168	26	0.028	102	2.856	Jager et al. (1995)
	Mean	168	26	0.028		2.856	
0-group sole							
Dollard	1992	224	4	0.011	46	0.506	Jager et al. (1995)
	Mean	224	4	0.011		0.506	

sole (more days marked in green) (Fig. 7b). In conclusion, the growth window in the western Wadden Sea is becoming increasingly unfavourable especially in summer for 0-group dab, plaice and flounder, but not for sole.

Based on an annual autumn survey (DFS) in Dutch, German and Danish coastal waters, Teal et al. (2008) did not find a clear trend in the mean size at the end of the growing season for 0-group plaice, whereas for 0-group sole, the mean size increased since the 1980s, coinciding with the increase in seawater temperature. Therefore, the effect of increased seawater temperatures in the Wadden Sea on growth appears to be species-specific and depends on physiological preference, in agreement with the expectation.

4.3. Expectation 3: Increased top predator abundance and fisheries have increased flatfish mortality

Mortality can be calculated from changes in densities over time when immigration and emigration can be determined or excluded. Mortality is often expressed as an instantaneous daily mortality rate calculated from the slope of a linear regression through log-transformed observed local densities over time (Beverton & Iles 1992).

Mortality estimates of 0-group flatfish species in the Wadden Sea are available for only a few semi-closed populations: for 0-group plaice (Zijlstra et al. 1982, van der Veer 1986, van der Veer et al. 2000b) and flounder (van der Veer et al. 1991) in the Dutch Wadden Sea in the Balgzand intertidal and for 0-group plaice, flounder and sole in the Dollard (Jager et al. 1995). For the North Frisian German Wadden Sea, mortality estimates are available for a 0-group plaice population in a mixed intertidal and subtidal setting (Berghahn 1986); however, these estimates also include shrimp fishery bycatch mortality in the subtidal area.

Comparison of mortality rates from the various intertidal areas and species showed a range from 0.002 to 0.034 d^{-1}, including interannual variability within and among species and areas (Table 1). The largest amount of information is available for the Balgzand intertidal area, where the mortality rate increased for 0-group plaice between 1973 and 1999 (Fig. 8a). Furthermore, the increase in instantaneous
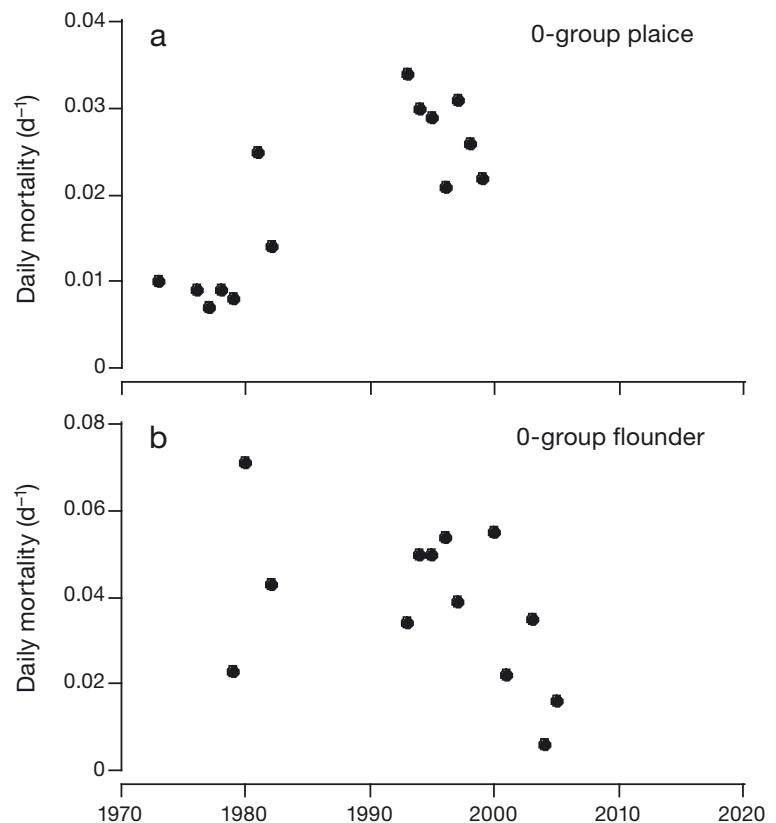

