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1 **Parallel changes of *Limecola (Macoma) balthica* populations in the Dutch**
2 **Wadden Sea**

3

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7

8 **Key words:** long-term data, population dynamics, recruitment, survival, synchronized
9 changes, climate change

10 **Abstract**

11 Long-term (>40 y, started in the 1970s) data series of *Limecola (Macoma) balthica* dynamics in
12 4 distant (>100 km) areas of the Dutch Wadden Sea are described and compared, including
13 annual recruitment, total abundance, age composition (recruits/adults) and adult survival. The
14 aim was to determine to what extent long-term changes in *L. balthica* population attributes
15 were synchronous in populations throughout the Dutch Wadden Sea and to identify possible
16 underlying causes. At all 4 sites studied, changes in annual recruitment (n m⁻² of spat-sized
17 animals in summer) was synchronous with long-term declining trends and peaks and lows
18 occurring in the same years at all sites. Adult survival was high for the first 15 to 20 y, but
19 irregular after 1990 with low values for periods of varying length. In contrast to the strongly
20 synchronized recruitment, the low-survival periods were not synchronous over the Wadden
21 Sea. Adult density and total biomass varied in parallel over most sites and were low throughout
22 the Dutch Wadden Sea (less than a quarter of the earlier long-term average) from 2005
23 onwards. The factors suggested to underly these changes in abundance were: (1) negative
24 effects of climate warming on recruitment, which includes higher abundance of predators on
25 young bottom stages, and (2) an unknown cause of enhanced adult mortality, possibly disease.
26 Synchronization in recruitment, adult density and total biomass of *L. balthica* populations
27 throughout the Dutch Wadden Sea indicates that they are part of a Wadden Sea-wide
28 metapopulation.

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34 Introduction

35 Synchrony in fluctuations of population size at distant locations has been observed in a wide
36 variety of species (Liebholt et al. 2004). Examples from the marine environment include rocky
37 shore communities in Shetland (Burrows et al. 2002), invertebrate recruitment on rocky
38 platforms in Chile (Lagos et al. 2007), recruitment in bivalves in the Wadden Sea (Beukema et
39 al. 2001), and mussel stock size in the Wadden Sea (Folmer et al. 2014, Beukema et al. 2015).

40 In the present paper, we compare changes in the population size of the bivalve *Limecola*
41 *balthica* in various parts of the Dutch Wadden Sea. In an earlier paper on dynamics at the
42 Balgzand site (Beukema et al. 2017), we showed that between-year variability in recruitment
43 success and subsequent adult survival together determined year-to-year variation in population
44 size of this species. Therefore, in the present paper, we study how these underlying processes
45 of recruitment and survival varied between different distant sites. In particular, we investigate
46 to what extent these variations were in unison, causing parallel fluctuations in *L. balthica* stock
47 size all over the Dutch Wadden Sea.

48 Some long-term monitoring programs, executed in 4 areas in the Dutch Wadden Sea
49 (Fig. 1), produced suitable data. Unfortunately, such data were not available for German and
50 Danish parts of the Wadden Sea. Data on dynamics of *L. balthica* are particularly suited for
51 studies in population biology. It is a common species in the Wadden Sea, occurring at almost all
52 sampling sites in fair numbers of 100 or more individuals m⁻². On the tidal flats of the Dutch
53 Wadden Sea, it ranked first for commonness (Beukema 1976). In this area, their ages can be
54 read from annual growth marks on the shell. During the 44 years of the study, recruits
55 appeared almost every year in numbers exceeding 10 m⁻² (Beukema and Dekker 2014). Annual
56 survival was relatively high and rarely catastrophic (Beukema et al. 2009). As a consequence,
57 interruptions of series of *L. balthica* numbers by absence of data are scarce: their numbers
58 rarely declined to levels below detection limit of the monitoring series. Among the 4 main
59 species of bivalves in the Wadden Sea, *L. balthica* was the one with the lowest coefficient of
60 variation for numbers and biomass (Beukema et al. 2001).

61 Various studies on possible consequences of fishery impact and of climate change point
62 to declining trends of Wadden Sea stocks of *L. balthica*. Sediment disturbance by cockle fishery
63 has been suggested to reduce bivalve recruitment for prolonged periods (Piersma et al. 2001),
64 but direct evidence for prolonged negative effects of the cockle fishery on *L. balthica*
65 abundance appear to be lacking. The mechanical cockle fishery in the Dutch Wadden Sea was
66 particularly intense in the 1980s and early 1990s, but ended in 2004 (in some areas already in
67 1993).

68 The climate in the study area is warming. Nowadays, mean annual water temperatures
69 in the Wadden Sea area show a rising trend and are about 1.5 °C higher than half a century ago
70 (Van Aken 2008, Beukema et al. 2009). The Wadden Sea population of *L. balthica* lives in the
71 warmer southern part of its distribution area (Beukema and Meehan 1985). Its reproductive
72 output (Honkoop and Van der Meer 1997, Philippart et al. 2003) and recruitment (Beukema et
73 al. 1998, 2009) were generally higher after cold than after mild winters. Recruitment success
74 was of overriding importance for population dynamics and production (Van der Meer et al.
75 2001, Dekker and Beukema 2007). Rising water temperatures initiated a chain of cause-effect
76 relationships by enhancing the pressure of epibenthic predation on tiny (<1 mm shell length)
77 just-settled bivalve post-larvae and thus reducing recruitment in several bivalve species,
78 including *L. balthica* (Beukema and Dekker 2014). Apart from recruitment, also annual survival
79 strongly affects *L. balthica* abundance and biomass (Beukema et al. 2010, 2017). In years with
80 elevated temperatures mortality rates were higher than in years with relatively low
81 temperatures (Beukema et al. 2009). Thus, a declining trend in *L. balthica* abundance may be
82 expected in a period with increasing temperatures. both from reduced recruitment as well as
83 from increased adult mortality.

