Growth and size-dependent loss of newly settled bivalves in two distant regions of the Wadden Sea

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ABSTRACT: Individual growth and the timing of life history events determine the course of individual body sizes. Hence, these factors can influence size-dependent species interactions, such as predation. In the Wadden Sea, predation by crustaceans plays an important role in the survival of pre-recruit bivalves. To investigate growth rates and size-dependent loss in 2 distant regions of the Wadden Sea, *in situ* marking with the fluorochrome calcein was combined with cage experiments. Through marking, we obtained, for the first time, size-increment data for the fragile newly settled juveniles of the species *Macoma balthica* and *Cerastoderma edule* in the field. Growth and size-selective mortality were analysed separately, whereas hitherto both have usually been inferred from size distributions at this life stage. Fluorescent marking also revealed that growth rates were very variable among individuals. Growth was temporarily higher at Texel than at Sylt in both species. In combination with the exclosure experiments and the sampling of predators and migrating bivalves, selective loss of smaller individuals was detected in both regions and was related to predation pressure. Climate influences on phenology have potentially strong effects on species interactions, altering survival and thus recruitment and population dynamics.

KEY WORDS: Individual marking · Predator-exclusion experiments · Benthic invertebrates · Soft-bottom intertidal · Early life history · Post-settlement mortality · Fluorescent dye · Bivalvia

INTRODUCTION

Life history characteristics, such as timing of reproduction and growth patterns, determine the course of body size during an organism's life. This has consequences for population dynamics because many fundamental ecological processes depend on body size. Species interactions, most notably predation, are especially influential and size-dependent. Predators can only handle a certain range of prey sizes (Fryxell & Lundberg 1998). Within this range, predators favour high profitability (Krebs & Davies 1981) or damage avoidance (Smallegange & van der Meer 2003, Hummel et al. 2011). In prey organisms, the ability to hide (Gibson & Robb 1992), escape (Schmidt et al. 2008) or defend against predation (Tollrian 1995) changes with body size. In the marine environment with taxa that commonly show indeterminate growth, organisms co-occur that span a large range of body sizes during their life. Together with the timing of life history events, such as hatching, organism growth rates will determine the duration of susceptibility to predation (Ebenman & Persson 1988).

Growth rates and the timing of seasonally dependent events are influenced by temperature and therefore are potentially subject to change with climate warming (Parmesan & Yohe 2003, Root et al. 2003). When reproductive timing and growth are altered in a species-specific way (Yang & Rudolf 2010), different stages of predators and prey will encounter each other (Visser et al. 2006). Thus, in addition to the physiological effects on organisms, size-dependent species interactions, such as predation, can be altered by shifting temperatures (Walther 2010).

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One illustration of this phenomenon can be found in our study system in the Wadden Sea. Here, spring temperatures trigger the spawning time of bivalves (Drent 2004), while prevailing winter temperatures influence the timing of the arrival of predatory shrimps and crabs on the tidal flats (Beukema 1991, 1992). Increased predation after persistently warmer winters in the past decade is an anticipated reason for the decline of the bivalve *Macoma balthica* in the western Wadden Sea (Beukema & Dekker 2005). High recruitment is usually observed after cold winters because crustacean predators arrive late (Strasser & Günther 2001), after bivalve offspring have already settled and grown in a period of high food availability (Philippart et al. 2003).

Field studies confirmed the importance of predation for bivalve recruitment in several systems (e.g. van der Veer et al. 1998, Strasser 2002, Flach 2003), and some studies also pointed to a role of body size (Strasser et al. 2001, Hiddink et al. 2002, Hunt & Mullineaux 2002, Strasser 2002). Some species perform predator-avoiding migrations (Hiddink et al. 2002). However, the interplay of processes makes each process hard to investigate. One hurdle used to be that size-dependent mortality as well as growth rates of the newly settled stage in the field had to be inferred from observations of size distributions because conventional physical tagging or marking techniques (Bachelet 1980, Gilbert 1973) cannot be used on the small breakable bivalves. Growth estimates based on averages are inaccurate if mortality is size-dependent, and size-dependence of mortality is difficult to detect if size variability increases through growth variability. Furthermore, secondary settlement can influence size distributions. With the fluorochrome shell marker calcein (Kaehler & McQuaid 1999, Moran 2000, Moran & Marko 2005), however, a tool has become available to obtain size-increment data of bivalves and gastropods that can also be applied to fragile young animals. This approach is used in the present study to distinguish growth from size-selective processes.

To investigate early bivalve growth and size-dependent loss, we used a novel combination of the more recently established fluorescent staining method with caging experiments (Hall et al. 1990). In our approach to study the general importance of body size for the survival of young bivalves that are preyed upon by crustacean predators field experiments were conducted, for the first time, simultaneously in 2 distant regions of the Wadden Sea. The winter sea-water temperature (Bundesamt für Seeschifffahrt und Hydrographie 2012, www.bsh.de/en/Marine_data/ Observations/Sea_surface_temperatures/index.jsp) as well as nutrient conditions (Loebl et al. 2009) and therefore algal food influencing growth (Bos et al. 2006) are lower at Sylt in the northern than at Texel in the western Wadden Sea. While the period of bivalve spawning is very similar over a large latitudinal range in Europe (Drent 2004), the reproductive season of *Crangon crangon* is delayed toward the northern Wadden Sea (Campos & van der Veer 2008). The selected island regions thus provided different conditions affecting body size and were chosen to study how the environment can shape species interactions via body size. As the recruitment phase strongly influences population size for the years which follow, research on mortality in the early phase of life will contribute to the understanding of population dynamics (van der Meer et al. 2001). The main objectives were to estimate and compare growth rates and to detect and compare size-dependent loss in the 2 regions with differing conditions.

MATERIALS AND METHODS

Field experiments were carried out simultaneously in 2 distant regions in the Wadden Sea to investigate growth and size-selective abundance changes under different conditions. The experiments started after peak settlement of the most abundant bivalve species, *Macoma balthica* and *Cerastoderma edule*. Caging experiments to exclude epibenthic predators during tidal submergence were combined with fluorescent shell marking to distinguish size-selective survival from variation in growth. The experiments were accompanied by observations of predators and migrating bivalves.

Study sites

The study regions in the Dutch Wadden Sea at the island of Texel and the German Wadden Sea at the island of Sylt are ~400 km of coastline apart (Fig. 1). We selected 2 sites per study region. Near Texel, 1 site lies in the south of the Balgzand tidal flat area. The site is sheltered, and the sediment can be characterized as muddy fine sand. In the northeast of the island lies an open site with fine sand on the sandflats of the Vlakte van Kerken. At Sylt, Gröningwatt is very sheltered with sand to muddy fine sand, and Oddewatt, with medium to coarse sand, is more open. The sites are not meant to represent the area but were chosen for their contrasting conditions. The
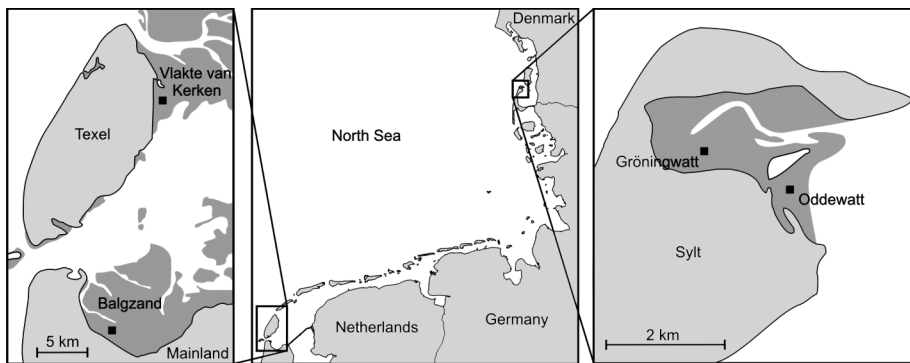
Fig. 1. Study sites in the middle intertidal zone near the islands of Texel (53° N, 5° E) and Sylt (55° N, 8° E) in the Wadden Sea, which constitutes the coastal transition zone to the North Sea. Vlakte van Kerken and Oddewatt are open; Balgzand and Gröningwatt sheltered sites

tidal flats at Texel stretch ~2 km from the high inter-tidal zone to the low water line; at the Sylt sites, this range was ~800 m. The tidal ranges are 1.5 and 2 m respectively. Experiments were carried out in the mid-intertidal zone because the highest number of predator–prey encounters is expected there.

