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

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12 **ABSTRACT**

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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18 western Dutch Wadden Sea, by analysing published and unpublished information from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

75 assessed. Growth reduction appears to be a general phenomenon among various 0-
76 group flatfish species, at least in shallow intertidal and coastal areas (van der Veer et al.,
77 2010; Freitas et al., 2012; Ciotti et al., 2014). It is unclear whether growth reduction
78 also operates in deeper waters and among elder flatfish age groups. This would require
79 information about growth in I- and II-group flatfish and information from deeper waters.

80   From an energetic perspective, growth reduction boils down to reduced energy
81 availability for growth. According to general Dynamic Energy Budget theory
82 considerations (Kooijman, 2010), this must translate to a reduced mobilization of stored
83 energy due to less food assimilated. Because juvenile flatfish in European waters are
84 mainly benthic polychaete and mollusc feeders (Edwards & Steele, 1968; de Groot,
85 1971; Kuipers, 1977; de Vlas, 1979), sudden decreases in benthic food availability seem
86 unlikely. Moreover, long-term intertidal macrozoobenthic data at the Balgzand intertidal
87 in the Dutch Wadden Sea suggest even an increase in food abundance in summer over
88 the last decades (Dekker, unpubl., in van der Veer et al., 2011). This implies that intra-
89 and/or interspecific food competition might be more likely candidates. If growth
90 reduction of 0-group plaice is caused by intraspecific food competition, a negative
91 relationship between realized growth of the 0-group and the total food uptake of the
92 flatfish species (0-, I- and II-group) would be expected. Growth reduction caused by
93 interspecific food competition would imply a negative relationship between realized
94 growth and food intake by other predatory epibenthic species (e.g., other fish species
95 and crustaceans). An alternative explanation could be resource competition due to
96 crowding, which would imply a negative relationship between realized growth in 0-group
97 plaice and the population density of all predatory epibenthic species.

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

108

109 **2. Material and methods**

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111 *2.1. Data sources*

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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*

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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*

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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*

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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,

sex can be responsible for a size variation at the end of the first year of life at Balgzand of between 8.0 cm (for a male) and 13.5 cm (for a female), a 70% difference. Temperature is a controlling factor (Fry, 1947; Neill et al., 1994) directly affecting growth. Temperature conditions at Balgzand can vary about 1 – 3°C between stations, which would mean a range in size of about 10 – 30% at 10°C, and of 5 – 15 % at 20°C. Salinity on the other hand is a masking factor, loading metabolism (Fry, 1947; Neill et al., 1994) and therefore potentially negatively affecting growth. The Balgzand surveys have illustrated that salinity conditions at Balgzand can be very variable, sometimes on the order of a few hundred percent; however, the quantitative impact on growth is unknown. Reduced growth rates have been reported for 0-group plaice at low salinities (Karakiri & von Westernhagen, 1989), but experimental work showed faster growth at the lowest salinity levels tested (Augley et al., 2008) in a situation of unlimited food. The interaction of food availability with other variables to generate variability in growth response is widely known (Jobling, 1994). Food resources are a limiting factor that can restrict maximum metabolism (Neill et al., 1994). In the Wadden Sea, clear indications of a relationship between food abundance and growth were found (van der Veer & Witte, 1993), whereby a range in growth of 50% was observed, but recently Freitas et al. (2016) could not confirm this relationship.

A comparison of temporal with spatial variability in size within and among local populations might give an insight into the relative importance of the various factors generating growth variability (van der Veer et al., 1994). However, size-selective processes such as size-selective mortality and migration (Kuipers, 1977; van der Veer et al., 1997) might interfere and bias such a comparison. By far the most important appears to be intrinsic factors such as sex, being able to generate differences in growth rates within populations on the order of 70%, and ontogenetic background generating a range of 50% in size. However, van der Veer et al. (2000) argued that the impact of ontogenetic background will vary among years and will normally be relatively low since most of the population will have a relatively similar background.

