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Possible causes for growth variability and summer growth reduction in juvenile plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea

Henk W. van der Veer [a,*], Alexa Sarina Jung [a], Vânia Freitas [a,b], Catharina J.M. Philippart [a], Johannes IJ. Witte [a]

[a] Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg Texel, The Netherlands
[b] CIIMAR/CIIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Universidade do Porto, Rua dos Bragas 289, 4050-123 Porto, Portugal

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ABSTRACT

Growth variability within individuals and among groups and locations and the phenomenon of summer growth reduction has been described for juvenile flatfish in a variety of European coastal areas whereby the underlying causes still remain elusive. Potential mechanisms were tested for juvenile plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea, by analysing published and unpublished information from long-term investigations (1986–present). Growth variability did occur and could be explained by differences induced by environmental variability (water temperature), and by non-genetic irreversible adaptation and sex. Dynamic Energy Budget analysis indicated that especially sexually-dimorphic growth in combination with variability in sex ratio could explain most of the variability in growth and the increase in the range of the size of individuals within the population over time. Summer growth reduction was not only observed among 0-group plaice in the intertidal, but also in the subtidal and tidal gullies as well as among I- and II-group plaice. Intraspecific competition for food was not detected but some support for interspecific competition with other predators was found. Also resource competition (due to crowding) with the other abundant epibenthic species (0-, I- and II-group flounder *Platichthys flesus*; the brown shrimp *Crangon crangon*; the shore crab *Carcinus maenas*; the goby species *Pomatoschistus minutus* and *Pomatoschistus microps*) could not explain the summer growth reduction. The observed growth reduction coincided with a decrease in stomach content, especially of regenerating body parts of benthic prey items. It is hypothesised that macrozoobenthos becomes less active after the spring phytoplankton bloom, reducing prey availability for juvenile plaice in summer, causing a reduction in food intake and hence in growth.

1. Introduction

Temperate shallow coastal areas such as the international Wadden Sea are important nurseries for various commercial and non-commercial fish species (Zijlstra, 1972), providing a combination of relatively low mortality and fast growth (Bergman et al., 1988). Hence, both of these aspects, as well as the carrying capacity of these areas, have been a research focus over many decades.

Over time, insight into the growth dynamics of shallow coastal areas has changed from the traditional view that field growth of juvenile fish was maximal and only determined by prevailing water temperatures (Zijlstra et al., 1982; van der Veer, 1986), the so-called 'maximum growth-optimal food condition hypothesis' (van der Veer and Witte, 1993; van der Veer et al., 1994), to the view that growth is variable among nursery areas (Karakiri et al., 1989, 1991; Berghahn et al., 1995) and only maximum just after settlement, slowing down during summer. This growth reduction has been found using various methods, annually, at a latitudinal scale, and in multiple juvenile flatfish species (van der Veer et al., 2010; Freitas et al., 2012; Ciotti et al., 2013a,b; Fox et al., 2014). In combination with experimental work, Fox et al. (2014) point to post-settlement habitat quality in general as the key factor modifying potential growth rates, without indicating in detail the underlying responsible processes.

All of the existing information about growth variability among juvenile flatfish in various nurseries and the evidence of summer growth reduction have been summarized recently by Ciotti et al. (2014). Their main conclusion was that, despite clear evidence for growth heterogeneity at numerous spatiotemporal scales, underlying causes remain elusive, and therefore might even be multifactorial. Nevertheless, there are also arguments in support of the presence of general patterns, such as the observation that summer growth reduction in European waters occurs each year in adjacent populations and among different species (see van der Veer et al., 2010; Freitas et al., 2012; Ciotti et al., 2013a,b).

In course of time, various factors have been suggested that might induce variability in juvenile growth, ranging from ontogenetic background (Kinne, 1962; van der Veer et al., 2000), sex (Lozan, 1992; van der Veer et al., 2009) and environmental conditions such as spatial and temporal variability in water temperature (Fonds et al., 1992), salinity (Augley et al., 2008) and food conditions (van der Veer and Witte, 1993); however, so far the quantitative impact of these factors

* Corresponding author.

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on field growth have not been assessed. Growth reduction appears to be a general phenomenon among various 0-group flatfish species, at least in shallow intertidal and coastal areas (van der Veer et al., 2010; Freitas et al., 2012; Ciotti et al., 2014). It is unclear whether growth reduction also operates in deeper waters and among elder flatfish age groups. This would require information about growth in I- and II-group flatfish and information from deeper waters.

From an energetic perspective, growth reduction boils down to reduced energy availability for growth. According to general Dynamic Energy Budget theory considerations (Kooijman, 2010), this must translate to a reduced mobilization of stored energy due to less food assimilated. Because juvenile flatfish in European waters are mainly benthic polychaete and mollusc feeders (Edwards and Steele, 1968; de Groot, 1971; Kuipers, 1977; de Vlas, 1979), sudden decreases in benthic food availability seem unlikely. Moreover, long-term intertidal macrozoobenthic data at the Balgzand intertidal in the Dutch Wadden Sea suggest even an increase in food abundance in summer over the last decades (Dekker, unpubl., in van der Veer et al., 2011). This implies that intra- and/or interspecific food competition might be more likely candidates. If growth reduction of 0-group plaice is caused by intraspecific food competition, a negative relationship between realized growth of the 0-group and the total food uptake of the flatfish species (0-, I- and II-groups) would be expected. Growth reduction caused by interspecific food competition would imply a negative relationship between realized growth and food intake by other predatory epibenthic species (e.g., other fish species and crustaceans). An alternative explanation could be resource competition due to crowding, which would imply a negative relationship between realized growth in 0-group plaice and the population density of all predatory epibenthic species.