Fig. 8. Average daily instantaneous mortality among 0-group (a) plaice and (b) flounder at the Balgzand intertidal. Note the differences in the *y*-axis scales between the 2 species. For more information, see Section 4.3 and Table 1

daily mortality rate of 0-group plaice correlated with the increase in mean seawater temperature in the Marsdiep in spring (Table 2), which suggests that part of the increased mortality might be due to increased seawater temperature conditions. Mortality estimates could not be made for the last 2 decades because of their earlier migration to deeper waters.

For 0-group flounder, instantaneous daily mortality rates at the Balgzand intertidal area did not change in time. On average, instantaneous daily mortality rates of 0-group flounder were roughly twice those of 0-group plaice (Fig. 8b), reflecting the settlement of flounder both at a smaller size and at a higher water temperature later in the year (van der Veer 1986, van der Veer et al. 1991). The instantaneous daily mortality rate of 0-group flounder did not correlate with the increase in mean seawater temperature in the Marsdiep in spring and summer (Table 2).

Shrimp fisheries are restricted to subtidal areas, so there is no bycatch-induced mortality in intertidal areas. Predation pressure by top predators has increased strongly since the 1990s because of increased

Table 2. Mean water temperature in the Marsdiep in spring (March–May; TSP), summer (June–August; TSU) and March–August (TMEAN) together with mean instantaneous mortality rate (M) of 0-group plaice and flounder at Balgzand. Spearman rank correlations (r_S) with p-values (ns: not significant): Plaice: M–TSP: $r_S = 0.70$, $p < 0.01$; M–TSU: $r_S = 0.36$, ns; M–TMEAN: $r_S = 0.58$, $p < 0.05$. Flounder: M–TSP: $r_S = 0.11$, ns; M–TSU: $r_S = 0.22$, ns; M–TMEAN $r_S = 0.17$, ns. Empty cells: years with insufficient data

Year	TSP (°C)	TSU (°C)	TMEAN (°C)	M (d^{-1}) Plaice	Flounder
1973	8.2	17.6	12.9	0.01	
1976	7.5	18.4	13.0	0.009	
1977	8.1	16.2	12.2	0.007	
1978	7.6	15.9	11.7	0.009	
1979	6.6	16.4	11.5	0.008	0.023
1980	7.9	16.7	12.3		0.071
1981	8.7	16.6	12.6	0.025	0.089
1982	8.3	18.3	13.3	0.014	0.043
1993	9.0	16.8	12.9	0.034	0.034
1994	8.3	17.8	13.1	0.03	0.050
1995	8.7	18.1	13.4	0.029	0.050
1996	6.4	17.0	11.7	0.021	0.054
1997	8.7	18.4	13.5	0.031	0.039
1998	9.8	16.8	13.3	0.026	
1999	10.0	18.2	14.1	0.022	
2000	10.1	17.2	13.6		0.055
2001	8.5	18.1	13.3		0.022
2002	9.7	18.4	14.0		
2003	9.3	19.2	14.2		0.035
2004	9.3	17.8	13.5		0.006
2005	8.3	17.0	12.7		0.016

abundance of cormorants, harbour seals and grey seals (Fig. 9). The mean daily mortality of 0-group plaice was significantly positively correlated to the index of predation by top predators (Spearman's rank correlation: n = 14; $r_S = 0.71$), in contrast to 0-group flounder (n = 14; $r_S = -0.55$).
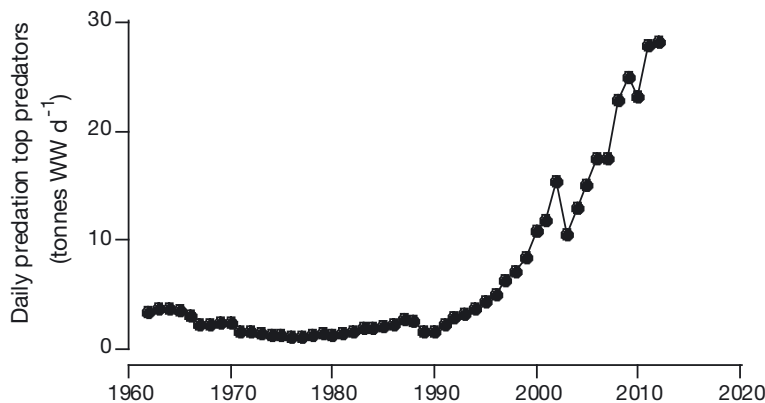