4.2. Summer growth reduction

The evidence of summer growth reduction in early juvenile flatfish is strong and has been reported for different years, different areas and different species based on different methods (Fonseca et al., 2006; Hurst and Abookire, 2006; van der Veer et al., 2010; Freitas et al., 2012; Ciotti et al 2013a,b). Summer growth reduction might be a general phenomenon: in this study, it was also observed in other age groups (I- and II-group plaice) and in areas other than the intertidal (subtidal, deeper channels). Recently, otolith microstructure analysis of individual flatfish confirmed earlier observations of

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

388   In this study no support was found that the observed summer growth reduction
389 was caused by direct competitive intraspecific interactions between juvenile plaice
390 themselves and only a weak support existed for interspecific competition with other
391 species. Also resource competition did not seem likely. However, these conclusions were
392 based on hauls with a length of about 100 m at high water, while growth heterogeneity
393 already seems to occur even at this small spatial scale of about 100 m (Ciotti et al.,
394 2013a,b). Therefore, it cannot be excluded that the sampling is inadequate for any
395 analysis of direct and indirect competition: at the scale of the length of a haul
396 heterogeneity in growth might already occur. Furthermore, the present analysis based
397 on mean densities does not take into account the spatial heterogeneity in
398 macrozoobenthos in the intertidal (Compton at al., 2013) and the spatial and temporal
399 variation in the distribution of 0-group plaice (Gibson, 1973; Kuipers, 1973; van der
400 Veer & Bergman, 1986). It cannot be excluded that the sampling design has been
401 inadequate for analysing competition and interactions among epibenthic predators and
402 that sampling should be conducted at a smaller scale, as was done for shore crabs
403 *Carcinus maenas* in the same area (Smallegange et al., 2009).

404   Growth reduction induced by changes in food availability does not seem likely at
405 first glance. For benthic predators such as juvenile plaice, predation pressure by juvenile
406 flatfish is rather low compared to food availability, at least for the Balgzand area
407 (Kuipers, 1977; de Vlas, 1979; van der Veer et al., 2011). Also, part of the diet of
408 juvenile flatfishes at Balgzand and in other areas consists of regenerating body parts of
409 benthic prey (among others Macer, 1967; Edwards & Steele, 1968; Kuipers, 1977; de
410 Vlas, 1979; Poxton et al., 1983; van der Veer & Witte, 1993) and maximum predation at
411 Balgzand appears to coincide with maximum productivity of the benthic invertebrates
412 (Kuipers, 1977). However, these considerations are based on potential food availability,
413 while for a predator only harvestable prey matters: the combination of not only density
414 and size (potential food availability), but also of accessibility (Zwarts & Wanink, 1993;
415 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).

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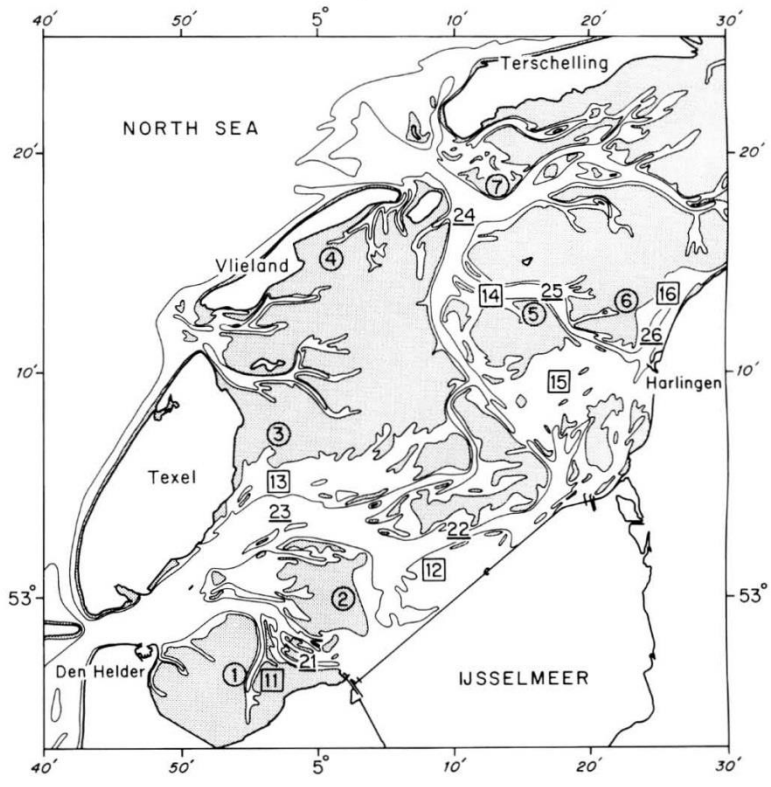
3   Figure 1   Location of the Balgzand and the EMOWAD-ZKO cruises Marsdiep (Station 1-3,

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).

