Size-dependent predation risk for young bivalves

VRIJE UNIVERSITEIT

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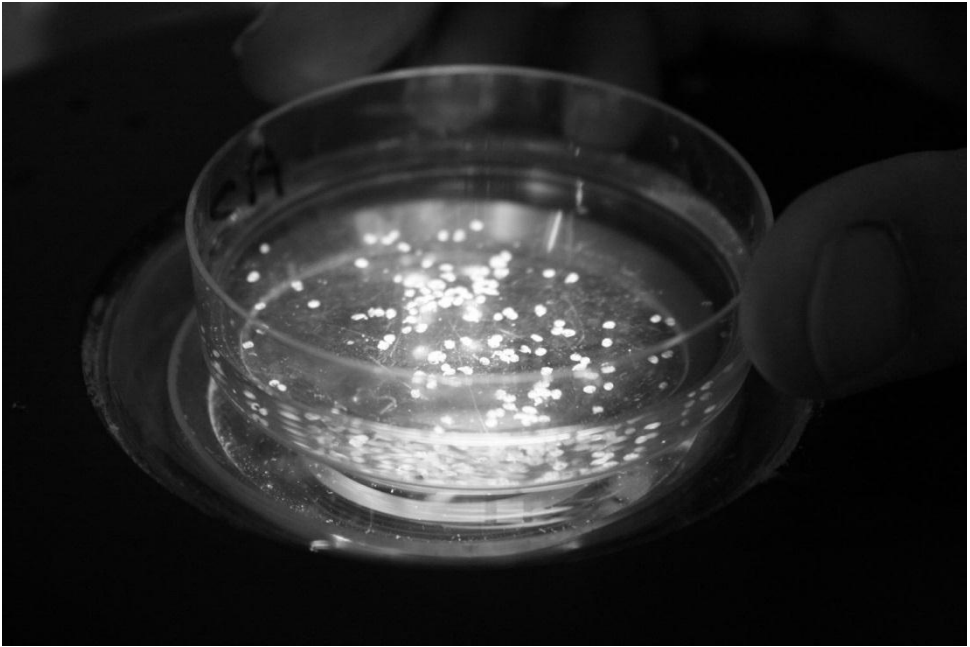in de aula van de universiteit,
De Boelelaan 1105

door

Henrike Andresen

geboren te Hamburg, Duitsland

promotor: prof.dr. J. van der Meer

Contents

Chapter 1

Introduction

Population dynamics and Wadden Sea bivalves

Population ecology is the study of population sizes and of the processes that determine these sizes (Begon et al. 1996). Population size changes by mortality or reproduction. Processes that can affect survival and reproductive success are, for example, resource availability, climate, diseases or predation, which effects can carry through via altered demographics (age structure or sex ratio). Investigating population dynamics is both academically fascinating and essentially important for conservation purposes (e.g. Armbruster and Lande 1993). Man induced population changes occur among other reasons through hunting or fisheries, and manipulation of habitats and resource availability (Ravera 1991).

The Wadden Sea is suited for studying marine population dynamics, because it is home to a comparably low number of species, with high numbers of individuals (Beukema 1976). As the world's largest uninterrupted system of intertidal flats, the Wadden Sea has recently received the world heritage status of
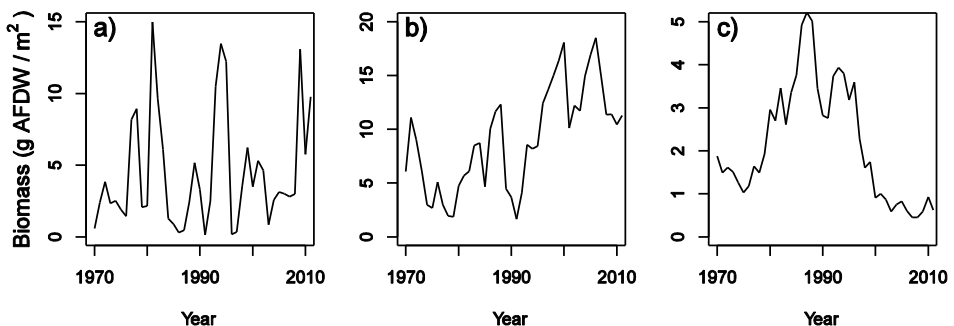
Fig. 1.1 Long-term changes of three bivalve populations at Balgzand in the Dutch Wadden Sea. a) *Cerastoderma edule*, b) *Mya arenaria*, c) *Macoma balthica* (Rob Dekker, pers. comm.). AFDW=ash-free dry weight.

the UNESCO. It is ecologically relevant beyond its geographic extension, because it functions as a stopover for migrating birds (van de Kam et al. 2004), and as a nursery ground for North Sea fish (van der Veer et al. 2001). Bivalves are a major component of this ecosystem; they usually comprise more than 50% of the biomass of the macrozoobenthos in the Wadden Sea (Beukema 1992a). Bivalves are also suitable for studying population dynamics, because their shells make age and growth determination possible, and they are quite hardy in experiments. Long-term observations (Beukema 1982) show that big year-to-year changes in bivalve abundance are the rule (Fig. 1.1 a). However, there are also long-term trends and changes which ask for research. In the past decades the share of the gaper clam *Mya arenaria* has increased (Fig. 1.1 b). New species, the razor clam *Ensis americanus* (Armonies and Reise 1999) and the Pacific Oyster *Crassostrea gigas* (Diederich et al. 2005), have been accidentally introduced. Mussels *Mytilus edulis* (Beukema 1993) and cockles *Cerastoderma edule* (Kraan et al. 2007) have been fished, and Baltic tellin *Macoma balthica* records are on their all-time low in the Western Wadden Sea (Fig. 1.1 c).

Population dynamics are determined by recruitment success

In many marine animal populations, the survival of juveniles is commonly decisive for population dynamics (Ólafsson et al. 1994). Early in life the mortality is high and variable, and after that the relative strength of an age class is more or less set, it decreases through a rather constant mortality, but does not change dramatically. The stage at which survivors of the youngest age group are regarded to be added to a population is called recruitment. The exact time is arbitrarily defined and involves practical reasons. For fish this is often when they become available for fisheries, but can also refer to a distinct biological phase, for example when they move to a different habitat. Bivalves in the Wadden Sea are usually termed "recruits" when they are retained on a 1 mm sieve at sampling in the end of the summer (Strasser et al. 2003), but sometimes after the first winter (van der Meer et al. 2001). The number of adult bivalves strongly correlates with their number as recruits observed in the first summer (Fig. 1.2 a). Conversely, there is no proportional increase of the number of offspring with increasing parent stock (Fig. 1.2 b). Juvenile mortality typically leads to asymptotic stock-recruitment curves. The numbers of parents in the gametes producing stock do not determine the numbers in the new generation the following year (van der Meer et al. 2001). The apparent lack of a stock-recruitment relationship is the central problem of fisheries science (Cushing 1996). Many fish and bivalve species spawn in excess,

this acts as an insurance against unpredictable dramatic events (Fuiman and Werner 2002). But then why do we not see huge year classes more often? Somewhere between larval phase and recruitment strong mortality takes place. The scattered observations about a horizontal line were often interpreted as lack of relationship, whereas it is evidence of strong density dependence worth consideration (Shepherd and Cushing 1980). There is still not sufficient understanding of how and when the magnitude of bivalve recruitment is determined.
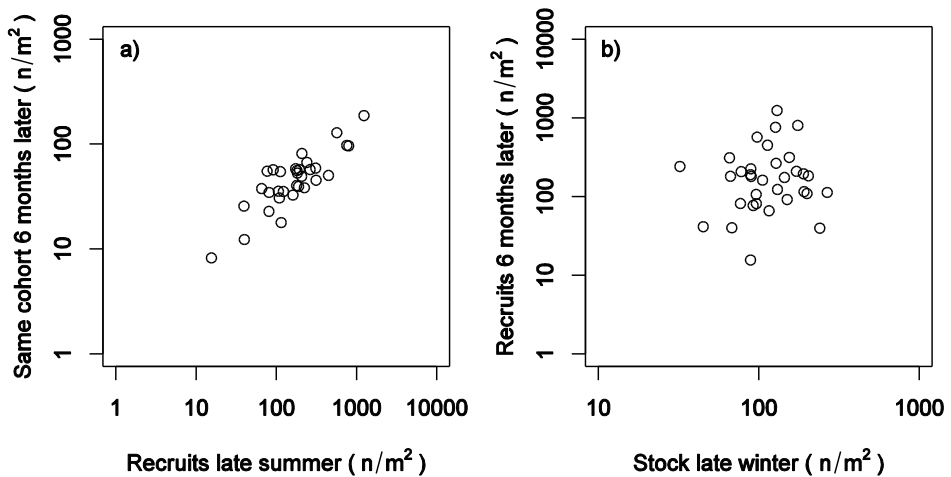
Fig. 1.2 a) Recruitment-stock relationship, b) stock-recruitment relationship of *Macoma balthica* at Balgzand in the Dutch Wadden Sea 1973-2005 (Rob Dekker and Jan Drent, pers. comm.).

Recruitment success is influenced by predation

Unusual events can teach us a lot about the processes that usually take place. From exceptional years in which recruitment was very good, we know that predation plays a big role in pre-recruit mortality. Good recruitment of several bivalve species all over the Wadden Sea was typically observed after cold winters (Beukema 1982, Jensen and Jensen 1985). After cold winters, the abundances of their crustacean predators, shrimp (*Crangon crangon*) and crabs (*Carcinus maenas*), increase later and stay lower than after mild winters (Beukema 1991, 1992b). Field experiments confirmed differential predation being the major reason behind the winter effect on bivalve recruitment (Strasser 2002). The importance of predation is further backed by the evolvement of predation

avoiding migration behavior in *Macoma balthica* (Hiddink et al. 2002). Predation on pre-recruits has been found relevant for other marine taxa, from sessile invertebrates (Osman and Whitlatch 2004) to flatfish (van der Veer and Bergman 1987).

Predation is influenced by prey size

The advantageous effect of the delayed shrimp arrival after cold winters is thought to act via body size (Strasser 2002). Most of the young bivalves are already too big to be consumed by the predators at the time they meet. After mild winters, when the crustaceans arrive earlier, the bivalves are still well within or below the preferred size range of the predators. This has been concluded from observations of recruit size distributions, which were shaped differently between contrasting years (Strasser 2002). These observations asked for studying the role of body size explicitly.

Body size is fundamental to predation risk (Kerfoot and Sih 1987). Predators can only ingest prey up to a certain maximum size (Nilsson and Bronmark 2000). Below that size, they may choose their prey according to energetic profitability (Krebs and Davies 1981) or to avoid damage of their feeding apparatus (Hummel et al. 2011, Smallegange and van der Meer 2003). In prey organisms the ability to hide (Gibson and Robb 1992), escape (Schmidt et al. 2008) or defend against predation (Tollrian 1995) changes with body size. Thus, different sized prey have a different risk of mortality. Size-selective predation is widespread and important for almost all animal taxa studied (Fryxell and Lundberg 1998). While typical terrestrial taxa such as holometabolic insects or birds reach a final body size early in life (Kooijman 2000), indeterminate growth is common among aquatic and marine taxa, such as mollusks and fish (Kozlowski 1996). As a consequence, marine predators and prey may co-occur over a large range of possible body size ratios during their lives.

Prey size is influenced by life history traits

Life history theory is concerned with strategies that increase the number of surviving offspring via scheduling of and investment in processes and events of the life cycle, such as development, number of offspring, parental care and reproductive lifespan (Stearns 1992). Two life history traits in particular, namely individual growth and timing of annual reproduction (e.g. Kooi and van der Meer 2010),

can influence the sizes of Wadden Sea bivalves at the time they encounter their crustacean predators.

Timing of life history events

Phenology is the timing of life history events depending on seasonal and interannual climate variations. For important events such as reproduction, migration or hiatus, the timing is essential. Temperature often functions as a cue to good circumstances, such as food availability. When different species react to changing cues in different ways, their interactions may be altered, because they encounter at different stages (Yang and Rudolf 2010). One example of this became famous through the documentary "An inconvenient truth" about effects of climate change: Caterpillar abundances in the Netherlands peak earlier and earlier in the year with increasing spring temperatures, but their bird predators, migratory great tits (*Parus major*), at their wintering grounds do not have knowledge of local temperatures when they decide to return to their breeding habitat in the Netherlands (Visser et al. 2004). As a result, the chicks now hatch mainly after the caterpillars pupate (Fig. 1.3). Consequences may be reduced hatchling survival, increased predation pressure on alternative prey, and limited control of the caterpillar population.

In the Wadden Sea, bivalve spawning is triggered by water temperature in spring (Drent 2004). This is usually a good indicator of algal food availability. In contrast, winter temperature decides when their crustacean predators arrive
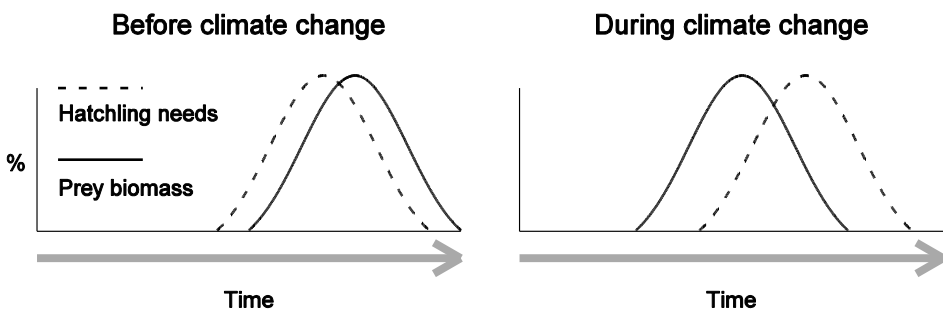
Fig. 1.3 Example how phenology affects stage-dependent species interactions. Warming climate promotes earlier appearance of caterpillars, an important food item of newly hatched great tits. Hatching of great tits however does not advance in time, because the adults have no information of the local environment at the time they decide to migrate from their wintering to their breeding grounds. They miss the time of highest caterpillar availability. Curves are scaled to the respective maximum. Adapted after Visser et al. (2006).

back from their winter retreat in the deeper North Sea and reproduce (Beukema 1991, 1992b). Therefore, although spring and winter temperature may be correlated, the relative timing of predators and prey varies between years (Strasser and Günther 2001). Yet, what that means for the body sizes that actually encounter had not been studied explicitly yet. This becomes especially important since cold winters are getting rare.

Individual growth rates

Most obviously body growth rate influences body size trajectories over time. Together with the timing of reproduction, growth rates will determine the duration of susceptibility to predation (Ebenman and Person 1988). *Cerastoderma edule* in Ireland for example experience high mortality during their whole life, they reproduce early and then grow rapidly. *Modiolus modiolus* in the same area suffer intense predation early in life, but after escaping further predation by growing large, they reproduce at slower growth rates and live long (Seed and Brown 1978). These "strategies" are the result of natural selection. In the past decades, man selected for lower growth rates in fish, because larger mesh sizes were used in fisheries with the aim to reduce overfishing (Nussle et al. 2011). Conversely, selection for small prey should promote fast growth. The investment in the best tactic is constrained within the energetic possibilities. Rapid growth was accompanied by increased susceptibility to predation in the fish *Menidia menidia*, this was explained with decreased physiological performance through the costs of rapid growth (Munch and Conover 2003). In larval Japanese anchovy (*Engraulis japonicas*) not only size-selective, but among individuals of the same size also growth-selective predation has been found, probably because a bad condition causes bad growth and at the same time ineffectiveness of antipredation behavior (Takasuka et al. 2003). Infaunal bivalves that feed at the sediment-water interface have to pay the predation avoiding effect of deep burrowing with reduced food intake (de Goeij and Luttikhuizen 1998). To investigate individual growth rates, either the age of the animals must be determined, or they must be marked. Both are difficult in the very small juvenile stage of bivalves, so it is hard to decide how far the observed size distributions are the result of selective mortality and for what part they are due individual growth rate variation. Individual chemical marking methods are now available (Moran 2000) that can be applied to disentangle these two factors, so that growth can be explicitly included when studying size-selective predation.

Predation is influenced by prey density

Prey size affects predation rates, among other reasons by influencing the time it takes to find and handle prey. The relative importance of these two components of the predation process depends on prey density. At low prey density, it takes longer to find prey than at high density. At very high prey density, when it is very easy to find prey, the time that it costs to consume a prey will limit predation rates. Accordingly, the effect of body size or of predation avoiding features on consumption rates cannot be considered independently of prey density (Aljetjawi et al. 2004, McCoy and Bolker 2008). The functional response expresses how predation rates change with density (Holling 1966). For a foraging predator, the functional response can in principle have two shapes. A hyperbolic form means high per capita mortality risk at low prey densities and decreasing risk with higher densities (Fig. 1.4). This has a destabilizing effect on the prey population. Or the functional response can have a sigmoid form, for which per capita mortality is highest at an intermediate density and becomes lower also at lower densities (Hassel 1979).
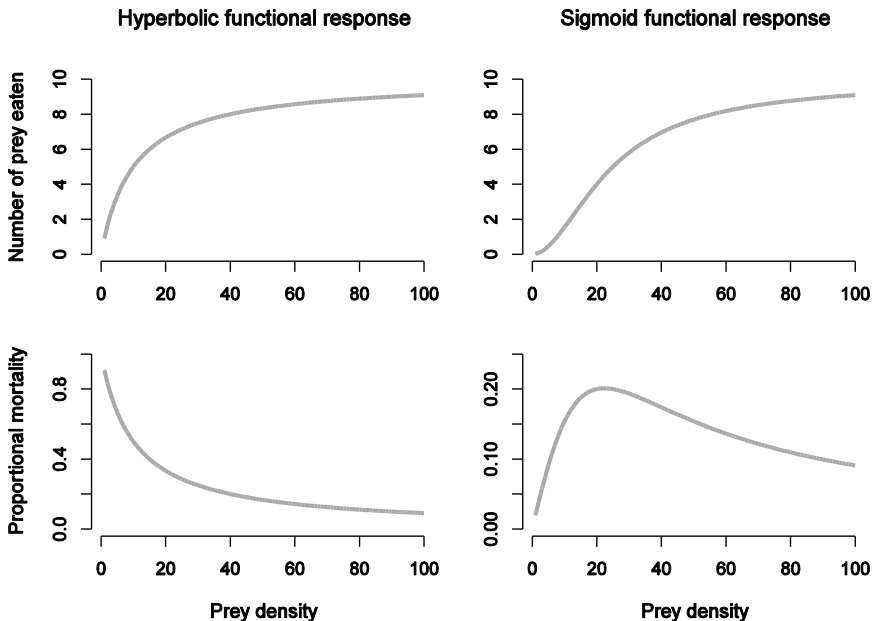
Fig. 1.4 The functional response describes how the predation rate depends on prey density. For a predator foraging by searching, it can in principle have two shapes. Both reach an asymptote at high densities, when predation is limited by handling time. Prey find a refuge at low density when a predator is unmotivated to search at a low reward rate (sigmoid shape).

As explained earlier, the lack of a stock-recruitment relationship implies that mortality must be density-dependent somewhere in the period from spawning until recruitment. Although the sigmoid functional response provides a low density refuge, it is unlikely that it alone is responsible for the uncoupling of recruitment from reproductive stock size, as this would mean that the reversal point would have to be at a very high density. A predation behavior that equalizes prey density in space would be the aggregative response, which means that predators move to places with high prey density (Charnov 1976, Cummings 1997). Of course, there are also potential sources of density-dependent mortality other than predation, such as competition or diseases.

Aims, approach and overview of thesis

Size dependence of predation on young bivalves and its interplay with seasonal timing, early growth and density is the central theme of this thesis. The overall question is: can predation by shrimp explain the mortality patterns of young bivalves in the Wadden Sea? The main aims were to detect size and density dependence of mortality in the field, to find out how variable predator and prey size ratios are with varying conditions, to obtain early growth rates, and to quantify how predation rates change with prey size and density. The focus is on the pre-recruit, but post-settlement period of the bivalve species *Macoma balthica* and *Cerastoderma edule*; two chapters deal with *M. balthica* exclusively, and one also includes *Mya arenaria*. They are all infaunal intertidal bivalve species with a pelagic larval phase.

It is good to tackle a research question with several approaches, from emphasis on investigating the most natural situation to getting the best grip on mechanisms. Field observations will give the most realistic results, but the processes that led to the observed patterns can often not be identified. In field experiments, under mainly natural conditions certain processes are manipulated, but other aspects cannot be controlled. In laboratory experiments, processes can be investigated in isolation, but they may not be relevant or behave the same way in the field. Modeling offers most control and understanding, and makes it possible to study hypothetical scenarios. Unrealistic results help to explore what else is needed to understand the situation outside. All these different approaches together are needed, because every one on its own only tells a part of the story and no one of them is controlled and natural enough at the same time (Underwood et al 2000, Virnstein 1980).

In chapter 2 we model *M. balthica* growth rates and size selection by shrimp on the basis of several years of field observations of pre-recruit bivalve and shrimp size distributions. Different combinations of growth rates with size preferences by shrimp or size-independent mortality are analyzed to see which parameter combination leads to similar bivalve sizes as observed. The main question is whether size selectivity by shrimp is able and necessary to reproduce the observed bivalve size distributions.

In chapter 3 we investigate growth and size selectivity of loss of newly settled bivalves with field experiments. Field sites in two distant regions of the Wadden Sea are chosen to get different growth and timing conditions and predator regimes. Exclosure cages are used to manipulate predator access. Bivalves are stained with a fluorescent dye to disentangle growth and size-selective loss. The main aims are to obtain individual growth rates for the fragile early life stage of bivalves, and to detect size-selective loss.

In chapter 4 we compile field observations of young bivalves and crustaceans from several years from two Wadden Sea regions. The main aim is to examine how the time lag between predators and prey and their resulting size ratios differ between years, regions and species.

In chapter 5 we carry out aquarium experiments on the functional response of shrimp foraging on different densities and sizes of *M. balthica*. The main aims are to determine the shape of density dependence, to estimate feeding rates, and to find out how much difference a larger body size makes for bivalve prey survival.

In chapter 6 we analyze observations of pre-recruit densities concerning density-dependent mortality. Simulations are used to account for measurement and process error. The main aim is to detect if and when density dependence of mortality in the pre-recruit phase occurs.

In chapter 7 the conclusions from the previous chapters are brought together, discussed, and compared to other research. The main aims are to establish their relevance to our understanding of bivalve recruitment, and to pinpoint directions for further research.

Acknowledgements

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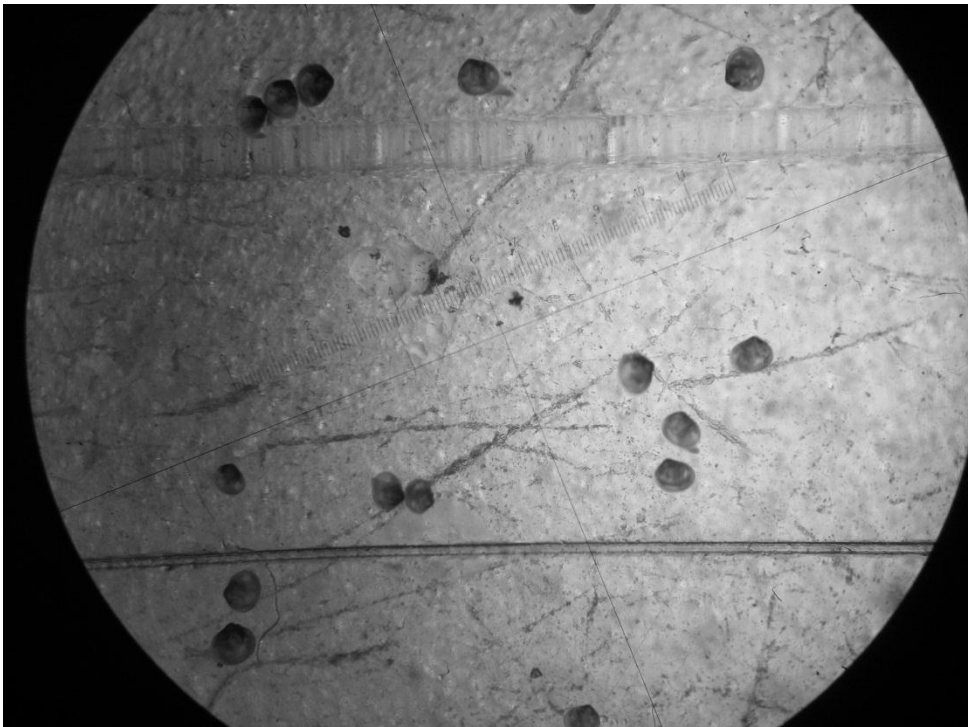
Chapter 2

Size-selective predation mortality and growth rates of 0-group bivalves *Macoma balthica* modeled from size distributions

Henrike Andresen, Rob Dekker, Jaap van der Meer

Abstract

We simulated growth and size-selective predation mortality of juvenile Wadden Sea bivalves, predicted size distributions of prey *Macoma balthica* shaped by their predators *Crangon crangon* (Brown shrimp), and compared these predictions with observations in the field. Under the assumption that all mortality is caused by shrimp, size-selective predation could explain bivalve size structure in several cases with quite realistic and consistent prey choice functions. In about half of the 14 studied time periods, bivalve size structures could not be reproduced by selective shrimp predation, but unselective mortality never led to a reliable fit of the field data. We conclude that size-dependent abundance changes are the rule in the early life of these bivalves. Though other size-dependent processes such as migrations can affect local abundances, the support for shrimp predation being a major determinant of young *M. balthica* abundance and size distribution of the survivors is strong.

Introduction

Body size is crucial to predator–prey interactions (Brooks and Dodson 1965). Prey capture and handling success depend on the sizes of both predator and prey (Claessen et al. 2002). As predation mortality depends on body size, predators can affect the size structure of their prey population (Rice et al. 1993, Sparevik and Leonardson 1999).

Predation by crustaceans is considered to play an important role in the recruitment success of bivalves in the Wadden Sea (Beukema et al. 2005, Hiddink et al. 2002, Strasser 2002). Relative timing of peak crustacean and bivalve settler abundances varies between years (Philippart et al. 2003, Strasser and Günther 2001), so that different predator and prey body sizes may encounter over time each year. Differences in bivalve size distributions between years at the time of recruitment in August have been observed (Strasser et al. 2001), and are possibly due to selective predation. Yet, up till now predator and prey size structures have not been brought together analytically.

We investigate the predator-prey relationship of young infaunal bivalves *Macoma balthica* (Baltic tellin) and their most abundant epifaunal predators *Crangon crangon* (Brown shrimp). Field observations of their size distributions over time in the Wadden Sea were the starting point of a simulation study. We analyzed what combinations of bivalve growth rates and size selection by the predators would be able to bring about the observed changes in bivalve size distributions. The outcomes of a model version assuming that all mortality was caused by size-selective predation by shrimp are compared to a version that assumes unselective mortality. Size-related mortality can also occur through processes other than predation (Green et al. 2004). If the estimated prey preference by shrimp turns out to be very variable between study periods or has to be unrealistic to achieve a good fit, then other processes must dominate over predation in determining bivalve size distribution and mortality.

Individual-based models are useful to evaluate whether effects of individual variability need to be considered in understanding year class variation, or whether an approach based on averages is already sufficient (Rice et al. 1993). Studies conducted in relation to fisheries research (e.g. Paradis and Pepin 2001) and also in systems with invertebrate prey (e.g. Sparevik and Leonardson 1999) show the necessity of including size structure in studies of early mortality. The aim of the present study is to determine how dominant size-selective predation by shrimp is in shaping the size distribution of the surviving young *M. balthica*.

Material and Methods

Data

Study site and temporal sampling design: Bivalves and crustaceans were sampled during low tide at the Balgzand tidal flats in the westernmost part of the Dutch Wadden Sea, at a site about 10 cm above mean sea level. Sampling took place in the years 1994 to 1998, at several occasions between May and November, the crucial phase determining *Macoma balthica* recruitment. See Tables 2.1 and 2.2 for the exact sampling dates each year for crustaceans and bivalves, respectively. Within these five years of field data, 14 periods occurred in which bivalve density decreased and shrimp observations were available.

Bivalve sampling: Bivalve samples were taken haphazardly within a plot of 100 m^2. Sampling area was adapted to decreasing bivalve densities by changing the number of samples taken at a sampling event (three to ten), as well as the number of cores pooled per sample (two to ten), and corer area (27 or 90 cm^2). Table 2.1 gives details of the total sampling area per date, and the number of *M. balthica* individuals found. Sampling depth was 8 cm in 1994 and 5 cm in later years. Samples were sieved in the lab over 300 μm mesh screen, only in 1998 a 150 μm sieve was used. At some occasions additional larger samples were taken, to a depth of 15 cm and sieved over larger mesh (1 mm), to get a better chance of catching the largest of the young bivalves, which occur in lower densities. The abundance estimates of the bivalves that are retained on a 1 mm sieve come from both the standard and the large samples; this gave smoother size-frequency distributions. The abundance they would have had in the area of the standard samples was calculated, because scaling the number of individuals up to a larger area would lead to a seemingly high accuracy of the subsequent statistical test. Bivalves were sorted live or preserved in 4% formalin in buffered seawater. Shell lengths were measured with 100 μm accuracy.