Experimental design, spatial arrangement and time course

Two experiments were conducted, one at the end of May and one at the beginning of June 2007. The experiments had 3 factors: site, exclosure and fluorescent marking with calcein. The factor 'site' had 4 levels. The 3 levels of the exclosure treatments were uncaged, simple cage and control cage. In half of the experimental units, a calcein solution was applied (i.e. 2 levels, calcein and no calcein) so that a potential effect of marking on growth or survival could be tested for. Each site × exclosure × calcein combination was replicated 4 times, but 2 cages each were lost in May and June. The experiments took place within square plots of 1600 m², marked with 25 poles. At 1 site, the plot was made rectangular (30 × 53 m) to fit between megaripples. The plots were divided into 400 squares of 2 × 2 m. The positions for cages and samples within a plot were selected from a random list of the 400 squares without resampling. A short duration of each 10 d was chosen because mortality is high in this early phase of life. Following Strasser's (2002) example, we conducted the experiment between spring tides to circumvent the period of strongest currents and be-cause *Cerastoderma edule* migratory activity is high-est at this time (Armonies 1992). There was a maximum of 2 d between the initiations of the experiments at all 4 sites. At the end of the 10 d experiments, samples were taken in the experimental units to measure abundance, body size and the size of the fluorescent growth ring to compare the abundance,

growth and size-selective survival of the 2 bivalve species *C. edule* and *Macoma balthica*.

Exclosure treatments

Predator-exclosure cages were cylindrical, 30 cm high and 30.5 cm in diameter. The construction was similar to Strasser's (2002), with a frame of 2 polyvinyl chloride (PVC) rings and 3 PVC straps. The sides and top were covered with 1 mm nylon mesh gauze (Kabel Zaandam) to exclude the smallest shrimp. During low tide, the cages were pushed 10 cm deep into the sedi-ment and protruded 20 cm. They were anchored with iron hooks of 50 cm length. To control for cage arte-facts, double-walled cages were used. A second, larger cage, 35 cm high and 39 cm in diameter, was placed around the cage, leaving a space of ~4 cm be-tween the 2 cage walls. In earlier experiments, we had found that the more commonly used incomplete control cage attracted predators, confounding poten-tial caging artefacts and predation pressure (H. An-dresen pers. obs.). This problem is not easy to solve (Peterson & Black 1994). The aim of the double control cage is to increase the intensity of potential artefacts, such as hydrodynamic modification or shading, and then test for interactions between artefact and treat-ment (Reusch & Williams 1999). The reasoning is that, if a difference in the response variable between sin-gle- and double-walled cages has the same direction and magnitude at the different sites, the effect can be assumed to be additive, and it is still possible to compare exclosure effects among sites (Reusch & Williams 1999). It was a priority not to disturb the sedi-ment at setup of the cages, even though this may have led to accidental enclosure of small shrimp that stayed buried in the sediment during low tide. However, the animals are inactive without water, while with high tide more and bigger shrimp enter the tidal flats to forage, so predation pressure was higher outside

the exclosures. Cages were cleaned of algae twice during each experimental period.

Dyeing with calcein

Size-increment data for juvenile bivalves were obtained using calcein blue dye. Calcein functions as a fluorescent label that binds to calcium and is incorporated into growing calcium carbonate structures (Moran & Marko 2005). It has been used in several studies to determine the growth of molluscs (e.g. Herrmann et al. 2009, Clarke et al. 2004). Calcein is suitable because it needs only short immersion times and causes little harm (Riascos et al. 2007, Mahe et al. 2010). It can be applied *in situ* without disturbing the bivalves (van der Geest et al. 2011). PVC rings 30.5 cm in diameter and 10 cm high were pushed halfway into the sediment, and 0.5 l solution consisting of 250 mg calcein per litre of seawater carefully poured into the cylinder. The ring was removed after 1.5 h. When it was not replaced with a cage, tent pegs were used to mark the spot for sampling.

Predator sampling and sample processing

To quantify epibenthic predators, once per experiment at high tide, 4 samples were taken with a drop trap (Pihl & Rosenberg 1984) just outside the plot at each site. The trap was made of aluminium, had a sampling area of 0.5 m^2 and was 70 cm high. To avoid deterring the predators, the trap was suspended from a 8 m long pole (made of 2 windsurf masts) by 2 persons. Sampling took place as soon as the water had receded far enough that it would not swash over the sides after the trap was dropped (i.e. below 70 cm). The content of the trap was intensively fished using a net with a stable rectangular frame and 1 mm mesh, following Polte et al. (2005). Drop trap sampling was not possible at Balgzand in June because of a combination of weather conditions and logistic constraints. Crustacean samples were stored frozen, and *Crangon crangon* lengths from scaphocerite to telson were measured with 1 mm accuracy.

Bivalve sampling and sample processing

At the end of the exclosure experiment, bivalves were sampled to a depth of 3 cm using a sharpened Perspex tube of 20 cm^2 area. Because of high abundances of *Macoma balthica*, a corer of 12.5 cm^2 area

was used in May at Oddewatt. Nine cores were pooled per experimental unit. Samples were sieved through a 500 µm mesh. Bivalve samples were frozen at −20°C or (bivalve samples without calcein at Sylt) stored in 4% formalin in seawater, buffered with borax to prevent decalcification (Sturm et al. 2006). The bivalve sample material was placed in small portions into Petri dishes and sorted systematically. Samples from Sylt were first repeatedly brought into suspension and decanted from the coarse sediment into a 250 µm sieve. Calcein-treated bivalves were measured under a stereomicroscope equipped with a Mercury ultraviolet (UV) lamp and appropriate emission and excitation filters. The length of the fluorescent growth ring was measured as the longest span from front to back, and ring-height was measured perpendicular to that through the umbo (top of the shells at the hinge). The calcein ring measurements were up to 10 µm accurate at the highest usable magnification. For larger measurement values, which had to be done at lower magnifications, accuracy was ~2%. The ring was often not complete, and the height was more frequently measurable than the length. Height and length of the complete growth rings were highly correlated (R^2 = 0.99). When ring length was not measurable but height was, the missing length was filled in using the correlation. The daily instantaneous growth rate (µ) was calculated per individual as follows:

$$\mu = \log (L_{10} / L_0) / t \qquad (1)$$

where L_{10} is the shell length at the end of the 10 d experiment, L_0 is the initial length measured based on the fluorescent ring, and t = 10 d is the duration of the experiment.