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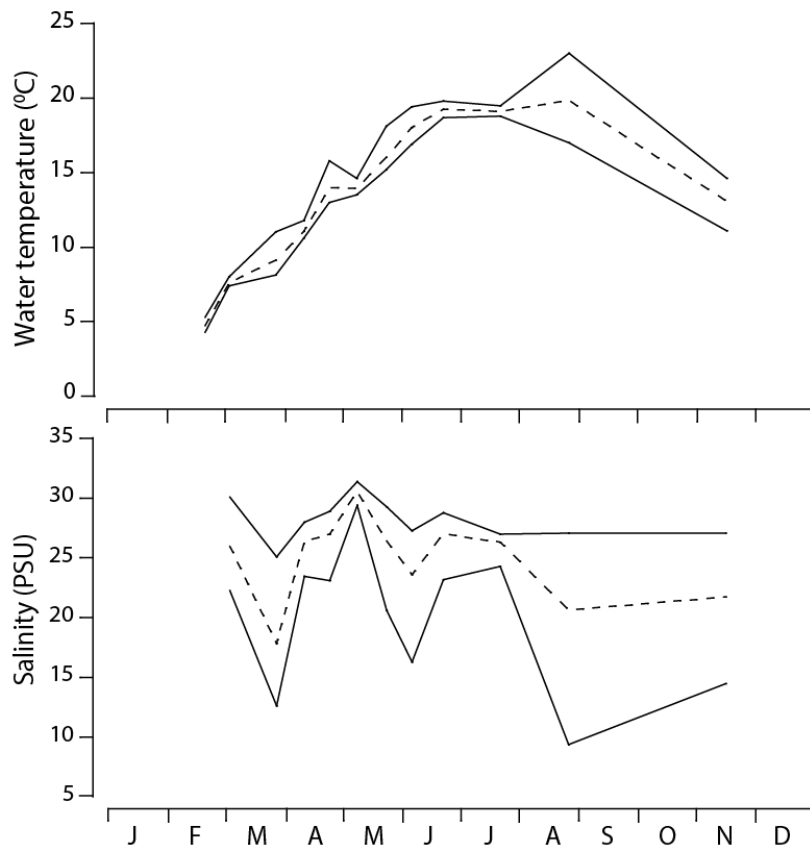
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14   Figure 2   Mean (dashed line), minimum (lower line) and maximum (upper line) bottom
15   water temperature (top panel; °C) and salinity (bottom panel; PSU) at
16   Balgzand at 36 fishing stations during high water in 2000.
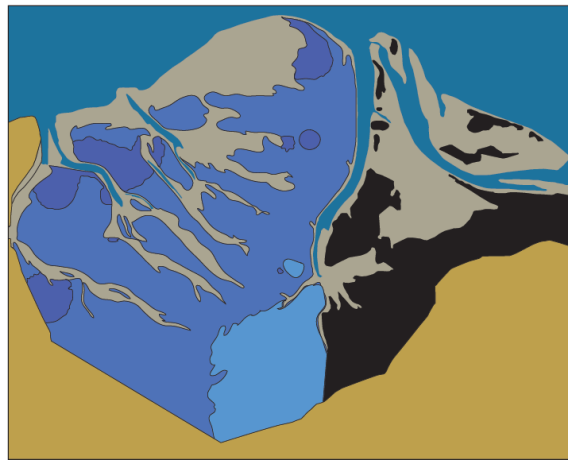
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19   Figure 3   Bottom water temperature (top panel; °C) and salinity (bottom panel; PSU)
20   on 18-19 April 2000 at Balgzand at 36 fishing stations. Temperature ranges
21   from 8°C (dark red) to 11°C (light red), salinity from 23 (light blue) to 28
22   (dark blue). Yellow area refers to mainland, light brown is subtidal area