Fig. 9. Index of predation pressure by top predators in the Dutch Wadden Sea. WW: wet weight. For more information and data sources, see van der Veer et al. (2015a)

The changes in daily mortality of 0-group plaice are in agreement with the expectation that the increase in abundance of top predators has increased the mortality of juvenile flatfish in the Wadden Sea. The results for 0-group flounder are not in line with this expectation. The available data are not sufficient to establish the contribution of bycatch-induced mortality by shrimp fisheries.

4.4. Expectation 4: Year-class strength of cold-water species will decrease in response to increased seawater temperatures offshore

The peak abundance of settling flatfish larvae, used as proxy for larval supply and 0-group at the Balgzand intertidal, showed the highest densities for plaice, followed by flounder and then sole throughout the time series (Fig. 5). Large interannual variations were observed in all 3 species. The temporal variations of the 3 species appeared to be similar, with relatively high peak densities in the 1990s, but there were no significant relationships between year-class strengths of the 3 species (plaice versus flounder and sole: $r^2_{adj} = 0.07$; flounder versus sole: $r^2_{adj} = 0.27$).

Time series of recruitment to the North Sea fish stocks are available for I-group plaice and sole from 1957 onwards and for dab from 2003 onwards (ICES 2017, 2018a,b). Recruitment estimates showed year-to-year fluctuations, with exceptionally strong recruitment of plaice in 1964, 1986 and 1997 and of sole in 1959, 1964, 1988 and 1992. After the peak in 1986, plaice recruitment decreased until 1992, and then stabilized but with a tendency to increase again. Sole recruitment did not change over time. Dab recruitment increased strongly from 2003 to 2014, and then decreased in 2015 and 2016. The decreasing trends for juvenile flatfish abundance in autumn in the Wadden Sea (Fig. 5) were not reflected in the recruitment estimates (Fig. 10). The results do not support the expectation that year-class strength of plaice and other cold-water species decreases in response of the increase in seawater temperature offshore.

5. DISCUSSION

5.1. Shifts in flatfish nursery function

The early studies starting in the 1890s (Petersen 1895, Redeke 1905, Johansen
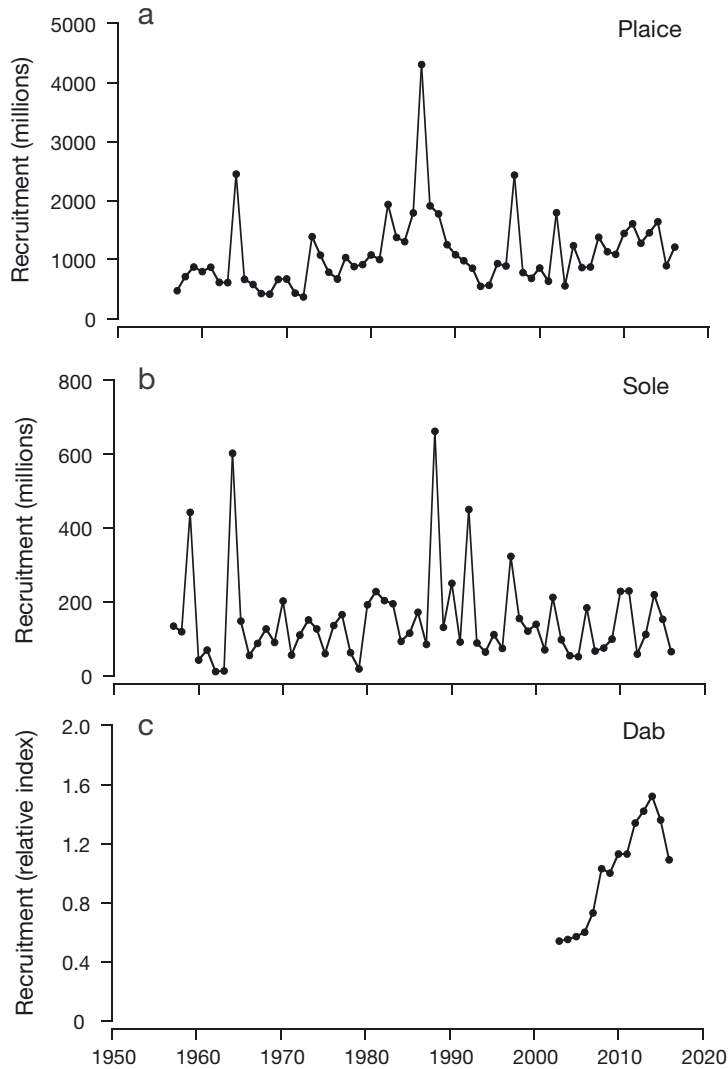
Fig. 10. Trends in recruitment to the fisheries of North Sea (a) plaice, (b) sole and (c) dab, according to ICES (2017, 2018a,b)

