Royal Netherlands Institute for Sea Research

This is a postprint of:

Article begins on next page]

1 **Possible causes for growth variability and summer growth reduction in juvenile**
2 **plaice *Pleuronectes platessa* L. in the western Dutch Wadden Sea**
3

4 Henk W. van der Veer*[1], Alexa Sarina Jung[1], Vânia Freitas[1,2], Catharina J. M. Philippart[1],
5 Johannes IJ. Witte[1]
6

7 [1] Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg Texel,
8 The Netherlands
9 [2] CIIMAR/CIIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental,
10 Universidade do Porto, Rua dos Bragas 289, 4050-123 Porto, Portugal
11

12 **ABSTRACT**
13

14 Growth variability within individuals and among groups and locations and the
15 phenomenon of summer growth reduction has been described for juvenile flatfish in a
16 variety of European coastal areas whereby the underlying causes still remain elusive.
17 Potential mechanisms were tested for juvenile plaice *Pleuronectes platessa* L. in the
18 western Dutch Wadden Sea, by analysing published and unpublished information from
19 long-term investigations (1986-present). Growth variability did occur and could be
20 explained by differences induced by environmental variability (water temperature), and
21 by non-genetic irreversible adaptation and sex. Dynamic Energy Budget analysis
22 indicated that especially sexually-dimorphic growth in combination with variability in sex
23 ratio could explain most of the variability in growth and the increase in the range of the
24 size of individuals within the population over time. Summer growth reduction was not
25 only observed among 0-group plaice in the intertidal, but also in the subtidal and tidal
26 gullies as well as among I-and II-group plaice. Intraspecific competition for food was not
27 detected but some support for interspecific competition with other predators was found.
28 Also resource competition (due to crowding) with the other abundant epibenthic species
29 (0-, I- and II-group flounder *Platichthys flesus*; the brown shrimp *Crangon crangon*; the
30 shore crab *Carcinus maenas*; the goby species *Pomatoschistus minutus* and *P. microps*)
31 could not explain the summer growth reduction. The observed growth reduction
32 coincided with a decrease in stomach content, especially of regenerating body parts of
33 benthic prey items. It is hypothesised that macrozoobenthos becomes less active after
34 the spring phytoplankton bloom, reducing prey availability for juvenile plaice in summer,
35 causing a reduction in food intake and hence in growth.
36

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 & 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) points 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 has 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 & Witte, 1993); however, so far the quantitative impact of these factors 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 & 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-group) 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 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 competition) 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 & Witte, 1993; van der Veer et al., 2000).

2. Material and methods

2.1. Data sources

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

115   The Balgzand high water programme covers the period 1975 to 2009 (1975-
116 1976, 1979-1983, 1986, 1991, 1993-2002, 2007, 2009). Fishing was conducted on a
117 grid of 36 stations distributed over the Balgzand, an isolated tidal flat system of 50 km^2
118 in the western part of the Wadden Sea (Fig. 1). Samples were collected using a standard
119 2-m beam trawl with one tickler chain from February onwards at frequent intervals (in
120 principle every 2 to 4 weeks) over a period of 3 h centred around high water, because
121 during this period the flatfish population is randomly distributed over the area (Kuipers,
122 1977). Over the years, methodology has remained the same: hauls of about 100 m have
123 been made during daytime at a speed of about 35 m min^{-1}, following the protocols of
124 Riley & Corlett (1966). Location of the hauls was established by wooden poles put in the
125 sediment at tow start, and later by GPS. The length of the trawls was assessed with a
126 meter-wheel fitted outside the trawl. During each cruise bottom water temperature, and
127 in later years also salinity, was measured. All samples were stored in plastic bags,
128 transported to the laboratory on the same day and preserved in 4 % formaline-seawater
129 (samples collected up till 1990) or deep-frozen (samples collected after 1990). All
130 samples were sorted to species level and each individual was measured to either the
131 nearest mm total length if 0-group flatfish, or to the nearest 5 mm for other specimens,
132 within a few weeks of collection. Juvenile flatfish were separated into age groups based
133 on their length–frequency distribution. In case of doubt, sagittal otoliths were removed
134 and were checked by eye for annual rings. Subsequently, data were stored in a
135 database.

136   The EMOWAD-ZKO programme was carried out in 1986 (12 stations) and 2009
137 (18 stations) in the Marsdiep and Vlie tidal basins of the western Dutch Wadden Sea
138 (Fig. 1). In 1986, stations in each basin were visited alternately (Marsdiep basin in odd
139 months, Vlie stations in even months), in 2009 both basins were sampled every month.
140 Stations were selected at the intertidal (areas with drained tidal flats at lower low water
141 spring tides, LLWS); subtidal (area between LLWS and LLWS - 5 m); and tidal channels
142 (areas deeper than 5 m below LLWS). Sampling was carried out every month from March
143 to October, for about 3 hours around high tide during daytime. Intertidal stations were
144 sampled with a 2-m beam trawl (5-mm mesh in codend, 1 tickler chain) towed from a
145 rubber dinghy powered by an outboard motor at a constant speed of 35 m min^{-1},
146 following the protocols of Riley & Corlett (1966). At each station 2-3 hauls of about 100
147 m each were conducted. In subtidal and channel stations, fishing was carried out with
148 the RV *Navicula* -a 20m, low-draft vessel equipped with a stern-mounted trawl gantry-
149 with a 3-m beam trawl (10-mm mesh in codend, 1 tickler chain). Depending on the size
150 of the area, 2-3 hauls were done in subtidal stations and 1 or 2 in the tidal channels. In

all cases the total distance covered at each station, from all tows combined, was on average 500 m. The geographic position of the trawls was recorded using a GPS and bottom temperature data were obtained at each trawl location with a CTD. Catches were sorted on board immediately and measured to the nearest mm (0-group) or in 0.5 cm total length classes. For all catches, juvenile flatfish were separated into age groups (i.e. 0-, I-, II-group) based on their length–frequency distribution. In rare cases in which the distributions overlapped and it was unclear to which age group an individual belonged, sagittal otoliths were removed and were checked by eye on board for annual rings. Subsequently, data were stored in a database.

The number of fish caught was corrected for size-selective mesh and catch efficiency according to Kuipers (1975) and Dapper (1978) for the 2-m beam trawl, and after Bergman et al. (1989) for the 3-m beam trawl, and converted into densities. For each station, the arithmetic mean of the plaice density and the mean length were estimated and used as indices of population density and size over time.

2.2. Growth variability

The effect of environmental variability (bottom water temperature and salinity) on growth was analysed for juvenile plaice at the Balgzand area. Unpublished data for 2000, representing an average year with respect to previous winter, were selected. For all cruises, temperature and salinity were measured during each haul (see above) with an accuracy of about 0.5^0C and 0.5 PSU.

The impact of ontogenetic background on growth was studied by analysing morphometric characteristics for juvenile plaice at the Balgzand area. Published information for 1995 was taken from van der Veer et al., (2000). In short, from each cruise, at least 100 individuals of 0-group were selected and they were rinsed with 1 % NaCl, and bleached individually in a 1 % NaCl, 0.45 % H_20_2 and 0.85 % KOH solution for 20 to 60 min depending on their size (Potthoff, 1983). Subsequently, the fish were kept overnight in 1 % KOH for maceration. Next day the fish skeletons were stained with analizarin red solution for about 3 d. Finally, after rinsing with a 1 % NaCl, 0.5 % KOH solution, the fish were stored and cleared in a solution consisting of 50 % glycerine and 50 % of 0.5 % KOH, 1 % NaCl. All of the dilutions were made with demineralized water. For each individual, the number of vertebrae, dorsal, and anal fin rays were counted, reflecting the temperature conditions experienced during the egg (vertebrae) and larval (fin rays) stages. For more details, see van der Veer et al. (2000).

The potential impact of sex on growth variation was analysed for juvenile plaice using the Dynamic Energy Budget (DEB) model. The DEB theory (Kooijman, 2010) describes the energy flows through an animal in relation to varying food densities and

189 temperatures conditions. Food uptake in plaice is assumed to follow a (Holling type-II)
190 functional response relationship with food density in line with observations on juvenile
191 flounder (Kiorbøe, 1978; Mattila & Bonsdorff, 1998) and whereby food conditions are
192 scaled between 0 to 1 (*ad libitum* food). With a set of species-specific parameters (for
193 plaice see: van der Veer et al. 2001, 2010), the DEB model can be applied for all
194 combinations of fish size, food conditions and temperature. Due to differences in food
195 intake and in energy participation, males and females have different parameter sets, and
196 hence, growth characteristics (Freitas et al., 2010). For a thorough description of the
197 model and relevant equations see van der Veer et al. (2009).