Crustacean sampling: Shrimp were sampled in four 10 m long transects just outside the 10x10 m^2 bivalve plot. Each time, 40 cores of each 90 cm^2 area were taken, adding up to a total sampling area of 0.36 m^2. Sampling depth was ca. 5 cm, and samples were sieved in the field over 1 mm mesh screen. *Crangon crangon* were sorted out live in the lab and their length measured from telson to scaphocerite to the nearest mm.

Table 2.1 Bivalve sampling dates, number of individuals and total sampling area per date.

		1994	1995	1996			1997	1998	
May	Date		22nd				21st	13th	28th
	n		87				391	42	11
	Area (cm^2)		807				672	403	403
Jun	Date	23rd	27th	13th			18th		
	n	63	27	142			125		
	Area (cm^2)	644	807	1340			403		
Jul	Date	19th	24th	3rd	16th	29th [1]	16th		
	n	57	19	234	54	63	143		
	Area (cm^2)	1076	807	2687	2687	672	538		
Aug	Date		22nd				28th		
	n		57				77		
	Area (cm^2)		5400				538		
Sep	Date	19th	21st	10th			15th		
	n	41	36	24			72		
	Area (cm^2)	1076	2700	540			672		
Oct	Date			9th*					
	n			30					
	Area (cm^2)			403					
Nov	Date			26th					
	n			305					
	Area (cm^2)			10200					

[1] No density decrease towards this sampling event.

Model

Simulations were carried out to find out which combination of bivalve growth rate and prey choice by shrimp could best predict the observed change in *M. balthica* size distribution. Random encounters between the observed predators and the observed initial bivalve prey were simulated, and a preference curve by the predator decided on the outcome of the encounter - consumption by the shrimp or survival of the bivalve. Mortality events and growth periods were alternated, so they were spread evenly over the time period, until the prey numbers were reduced to the abundance observed at the end of a time period. The resulting size distributions were compared to the field distributions by Kolmogorov-Smirnov tests (Zar 1999). The steps of the procedure are explained in more detail below and are illustrated in Fig. 2.1.
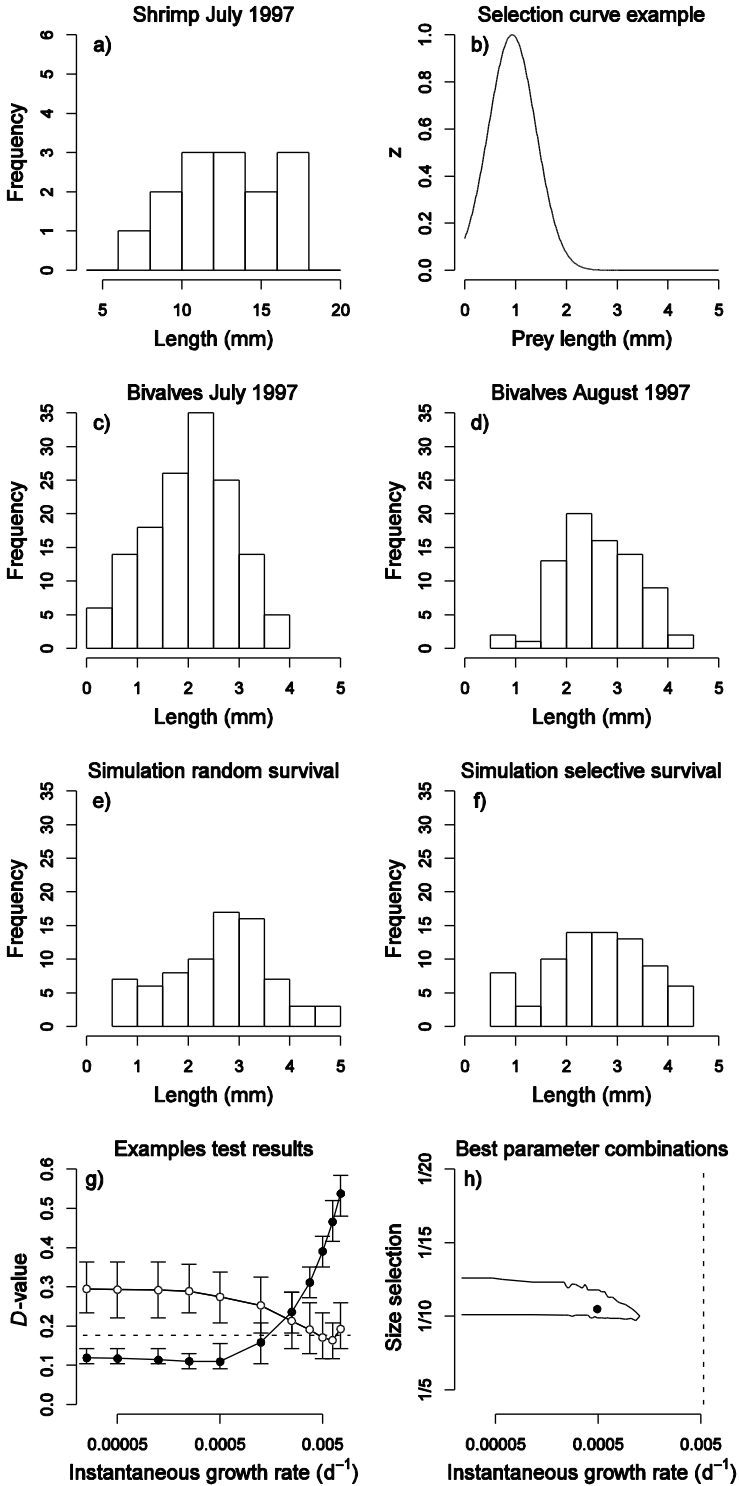
Exponential growth was assumed for the bivalve, with a single mean in-stantaneous growth rate parameter. On top of this average rate, for each period and for each individual a small randomly chosen and normally distributed growth variation was added with a standard deviation of 0.15 times the mean growth rate. Prior analyses showed that such growth variation gives a natural looking size distribution and that the results are quite robust to the amount of growth rate vari-ation. Growth created much smaller size increments in the simulations than the measurement accuracy in the observed data had been. For this reason, bivalve lengths were drawn from a uniform distribution within 0.1 mm of the measure-ments.

The predator-prey encounter rate was scaled to predator body size. The searching rate as well as the width of the searched area scales with predator length, thus the encounter rate scales with squared predator length (Kooijman 2000). The body size of the small bivalve prey was considered negligible for scaling the probability of predator-prey encounters. For all predator sizes, selec-tion takes place on the basis of predator/prey length ratio. For a given predator size, it has been suggested that the chance that a prey encounter results in a kill should be a dome-shaped function of prey body size. (Lundvall et al. 1999). We used the normal curve as the shape of the preference curve. The preference curve

Table 2.2 Shrimp sampling dates and density. Total sampling area per date was always 0.36 m^2.

		1994	1995	1996	1997	1998
May	Date					13th
	Density/m^2					54
Jun	Date	30th	12th	26th	5th	
	Density/m^2	25	56	72	51	
Jul	Date		12th	16th	2nd and 31st	
	Density/m^2		31	78	111 and 38	
Aug	Date	23rd	9th	22nd	25th	
	Density/m^2	36	117	3	77	
Sep	Date		5th			
	Density/m^2		59			
Oct	Date			9th		
	Density/m^2			36		
Nov	Date					
	Density/m^2					

gives the probability that an encounter results in prey death as a function of relative prey length. The maximum value is obtained at the preferred relative prey length. The standard deviation was chosen to be 1/3 of the preferred relative prey length. If the predators were not able to reduce the prey to the target abundance through their prey choice after 5000 encounters, the simulation was terminated. For the case of unselective mortality, the bivalves to be removed from the cohort were drawn randomly. After a bivalve was removed from the cohort, the remaining bivalves grow.

When the bivalves were reduced to the final abundance, the simulated size distribution resulting from the respective parameter combination of growth rate and preferred relative prey length was compared with the observed field size distribution by a Kolmogorov-Smirnov test (KS-test). The aim was to find the combination of the two parameters that do not lead to a significant difference in size distribution between observed and simulated. For every parameter combination, the simulation with alternating mortality and growth and the KS-test in the end was repeated 500 times. The parameter combinations for which the 97.5%-quantile of the *D*-values remained under the critical *D*-value for the particular *n* are concluded to be able to explain the observed bivalve size distribution.

Recall that the bivalve sampling area in the field was adjusted to bivalve density. This implies that the difference in the counts of individuals sampled between dates does not directly resemble the change in density. Therefore, the

◄ **Fig. 2.1** Illustration of the modeling procedure. a) Observed size distribution of shrimp, example from July 1997. b) Example of a prey selection curve, for a 14 mm long shrimp that chooses prey 1/15 of the predator length. c) Observed size distribution of *Macoma balthica* in July 1997. d) Observed size distribution of *M. balthica* the next month. e) Example of a simulated size distribution of *M. balthica*, using the July data as a starting point for growing and random mortality. f) Example of a simulated size distribution of *M. balthica*, using the July data as a starting point for growing and selective predation. g) Resulting *D*-statistic of the Kolmogorov-Smirnov tests comparing simulated with observed data, set out against the tested growth rates. As examples, the black dots are the averages of each 500 *D*-values obtained using a prey preference for 1/11 of the predator length, the white dots were obtained with size-independent mortality. The error bars represent 95% confidence intervals. The horizontal dashed line marks the critical *D*-value. Values below it indicate that the compared size distributions are not significantly different. h) Contour plot of the best parameter combinations for the example period. The black dot represents the combination of growth rate and prey preference that leads to the lowest average *D*-value when simulated and observed data are compared. For all parameter combinations within the contour, at least 95% of the resulting *D*-values are below the critical *D*-value. The vertical dashed line marks the best fitting growth rate for the case of unselective mortality; however, no growth rate led to sufficiently low *D*-values in combination with random mortality.

number of animals at the beginning of a time period was changed, while keeping the body size composition, such that the decrease in *n* until the end of the time period corresponds to the density decrease. The *n* at the end must not be changed, as this changes the apparent power of the KS-test. Further, when the smallest individuals in the end of a time period were smaller than the smallest in the beginning, they were removed, as this is probably due to later settlement into the area.

Results

In seven out of the 14 investigated periods, simulations with size-selective predation by the observed shrimp were able to reproduce the observed size distributions of *Macoma balthica* (Fig. 2.2). In the other cases, neither selective predation by the present shrimp nor random mortality led to a resemblance with the observed bivalve size distributions. That means size-dependent abundance changes must have taken place, but not, or not only, caused by shrimp predation. These periods were mainly early in the season, and in the whole year of 1996.

In the cases where size-selective shrimp predation produced bivalve size distributions similar to the field observations, the selected prey size was often around a tenth of the predator size. One time, the estimated choice was half of the predator size, and in one case the estimated selected size was much smaller, 1/50 of the predator's size. The corresponding estimates of the bivalves' instantaneous growth rates range from 0.00025^{-d} to 0.025^{-d} between all investigated time periods that got a fit with the data.

Turning to the prey point of view, the results also point to which sizes of the bivalves were most affected. In most of the cases where predation could explain the bivalves' size distribution, estimated growth rates were lower than those assuming unselective mortality. This means that of the available bivalves, the

► **Fig. 2.2** Estimates of prey selection by shrimp and bivalve daily instantaneous growth rate. A size selection of e.g. 1/10 means that a shrimp selects bivalves of a tenth of its own length. The black dot indicates the best fitting combination of prey preference and growth rate from simulations with size-selective predation. The solid contour contains all parameter combinations that resulted in prey size distributions similar to the observed size distribution in at least 95% of the simulations. When there is no contour drawn, no parameter combination led to a fit with the field data, and the dot is filled white. The dashed vertical line indicates the best fitting growth rate from simulations with size-independent, random mortality. No growth rate value led to a fit with the field data in combination with unselective mortality, so no confidence region is drawn around the dashed line.
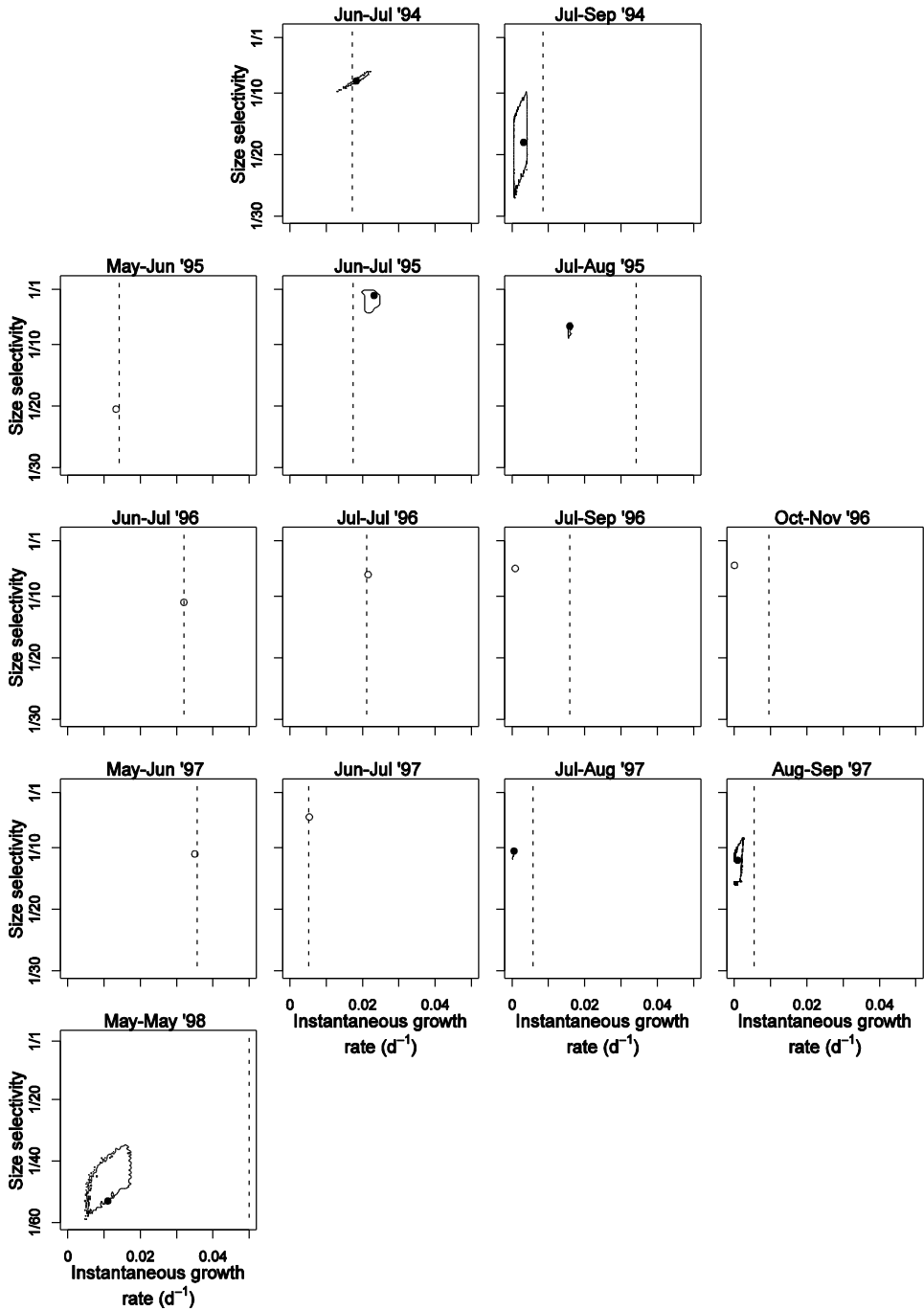
smallest ones have been fed on, as ignoring predation gives the illusion of faster growth. Only in the first investigated time period, growth rate estimates were similar with or without size-selective predation.

Discussion

For many of the investigated periods of the five summers studied, simulations supported size-selective predation by shrimp as the driving force. Usually bivalves at the lower end of the present size spectrum were affected. With about a tenth of the predator's size, these smaller sizes often represented the maximum of what shrimp could take (Hiddink et al. 2002, Keus 1986 cited at van der Veer et al. 1998). This points to the possibility for the bivalves to outgrow this predator. The choice for prey half the predator's size found in one instance (June to July 1995) is unrealistic. Also the preference for extremely small prey, relative to the predator and also compared to the available prey size range (May 1998), is in conflict with feeding on the center of the available size distribution at the maximum of the predator's ability (June to July 1994). Of the estimated values of the resulting growth rates, the higher ones are similar to growth rates obtained by individual marking in situ (Chapter 3).

Are there methodological limitations that could have had an effect on the results? The observed size structures of the bivalves can often not be explained by shrimp predation alone, but they can never be explained by simple bivalve growth in combination with unselective mortality, not even when the predator abundance was very low (July to September 1996, Fig. 2.2, Table 2.2). One might question the adequacy of the very simple growth model that has been assumed. Yet, assuming constant instantaneous growth is realistic for the early period, when growth is indeed almost exponential. In individual marking experiments (Chapter 3) we found that the lines of Ford-Walford plots were not converging, and that instantaneous growth rates did not change with bivalve size. It should be mentioned for completeness that out of curiosity simulations for growth with random mortality were also done with von Bertalanffy growth, in which the ultimate length was fixed. Even then, only in one out of 14 cases did unselective mortality lead to a matching size distribution at the end of the period. Thus, size-dependent processes are the rule in the early months of a bivalve cohort. Also in the periods where the estimated preference values deviate strongly from the other estimates (June to July 1995 and within May 1998), size-selective loss probably occurred through another process, but the attempt to link this to the present shrimp sizes led to the exceptional estimates. There could be additional predators, such as in-

faunal polychaetes, but also dissolution mortality (Green et al. 2004), competitive ability and starvation resistance or susceptibility to diseases could depend on size. One well known process in the early benthic life of young *Macoma balthica* is their secondary migration (Beukema 1993, Hiddink and Wolff 2002), which is also size-specific (Armonies 1992). Sometimes additional settlement was identified in the present data by the appearance of smaller individuals, which were removed from the analysis, but not all additional settlers may have been able to be identified that way, and that could give a distorted image.

The estimates of the preferred prey size were often at or just above the limit of the experimentally determined ability of shrimp (Hiddink et al. 2002). An underestimation of the number of big shrimp through sampling during low tide could have led to an overestimation of the preferred prey size by the observed shrimp. At high tide bigger shrimp enter the tidal flats for foraging (Janssen and Kuipers 1980). This could also lead to an underestimation of the bivalve growth rates, because lower growth fits better with the lack of bigger bivalve individuals that may have been consumed by the undocumented bigger shrimp.

The simulations were done under the far-reaching assumption that all mortality is due to shrimp predation. Considering that a lot of other processes can potentially affect bivalve size distributions, it is still remarkable that parameter estimates were consistent and realistic in so many cases. Even more so since the investigated time spans were short, while a comparable study in a piscivore system showed that size-selective mortality is more easily predicted in longer periods (Paradis and Pepin 2001). Hence it is plausible that size-selective shrimp predation is an influential process, which not only has a strong impact on size distributions, but also must make a major contribution to total pre-recruit mortality. Selective loss is dominated by the predator type with the greatest impact on the survivors (Paradis and Pepin 2001).

Concerning further research, an approach that tackles the problem from the other side would use detailed information on prey choice to quantify predation rates. Prey choice experiments until now (Hiddink et al. 2002, Keus 1986 cited at van der Veer et al. 1998) have established the upper limit of the predation window of shrimp feeding on *M. balthica*. The required experiments are not simple, because prey choice may depend on relative densities and alternative prey. Further, our results show that estimating growth rates from size distributions alone is inaccurate and individual marking methods (Chapter 3) are needed. Strong selectivity implies that there are important differences among individuals. In the future it will be interesting to not only investigate the consequences of variability among individuals of a bivalve cohort, but also the sources of variability.

Acknowledgements

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Chapter 3

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

Henrike Andresen, Ine Dorresteijn, Jaap van der Meer

Abstract

Individual growth and the timing of life history events determine the course of individual body sizes. By that, they can influence size-dependent species interactions such as predation. In the Wadden Sea, predation by crustaceans plays an important role for survival of pre-recruit bivalves. To investigate growth rates and size-dependent loss in two 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 of the fragile newly settled juveniles in the species *Macoma balthica* and *Cerastoderma edule* in the field. By this, growth and size-selective mortality were disentangled, while hitherto both were usually inferred from size distributions at this life stage. Fluorescent marking also revealed that growth rates were very variable between individuals. Growth was temporarily higher at Texel than at Sylt in both species. In combination with the exclosure experiments and sampling of predators and migrating bivalves, selective loss of smaller individuals was detected in both regions and could be related to predation pressure. Climate influences on phenology have potentially strong effects on species interactions, altering survival and thus recruitment and population dynamics.

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 and Lundberg 1998). Within this range, predators have preferences that favor high profitability (Krebs and Davies 1981) or avoid damage (Hummel et al. 2011, Smallegange and van der Meer 2003). In prey organisms the ability to hide (Gibson and 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, their growth rates will determine the duration of susceptibility to predation (Ebenman and Persson 1988).

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

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 and Dekker 2005). High recruitment is usually observed after cold winters, because crustacean predators arrive late (Strasser and Günther 2001), after bivalve offspring has 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 for several systems (e.g. Flach 2003, Strasser 2002, van der Veer et al. 1998), and some studies also pointed to a role of body size (Hiddink et al. 2002,

Hunt and Mullineaux 2002, Strasser 2002, Strasser et al. 2001). Some species perform predator avoiding migrations (Hiddink et al. 2002). However, the interplay of processes makes every one of them 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 act on size distributions. With the fluorochrome shell marker calcein (Kaehler and McQuaid 1999, Moran 2000, Moran and Marko 2005), a tool is available to obtain size-increment data of bivalves and gastropods, that can also be applied to fragile young animals. It is used in this study to disentangle growth from size-selective processes.

To investigate early bivalve growth and size-dependent loss, we combined the more recently established fluorescent staining method with already widely applied 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, for the first time field experiments were conducted simultaneously in two distant regions of the Wadden Sea. The winter seawater temperature (Bundesamt für Seeschiffahrt und Hydrographie 2012) 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 towards the northern Wadden Sea (Campos and 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 coming years, 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 detect and compare size-dependent loss in the two regions with differing conditions.

Material and Methods

Field experiments were carried out simultaneously in two 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 disentangle 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 about 400 km coastline apart (Fig. 3.1). Near Texel, one 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 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. Thus, in the two regions, two sites each were selected. They are not meant to represent the area, but were chosen for their contrasting conditions. The tidal flats at Texel stretch about 2 km from the high intertidal zone to the low water line, at the sites at Sylt this was about 800 m. The tidal ranges are 1.5 m and 2 m respectively. Experiments were carried out in the middle intertidal zone, because there the highest number of predator-prey encounters is expected.
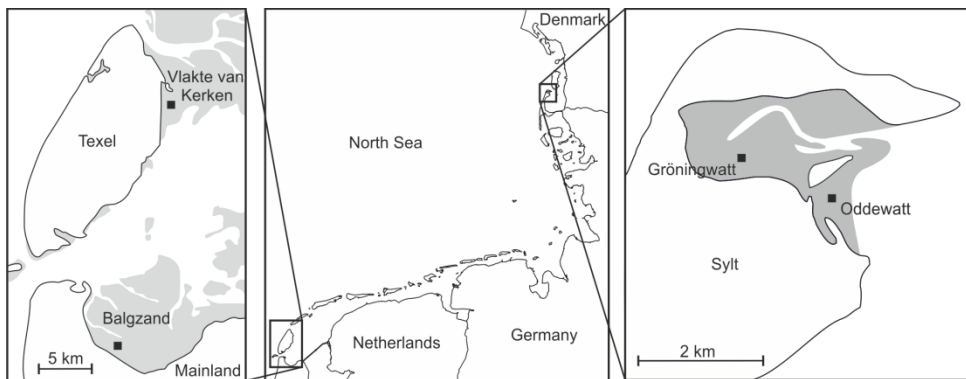
Fig. 3.1 Study sites in the middle intertidal zone near the islands of Texel and Sylt in the Wadden Sea, which constitutes the coastal transition zone to the North Sea. Vlakte van Kerken and Oddewatt are open, Balgzand and Gröningwatt sheltered sites.

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 three factors: site, exclosure and fluorescent marking with calcein. The factor site had four levels. The three levels of the exclosure treatments were uncaged, simple cage, and control cage. In half of the units calcein solution was applied (i.e. two 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 four times, but two cages each got lost in May and June. The experiments took place within square plots of 1600 m^2, marked with 25 poles. At one site the plot was made rectangular (30 m by 53 m) to fit between megaripples. The plots were divided into 400 squares of 2×2 m^2. For each cage or sample, one of them was picked from a random list without resampling. A short duration of each 10 days was chosen because the 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 because *C. edule* migratory activity is highest during spring tides (Armonies 1992). There were maximally two days between the initiations of the experiments at all the four sites. At the end of the 10-day experiments, samples were taken in the experimental units to measure abundance, body size and size of the fluorescent growth ring, to compare abundance, growth and size-selective survival of the two bivalve species *C. edule* and *M. balthica*.

Exclosure treatments

Predator-exclosure cages were cylindrical, 30 cm high with 30.5 cm diameter. The construction was similar to Strasser's (2002) with a frame of two PVC rings and three PVC straps. 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 sediment and protruded 20 cm. They were anchored with iron hooks of 50 cm length. To control for cage artifacts, double-walled cages were used. A second, larger cage with 39 cm diameter and 35 cm high was placed around the cage, leaving a space of about 4 cm between the two cage walls. In earlier experiments we had found that the more commonly used incomplete control cage attracted predators, so that potential caging artifacts and predation pressure are confounded (Andresen, in prep.). This problem is not easy to solve (Peterson and Black 1994). The aim of the double control cage is to increase the intensity of potential artifacts such as hydrodynamic modification or shading, and then test for interaction between artifact and treatment (Reusch and Williams 1999). The reasoning is that, if a difference in the response variable

between single 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 between sites (Reusch and Williams 1999). It was a priority not to disturb the sediment 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 from algae twice during each experimental period.

Dyeing with calcein

Size-increment data of juvenile bivalves were obtained by dyeing with calcein blue. Calcein functions as a fluorescent label that binds to calcium and is incorporated into growing calcium carbonate structures (Moran and Marko 2005). It has been used in several studies to determine growth of mollusks (e.g. Clarke et al. 2004, Hermann et al. 2009). Calcein is suitable because it needs only short immersion times and causes little harm (Mahe et al. 2010, Riascos et al. 2007). It can be applied in situ without disturbing the bivalves (van der Geest et al. 2011). PVC rings of 30.5 cm diameter and 10 cm high were pushed halfway into the sediment and 0.5 l solution of 250 mg l^{-1} calcein in 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

For quantifying epibenthic predators, once per experiment at high tide four samples were taken with a drop trap (Pihl and Rosenberg 1984) just outside the plot at each site. The trap was made of aluminum, had 0.5 m^2 sampling area and was 70 cm high. To avoid scaring the predators away, it was operated hanging from a 8 m long pole (made of two windsurf masts) by two persons. Sampling took place as soon as the water had receded enough that it would not swash over the sides after dropping the trap (i.e. below 70 cm). The content of the trap was intensively fished with 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, through a combination of weather conditions and logistic constraints. Crustacean samples were stored frozen and *Crangon crangon* length from scaphocerite to telson measured with 1 mm accuracy.

Bivalve sampling and sample processing

At the end of the exclosure experiment, bivalves were sampled with a sharpened Perspex tube of 20 cm^2 area to a depth of 3 cm. Because of high abundances of *M. balthica*, in May at Oddewatt a corer of 12.5 cm^2 area was used. 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 material of the bivalve samples was sorted in portions systematically from Petri dishes. Samples from Sylt were first repeatedly brought in suspension and decanted from the coarse sediment into a 250 µm sieve. Calcein-treated bivalves were measured under a stereomicroscope equipped with a Mercury UV-lamp and appropriate emission and excication 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 about 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

$$\mu = \log (L_{10} / L_0) / t \tag{3.1}$$

where L_{10} is the shell length at the end of the 10-day experiment, L_0 is the initial length measured by fluorescent ring, and $t = 10$ days is the duration of the experiment.