84 The aims of the present paper are:

- 85 1. Showing to what degree changes in the size of various *L. balthica* populations all over
86 the Dutch Wadden Sea were in synchrony and point to the presence of a single
87 population in this area;
- 88 2. Relating the changes in stock size to underlying changes in rates of recruitment and
89 adult survival (as shown in detail for the Balgzand population in Beukema et al. 2017);
- 90 3. Showing in how far fluctuations in recruitment and survival were in unison all over the
91 Dutch Wadden Sea;
- 92 4. Trying to find underlying causes of changes in population attributes of *L. balthica*.

93 **Methods**

94 **Sampling areas**

95 The 4 sampling areas were, arranged from west to east: Balgzand, Sublitoral, Piet Scheveplaat,
96 and Groninger wad (Fig. 1). We give short descriptions and refer to publications for more
97 details.

98 The Balgzand area of 50 km² of tidal flats, with 15 sampling sites (mostly 1-km transects)
99 at strongly varying intertidal levels (between about +0.2 and -0.8 m relative to mean-tide level)
100 and with a wide range of sediment composition, is described in detail in Beukema and Cadée

101 (1997). Median grain size of the sediment varied from about 90 to 250 μm and silt content
102 (proportion $<16 \mu\text{m}$) from 0.1 to 30%.

103 The Sublitoral area is an extensive subtidal area with 3 transects of 1.5 km at depth of
104 between 1.5 and 4.7 m below mean tide level. Median grain size of the sediment varied from
105 about 140 to 175 μm and silt content (proportion $<16 \mu\text{m}$) from about 2 to 6% (Dekker 2012).

106 The Piet Scheveplaat area is a tidal flat of a few km^2 with 3 transects of 760 m at a level
107 of +0.5 to -0.7 m relative to mean-tide level, median grain sizes of 145 to 181 μm and silt
108 contents of 0.5 to 6.5 % (Dekker 2009).

109 The Groninger wad area is a 10 km^2 tidal flat area with 5 sampling squares of 900 m^2 at a
110 level of about 0 to -0.5 m relative to mean-tide level, median grain size of 100 to 145 μm and
111 silt contents of 1 to 10% (Van der Graaf and Tydeman 2008).

112 A 17-year data series for a part of the western Wadden Sea that was reported by
113 Compton et al. (2016) could not be used, because the animals were not properly aged (only
114 divided into 2 size classes).

115 **Bivalve sampling**

116 Most areas were sampled in a consistent way twice a year: in late winter/early spring
117 and in late-summer. Bivalves were sorted from the sieved (1-mm mesh size) samples, assigned
118 to age classes (cohorts were indicated by the year of birth), and counted. Numerical densities
119 were expressed in n m^{-2} and presented as multi-station means. Surface areas sampled annually
120 amounted to about 15 m^2 on Balgzand, 3 m^2 in the Subtidal, 1.6 m^2 on Piet Scheveplaat and 1
121 to 2 m^2 on Groninger wad. Core size varied from 0.01 to 0.1 m^2 and sampling depth from 20 to
122 30 cm. This variation will not have affected the estimates of *L. balthica* abundance.

123 Recruitment (numerical density of a new cohort) was assessed at a bivalve age of about
124 0.3 y in late-summer. At that time the animals were still of spat size (mostly $< 7 \text{ mm}$ shell
125 length).

126 Annual survival of adults was expressed as the percentage of the total numbers of 1.8 or
127 more years old individuals in a certain year that were still alive 1 y later: $100 \cdot (\text{n m}^{-2} \text{ of } 2.8^+\text{y-}$
128 $\text{olds in year } n+1 / \text{n m}^{-2} \text{ of } 1.8^+\text{y-olds in year } n)$. To avoid extreme variability by the use of too
129 low numbers of departure, we did not use percentages that were based on numbers of 1.8⁺y-
130 olds of less than 10 m^{-2} .

131 The size of the total *L. balthica* stocks was expressed in 2 ways: in units of numerical
132 density (n m^{-2}) of adult individuals and in units of biomass ($\text{g ash-free dry mass [AFDM] m}^{-2}$).

133 The statistical method used was the Pearson correlation test. Because of the extreme
134 variability in recruitment success, recruit densities were evaluated after ¹⁰log transformation.

135

136

Data sources

137 Balgzand data were collected by JJB and RD and are stored in the NIOZ (Royal Netherlands
138 Institute for Sea Research) data base. Sublittoral data were collected by RD and published in a
139 series of reports (Dekker 2012 and earlier reports in the same series). Data for years after 2010
140 are stored in the NIOZ data base.

141 Piet Scheveplaat data were reported by Laufer (1992) for 1978-1990, by RD (1991-2008,
142 see Dekker 2009 and earlier reports) and by some other investigators in later years (see Wanink
143 et al. 2014 and earlier reports in the same series). Biomass data in Laufer (1992) were
144 converted to late-winter values.