198

199 *2.3. Growth reduction*

200

201 Summer growth conditions among I- and II-group plaice were studied for the
202 Balgzand programme. Until the beginning of the 1980s, both I- and II-group occurred in
203 substantial densities (see Bergman et al., 1988 and van der Veer et al., 2011) to allow a
204 reliable growth analysis. For the period 1975 – 1978, observed growth in between two
205 successive sampling periods was compared with predicted maximum possible growth
206 according to the DEB model [sensu the same method as described in Freitas et al.
207 (2012)]. Under constant food conditions (or at abundant food due to the hyperbolic
208 shape of the functional response), DEB differential equations can be analytically solved
209 and the dynamics of growth then simplifies to Von Bertalanffy growth curve (Kooijman,
210 2010). This allows predictions of maximum possible growth predictions in between two
211 successive sampling periods and a comparison with observed growth. This approach has
212 already been applied for juvenile plaice previously and for a thorough description of the
213 method and relevant equations, see van der Veer et al. (2010) and Freitas et al. (2012).
214 Summer growth conditions in the subtidal and channel stations were analysed for
215 0-group plaice for the EMOWAD-ZKO programme in 1986 and 2009. For all field
216 observations, the observed growth rate dL (cm d^{-1}) between time $t = i$ and $t = i + 1$ was
217 compared with maximum growth as predicted by the standard Dynamic Energy Budget
218 (DEB) model (sensu Freitas et al., 2012, see above) for the intertidal, subtidal and
219 channel stations. Results are taken from Freitas et al. (2016).

220

221 *2.4 Growth relationships*

222

223 The presence of intraspecific, interspecific and resource competition was analysed
224 for the Balgzand data. First of all, for all data, the ratio of observed and DEB predicted
225 maximum growth rates was estimated and analysed over time. To help visualize
226 patterns, a smoothing curve was added using the LOESS function in R (R Development

227 Core Team, 2014). Next, daily food intake for juvenile flatfish and the other epibenthic
228 species was estimated in mg ash free dry weight per m^2 per d (mg AFDW m^{-2} g^{-1})
229 separately for each Balgzand survey, based on specific energy requirements following de
230 Vlas (1979) with some slight modifications (van der Veer et al., 2010), whereby energy
231 requirements were based on two components: contribution for metabolism (daily
232 maintenance requirements), and contribution for observed growth (daily growth
233 requirements). Energy required for locomotion and other expenditures was not
234 considered and was assumed to be included in the estimate of metabolism. The various
235 coefficients were adjusted for each species separately (Table 1). Finally, for each
236 Balgzand survey over the years, the ratio between observed and DEB predicted
237 maximum possible growth for 0-group plaice was compared with the estimated daily
238 food intake of all juvenile plaice (0-, I- and II-group) (proxy for intraspecific
239 competition); with the estimated daily food intake of all epibenthic predators present
240 (proxy for interspecific competition) and with the density of all epibentic species (proxy
241 for resource competition).

242

243 *2.5. Statistical analyses*

244

245 All calculations were carried out in R version 3.1.1. Linear mixed effects models
246 were fitted using the nlme package (Pinheiro et al., 2009). Generalized additive models
247 using a Normal distribution with log-link were applied using the GAM functions in the
248 mgcv package (Wood, 2006).

249

250 **3. Results**

251

252 *3.1. Growth variability*

253

254 3.1.1. Environmental conditions

255

256 Variability in water temperature and salinity was low in spring, but increased with
257 increasing temperature and was on the order of 1 – 3 °C during the year (Fig. 2).
258 Salinity showed large fluctuations during the year and also among stations on the order
259 of 2 – 18 PSU difference. Variability was not random among stations but showed clear
260 spatial patterns; e.g., relatively cold and saline waters at the lower parts of the tidal flats
261 in spring (Fig. 3). According to the maximum growth model of Glazenburg (1983), for 0-
262 group plaice each degree Celcius in water temperature potentially accounted for 1.3 mm
263 mo^{-1} growth difference.

264

265   3.1.2. Ontogenetic background

266

267   From the onset of larval immigration in March 1995, individual variability in the
268   number of vertebrae (40 – 45), anal (49-60) and dorsal (66-82) fin rays was found and
269   remained present in substantial enough numbers during the season to identify
270   subgroups (Fig. 7 in van der Veer et al., 2000). Trends in mean length over time
271   indicated that differences between subgroups were significantly correlated with the
272   number of vertebrae, but not with the number of anal fin or dorsal fin rays (Fig. 4). As a
273   consequence, there was a significant relationship between mean growth and number of
274   vertebrae (r_s= 1.00, P < 0.05) and by the end of June mean length of the various
275   subgroups varied from around 45 to 60 mm (Fig. 4).

276

277   3.1.3. Sex

278

279   The potential impact of sex on growth was illustrated by the predicted difference
280   in growth of male and female 0-group plaice at Balgzand in 1975. Growth curves for
281   both males and females constructed by means of the DEB model at prevailing water
282   temperatures showed clear differences. Starting at a similar size (15 mm) at settlement,
283   predicted mean length differed by more than 4 cm by the end of the season (Fig. 5).
284   Plaice growth as predicted by the experimentally established maximum growth model
285   (for an unknown mixture of male and female plaice) by Fonds et al. (1992) was in
286   between male and female growth. Applying the DEB growth model of males and females
287   for 0-group plaice and water temperature data from 1975 (de Vlas, 1979), showed that
288   much of the observed variation in size at the end of the growing season could be
289   explained by differences in settlement time and in sex (Fig. 6).

290

291   *3.2. Growth reduction*

292

293   Growth reduction was not restricted to 0-group and could also be observed in I-
294   and II-group plaice at Balgzand: the ratio observed growth/maximum possible growth
295   for both groups showed a decrease over time from values around 1.0 in the beginning of
296   the season to values around 0.5 at the end of the summer season (Fig. 7).

297   Growth reduction was also not restricted to the intertidal.The ratio observed
298   growth/maximum possible growth for 0-group plaice in the subtidal and channel areas
299   decreased over time in both years for all stations from values around or above 1.0 to
300   about 0.3 at the end of the summer season (Fig. 8).

301

302   *3.3. Growth relationships*

303

304   Intraspecific food competition for 0-group plaice did not seem present at
305 Balgzand: there was no relationship between the ratio of observed and maximum
306 possible growth according to the DEB model and the estimated daily food intake of all
307 juvenile plaice (0-, I- and II-group) (Fig. 9). Applying a GAM showed that no significant
308 relationship existed: the smoother could be described by a straight line and 0 (no
309 relationship) was within the 95% confidence limits (Fig. 9).

310   To analyse interspecific food competition at Balgand, the ratio between observed
311 and maximum possible growth for 0-group plaice according to the DEB model was
312 compared with the estimated daily food intake of all epibenthic predators present (Fig.
313 10). Applying a GAM showed that a weak significant relationship existed (P < 0.05): 0
314 (no relationship) was not completely within the 95% confidence limits (Fig. 10) of the
315 smoother.

316   Possible resource competition at Balgzand did not seem present: there was no
317 relationship between density of all epibenthic species (flatfishes, gobies and crustaceans)
318 and observed growth reduction in 0-group plaice (Fig. 11).

319

320 **4. Discussion**

321

322 **4.1 Growth variability**

323

324   Growth, and as a consequence size, is a key life history parameter due to the
325 strong link between growth and mortality, especially in early life (Ware, 1975; Anderson,
326 1988; Pepin, 1991; Houde, 1997; van der Veer et al., 1997). Hence, variability in growth
327 during early life may directly affect survival, and ultimately recruitment, via size-
328 selective mortality and/or size-dependent onset of maturation (van der Veer et al.,
329 1994).

330   Variability in growth is the integrated effect of multiple factors acting ultimately
331 on energy consumption and participation between maintenance, growth and
332 reproduction (Kooijman, 2010; van der Veer et al., 2009). They consists of drivers at
333 various levels, as summarized by Ciotti et al. (2014). In this study the focus is on
334 especially some intrinsic (ontogenetic background, sex) and extrinsic (temperature,
335 salinity, food conditions) drivers. Quantification of the various drivers is complicated
336 since they are acting simultaneously and are also partly opposing. Ontogenetic
337 background results in a variability in mean growth during the season of between 0.40 –
338 0.75 mm d^{-1}; however, most of the population falls within 0.50 – 0.75 mm d^{-1} (van der
339 Veer et al., 2000), a range of 50%. Lozan (1992) was among the first who pointed at
340 sexual differences in food intake and growth performance. According to the DEB theory,