To be retained by a 500 µm mesh, *Cerastoderma edule* must be 0.7 mm long and *Macoma balthica* must be 0.75 mm. Especially for *M. balthica* at Sylt in May, we missed the smallest individuals (Fig. 2c). When growth rates differed between exclosure treatments, individual counts were corrected for the sieve selection, using the measured growth rates. For the data involving growth ring size, we also corrected for a sieve artefact. Individuals with a small initial size were caught on the sieve only when they had a high growth rate (missing lower left corner in Fig. 3). Individuals with growth rings <0.7 mm were excluded from the analysis of growth rates and growth ring sizes. Without correction, average growth rates would have been overestimated when the initial size was small. Average growth ring size would have been overestimated when growth was slow because slow-growing individuals with a small initial size were missed by the sieve. On average, the mean
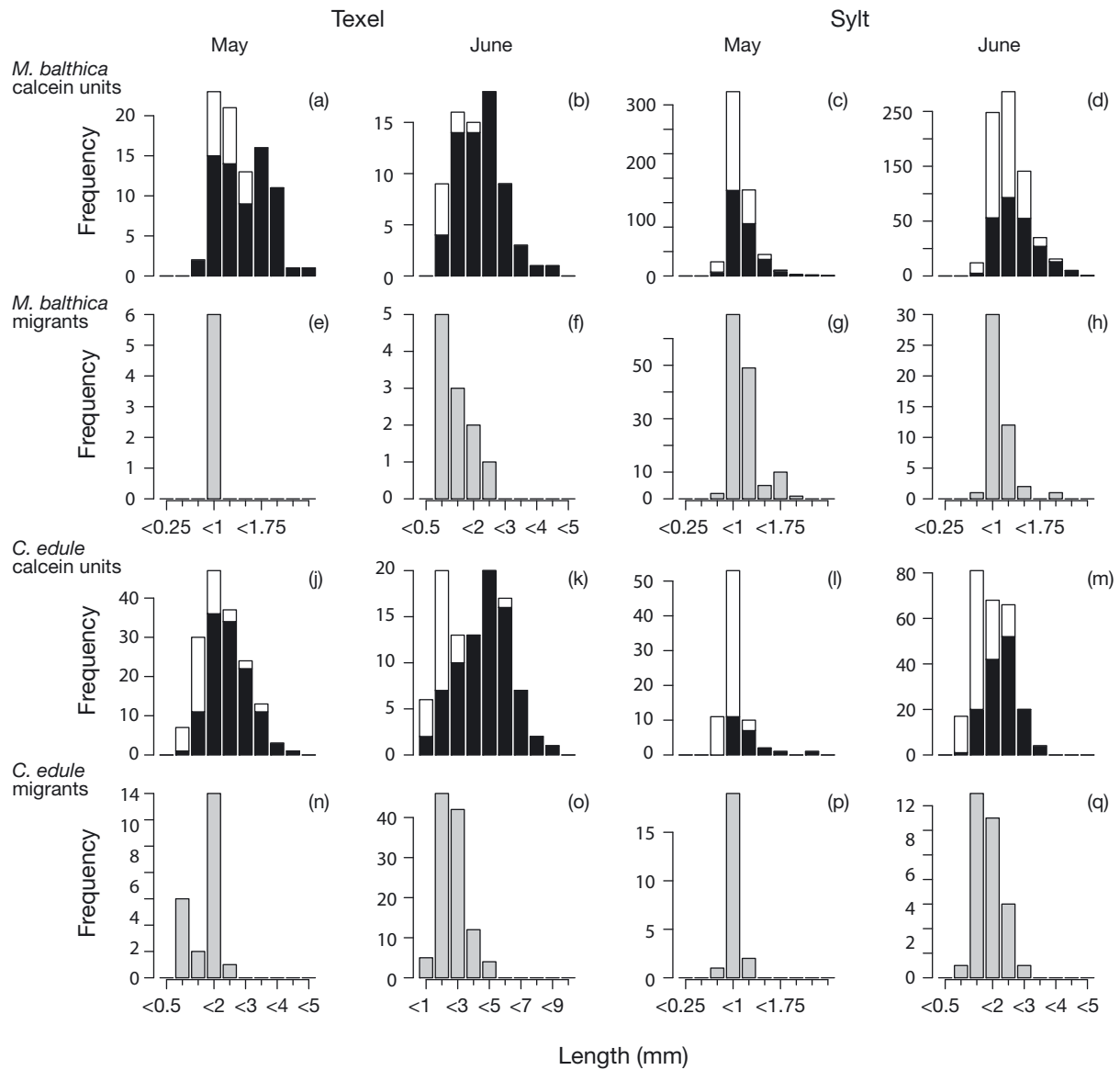
Fig. 2. (a–h) *Macoma balthica* and (j–q) *Cerastoderma edule*. Size frequency distributions of shells in calcein-treated experimental units with (black) and without (white, stacked) fluorescent marking and in migration nets (grey). For the migrants, which were caught on 2 occasions during the 10 d experiment, the theoretical final length at the end of the 10 d was estimated using growth rates obtained from the marking experiment. Note the varying scales for frequencies and for sizes

growth rate and median growth ring size are based on ~10 individuals per sample, sometimes only 1 or 2; the maximum was 68 marked individuals in 1 sample. A low n within a sample will lead to higher variation among samples.

Assessment of immigration

In the early benthic phase, *Macoma balthica* and *Cerastoderma edule* can perform secondary migra-

tions. A difference in bivalve size or abundance between exclosures and uncaged samples could be caused by (size-specific) migration. In the samples treated with calcein, not all individuals had a fluorescent mark. These could have settled into the plots after initiation of the experiments. To evaluate this, migrating bivalves were sampled over two 24 h periods during each experiment. A migration net consisting of a nylon bag of 500 µm mesh size, glued to a PVC ring of 20 cm diameter, which was mounted on a pole 10 cm above the sediment (similar to the
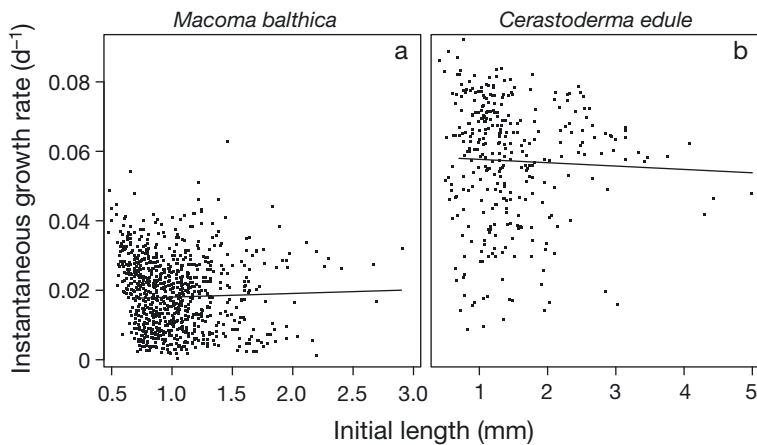
Fig. 3. *Macoma balthica* and *Cerastoderma edule*. Individual growth from size-increment data in relation to initial size. Analyses of experimental effects regarding individuals with growth rings only were conducted omitting growth rings <0.7 mm to avoid bias through sieve selection. When growth rings <0.7 mm are omitted, the slopes presented here are not significant for either species (p > 0.05), and instantaneous growth rates could be averaged over sizes within a sample

plankton net in Armonies 1994). The opening could rotate freely to face water current directions. Four migration nets were installed at each site just outside the sampling plot. The aim was to compare the sizes of the bivalves caught in the water column with the ones from the benthic samples of the experiments. As the sampling of migrating bivalves took place twice during the experimental periods, for comparison, their hypothetical size at the end of experiments was calculated using the obtained growth rates from the marked animals. The size distributions of the animals caught in the nets mostly resembled the size distributions of the animals without a fluorescent mark in the calcein-treated samples (Fig. 2). It was concluded that individuals without a mark had entered the experimental units later. For the subsequent analyses of abundances, such individuals were excluded from the data. As immigrants could not be identified in undyed samples, analyses of exclosure effects used dyed samples only.

Data analysis

The experimental results were analysed separately per species and per experimental period with gener-alised linear models (GLM) in R (R Development Core Team 2008). The factors were site, exclosure and marking with calcein solution. *Macoma balthica* counts were overdispersed (dispersion parameter be-tween 4.3 and 6.7), and the quasi-Poisson family was used; for *Cerastoderma edule* counts, the Poisson

family was suitable (dispersion parameter ~1). In a few cases, the counts in all the 4 replicates of a given treatment were zero, and the function would try to predict infi-nitely small log values. In that case, 1 was added to one of the 4 replicates to aid the estimation. Sampling area was in-corporated in the model as a so-called offset variable (McCullagh & Nelder 1998). For size data, the median shell length per sample was calculated, and the Gamma family gave the best looking residual distri-bution plot. For growth, the mean per sam-ple and the Normal family could be used. As there was no significant relationship of instantaneous growth rate with initial size within the presented range, it was not nec-essary to include initial size as a covariable in the analysis of growth rates (Fig. 3). Models including different combinations of main and interactive effects (Table 1) were compared simultaneously with Akaike's information criterion and corrected for small sample size (Ander-son 2008), using the R package 'MuMIn' (Bartoń 2012):

$$AIC_c = -2(\text{log-likelihood}) + 2p[n / (n - p - 1)] \quad (2)$$

where p is the number of estimated parameters of the respective model including the intercept, and n is the number of observations.

For *Macoma balthica* counts, the QAIC$_c$ for overdis-persed count data was used.

$$QAIC_c = -2(\text{log-likelihood}) / \hat{c} + 2p[n / (n - p - 1)] \quad (3)$$

where $\hat{c}$ is the dispersion parameter estimated from the full model, calculated by dividing the deviance by the residual degrees of freedom. The number of model parameters was increased by 1 to account for estimating the dispersion parameter. The log-like-lihood was obtained from the Poisson fitted model. Every model that contains 'exclosure' was estimated in 2 versions: (1) double cages and single cages were regarded as separate levels; and (2) these 2 exclosure types were not distinguished (lowercase letters in all tables) to assess caging artefacts.