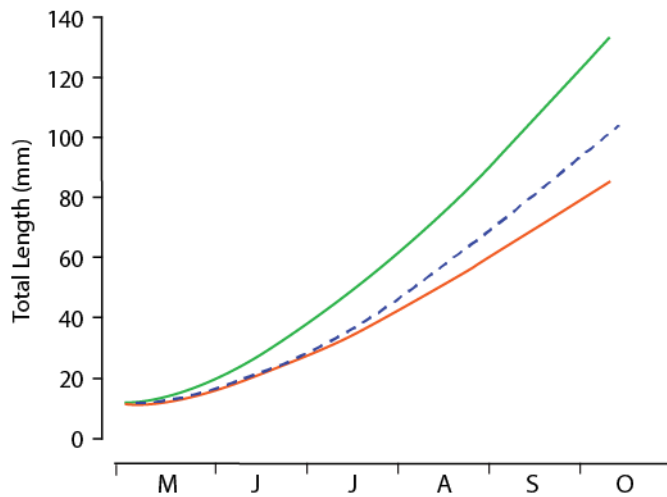23   (between low water and low water − 5m and black area is no data available
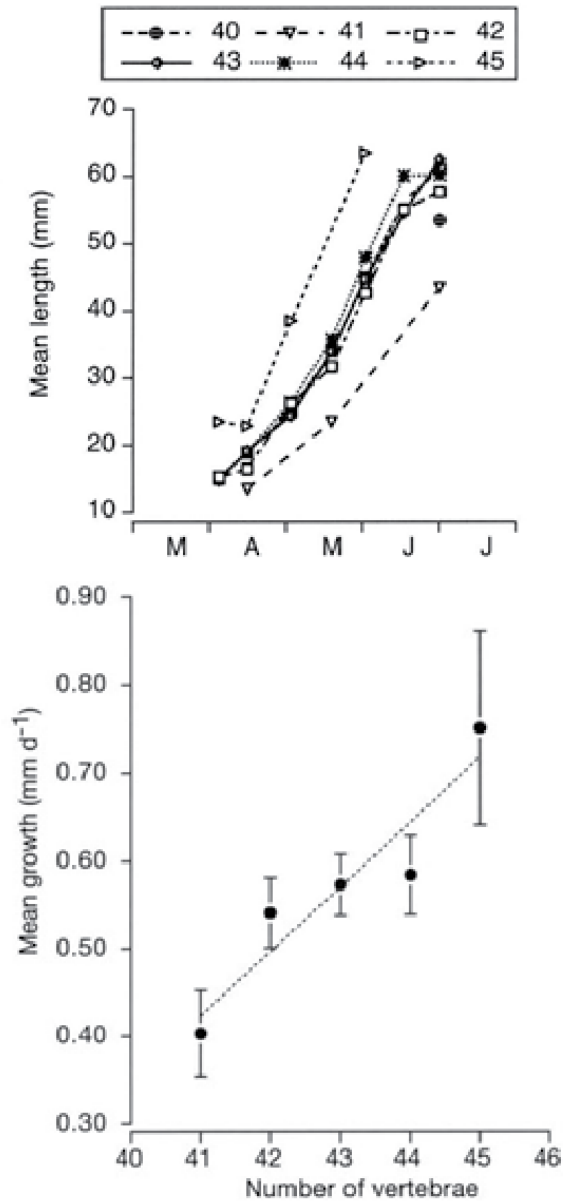
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25 Figure 4   Seasonal pattern of mean length (mm) (top panel) and mean growth (bottom
26   panel) of the various meristic subpopulations of 0-group plaice at the
27   Balgzand in 1995 in relation to number of vertebrae.
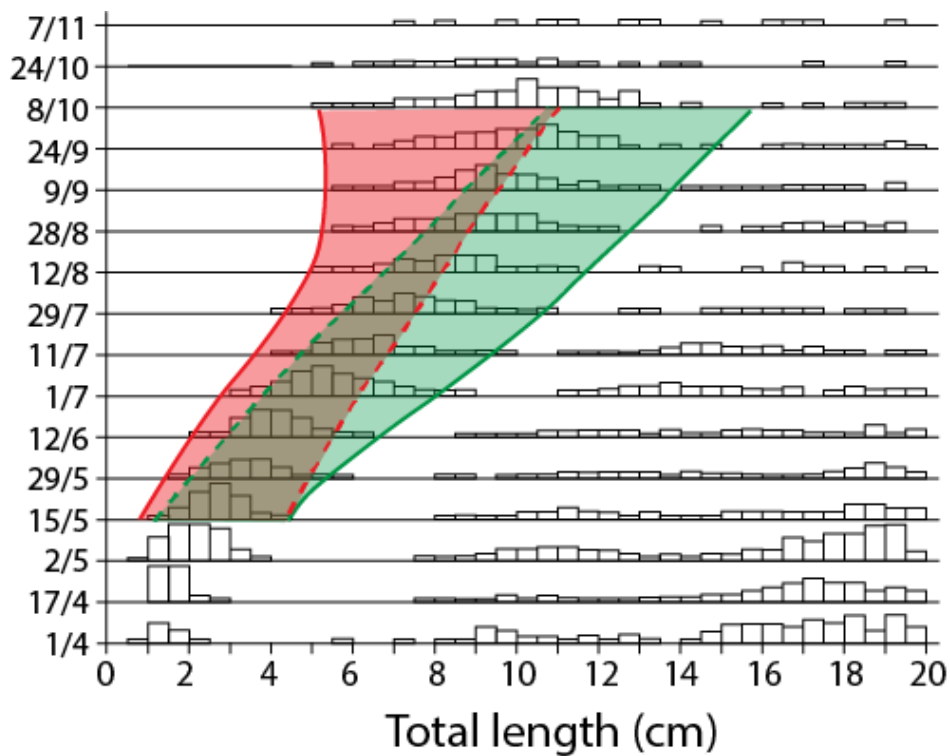
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29   Figure 5   Predicted growth of male (red) and female (green) 0-group plaice at the
30   Balgzand in 1995 from May 1th onwards according to the DEB model and
31   according to the experimentally established growth model of Fonds et al.
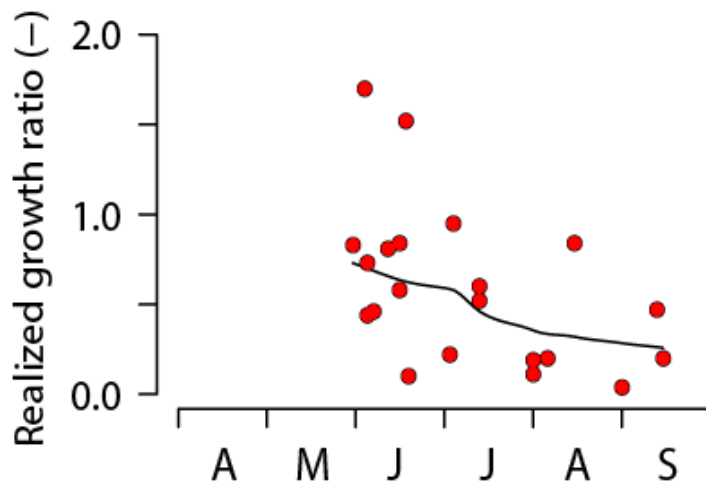32   (1992) (blue).