341 sex can be responsible for a size variation at the end of the first year of life at Balgzand
342 of between 8.0 cm (for a male) and 13.5 cm (for a female), a 70% difference.
343 Temperature is a controlling factor (Fry, 1947; Neill et al., 1994) directly affecting
344 growth. Temperature conditions at Balgzand can vary about $1 - 3°C$ between stations,
345 which would mean a range in size of about $10 - 30$% at 10°C, and of $5 - 15$ % at 20°C.
346 Salinity on the other hand is a masking factor, loading metabolism (Fry, 1947; Neill et
347 al., 1994) and therefore potentially negatively affecting growth. The Balgzand surveys
348 have illustrated that salinity conditions at Balgzand can be very variable, sometimes on
349 the order of a few hundred percent; however, the quantitative impact on growth is
350 unknown. Reduced growth rates have been reported for 0-group plaice at low salinities
351 (Karakiri & von Westernhagen, 1989), but experimental work showed faster growth at
352 the lowest salinity levels tested (Augley et al., 2008) in a situation of unlimited food. The
353 interaction of food availability with other variables to generate variability in growth
354 response is widely known (Jobling, 1994). Food resources are a limiting factor that can
355 restrict maximum metabolism (Neill et al., 1994). In the Wadden Sea, clear indications
356 of a relationship between food abundance and growth were found (van der Veer & Witte,
357 1993), whereby a range in growth of 50% was observed, but recently Freitas et al.
358 (2016) could not confirm this relationship.
359 A comparison of temporal with spatial variability in size within and among local
360 populations might give an insight into the relative importance of the various factors
361 generating growth variability (van der Veer et al., 1994). However, size-selective
362 processes such as size-selective mortality and migration (Kuipers, 1977; van der Veer et
363 al., 1997) might interfere and bias such a comparison. By far the most important
364 appears to be intrinsic factors such as sex, being able to generate differences in growth
365 rates within populations on the order of 70%, and ontogenetic background generating a
366 range of 50% in size. However, van der Veer et al. (2000) argued that the impact of
367 ontogenetic background will vary among years and will normally be relatively low since
368 most of the population will have a relatively similar background.
369
370 **4.2. Summer growth reduction**
371
372 The evidence of summer growth reduction in early juvenile flatfish is strong and
373 has been reported for different years, different areas and different species based on
374 different methods (Fonseca et al., 2006; Hurst and Abookire, 2006; van der Veer et al.,
375 2010; Freitas et al., 2012; Ciotti et al 2013a,b). Summer growth reduction might be a
376 general phenomenon: in this study, it was also observed in other age groups (I- and II-
377 group plaice) and in areas other than the intertidal (subtidal, deeper channels). Recently,
378 otolith microstructure analysis of individual flatfish confirmed earlier observations of

summer growth reduction at Balgzand; the reduction was however, relatively smaller than the one observed from shifts in population size (Cardoso et al., 2015). This difference is most likely caused by size-selective processes, such as size-selective predation (van der Veer et al., 1997) and migration (Kuipers, 1977) biasing estimates from size-frequency distributions. Furthermore, Cardoso et al. (2015) suggested that the observed reduction in growth was most likely caused by an external factor: the growth reduction did not start at a certain fish size (which would suggest being caused by an ontogenetic change such as a shift in prey preference, sensu de Vlas, 1979), but the decline occurred at about the same time in different years irrespective of fish size.

In this study no support was found that the observed summer growth reduction was caused by direct competitive intraspecific interactions between juvenile plaice themselves and only a weak support existed for interspecific competition with other species. Also resource competition did not seem likely. However, these conclusions were based on hauls with a length of about 100 m at high water, while growth heterogeneity already seems to occur even at this small spatial scale of about 100 m (Ciotti et al., 2013a,b). Therefore, it cannot be excluded that the sampling is inadequate for any analysis of direct and indirect competition: at the scale of the length of a haul heterogeneity in growth might already occur. Furthermore, the present analysis based on mean densities does not take into account the spatial heterogeneity in macrozoobenthos in the intertidal (Compton at al., 2013) and the spatial and temporal variation in the distribution of 0-group plaice (Gibson, 1973; Kuipers, 1973; van der Veer & Bergman, 1986). It cannot be excluded that the sampling design has been inadequate for analysing competition and interactions among epibenthic predators and that sampling should be conducted at a smaller scale, as was done for shore crabs *Carcinus maenas* in the same area (Smallegange et al., 2009).

Growth reduction induced by changes in food availability does not seem likely at first glance. For benthic predators such as juvenile plaice, predation pressure by juvenile flatfish is rather low compared to food availability, at least for the Balgzand area (Kuipers, 1977; de Vlas, 1979; van der Veer et al., 2011). Also, part of the diet of juvenile flatfishes at Balgzand and in other areas consists of regenerating body parts of benthic prey (among others Macer, 1967; Edwards & Steele, 1968; Kuipers, 1977; de Vlas, 1979; Poxton et al., 1983; van der Veer & Witte, 1993) and maximum predation at Balgzand appears to coincide with maximum productivity of the benthic invertebrates (Kuipers, 1977). However, these considerations are based on potential food availability, while for a predator only harvestable prey matters: the combination of not only density and size (potential food availability), but also of accessibility (Zwarts & Wanink, 1993; Piersma, 1994).

The potential benthic prey items for juvenile plaice, all live at least partly burrowed in the sediment where they are relatively well hidden and only available for predators when they are actively exposing body parts at the sediment surface for instance during feeding, defecation and spawning. At Balgzand, the growth reduction in plaice corresponds with a (temporal) disappearance of regenerating body parts in the stomachs of juvenile flatfish (Fig. 6 in de Vlas, 1979). At the same period of time, mean stomach content of I- and II-group plaice at Balgzand also showed a dip (Fig 13; after Kuipers, 1977). Macrozoobenthic biomass shows a seasonal pattern (Beukema, 1974) in synchrony with primary production in the system (Cadée & Hegeman, 1974a,b) and the (temporal) disappearance of regenerating body parts in the stomachs of juvenile flatfish in summer corresponds with the decrease in primary production after the spring bloom, in between and before the second lower autumn bloom (Philippart et al., 2010; Beukema et al., 2014). This suggests that growth reduction in summer in plaice at Balgzand and possibly in other European waters might be caused by a reduced activity of the benthos after the spring phytoplankton bloom. Temperate coastal benthic ecosystems indeed seem to show a clear seasonality (Coma et al., 2000).

However, to test whether prey searching and handling are indeed key factors determining food intake of juvenile flatfish underlying the widespread reported summer growth reduction would require underwater observations of seasonal activity patterns of the benthic community. If true, also spatial differences in prey species composition and abundance would affect food intake of juvenile flatfish and hence growth (sensu van der Veer & Witte, 1993).

References

Anderson, J.T., 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest Alt. Fish. Sci. 8, 55-66.

Augley, J., Huxham, M., Fernandes, T.F., Lyndon, A.R., 2008. The effect of salinity on growth and weight loss of juvenile plaice (*Pleuronectes platessa*, L): an experimental test. J. Sea Res. 60, 292-296.

453   Berghahn, R., Lüdemann, K., Ruth, M., 1995.Differences in individual growth of newly
454   settled O-group plaice (*Pleuronectes platessa* L.) in the intertidal of neighbouring
455   Wadden Sea areas. Neth. J. Sea Res. 34, 131-138.

456   Bergman, M.J.N., van der Veer, H.W., Zijlstra, J.J., 1988. Plaice nurseries: effects on
457   recruitment. J. Fish Biol. 33 (Suppl A), 201-218.

458   Bergman, M.J.N., van der Veer, H.W., Stam, A., Zuidema, D., 1989. Transport
459   mechanisms of larval plaice (*Pleuronectes platessa* L.) from the coastal zone into
460   the Wadden Sea nursery area. Rapp. P-v. Réun. Int. Explor. Mer 191, 43-49.

461   Beukema, J.J., 1974. Seasonal changes in the biomass of the macro-benthos of a tidal
462   flat area in the Dutch Wadden Sea. Neth. J. Sea Res. 8, 94-107.

463   Beukema, J.J., Cadée, G.C., 1997. Local differences in macrozoobenthic response to
464   enhanced food supply caused by mild eutrophication in a Wadden Sea area: food
465   is only locally a limiting factor. Limnol. Oceanogr. 42, 1424–1435.

466   Beukema, J.J., Cadée, G.C., Dekker, R., Philippart, C.J.M., 2014. Annual and spatial
467   variability in gains of body weight in *Macoma balthica* (L.): Relationships with
468   food supply and water temperature. J. Exp. Mar. Biol. Ecol. 457, 105–112

469   Brey, T., Müller-Wiegmann, C., Zittier, Z.M.C., Hagen., W., 2010. Body composition in
470   aquatic organisms — a global data bank of relationships between mass, elemental
471   composition and energy content. J. Sea Res. 64, 334-340.

472   Cadée, G.C., Hegeman, J., 1974a. Primary production of the phytoplankton in the Dutch
473   Wadden Sea. Neth. J. Sea Res. 8, 240-259.

474   Cadée, G.C., Hegeman, J., 1974b. Primary production of the benthic microflora on tidal
475   flats in the Dutch Wadden Sea. Neth. J. Sea Res. 8, 260-291.

476   Cardoso, J.F.M.F., Freitas, V., De Paoli, H., Witte, J.IJ., van der Veer, H.W., 2015. Intra-
477   and inter-annual variation in growth of 0-group plaice *Pleuronectes platessa* in
478   the western Wadden Sea. J Sea Res. (submitted)

479   Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013a. Spatial variation in growth rate of early
480   juvenile European plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 475, 213–
481   232.