RESULTS

Effect of calcein marking on abundance and size

A side question but a prerequisite in the combined caging and staining experiment was whether the fluo-

Table 1. Description of models of different complexity that were estimated separately for each combination of period (May and June) with species (*Cerastoderma edule* and *Macoma balthica*) and response variable (abundance and size). s: site, e: exclosure, m: marking with calcein solution. The response variables growth, abundance of marked animals and initial size were estimated from the calcein-treated samples only, so models including marking do not apply, and 'J' functions as the full model. Each model including the factor exclosure was tested in 2 versions, once with the 3 levels separately (upper case letters) and once without differentiating between the single cages and double-control cage (lower case letters). Models were compared simultaneously with Akaike's information criterion (Tables 2 & 3)

Model complexity	Model	Model description
Full model	A, a	s + e + m + s:e + s:m + e:m + s:e:m
Three 2-way interactions	B, b	s + e + m + s:e + s:m + e:m
Two 2-way interactions	C, c	s + e + m + s:e + s:m
	D, d	s + e + m + s:e + e:m
	E, e	s + e + m + s:m + e:m
One 2-way interaction	F, f	s + e + m + s:e
and 3 main effects	G, g	s + e + m + s:m
	H, h	s + e + m + e:m
2-way interaction and	J, j	s + e + s:e
2 main effects	K	s + m + s:m
	L, l	e + m + e:m
3 main effects	M, m	s + e + m
2 main effects	N, n	s + e
	O	s + m
	P, p	e + m
1 main effect	Q	s
	R, r	e
	S	m
Null model	T	Intercept

rescent marking method affects the survival and growth of first year bivalves. For *Macoma balthica* in June and *Cerastoderma edule* in May, calcein did not need to be included in the models (Model j for abundances, Models Q and j for size, respectively, Tables 1 & 2). The application of the marking solution seemed to lower *M. balthica* abundances in May (Fig. 4a,b; only significant factors plotted). The effect was small but significant and showed in the exclosures. The marking and exclosure interaction (Model h; Tables 1 & 2) did not affect the direction but only the strength of the exclosure effect and was similar at all sites (Fig. 4a,b). Also, *C. edule* abundances in June differed between calcein treatments (Model C): at Oddewatt, they were higher in the calcein-treated units (Fig. 4c,d). Still, there was no interaction with exclosure, and the calcein effects were weak compared to the exclosure effects. Concerning size, *M. balthica* median length in May was lower in the calcein samples at Sylt, while at Vlakte van Kerken, the individuals were smaller in the experimental units that had not been treated with calcein, independent of exclosure treatment (Model K; Fig. 5a). There was no significant influence of calcein on body size of *C. edule* in

June after 1 influential value was removed (Model n; Fig. 5d). Overall, in some cases, calcein may change the effect sizes in the following analyses but not the qualitative conclusions.

Growth

Under natural (uncaged) conditions, the growth of *Macoma balthica* was similar at all sites in May (Fig. 6a), but in June, growth decreased at Sylt (Fig. 6b). In contrast, for *Cerastoderma edule*, growth appeared to be lower at Sylt in May (Fig. 6c) and the same everywhere by June (Null model; Fig. 6d). *C. edule* had the fastest growth observed; their average daily instantaneous growth rate of 0.06 d^{-1} in June amounts to 60 µm in 1 d for a 1 mm long individual. The instantaneous growth rate of ~0.02 d^{-1} for *M. balthica* in May corresponds to a 20 µm length increase in 1 d for a 1 mm long individual. However, it is remarkable how variable the individual growth rates were (Fig. 3). *M. balthica* grew at up to 0.06 d^{-1}, but some individuals hardly grew at all; the maximum individual growth rate observed was 0.08 d^{-1} in *C. edule*. Except for *C. edule* in June, caging had an influence on bivalve growth (Fig. 6). In most of the observable cases, growth was higher in the cages (Model n; Table 3), but for *M. balthica* in May, the influence of caging differed between sites (Model j). Growth was decreased in the cages at Sylt, indicating habitat-dependent modification of growth conditions (Fig. 6a). If growth had been calculated only from observations of size (from the end of the May experiment to the end of the experiment in June) and the small immigrants had been included, the estimates would be up to 70% lower than the measured growth rates.

Exclosure effect on abundance and size-selectivity of loss

For *Macoma balthica* as well as *Cerastoderma edule*, abundances in May were always lower in the uncaged experimental units to which predators had access (Fig. 7a,c). The loss, presumably mainly preda-

Table 2. Akaike's information criterion values (bias corrected for small sample size: AIC_c) for general linear models that include all experimental treatments to assess a possible effect of calcein marking on the response variables bivalve abundance and size. For *Macoma balthica* counts, $QAIC_c$ a version of AIC_c for overdispersed count data (Eq. 3) was used. The lowest values are in **bold**. For a description of each model, see Table 1. *C. e.: Cerastoderma edule*, *M. b.: Macoma balthica*. Fit: 1 − deviance$_{best fitting model}$ / deviance$_{Null model}$ is given as a measure of fit

Model	Counts				Size			
	M. b. May	*M. b.* June	*C. e.* May	*C. e.* June	*M. b.* May	*M. b.* June	*C. e.* May	*C. e.* June
A	207.0	190.5	405.0	457.4	−76.06	31.83	2.216	135.9
B	198.4	178.9	391.4	454.6	−88.73	17.89	−7.057	123.5
C	196.5	174.2	388.3	**449.3**	−94.70	12.00	−4.646	116.9
D	192.7	174.2	383.7	461.0	−84.79	11.45	−14.00	120.6
E	183.1	179.5	388.3	466.6	−99.15	13.09	−9.152	109.0
F	191.8	170.2	380.7	456.8	−88.57	5.967	−10.87	114.5
G	182.1	175.9	385.6	462.6	−102.5	8.549	−4.948	103.5
H	178.8	176.3	381.4	474.8	−93.49	7.562	−15.24	106.5
J	192.9	167.6	378.6	458.9	−88.57	3.194	−13.27	111.4
K	198.1	177.3	427.4	562.9	**−107.4**	4.125	−8.139	107.6
L	480.1	523.6	712.2	780.0	−41.32	80.67	117.2	213.4
M	178.7	173.1	379.1	471.2	−95.98	3.347	−11.02	101.7
N	180.1	170.8	377.4	473.9	−96.26	1.072	−13.35	99.34
O	195.0	174.9	421.3	571.9	−100.4	−0.7780	−13.74	107.1
P	480.3	519.8	710.2	776.0	−44.14	76.29	114.1	209.1
Q	196.5	172.7	419.7	574.3	−100.6	**−2.898**	−15.86	105.0
R	481.9	517.6	708.7	780.1	−45.34	74.230	111.9	206.9
S	493.3	524.3	752.3	879.9	−48.54	72.10	111.1	207.5
T	495.0	522.1	750.8	883.4	−49.66	70.16	109.0	205.4
a	190.5	178.8	386.5	460.8	−95.17	13.48	−11.12	116.4
b	187.9	170.3	378.6	454.4	−102.4	7.925	−15.41	111.1
c	187.7	167.6	378.8	451.8	−104.5	5.765	−15.80	108.0
d	183.8	167.0	372.1	462.5	−99.15	2.435	−20.40	107.8
e	181.0	178.3	384.6	463.2	−103.2	7.971	−8.699	103.5
f	184.0	164.4	372.0	460.0	−99.95	0.4271	−20.68	105.0
g	181.1	175.7	384.5	460.7	−105.1	5.962	−7.303	100.8
h	**177.5**	175.5	378.0	471.7	−97.45	2.768	−14.15	101.5
j	185.3	**162.1**	370.2	462.8	−99.65	−1.965	**−22.67**	102.4
l	478.0	523.6	709.4	776.2	−44.72	76.22	113.9	209.2
m	177.8	173.1	378.2	469.4	−98.49	0.9214	−13.14	99.20
n	179.3	170.9	376.5	472.2	−98.69	−1.298	−15.38	**96.90**
p	478.5	521.4	709.7	774.0	−46.34	74.30	112.1	206.9
r	480.1	519.2	708.2	778.2	−47.52	72.28	109.9	204.7
Fit	0.7702	0.8060	0.8013	0.7914	0.6269	0.6466	0.8509	0.7905

tion mortality, was similar between sites (Model n). In June for both species, abundances differed between the single cages and the double control cages in different ways between sites (Model J, Fig. 7b,d). Although sometimes the abundances were clearly higher in the cages, it cannot be safely concluded that this is due to protection from predation. The varying differences between cage types are an indication that caging could have had an influence on local survival other than through the exclosure of predators alone.