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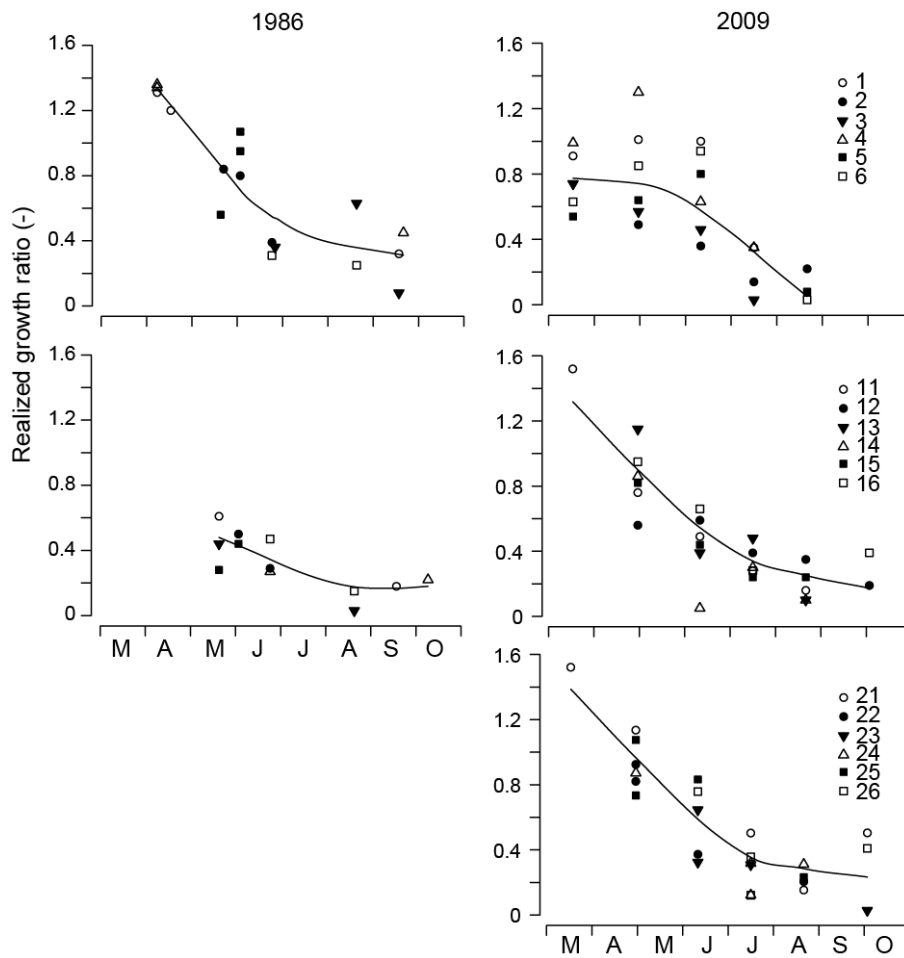
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44 Figure 7   Realized growth (ratio between observed growth and maximum possible
45   growth according to the DEB model) for I- and II-group plaice at Balgzand in
46   the period 1975 – 1978. For methodology see Freitas et al. (2012).