482   Ciotti, B.J., Targett, T.E., Burrows, M.T., 2013b. Decline in growth rates of juvenile
483   European plaice (*Pleuronectes platessa*) during summer at nursery beaches along
484   the west coast of Scotland. Can. J. Fish. Aquatic Sci. 70, 720–734.

485   Ciotti, B.J., Targett, T.E., Nash, R.D., Geffen, A.J., 2014. Growth dynamics of European
486   plaice *Pleuronectes platessa* L. in nursery areas: A review. J. Sea Res*.* 90, 64-82.

487   Coma, R., Ribes, M., Gili, J.-M., Zabala, M., 2000. Seasonality in coastal benthic
488   ecosystems. TREE 15, 448-453.

489   Compton, T., Holthuijsen, S., Koolhaas, A., Dekinga, A., Ten Horn, J., Smith, J., Galama,
490   Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H.W., Piersma,

T., 2013. Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. J. Sea Res 82, 103-116.

Creutzberg, F., Eltink, A.Th.G.W., van Noort, G.J., 1978. The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In: McLusky, D.S., Berry, A.J. (Eds.) Physiology and behaviour of marine organisms. Proc. 12th Europ. Mar. Biol. Symp. Pergamon Press, New York, 243-251

Dapper, R., 1978. De Balgzand scholgegevens 1975, 1976, 1977. NIOZ internal report 1978-12, 53 pp.

de Groot, S.J., 1971. On the interrelationships between morphology of the alimentary track, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5, 121-196.

de Vlas, J., 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating parts of macrobenthic prey. Neth. J. Sea Res. 13, 117-153.

Edwards, R., Steele, J.H., 1968. The ecology of 0-group plaice and commen dab at Loch Ewe. I. Population and food. J. Exp. Mar. Biol. Ecol. 2, 215-238.

Fonds, M., Cronie, R., Vethaak, A.D., van der Puyl, P., 1992.Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Neth. J. Sea Res. 29, 127-143.

Fonseca, V.F., Vinagre, C., Cabral, H.N., 2006. Growth variability of juvenile soles *Solea solea* and *Solea senegalensis*, and comparison with RNA:DNA ratios in the Tagus estuary, Portugal. J. Fish Biol. 68, 1551–1562.

Fox, C.J., Targett, T.E., Ciotti, B.J., de Kroon, K., Hortsmeyer, L., T. Burrows, M., 2014. Size variation of 0-group plaice: Are earlier influences on growth potential a contributing factor? J. Sea Res. 88, 59-66.

Freitas, V., Cardoso, J.F.M.F., Lika, K., Peck, M.A., Campos, J., Kooijman, S.A.L.M., van der Veer, H.W., 2010. Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species. Phil. Trans. R. Soc. B 365, 3553-3565.

Freitas, V., Kooijman, S.A.L.M., van der Veer, H.W., 2012. Latitudinal trends in habitat quality of shallow water flatfish nurseries. Mar. Ecol. Prog. Ser. 471, 203-214.

Freitas, V., Witte, J.IJ., Tulp, I., van der Veer, H.W., 2016. Subtidal areas replacing intertidal flats as the main nursery habitat for plaice *Pleuronectes platessa* L. in the western Wadden Sea. J. Sea Res. (submitted)

Fry, F.E.J., 1947. Effects of the environment on animal activity. Univ. Toronto Stud., Biol. Ser. 55, 1-62.

528   Gibson, R.N., 1973. The intertidal movements and distribution of young fish on a sandy
529   beach with special reference to the plaice (*Pleuronectes platessa* L.) J . Exp. Mar.
530   Biol. Ecol. 12, 79-102.

531   Glazenburg, B., 1983. Een experimenteel onderzoek naar de groei van 0-groep school en
532   bot in relatie tot de watertemperatuur. Interne Verslagen Nederlands Instituut
533   voor Onderzoek der Zee, Texel, 1983-5, 1-19.

534   Houde, E.D., 1997. Patterns and consequences of selective processes in teleost early life
535   histories. In: Chambers, R.C., Trippel, E.A. (Eds.). Early life history and
536   recruitment in populations. Chapman and Hall, London, 173-196.

537   Hurst, T.P., Abookire, A.A., 2006. Temporal and spatial variation in potential and realized
538   growth rates of age-0 year northern rock sole. J. Fish Biol. 68, 905-919.

539   Jobling, M., 1994. Fish bioenergetics. Chapman &Hall, London, UK.

540   Karakiri, M., Berghahn, R., von Westernhagen, H., 1989. Growth differences in 0-group
541   plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. Mar.
542   Ecol. Prog. Ser. 55, 15-22.

543   Karakiri, M., von Westernhagen, H., 1989. Daily growth patterns in otoliths of larval and
544   juvenile plaice (*Pleuronectes platessa* L.): influence of temperature, salinity, and
545   light conditions. Rapp. P-v.Réun. Int. Explor. Mer191, 390–399.

546   Karakiri, M., Berghahn, R., van der Veer, H.W., 1991. Variations in settlement and
547   growth of 0-group plaice (*Pleuronectes platessa* L.) in the Dutch Wadden Sea as
548   determined by otolith microstructure analysis. Neth. J. Sea Res. 27, 345-351.

549   Kinne, O., 1962. Irreversible nongenetic adaptation. Comp. Biochem. Physiol. 5, 265-
550   282.

551   Kiorbøe, T., 1978.Feeding rate in juvenile flounder in relation to prey density. Kieler
552   Meeresforsch. Sonder. 4, 275–281.

553   Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organization.
554   Cambridge University Press, Cambridge, UK.

555   Kuipers, B.R., 1973. On the tidal migration of young plaice (*Pleuronectes platessa*) in the
556   Wadden Sea. Neth. J. Sea Res. 6, 376-388.

557   Kuipers, B.R., 1975. On the efficiency of a two metre beam trawl in juvenile plaice
558   (*Pleuronectes platessa*). Neth. J. Sea Res. 9, 69-85.

559   Kuipers, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea.
560   Neth. J. Sea Res. 11, 56-91.

561   Lozan, J.L., 1992. Sexual differences in food intake, digestive track size, and growth
562   performance of the dab, *Limanda limanda* L. Neth. J. Sea Res. 29, 223-227.

563   Macer, C.T., 1967. The food web in Red Wharf Bay (N. Wales) with particular reference
564   to young plaice. Helgolander wiss. Meeresunters. 15, 560-573.

565 Mattila, J., Bonsdorff, E., 1998. Predation by juvenile flounder (*Paralichthys flesus* L.): a
566   test of prey vulnerability, predator preference, switching behaviour and functional
567   response. J. Exp. Mar. Biol. Ecol. 227, 221–236.

568 Neill, W.H., Miller, J.M., van der Veer, H.W., Winemiller, K.O., 1994. Ecophysiology of
569   marine fish recruitment: a conceptual framework for understanding interannual
570   variability. Neth. J. Sea Res. 32, 135-152.

571 Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival
572   rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquatic
573   Sci. 48, 503–518.

574 Piersma, T., 1994. Close to the edge: energetic bottlenecks and the evolution of
575   migratory pathways in knots. PhD thesis Rijksuniversiteit Groningen.

576 Philippart, C.J.M., Van Iperen, J.M., Cadée, G.C., Zuur, A.F., 2010. Long-term field
577   observations on seasonality in chlorophyll-a concentrations in a shallow coastal
578   marine ecosystem, the Wadden Sea. Estuar. Coasts 33, 286–294.

579 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., the R Core team, 2009. nlme: linear and
580   nonlinear mixed effects models. R package version 3, 1-96.

581 Potthoff, T., 1983. Clearing and staining techniques. Am Soc. Ichthyol. Herpetol. Spec.
582   Publ. 1, 35-37.

583 Poxton, M.G., Eleftheriou, A., McIntyre, A.D., 1983. The food and growth of 0-group
584   flatfish on nursery grounds in the Clyde Sea area. Estua. Coast. Shelf Sci. 17,
585   319-337.

586 R Development Core Team, 2014. R: A language and environment for statistical
587   computing. R Foundation for Statistical Computing, Vienna, Austria.URL
588   http://www.R-project.org.

589 Riley, J.D., Corlett, J., 1966. The numbers of 0-group plaice in Port Erin Bay 1964-66.
590   Rep. mar. biol. Stn Port Erin 78, 51-56.

591 Smallegange, I.M., van Noordwijk, C.G.E., van der Meer, J., van der Veer, H.W., 2009.
592   Spatial distributions of shore crabs (*Carcinus maenas*) in an intertidal
593   environment in relation to their morphology, prey availability and competition.
594   Mar. Ecol. Prog. Ser. 392, 143-155.