145 Groninger wad data were collected by K. Essink and R. Koeman and compiled by JD
146 (1976-2003). Part of the data are reported in Van der Graaf et al. (2009) (1975-2006), Van der
147 Graaf and Tydeman (2008) (courtesy R.Koeman) (1998-2007), Wanink et al. (2014) and earlier reports
148 in the same series (2008-2014).

149

150 Results

151

Recruitment

152 Annual recruitment ($n\ m^{-2}$ of spat) of *Limecola balthica* as assessed in late summer was highly
153 variable among years, varying over 3 orders of magnitude. Therefore, these data were plotted
154 at a ¹⁰log scale for clarity (Fig. 2). At first sight, the long-term patterns for the 4 areas shown in
155 Fig. 2 revealed a clear resemblance, indicating that success or failure in the 4 areas took place
156 mostly in the same years. Indeed, this synchrony proved to be statistically significant for 5 of
157 the 6 possible comparisons (Table 1a). The strongest correlations ($r > 0.6$, $r^2 > 0.4$; Pearson
158 correlation) were found in pairs of nearby places: the westernmost comparison between
159 Balgzand and Sublittoral and the easternmost comparison between Piet Scheveplaat and
160 Groningen.

161 In the years after 2000, recruitment failed ($n < 20\ m^{-2}$) several times and more or
162 less synchronized. Extremely low recruitment occurred particularly around 2007: Balgzand:
163 2004-2012, sublittoral: 2007-2011, Piet Scheveplaat: 2006-2008, and Groningen 2005-2008.
164 Significantly declining trends over the entire periods of observation were found in 3 out of the 4

165 studied areas. On Balgzand, the Pearson-r value for the correlation of log recruit density with
166 year number amounted to -0.70 ($n = 43$, $p < 0.0001$), in the sublittoral area to $r = -0.80$ ($n = 27$,
167 $p < 0.0001$), and at Groninger wad to $r = -0.43$ ($n = 37$, $p < 0.01$). At the Piet Scheveplaat, no
168 significant negative trend was observed ($r = -0.18$, $n = 34$, $p = 0.3$).

169 For the first 20 to 25 years of the period of observation, recruitment was generally
170 successful (about 100 or more spat individuals m^{-2}) in the 3 intertidal areas (Fig. 2). During these
171 initial periods, peaks and lows frequently occurred in the same years in the 3 areas. Peak values
172 were found particularly after the 3 coldest winters of the period: in 1979, in 1987, and in 1996 (
173 Wadden Sea water temperatures in winter can be found in figure 3 of Beukema and Dekker
174 (2014)). Indeed, in all 3 areas, recruitment in this initial period was negatively correlated with
175 water temperature in the preceding winter: Balgzand $r = -0.74$ ($p < 0.001$), Piet Scheveplaat $r = -$
176 0.51 ($p < 0.02$), and Groningen $r = -0.59$ ($p < 0.01$).

177 **Adult survival**

178 For prolonged initial periods, the proportions of adults that survived from one year to the next
179 were rather constant in all areas, amounting to 60 to 80% in the 3 intertidal areas and to 70 to
180 100% in the sublittoral area (Fig. 3). After 1989, long periods with high survival alternated with
181 short periods with seriously reduced survival rates: single years in some locations (e.g.
182 Groninger wad) and in other locations periods up to 7 years (e.g. Balgzand). Generally, these
183 short periods did not occur simultaneously in the 4 areas: Balgzand 1999-2005 and again 2014;
184 sublittoral 2005-2006; Piet Scheveplaat 2009-2010; and Groningen 1990, 1995, 1997-1998, and
185 2009 (Fig. 3). As a consequence of this lack of synchronization, survival rates in the 4 areas were
186 not significantly correlated: the 6 Pearson-r values shown in Table 1b ranged from -0.24 to
187 $+0.09$ ($p > 0.5$ in all cases). None of the long-term trends in Fig. 3 was statistically significant.

188 For the 1975-1995 period (i.e. the period before the sudden declines in survival in most
189 locations), we found a negative correlation between winter water temperatures and
190 subsequent survival exclusively at Balgzand. In the other areas, this correlation was close to 0
191 and non-significant. At Balgzand, survival rates were lower by 2% for each $^{\circ}C$ water
192 temperatures were higher (for details see Beukema et al. 2017).

193 **Stock size**

194 In all 4 sampling areas, annual values of adult density (Fig. 4) and total biomass (Fig. 5) varied
195 strongly, from close to 0 to about 3 times their long-term average. The long-term means of
196 adult density estimates amounted to about $50 m^{-2}$ in the sampled areas in the western Dutch
197 Wadden Sea (Fig. 4a) and substantially higher values of about 100 and $200 m^{-2}$ in the eastern
198 half of the Dutch Wadden Sea (Fig. 4b). The long-term mean biomass values amounted to about

199 2 g m⁻² in the 2 areas in the western part (Fig. 5a) and to higher values in the 2 areas in the
200 eastern part (Fig. 5b: about 3 g m⁻² on Piet Scheveplaat and about 6 g m⁻² on Groninger wad).