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50 Figure 8   Realized growth (ratio between observed growth and maximum possible
51   growth according to the DEB model) in 1986 and 2009 at stations located in
52   the intertidal (top panels), subtidal (middle panels) and channels (bottom
53   panel). Solid lines are the LOESS smooth functions fitted to the realized
54   growth ratio data to capture trends over time. For locations of EMOWAD-ZKO
55   stations see Fig. 1. Data for 2009 were originally published in Freitas et al.
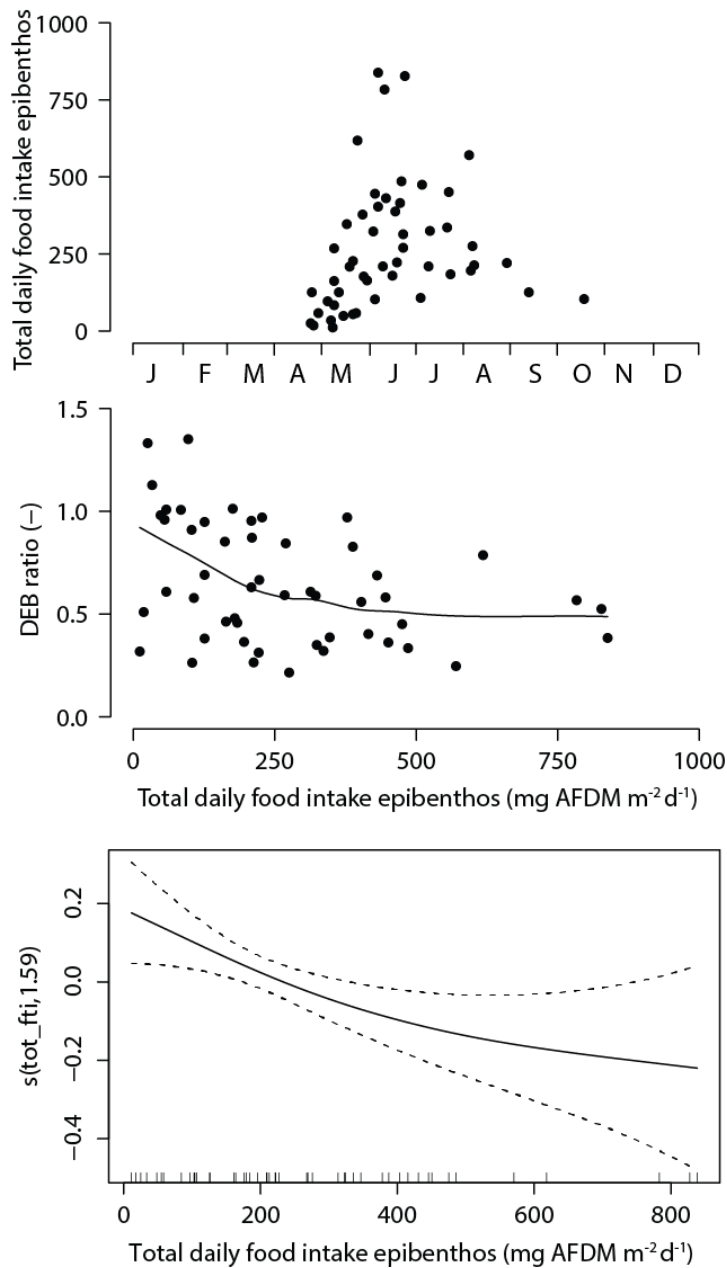56   (2016).
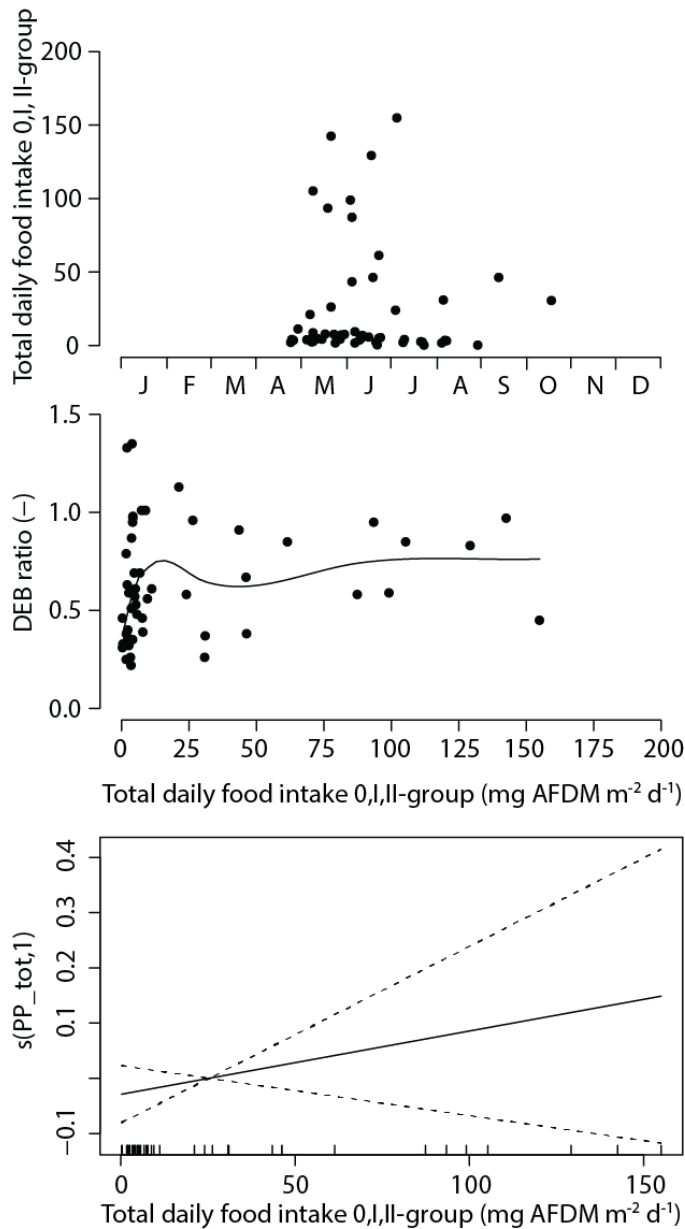