To be retained by a 500 µm mesh *C. edule* have to be 0.7 mm long and *M. balthica* 0.75 mm. Especially for *M. balthica* at Sylt in May, we missed the smallest individuals (Fig 3.2 c). 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 artifact. 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. 3.3). That means average growth rates would be overestimated where the initial size is small. Average growth ring size would be overestimated where growth is slow, because slow growing individuals with a small initial size are missed by the

sieve. Individuals with growth rings smaller than 0.7 mm were excluded from the analysis of growth rates and growth ring sizes. On average the mean growth rate and median growth ring size are based on about ten individuals per sample, sometimes only one or two; the maximum was 68 marked individuals in one sample. A low *n* within a sample will lead to higher variation between samples.
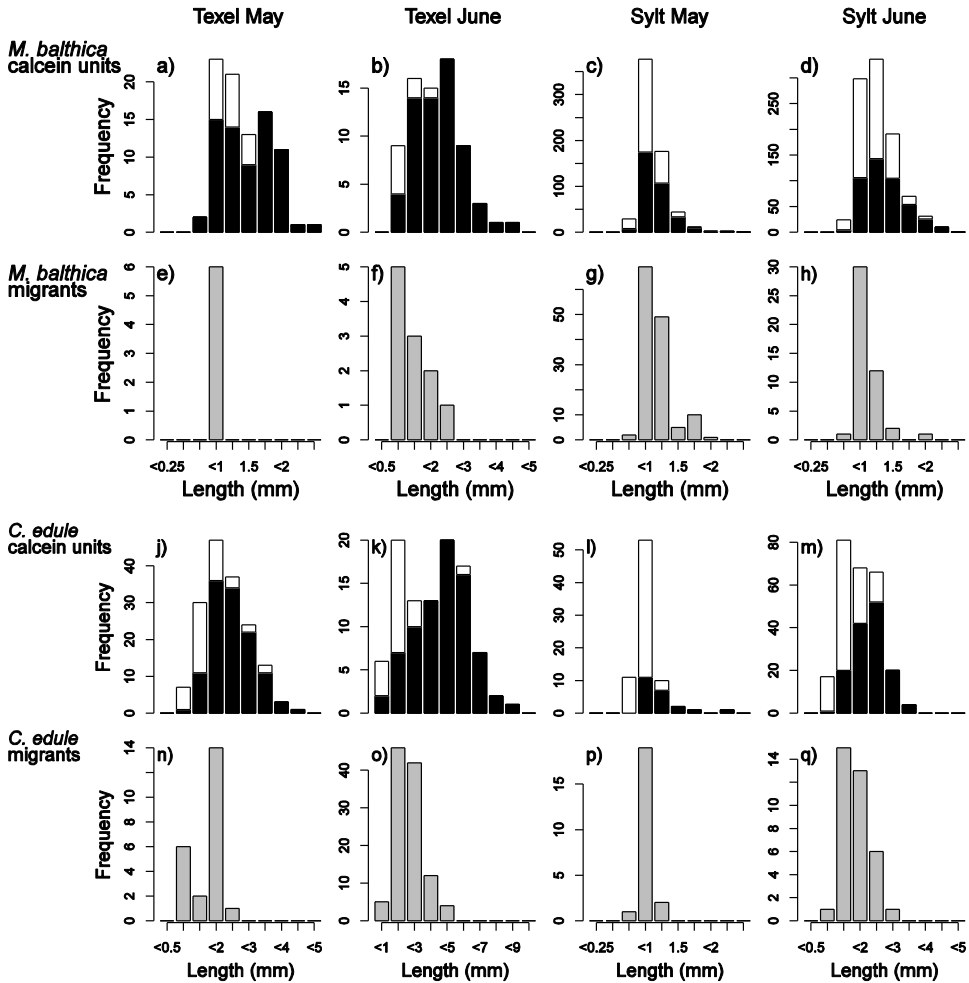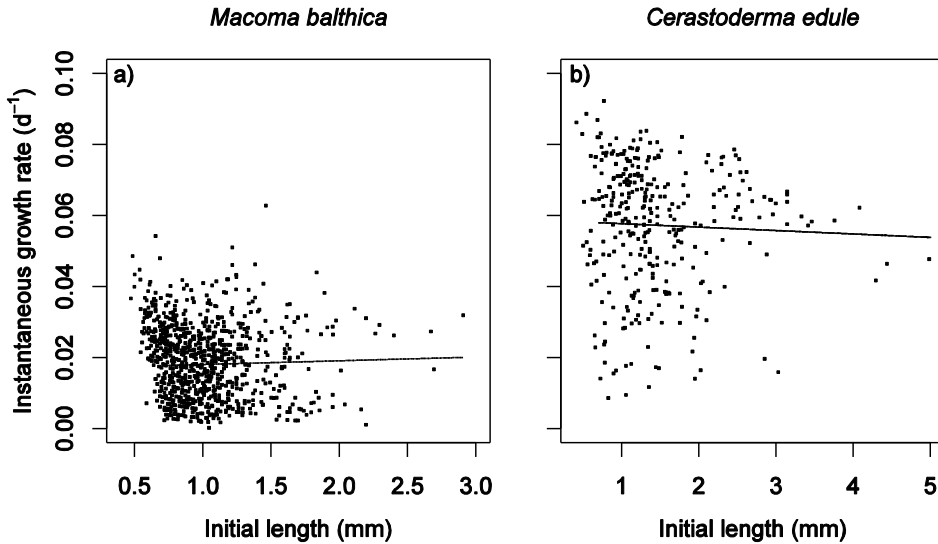

Fig. 3.2 *Macoma balthica* and *Cerastoderma edule*. Size-frequency distributions of shells in calcein treated experimental units with (black) and without (white, stacked) fluorescent mark, and in migration nets (grey). For the migrants, which had been caught at two occasions during the 10-day experiment, the theoretical final length at the end of the ten days was estimated using growth rates obtained from the marking experiment. Note the varying scales for frequencies and for sizes.

Assessment of immigration

In the early benthic phase, *M. balthica* and *C. edule* can perform secondary migrations. 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 consisted 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 plankton net in Armonies 1994). The opening could rotate freely pointing towards 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 at two times 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 resemble the size distributions of the animals without a fluorescent mark in the calcein-treated samples (Fig. 3.2). It was concluded that individuals without a mark had entered the sampling units later. For the subsequent analyses of abundances, they 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 analyzed separately per species and per experimental period with Generalized Linear Models (GLM) in R (R Development Core Team, 2008). Factors were site, exclosure and marking with calcein solution. *M. balthica* counts were overdispersed (dispersion parameter between 4.3 and 6.7), and the quasipoisson family was used, for *C. edule* counts, the poisson-family was suitable (dispersion parameter around 1). In a few cases the counts in all the four replicates of one treatment were zero, and the function would try to predict infinitely small log values. In that case, 1 was added to one of the four replicates to aid the estimation. Sampling area was incorporated in the model as a so-called offset variable (McCullagh and Nelder 1998). For size data, the median shell length per sample was calculated and the Gamma family gave the best looking residual distribution plot. For growth, the mean per sample 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

Fig. 3.3 *Macoma balthica* and *Cerastoderma edule*. Individual growth from size-increment data in dependence of initial size. Further calculations were done omitting growth rings <0.7 mm in length to avoid bias through sieve selection. Then the slopes were not significant for both species (p > 0.05), and instantaneous growth rates could be averaged over sizes within a sample.

necessary to include initial size as a covariable in the analysis of growth rates (Fig. 3.3). Models including different combinations of main and interactive effects (Table 3.1) were compared simultaneously with Akaikes information criterion, corrected for small sample size (Anderson 2008), using the R package 'MuMIn' (Bartoń 2012):

$$AIC_c = -2(\text{log-likelihood}) + 2p(n/(n\text{-}p\text{-}1)) \tag{3.2}$$

where p is the number of estimated parameters of the respective model including the intercept, and n is the number of observations. For *M. balthica* counts, the $QAIC_c$ for overdispersed count data was used.

$$QAIC_c = -2(\text{log-likelihood})/\hat{c} + 2p(n/(n\text{-}p\text{-}1)) \tag{3.3}$$

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 is increased by 1 to account for estimating the dispersion parameter.

The log-likelihood was obtained from the poisson fitted model. Every model that contains "exclosure" was estimated in two versions, once double cages and single cages were regarded as separate levels, and once these two exclosure types were not distinguished (lowercase letters in Tables 3.1 – 3.3), to assess caging artifacts.

Table 3.1 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 two versions, once with the three levels separately (capital letters) and once not differentiating between single cage and double control cage (lower case letters). Models were compared simultaneously with Akaikes information criterion (Tables 3.2 and 3.3).

| Model complexity	Model No.	Model description
Full model	A, a	s + e + m + s:e + s:m + e:m + s:e:m
3 two-way interactions	B, b	s + e + m + s:e + s:m + e:m
2 two-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
1 two-way interaction and 3 main effects	F, f	s + e + m + s:e
	G, g	s + e + m + s:m
	H, h	s + e + m + e:m
two-way interaction and 2 main effects	J, j	s + e + s:e
	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

Results

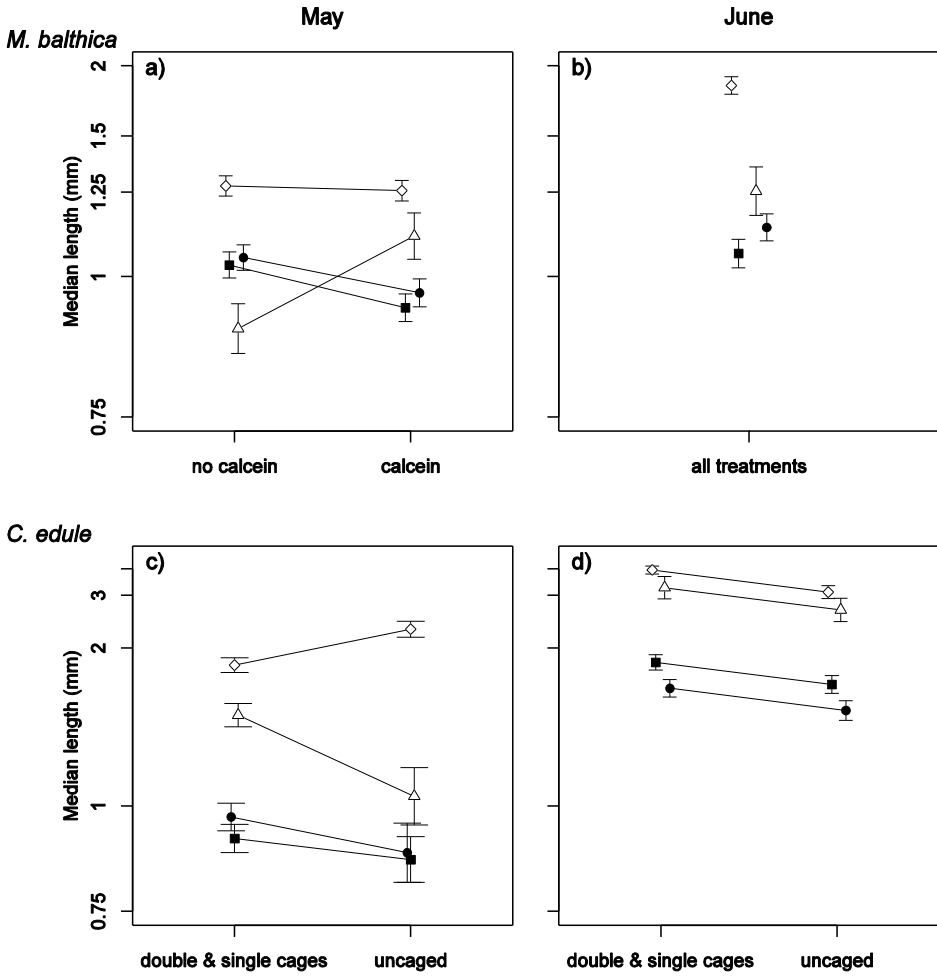## *Effect of calcein marking on abundance and size*

A side-question but prerequisite in the combined caging and staining experiment was whether the method of fluorescent marking affects 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, Table 3.1 and 3.2). The application of the marking solution seems to have lowered *M. balthica* abundances in May (Fig. 3.4 a and b, only significant factors plotted). The effect was small but significant and showed in the exclosures. The m(marking):e(exclosure) interaction (model "h", Table 3.1 and 3.2) did not affect the direction but only the strength of the exclosure effect, and was similar at all sites (Fig. 3.4 a and b). Also *C. edule* abundances in June differed between calcein treatments (model "C"), at Oddewatt they were higher in the calcein treated units (Fig. 3.4 c and 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. 3.5 a). There was no significant influence of calcein on body size of *C. edule* in June after one influential value was removed (model "n", Fig. 3.5 d). Overall, in some cases calcein may change the effect sizes in the following analyses, but not the qualitative conclusions.

Growth

Under natural (uncaged) conditions, growth of *M. balthica* was similar at all sites in May (Fig. 3.6 a), but in June growth got lower at Sylt (Fig 3.6 b), whereas in *C. edule*, growth appeared to be lower at Sylt in May (Fig 3.6 c), and the same everywhere by June (Null model, Fig 3.6 d). *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 one day for a 1 mm long individual. The instantaneous growth rate of around 0.02 d^{-1} for *M. balthica* in May corresponds to 20 µm length increase in one day for a 1 mm long individual. However, it is remarkable how variable the individual growth rates were (Fig. 3.3). *M. balthica* grew at up to 0.06 d^{-1}, but some had hardly grown 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. 3.6). In most of the observable cases, growth
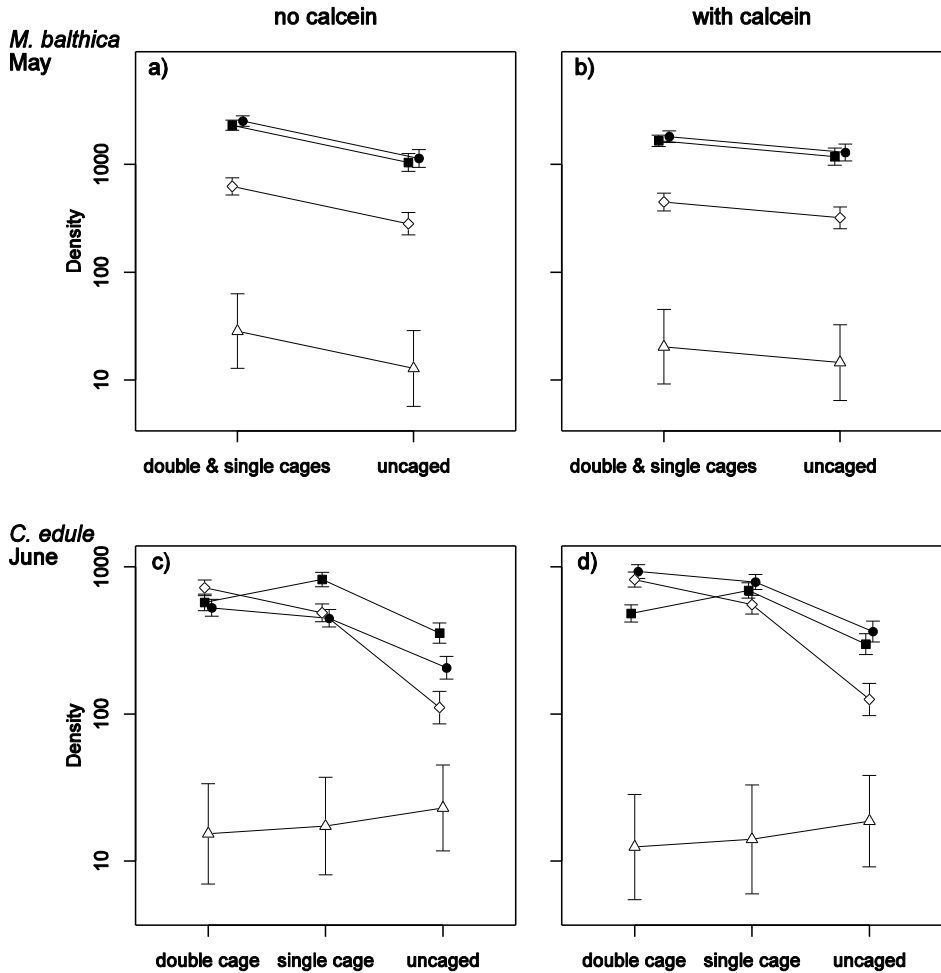
Fig. 3.4 *Macoma balthica* and *Cerastoderma edule*. Model predictions and standard errors of the models that assess the effect of calcein marking on bivalve abundance. Only significant factors are plotted. The factor marking was not significant for M. balthica in June and for *C. edule* in May (not shown). ■ = Gröningwatt (at Sylt), ● = Oddewatt (at Sylt), ◇ = Balgzand (at Texel), △ = Vlakte van Kerken (at Texel).
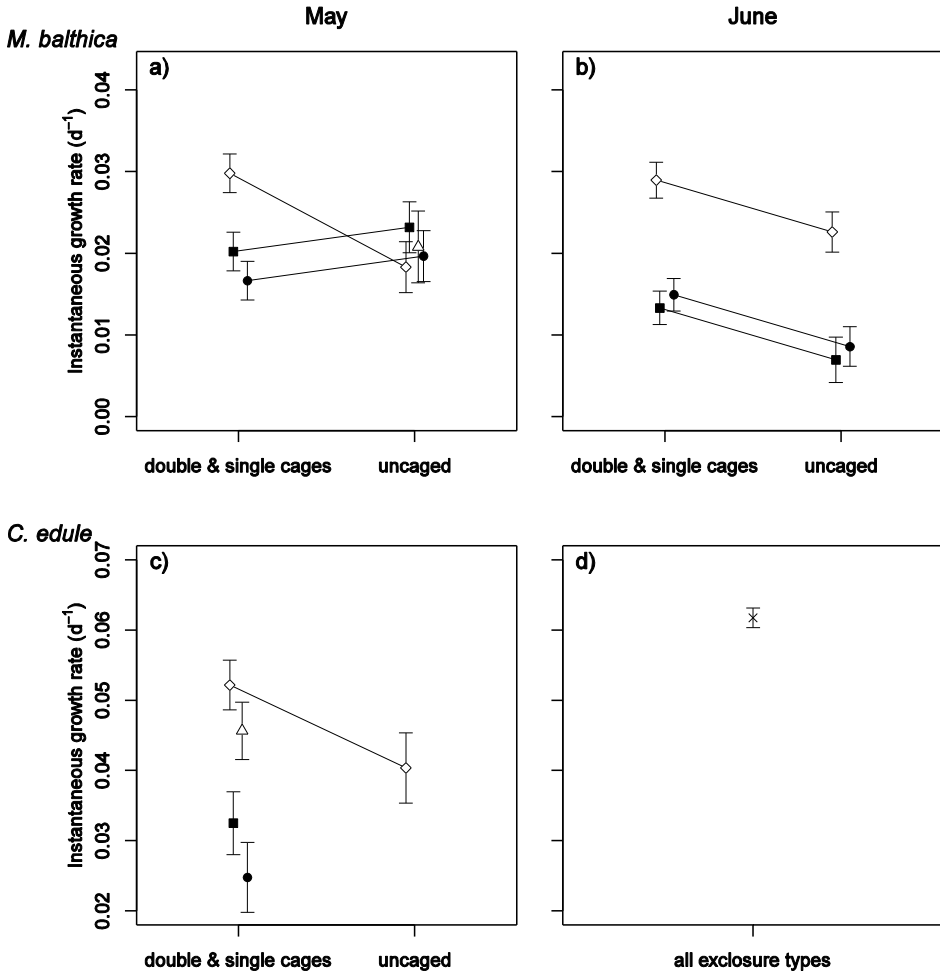
Fig. 3.5 *Macoma balthica* and *Cerastoderma edule*. Model predictions and standard errors of the models that assess the effect of calcein marking on bivalve size. Only significant factors are plotted. Note the compressed scale. ■ = Gröningwatt (at Sylt), ● = Oddewatt (at Sylt), ◇ = Balgzand (at Texel), △ = Vlakte van Kerken (at Texel).

Table 3.2 Akaikes 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, $QAIC_c$ for overdispersed count data was used. The lowest values are highlighted in bold. For the description of each model number see Table 3.1.
C. e: *Cerastoderma edule*, *M. b.*: *Macoma balthica.*
Fit: $1 - \text{deviance}_{\text{best fitting model}} / \text{deviance}_{\text{Null model}}$ is given as a measure of fit.

| Model number	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

Fig. 3.6 *Macoma balthica* and *Cerastoderma edule*. Model predictions and standard errors of models on mean daily instantaneous growth rates in exclosure experiment, obtained from size-increment data. Only significant factors are plotted. ■ = Gröningwatt (at Sylt), ● = Oddewatt (at Sylt), ◇ = Balgzand (at Texel), △ = Vlakte van Kerken (at Texel), ✕ = all sites together.

was higher in the cages (model "n", Table 3.3), but in *M. balthica* in May the influence of caging differed between sites (model "j"). Growth was decreased in the cages at Sylt, hinting to habitat-dependent modification of growth conditions (Fig. 3.6 a). 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.

Table 3.3 Akaikes 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, and size selectivity of loss. For *Macoma balthica* counts, $QAIC_c$ for overdispersed count data was used. The lowest values are highlighted in bold. For the description of each model number see Table 3.1. *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 No.	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	-147	-205.6	95.6	**121.3**	160.8	**194.7**	-3.945	6.162	1.161	17.49
N	-236.2	-225.7	-159	-217.5	81.1	126.3	147.9	203.9	-14.85	-4.203	-5.785	11.07
Q	-241.3	-221.6	-161	-222.5	80.6	131.7	151.4	263.9	-16.15	**-9.9**	-8.956	**5.23**
R	-237.3	-201.6	-147	-223.3	139.3	250.7	288.6	292.5	-20.23	10.26	17.92	68.27
T	-241.7	-204.8	-152	**-227**	139.9	259	292.9	353.9	-21.07	6.27	21.45	63.39
j	**-242**	-222	-161	-216.2	82.92	121.5	150.8	203.4	-13.67	-4.708	**-8.97**	9.171
n	-239	**-226**	**-161**	-220.7	**78.8**	123.5	**145.9**	204.8	-18	-7.255	-8.966	8.096
r	-239.8	-203.9	-150	-225.8	138.3	248.7	286.8	292.9	**-22.76**	7.851	15.96	65.8
Fit	0.3994	0.5941	0.536	0	0.6335	0.7975	0.7867	0.8239	0.1096	0.4831	0.7794	0.8527
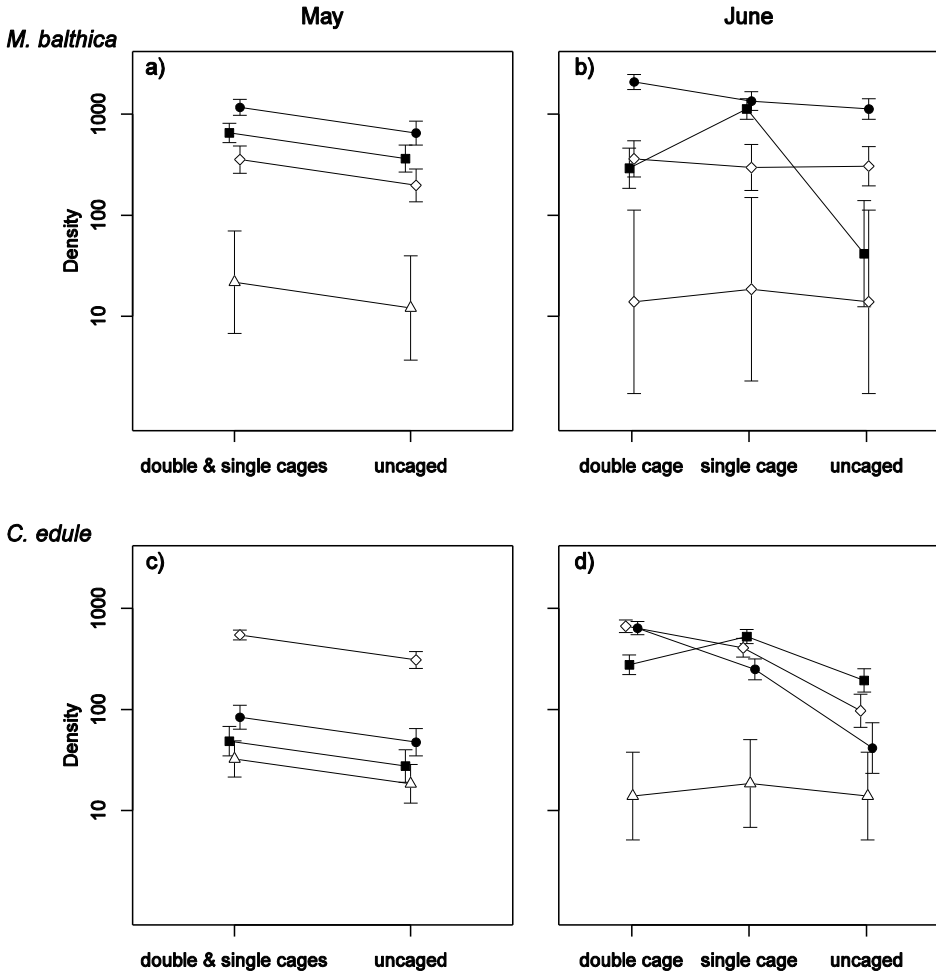
Fig. 3.7 *Macoma balthica* and *Cerastoderma edule*. Model predictions and standard errors of models on abundance of marked bivalves in the exclosure experiment. Only significant factors are plotted. ■ = Gröningwatt (at Sylt), ● = Oddewatt (at Sylt), ◇ = Balgzand (at Texel), △ = Vlakte van Kerken (at Texel).

## *Exclosure effect on abundance and size-selectivity of loss*

In *M. balthica* as well as in *C. edule*, in May abundances were always lower in the uncaged sampling units where predators had access (Fig. 3.7 a and c). The loss, presumably mainly predation mortality, was similar between sites (model "n"). In June, in both species abundances differed between the single cages and the double control cages in different ways between sites (model "J", Fig. 3.7 b and d). Although sometimes the abundances were clearly higher in the cages, it
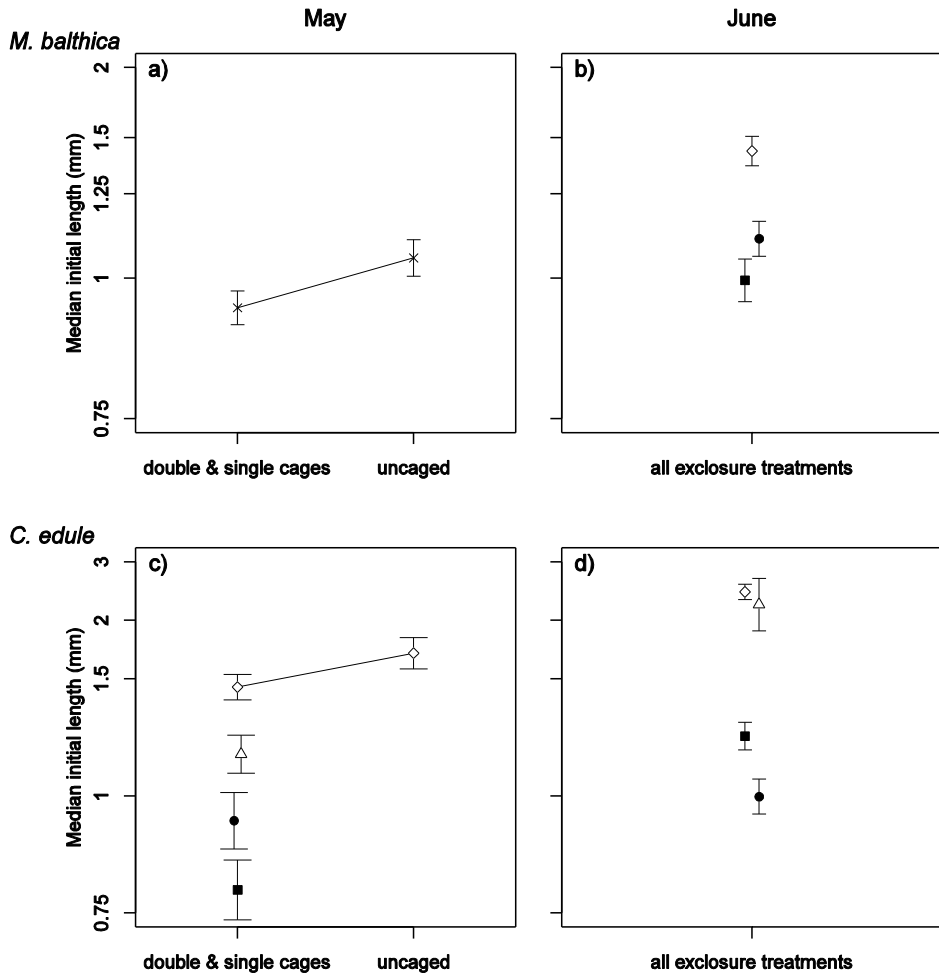
Fig. 3.8 *Macoma balthica* and *Cerastoderma edule*. Model predictions and standard errors of models on initial bivalve size in exclosure experiments to investigate size-selectivity of loss. The initial size of the survivors is the size of their artificial growth rings produced with calcein at the beginning of the experiment. Only significant factors are plotted. For *C. edule* in May, only at Balgzand unbiased growth ring observations were available. ■ = Gröningwatt (at Sylt), ● = Oddewatt (at Sylt), ◇ = Balgzand (at Texel), △ = Vlakte van Kerken (at Texel), ✕ = all sites together.

cannot be safely concluded that this is due to protection from predation. The varying differences between cage types are a hint 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, both in *M. balthica* and *C. edule* (model "r" and "j", Fig. 3.8 a and c). This hints to 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 that in *M. balthica* (Fig. 3.5 a). The fluorescent record in the shells 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 both species (model "Q", Fig, 3.8 b and 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. 3.7 d), but through marking, it becomes evident that smaller individuals had immigrated (Fig. 3.2 k). Unfortunately, for *C. edule* in May, there are no unbiased growth ring observations (truncation at 0.7 mm) from uncaged sampling units at three sites. Inspection of the final shell sizes would suggest selective loss of bigger individuals (Fig. 3.7 c) but the above contradictions show that final shell size can be misleading.
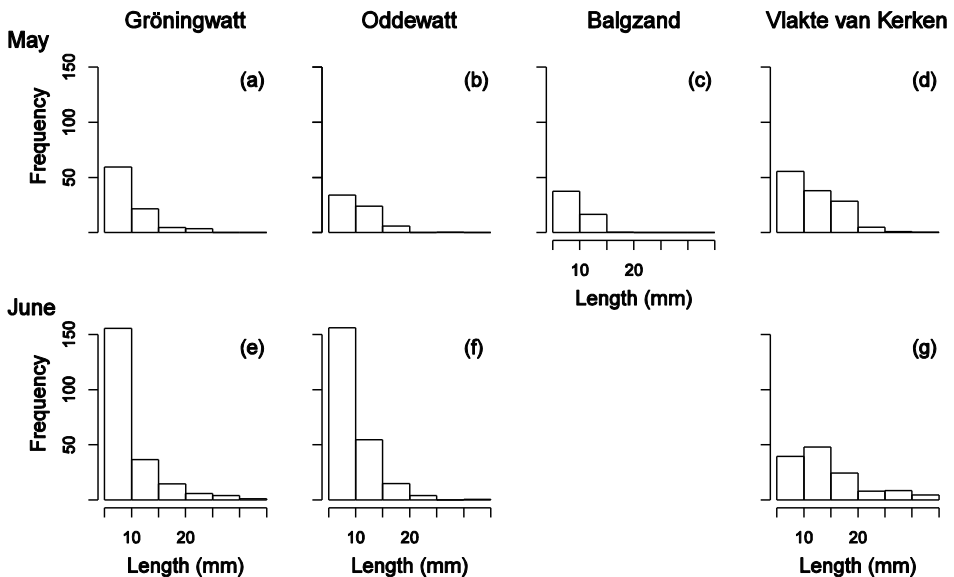
Fig. 3.9 *Crangon crangon*. Length-frequency distributions during the experiments, sampled at high tide (not possible at Balgzand in June). Gröningwatt and Oddewatt are at Sylt, Balgzand and Vlakte van Kerken are at Texel. Frequencies are given per m^2, total sampling area each time was 2 m^2.