595 van Beek, F.A., 1976. Aantallen, groei, productie en voedselopname van de zandgrondel
596   (*P. minutus*) en de wadgrondel (*P. microps*) op het Balgzand. Netherlands
597   Institute for Sea Research - Internal Report 1976-9

598 van der Veer, H.W., 1986. Immigration, settlement and density-dependent mortality of a
599   larval and early post-larval 0-group plaice (*Pleuronectes platessa*) population in
600   the western Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 29, 223-236.

601 van der Veer, H.W., Berghahn, R., Rijnsdorp, A.D., 1994. Impact of juvenile growth on
602   recruitment in flatfish. Neth. J. Sea Res. 32, 153-173.

van der Veer, H.W., Bergman, M.J.N., 1986. Development of tidally related behaviour of a newly settled 0-group plaice (*Pleuronestes platessa* L.) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 31, 121-129.

van der Veer, H.W., Bies, B., Witte, J.IJ., 2000. Selective growth and mortality of juvenile 0-group plaice *Pleuronectes platessa* L. in the Dutch Wadden Sea: a consequence of irreversible non-genetic adaptation during early pelagic life. Mar. Ecol. Prog. Ser. 197, 273-283.

van der Veer, H.W., Cardoso, J.F.M.F., Peck, M.A., Kooijman, S.A.L.M., 2009. Physiological performance of plaice *Pleuronectes platessa* (L.): A comparison of static and dynamic energy budgets. J. Sea Res. 62, 83-92.

van der Veer, H.W., Ellis, T., Miller, J.M., Pihl, L., Rijnsdorp, A.D., 1997. Size-selective predation on juvenile North Sea flatfish and possible implications for recruitment. In: Chambers, R.C., Trippel, E.A. (Eds.). Early life history and recruitment in populations. Chapman and Hall, London, 279-303.

van der Veer, H.W., Freitas, V., Koot, J., Witte, J.IJ., Zuur, A.F., 2010. Food limitation in epibenthic species in temperate intertidal systems in summer: analysis of 0-group plaice *Pleuronectes platessa.* Mar. Ecol. Prog. Ser. 416, 215−227.

van der Veer, H.W., Kooijman, S.A.L.M., Van der Meer, J., 2001. Intra- and interspecies comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets. J. Sea Res. 45, 303-320.

van der Veer, H.W., Koot, J., Aarts, G., Dekker, R., Diderich, W., Freitas, V., Witte, J.IJ., 2011. Long term trends in juvenile flatfish predation on the Balgzand intertidal, Dutch Wadden Sea, indicate a dramatic reduction in nursery function. Mar. Ecol. Prog. Ser. 434, 143−154.

van der Veer, H.W., Witte, J.IJ, 1993. The 'maximum growth/optimal food condition' hypothesis, a test for 0-group plaice *Pleuronectes platessa* in the Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 101, 81-90.

van Lissa, J.H.L., 1977. Aantallen, voedselopname, groei en produktie van de garnaal (*Crangon crangon* L.) in een getijdengebied, alsmede de voedselopname en groei onder laboratoriumomstandigheden. Netherlands Institute for Sea Research - Internal Report 1977-10.

Ware, D.M., 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Bd Can. 32, 2503−2512.

Wood, S., 2006. Generalized Additive Models: An introduction with R, vol. 66.Chapman & Hall/CRC, Boca Raton.

Zijlstra, J.J., 1972. On the importance of the Waddensea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp. zool. Soc. Lond. 29, 233-258

641 Zijlstra, J.J., Dapper, R., Witte, J.IJ., 1982.Settlement, growth and mortality of post-
642   larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea
643   Res. 15, 250-272.
644 Zwarts, L., Wanink, J.H., 1993. How the food supply harvestable by waders in the Dutch
645   Wadden Sea depends on the variation in energy density, body weight, burying
646   depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31, 441-476.

1

2
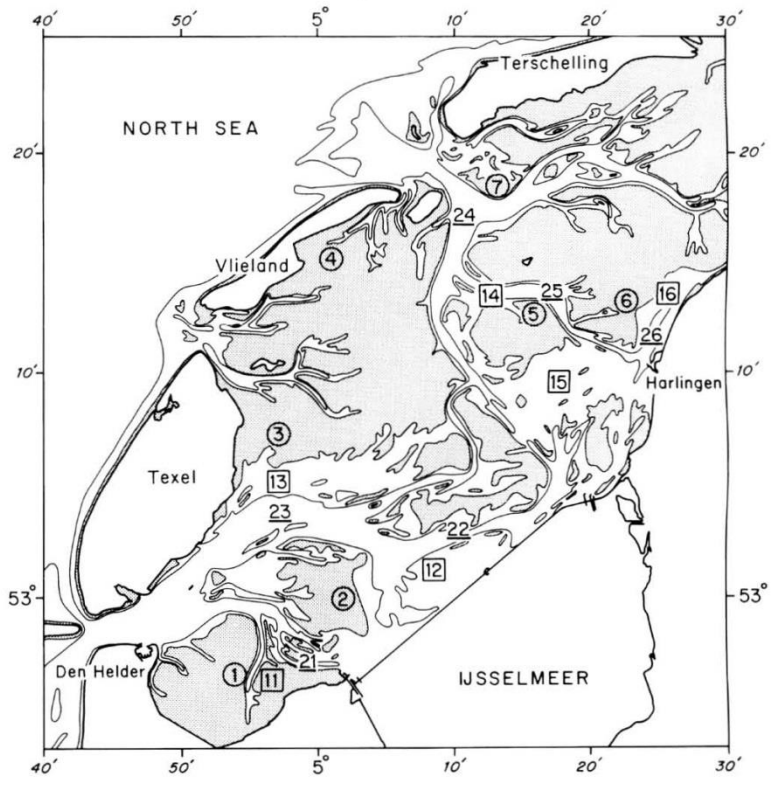
3 Figure 1 Location of the Balgzand and the EMOWAD-ZKO cruises Marsdiep (Station 1-3,
4   11-13, 21-23) and Vlie (Station 4-7, 14-16, 24-26) tidal basin in the western
5   Dutch Wadden Sea. Note EMOWAD-ZKO Station 1: Balgzand area (where the
6   36 gridded stations of the Balgzand cruises are located). Stations 1 to 6:
7   intertidal stations; Stations 11 to 16: subtidal stations; Stations 21 to 26: tidal
8   channels. Station numbers refer to code used in van der Veer & Witte (1993).
9   Grey areas refer to the intertidal. After van der Veer & Witte (1993).

10

11
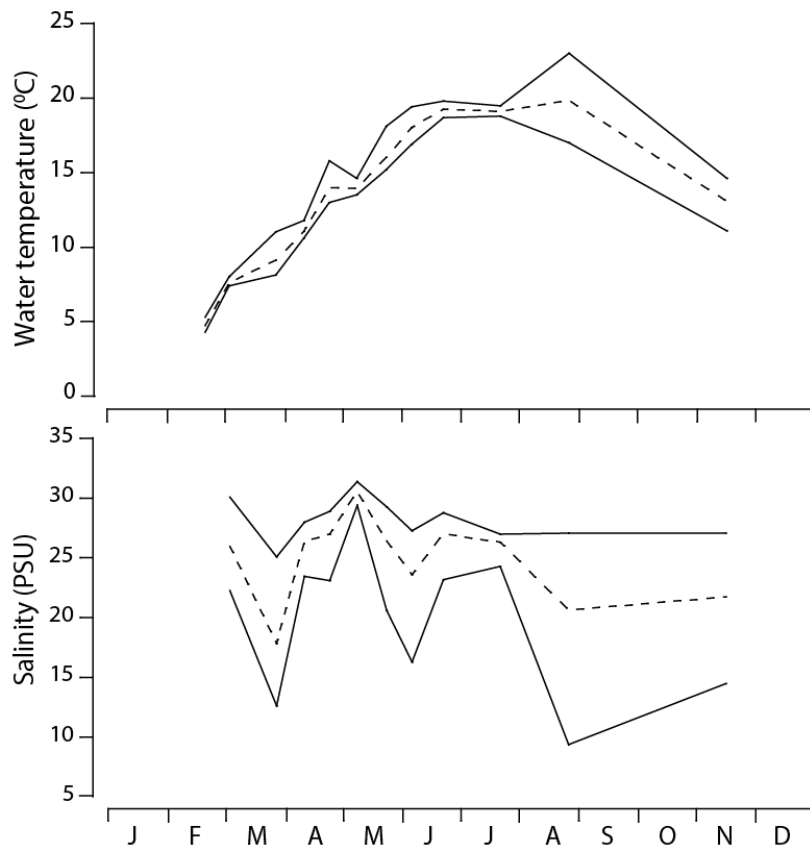
12

13

14 Figure 2 Mean (dashed line), minimum (lower line) and maximum (upper line) bottom
15   water temperature (top panel; °C) and salinity (bottom panel; PSU) at
16   Balgzand at 36 fishing stations during high water in 2000.