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59 Figure 9   Modelled intraspecific competition for food at Balgzand, where daily food
60   intake was estimated on the basis of specific energy requirements, using data
61   that were combined for 1975 – 2009.
62   Top panel: Estimated total daily 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}).
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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.
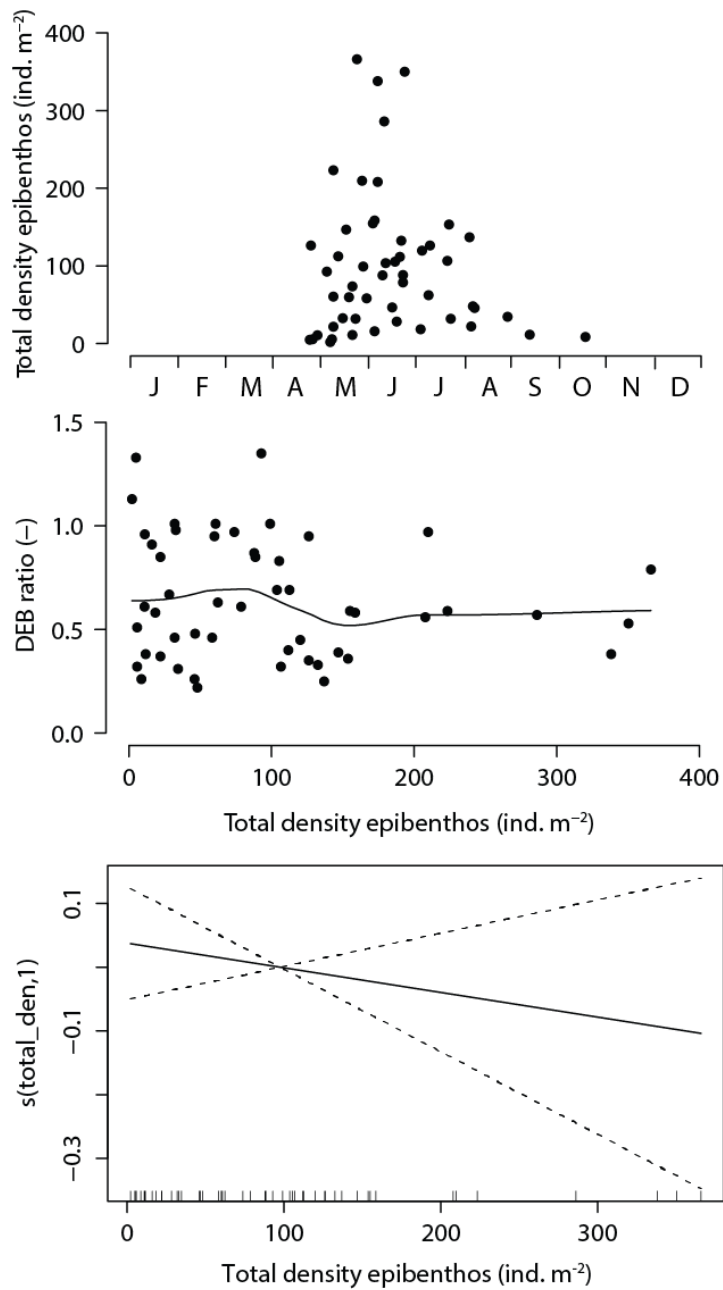
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86　Figure 11　Potential for resource competition for food due to crowding, at Balgzand,