Crangon crangon have to be about ten times longer than *M. balthica* to be able to consume them (Hiddink et al. 2002), for eating *C. edule* they probably have to be even bigger because of the harder shell and globose shape. In May there were plenty shrimp present that would feed on small bivalves (Fig. 3.9). In June, more small shrimp had entered the study sites, and also the numbers of larger individuals had increased. Although the bivalves had grown, there was still prey in the size range of the shrimp present.

Discussion

Body size is central to species interactions that influence survival, and individual growth determines the body sizes of species that encounter. With a combined fluorescent staining and caging experiment, we disentangled growth from size-dependent abundance changes of juvenile bivalves *Macoma balthica* and *Cerastoderma edule*. We obtained individual growth rates and compared average growth in two 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 one of the two study periods, resulting in bigger individuals at Texel at the end of the study. If only the change in average size had been used to estimate average growth rates, growth would have been strongly underestimated due to immigration of smaller individuals. The possibility to identify immigrants from size distributions is limited. Individual marking also showed that growth is highly variable between individuals.

The other objective of using individual staining was to identify size-dependent loss, which has population 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 additionally to predator access, emigration is another possible 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 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 had also been 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 support that during the study, the middle intertidal zone experienced net immigration. In June, when no size-selective loss was found, still many small *C. edule* and *M.*

balthica were caught with drift nets during migration. If these had been mainly emigrants, then why did we not get 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 and Hellwig-Armonies (1992) also found that the middle intertidal zone at Oddewatt was subject to net immigration until July in 1991, when *M. balthica* gradually moved up higher in the intertidal. (3) The predators present were able to consume the missing bivalves, both concerning their size (Hiddink et al. 2002) and their intake rates (Andresen and 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 *C. edule* as well as *M. balthica* occurred in the first experiment in May. Although young shrimp had arrived earlier at Texel than at Sylt (own observations), there was no systematic difference in predator regimes between 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 two 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 number of the four sites. The topology of the Balgzand mudflats may have delayed immigration of larger shrimps. Hence, no simple general one-line conclusion can be drawn, and here one of the limitations of the study becomes obvious. Field experiments and the measurements under UV-light are very laborious, which restricted the temporal and spatial replication and scope of the 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 speed. At Texel the potential for the bivalves to outgrowth their predators soon was better than at Sylt.

Caging and calcein marking each come with their own problems. While other studies found no harmful influence of calcein (Moran and Marko 2005), our findings show that this should be assessed each time when applied in a new system. Even if the methods do not give absolute quantitative results, it is still possible to compare between levels of each factor as long as there are no interactions of the two factors. This was the case for the effect of calcein on *M. balthica* growth in May and on *C. 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. As this reduced the effects of exclosure treatments, qualitative conclusions that were drawn from calcein samples are merely more con-

servative. Further, cage artifacts cannot be excluded if the effects of single and double cage walls are all-or-nothing. Artifacts are always created by an experimental procedure (Fernandes et al. 1999), but 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 which are otherwise obscured. If we had not combined them, we could have drawn wrong conclusions, or would have missed an interesting process (compare e.g. Fig. 3.6 with Fig. 3.8). Sometimes we noticed that scouring 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 emphasized 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 since the beginning. When in past exclosure studies size differences between cages had been observed, it was not known for sure whether that was just the influence of the cage on growth or size-dependent loss. Here 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 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 surrogate for the examination of otolith microstructures in fish. Concerning the consequences for population dynamics, size-selective mortality in the early life phase has in the first instance an effect on the population density. Size-selective mortality will affect recruitment variability if the factors governing size-based processes vary between 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 size-selective mortality of salmon fry was flood and drought related (Good et al. 2001). Additionally to abundance, size-selective mortality will also affect the size structure of a cohort. In our study the smallest individuals were most vulnerable, but after a warm winter in 1997, it was the smallest *C. edule* that survived until recruitment (Strasser et al. 2001). When predation is directed towards small individuals, fast growth would increase survival, but slow growth can be advanta-

geous if relatively big gape limited predators are present only temporarily (Urban 2007). Under constant unidirectional selection pressure through persistently warmer winters and consequently earlier arriving shrimps, the possibility for the young bivalves to adapt by increased growth rates is limited by food availability (Freitas et al. 2007, Philippart et al. 2003). 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 behavior, also in the presence of alternative food. Yet, our new data on individual growth rates should, together with information on seasonality and prey choice, help to further investigate recruitment success under various scenarios.

Acknowledgements

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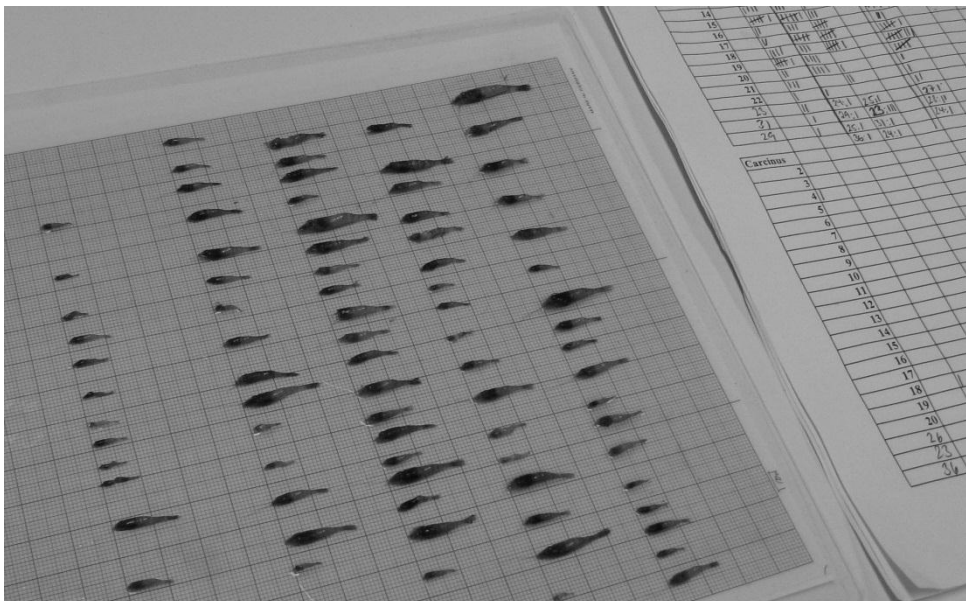
Chapter 4

Seasonal timing of bivalve settlement and arrival of crustaceans in the Wadden Sea, and resulting predator-prey body size ratios

Henrike Andresen, Rob Dekker, Ine Dorresteijn, Matthias Strasser, Jaap van der Meer

Abstract

Phenology is the timing of life history events in dependence of climate variations within and between years. Species specificity in phenological responses can influence interspecific interactions. Correlated climate effects on early predation mortality are a proposed cause of corresponding bivalve recruitment successes throughout the Wadden Sea. Bivalve recruitment is usually high after cold winters through delayed predator arrival. We compared four years of bivalve settlement timing between two distant regions of the Wadden Sea that generally differ in winter temperatures. In one year, also their epibenthic crustacean predators were measured and the prey-predator size ratio frequencies were compared. At one site, size ratios were compared between five years. Timing of settlement of the studied bivalves *Macoma balthica*, *Cerastoderma edule* and *Mya arenaria* was quite similar between the two regions. While their shrimp predators (*Crangon crangon*) were delayed at the colder region, the resulting prey-predator size ratios were similar between regions as well. Timing of bivalves differed between years, and a stronger phenological response in crustaceans than in bivalves caused diverse size ratio distributions of predators and prey. The results support that climate driven conditions for predation can be an influential factor for annual fluctuations of recruitment success as well as spatial population synchrony.

Introduction

Phenology, the timing of life history events depending on seasonal and interannual climate variations, can influence species interactions and by that population dynamics (Yang and Rudolf 2010). In our study system, the Wadden Sea, bivalves typically have good recruitment after cold winters (Beukema 1982). Recruitment is the subjectively defined stage at which juvenile survivors are regarded to be added to a population and year class strength is determined, in the case of Wadden Sea bivalves usually at the end of the summer (Strasser et al. 2003), but sometimes the definition includes the first winter (van der Meer et al. 2001). With the issue of climate change emerging, several studies in the 1990s investigated processes determining bivalve recruitment in the Wadden Sea (Hiddink 2002, Honkoop 1998, Strasser 2000). Variations in reproductive output through winter temperature differences had little influence on bivalve population dynamics (Honkoop et al. 1998). Predation by crustaceans on small settlers appears to play an important role for the survival until recruitment (Hiddink et al. 2002, Strasser 2002). After cold winters crustacean arrival on the tidal flats is delayed (Beukema 1991, 1992, Strasser and Günther 2001), giving their bivalve prey a head start. This is regarded a major process behind synchronized popula-
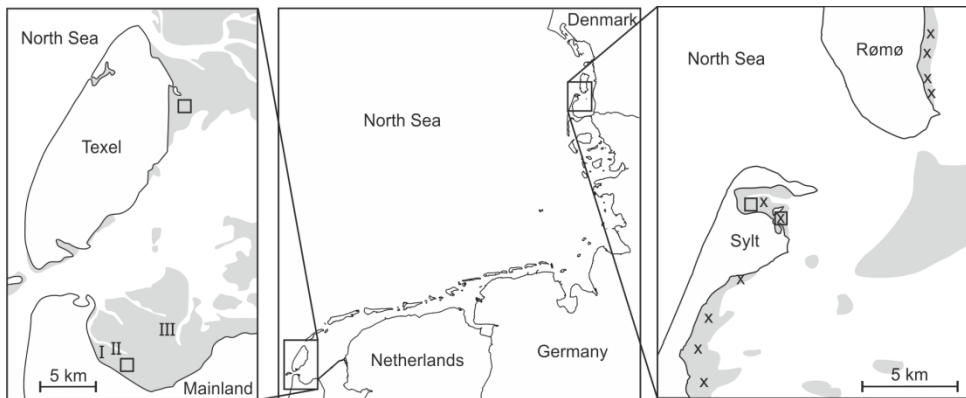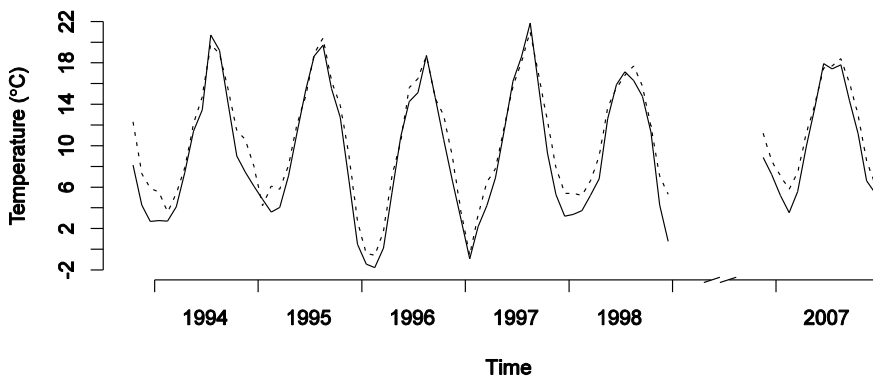

Fig. 4.1 Map of the Wadden Sea at the south-eastern edge of the North Sea (middle). Details of the study regions at Texel (left) and Sylt (right), with tidal flats shaded grey. Boxes indicate the sampling sites for bivalves and crustaceans in 2007 at both islands. Site I at Texel was sampled 1994 to 1998 for bivalves and crustaceans. Site II was sampled 1994 to 1998 for crustaceans. Site III at Texel was sampled from 1995 to 1998 for bivalves and in 1998 additionally for crustaceans. X marks the sampling sites in the Sylt region for bivalves in 1996 to 1998.

tion dynamics over a large geographic area of the Wadden Sea (Beukema et al. 1996). Spatial synchrony of population dynamics is a general phenomenon in many taxa and usually induced by correlated climatic factors (Hudson and Cattadori 1999).

Some questions still remain unanswered. Why does one bivalve species profit from cold winters over the whole Wadden Sea and others only in certain regions (Strasser et al. 2003)? Winter temperatures differ between the ends of the Wadden Sea, does this lead to differences in timing between regions? If so, does this alter the size ratio of predators and prey that encounter? This has not been compared yet.

We observed the time course of bivalve and crustacean abundances and body sizes in the year 2007 simultaneously in two distant regions of the Wadden Sea, namely at the island of Texel in the southwest and at the island of Sylt in the northeast. We also got a data set out of the drawer of bivalve settler observations at Texel 1994 to 1998, which includes the same three years that were studied by Strasser et al. (2001) at Sylt. This gave us the opportunity to compare bivalve timing between regions in three recruitment periods that followed winters of contrasting conditions. Crustacean predators had been sampled as well in all the years at Texel, so predator-prey size ratios could be compared between years in one region. The main aim of comparing timing and resulting size ratios was to assess whether they can explain differences or similarities in recruitment between years, sites and species.

Fig. 4.2 Sea water surface temperatures at Texel (dashed line) and Sylt (solid line) in the study years (van Aken 2008, van Beusekom, pers. comm.).

Material and Methods

Study area

The Wadden Sea at the south-eastern edge of the North Sea is a system of inter-tidal flats between barrier islands and the mainland. The two sampling regions, at the island of Texel in the westernmost part of the Dutch Wadden Sea, and at the island of Sylt in the northernmost part of the German Wadden Sea, are approximately 400 km coastline apart (Fig. 4.1). The tidal range at Texel is about 1.5 m, at Sylt about 2 m. All data used in this study are from the middle intertidal zone. Seawater temperatures range from around 0°C in winter up to around 20°C in summer, but in winter are usually lower at Sylt than at Texel (Fig. 4.2).

Sampling

Sampling focused on spring and summer, to cover the period from bivalve settlement to recruitment. In 2007 two sampling sites were chosen in each of the two study regions (Fig. 4.1). Bivalve and crustacean samples were taken within a plot of 40 x 40 m^2, in one to two week intervals. Bivalve sample area, number of samples, sampling depth and sieve mesh size were adjusted over time to their abundance and size, see Tables 4.1 and 4.2 for details per date. Samples were taken with corers, sieved in the lab and preserved in buffered formalin. They were sorted and bivalve lengths measured under stereo microscopes to the nearest 10 μm for the smallest animals or with 2% accuracy when lower magnifications were used for bigger individuals. Crustaceans were sampled by scooping out the sediment and sieving in the field over 1 mm punch plate. Usually four crustacean samples of 0.5 m^2 each were taken. Only three samples were taken at Texel at the first sampling event at each site. At one site at Texel the area was reduced to 0.125 m^2 in April, June and July because of high shrimp abundance. Crustacean samples were sorted life or stored frozen; *Crangon crangon* length from telson to scaphocerit and *Carcinus maenas* caparax width were measured to the nearest millimeter.

The Sylt bivalve data from 1996 to 1998 origin from ten sites (Fig. 4.1), sampled about every six weeks within roughly 9 m^2 at each site. Sampling of the ten sites was usually completed with a week. See Table 4.1 for number of samples, sample areas and sieve mesh sizes per sampling event. No epibenthic crustaceans were sampled 1996 to 1998 at Sylt.

At Texel, in 1994 bivalves were sampled at one site, from 1995 to 1998 at two sites (Fig. 4.1), within plots of 10 x 10 m^2. Sampling took place one to

Table 4.1 Sylt bivalve sampling details. If sampling differed within one event, sites are separated by slashes (/).

Year	Date	No. of samples per site	Area per sample (cm^2)	Sampling depth (cm)	Sieve mesh size (µm)
1996	end of May	4	5	1	125
	end of Jun	4	10	3	125
	middle of Aug	4	10	3	125
	beginning of Oct	4	284	10	1000
1997	beginning of Apr	4	10	1	125
	middle of May	4	10	1	125
	end of Jun	4	10	1	125
	beginning of Aug	4	20	3	125
	middle of Sep	4	284	10	1000
1998	end of May	4	10	1	125
	beginning of Jul	4	20	3	125
	middle of Aug	4	20	3	125
	beginning of Oct	4	284	10	1000
2007	11/12 Apr	3	80	1	125
	18/19 Apr	3	80	1	125
	25/26 Apr	3	80	1	125
	4/5 May	4	80	1	250
	14/15 May	4	180/113	1	250
	19/20 May	8	80	3	250
	29/30 May	4	180	3	250
	4/6 Jun	8	50/80	3	250
	14/15 Jun	4	80/180	3	250

three times per month, see Table 4.2 for details. Bivalve lengths were measured to the nearest 100 µm. Crustaceans were sampled at two sites from 1994 to 1997, one of them was identical with one of the bivalve sites. In 1998 crustaceans were additionally sampled at the second bivalve site (Fig. 4.1). For crustaceans, total sampling area per date was 0.36 m^2, taken in 40 cores in four 10 m long transects just outside the 10 x 10 m^2 plot. They were sieved in the field over 1 mm screen mesh, sorted in the lab and measured to the nearest millimeter.

Table 4.2 Texel bivalve sampling details. If sampling differed within one event, sites are separated by slashes (/) and different samples within a site by plus-symbols (+).

Year	Date	No. of samples per site	Area per sample (cm^2)	Sampling depth (cm)	Sieve mesh size (µm)
1994	24 May	4	81	4	300
	23 Jun	4	161	8	300
	19 Jul	4	269	8	300
	19 Sep	4	269	8	300
1995	16/22 May	3	269	5	300
	26/27 Jun	3+3	269+900	5+15	300+1000
	24/25 Jul	3+3	269+1800	5+15	300+1000
	22/23 Aug	3+3	269+1800	5+15	300+1000
1996	14/15 May	20/10	14	5	300
	29/31 May	5+5/10	134+360/28	5+15	300+1000
	12/13 Jun	10	28/134	5	300
	2/3 Jul	10	161/269	5	300
	15/16 Jul	5+5	134+360	5+15	300+1000
	29/30 Jul	5+5	134+360	5+15	300+1000
	7/9 Oct	3	134	5	300
1997	21/22 May	5	134/54	5	300
	18/19 Jun	5+5	81+180/134+180	5+15	300+1000
	16/17 Jul	5+5	108+360/134+360	5+15	300+1000
	18/25 Aug	5+5/5	134+360/108+360	5+15	300+1000
1998	11/13 May	3	134	5	150
	26/28 May	3	134	5	150
	8/10 Jun	3+3	81+360	5+15	150+1000
	22/24 Jun	3+3	134+1560/134+360	5+15	150+1000
2007	6/12 Apr	3	80	1	125
	18/28 Apr	3	80	1	125
	6/7 May	4	80	1	250
	15/16 May	4	180	1	250
	20/21 May	8	80	1	250
	30/31 May	4	180	3	250
	3/4 Jun	7	180/80	3	250
	13/14 Jun	4	180	3	500

Data interpretation

The periods of steepest abundance increase of juveniles before the maximum abundance were considered peak settlement for comparing timing between species, regions and years. In crustaceans, cohorts are not as distinct as in the bivalves. To make sure to include all juveniles in spite of growth between sampling events, *C. crangon* individuals ≤ 10 mm and *Carcinus maenas* individuals ≤ 6 mm were considered, while they are 5 mm and 1 mm big at settlement, respectively. For the assessment of body size relationships of the bivalves with *C. crangon*, all ages of *C. crangon* were included. From the data obtained at the sampling event closest to the middle of each month, for all possible bivalve-shrimp encounters the body size ratios were calculated for a representation in size ratio frequency histograms. Bivalve size frequencies were weighed according to sampling area if different areas were used within one event.
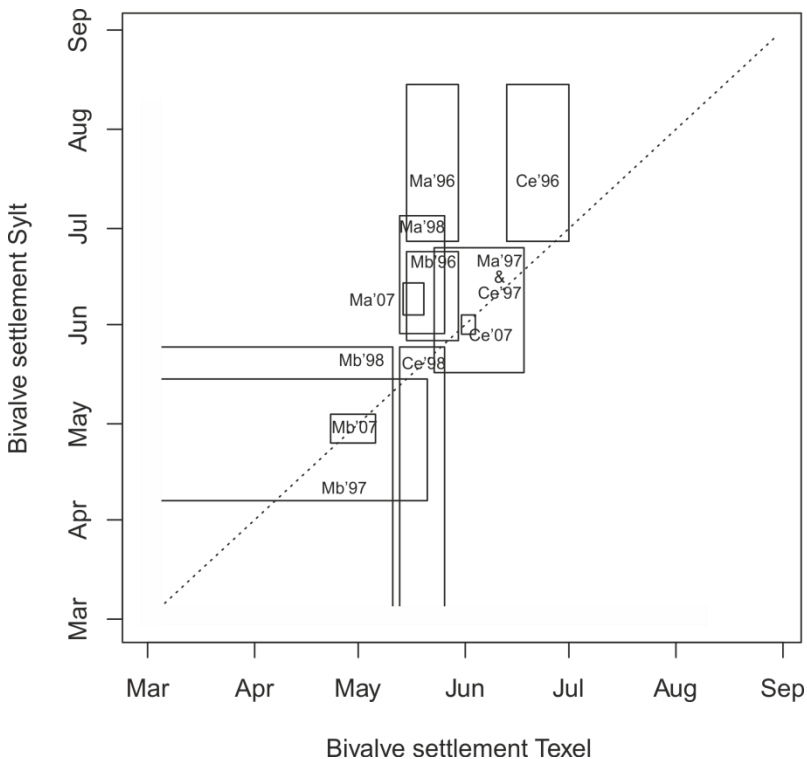
Fig. 4.3 Bivalve settlement time at Sylt versus Texel. Boxes mark periods of steepest abundance increase in the years 1996, 1997 and 1998 and 2007. Mb = *Macoma balthica*, Ce = *Cerastoderma edule*, Ma = *Mya arenaria*.

Results

Settlement timing

The timing of bivalve settlement was quite similar between the sampling regions at the islands of Sylt and Texel (Fig. 4.3). Only in 1996, that is after the coldest winter (Fig. 4.2), the spatfall was later at Sylt than at Texel. Accordingly, variation in timing between the four studied years was higher at Sylt than at Texel. *Macoma balthica* was generally the first or among the first to arrive. The biggest difference in settlement time between the two islands was in *Mya arenaria*.

The arrival of crustaceans was monitored in 2007 at both islands to compare the relation of predator and prey timing between study regions (Fig. 4.4). A striking difference was found in the arrival of *Crangon crangon*: it peaked two months earlier at Texel, in April, and by that before the main period of bivalve settlement. Predator arrival versus prey settlement timing was also compared between years within the Texel region (Fig. 4.5). Annual variation in seasonal timing was higher in crustaceans than in the bivalve species. *Carcinus maenas* generally arrived later.
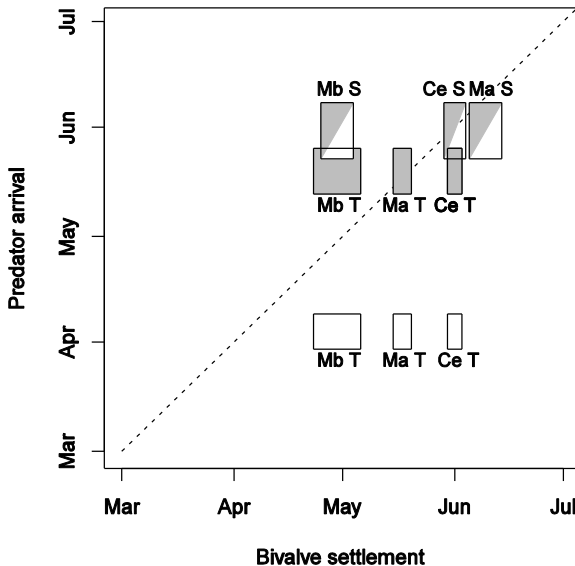
Fig. 4.4 Predator arrival versus bivalve settlement time in 2007. Boxes mark periods of steepest abundance increase before maximum abundance, at Sylt and at Texel. Mb: *Macoma balthica*, Ce: *Cerastoderma edule*, Ma: *Mya arenaria*, S: Sylt, T: Texel. White boxes: predator *Crangon crangon*, grey boxes: predator *Carcinus maenas*.
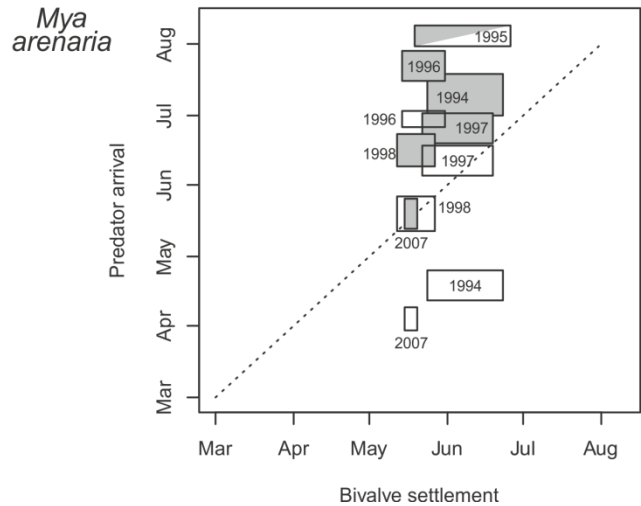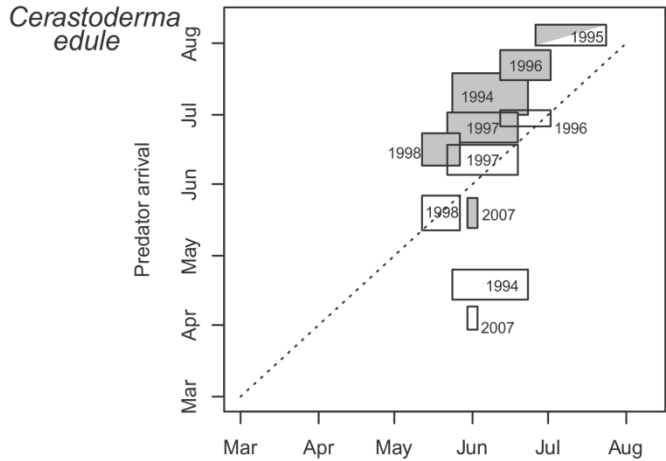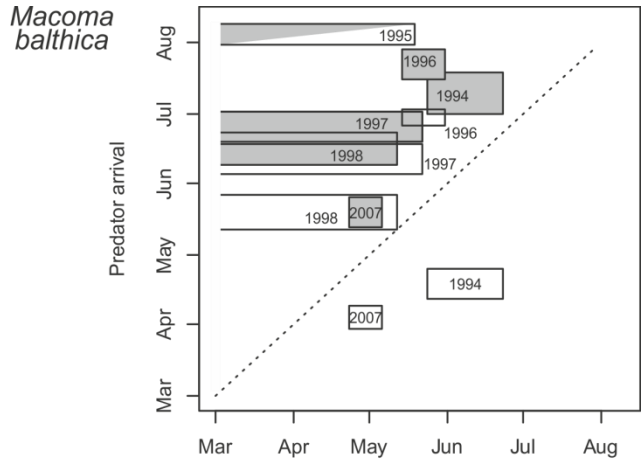
Fig. 4.5 Predator arrival versus bivalve settlement time at Texel. Boxes mark periods of steepest abundance increase before maximum abundance, for the years 1994 to 1998 and 2007, per bivalve species. White boxes: predator *Crangon crangon*, grey boxes: predator *Carcinus maenas*.