Concerning size-selectivity of the observed loss, individuals that survived under predator access in May had, on average, bigger fluorescent growth rings than the protected survivors for both *Macoma balthica* and *Cerastoderma edule* (Models r and j; Fig. 8a,c). This hints at selective loss of individuals with a smaller initial size (smaller than the respective median). The mere observation of the final shell size had given no indication of such loss in *M. balthica* (Fig. 5a). The fluorescent record of the size at the initiation of the experiment avoids bias by subsequent growth differences and immigration. In June, the average of the initial body size of the survivors was not influenced by exclosure treatments in either species (Model Q; Fig. 8b,d). Note that the observation of final body size would have suggested a better survival of smaller *C. edule* under predation risk in June (Fig. 7d), but through marking, it becomes evident that smaller individuals had immigrated (Fig. 2k). Unfortunately, there were no unbiased growth ring observations (truncation at 0.7 mm) from uncaged experimental units for *C. edule* in May at 3 sites. Inspection of the final shell sizes would suggest selective loss of bigger individuals (Fig. 7c), but the above contradictions show that final shell size can be misleading.

Crangon crangon have to be ~10 times longer than *Macoma balthica* to be able to consume them (Hiddink et al. 2002), and they probably have to be even bigger to consume *Cerastoderma edule* because of the latter's harder shell and globose shape. In May, there were plenty of shrimp present that would feed on small bivalves (Fig. 9). In June, more small shrimp had entered the study sites, and the numbers of larger individuals had also increased. Although the bivalves had grown, there was still prey available of a size suitable for predation by *C. crangon*.

DISCUSSION

Body size is central to species interactions that influence survival, and individual growth determines
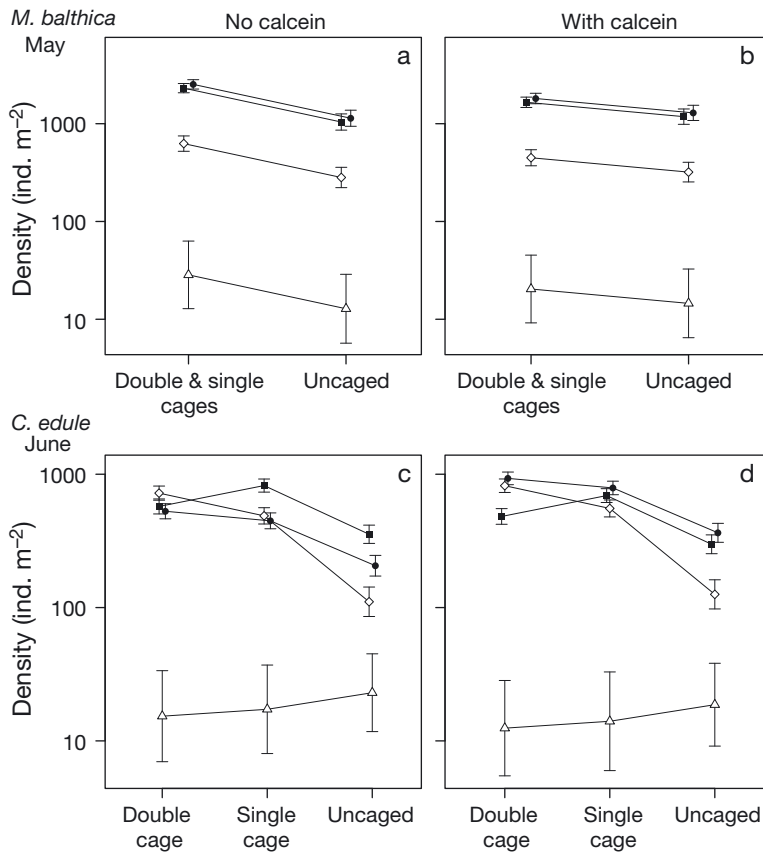
Fig. 4. (a,b) *Macoma balthica* and (c,d) *Cerastoderma edule*. Model predictions and standard errors of the models that assess the effect of calcein marking on bivalve abundance. Only significant factors are plotted. The factor marking was not significant for *M. balthica* in June or for *C. edule* in May (not shown). ■: Gröningwatt (Sylt), ●: Oddewatt (Sylt), ◇: Balgzand (Texel), △: Vlakte van Kerken (Texel). The lines connecting the symbols identify the interactions between factors and do not represent any formal relationship between treatment levels

the body sizes of species that encounter each other. With a combined fluorescent staining and caging experiment, we distinguished growth from size-dependent abundance changes of juvenile bivalves *Macoma balthica* and *Cerastoderma edule*. We obtained individual growth rates and compared average growth in 2 distant regions in the Wadden Sea, detected size-dependent loss and identified the affected sizes.

In both species, individual growth was faster at Texel than at Sylt in 1 of the 2 study periods, resulting in bigger individuals at Texel at the end of the present study. If only the change in average size had been used to estimate the average growth rates, growth would have been strongly underestimated due to immigration of smaller individuals. The possibility of identifying immigrants from size distributions is limited. Individual marking also showed that growth is highly variable among individuals.

The other objective of using individual staining was to identify size-dependent loss, which has population-scale ecological consequences. In combination with a caging experiment, we found evidence of selective loss of small bivalves in both regions in the first study period. The caging experiment was intended to manipulate predation mortality, but in addition to predator access, emigration is another process that could cause an abundance decrease and could be affected by the cages. We think that the main cause of the size-dependent loss outside of the exclosures was predation, for several reasons: (1) The missing bivalve sizes were theoretically small enough to pass through the cage mesh. Immigration into similar cages was also observed by Strasser (2002). Admittedly, emigration would require some water current, but then we would expect a difference between single and double cages, which we did not find. (2) There is strong evidence that during the present study, the middle intertidal zone experienced net immigration. In June, no size-selective loss was found, but many small *Cerastoderma edule* and *Macoma balthica* were caught with drift nets during migration. If these were mainly emigrants, then why did we not find size-selective loss? Thus, we conclude that migrants were mainly immigrants, which is further supported by the size similarity of the unmarked individuals in the sediment and the migrating bivalves. Armonies & Hellwig-Armonies (1992) also found that the middle intertidal zone at Oddewatt was subject to net immigration until July 1991, when *M. balthica* gradually moved up higher in the intertidal. (3) The predators present were able to consume the missing bivalves, both with respect to their size (Hiddink et al. 2002) and their intake rates (Andresen & van der Meer 2010). While it is possible that some of the loss is due to movements of bivalves, mortality is plausible as the main reason.

There were no systematic differences in predation patterns between the islands of Sylt and Texel. Size-selective predation on *Cerastoderma edule* and on *Macoma balthica* occurred in the first experiment in May. Although young shrimp had arrived earlier at Texel than at Sylt (authors' pers. obs.), there was no
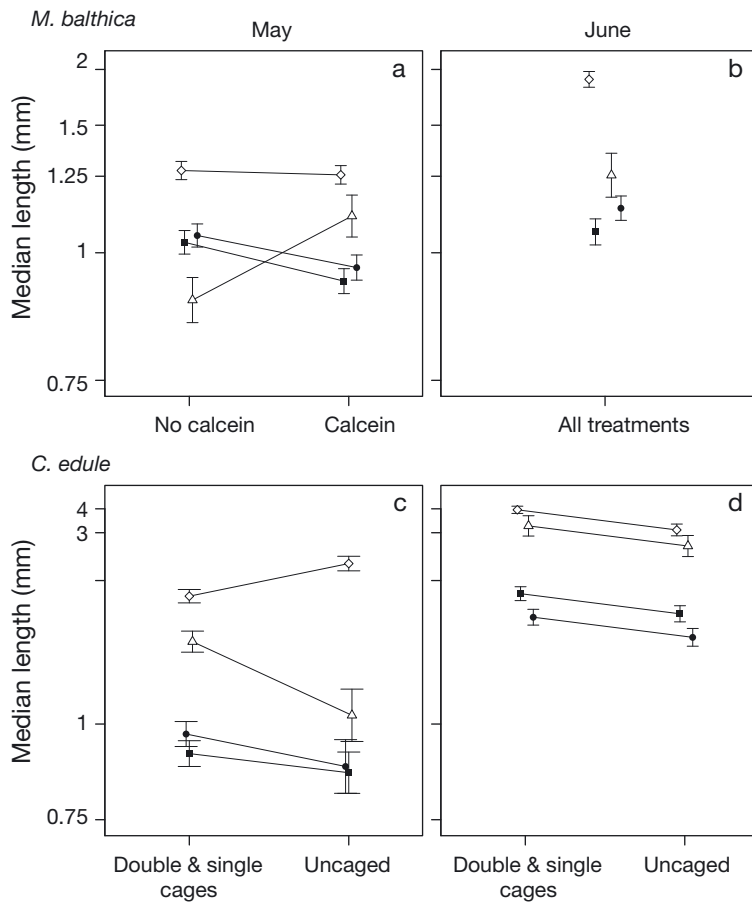
Fig. 5. (a,b) *Macoma balthica* and (c,d) *Cerastoderma edule*. Model predictions and standard errors of the models that assess the effect of calcein marking on bivalve size. Only significant factors are plotted. The lines connecting the symbols identify the interactions between factors and do not represent any formal relationship between treatment levels. Note the compressed scale. ■: Gröningwatt (Sylt), ●: Oddewatt (Sylt), ◇: Balgzand (Texel), △: Vlakte van Kerken (Texel)