17

18
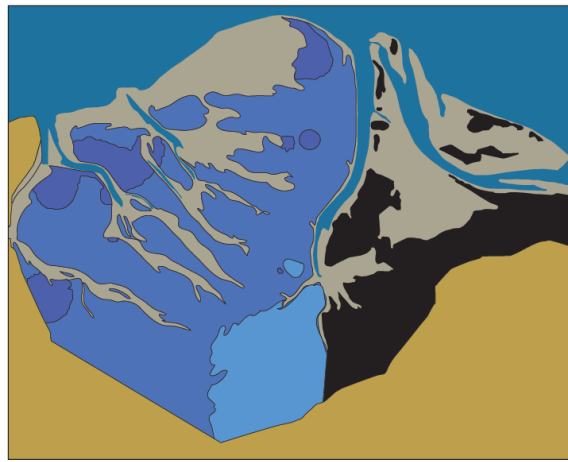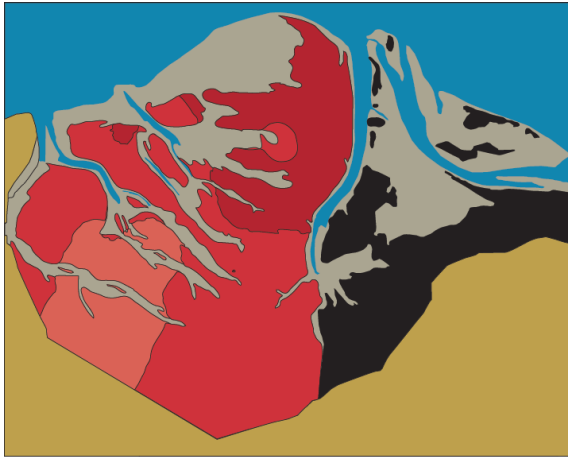
19 Figure 3   Bottom water temperature (top panel; °C) and salinity (bottom panel; PSU)
20   on 18-19 April 2000 at Balgzand at 36 fishing stations. Temperature ranges
21   from 8°C (dark red) to 11°C (light red), salinity from 23 (light blue) to 28
22   (dark blue). Yellow area refers to mainland, light brown is subtidal area
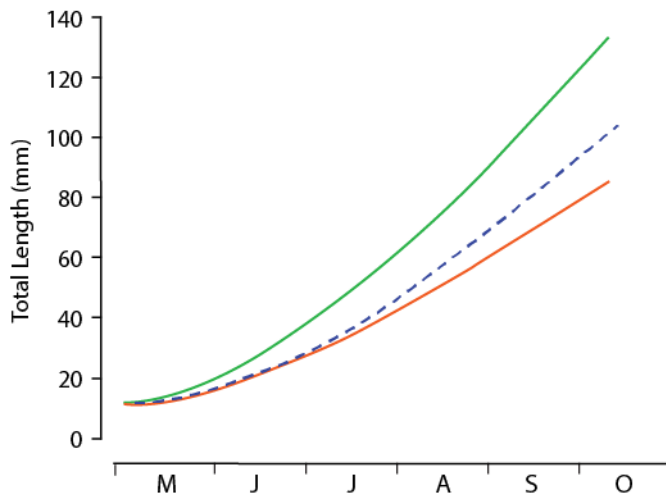23   (between low water and low water – 5m and black area is no data available
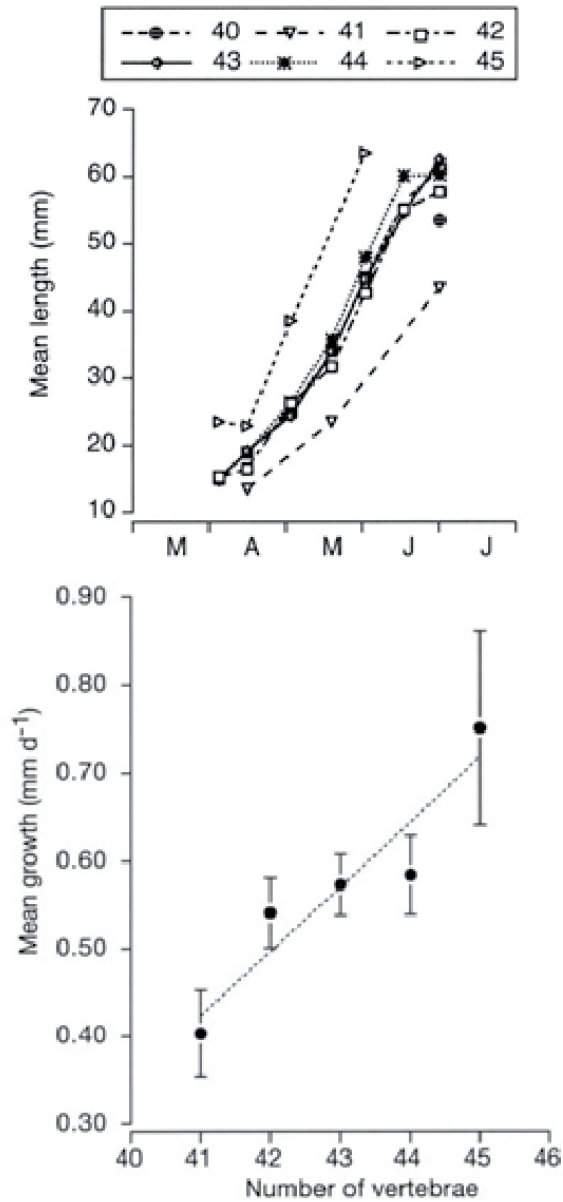
24

25   Figure 4   Seasonal pattern of mean length (mm) (top panel) and mean growth (bottom

26   panel) of the various meristic subpopulations of 0-group plaice at the

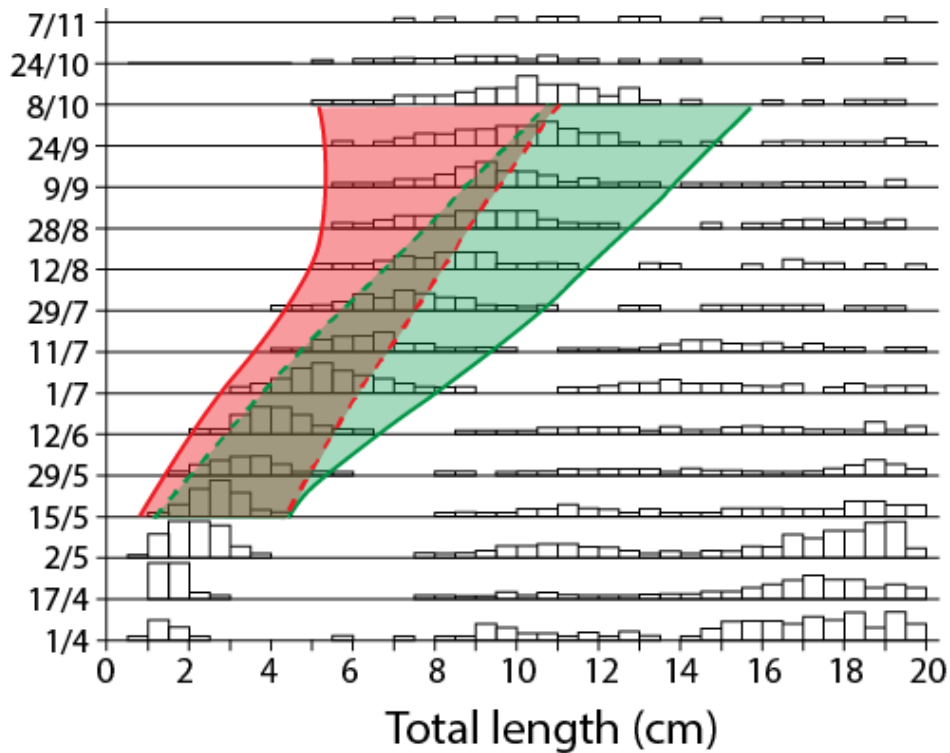27   Balgzand in 1995 in relation to number of vertebrae.

28

29   Figure 5   Predicted growth of male (red) and female (green) 0-group plaice at the
30   Balgzand in 1995 from May 1th onwards according to the DEB model and
31   according to the experimentally established growth model of Fonds et al.
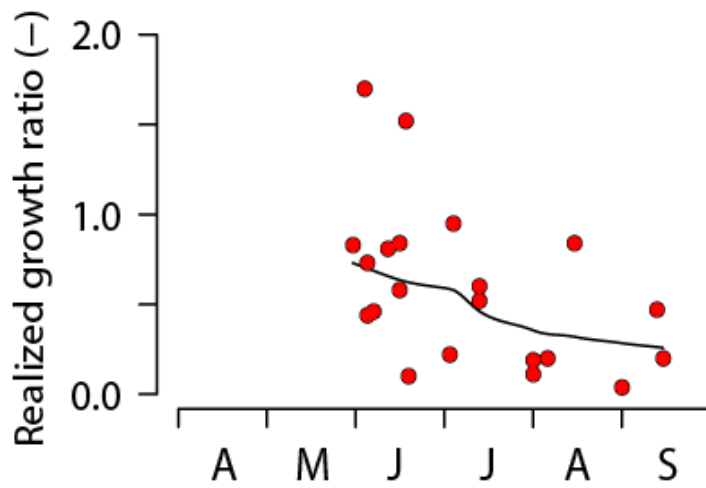32   (1992) (blue).