Prey-predator body size relationships

The reason that timing is thought to be so important is because it influences with what body sizes crustaceans and bivalves – predator and prey – encounter. Shrimp have to be about at least ten times bigger than *M. balthica* to be able to eat them (Beukema et al. 1998, Hiddink et al. 2002). We calculated body size ratios for all possible bivalve-shrimp encounters at a given time and place (Fig. 4.6 and 4.7). A grey bar indicates that a bivalve is a tenth or less of the predator length and thus vulnerable to predation. To consume the harder shelled and more globose *Cerastoderma edule*, shrimp probably have to be even more than ten times bigger, but as no experimental evidence is available, the same size-ratio as for *M. balthica* was used for illustration purposes.

The distribution of size ratios of bivalves and their predators each month was comparable between Sylt and Texel in the observation year 2007 (Fig. 4.6). In April, nearly every encounter between a shrimp and a *M. balthica* could potentially have led to predation; the bivalves that were already present at that time were almost all in the predators' size range. In May it became possible that a *M. balthica* was too big to be eaten by a predator it was encountered by. In June, at both islands *M. balthica* at the larger end of the size distribution were out-growing the shrimp predators. In *M. arenaria*, quick growth made up for later arrival and resulted in similar susceptibility to predation as the early arriving *M. balthica*. *C. edule* under the same predator regime reached safe body sizes most rapidly by fast growth. The similarity of the cockle-to-shrimp size ratios between Texel and Sylt is remarkable, although they are the result of different absolute sizes. At Texel cockles had grown faster, but at Sylt small shrimp were more abundant (chapter 3).

At Texel, between the study years 1994 to 1998 a variety of size ratio frequencies was found for the three bivalve species (Fig. 4.7). There was the case of continuously outgrowing the predators (e.g. *M. balthica* 1997), yet sometimes there was no apparent progress at all (e.g. *C. edule* 1995), or some of the individuals attained a safe body size while a vulnerable group remained (e.g. *M. arenaria* 1996). *M. balthica* showed some consistency among the seasons following mild winters (1994, 1995 and 1998, Fig. 4.2 and 4.7), whereas *C. edule* size ratios with shrimp were most variable and extreme between years. Furthermore, within a year, usually each species had unique size ratio distributions through their specific settlement and growth patterns under the same predator regime. A high frequency of large prey-predator size ratios did not only and not necessarily occur in connection with a delayed predator arrival (Fig. 4.8).
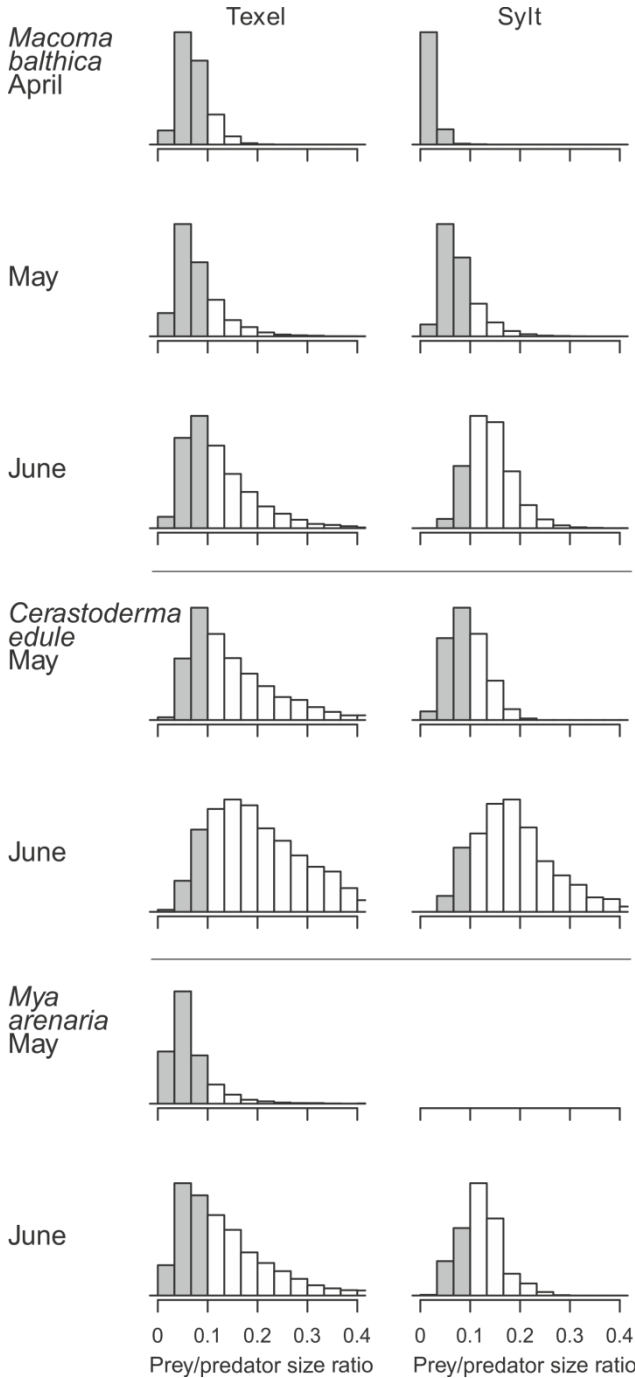
Fig. 4.6 Prey-predator size-ratio frequencies per month and bivalve species at Sylt and Texel in 2007. Grey bars stand for shrimp-bivalve encounters that can potentially lead to consumption of the bivalve. White bars stand for encounters with relatively larger bivalves that are safe from predation. The heights of the frequency distributions are not of informative value due to varying sample sizes and predator and prey numbers.

Prey/predator size ratio
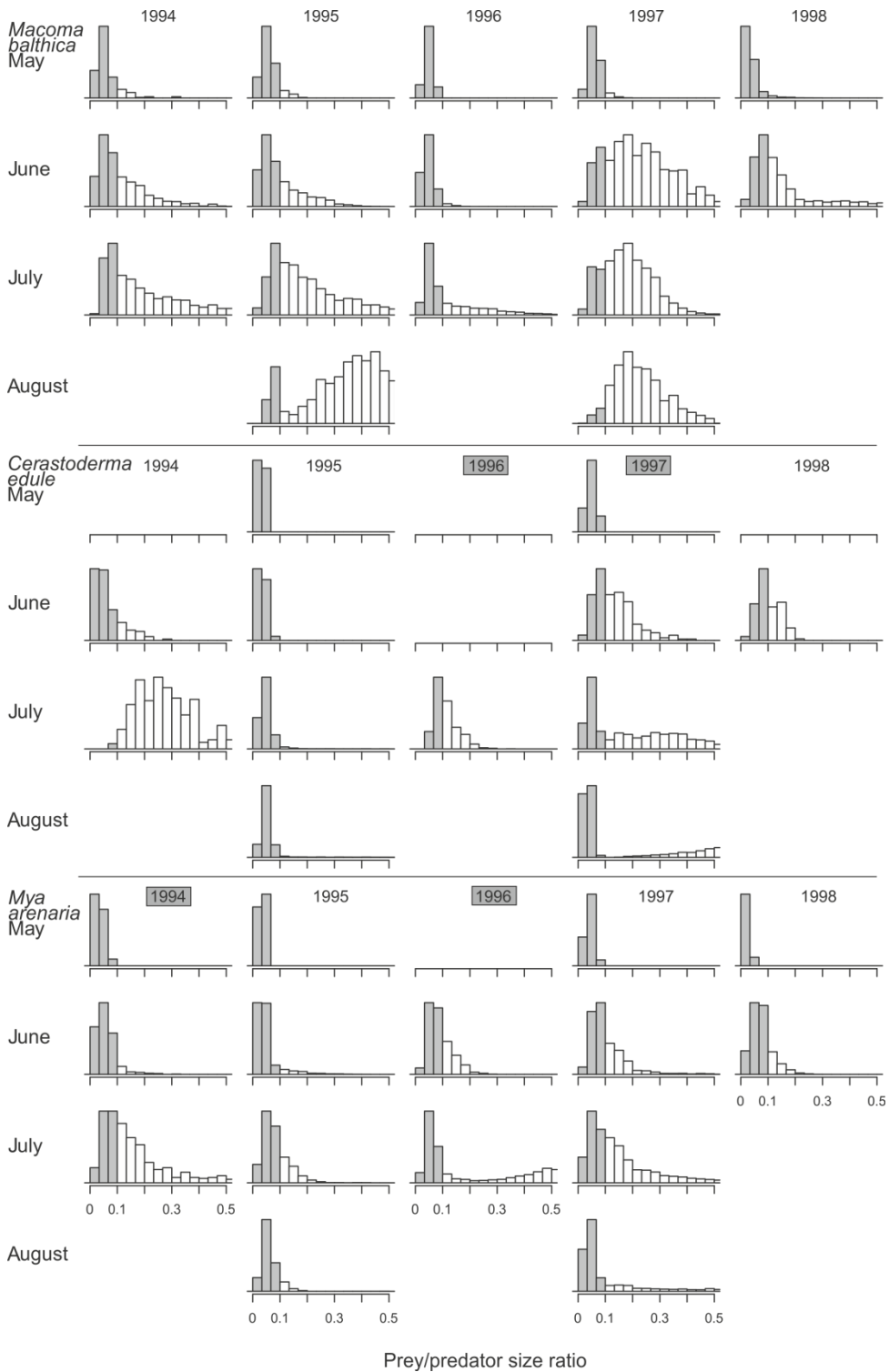
Discussion

Climatic effects on timing of annual reproduction of bivalves and the arrival of their crustacean predators are thought to affect bivalve recruitment Wadden Sea wide via an influence on size-dependent predation mortality (Beukema et al. 1996). We found indeed quite similar timing in bivalve settlement between distant regions but differing between years. Crustacean arrival showed more regional and annual variation in seasonal timing than bivalve settlement. There were strong differences in the resulting prey-predator size ratios between years, but a remarkable similarity between study regions. This fits together with spatially synchronized strong annual fluctuations in bivalve recruitment success (Strasser et al. 2003).

A head start for bivalve settlers did not necessarily result in a beneficial size ratio with the predators (Fig. 4.8). We used the steepest abundance increase before the maximum abundance of juveniles to compare arrival times, but size distributions are also shaped by additional settlement, growth and selective mortality. During summer 1996, a year with late predator arrival that is known for good *Macoma balthica* recruitment in the rest of the southern Wadden Sea (Strasser et al. 2003), *M. balthica* remained in the predator's size range at Texel. Yet, a simulation study (chapter 2) did not support selective predation as the main determinant of *M. balthica* size structure and low abundance in that year at Texel. Unfortunately, no temporal size observations are available for successful sites. A local exception from population synchrony may be a hint to man-made disturbance (Beukema et al. 1996). Sensitivity to other meteorological conditions is discussed as a possible reason that *M. balthica* and *Mya arenaria* did not profit from the predator delay through the severe winter in the eastern part of the Wadden Sea (Strasser et al. 2003). A size ratio distribution that appeared truncated was also observed in 1997 in *Cerastoderma edule* at Texel (Fig. 4.7), and *C. edule* recruit sizes of 1997 were truncated in the Sylt region as well (Strasser et al. 2001). This is probably due to continuing larval settlement in combination with predation on growing individuals as soon as they reach a certain body size. The

◀ **Fig. 4.7** Prey-predator size-ratio frequencies at Texel per month from 1994 to 1998. Grey bars stand for shrimp-bivalve encounters that can potentially lead to consumption of the bivalve. White bars stand for encounters with relatively larger bivalves that are safe from predation. The heights of the frequency distributions are not of informative value due to varying sample sizes and predator and prey numbers. Grey boxes mark years with recruitment higher than the average of the years 1988 to 2000 (Strasser et al. 2003). *Macoma balthica* had the last exceptionally good recruitment in 1991.

very coarse sand at Sylt is a conceivable explanation for foraging above a detection threshold (Strasser et al. 2001), but as a similar pattern developed at Texel with finer sediment, it should be considered that the predators have energetic prey choice criteria.

While the sampling frequencies were very high, the possibilities to make generalizations from this study are limited by the number of years and sites studied. Further, the sampling design was not the same everywhere all the time, but as long as the obtained individual numbers are high enough, they can be used to compare timing and sizes between years and regions. Only data from the middle intertidal were included in this study, which does not represent the entire intertidal populations, but the time course of bivalve abundances is similar to the time course from all tidal levels (comp. Fig. 4.A1 in the Appendix of this chapter with Strasser et al. 2001). Crustaceans were sampled at low tide, although with high tide bigger shrimp enter the tidal flats (Janssen and Kuipers 1980). Thus, the predation risk is probably even underestimated in this study.

In spite of differing sampling designs, it is valuable that these data sets, that include the key year 1996 after the cold winter, have been brought together now. Processes that can synchronize recruitment over large spatial scales are undoubtedly so dominant that they will also have a major influence on temporal population changes. The results substantiate that similar processes take place in the two distant regions, just at different absolute sizes and moments in time. They also show that subtle changes can tip the scales. Strong differences in year class strength caused by changes in predation mortality through annual climate variations have been found also for example in flatfish, in this case through temperature induced differences in prey growth (Nakaya et al. 2007). In our system, comparing the size ratios with recruitment success (Strasser et al. 2003), an advantageous size ratio distribution seems to be a prerequisite but not a warranty for good bivalve recruitment (Fig. 4.7 and 4.8).

The intent of the present study was to compare the conditions for predation related to body sizes. Future research needs to include individual numbers and feeding rates for a quantitative perspective on pre-recruit predation mortality. A phenomenon that has received little attention yet in this system is selection for prey above a minimum size. Experiments could establish the lower end of the predation window and its behavioral basis. Staying small through extended or late spawning or slow growth, until the predation risk decreases towards the end of the year, could be an alternative life history strategy.
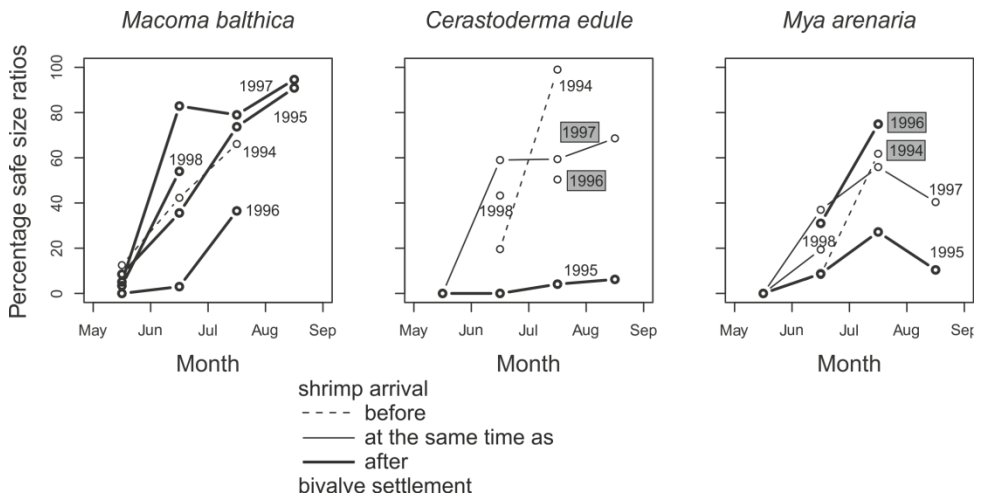
Fig. 4.8 Link between relative timing, prey-predator size ratios over the season, and final recruitment, at Texel in 1994 to 1998. For the relative timing, the periods of steepest increase of juveniles before the maximum abundance observed are compared. In an encounter with a shrimp, bivalves are considered safe from predation if they are larger than a tenth of the predator size. Grey boxes mark years with final recruitment above the average of the years 1988 to 2000 (Strasser et al. 2003). *Macoma balthica* had the last exceptionally good recruitment in 1991.

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Appendix
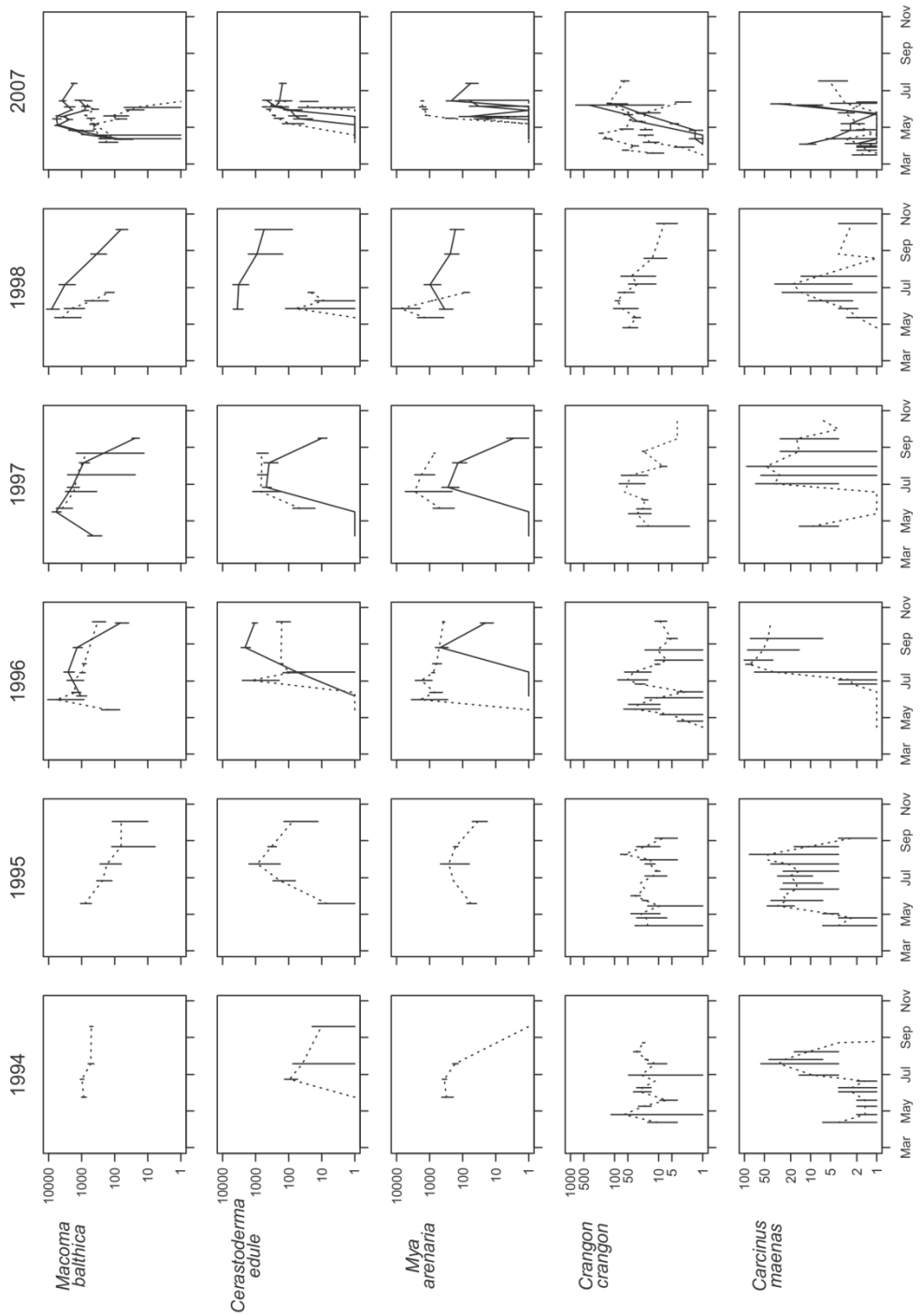
◄ **Fig. 4.A1** Densities of juvenile bivalve and crustacean individuals over time per species and year at the island of Texel in the Netherlands (dotted line) and the island of Sylt in Germany (solid line). In 1995 to 1998 the two, three or ten sampled sites are summarized, error bars represent standard errors between sites. In 1994 and 2007 error bars show standard errors between samples within a site. In the crustacean species, cohorts are not as distinct as in bivalves and individuals grow quickly. *Crangon crangon* are 5 mm and *Carcinus maenas* 1 mm big at settlement to the benthos. Densities plotted are of individuals of ≤ 10 mm long (*C. crangon*) and ≤ 6 mm wide (*C. maenas*) at each time step.
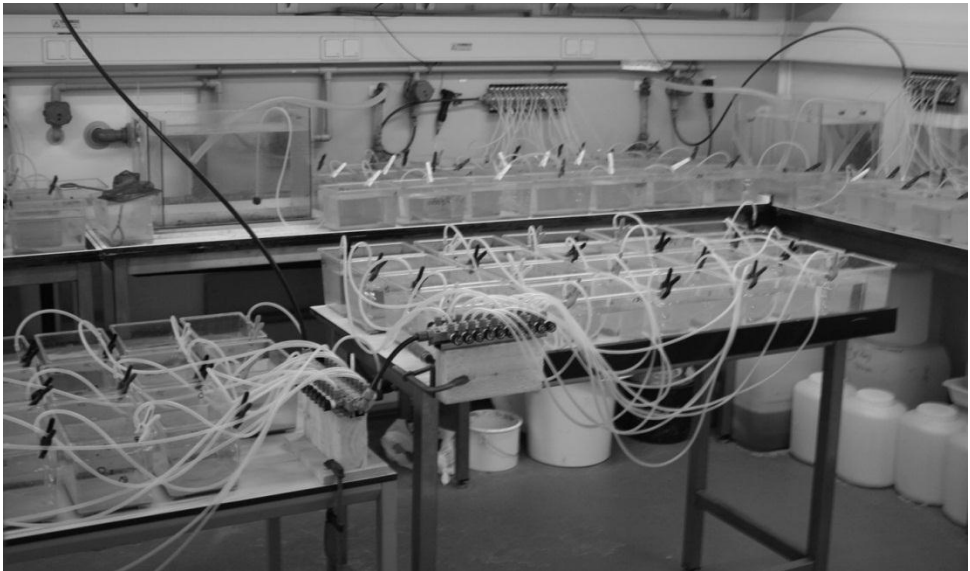
Chapter 5

Brown shrimp (*Crangon crangon*, L.) functional response to density of different sized juvenile bivalves *Macoma balthica* (L.)

Henrike Andresen, Jaap van der Meer

Abstract

Variability in infaunal bivalve abundance in the Wadden Sea is largely determined by recruitment variability. Post-settlement, but pre-recruitment bivalve mortality is high and related to the occurrence of their most abundant predator, the brown shrimp *Crangon crangon*. To investigate if the mortality patterns of newly settled bivalves can be explained by the foraging behavior of brown shrimp, we carried out experiments on shrimp functional response to three size classes of juveniles of the Baltic Tellin *Macoma balthica*. The functional response curves for all three prey sizes (0.62 mm, 0.73 mm, and 0.85 mm) were the hyperbolic Holling's type II. The attack rate was highest for the smallest prey size (a=0.31, medium and large prey a=0.22); the handling time was longest for the largest prey size (T_h=29 s, small and medium prey T_h=15 s). Thus, a large body size is advantageous for the bivalves over the whole density range. Knowledge of individual foraging behavior is needed to model predation mortality of bivalves. The consumption rates in the experiment were theoretically high enough to account for *M. balthica* mortality in the field.

Introduction

Populations of broadcast spawning bivalves in the Wadden Sea fluctuate consid-
erably in abundance among years. Year class strength is only weakly influenced
by the production of eggs, the amount of larvae or even settlers (Beukema et al.
1998, Bos et al. 2007, Honkoop et al. 1998). Rather, mortality of benthic marine
invertebrates is commonly high and variable in the early post-settlement period
(Gosselin and Qian 1997) and uncouples settlement from recruitment (Ólafsson et
al. 1994). As recruitment, here defined as the abundance of the 0-year class after
their first winter, largely determines bivalve population size for subsequent years
(van der Meer et al. 2001), it is crucial to understand what controls juvenile mor-
tality.

This question is especially pressing because dramatic changes are taking
place in macrozoobenthic populations of the Western Wadden Sea. In particular
the Tellinid bivalve *Macoma balthica* is declining so strongly and suddenly (van
Gils et al. 2009), that anthropogenic influences cannot be ruled out. The two
prime suspects are climate warming and shellfish fisheries (Beukema and Dekker
2005). Fisheries could affect *M. balthica* recruitment via the loss of fine sediment
(Piersma et al. 2001). Climate warming is proposed to alter species interactions
through phenological shifts, which result in more intensive predation, in particu-
lar by the brown shrimp *Crangon crangon*, on *M. balthica* pre-recruits (Philippart
et al. 2003). Predation is one of the most important and best documented pro-
cesses that lead to high mortality of newly settled benthic invertebrates (Hunt and
Scheibling 1997, Ólafsson et al., 1994). With this study we aim to get quantitative
estimates of predator consumption rates to assess if predation pressure by shrimp
can potentially explain the observed mortality of juvenile *M. balthica*.

Due to global warming, the seasonal timing of life history events can be
altered, and the response may differ among species (Lawrence and Soame 2004).
After cold winters, a delayed arrival of predatory crustaceans led to high survival
of bivalve settlers (Strasser and Günther 2001), and cold winters are now
becoming rare (Shabalova and van Engelen 2003). Conversely, after warm win-
ters, peak abundances of bivalves and predators coincide (Beukema 1992b).
Moreover, shrimps then encounter the young bivalves when these are still small
and more suitable as prey (Hiddink et al. 2002b).

The phenomenon of high bivalve recruitment after cold winters is known
for decades (Beukema 1982, Kreger 1940), and the idea that differential predation
is the decisive underlying mechanism has been confirmed by field exclosure
experiments (Strasser 2002). Size-selective predation is sometimes reflected in

skewed size distributions of bivalve recruits (Strasser et al. 2001). The existence of a strong top-down control is further supported by a negative correlation of bivalve recruitment with shrimp abundances (Beukema and Dekker 2005, Beukema et al. 1998). However, there is still a lack of quantitative mechanistic studies on predation mortality for this system.

We performed laboratory experiments to study in more detail the apparently important role of prey size for the consumption rate of *C. crangon*. Clearly there is a limit to the size of prey a predator can eat, but also within the size window the consumption rate will differ between sizes. Very small and very large prey are probably difficult to handle (Aljetlawi et al. 2004, McCoy and Bolker 2008). The detectability of smaller prey may be lower, yet larger prey may have better escape mechanisms (McCoy and Bolker 2008, Streams 1994). These two potentially size-dependent aspects, handling and searching, are the behavioral components that the functional response comprises (Holling 1966). The functional response is essential for modeling predator–prey interactions (Hassel 1978). It describes how the consumption rate of a predator changes with prey density (Holling 1966). The relative importance of searching and handling time changes with prey density. Searching, which becomes manifested in the attack rate, is most influential at low densities. Handling time limits the predation rate at high densities (Seitz et al. 2001).

We evaluated the functional response by *C. crangon*, which were fed young *M. balthica* of three size classes separately (0.62–0.85 mm average length) in a range of densities, to (1) find out how prey size affects predation rates, (2) get quantitative estimates of the predation intensity, and (3) infer if these processes can explain the observed mortality patterns in the field. This will add a new piece of understanding that is needed to model size-dependent predation on bivalve pre-recruits.

Materials and methods

Experimental design

To investigate the functional response of *Crangon crangon* on juvenile *Macoma balthica*, a two-factorial randomized-block experiment was set up. Factors were bivalve density (9 levels) and bivalve size class (3 levels). In each experimental unit, prey mortality was determined in the presence of one shrimp. The experiment was spread over six trial days (blocks) in June and July 2008 (Table 5.1). The attack rate and handling time were determined indirectly by fitting Royama–

Rogers random predator equation (Rogers 1972) to the number of prey consumed.

Study system

In the Wadden Sea, the brown shrimp *C. crangon* is, with average peak densities of about 60 individuals per m^2 (Beukema 1992a), the most abundant epibenthic predator of young bivalves. Shrimp size distribution remains relatively stable during summer, because their spawning is spread over several months (Siegel et al. 2008), and through size-dependent habitat choice; they start tidal migrations into the subtidal at a size larger than 2.5 cm (Janssen and Kuipers 1980). *C. crangon* are opportunistic omnivores (Pihl 1985) that find their prey by chemo- and mechanoreception (Campos and van der Veer 2008). The Tellinid bivalve *M. balthica* is a thin-shelled suspension and deposit feeder that avoids predators by burying deep (de Goeij et al. 2001). Their spawning in the Wadden Sea is concentrated to the spring period (Drent 2004). They can reach peak densities that exceed 10,000 individuals m^{-2} just after settlement (Hiddink and Wolff 2002). At settlement, they are just above 250 μm long (Bos et al. 2007) and reach several millimeters in the end of the summer (Strasser 2002).

Table 5.1 Densities of *Macoma balthica* of three size classes fed to individual *Crangon crangon* in six time blocks to investigate the functional response. Size classes were divided by fractionated sieving, lengths ± SD were measured under a stereo microscope at 40× magnification in four time blocks (*n*=211 for small, *n*=201 for medium and *n*=242 for large prey).