201 Stock changes from one year to the next were generally only moderate: the observed
202 fluctuations (Figs 4 and 5) were characterized by prolonged periods with either continually
203 increasing or continually declining trends. In the 2 sampling areas in the eastern Dutch Wadden
204 Sea, patterns of fluctuations in numbers and biomass resembled each other rather closely and
205 the correlations of their annual values were highly significant (Table 1c and 1d: Pearson r =
206 +0.80 and +0.85, n = 34, p<0.001, for adult numbers and total biomass, respectively). The
207 pattern found in the sublittoral of the western Dutch Wadden Sea showed some resemblance
208 with the 2 patterns found in the eastern Dutch Wadden Sea with statistically significant (mostly
209 p<0.01) r-values of around +0.6 (Table 1c and 1d). Only the Balgzand patterns for both adult
210 densities as well as biomass clearly differed from the 3 other areas: with non-significant r values
211 of mostly around 0.3 for all 6 correlations with the other areas. Unique characteristics at
212 Balgzand were peaks around 1987 and 1993, and a lack of the peaks that occurred in the 3
213 other areas around 2002.

214 More or less consistently declining long-term trends were observed on Balgzand already
215 from 1993-1996 on, in the sublittoral from 2000-2002 on, on P.Scheveplaat from 2001-2003 on,
216 and on Groninger wad from 2000-2002 on. The synchronized declines in the latter 3 areas
217 which started in 2001 were all statistically significant (p<0.02) with Pearson r-values for
218 correlations with year number of around -0.7.

219 **Discussion**

220 **Synchronized recruitment**

221 Years of successful and failing recruitments alternated in largely similar ways in the 4 sampling
222 areas. Moreover, the areas had a downward long-term trend in common. Such synchronization
223 points to a common controlling mechanism that is effective all over the Wadden Sea. The
224 warming climate could be such a cause: water temperatures increased between 1970 and 2010
225 all over the Dutch Wadden Sea and fluctuated in harmony (Tulp et al. 2012). Recruitment was
226 indeed high everywhere after the 3 coldest winters (1979, 1987, and 1996) of the study period
227 and we found negative correlations between winter temperatures and subsequent recruitment
228 for the first half of the period of observation when recruitment was still at a high level. Cold
229 winters cause low abundance of the main predators, shrimps and shore crabs, of tiny, just-
230 settled, bivalve spat (Strasser 2002; Strasser et al. 2003; Beukema and Dekker 2005, 2014). As a
231 consequence, high proportions of the spat survive. Shore crab abundance strongly increased
232 (about 5-fold) all over the Dutch Wadden Sea between 1994 and 2010 (Tulp et al. 2012). Shrimp
233 abundance strongly increased during the last 4 decades in the western half of the Dutch

234 Wadden Sea, remained at roughly the same level in the area around Piet Scheveplaat and
235 halved in the area around Groninger wad (Campos et al. 2010, Tulp et al. 2012). The increases
236 in total (crab + shrimp) epibenthic predation pressure might largely explain the observed
237 declining trends in recruitment success in *L. balthica* all over the Dutch Wadden Sea, but
238 probably not the sudden and dramatic declines between 2005 and 2010.

239 Synchronization in *M. balthica* recruit abundance appears not to be restricted to the
240 Dutch Wadden Sea. For the 1976-1999 period, recruitment at the German island of Norderney
241 was reported to be significantly positively correlated with that in Groningen and Balgzand
242 (Beukema et al. 2001). The peaks observed on Balgzand in 1979 and 1987 were also found at
243 Norderney (Strasser et al. 2003).

244 **Non-synchronized survival**

245 For a long initial period (before 1989), survival rates were invariably high, around 60% y^{-1} or
246 higher. Starting from 1990, however, years or groups of years were observed at all locations
247 with substantially lower survival. These years were not synchronized, pointing to local causes,
248 which are as yet unknown. A detailed study on Balgzand revealed a shifting geographic pattern
249 of survival rates, suggesting the expansion of a contagious disease, taking about 5 years to
250 reach all sampling sites within the 50-km² area (Beukema et al. 2017). However, the exact cause
251 of the catastrophic mortalities is still an object of investigation. So far, the earlier stable
252 situation has not yet been restored anywhere: years with low survival still occasionally occur in
253 all sampling areas.

254 **Partly synchronized stock sizes**

255 At any moment, stocks of *L. balthica* are made up of several year classes. As a consequence,
256 between-year changes in stock size were relatively small (by the autocorrelation of data of
257 successive years). Generally, dramatic changes only occurred over periods of several years.
258 Gradual changes were also promoted by the non-simultaneous occurrence of incidences of
259 reduced survival at nearby sampling places (as shown within the Balgzand area in Beukema et
260 al. 2017). The monitored tidal-flat areas were relatively rich in *L. balthica*: Dutch Wadden Sea-
261 wide mean biomass values of this species on tidal flats were 2.2 and 1.3 g AFDM m⁻² in the
262 1970s (Beukema 1976) and 2000s (Compton et al. 2013), respectively.

263 The long-term patterns for adult densities and total biomass were clearly similar
264 between the 2 easternmost sites with peaks in the early 1980s and again around 2000. For the
265 1990-2007 period, the observations by De Mesel et al. (2011) revealed a similar pattern not
266 only in the entire eastern half of the Dutch Wadden Sea, but also in the nearby coastal zone of

267 the North Sea . A similar pattern for biomass was also observed about 60 km east of Groninger
268 wad, at the German island of Norderney (Beukema et al. 1996).

