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Growth conditions of 0-group plaice *Pleuronectes platessa* in the western Wadden Sea as revealed by otolith microstructure analysis

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ABSTRACT

Growth studies based on population-based growth estimates are limited by the fact that they do not take into account differences in age/size structure within the population. To overcome these problems, otolith microstructure analysis is often used to estimate individual growth. Here, we analyse growth of 0-group plaice in the western Wadden Sea in two years: a year preceded by a mild winter (1995) and a year preceded by a severe winter (1996). Growth was analysed by combining information on individual growth based on otolith analysis with predictions of maximum growth (= under optimal food conditions) based on a Dynamic Energy Budget model. Otolith analysis revealed that settlement occurred earlier in 1995 than in 1996. In both years, one main cohort was found, followed by a group of late settlers. No differences in mean length-at-age were found between these groups. DEB modelling suggested that growth was not maximal during the whole growing season: realized growth (the fraction of maximum growth realized by 0-group plaice) declined in the summer, although this decline was relatively small. In addition, late settling individuals exhibited lower realized growth than individuals from the main cohort. This study confirms that growth conditions for 0-group plaice are not optimal and that a growth reduction occurs in summer, as suggested in previous studies.

1. Introduction

Since the late 1960s, shallow coastal areas have been found to be important nurseries for a variety of fish species (Zijlstra, 1972). Hence, the growth dynamics and carrying capacity of these areas have been a research focus for many decades. Crucial for these types of studies has been the development of quantitative sampling devices, especially the development of small demersal trawls (Kuipers et al., 1992). This resulted in a number of classical studies (1960s–1970s) in European coastal areas focussing on demersal juvenile flatfishes, especially plaice *Pleuronectes platessa* (Edwards and Steele, 1968; Kuipers, 1977; Lockwood, 1980; Macer, 1967; Riley and Corlett, 1966). Advances in methodology led to an increasing knowledge on growth dynamics of this species in shallow coastal areas.

The first approaches to studying flatfish growth dynamics compared potential growth of small fish under experimental conditions with observed shifts in mean size of individuals within populations in the field and these studies led to the conclusion that optimal growth occurred in various European coastal areas (Bergman et al., 1988; van der Veer, 1986; Zijlstra et al., 1982). These findings were subsequently confirmed by a multi-scale spatial survey in the Dutch Wadden Sea and led to the formulation of the 'maximum growth/optimal food condition' hypothesis that proposed that field growth was only determined by prevailing water temperatures (van der Veer and Witte, 1993). However, these studies and conclusions were hampered by the fact that plaice growth estimates were based on shifts in mean population size and that the experimental growth model used was only applicable for small fish and did not take into account fish size (Fonds et al., 1992). Nevertheless, substantial progress has been made since then to try to solve these problems.

Growth studies based on otolith microstructure analysis (Karakiri et al., 1991) and on individual tagged fish (Nash et al., 1994), as well as studies on the effect of temperature on growth (Freitas et al., 2010; Teal et al., 2008), questioned the 'maximum growth/optimal food condition' hypothesis, at least in relation to the summer growth. However, these studies suffered from the same problems; i.e. they were based on growth models defined under a set of experimental conditions that limited their application to a wider size range.

Problems related to the application of growth models to wider size ranges were partially solved with the introduction of the Dynamic Energy Budget (DEB) model (Kooijman, 2000; van der Veer et al., 2001, 2009), a model that can predict maximum possible growth in relation to temperature and fish size. An analysis of population-level growth using this approach rejected the 'maximum growth/optimal food condition' hypothesis and suggested a reduction in growth during summer and autumn (van der Veer et al., 2010). This growth reduction was

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also observed at a latitudinal scale among various flatfish species (Fonseca et al., 2006; Freitas et al., 2012; Hurst and Abookire, 2006). A completely different approach, using an RNA-based growth index applied on a multi-spatial scale, led recently to the same conclusion: growth is variable among nursery areas and seems to be only maximum immediately after settlement, slowing down during summer (Ciotti et al., 2013a, 2013b). However, these studies are still based on the analysis of average length over time and may suffer from bias due to processes affecting size structure within the population.

Flatfish populations are a built-up of individuals that differ considerably in size since settlement takes place in a time frame of weeks to months, depending on the location and the species. During the first year of life, and especially early in life, size-selective processes might operate affecting the size distribution of the population and hence biasing perceived growth estimates. Size-selective predation may occur as several species of fish predate on small 0-group plaice (Ellis and Gibson, 1995; van der Veer et al., 1997 and references therein). In addition, also size-selective emigration may influence the observed size distribution as larger 0-group plaice tend to move out of the shallow grounds earlier (Geffen et al., 2011; Gibson et al., 1996). To overcome these problems, an analysis based on individual growth is necessary such as by analysing otolith microstructure in terms of daily rings. This approach has already been validated and applied to analyse individual growth in plaice (Al-Hossaini et al., 1989; Bolle et al., 2004; Geffen et al., 2011; Karakiri et al., 1989; Rijnsdorp et al., 1990; van der Veer et al., 2000; among others). Nevertheless, a study combining otolith analysis with DEB modelling, which would provide an unbiased growth analysis of 0-group plaice, has been lacking so far.