Density m^{-2}	Number per bucket (314 cm^2)	Number of replicates realized per size class and density (in brackets by time block)		
		Small 616 ± 53 μm long 350-430 μm sieve	Medium 728 ± 52 μm long 430-500 μm sieve	Large 853 ± 67 μm long 500-600 μm sieve
100	3	10 (2, 2, 2, 2, 2, 0)	13 (2, 0, 2, 3, 4, 2)	11 (2, 2, 1, 3, 1, 2)
178	6	11 (2, 2, 1, 1, 2, 3)	13 (2, 1, 2, 1, 3, 4)	15 (2, 2, 2, 1, 2, 6)
316	10	6 (2, 0, 1, 2, 1, 0)	8 (2, 1, 1, 1, 1, 2)	6 (2, 1, 1, 1, 1, 0)
562	18	9 (1, 1, 1, 2, 2, 2)	8 (1, 0, 1, 2, 2, 2)	11 (1, 1, 1, 2, 2, 4)
1,000	31	8 (1, 1, 1, 1, 2, 2)	7 (1, 1, 1, 1, 1, 2)	8 (1, 1, 1, 1, 2, 2)
1,778	56	6 (1, 1, 0, 2, 2, 0)	7 (1, 1, 1, 2, 2, 0)	8 (1, 1, 1, 2, 1, 2)
3,162	99	4 (1, 1, 0, 1, 1, 0)	4 (1, 0, 1, 1, 1, 0)	5 (1, 0, 1, 0, 1, 2)
5,623	177	4 (1, 1, 0, 1, 1, 0)	6 (1, 0, 1, 1, 1, 2)	4 (1, 1, 0, 0, 2, 0)
10,000	314	5 (1, 0, 0, 1, 1, 2)	4 (1, 1, 0, 1, 1, 0)	4 (1, 0, 1, 1, 1, 0)

Collection and maintenance of experimental animals

Predators *C. crangon* were collected nine days before each of the six trial days. They were caught by dredging with a small hand operated beam trawl in shallow water near the institute on the island of Texel, the Netherlands. The animals were brought into a climate chamber with the natural summer photoperiod (16:8) and a temperature of 15°C, the average seawater temperature in the western Wadden Sea in June (van Aken 2008). Each time 110 individuals of 19–21 mm length were sorted into individual tanks of 19×11 cm^2 surface, filled with a 1 cm layer of clean sand and ca. 10 cm high aerated seawater. The animals were fed with fish (commercial refrigerated Pollack) every two days but were starved for four days before the trials (compare Feller 2006). To make sure that the animals were all in an equal and healthy condition, only shrimps that molted during the acclimation period until two days before the trials were used in the experiment. Through molting they reached an average length of 22 mm (±1 mm SD) and a maximum length of 24 mm (measured after the trial). This is in the upper end of the size range at which shrimps still spend most of the foraging time on the mudflats, before they start tidal migrations (Janssen and Kuipers 1980). It is also below 25 mm, at which males and females start to exhibit different growths and molt patterns (Campos and van der Veer 2008).

The prey, newly settled *M. balthica*, were sparse around Texel, so they were collected at the island of Sylt in the German Wadden Sea in two visits at the end of May and the middle of June. The upper layer of the sediment was scraped off, and the material that passed through an 800 μm sieve but not through 250 μm was swirled and decanted to separate the animals from most of the sediment. The decanted matter contained bivalves, but also other organisms and still some sediment. The decanted portion was maintained in mesocosms at 10°C to keep growth and mortality low. The animals were fed with algae suspension (Isochrysis 1800, Reed Mariculture) every two days. In each time block, one day before the trials the material was separated into three size classes (Table 5.1) by thorough fractionated sieving, after which the bivalves were selected with tweezers under stereo microscopes. They were counted into little sieves of 100 μm mesh size, in which they were kept, standing in water in the climate chamber of 15°C, until the trial started. Each shrimp was used only once, but some bivalves were used a second time in the last two time blocks.

Experimental conditions and procedure

The nine bivalve densities were chosen in the range from 100 to 10,000 m^{-2}, with logarithmic distance between densities. This range resembles the field situation

(Hiddink and Wolff 2002). High numbers of replicates are necessary at low prey densities, when the number of prey eaten is often zero (Trexler et al. 1988). We aimed to distribute the replicates as evenly as possible over the six time blocks (Table 5.1), yet this was not perfectly achievable due to the number of molted shrimps available and the cases we had to exclude afterwards (see Section "Controls"). For functional response experiments aimed at studying short term behavior at distinct prey densities, it is desirable to avoid a decrease in prey abundance during a trial (Jensen et al. 2007). Replacement of consumed prey was not possible in this set up, but the area and the duration of the experiment were chosen such that depletion was limited. The trials were conducted in round buckets of 314 cm^2 bottom surface area and lasted 15 min. A short duration also prevents satiation. The buckets were filled with a 1 cm layer of clean sand of 100–200 μm grain size, and then with ca. 4 L of previously aerated seawater. The chosen grain size is common in the sediments around Texel, and also convenient to separate from the bivalves by sieving. The trials took place in the middle of the day at ceiling lighting in the 15°C climate chamber. Bivalves were randomly distributed in the buckets and allowed to bury for 1 h before the start of the trial (based on own observations, see also van Colen et al. 2009). Predators were placed into the trial buckets with a time lag of 1 min between consecutive buckets, and each shrimp was removed after 15 min by a second experimenter, so that all trials in one time block took place within roughly an hour. The contents of the buckets were sieved over a 250-μm sieve and the remaining bivalves, dead or alive, were counted as not consumed.

Controls

Procedural controls: To test for losses during sorting, the experiment was also carried out without predators, with three replicates for each size×density combination. We assumed a loss of a constant proportion and did a weighted linear regression through the origin (weighted with the square root of the initial density, because this was also applied in the analysis of the trial data). In the smallest size class, 2.4% of the bivalves were missing; in the two larger size classes 0.9% was lost. The percentage lost in controls was subtracted from the intended initial densities before the statistical analysis.

State of individuals: To avoid studying abnormal behavior of predator individuals that were in a bad condition, we defined three different criteria for high-density, medium-density, and low-density trials to control for the state of the experimental animals. At the three highest prey densities (99, 177 and 314 per bucket), cases

when the consumption was zero (or not higher than the losses in the procedural controls) were excluded, assuming that the predator was in a too bad condition to search for prey. These were four out of 45 cases. At the three lowest densities (3, 6 and 10), the consumption is expected to be zero often due to unsuccessful searching. The shrimps from these treatments were fed again after the trial with bivalves that were easy to find. Four out of 97 cases were excluded because the shrimp ate neither in the trial nor afterwards and probably were in a bad state. At the three intermediate densities (18, 31 and 56), zero consumption is probably still the correct trial outcome in some cases, but we realized that only through the study results and had not fed shrimps from these trials afterwards. Yet, from time block 4 on, we had done scans of the activity of the shrimps every five minutes during each trial. Of the 16 shrimps that did not eat at intermediate densities, five had been observed actively searching and these cases were included, three shrimps had been inactive and these cases were excluded. For the remaining eight cases we had no observations; here the same proportion, that is three cases, were randomly chosen and removed; in total six out of 78 cases were excluded at intermediate densities. There was no difference in the proportion of inactive predators between low, intermediate and high prey densities (binomial proportions test, p=0.70). Thus, activity does not reflect a density-dependent stimulus to search but rather is an indicator of the individual predator condition. See the Appendix for the robustness of these selection decisions.

Finally, one case was excluded where at the highest density of the largest size class 96 bivalves had disappeared. This value is higher than all other observations, and more than four times higher than the measurements of the same treatment. Including the case changes the parameter estimates and the residual plot enormously, so not much biological importance was attached to this single value. It is more likely due to an unnoticed accident than to a voracious predator.

Statistical analysis

Holling's type II and III functional response curves cannot directly be used when prey density is not constant. For type II, the Royama–Rogers random predator equation (Rogers 1972) takes account of such decreasing prey density during an experiment by integrating over time.

$$N_e = N_0 \left(1 - \exp\left(a \left(N_e T_h - T\right)\right)\right) \tag{5.1}$$

where N_e is the number of prey consumed, N_0 is the initial prey density, a is the attack rate, T_h is the handling time and T is the total time prey was exposed to

Table 5.2 Sum of squares and AIC values of 16 models to identify differences in functional response parameters for three prey size classes. a = attack rate, T_h = handling time; subscripts: s = small prey, m = medium prey, l = large prey. In bold: selected model (lowest AIC) with two different attack rates and two different handling times.

		$T_{h,sml}$	$T_{h,s} + T_{h,ml}$	$T_{h,sm} + T_{h,l}$	$T_{h,s} + T_{h,m} + T_{h,l}$
a_{sml}	SSQ	114.58	110.26	110.52	109.11
	AIC	4.76	4.73	4.73	4.73
$a_s + a_{ml}$	SSQ	109.16	108.53	107.27	107.26
	AIC	4.72	4.73	**4.71**	4.72
$a_{sm} + a_l$	SSQ	111.68	109.02	110.29	108.74
	AIC	4.74	4.73	4.74	4.74
$a_s + a_m + a_l$	SSQ	108.75	108.17	107.22	107.22
	AIC	4.73	4.73	4.72	4.73

predation. For the type III functional response, where the attack rate increases with prey density, the appropriate equation is:

$$N_e = N_0 (1 - \exp ((d + bN_0)(N_e T_h - T) / (1 + cN_0)))$$
(5.2)

where b, c and d are constants in the hyperbolic function that describes the change in the attack rate with initial prey density. If b and c are equal to 0, this equation reduces to type II (Juliano 2001). Both curve types were fitted to the data of each size class separately. Parameter estimates were located by minimizing the sum of squares, using the optim function in R (R Development Core Team 2008). Observations were weighted with $\sqrt{N_0}$ to reduce heterogeneity of variances. To identify the type of curve for each size class, the full type III model was compared by *F*-tests to the models with simpler relationships of the attack rate with N_0 that are nested within it (c=0 and/or d=0, and the type II model). After the curves for the size classes separately were each classified as type II (*F*-tests, $p>0.05$), all data were analyzed together and dummy variables (Juliano 2001) were used to allow and test for differences in the parameters between prey sizes (Table 5.2). The best model was selected using the Akaike information criterion (AIC):

$$\text{AIC} = \log (\text{SSQ}_k) + 2 \, k / n$$
(5.3)

(Hilborn and Mangel 1997) where SSQ_k is the minimum sum of squares for the model with k parameters and n is the number of observations. The joint confi-

dence regions for the attack rate and the handling time are bounded by the points that produce the sum of squares (Draper and Smith 1966):

$$SSQ_\alpha = SSQ_k \left(1 + (k / (n-k)) F_{k,n-k,1-\alpha}\right) \qquad (5.4)$$

where α is the approximate significance level and F is the F-ratio.

Results

Foraging by *Crangon crangon* followed Holling's type II functional response for all three size classes of the prey *Macoma balthica* that we examined (Fig. 5.1). That means the predators were sufficiently motivated to search at low densities
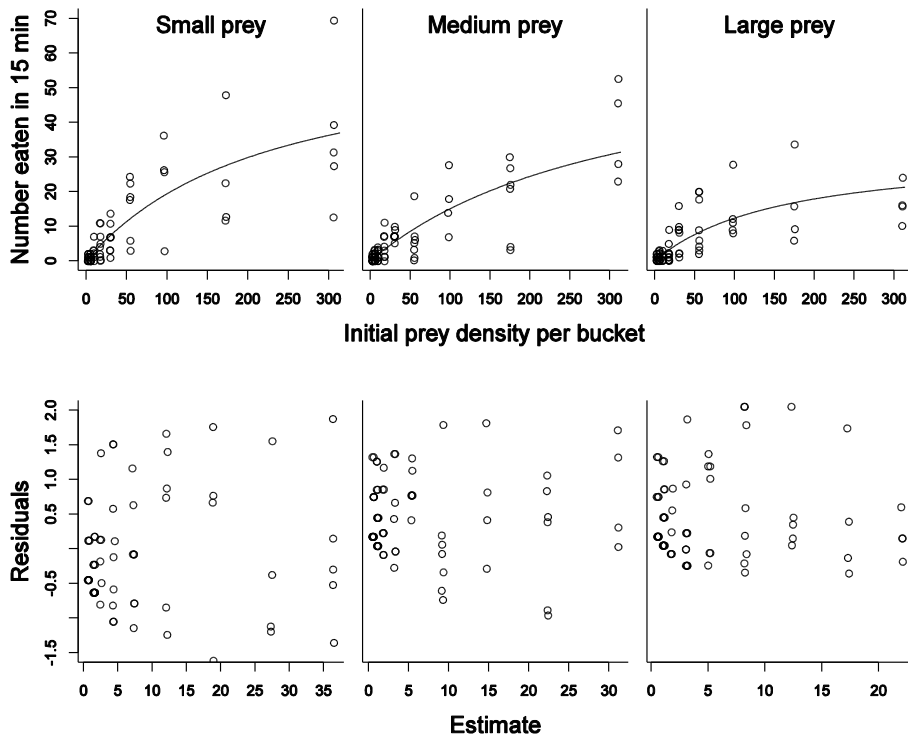
Fig. 5.1 Top: Number of prey consumed by *Crangon crangon* preying on one size class at a time of three size classes of young *Macoma balthica*. Individual observations (dots) and values predicted by fitting the Royama–Rogers random predator equation (lines). Bottom: Residual plots obtained by weighting with the square root of the initial density. Slight random jitter added to show overlapping points.

and efficiently foraging even when there were only one or two prey items per square decimeter. Through the type II functional response, proportional prey mortality decreases with increasing density (Fig. 5.2). For none of the prey size classes did the curves reach an asymptote (Fig. 5.1), which means that predation is not bounded by handling times at the densities investigated.
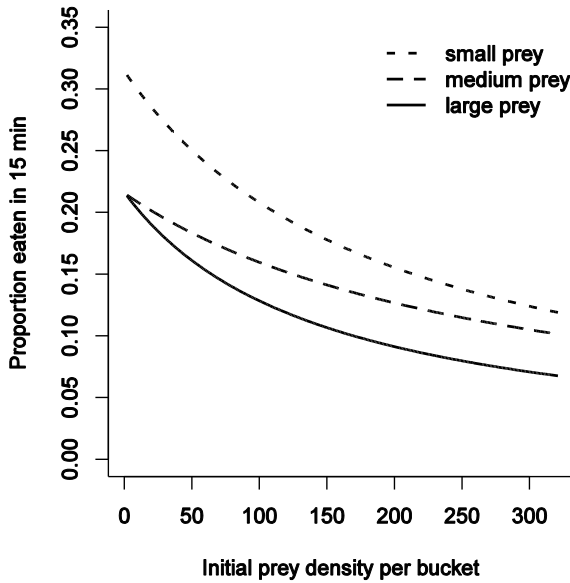

Fig. 5.2 Density-dependent proportional mortality through predation by *Crangon crangon* for three size classes of the prey *Macoma balthica*.

The number of prey consumed at each prey density showed much varia-tion (Fig. 5.1), but still a change of predation rate with size could be identified (Fig. 5.2). Shrimp consumed lower numbers of larger prey. According to AIC, all models that included at least one additional parameter describing the shrimp's response to varying prey sizes were better than the model with only one set of parameters, despite of the penalty for additional parameters (Table 5.2). Allowing for two different attack rates most improved the fit to the data, and a model with two different attack rates and two different handling times had the lowest AIC value (Table 5.2). The smallest prey experienced the highest rate of successful search (a_s=0.313, a_{ml}=0.215, Fig. 5.3), while the largest prey required twice as
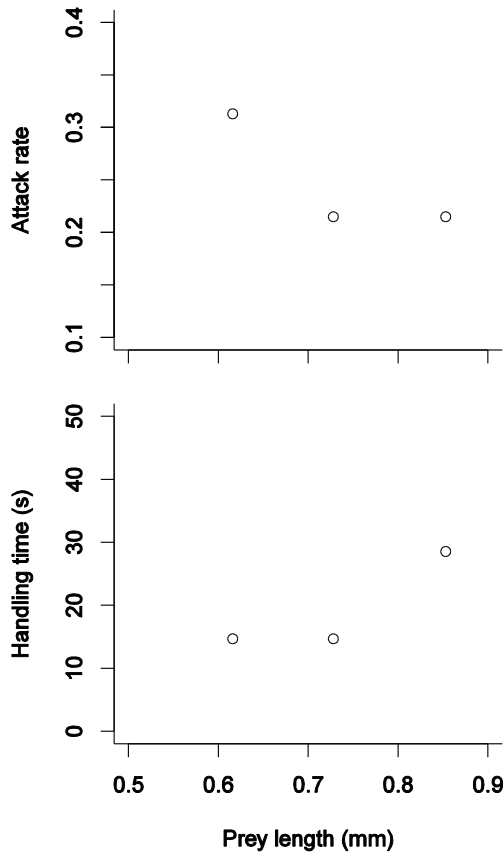
Fig. 5.3 Attack rate and handling time of the type II functional response by *Crangon crangon* to *Macoma balthica* in relation to prey length. Differences in parameters identified by AIC, for confidence regions on estimates see Fig. 5.4.

much handling time as the two smaller prey sizes ($T_{h,sm}$=15 s, $T_{h,l}$=29 s, Fig. 5.3). As a consequence, at low as well as at high densities, predation mortality is highest for small prey (Fig. 5.2). Attack rates were similar for large- and medium-sized prey, and handling times similar for small- and medium-sized prey (Table 5.2, Fig. 5.4). We treated the influence of prey size on parameters phenomenological via dummy variables and not in functions of size-dependent parameters, because we only investigated three prey sizes and had no a priori assumptions about the shape of the relationship.
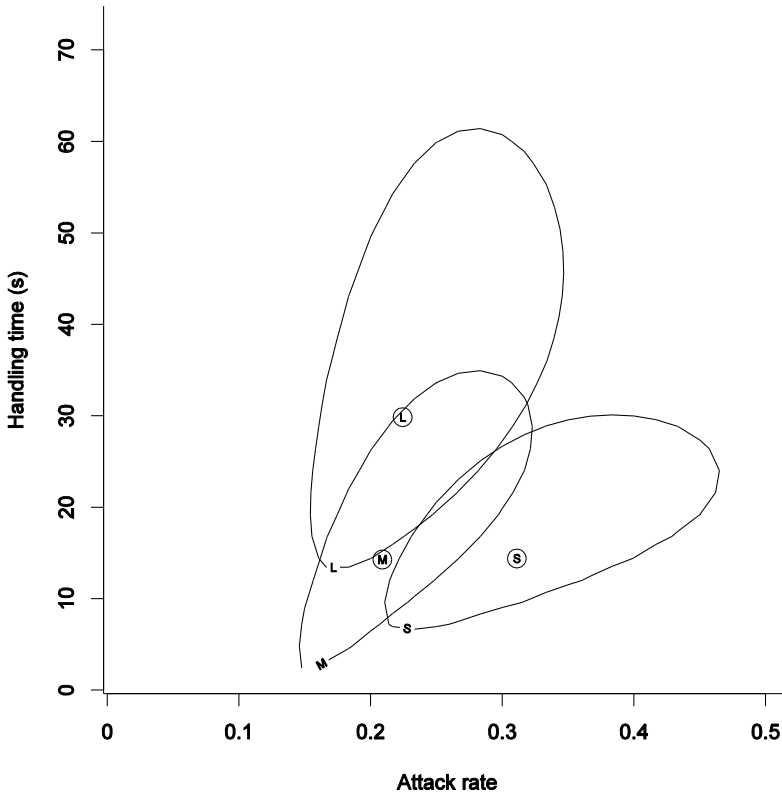
Fig. 5.4 Joint parameter estimates and 95% confidence regions of the type II functional response by *Crangon crangon* to three separate size classes of the prey *Macoma balthica*. (L = large prey, M = medium-sized prey, S = small prey, see also Table 5.1).

Discussion

The functional response of shrimp *Crangon crangon* on young bivalves *Macoma balthica* in fine sand, regardless of prey size examined (<1mm),was type II (Fig. 5.1). A larger body size of the prey reduced attack rate and increased handling time (Figs. 5.3 and 5.4), leading to a survival advantage over the whole density range (Fig. 5.2).

Despite their smaller body surface, small prey were attacked more frequently than larger ones. The attack rate is composed of the probability of an encounter, the probability of the encounter resulting in an attack, and the probability of the success of an attack (Streams 1994), each of these attack components can change with prey size. For our system we hypothesize that the probability of

an encounter is reduced for the larger *M. balthica* investigated, because they can hide better than the smallest ones. Deep burying is the main defense strategy of this species (de Goeij et al. 2001, Seitz et al. 2001).

The handling time was higher for larger bivalves. This may again be due to the deeper burying, because digging out the prey is part of the handling time. We found a sudden increase in handling time from the two smaller prey sizes to the largest prey. Provided that this is due to shrimp behavior and not to a low precision of the estimate (Fig. 5.4), an explanation may be that the predators have to change their feeding method, such as changing from swallowing to breaking. Size-related different opening methods have also been observed for shore crabs (Elner 1978, Smallegange and van der Meer 2003).

Several functional response studies also report highest consumption rates for the smallest prey, through a decreasing attack rate and increasing handling time with increasing prey size (Aljetlawi et al. 2004, Gibson et al. 1995, Hohberg and Traunspurger 2005, Krylov 1992, McArdle and Lawton 1979, Reynolds and Geddes 1984, Thompson 1975). Yet, also the theoretically expected dome-shaped relationship of proportional prey mortality with prey body size has been observed (Cowan et al. 1996, Lundvall et al. 1999, Taylor 2003), with at intermediate size the minimum handling time and the maximum attack rate (Spitze 1985). Clearly, this depends on the size range investigated. In our study system shrimps are probably able to forage on prey smaller than the sizes we included.

Regarding the vulnerability of different prey sizes in the field, the advantage of the large body size might disappear through size-dependent prey choice if predators can choose their prey such as for higher profitability (Mascaro and Seed 2000), provided that an increased biomass gain compensates for the longer handling time. However, crustaceans do not necessarily select for the highest energy reward, most crabs forage selectively on small-sized molluscan prey below the most profitable size and far below the critical size that can be opened (Seed and Hughes 1995, Smallegange and van der Meer 2003). As shrimp are characterized as opportunistic omnivores, they may as well select their prey on the basis of relative availability (Pihl 1985).

Knowing the feeding rates observed in the experiments, a rough estimation using field abundances suggests that shrimps theoretically would be able to wipe out the new year class before the end of the summer. For the calculation we started with 10,000 m^{-2} bivalve settlers. Densities of shrimp $\geq$ 20 mm were taken from field observations in the Wadden Sea (0.5 m^{-2} in April 2007, 2 m^{-2} in May and 4 m^{-2} in June). Smaller shrimps were neglected. Functional response parameters for small prey were used for the first month, medium prey for the second month and large prey for the third month. The consumption and reduction in

bivalve density was calculated from day to day. Then, only 2 h foraging time per day would be needed to deplete the bivalves to a density below 1 m^{-2} by the end of the third month.

The experiments were carried out in the laboratory under simplified foraging conditions, but in the field, predators and prey experience more complex situations. A first difference might be that we investigated starved predators; satiation would reduce the consumption rate (Jeschke and Hohberg 2008). Pre-starving of the experimental animals may though be appropriate, because feeding time is in reality also limited in the intertidal (Janssen and Kuipers 1980), and thus predators in the field will experience a certain hunger level. Minimum inundation time in the Wadden Sea is 8 h per day (4 h per tidal cycle) except for very high sites (Kraan et al. 2010). Reducing foraging time to 25% of that, i.e. the assumed 2 h per day, should roughly account for satiation effects on maximum predation rates (compare Ali et al. 1996, Holling 1966 for other arthropods). Second, earlier studies showed that sediment grain size may affect the searching efficiency. Shrimp reduced the abundance of juvenile cockles in lab experiments in fine sediment much more than in coarse sediment (Reise 1985). Coarser sediment can increase searching time and even change the functional response from type II to type III (Lipcius and Hines 1986, Seitz et al. 2001). Our results were obtained by using fine sediment and if applied to other habitats, caution is warranted. Third, avoidance of top-predators (Ejdung 1998) and interference with competitors (van der Meer and Smallegange 2009) may affect foraging behavior. Fourth, and maybe most important, the presence of alternative prey and even non-prey items will reduce the consumption rate derived from experiments compared to the field (Kratina et al. 2007). Not only do the predators have other food sources available, such as polychaetes, other bivalve species and crustaceans (Feller 2006, Pihl 1985), but also the foraging efficiency is reduced when various prey species are present, as different types of prey require different feeding strategies (Persson 1985). The four aforementioned circumstances would reduce the predation rate by *C. crangon* on *M. balthica* in the field as compared to our lab values. On the contrary, in nature, bivalves are confronted with many other predators. Shrimps are very abundant in the Western Wadden Sea, but shore crabs (*Carcinus maenas*) may be more efficient or have higher consumption rates, which would increase bivalve mortality.

For a realistic estimate of predation mortality in the field, it is the co-occurrence of other species that is particularly difficult to take account of. As the Wadden Sea is a relatively species poor ecosystem (Beukema 1976), potentially strong interactions between few dominant species can occur (McCann et al. 1998), which makes it a most suitable system to study species interactions

(Williams et al. 2004). To reconcile experimentally derived parameter estimates with those realized in the field, a consumption model based on high-quality field data of predator- and prey size-distributions over time is required. Aljetlawi et al. (2004) accepted the challenge and did this for an Isopod–Amphipod system. They found that attack rates from the laboratory experiment had to be reduced by two orders of magnitude to obtain realistic prey survival, and that in the species poor Baltic Sea.

Differences between experimental predictions and empirical results suggest that there are more aspects of predator behavior that should be investigated now, and we need to know what the animals actually do in a more complex situation. In the absence of alternatives, the predation risk in the experiments was highest at low prey densities (Fig. 5.2). In contrast, juvenile bivalve mortality in the Wadden Sea was positively density dependent in field observations (Beukema 1982, Beukema et al. 1998, Dekker and Beukema 2007). An explanation may be that shrimps focus on abundant prey when confronted with multiple prey species (Charnov 1976b, Schenk and Bacher 2002), which would lead to lower mortality at low densities. The aggregative response, moving to patches of high prey abundance (Charnov 1976a, Cummings et al. 1997), is another behavior that would have a stabilizing effect at least in space, but also non-predatory processes such as bivalve migration (Hiddink et al. 2002a) have to be considered.

In conclusion, we demonstrated that even within the ingestible prey size range, differences of little more than 0.1 mm in prey length can reduce the proportional mortality by about 30% (Fig. 5.2) at these small absolute prey sizes. Strong size-selective predation can have life history consequences (Commito 1982), and for the survival of young bivalves, reproductive timing as well as early growth rates will be crucial. Our experiments show that shrimp have the ability to substantially reduce *M. balthica* settlers, thus changes in shrimp abundance and arrival time potentially have consequences for the bivalve population. However, the functional response is only one piece of the puzzle. To more realistically estimate how much of the mortality of young bivalves in the field can be explained by predation, not only detailed information on prey and predator size structures is needed, but also shrimp behavior, with spatially heterogeneous prey (Englund and Leonardsson 2008) and in the presence of other species while taking satiation into account, has to be investigated.

Acknowledgements

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# Appendix: Robustness of data selection

We had excluded 14 out of 219 cases from the analysis on the basis of activity and consumption observations that hint to a bad condition of individual predators. To investigate the robustness of these decisions, we did the analysis once with even stricter selection criteria and once with all data. In the stricter selection (*n*=192), additionally to the criteria applied before (see Methods Section "Controls"), all trials in which predators had been observed inactive, even if they ate something, were excluded, and predators that had not grown through molting were excluded. This barely affected parameter estimates, but reduced the overlap of confidence regions (Fig. 5.A1). A model with a higher handling time for large bivalves and a higher attack rate for small bivalves was still identified as the best model according to AIC.
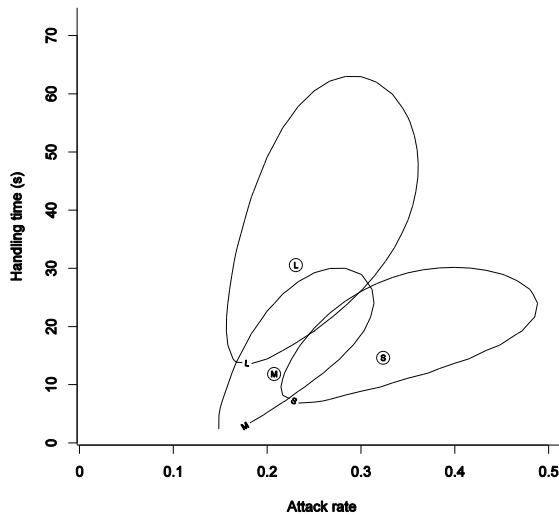
Fig. 5.A1 Influence of stricter data selection (*n*=192) on joint parameter estimates and 95% confidence regions for the type II functional response by *Crangon crangon* to three separate size classes of the prey *Macoma balthica*. Compare with Fig. 5.4 (L = large prey, M = medium-sized prey, S = small prey, see also Table 5.1).