269 On Balgzand, however, a unique pattern was found, with a strong abundance peak in
270 1992-1993 (due to an extraordinarily successful recruitment in 1991), followed by a prolonged
271 decline for a long period that was characterized by declining recruitments and adult survival
272 rates. Only in the most recent years, recruitment increased again to near earlier levels. For the
273 last 2 decades, such patterns were also observed in part of the western half of the Dutch
274 Wadden Sea (Compton et al. 2016; De Mesel et al. 2011) and also in the coastal zone of the
275 main land south of the Wadden Sea (De Mesel et al. 2011). Even farther south, in the south-
276 westernmost part of The Netherlands, they found different patterns. Thus, the Balgzand
277 patterns of adult densities and recruitment were representative for a wider area, including the
278 westernmost part of the Dutch Wadden Sea and the main-land coast south of it (almost 200
279 km).

280 In all Wadden Sea areas outside Balgzand, consistent declines in adult abundance and
281 biomass started several years later than on Balgzand: only around 2003. In these areas,
282 recruitment success remained high until around 2003. Everywhere in the Dutch Wadden Sea,
283 adult numbers and biomass were low after 2005 and recruitment was low for these years,
284 whereas years with low adult survival were still frequent. Both recruitment and survival
285 (mortality) are known to seriously affect biomass in *L. balthica* and other bivalves (Van der
286 Meer et al. 2001, Beukema et al. 2010, Magelhaes et al. 2016).

287 **Conclusions**

288 In the 4 sampling areas scattered over the Dutch Wadden Sea, we found several similarities in
289 the long-term patterns of recruitment success and total abundance. Low values were observed
290 everywhere in the Dutch Wadden Sea for the most recent decade, when recruitment was low
291 and years of low survival were frequent. Such similarities point to the existence of one single
292 population of *L. balthica* in the Dutch Wadden Sea (extending to the near-coastal areas of the
293 North Sea along the Dutch mainland coast and the Dutch Frisian islands). This population was
294 struck by incidences of sudden marked reductions in survival that occurred everywhere in the
295 Dutch Wadden Sea since 1990, but at different times and lasting for 1 to 7 years. Together with
296 reduced recruitment, occurring everywhere in the Dutch Wadden Sea since 2000, adult stocks
297 declined since around 2000. It is difficult to tease apart the influences of recruitment and
298 survival. An attempt for the Balgzand data (Beukema et al. 2017) pointed to a decisive influence
299 of reduced survival, affecting recruitment via adult stock size, the latter becoming too small to
300 produce sufficient offspring.

301 Negative fishery effects cannot explain the ubiquitous decline of stocks around 2000, as
302 fishery for cockles and mussels on tidal flats completely ended near that time (2004), and in
303 some areas (such as Balgzand: 1993) already several years before. Stock declines continued
304 after the fishery had stopped and stock increases were found in the eastern Dutch Wadden Sea
305 for the years just before 2004. We conclude that no consistent effects of fisheries on *L. balthica*
306 abundance can be discerned.

307 An influence of the warming climate could be shown for the period before survival and
308 recruitment strongly declined: throughout the Dutch Wadden Sea we found negative
309 correlations (with r values of around -0.6) between winter temperatures and subsequent
310 recruitment. On Balgzand also survival declined with increasing temperatures (Beukema et al.
311 2009, 2017). After around 1995, however, the influence of catastrophic mortality rates became
312 overwhelming, obscuring possible temperature effects. Nowadays, a return to the usual
313 survival rates appears to be still incomplete. Whenever survival recovers to more normal
314 values, we would expect a somewhat lower abundance of *L. balthica* at the ongoing climate
315 warming as a consequence of lower recruitment and survival at the mostly higher
316 temperatures. Caution, however, is warranted in predictions of temperature effects. As Van der
317 Meer et al. (2013) have shown, the effects of temperature change on benthic fauna in the
318 Wadden Sea are poorly predictable.

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321

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421

422 **Legends**

423 Fig.1. Map of the western part of the Wadden Sea, showing locations of the long-term
424 monitoring of the macrozoobenthos. From West to East: Balgzand, subtidal western Wadden
425 Sea, Piet Scheveplaat, and Groninger wad.

426 Fig. 2. Long-term data series of annual *Limecola balthica* recruitment, expressed in $n\ m^{-2}$ of
427 spat-size individuals, assessed in late summer in 4 areas in the Dutch Wadden Sea:

- 428 (a) (solid points) Averages of 15 sampling places scattered on tidal flats of Balgzand, in the
429 43 yr of the 1973-2015 period.
430 (open points) Averages of 3 transects in a sublitoral area about 25 km northeast of
431 Balgzand in the 27 yr of the 1989-2015 period.
- 432 (b) (solid points) Averages of 3 transects on tidal flats called Piet Scheveplaat, sampled in 34 yr
433 within the 1978-2014 period.
434 (open points) Averages of 5 sampling places in a tidal-flat area north of Groningen, sampled in
435 37 yr of the 1975-2014 period.

436 Fig. 3. Long-term data series of annual *Limecola balthica* survival, expressed as a percentage of
437 individuals of >1.8 y old that were still alive 1 yr later. Numbers assessed in late winter/early
438 spring in 4 areas in the Dutch Wadden Sea:

- 439 (a) (solid points) 15 sampling places scattered on tidal flats of Balgzand, in the 44 yr of the
440 1973-2016 period.
441 (open points) 3 transects in a sublitoral area about 25 km northeast of Balgzand in the
442 26 yr of the 1990-2015 period.
- 443 (b) (solid points) 3 transects on tidal flats called Piet Scheveplaat, sampled in 33 yr of the 1978-2010
444 period.
445 (open points) 5 sampling places in a tidal-flat area north of Groningen, sampled in 33 yr of the
446 1976-2010 period.