33

34

35

36   Figure 6   Length frequency distribution of juvenile plaice at Balgzand in 1975. Data
37   after de Vlas (1979), together with simulated maximum growth for 0-group
38   plaice according to the DEB model for first settlers and last settlers at
39   prevailing water temperatures. Green: female; red: males. For more
40   information see text.
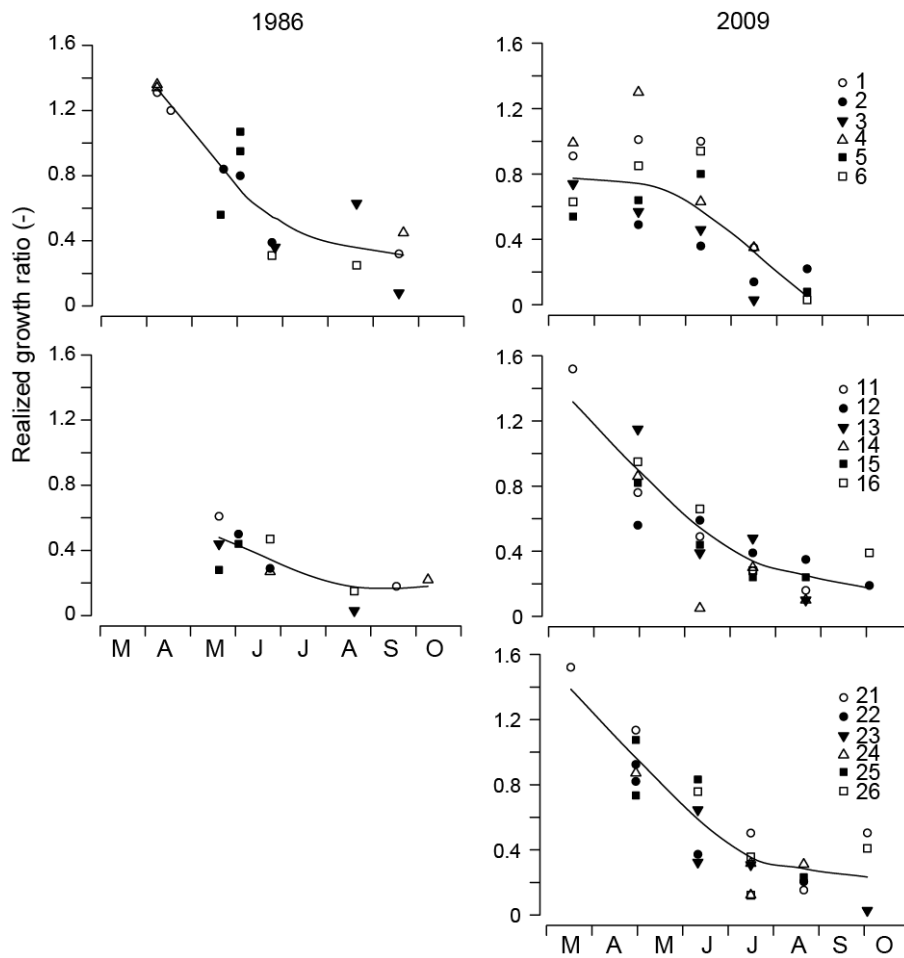
41

42
43
44   Figure 7   Realized growth (ratio between observed growth and maximum possible
45   growth according to the DEB model) for I- and II-group plaice at Balgzand in
46   the period 1975 – 1978. For methodology see Freitas et al. (2012).
47

Figure 8   Realized growth (ratio between observed growth and maximum possible growth according to the DEB model) in 1986 and 2009 at stations located in the intertidal (top panels), subtidal (middle panels) and channels (bottom panel). Solid lines are the LOESS smooth functions fitted to the realized growth ratio data to capture trends over time. For locations of EMOWAD-ZKO stations see Fig. 1. Data for 2009 were originally published in Freitas et al. (2016).

57

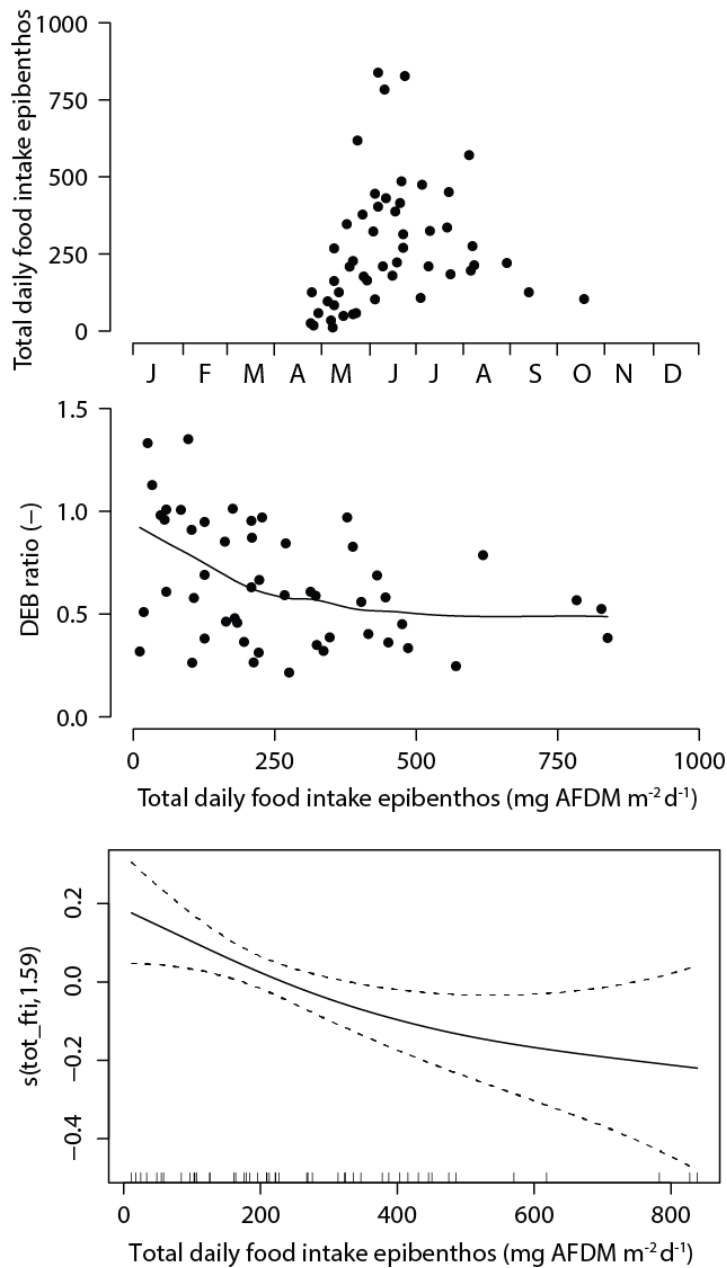58
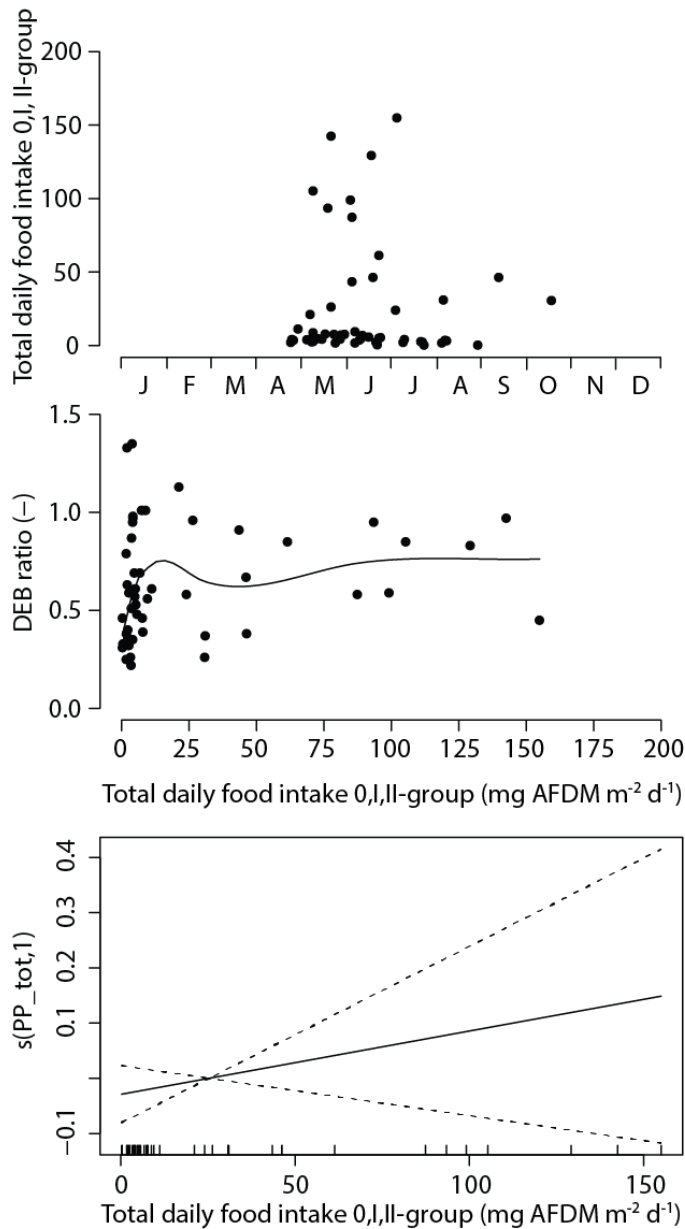
59 Figure 9   Modelled intraspecific competition for food at Balgzand, where daily food