When all data (except for the case last mentioned in Methods Section "Controls") were included (*n*=219), attack rates were slightly reduced, and the handling time for the intermediate size decreased noticeably. At the same time the

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overlap of the confidence regions increased (Fig. 5.A2). Through this, the handling time of the best model identified by AIC was similar for all three prey size classes. The model for the data originally selected, despite some overlap of the confidence regions (Fig. 5.4), distinguished a different handling time for the largest prey (Table 5.2). The proportion of cases excluded did not differ significantly between size classes (5, 7 and 2 out of 68 small, 77 medium and 74 large prey trials, respectively).
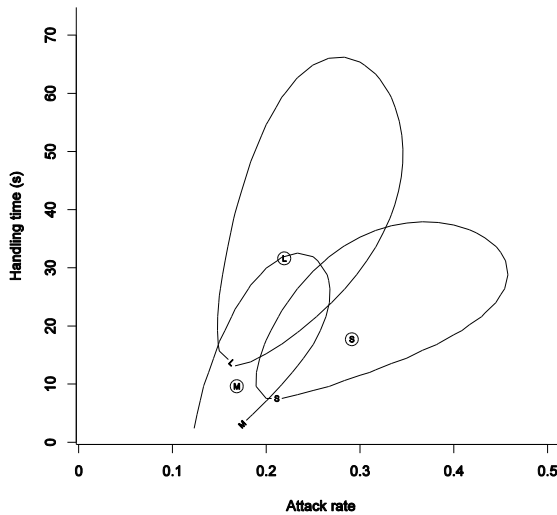
Fig. 5.A2 Consequences of inclusion of all doubtful data (*n*=219) on joint parameter estimates and 95% confidence regions for the type II functional response by *Crangon crangon* to three separate size classes of the prey *Macoma balthica*. Compare with Fig. 5.4 (L = large prey, M = medium-sized prey, S = small prey, see also Table 5.1).

Chapter 6

Estimation of density-dependent mortality of juvenile bivalves in the Wadden Sea

Henrike Andresen, Matthias Strasser, Jaap van der Meer

Abstract

We investigated density dependence of mortality within the early months of life of the bivalves *Macoma balthica* (Baltic tellin) and *Cerastoderma edule* (common cockle) in the Wadden Sea. Mortality is thought to be density-dependent in juvenile bivalves, because there is no proportional relationship between the size of the reproductive adult stocks and the numbers of recruits. It is not known however, when exactly density dependence in the pre-recruitment phase occurs and how prevalent it is. The magnitude of recruitment determines year class strength in bivalves. Thus, understanding pre-recruit mortality will improve the understanding of population dynamics. We analyzed count data from three years of temporal sampling during the first months after bivalve settlement at ten transects in the Sylt-Rømø-Bay in the northern German Wadden Sea. Analyses of density dependence are sensitive to bias through measurement error. Measurement error was estimated by bootstrapping, and residual deviances were adjusted by adding process error. With simulations the effect of these two types of error on the estimate of the density-dependent mortality coefficient was investigated. In three out of eight time intervals density dependence was detected for *M. balthica*, and in zero out of six time intervals for *C. edule*. Biological or environmental stochastic processes, such as variable predator access or physical disturbance, dominated over density dependence at the investigated scale.

Introduction

Survival during the early life phase takes a central role in population dynamics of marine invertebrates (Ólafsson et al. 1994). Many marine species produce an excess of larvae that prepares the population for unpredictable events (Fuiman and Werner 2002). Broadcast spawning by bivalves can create a wide range of larval densities. When comparing between years, the number of offspring does not increase proportionally with increasing stock of reproductive animals (van der Meer et al. 2001a). Early juvenile mortality typically leads to asymptotic stock-recruitment curves

This shape of relationship points towards density-dependent mortality in the pre-recruit phase. Recruitment is the subjectively defined stage at which juvenile survivors are regarded to be added to a population. In our study system in the Wadden Sea, juvenile bivalves are usually termed recruits at sampling in August (e.g. Strasser et al. 2003). Pre-recruit and early post-recruit survival of Wadden Sea bivalves is indeed higher in years with low densities (Beukema 1982, Dekker and Beukema 2007, van der Meer et al. 2001b). The recruitment period is the key to marine population dynamics, as it largely sets year class strength. Still, we do not know much about the causes of density dependence of mortality in this early life phase, how prevalent it is in the first place, and when exactly mortality is density-dependent during this critical period of the life-history.
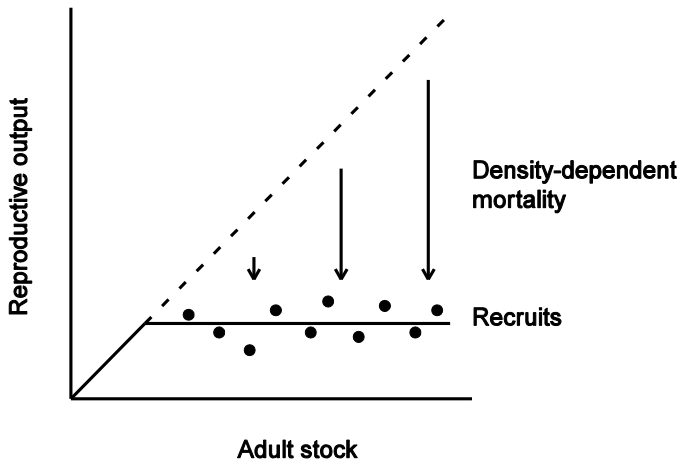
Fig. 6.1 Scheme of an asymptotic stock-recruitment relationship. Reproductive output of the adult stock is proportional to the stock size, but through density-dependent mortality during the pre-recruit phase, a stock-recruitment relationship is lacking (after Bos et al. 2007).

Mechanisms that could lead to density-dependent mortality are competition, infections, and behavior such as emigration (Hiddink et al. 2002, Powers and Peterson 2000). Density-independent mortality can be age related or have extrinsic causes such as weather events or food supply. Mortality through predation can have both density-dependent (Oaten and Murdoch 1975, Solomon 1949) and -independent aspects. If mortality is density-independent, the mortality rate is constant over all densities, and the more eggs are produced, the more recruits will be there. If mortality is density-dependent, it is higher at high densities. A higher reproductive output means proportionally less survivors (Fig. 6.1).

The bivalve species investigated in this study are the Baltic tellin *Macoma balthica* (L.) and the common cockle *Cerastoderma edule* (L.). Both are abundant infaunal bivalve species in the Wadden Sea. They spawn large quantities in spring or early summer, and after a planktonic larval phase of several weeks, the juveniles settle to the soft sediment. *C. edule* has a hard shell and is a suspension- (filter-) feeder, while *M. balthica* bury deep to avoid predators, they predominantly feed on surface deposit. *C. edule* densities show stronger variability between years (van der Meer et al. 2001a), and their spatial distribution is more patchy (Kraan et al. 2009) compared to *M. balthica*. *M. balthica* is less variable in occurrence in time and space, suggesting a weaker role of density independence.

We analyzed a data set that addressed the first half year of life of the bivalves, from settlement to recruitment. The young bivalves have been sampled in ten transects four to five times during spring and summer of three years. Our main aim is to determine when mortality was spatially density-dependent.

Material and Methods

Theoretic background

Beverton and Iles (1992) present a procedure for analyzing density dependence using a regression between pairs of densities of successive sampling events. It assumes mortality according to the following equation:

$$D_t = e^{\frac{\mu_1}{\mu_2} \cdot (e^{-\mu_2 t} - 1)} \cdot D_0^{e^{-\mu_2 t}} \tag{6.1}$$

where D_t is the density at any time t, D_0 is the initial density at $t=0$, μ_1 is the density-independent mortality coefficient and μ_2 is the density-dependent coefficient. Then in the regression of the densities at the end ($\log D_{t+1}$) on the corresponding

densities at the beginning ($\log D_t$) of a specific time interval, the slope is $e^{-\mu 2}$ and thus the density-dependent component of mortality can be estimated. The slope of the regression should be < 1 to diagnose density dependence. Stronger deviation from a slope of 1 means stronger density dependence. However, in the presence of measurement error, a simple linear regression of $\log D_{t+1}$ on $\log D_t$ would yield estimates of slopes that are biased downward (and hence of μ_2 that are too large), exaggerating a departure from the null hypothesis of no density dependence. To solve this without quantitative knowledge of the measurement error, one could fit a density-independent model and then ask retrospectively how much census error would have been required to produce the observed levels of density dependence (Freckleton et al. 2006). If much error would have been required, the conclusion of density-dependent mortality may be regarded as robust. In another approach, abbreviated SIMEX (Simulation-extrapolation, Cook and Stefanski 1994), a method that needs an error model, additional observation error is put into the data. From the resulting parameters it is then extrapolated back to predict what happens under reduced observation error. These two approaches inspired our method. We compared the observed apparent level of density dependence with the results of simulations for various given strengths of density dependence. The simulations incorporated the effects of measurement error and process error, i.e. actual biological variability as opposed to sampling variation (Dennis et al. 2006, de Valpine and Hastings 2002), in two separate steps.

Data

The study was conducted in the Sylt-Rømø-Bay, a tidal basin in the northern Wadden Sea (German Bight). The tidal range in the bay is about 2 m; a third of the basin consists of intertidal flats. Samples of post-settlement bivalves were collected in the intertidal. Ten transects were placed perpendicular to the coast along 20 km of shoreline. There were three stations on each transect, one site in the upper intertidal, one in the middle and one in the low intertidal. Every station on the transect was sampled with four replicates. Sampling took place four to five times per year in regular intervals of about six weeks, starting in spring and ending in autumn, in the years 1996 to 1998. A sampling round covering all ten transects took usually about one week. The area of the corers used was increased during the year to adjust sampling effort to declining individual densities (Table 6.1). Samples were fixed in buffered 5% formalin in seawater. Before sorting and counting they were sieved through a 0.125 mm screen; in the last sampling round each year the mesh size was increased to 1 mm due to the increased size of the bivalves. For details see Strasser et al. (2001). The abundances were summarized

per transect and not per site, because *Macoma balthica* and *Cerastoderma edule* can migrate to the higher intertidal during summer, which could give the impression of density dependence but would be only due to a habitat shift. One missing value was substituted with the average of the other three replicates. In 1996 the mid intertidal was not sampled in one transect, here the values were not imputed but the transect was left out for that year. Originally this data collection was part of a study on settlement timing and recruitment in relation to winter temperature (Strasser et al. 2001), but the sampling design makes it suitable to analyze the data for density dependence of mortality as well. In this analysis only data from the observed settlement peak onwards were included. In *M. balthica* there were eight periods beyond the settlement peaks in the three years; for the later arriving *C. edule,* six periods of density decline could be analyzed.

Table 6.1 Sampling time scheme with corer areas (cm^2).

year	Apr	May	Jun	Jul	Aug	Sep	Oct
1996		5	10		10		284
1997	10	10	10		20	284	
1998		10		20	20		284

Data analysis

Accounting for measurement error only: In the data analysis procedure, first, a linear regression was fit of the log counts in the ten transects at the end of a time step on the log counts+1 at the beginning of the time interval (example Fig. 6.2a). The regression was done as a GLM (Generalized linear model) with the quasipoisson family to allow for overdispersion, while the associated log link suits the exponential nature of mortality and realizes that density dependence is modeled as a function of log density. Sampling areas were changed over time and this was accounted for by using an offset, namely the log of the ratio of the sampling areas at the end and at the beginning of a time interval. For both species a regression model was fitted for every period. The estimated slope was subsequently compared to the outcomes of simulations. The statistical question to be answered is, which hypothetical true slopes may lead to the observed slope under the observed measurement error? For this, a density-independent model (slope = 1) and models with different predefined levels of density dependence (slopes < 1) were forced through the observed data (example Fig. 6.2b). The preset slopes and the respective resulting intercepts were then used to calculate deterministic

data without error (Fig. 6.2c) from the observed data. Next, error was added by generating random deviates with the observed measurement error (details on quantification of measurement error below). Through these simulated data, a regression was fit again (example Fig. 6.2d). Adding the error and fitting the regression was repeated 10,000 times per predefined slope, and the average resulting slope with 95% prediction intervals (white line and grey area in example Fig. 6.2f) plotted against the preset slope to compare it with the slope calculated from the observed field data (dashed line in Fig. 6.2f).

The measurement error to be added to the data was estimated with bootstrapping: the counts in the four cores for each of the three sites per transect were sampled with replacement, and the drawings of the three sites per transect were summed. This was repeated 100,000 times and the variance of the sum per transect was calculated. For each species, per time step one dispersion parameter was used for all transects for the generation of stochastic data; it was modeled as variance=mean^b, which is known as Taylor's power law (Taylor and Woiwod 1982). The exponent b had values around 1, pointing to a Poisson distribution, though it was significantly > 1 ($p < 0.05$) in 6 out of 20 cases (time steps × species). To be conservative, as the effect of measurement error is central to this study, when the exponent was > 1, whether significant or not, the variance calculated with the actual value of b was used for generating stochastic data with the negative binomial distribution. When b was ≤ 1, Poisson distributed values were generated.

► **Fig. 6.2** An illustration of the steps within the analysis of density dependence, using data of *Macoma balthica* for the time interval May to June 1997. a) regression through observed data. b) predefined slope forced through observed data (here slope=1 for density independence). c) deterministic data calculated from observed data to lie on hypothetical regression line from previous step. d) regression after measurement error, estimated by bootstrapping, was added to deterministic data, one example of 10000 simulations. e) additionally, before adding measurement error, process error was added to $\log D_{t+1}$, to arrive at observed residual deviance from first step, one example of 10000 simulations. f) resulting slope values with prediction intervals for various preset slopes, simulated with observed measurement error alone (white line for slope values and grey bootstrap interval) and observed process error additionally (black dots and whiskers). The dashed line gives the estimated slope from step a). In this case this estimated slope falls within the prediction interval, whatever the assumed true slope is.
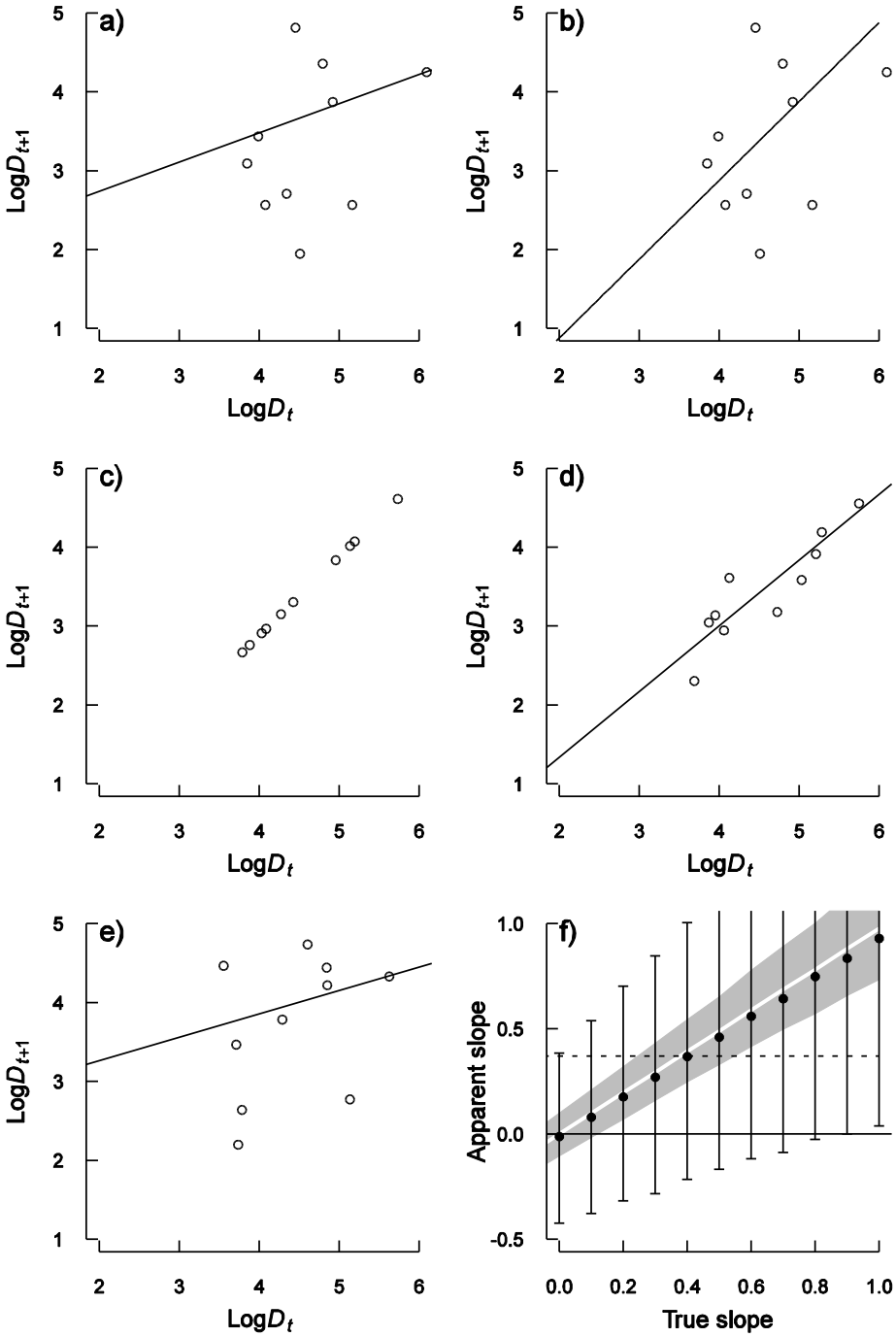
Incorporating process error: The residual deviance in the simulations with measurement error was much lower than in the original regression (compare Fig. 6.2a and d). The measurement error was estimated from the data by bootstrapping, so the remaining error must be process error, due to environmental variation and biological processes. This was included in an extra step before incorporating measurement error. Lognormal errors were added to the abundance at the end of a time interval. By that, process error is treated as an additional source of density-independent fluctuation (Ruesink 2000). In case the abundance after adding process error was < 1, the simulated value was set to 0, because the dispersions parameter of the negative binomial distribution is not defined when the variance is smaller than the mean (through the relationship variance = mean^b). For each slope the amount of process error was found that, together with the subsequently added measurement error, on average resulted in a regression with the original residual deviance ($\pm$ 2%). In the same way as for the measurement error, the average resulting slopes (example Fig. 6.2e) and the enlarged confidence intervals were plotted against the preset slope (example Fig. 6.2f). If, at preset slope 1, the lower end of the confidence interval is above the original slope, then one could conclude that the slope is indeed different from 1 and that there is density-dependent mortality.

Results

Three incidences of density dependence were found for *Macoma balthica*, one of them in the middle of the summer 1996 and another two in 1998 in the time intervals in the middle and at the end of the summer (Fig. 6.3 a, g and h). Density dependence is concluded when the lower end of the confidence interval for the predefined slope 1 (no density dependence) ends above the observed slope value (arrows in Fig. 6.3), that means the observed slope differs significantly from 1. In *Cerastoderma edule* this was never the case (Fig. 6.4). The time intervals with density-dependent mortality did not start with an especially high density or large range of densities, nor were the mortalities exceptional (Fig. 6.5).

Adding measurement error to deterministic data of a given strength of density dependence generally lowered the average apparent slope of regressions of $\log D_{t+1}$ on $\log D_t$ (white lines in Fig. 6.3 and 6.4). The slope could take on a range of values in simulations with random error added (grey area in Fig. 6.3 and 6.4). The residual deviances of the regressions including measurement error were much lower than those of the original regressions through the observed data. Thus, the remaining variability must have been due to process variability. After
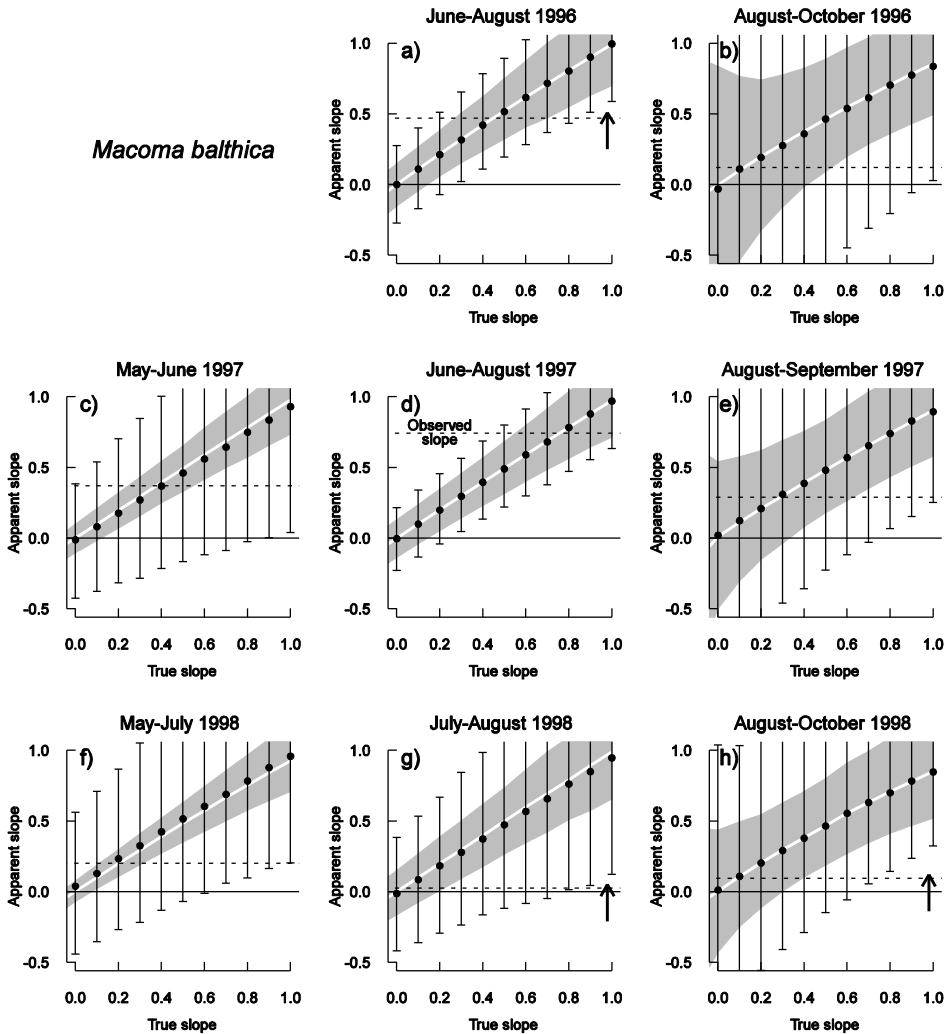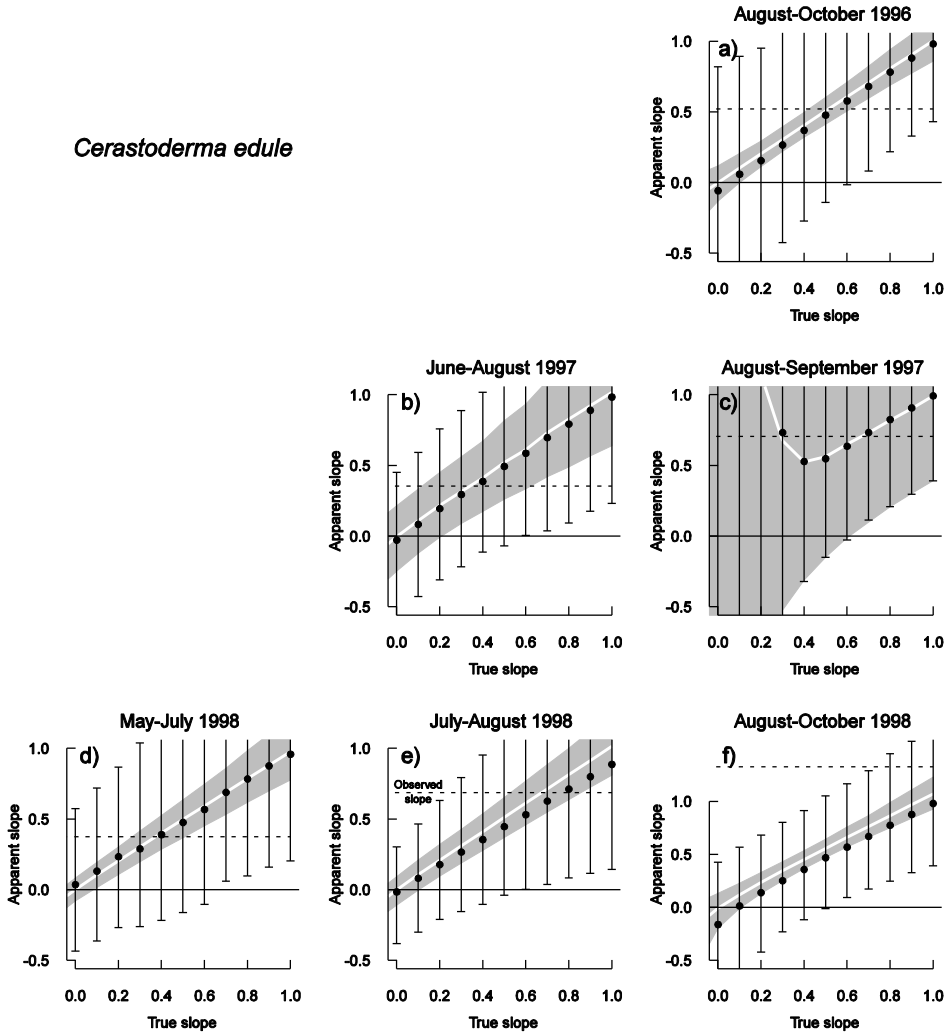
Fig. 6.3 Simulation results for *Macoma balthica* in the time intervals of density decline. Dashed line: slope value of the original regression through the observed data. White line: average slope values resulting when measurement error is added to deterministic data on predefined "true" regression lines. Grey area: corresponding 95% confidence intervals. Black dots: average slope values resulting when process error and measurement error are added to deterministic data on predefined "true" regression lines. Whiskers: corresponding 95% confidence intervals. When the lower end of the confidence interval for the predefined slope 1 ends above the observed slope value, the observed slope differs significantly from 1 and density dependence is concluded (arrows).

extra error was added to $\log D_{t+1}$ to reach the original residual deviance, the average apparent slope changed only slightly (black points in Fig. 6.3 and 6.4), which is expected when error is added only to the y-variable and not to the x-variable. However, the range of possible slope values increased enormously (whiskers).

Concerning the strength of density dependence, in the first period where density dependence has been observed for *M. balthica*, the predefined slope that best predicts the observed slope when errors are included, lies at about 0.45. By taking the logarithm and changing sign, the density-dependent mortality coefficient is obtained: $\mu_2 = 0.8$. In practice this means for example that a 10-fold difference in initial abundances results only in a 2.8-fold difference in final abundances. The estimates for the last two time intervals for *M. balthica*, for which density dependence was concluded, have slopes predicted near to zero, which would mean that density-dependent mortality would almost equal out all differences in initial densities. However, the estimates are not very precise. The range of slopes that can result from the simulations go up as high as around 0.8, or a μ_2 around 0.2. To illustrate this, a 4-fold difference in initial abundances, as was found for example between peak total densities of the three years (Strasser et al. 2001), would then still lead to a 3-fold difference in final densities. A 20-fold difference, as could be found between initial densities in space, would lead to an 11-fold difference in the end of the time interval. In the other investigated periods for *M. balthica*, and for *C. edule*, there was no evidence of density-dependent mortality, but with the large spread of possible results, it cannot be excluded either. The graph for *C. edule* in the last period of 1997 has matching measurement error and process error prediction intervals, this is because the measurement error estimated by bootstrapping was small, but we did not simulate underdispersed data. Through that even without process error the residual deviance was already higher than in the original regression.

Discussion

Density-dependent decrease was detected for pre-recruit *Macoma balthica* in three of eight investigated time periods, but there was no evidence for density dependence in *Cerastoderma edule*. Stronger regulation in *M. balthica* than in *C. edule* is expected from the higher variability of *C. edule* abundances (van der Meer et al. 2001b). While this gives confidence that the findings are due to actual processes, first we discuss the reliability of the results in relation to methodological aspects.

Fig. 6.4 Simulation results for *Cerastoderma edule* in the time intervals of density decline. Dashed line: slope value of the original regression through the observed data. White line: average slope values resulting when measurement error is added to deterministic data on predefined "true" regression lines. grey area: corresponding 95% confidence intervals. Black dots: average slope values resulting when process error and measurement error are added to deterministic data on predefined "true" regression lines. Whiskers: corresponding 95% confidence intervals. If the lower end of the confidence interval for the predefined slope 1 would end above the observed slope value, the observed slope would differ significantly from 1 and density dependence would be concluded.