447 Fig. 4. Long-term data series of annual estimates of numerical density of adult (age 1.8 yr or
448 more) *Limecola balthica* in late-winter/early spring, expressed in $n\ m^{-2}$, in 4 areas in the Dutch
449 Wadden Sea:

- 450 (a) (solid points) Averages of 15 sampling places scattered on tidal flats of Balgzand,
451 sampled in the 44 yr of the 1973-2016 period.
452 (open points) Averages of 3 transects in a sublitoral area about 25 km northeast of
453 Balgzand, sampled in the 27 yr of the 1990-2016 period.
- 454 (b) (solid points) Averages of 3 transects on tidal flats called Piet Scheveplaat, sampled in 34 yr
455 within the 1978-2011 period.

456 (open points) Averages of 5 sampling places in a tidal-flat area north of Groningen, sampled in
457 36 yr of the 1976-2011 period.

458 Fig. 5. Long-term data series of annual total *Limecola balthica* biomass in late-winter/early
459 spring, expressed in g AFDM m⁻², in 4 areas in the Dutch Wadden Sea: as detailed in the legend
460 of Fig. 4, but a few values added of estimates for years with lacking age distributions.

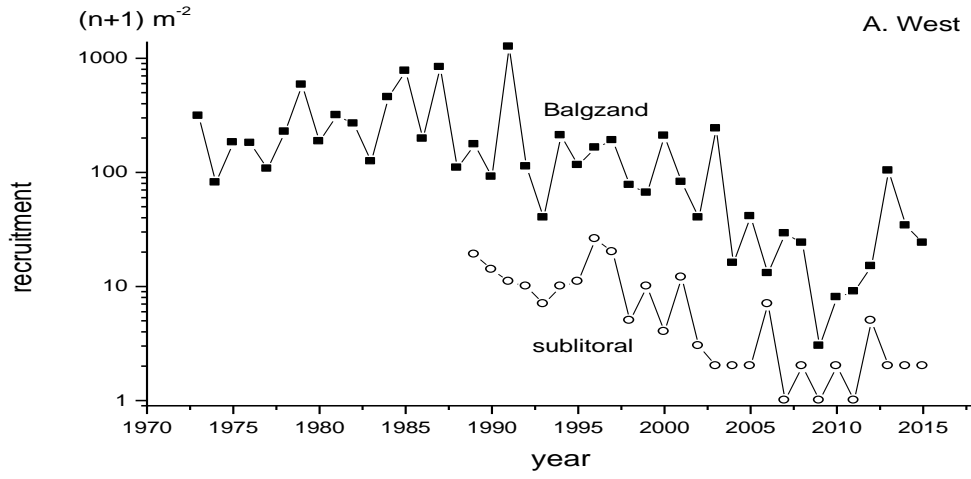
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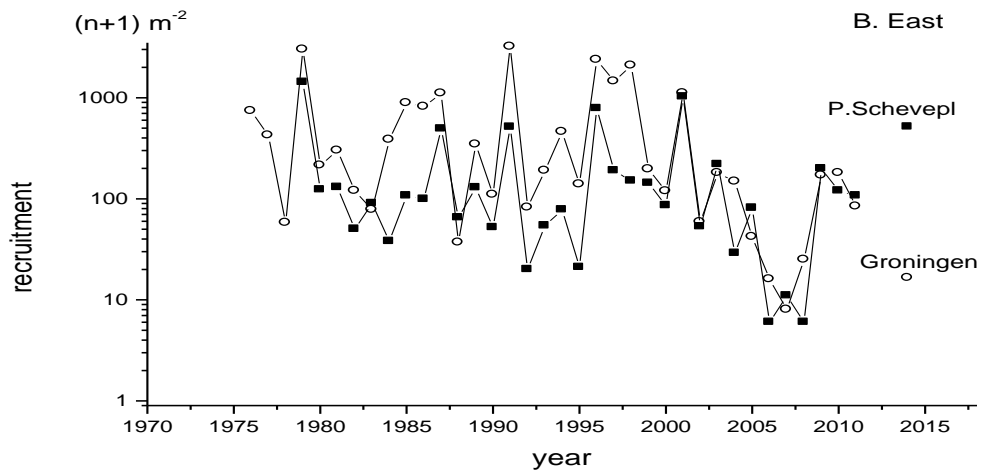
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468 Fig. 2