systematic difference in predator regimes between the regions. The size composition of shrimp on tidal flats is primarily determined by size-dependent habitat use rather than by local growth conditions (Beukema 1992). The 2 sites at Sylt were similar in predator composition, but in May, Vlakte van Kerken had the highest number of large predators and Balgzand the lowest among the 4 sites. The topology of the Balgzand mudflats may have delayed immigration of larger shrimps. Hence, no simple, general, 1-line conclusion can be drawn, and here, one of the limitations of the present study becomes obvious. The field experiments and measurements under UV light were very laborious, which restricted the temporal and spatial replication and scope of the present study. Given the inherent variability of the phenomena, such replication is apparently needed. The results suggest that similar processes are taking place at both islands, albeit at different speeds. At Texel, the potential for the bivalves to outgrow their predators quickly was better than at Sylt.

Caging and calcein marking each have disadvantages. While other studies found no harmful influence of calcein (Moran & Marko 2005), our findings show that this potential should be assessed each time that the method is applied in a new system. Even if the methods do not give

Table 3. Akaike's information criterion values (bias corrected for small sample size: AIC_c) for general linear models that include only bivalves with a fluorescent mark to investigate growth, exclosure effects on abundance (numbers of individuals with calcein mark only) and size selectivity of loss. For *Macoma balthica* counts, $QAIC_c$ for overdispersed count data was used. The lowest values are in **bold**. For the description of each model, see Table 1. *C. e.*: *Cerastoderma edule*, *M. b.*: *Macoma balthica*. Fit: 1 − deviance$_{best fitting model}$ / deviance$_{Null model}$ is given as a measure of fit

| Model		Growth				Count marked individuals				Initial size (size of growth ring)		
	M. b. May	*M. b.* June	*C. e.* May	*C. e.* June	*M. b.* May	*M. b.* June	*C. e.* May	*C. e.* June	*M. b.* May	*M. b.* June	*C. e.* May	*C. e.* June
J	−238.3	−219.0	−147.0	−205.6	95.60	**121.3**	160.8	**194.7**	−3.945	6.162	1.161	17.49
N	−236.2	−225.7	−159.2	−217.5	81.10	126.3	147.9	203.9	−14.85	−4.203	−5.785	11.07
Q	−241.3	−221.6	−160.5	−222.5	80.60	131.7	151.4	263.9	−16.15	**−9.897**	−8.956	**5.230**
R	−237.3	−201.6	−147.1	−223.3	139.3	250.7	288.6	292.5	−20.23	10.26	17.92	68.27
T	−241.7	−204.8	−152.4	**−227.0**	139.9	259.0	292.9	353.9	−21.07	6.270	21.45	63.39
j	**−242.4**	−222.0	−161.4	−216.2	82.92	121.5	150.8	203.4	−13.67	−4.708	**−8.966**	9.171
n	−239.0	**−225.8**	**−161.4**	−220.7	**78.80**	123.5	**145.9**	204.8	−18.00	−7.255	−8.966	8.096
r	−239.8	−203.9	−149.9	−225.8	138.3	248.7	286.8	292.9	**−22.76**	7.851	15.96	65.80
Fit	0.3994	0.5941	0.5355	0	0.6335	0.7975	0.7867	0.8239	0.1096	0.4831	0.7794	0.8527
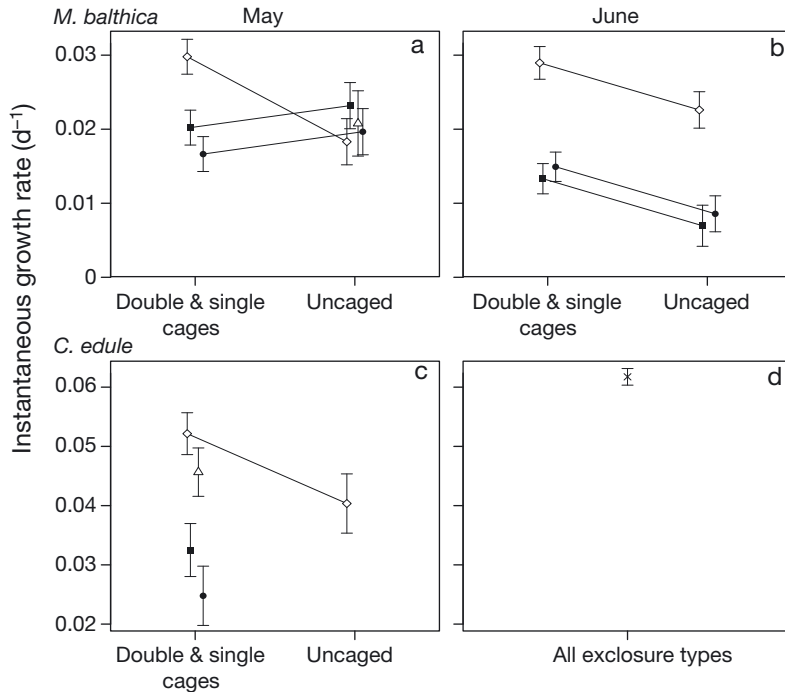
Fig. 6. (a,b) *Macoma balthica* and (c,d) *Cerastoderma edule*. Model predictions and standard errors of models of mean daily instantaneous growth rates in the exclosure experiment, obtained from size-increment data. Only significant factors are plotted. The lines connecting the symbols identify the interactions between factors and do not represent any formal relationship between treatment levels ■: Gröningwatt (Sylt), ●: Oddewatt (Sylt), ◇: Balgzand (Texel), △: Vlakte van Kerken (Texel), ×: all sites together
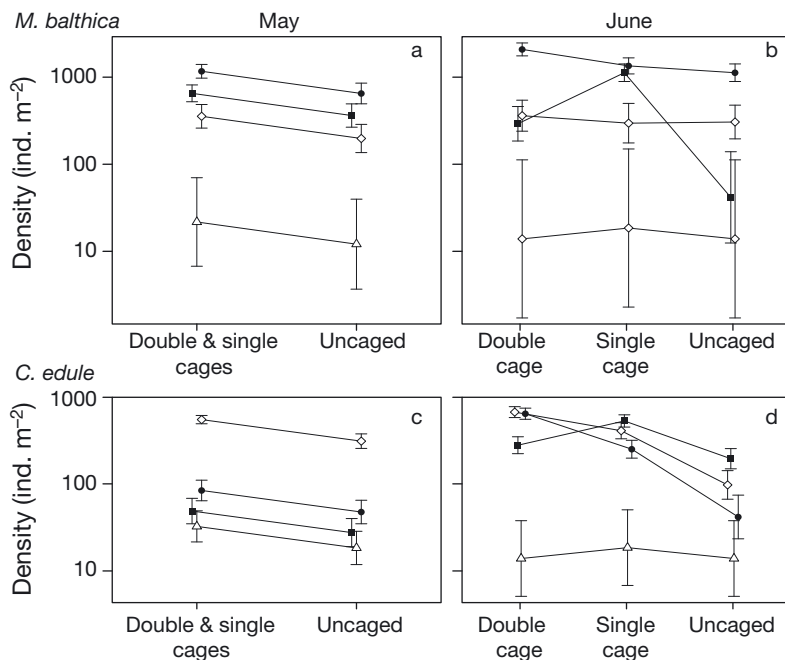

Fig. 7. (a,b) *Macoma balthica* and (c,d) *Cerastoderma edule*. Model predictions and SEs of count data (shown as density) of marked bivalves in the exclosure experiment. Only significant factors are plotted. The lines connecting the symbols identify the interactions between factors and do not represent any formal relationship between treatment levels ■: Gröningwatt (Sylt), ●: Oddewatt (Sylt), ◇: Balgzand (Texel), △: Vlakte van Kerken (Texel)

absolute quantitative results, it is still possible to compare levels of each factor as long as there are no interactions between the 2 factors. This was the case for the effect of calcein on *Macoma balthica* growth in May and on *Cerastoderma edule* abundance in June, which did not interact with exclosure treatments. There was an interactive effect on *M. balthica* abundances in May. Abundances were lowered in the exclosures but not in the uncaged units treated with calcein. Because this reduced the effects of exclosure treatments, qualitative conclusions that were drawn from calcein samples were merely more conservative. Further, cage artefacts cannot be excluded if the effects of single and double cage walls are all-or-nothing. Artefacts are always created by an experimental procedure (Fernandes et al. 1999), but by combining an interpretation of the results with natural history observations, caging experiments can contribute to the solution of important ecological questions (Reise 1985).