1913, Lübbert 1925, Bückmann 1935a,b, Smidt 1951), the systematic inventories in the western Wadden Sea in 1963–1964 (Creutzberg & Fonds 1971, Fonds 1983), in 1986 (van der Veer & Witte 1993) and in 2009 (Freitas et al. 2016), the studies of the intertidal Balgzand area in the 1970s (Kuipers 1977), the long-term fyke catches since 1960 (van der Veer et al. 2015a) and the annual DFS since 1970 (Zijlstra 1972, Tulp et al. 2008, this study) all show that until the 1980s, the Wadden Sea was a system with numerous seasonally immigrating juvenile plaice, flounder, sole and dab of different age groups.

From the 1970s onwards, the Wadden Sea has experienced major changes. The western Wadden Sea has become a system with higher and still increasing seawater temperatures (van Aken 2010),

while returning to lower primary production levels after a period of eutrophication in the 1980s (Jacobs et al. 2020), but nevertheless with a higher intertidal macrozoobenthic bio-mass (Beukema & Dekker 2020), higher numbers of top predators and an increased shrimp fishery (van der Veer et al. 2015a). In the Jade tidal basin in the German part of the Wadden Sea, climate warming, decreasing nutrient loads and species introductions occurred between the 1970s and 2009 with resulting changes in the macrofauna communities (Schückel & Kröncke 2013) and with decreasing abundances of juvenile plaice and dab while abundances of juvenile sole increased (Meyer et al. 2016). The functional changes for the western Wadden Sea and Jade, caused by increased water temperature and a eutrophication event, are most likely indicative of changes in the whole international Wadden Sea (see also Kloepper et al. 2017).

Since the 1980s, the nursery function of the Wadden Sea for flatfish species has changed substantially, resulting in decreased suitability for juvenile plaice and dab (Tulp et al. 2008, van der Veer et al. 2011, Meyer et al. 2016, ICES 2018c). The question is to what extent these changes were caused by internal (local) or external (large-scale) factors, and whether they result from bottom-up or top-down regulation. There are strong indications that increased seawater temperature, both locally and offshore, is an important causal factor. For North Sea plaice, the timing of spawning is negatively correlated with seawater temperature (Rijnsdorp 1989). For the Southern Bight spawning population that supplies the Balgzand intertidal area with larvae (Harding & Talbot 1973, Talbot 1977, van der Veer et al. 1998, Bolle et al. 2009), the observed trend of increasing seawater temperatures in the coastal zone (van Aken 2008a) is expected to cause earlier spawning, faster egg and larval development, and earlier settling. In contrast, Hovenkamp (1990) argued, based on RNA:DNA-ratios and otolith growth rates, that plaice larvae experience periods of food limitations causing growth retention, which counteracts a faster development. This agrees with smaller observed reductions in development time than expected from laboratory data (van der Veer et al. 2009). Nevertheless, the peak in plaice larval immigration occurs about 1 mo earlier at the Balgzand intertidal compared to 4 decades ago. The similar trend in earlier immigration

of flounder larvae suggests a relationship between increased seawater temperatures, earlier timing of spawning and shorter egg and larval development times for these species.