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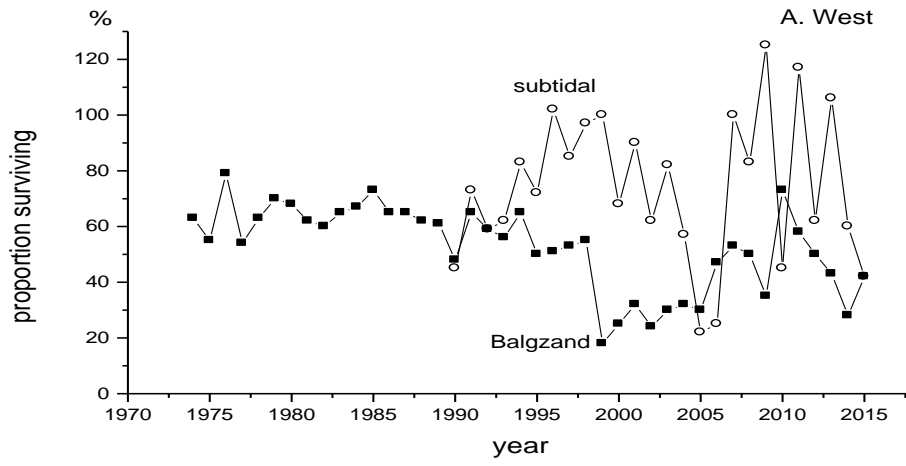
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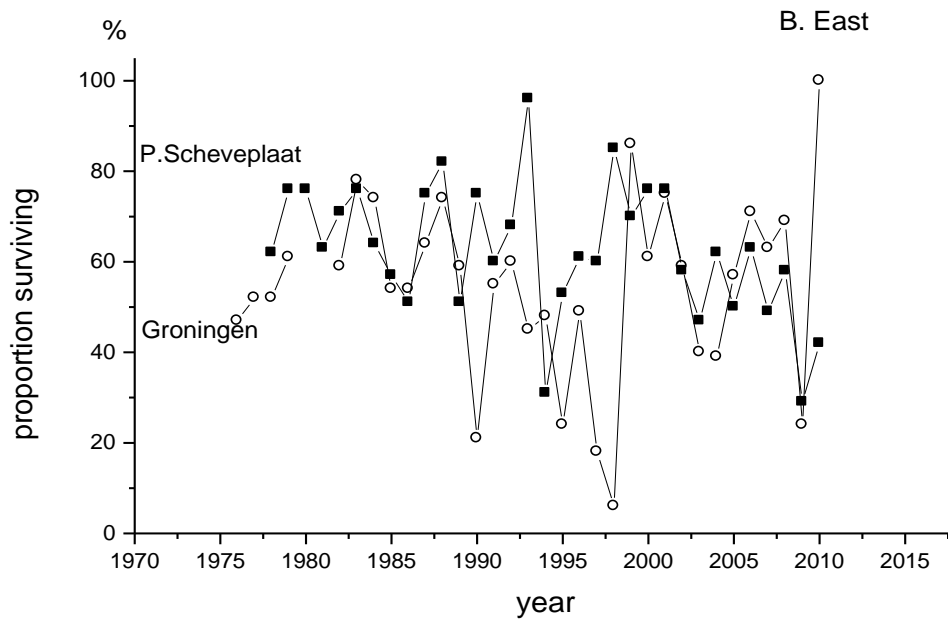
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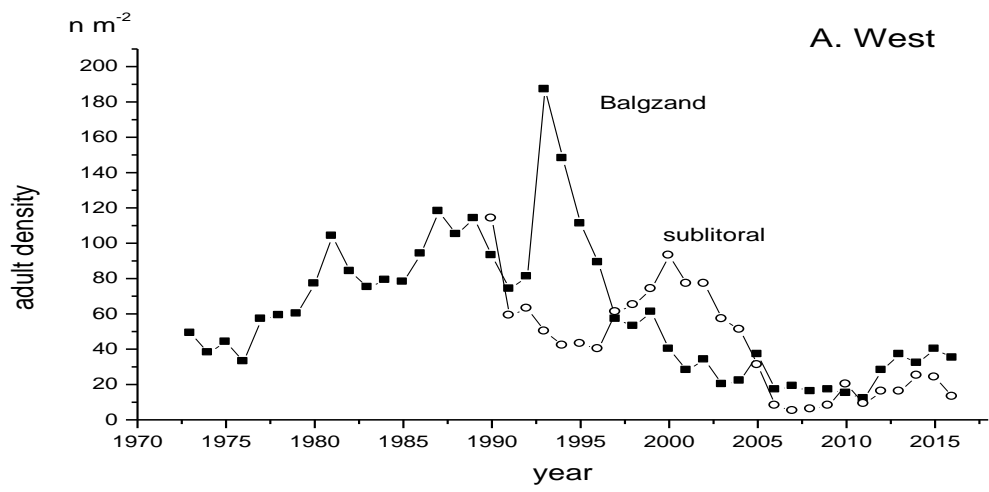
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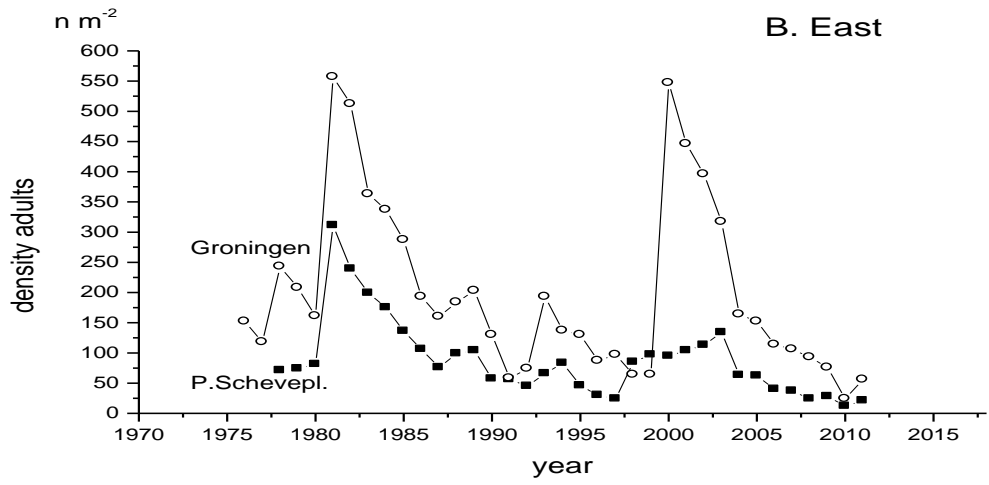