The combination of caging and marking provides valuable information on processes that are otherwise obscured. If we had not combined the methods, we could have drawn wrong conclusions or missed an interesting process (compare, for example, Fig. 6 with Fig. 8). We noted that scouring sometimes led to puddles in the cage area at low tide, which may prolong submersion and explain the increased growth in some cases (Freudendahl et al. 2010). We cannot exclude the possibility that this also had an influence on survival, but this effect would probably be small compared to that of predation. It must be emphasised that other caging studies probably have the same issues, which only become visible here through the combination of methods. The most important advantage of individual marking is that we know the size of the local survivors from the beginning. In past exclosure studies, when size differences between cages were observed, it was not known for sure
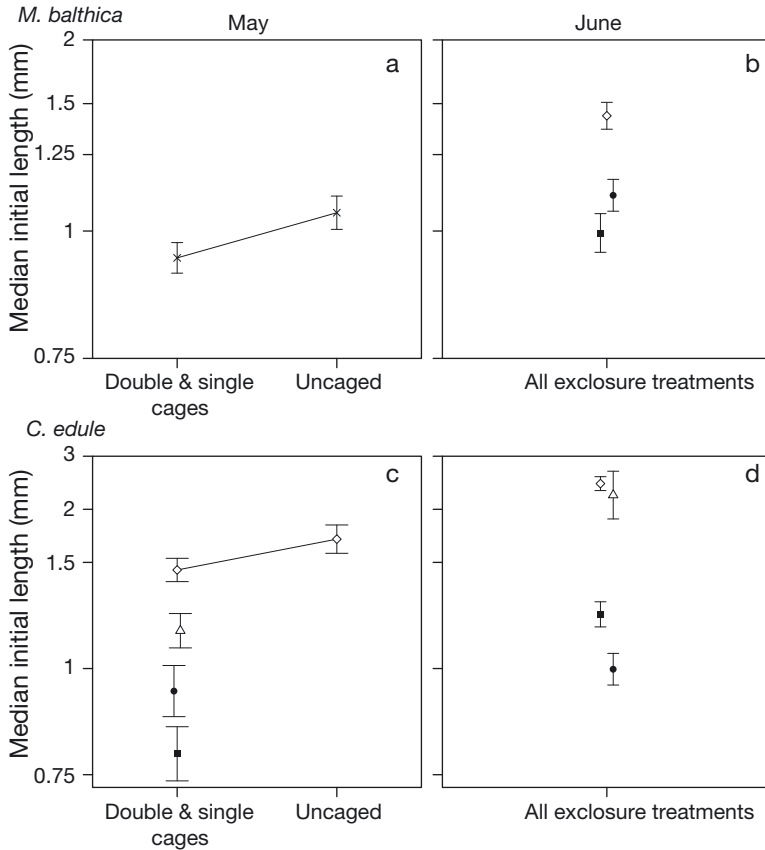
Fig. 8. (a,b) *Macoma balthica* and (c,d) *Cerastoderma edule*. Model predictions and standard errors of initial bivalve size in exclosure experiments to investigate size-selectivity of loss. The initial size of the survivors is the size of their artificial growth rings produced with calcein at the beginning of the experiment. Only significant factors are plotted. For *C. edule* in May, unbiased growth ring observations were available only at Balgzand. Lines connecting the symbols identify the interactions between factors and do not represent any formal relationship between treatment levels. ■: Gröningwatt (Sylt), ●: Oddewatt (Sylt), ◇: Balgzand (Texel), △: Vlakte van Kerken (Texel)

whether that was just the influence of the cage on growth or a size-dependent loss. In the present study, growth could be quantified and the recorded initial size of the survivors compared irrespective of subsequent growth.

Predation on the early post-settlement stages largely determines the recruitment and population dynamics of bivalves in the Wadden Sea (van der Meer et al. 2001). Much insight on size-structured populations and recruitment originates from fisheries science. While keeping potential harmful effects in mind for the early life stage of bivalves, calcein marking can function as a surrogate for the examination of otolith microstructures in fish. Concerning the consequences for population dynamics, size-selective mortality in the early life phase has a primary effect on the population density. Size-selective mortality will affect recruitment variability if the factors governing size-based processes vary among years (Sogard 1997). For example, Nakaya et al. (2007) found annual variation in shrimp predation on flatfish through an influence of variation in bottom water temperature on fish size but not on shrimp size. Annual variation in the size-selective mortality of salmon fry was flood- and drought related (Good et al. 2001). In addition to abundance, size-selective mortality will also affect the size-structure of a cohort. In our
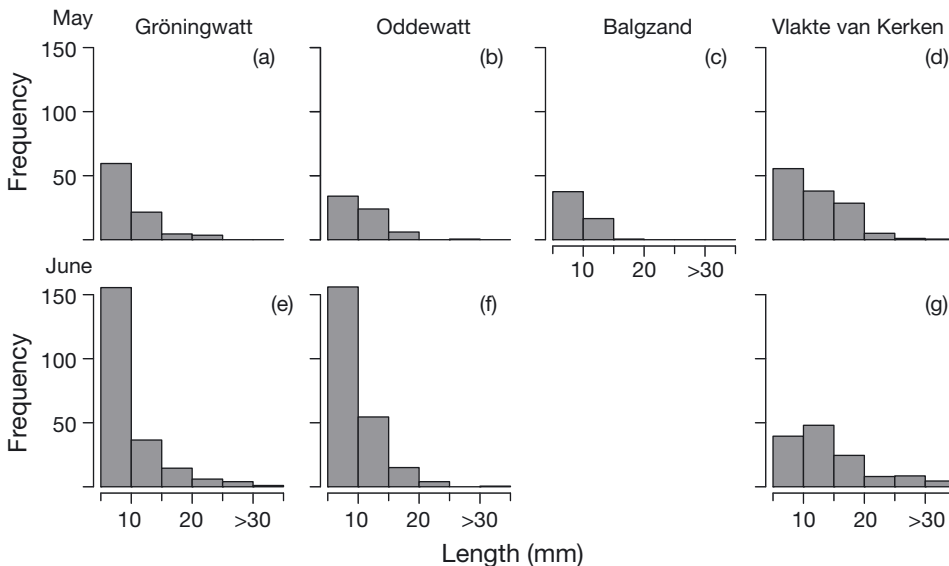

Fig. 9. *Crangon crangon*. Length–frequency distributions during the experiments, sampled at high tide (not possible at Balgzand in June). Gröningwatt and Oddewatt are at Sylt; Balgzand and Vlakte van Kerken are at Texel. Frequencies are given per m²; total sampling area each time was 2 m²

study, the smallest individuals were most vulnerable, but after a warm winter in 1997, it was the smallest *Cerastoderma edule* that survived until recruitment (Strasser et al. 2001). When predation is directed toward small individuals, fast growth would increase survival, but slow growth can be advantageous if relatively big gape-limited predators are present only temporarily (Urban 2007). Under constant unidirectional selection pressure through persistently warmer winters and thus the earlier arrival of shrimps, the possibility for the young bivalves to adapt by an increase in growth rates is limited by food availability (Philippart et al. 2003, Freitas et al. 2007). Texel cannot be used to forecast the situation at Sylt under climate warming.

The novel experimental evidence of size-selective predation in the field brings us one step closer to understanding observed recruitment patterns. From here, it would be interesting to look further into the sources and consequences of growth variability. For prognoses on a mechanistic basis, we would still need more detailed knowledge of shrimp behaviour, including behaviour in the presence of alternative food. Yet, together with information on seasonality and prey choice, our new data on individual growth rates should help to further investigate recruitment success under various scenarios.