Locally, increased seawater temperatures in the Wadden Sea are expected to be a critical factor for the observed changes in habitat use by and growth performance of the various flatfish species. The decrease in abundance of juvenile plaice and dab from their 1980s levels (Tulp et al. 2008, van der Veer et al. 2011, ICES 2018c) coincides with the start of the increase in seawater temperatures (van Aken 2008a). After the 1980s, seawater temperatures during the growing season increasingly exceeded the optimum for plaice, flounder and dab. Thermal limits are thought to be caused by an increasing mismatch between oxygen demand and the capacity of oxygen supply to tissues, and has been suggested to cause the decline of eelpout *Zoarces viviparus* in the Wadden Sea (Pörtner & Knust 2007). For sole, a warm-water species, seawater temperatures are still within their preferred temperature range. Increased water temperatures may also cause the observed shifts in habitat use. Shallow waters, such as intertidal areas, warm up more quickly than deeper waters in summer (van der Veer & Bergman 1986), causing juvenile plaice and flounder to abandon the intertidal areas earlier in the season.

As a result of the warming, summer seawater temperatures in the Wadden Sea exceed the tolerance range of juvenile dab, as well as the optimum for juvenile plaice and flounder, but have improved conditions for 0-group sole. Juvenile dab have vanished almost completely from the Wadden Sea. Juvenile plaice and flounder still grow up in the Wadden Sea, but they increasingly use deeper waters. For juvenile sole, the increased temperatures enhance growth (Teal et al. 2008). In the adjacent North Sea, seawater temperatures have increased by 0.2 to 0.6°C per decade between 1980 and 2009 (Belkin 2009), positively affecting the growth potential of sole but also plaice (Teal et al. 2012).

The period of eutrophication in the 1980s has been suggested to have caused an increase in fish production and a shift in the distributions of flatfishes. Assuming that fish growth is food limited, Boddeke & Hagel (1991) stated that the eutrophication of the Dutch coastal zone caused enhanced production. Inversely, the reduction in nutrient loads to the Wadden Sea reduced fish production, an effect also suggested by Støttrup et al. (2017) for juvenile flatfish abundance in Danish coastal waters. In the western Wadden Sea, flatfish growth was not affected by eutrophication. The pattern before, during and after the period of eutrophication was the same: juvenile flatfish growth appears to be optimal (for plaice, flounder, sole) in spring and early summer, and limited in summer not only in the Wadden Sea but also in other flatfish nurseries (Freitas et al. 2012, van der Veer et al. 2016). Growth rates for 4 resident fish species in the Wadden Sea (twaite shad *Allosa fallax*, bull-rout *Myoxocephalus scorpius*, thick-lipped grey mullet *Chelon labrosus* and eelpout) are even higher at present than during the period of eutrophication (Bolle et al. 2021).

The correlation of mortality of 0-group plaice in intertidal areas with the mean seawater temperature in spring suggests contributions from increased predation by shrimps, crabs and fishes (van der Veer & Bergman 1987b) at higher temperatures; however, in that case a similar relationship for 0-group flounder is expected. On the other hand, the lower daily mortality for 0-group plaice at the Balgzand intertidal area during the 1980s compared with the 1990s (this study; Table 1) suggests that enhanced system productivity in response to eutrophication in the 1980s (Philippart et al. 2007) reduces predation pressure. Most of the top predators strongly increased in abundance since the 1990s and consume juvenile flatfishes. Cormorants were estimated to cause substantial mortality during the period July–September in the 1990s (Leopold et al. 1998). Since then, cormorant numbers have increased (van der Veer et al. 2015a).