Therefore, in the present paper, we combine the analysis of individual growth based on otolith microstructure analysis with predictions of maximum growth based on the Dynamic Energy Budget model (Kooijman, 2000) for 0-group plaice in the western Wadden Sea. Since temperature is an important factor influencing growth in plaice (Al-Hossaini et al., 1989; Geffen et al., 2011; Gunnarsson et al., 2010; Modin and Pihl, 1994; Nash et al., 1994; van der Veer et al., 2000), growth of 0-group plaice was compared between two contrasting years with different temperature patterns (van der Veer et al., 2000): 1995, a year after a mild winter, and 1996 after a severe winter. In addition, intra-annual differences in individual growth were also analysed by following different settling cohorts.

2. Materials and methods

2.1. Sampling

Juvenile 0-group plaice *P. platessa* were sampled at the Balgzand, a large tidal flat area in the western Dutch Wadden Sea (Fig. 1). Flatfish were collected at frequent intervals (2 to 4 weeks) from February to August in 1995 and from March to August in 1996. Fishing was carried out on a grid of 36 stations distributed over the study area at a period of 3 h around high tide, since during this period the population is randomly distributed over the area (Kuipers, 1977). Nine transects each consisting of 4 stations of about 100 m in length were sampled during daytime with a 1.9 m beam trawl (1 ticker chain, net mesh size of 5 × 5 mm) towed by a rubber dinghy with a 25 HP outboard motor at a speed of approximately 35 m·min^{-1}. The location of the hauls was established by GPS, and the length of the hauls was assessed with a metre-wheel attached to the trawl. For more information see Zijlstra et al. (1982) and van der Veer (1986). Catches were transported to the laboratory and stored at −20 °C for further analysis. Water temperature was measured during each sampling campaign and compared to a daily temperature series collected at the Marsdiep jetty, a fixed sampling station in the Texel inlet just off the southern coast of the island of Texel (van Aken, 2008; Fig. 1).

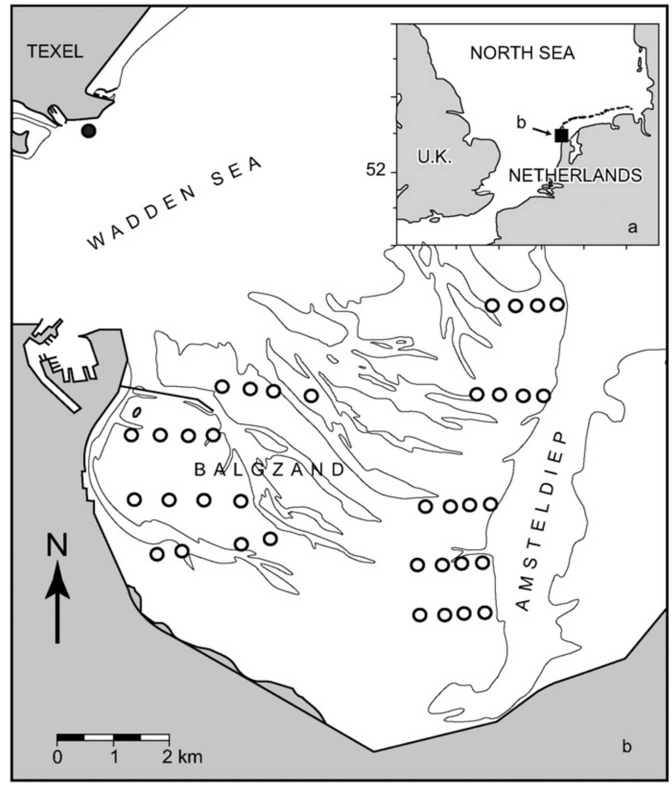

Fig. 1. The Balgzand intertidal area in the western Dutch Wadden Sea with the sampling stations (○). The full circle (●) shows the location of the Marsdiep jetty, where long-term temperature data is measured. Thin lines indicate the low water mark, thick lines indicate the high water mark.

2.2. Processing of samples

In the laboratory, samples were thawed and sorted within a few days of their capture. 0-group plaice were measured to the nearest mm total length and fixed in 96% ethanol. For each sampling date of each year, 16 or 17 individuals of different sizes were selected (in total 104 fishes in 1995 and 114 in 1996, mostly ≥19 mm). From each fish, the sagittal otolith pair was removed and, whenever possible, the left otolith was selected, cleaned and air-dried. In some small otoliths, counting of daily annuli could be done directly; however, most otoliths had to be polished prior to reading. For this, a drop of a liquid thermoplastic adhesive (Crystalbond, Buehler, USA) was placed on the centre

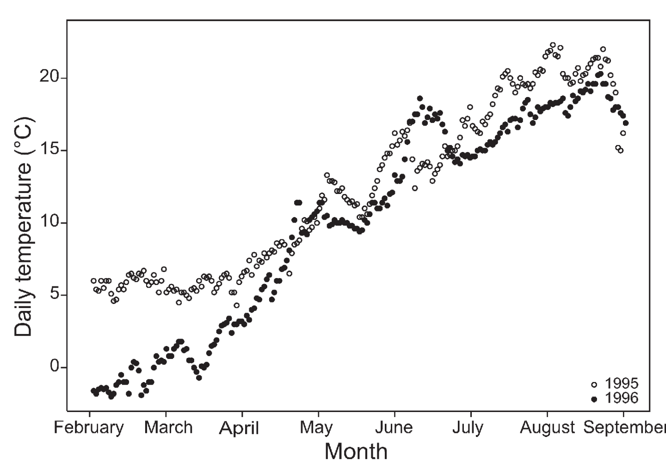

Fig. 2. Mean daily water temperature (°C) at the Marsdiep jetty from February to September in 1995 and 1996 (NIOZ unpublished data; van Aken, 2008).