In this paper, we first focus on the possible (multifactorial) causes for the observed heterogeneity in size as a consequence of variability in growth among juvenile fish and, secondly, we investigate whether similar factors might be operating in space and time by testing various hypotheses (intraspecific, interspecific and resource competitions) dealing with the observed growth reduction in summer. The focus is on juvenile plaice, *Pleuronectes platessa* L., because this species has been the subject of numerous studies in the western Dutch Wadden Sea and a wealth of published and unpublished information on various aspects of its ecology is available (for overview see Creutzberg et al., 1978; Kuipers, 1977; de Vlas, 1979; Zijlstra et al., 1982; van der Veer, 1986; van der Veer and Witte, 1993; van der Veer et al., 2000).

2. Material and methods

2.1. Data sources

Published and unpublished data of two fish sampling programmes in the western Dutch Wadden Sea were used: the Balgzand and the EMOWAD-ZKO programme.

The Balgzand high water programme covers the period 1975 to 2009 (1975–1976, 1979–1983, 1986, 1991, 1993–2002, 2007, 2009). Fishing was conducted on a grid of 36 stations distributed over the Balgzand, an isolated tidal flat system of 50 km^2 in the western part of the Wadden Sea (Fig. 1). Samples were collected using a standard 2-m beam trawl

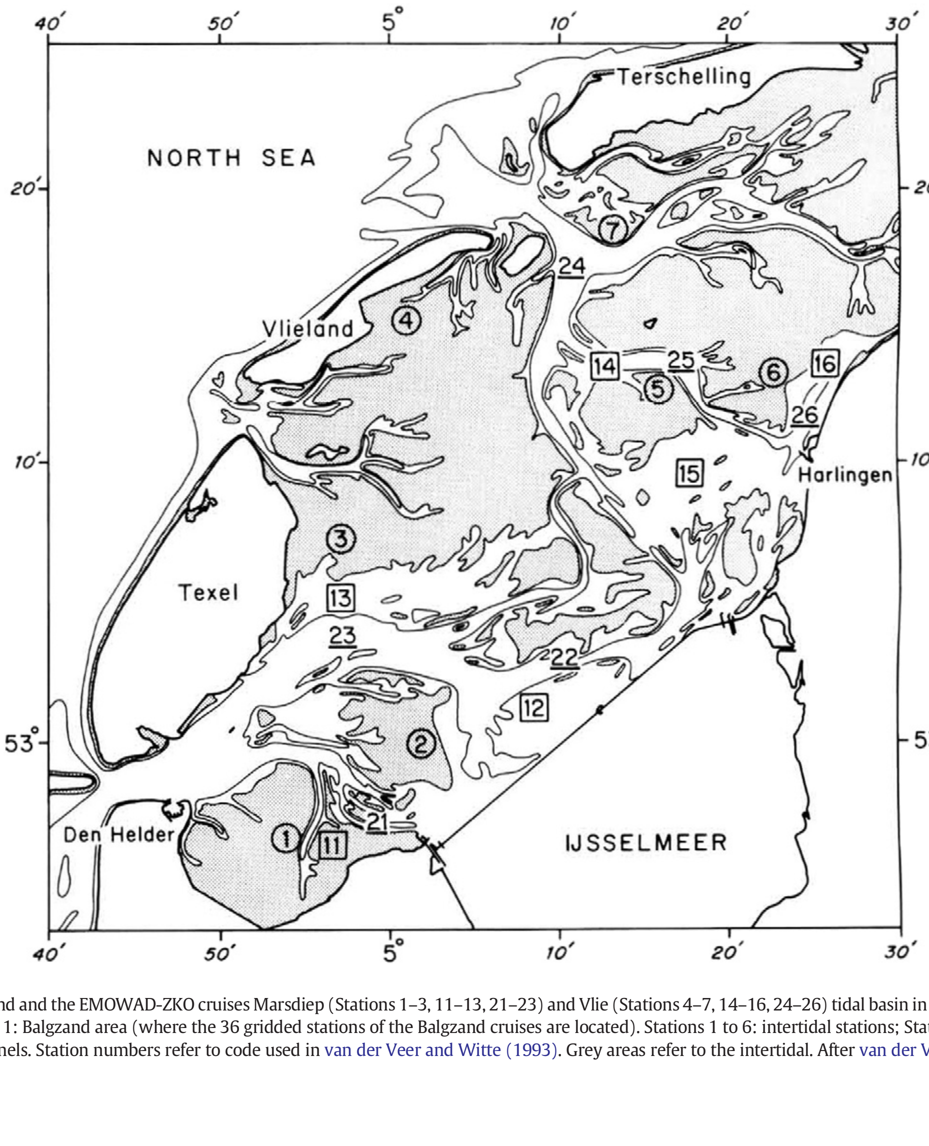

Fig. 1. Location of the Balgzand and the EMOWAD-ZKO cruises Marsdiep (Stations 1–3, 11–13, 21–23) and Vlie (Stations 4–7, 14–16, 24–26) tidal basin in the western Dutch Wadden Sea. Note EMOWAD-ZKO Station 1: Balgzand area (where the 36 gridded stations of the Balgzand cruises are located). Stations 1 to 6: intertidal stations; Stations 11 to 16: subtidal stations; Stations 21 to 26: tidal channels. Station numbers refer to code used in van der Veer and Witte (1993). Grey areas refer to the intertidal. After van der Veer and Witte (1993).