LITERATURE CITED

Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, Berlin

Andresen H, van der Meer J (2010) Brown shrimp (*Crangon crangon*, L.) functional response to density of different sized juvenile bivalves *Macoma balthica* (L.). J Exp Mar Biol Ecol 390:31−38

Armonies W (1992) Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar Ecol Prog Ser 83:197−206

Armonies W (1994) Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgol Meersunters 48:299−320

Armonies W, Hellwig-Armonies M (1992) Passive settlement of *Macoma balthica* spat on tidal flats of the Wadden Sea and subsequent migration of juveniles. Neth J Sea Res 29:371−378

Bachelet G (1980) Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geo-graphical distribution, the Gironde Estuary (SW France). Mar Biol 59:105−117

Barto K (2012). MuMIn: multi-model inference. R package version 1.7.7 http://R-Forge.R-project.org/projects/mumin/

Beukema JJ (1991) The abundance of shore crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. J Exp Mar Biol Ecol 153:97−113

Beukema JJ (1992) Dynamics of juvenile shrimp *Crangon crangon* in a tidal-flat nursery of the Wadden Sea after mild and cold winters. Mar Ecol Prog Ser 83:157−165

Beukema JJ, Dekker R (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar Ecol Prog Ser 287:149−167

Bos OG, Hendriks IE, Strasser M, Dolmer P, Kamermans P (2006) Estimation of food limitation of bivalve larvae in coastal waters of north-western Europe. J Sea Res 55: 191−206

Campos J, van der Veer HW (2008) Autecology of *Crangon crangon* (L.) with an emphasis on latitudinal trends. Oceanogr Mar Biol Annu Rev 46:65−104

Clarke A, Prothero-Thomas E, Beaumont JC, Chapman AL, Brey T (2004) Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. Polar Biol 28:62−71

Drent J (2004) Life history variation of a marine bivalve (*Macoma balthica*) in a changing world. PhD thesis, Rijksuniversiteit Groningen

Ebenman B, Persson L (1988) Size-structured populations: ecology and evolution. Springer, Berlin

Fernandes TF, Huxham M, Piper SR (1999) Predator caging experiments: a test of the importance of scale. J Exp Mar Biol Ecol 241:137−154

Flach EC (2003) The separate and combined effects of epibenthic predation and presence of macro-infauna on the recruitment success of bivalves in shallow soft-bottom areas on the Swedish west coast. J Sea Res 49:59−67

Freitas V, Campos J, Fonds M, Van der Veer HW (2007) Potential impact of temperature change on epibenthic predator−bivalve prey interactions in temperate estuaries. J Therm Biol 32:328−340

Freudendahl ASL, Nielsen MM, Jensen T, Jensen KT (2010) The introduced clam *Ensis americanus* in the Wadden Sea: field experiment on impact of bird predation and tidal level on survival and growth. Helgol Mar Res 64: 93−100

Fryxell JM, Lundberg P (1998) Individual behavior and community dynamics. Chapman & Hall, New York, NY

Gibson RN, Robb L (1992) The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. J Fish Biol 40: 771−778

Gilbert MA (1973) Growth rate, longevity and maximum size of *Macoma balthica* (L.). Biol Bull 145:119−126

Good SP, Dodson JJ, Meekan MG, Ryan DAJ (2001) Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. Can J Fish Aquat Sci 58:1187−1195

Hall SJ, Raffaelli D, Turrell WR (1990) Predator-caging experiments in marine systems: a reexamination of their value. Am Nat 136:657−672

Herrmann M, Lepore ML, Laudien J, Arntz WE, Penchas-zadeh PE (2009) Growth estimations of the Argentinian wedge clam *Donax hanleyanus*: a comparison between length-frequency distribution and size-increment analysis. J Exp Mar Biol Ecol 379:8−15

Hiddink JG, Marijnissen SAE, Troost K, Wolff WJ (2002) Predation on 0-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and

intertidal distribution of epibenthic predators. J Exp Mar Biol Ecol 269:223–248

Hummel C, Honkoop P, van der Meer J (2011) Small is profitable: no support for the optimal foraging theory in sea stars *Asterias rubens* foraging on the blue edible mussel *Mytilus edulis.* Estuar Coast Shelf Sci 94:89–92

Hunt HL, Mullineaux LS (2002) The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). Limnol Oceanogr 47:151–164

Kaehler S, McQuaid CD (1999) Use of the fluorochrome calcein as an in situ growth marker in the brown mussel *Perna perna.* Mar Biol 133:455–460

Krebs JR, Davies NB (1981) An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford

Loebl M, Colijn F, van Beusekom JEE, Baretta-Bekker JG and others (2009) Recent patterns in potential phytoplankton limitation along the Northwest European continental coast. J Sea Res 61:34–43

Mahe K, Bellamy E, Lartaud F, de Rafelis M (2010) Calcein and manganese experiments for marking the shell of the common cockle (*Cerastoderma edule*): tidal rhythm validation of increments formation. Aquat Living Resour 23: 239–245

McCullagh P, Nelder JA (1998) Generalized linear models. Chapman & Hall, London

Moran AL (2000) Calcein as a marker in experimental studies newly-hatched gastropods. Mar Biol 137:893–898

Moran AL, Marko PB (2005) A simple technique for physical marking of larvae of marine bivalves. J Shellfish Res 24: 567–571

Nakaya M, Takatsu T, Joh M, Nakagami M, Takahashi T (2007) Annual variation of potential predation impacts on larval and juvenile marbled sole *Pseudopleuronectes yokohamae* by sand shrimp *Crangon uritai* in Hakodate Bay, Hokkaido. Fish Sci 73:112–122

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. Mar Ecol Prog Ser 111:289–297

Philippart CJM, van Aken HM, Beukema JJ, Bos OG, Cadee GC, Dekker R (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica.* Limnol Oceanogr 48:2171–2185

Pihl L, Rosenberg R (1984) Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. Mar Ecol Prog Ser 15:159–168

Polte P, Schanz A, Asmus H (2005) Effects of current exposure on habitat preference of mobile 0-group epibenthos for intertidal seagrass beds (*Zostera noltii*) in the northern Wadden Sea. Estuar Coast Shelf Sci 62:627–635

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reise K (1985) Tidal flat ecology, Vol 54. Springer, Berlin

Reusch TBH, Williams SL (1999) Macrophyte canopy structure and the success of an invasive marine bivalve. Oikos 84:398–416

Riascos J, Guzman N, Laudien J, Heilmayer O, Oliva M (2007) Suitability of three stains to mark shells of *Concholepas concholepas* (Gastropoda) and *Mesodesma donacium* (Bivalvia). J Shellfish Res 26:43–49

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Schmidt M, Philipp EER, Abele D (2008) Size and age-dependent changes of escape response to predator attack in the Queen scallop *Aequipecten opercularis.* Mar Biol Res 4:442–450

Smallegange IM, van der Meer J (2003) Why do shore crabs not prefer the most profitable mussels? J Anim Ecol 72: 599–607

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull Mar Sci 60: 1129–1157

Strasser M (2002) Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. Mar Ecol Prog Ser 241:113–123

Strasser M, Günther CP (2001) Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. J Sea Res 46: 57–67

Strasser M, Hertlein A, Reise K (2001) Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters. Helgol Mar Res 55:182–189

Sturm CF, Pearce TA, Valdés Á (2006) The mollusks: a guide to their study, collection, and preservation. American Malocological Society, Pittsburgh, PA

Tollrian R (1995) *Chaoborus crystallinus* predation on *Daphnia pulex*: Can induced morphological changes balance effects of body-size on vulnerability? Oecologia 101: 151–155

Urban MC (2007) Predator size and phenology shape prey survival in temporary ponds. Oecologia 154:571–580

van der Geest M, Van Gils JA, Van der Meer J, Olff H, Piersma T (2011) Suitability of calcein as an *in situ* growth marker in burrowing bivalves. J Exp Mar Biol Ecol 399:1–7

van der Meer J, Beukema JJ, Dekker R (2001) Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. J Anim Ecol 70:159–169

van der Veer HW, Feller RJ, Weber A, Witte JIJ (1998) Importance of predation by crustaceans upon bivalve spat in the intertidal zone of the Dutch Wadden Sea as revealed by immunological assays of gut contents. J Exp Mar Biol Ecol 231:139–157

Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172

Walther GR (2010) Community and ecosystem responses to recent climate change. Philos Trans R Soc Lond B 365: 2019–2024

Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecol Lett 13:1–10