60   intake was estimated on the basis of specific energy requirements, using data

61   that were combined for 1975 – 2009.

62   Top panel: Estimated total daily food intake (mg AFDW m^{-2} d^{-1}) of 0-, I-, and

63   II-group plaice in relation to day number.

64   Middle panel: Realized growth of 0-group plaice (-) in relation to estimated

65   total daily food intake (mg AFDW m^{-2} d^{-1}) of 0-, I-, and II-group plaice.

66   Bottom panel: GAM smoother (n.s.) of relationship between realized growth

67   (-) of 0-group plaice and estimated total daily food intake of 0-, I-, and II-

68   group plaice (mg AFDW m^{-2} d^{-1}).

69

70

71

72

73 Figure 10 Modelled interspecific competition for food at Balgzand, where daily food
74 intake was estimated on the basis of specific energy requirements, using data
75 that were combined for 1975 – 2009.

76 Top panel: Estimated total daily food intake (mg AFDW m^{-2} d^{-1}) of all
77 epibenthic predators (flatfish, gobies and crustaceans) in relation to day
78 number.

79 Middle panel: Realized growth (-) of 0-group plaice in relation to estimated
80 total daily food intake (mg AFDW m^{-2} d^{-1}) of all epibenthic predators.

81 Bottom panel: GAM smoother for thr relationship between realized growth of
82 0-group plaice and estimated total daily food intake (mg AFDW m^{-2} d^{-1}) of all
83 epibenthic predators.
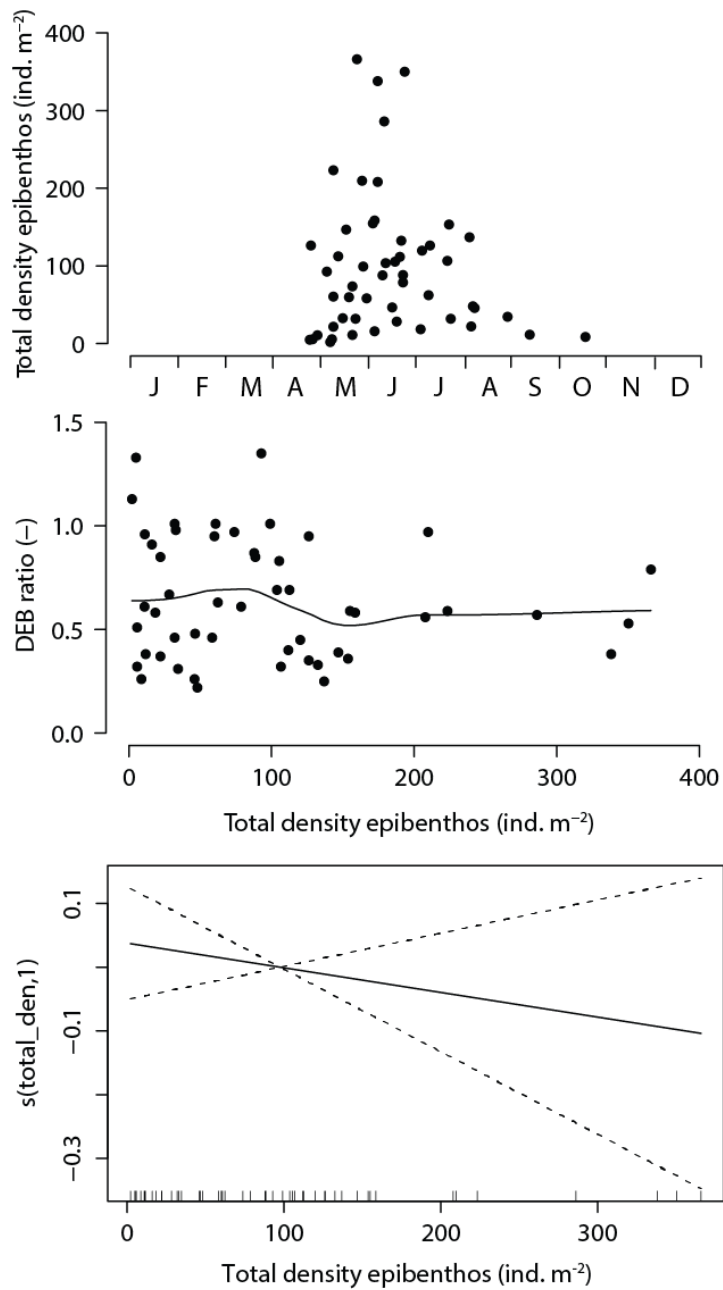
84

85

86   Figure 11   Potential for resource competition for food due to crowding, at Balgzand,
87   using data that were combined for 1975 – 2009.
88   Top panel: Total density (ind. m^{-2}) of all epibenthic predators (flatfish, gobies
89   and crustaceans) in relation to day number.
90   Middle panel: Realized growth (-) of 0-group plaice in relation to total density
91   (ind. m^{-2}) of all epibenthic predators.
92   Bottom panel: GAM smoother (n.s.) of relationship between realized growth
93   (-) of 0-group plaice and total density (ind. m^{-2}) of all epibenthic predators.
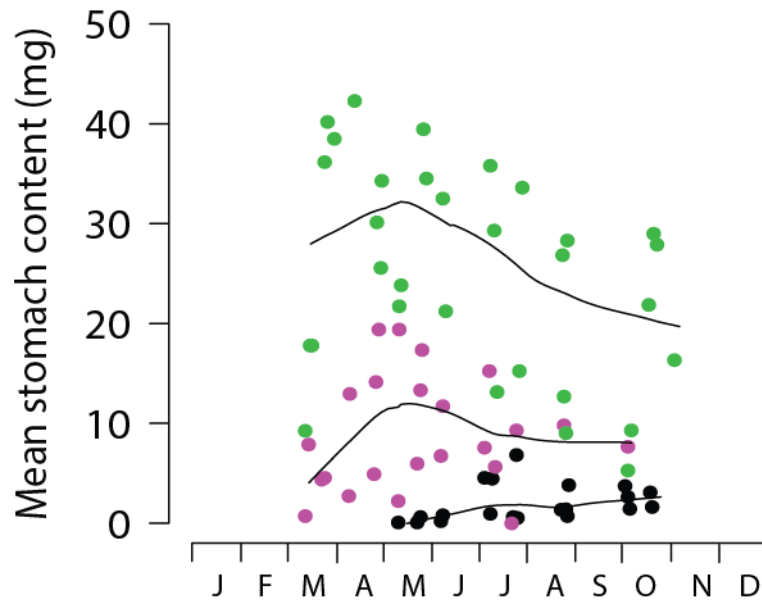
Figure 12 Mean stomach content of juvenile plaice at Balgzand in 1973. Data after Fig.6 in Kuipers (1977). Black: 0-group plaice; pink: I-group plaice; green: II-group plaice. Solid lines represent LOESS smooth functions fitted to the data to capture trends over time.

Table 1: Adjusted coefficients for different fish species for estimating daily food intake. For description of methodology see text and van der Veer et al. (2011). Q_{10} values were taken from Freitas et al. (2010), the wet weight- ash-free dry mass conversion factors (WA) and maintenance coefficients (Main) were taken from de Vlas (1979), van Beek (1976), Brey et al. (2010), van der Veer et al. (2001) and van Lissa (1977).

Species	Q10	WA	Main
Solea solea	2.79	0.20	0.02
Pleuronectes platessa	2.33	0.17	0.02
Pomatoschistus microps	1.53	0.19	0.01
Pomatoschistus minutus	1.53	0.19	0.01
Platichthys flesus	2.33	0.17	0.02
Carcinus maenas	2.16	0.14	0.01
Crangon crangon	2.90	0.19	0.02