Year-class strength in marine flatfishes is controlled in early life history in agreement with the hypothesis postulated by Hjort (1914, 1926), through a combination of density-independent processes related to fluctuations in the physical environment and density-dependent processes caused by either predation or food competition (Leggett & DeBlois 1994, van der Veer et al. 2000a,b, 2015b, Beggs & Nash 2007, Taylor et al. 2010). Various field and hydrodynamic modelling studies demonstrated the importance of hydrodynamic conditions in connecting spawning grounds to nursery areas and causing interannual fluctuations in larval supply to nursery grounds (Harding & Talbot 1973, Talbot 1977, Harding et al. 1978, van der Veer et al. 1998, de Graaf et al. 2004, Fox et al. 2006, Bolle et al. 2009, Erftemeijer et al. 2009, Savina et al. 2010, Hufnagl et al. 2013, Lacroix et al. 2013, Tiessen et al. 2014, Barbut et al. 2019, Cabral et al. 2021). Various studies also point to negative relationships between seawater temperatures and year-class strength. Van der Veer (1986) and van der Veer & Witte (1999) observed an inverse relationship between seawater temperatures during

larval drift and the abundance of settling plaice larvae at Balgzand. Such a negative relationship between seawater temperature in the first few months of the year and subsequent year-class strength was confirmed for most plaice stocks around the UK (Fox et al. 2000) and several areas in the North Sea for plaice and sole (Akimova et al. 2016). The expectation that year-class strength of plaice and other cold-water species would decrease as a consequence of the increase in seawater temperature offshore in the North Sea (van Aken 2010) is so far not reflected in the abundance of immigrating and settling larvae at the Balgzand intertidal.

5.2. Future perspectives

Most climate change studies predict increases in sea level and water temperature for the North Sea, alongside decreases in salinity and primary production, with regional differences and uncertainties in estimates of both magnitudes and consequences for hydrodynamic circulation (Schrum et al. 2016). For the Wadden Sea, a further rise in sea level (Vermeersen et al. 2018) and an increase in atmospheric temperatures by 1 to 5°C towards the end of the 21st century is predicted (Oost et al. 2017). Rijnsdorp et al. (2009) predicted a general (further) shift in abundance and distribution with latitude and depth for marine species and suggested that the response of demersal species, including flatfishes, may be hampered by geographically fixed habitats, such as nursery areas. However, spawning adults and embryos appear to be the most vulnerable life stages to climate warming due to their narrower temperature tolerance ranges (Dahlke et al. 2020). This means that further climate change may especially affect spawning in the open sea (see also the CERES project: https://ceresproject.eu). Until the mid-2000s, the increase in temperatures of coastal waters by 1.5°C (van Aken 2008a) did not change larval plaice settling at the Balgzand intertidal area. The broad spatial distribution of plaice in the North Sea, with spawning grounds in the English Channel, Southern Bight and German Bight, may provide potential for the Balgzand nursery and other areas of the Wadden Sea to shift to larvae from other spawning areas in the future.

Nursery use in the Dutch Wadden Sea has decreased over time especially for plaice and dab. This trend will likely continue with the predicted increase in seawater temperatures. However, at present, the Wadden Sea is still an important area for juvenile flatfish. Furthermore, the area is still within the tolerance limits of juvenile dab in autumn and winter, when temperatures are lower. Moreover, species with a high temperature tolerance and optimum, such as the tub gurnard *Chelidonichthys lucerna*, can benefit from the higher temperatures (Tulp et al. 2017).

The distribution of juvenile and adult plaice has shifted to deeper and northern areas in the North Sea, most likely in response to climate change (warming) (van Keeken et al. 2007, Engelhard et al. 2011). Further climate change will reduce the 'temperature window' for the remaining age groups of the cold-water species in the Wadden Sea (plaice, dab and to a lesser extent flounder), and growing conditions in late spring and summer will become less favourable as temperatures exceed their respective thermal tolerance range. Only sole can cope with higher water temperatures. However, other, new Lusitanian (warm-water) fish species may settle in the Wadden Sea as water temperatures increase.

The nursery function of the Wadden Sea will continue to change, and suitable nursery areas will shift towards the coastal zone in the North Sea, in agreement with expectations that habitat availability for North Sea plaice will reduce with further climate change (Petitgas et al. 2013). However, so far the decreasing abundances of juvenile plaice and dab in the Wadden Sea have not changed recruitment estimates for the North Sea, suggesting that the juveniles of these species have apparently found other alternative nursery areas.

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