478 Fig. 3

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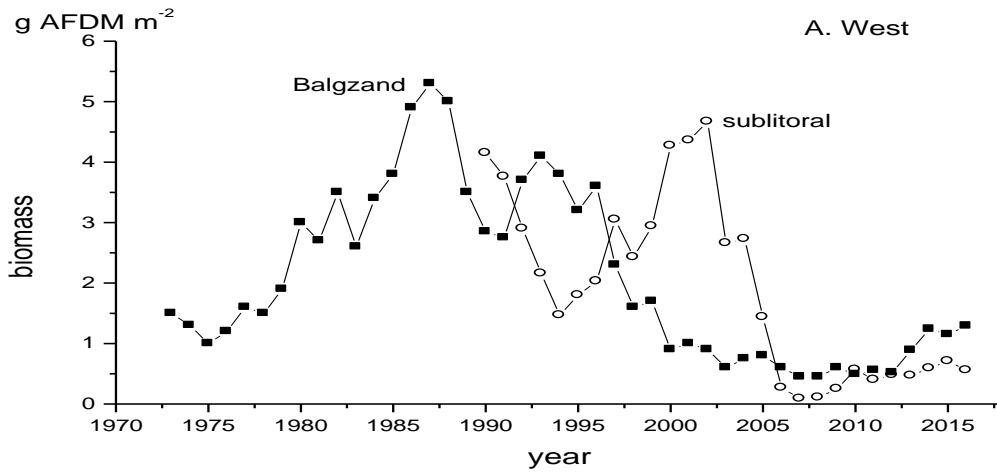
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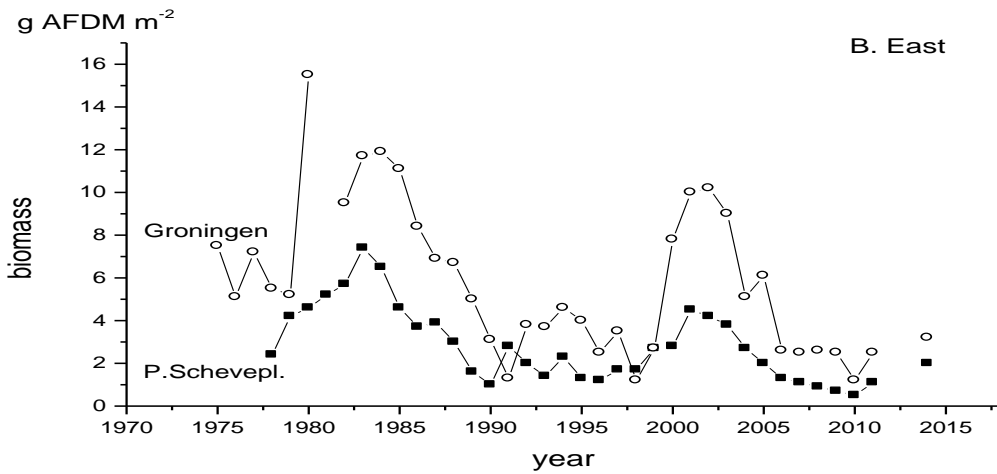
483 Fig. 4

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488 Fig. 5

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490 Table 1. Pearson-r values for correlations between time series for annual estimates of (a)
 491 recruitment, (b) survival, (c) adult numbers, and (d) total biomass as observed in 4 areas in the
 492 Dutch Wadden Sea (compare Fig. 1). Numbers of observation between brackets. Statistical
 493 significance indicated by * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

494

495 (a) recruit densities ($^{10}\log n \text{ m}^{-2}$) in late summer

	Sublitoral	P.Scheveplaat	Groningen
497 Balgzand	+0.64***(27)	+0.35* (34)	+0.55***(37)
498 Sublitoral		+0.24 (24)	+0.60** (24)
499 P.Scheveplaat			+0.69***(34)

500 (b) adult survival (% of initial number in late winter/early spring)

	Sublitoral	P.Scheveplaat	Groningen
502 Balgzand	+0.02 (26)	+0.06 (33)	+0.09 (33)
503 Sublitoral		-0.15 (21)	-0.24 (21)
504 P.Scheveplaat			+0.05 (31)

505 (c) numerical densities ($n \text{ m}^{-2}$) of adults in late winter/early spring

	Sublitoral	P.Scheveplaat	Groningen
507 Balgzand	+0.36 (27)	+0.27 (34)	+0.09 (36)
508 Sublitoral		+0.61**(22)	+0.50* (24)
509 P.Scheveplaat			+0.80***(34)

510 (d) Biomass (g AFDM m^{-2}) in late winter/early spring

	Sublitoral	P.Scheveplaat	Groningen
512 Balgzand	+0.34 (27)	+0.30 (35)	+0.24 (37)
513 Sublitoral		+0.55**(22)	+0.68***(24)
514 P.Scheveplaat			+0.85***(34)

515