87　　　　　　using data that were combined for 1975 – 2009.
88　　　　　　Top panel: Total density (ind. m^{-2}) of all epibenthic predators (flatfish, gobies
89　　　　　　and crustaceans) 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.
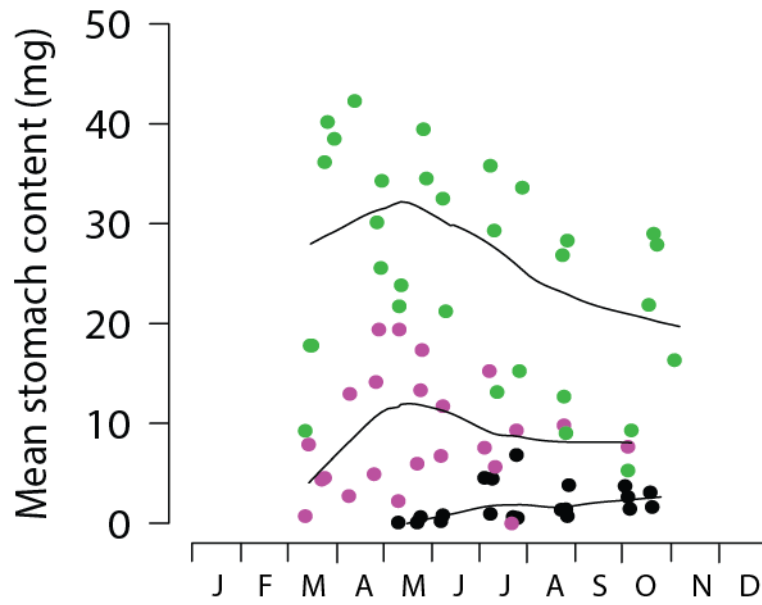
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96　　Figure 12　Mean stomach content of juvenile plaice at Balgzand in 1973. Data after Fig.6

97　　　　　　　in Kuipers (1977). Black: 0-group plaice; pink: I-group plaice; green: II-

98　　　　　　　group plaice. Solid lines represent LOESS smooth functions fitted to the data

99　　　　　　　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