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Few methodological drawbacks could have affected the results. An underestimation of the measurement error could have promoted the detection of density dependence (type I error). Within a transect, the choice of the positions of the sampling sites at the three tidal levels might have been an additional source of variation, that could not be quantified. As a consequence, the average resulting slope could have been too high, leading to false positive results. Also movements of animals between habitats can lead to population change appearing density-dependent (Freckleton et al. 2006). In the first interval of abundance decrease in 1996, where density dependence was concluded for *M. balthica*, indeed an increase in density occurred in the two northernmost transects, pointing to a possible additional transport alongshore into the area that could have led to the significant result. However, in both bivalve species density-independent mortality dominated. Are there issues through which density dependence could have been missed? In *C. edule,* the occurrence of planktonic larvae is spread over a longer time (Strasser and Günther 2001), and smaller numbers of individuals might have settled into the area later, although this had not led to a detectable increase of pre-
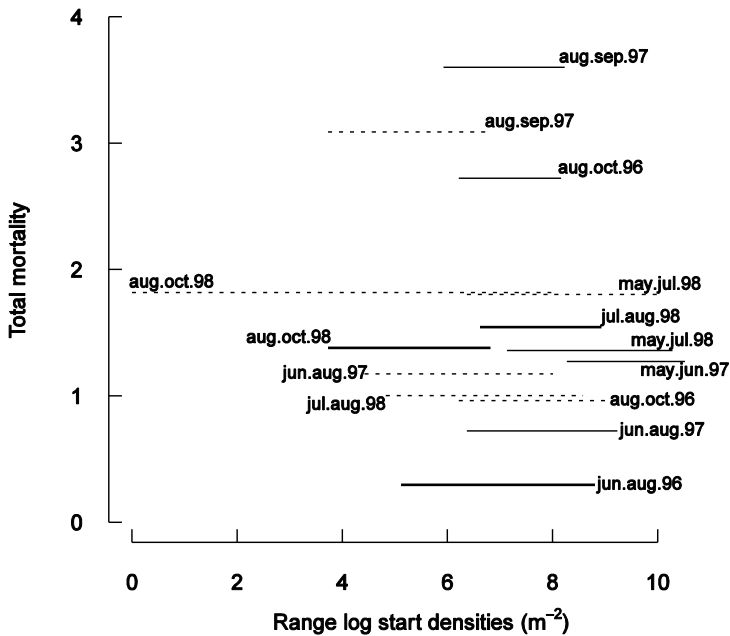
Fig. 6.5 Range of log densities per m^2 at the beginning of a time interval, and total mortality (mean logD_t - mean logD_{t+1}) during the time interval. Solid line: *Macoma balthica* (bold: density dependence detected). Broken line: *Cerastoderma edule*.

recruits. Further, the process error was generally large, which led to a large uncertainty of the estimate of the density-dependent coefficient to a large uncertainty of the estimate of the density-dependent coefficient of mortality. In some cases only extremely strong density dependence of mortality would have been detectable (Fig. 6.3b and c). Thus, occurrences of weak density dependence may have been overlooked due to a lack of power (type II error). What could have contributed to the problem is the circumstance that a sampling round lasted several days, which adds more apparent "process" variation. For the population perspective, one has to bear in mind that we solely analyzed spatial density dependence, while temporal density dependence is more important for population dynamics (Forrester et al. 2008). To predict temporal density dependence from spatial density dependence one has to know the underlying biological mechanism (Forrester et al. 2008). Several density-dependent mechanisms can have an effect in space and in time. However, if predators react in aggregative response to relative density at a single point in time and not to absolute density, this is not necessarily a stabilizing process (Stewart-Oaten and Murdoch 1990). Limits to generalizations from this study are also set by its spatial and temporal extent.

Besides stating the presence or absence of density-dependent mortality, can we say more about the possible causes? That the process error is big is not only to be seen as something that reduces power, but, unlike the problems arising from inaccurate data, also has an ecological meaning. Stochastic processes dominated over density-dependent mortality. Physical disturbance would affect the newly settled bivalves independently of their density. We did not investigate mechanisms directly, but anticipated to find differences in density-dependence in time and between species, and get indications for the underlying processes from additional available information. In August-September 1997 the highest mortalities in *M. balthica* as well as in *C. edule* were measured, both species probably suffered a common density-independent mortality source, such as physical disturbance. The data collection presented here accompanied predator exclosure experiments near one of the transects (Strasser 2002). No predation was detected in 1996, when predator arrival after the cold winter was delayed (Strasser and Günther 2001). Predation on *M. balthica* and *C. edule* did occur in August 1997 and June 1998. These months do not match the periods with density-dependent mortality in *M. balthica*. Because of the smaller spatial extent, the exclosure experiment cannot be compared directly with this study. In any case there is no support for predators causing density-dependent mortality in this study. Predation might rather distort the effects of density-dependent mortality if predator access differs between sites. In contrast, van der Veer et al. (2000) attributed density-dependent mortality in juvenile flatfish in the Wadden Sea to generalist predators

shifting their diet to abundant prey, and 1996 with late crustacean arrival broke free of that relationship.

A potentially informative difference between the two species is in feeding mode. Competition for food has been found stronger in deposit- than in suspension-feeding (Kamermans et al. 1992, Ólafsson, 1986), leading to more constant population densities in deposit feeders and higher variability in suspension feeders (Levinton 1972). Competition has not received much attention in the soft bottom intertidal, because it is not thought to be so important, even less so in millimeter sized juveniles. In the two years with density dependence in *M. balthica*, planktonic chlorophyll a, as a proxy for primary production they could have competed for, did not differ in the same way from the year with no density dependence detected (van Beusekom et al. 2009). There are examples of a negative influence of high adult abundances on juveniles (Hewitt et al. 1997). Adult-juvenile interactions have been proposed as a reason for the horizontal stock-recruitment relationship in *C. edule* (Beukema et al. 1996), but the adults should affect juveniles of other species as well. We investigated and found evidence for spatial density-dependence among juvenile *M. balthica*, but in this species adult and juvenile distributions are not even correlated, because of an ontogenetic habitat shift. Habitat choice might be a relevant keyword here for the explanation of density independence of bivalve settler mortality. High density may be correlated with good survival as secondary settlers choose sites with high quality, and this overrules any density-dependent mortality.

Much of the literature and debate on density dependence is about annual population changes. Fewer studies are concerned with density dependence within a single cohort (e.g. Myers and Cadigan 1993, Planes et al. 1998, Ruesink, 2000), and several different approaches are used. Density dependence within cohorts in time intervals shorter than a year has hardly been addressed. This study is the first to investigate density dependence within the early months of the life of Wadden Sea bivalves at a regional scale, on the basis of a well-defined statistical model, and assessing the effects of measurement and process error on the precision of parameter estimates by means of simulation studies. Our analysis method can be used for other systems as well, and for other data arrangements that do not confound density with age (Beverton and Iles 1992). We found evidence for both density-dependent and independent mortality, but density independence was more common. This is a reminder that, although density-dependence is expected from the stock-recruitment relationship, also the enormous variation around the horizontal part of the curve should be acknowledged. Previous studies on bivalve recruitment have been on an important track (Bos 2005, Hiddink 2002, Strasser 2000). Grasping recruitment remains difficult, as hardly any factors can be

dependably predicted. Knowledge of the processes that shape survival until recruitment is important, because it is the key to population dynamics of mass spawners. In recent years *M. balthica* abundances in the Western Wadden Sea strongly decreased (van Gils et al. 2009) and now at low stock a stock-recruitment relationship becomes apparent (Fig. 7.2 in Chapter 7, Rob Dekker, pers. comm.). One should remember that density-dependent mortality does not necessarily mean that populations have the ability to recover when they are reduced to low numbers (Sale and Tolimieri 2000). In broadcast spawners, ultimately reproductive success will decrease at low adult density as fertilization fails through dilution of gametes (Luttikhuizen et al. 2011). It is not known whether the decrease in abundances of both adult and juvenile *M. balthica* is an internal dynamic, or if they suffer from an extrinsic mortality source they have in common.

In this observational study, comparisons between species and time periods did not shed enough light on the processes behind density-dependent mortality. In future research, the mechanisms should be studied directly. Density-dependent infections with pathogens are becoming a strong candidate and have hardly been studied. Further, the theoretical consequences of density-dependence at different times in the life cycle on population dynamics could be investigated.

Acknowledgements

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Chapter 7

Discussion

Inter-annual variation in the abundance of broadcast spawning bivalves is merely determined in the period before recruitment (van der Meer 2001a). High recruitment after cold winters with delayed predator arrival pointed to an influential role of size-dependent predation (Beukema et al. 1998, Strasser 2000). This had been concluded from investigations of long-term surveys. The present study aimed to show size-selective predation in the field, and to take steps towards a more quantitative understanding of bivalve recruitment by including body size explicitly. Overall, we conclude that size-dependent predation on young bivalves is prevalent and substantial. The findings stress the pivotal role of life history characteristics that determine encounter sizes of predator and prey.

In a simulation study, we found that size-dependent predation was needed to explain observed size distributions of pre-recruit *Macoma balthica* (Chapter 2). Size-selective loss of young bivalves was proven experimentally in the field. By combining fluorescent marking and caging, we solved the problem of two entangled processes, growth and size-selective predation, acting on size distributions. We obtained individual in situ growth rates for juvenile *M. balthica* and *Cerastoderma edule* for the first time, and demonstrated selective loss of smaller individuals. Size selectivity was similar in the two distant study regions in the Wadden Sea, at the islands of Texel and Sylt (Chapter 3). A complementary compilation of several years of intra-annual field observations from Texel and Sylt supported that the settings for size-selective predation are rather similar in the two regions with differing but correlated winter temperatures. In contrast, between years, size ratios of predators and prey that encounter can differ completely due to a stronger phenological response of crustaceans than of bivalves (Chapter 4). The smallest bivalves suffered from the highest predation rates in aquarium experiments with different *M. balthica* sizes offered separately. Hungry shrimp (*Crangon crangon*) foraged effectively even at low bivalve densities and consumed disturbingly high numbers of *M. balthica*. The experimentally derived predation rates are higher than needed to explain bivalve field mortality (Chapter 5). Further, we could

demonstrate the occurrence of density-dependent bivalve pre-recruit mortality in spatio-temporal field data in a few cases, but could not pinpoint circumstances under which it typically occurs that might hint to underlying processes (Chapter 6).

I will now first discuss the limitations concerning methodological aspects and scope of the study. Then I will link my findings to related studies and point out directions for further research. Finally, I will envisage the future of our bivalve populations under changing circumstances.

Limitations of the study

Strong differences in bivalve recruitment success between years pointed to the importance of crustacean predation (Beukema et al. 1998). At the same time however, this high variability between years is also a major difficulty in studying bivalve recruitment. The cockle recruitment in the summer of 2011, that is after all the field work for this thesis was completed, was the highest ever recorded at Balgzand (Fig. 7.1)! The chapters that are concerned with the field situation (2 to 4 and 6) deal with one to six years, and different processes may dominate from year to year.
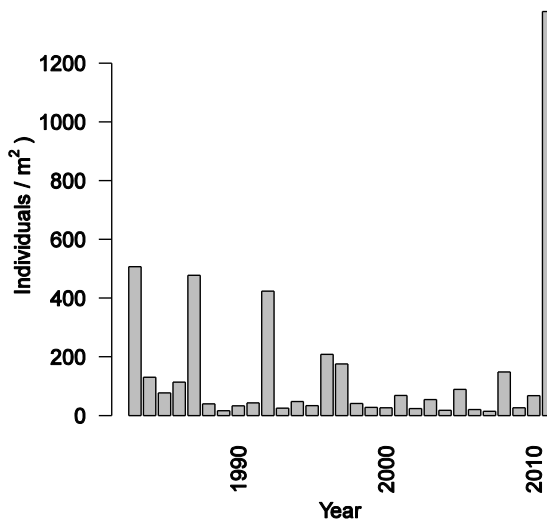
Fig. 7.1 *Cerastoderma edule* recruitment at Balgzand 1983 to 2011 (Rob Dekker, pers. comm).

Another complication in studying mortality in the early life phase of bivalves is that abundance changes are not only due to settlement and mortality, but also occur through bivalve mobility early after settlement, when they gradually move up to the higher intertidal (Armonies and Hellwig-Armonies 1992, Beukema 1993). In the three chapters dealing with mortality in the field (Chapters 2, 3 and 6), this problem was tackled differently each time. For the analysis of density dependence, the sampling design was stratified in the intertidal (Chapter 6). In the simulations aiming to reproduce observed bivalve size distributions, we investigated whether the simplifying assumption that all observed loss is due to predation still supports shrimp being a major determinant of prey size structure (Chapter 2). In the field experiments, several controls were built in: by individual marking, sampling migrants, caging with cage controls, as well as conducting the experiments in contrasting sites and in two periods, we concluded that we captured a time of net immigration. We can not exclude that the better survival in the cages is not all due to protection from predators. However, the average daily loss of bivalves exposed to predators in the field was only a fraction of the consumption reached in the lab (Chapter 5), so it is plausible that shrimp had a great share in field mortality of bivalves.

The studies reported in chapters 2 to 4 focus on the middle intertidal zone. Shrimp abundances decrease towards the higher intertidal (Janssen and Kuipers 1980), while the abundances of the studied bivalves increase towards the higher intertidal soon after settlement (Armonies and Hellwig-Armonies 1992, Beukema 1993). Thus, the highest number of encounters between predators and prey occurs in the middle intertidal, and this tidal zone is therefore suitable to study the phenomenon of size-selective predation. However, it must be kept in mind that the studied part of the bivalve populations does not necessarily represent the entire respective population.

Size-dependent predation, its effects and aftereffects

The aquarium experiments with shrimp feeding on different size classes of *Macoma balthica* (Chapter 5) show that already a small difference in prey size can make a big difference in mortality. Size-selective predation mortality in the field can change within a short time (Chapters 2 to 4). Thus, even small changes in life history characteristics, which determine the sizes of predator and prey at encounter, could tip the scales. The interplay of seasonality of the environment with predator and prey phenology and growth has been investigated in several aquatic and marine systems (e.g. Huusko and Sutela 1997, Urban 2007). For most

systems the "bigger is better" slogan applies, but in rare cases being small gives a survival advantage (e.g. Sogard 1997). Former experiments with *M. balthica* as prey had established the upper end of the predation window by shrimp (Hiddink et al. 2002, Keus 1986 cited at van der Veer et al. 1998). Yet, at least in *Cerastoderma edule*, the lower end of the predation window appears to influence predation mortality as well (Chapter 4, Strasser 2002).

We found in the lab experiment that shrimp predation can be very effective, and theoretically has the potential to cause 100% mortality under the right circumstances. However, in the field, shrimp do not reach consumption rates that high. To develop a basic model such as in Chapter 2 further towards quantification, more knowledge on shrimp foraging behavior is needed. The preference within the prey size range should be investigated, and we need to know if and how prey choice and feeding rates are affected by satiation, alternative prey and relative densities of different prey types. For predictions, statistical relationships can only be used when the populations as well as the environment stay in the known range, but behavioral information has to be applied for novel situations (Bradbury et al. 2001).

A question that arises from the observation that size distributions are sometimes strongly altered by selective loss (Chapters 2 to 4) is whether this has follow-up consequences not only on cohort size but also for later fitness. Body size determines burying depth (Zaklana and Ydenberg 1997), the amount of reserves (Kooijman 2000) and dissolution resistance of bivalves (Waldbusser et al. 2010) which all affect subsequent survival. Body size also determines the amount of gametes that can be produced (Honkoop and van der Meer 1997).

The stock-recruitment relationship

Bivalve recruitment does not increase proportionally with the reproductive adult stock. Juvenile survival is strongly influenced by predation mortality, but the stock-recruitment relationship implies that it is also density-dependent. An appealing conception to bring these two factors together would be an interaction between competition and predation. If competition at high individual densities reduces growth, then young bivalves would stay longer in the predators' size window and suffer higher mortality. However, this interaction was investigated experimentally for *Cerastoderma edule* in Western Brittany (Masski and Guillou 1999) and for *Mya arenaria* in Maine (Beal 2006) and was not confirmed, because juvenile growth was not reduced at high density in the first place. *C. edule* growth was reduced in the western Wadden Sea in the year 2011 with the

enormous recruitment (Rob Dekker, pers. comm.), but intra-cohort competition had not the proposed but the opposite effect at least on predation by their avian predators: the condition of *C. edule* was so bad at high densities that it was less profitable for Red Knots (*Calidris canutus*) to forage on them (Allert Bijleveld, pers. comm.).

We found occurrences of density-dependent bivalve mortality in the pre-recruitment phase (Chapter 6), but no particular process could be brought forward as the potential main underlying cause. Predation rather seems to add variation around the stock-recruitment relationship, through processes such as their timing of arrival, and their abundance and size composition, which are not influenced by a feedback from bivalve density. However, in the density dependence study (Chapter 6) we are dealing with limited circumstantial evidence from observational data. It is still possible that predation also has a density-dependent component, for example through density-dependent prey choice, and this should be investigated experimentally. Also competition for resources as a cause behind density-dependent mortality of bivalves deserves new attention. It may involve interspecific competition, as populations of many species co-vary (Beukema et al. 2001). This was beyond the scope of this project, so the quest is not over.

The stock-recruitment relationship is the backbone of fisheries research (Cushing 1996). Recruitment overfishing is a particular problem; it means that the reproductive stock is reduced so much that it is not able to replenish the population (Pauly 1988). At some point the stock-recruitment curve has to go through the origin. Usually, pre-recruitment processes are more important in determining year class strength, but larval supply is a precondition and ultimately limiting. This has recently become apparent for *Macoma balthica* (Fig. 7.2). In the past few years the lowest stock sizes and the lowest recruitment have been measured in the Balgzand time series, which covers almost 40 years. The size of the reproductive stock is for *M. balthica* now becoming more influential than it was in the past, and density dependence among offspring is less relevant. One might ask why the population is not replenished from adjacent areas. The rapid spread of the introduced species *Ensis americanus* in the Wadden Sea within a few years is a prominent example of larval dispersal (Armonies 2001). However, dispersal abilities not only depend on hydrodynamic conditions but are also species specific, through duration of the larval phase, larval behavior and buoyancy (Lundquist et al. 2004). There is evidence of self-recruitment back to benthic source populations in spite of the openness of coastal systems (Swearer et al. 2002). An exchange between sub-populations that equals out spatial density differences would also have been an alternative explanation for the disconnection of recruitment from the present stock. The detection of local density dependence in

this study (Chapter 6) speaks for local mortality rather than dispersal as the main reason behind the uncoupling of recruitment from stock size. Local mortality sources for newly settled bivalves, which reduced the population to the present low, would affect resident young bivalves and potential new arrivals alike.
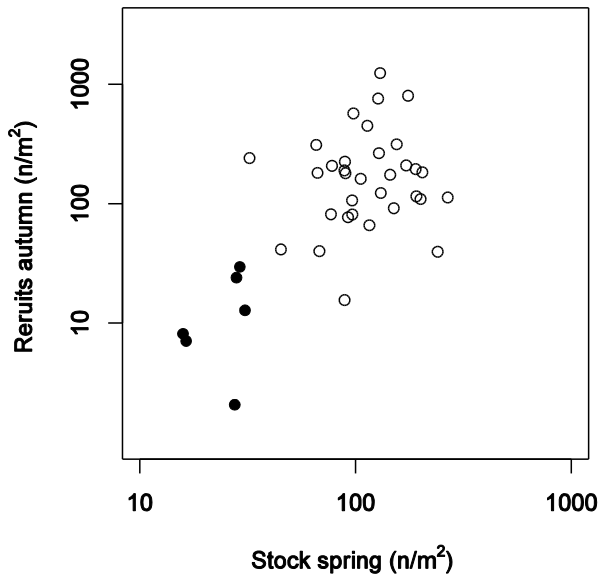
Fig. 7.2 Stock-recruitment relationship of *Macoma balthica*. White: years 1973 to 2005; black: years 2006 to 2011 (Rob Dekker and Jan Drent, pers. comm).

Bivalve population dynamics at a larger scale

Bivalve recruitment is correlated within the Wadden Sea at a scale much larger than could be covered by dispersal within the duration of the larval phase (Strasser et al. 2003). This is another support that recruitment is determined by winter effects working on species interactions. The "Moran effect" explains the phenomenon of spatially synchronized population dynamics with correlated climate conditions, provided that local density-dependent dynamics are similar (Hudson and Cattadori 1999). I approached the question how populations in two distant regions of the Wadden Sea can have similar recruitment successes in spite of differing winter temperatures, by investigating predator-prey interactions with simultaneous experiments in the field (Chapter 3). In the studied period, quite

similar processes took place, only at different speed and absolute sizes. Concerning the larger range of the European distributions of bivalves and their predators, Drent (2004) and Freitas (2011) investigated preconditions for size-specific predation, namely energetic aspects and life history variation. Temperature thresholds for *Macoma balthica* spawning become lower further north, resulting in spawning more or less at the same time along the European coast (Drent 2004). Shrimp grow well at all latitudes, but bivalves are food limited, so that they can not compensate for shorter growing seasons with higher intrinsic growth rates (Freitas 2011). In this context it is interesting what the causes and consequences are of the high growth variability we observed within a region by individual marking (Chapter 3).

Future prospects for Wadden Sea bivalve populations: limited adaptation options

What chances do the bivalves, and especially *Macoma balthica*, have to cope with a stronger phenological shift as a response to winter warming in shrimp than in the bivalves themselves? Through variation, selection and inheritance their life history could develop towards avoiding the predators by even earlier spawning. The dilemma is, if the larvae are too early they don't have enough algal food yet, which may delay development and reduce growth (Bos et al. 2006, Philippart et al. 2003). Reduced growth through food shortage in turn prolongs the period that they are in a size range susceptible to predation (Fig. 7.3). Many species are shifting or expanding their distributions to higher latitudes in recent years (Doney et al. 2012). Moving up north would make up for the distorted temperature trigger in respect to food availability, yet confront them with predators again.

Spawning does not happen at one distinct moment. It may be spread out over several weeks, or there may be another spawning event in autumn (Günther et al. 1998). Could this be a strategy to spread the chance that at least some offspring catch a good moment and survive at a best compromise between predator avoidance and growth conditions? Not at a low adult stock as we have now in *M. balthica*. At very low adult density, gametes are diluted so much that external fertilization may fail (Luttikhuizen et al. 2011). Now it becomes even more important that spawning is synchronized, which takes away the option to spread the timing.

Bivalves make for a big share of the Wadden Sea benthic communities, and play a central role in the ecosystem. If they don't thrive, many interactions with other species will be affected. Shrimp will probably not suffer from

depleting this prey, as they are omnivores and have alternative food. Migrating shorebirds depend much more on reliable high quality prey. A weakened bivalve population will be vulnerable to other anthropogenic or biological impacts. Studies on migration of *M. balthica* had shown that the high intertidal is important in the early life phase (Beukema 1993, Hiddink 2003), but with sea level rise these areas fall victim to diking and coastal defense. One overdue measure has been taken when habitat modifying cockle fisheries were finally banned from the Dutch Wadden Sea (van Gils et al. 2006). Climate change is a much less tangible problem. It remains to be seen whether a process will emerge that controls the epibenthic predators.

► **Fig. 7.3** Symbolic illustration of the interplay of size selection, individual growth and seasonal timing. a) before climate change: Bivalves settle before the peak arrival of epibenthic predators and soon outgrow their prey spectrum. b) during climate change: shrimp arrive even earlier than the advanced bivalve settlement, so they can feed on small bivalves immediately. c) hypothetic adaptation: selection for still earlier bivalve settlement is unlikely, as poor growth conditions earlier in the year would prolong the period needed to outgrow the predation window.
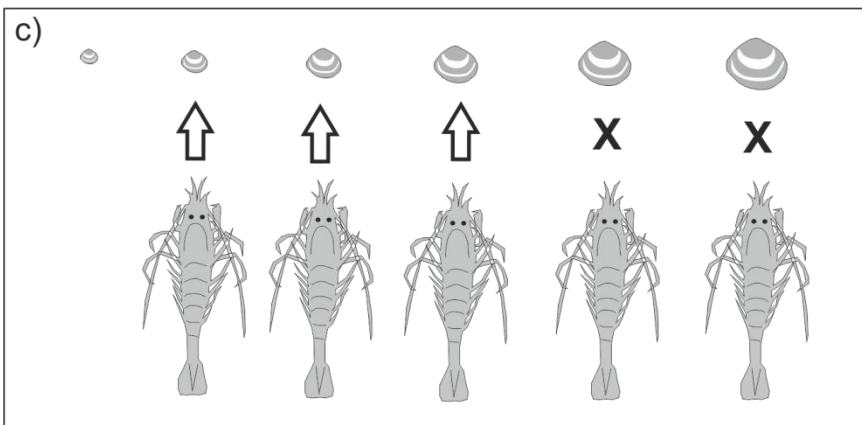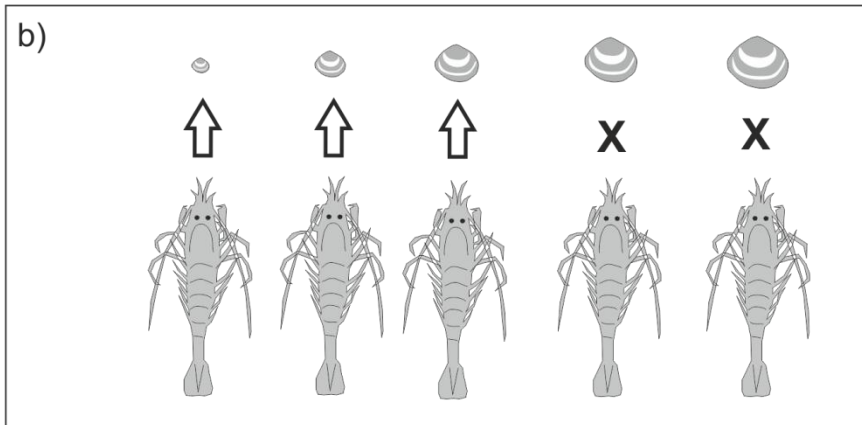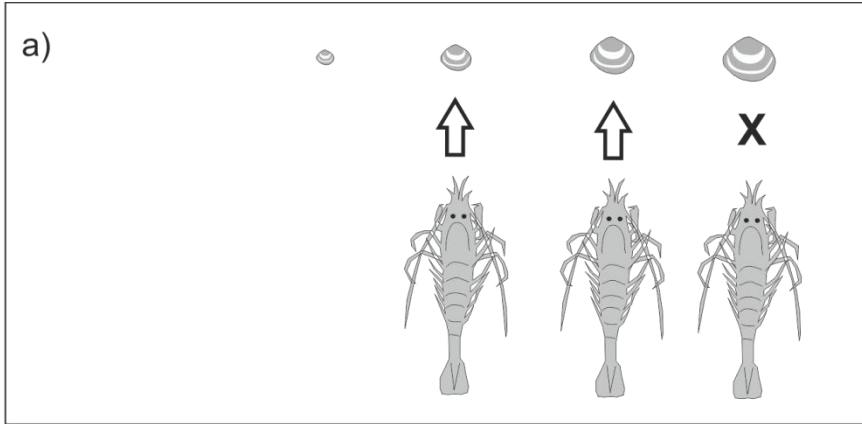
time

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Summary

Bivalve shellfish play an important ecological role in intertidal areas. They make up about half of the biomass of animals living in and on the bottom of the Wadden Sea and, among other things, are an important food source for migratory birds. The population size of different bivalve species often fluctuates strongly from year to year. Analyses of long-term observations have shown that the number of young bivalves that survived until August in the Wadden Sea, also termed recruitment, is decisive for the strength of that year-class in the future. After that the death rate of the animals does not change the overall picture. It is especially remarkable, that the number of reproductive bivalves hardly has an influence on the number of surviving offspring. At some point after fertilization in spring, between the planktonic larval phase and the end of the first summer in the sea bottom, a high and variable mortality must take place. Years with extremely good recruitment have given a hint, what might cause this mortality. In summers after very cold winters, the predators of the millimeter sized bivalves – Brown shrimp (*Crangon crangon*) and Shore crabs (*Carcinus maenas*) – arrived late and in lower numbers at the tidal flats. The young shellfish had a head start and had soon grown too large to be eaten by the crustaceans.

In this thesis "Size-dependent predation risk for young bivalves" I studied more deeply the role of body size in this predator-prey relationship. Can size-dependent predation really be one of the main causes of mortality of bivalves in the early bottom-living phase? What is the influence of different winter temperature between regions? How fast do bivalves grow anyway when they are so small, and how big is the influence of bivalve size on the predation rate of brown shrimp exactly?

First I report in **chapter 2** the results of a simulation study. Wadden Sea ecologist Rob Dekker had been following the size development of young bivalves during summers in several years at the Dutch island Texel, and at the same time also observed the sizes of the present crustaceans. Using data of the Baltic tellin (*Macoma balthica*) and the Brown shrimp we tried to reproduce the observed change in the size distribution of the bivalves from one month to the next, under the assumption that the shrimp feed size-dependently on the young, growing bivalves. The model calculations were run with different size preferences by the shrimp and different growth rates of the bivalves. In half of the 14 investigated time periods, it was indeed possible to simulate size distributions that did not differ significantly from the bivalves collected in the field. In most of the cases also the best fitting size preferences and growth rates were realistic. That is remarka-

ble, considering that we assumed that the decrease in bivalve numbers is solely due to predation by shrimp. In contrast, when assuming that the loss of bivalves is random and size-independent, the size distribution simulated only with bivalve growth never fits the observed one.

In the simulation study, growth rates were estimated indirectly. It was plausible, that a considerable part of bivalve mortality was caused by shrimp. In **chapter 3** we report the results of an elaborate field experiment, in which we measured individual growth of bivalves and size selective loss directly. Young bivalves in the field were stained in the sediment with the fluorescent dye calcein. Ten days later samples were taken and under a special microscope with UV-lamp it was measured, how much shell material had been added since the uptake of the dye. This way individual growth of Baltic tellins and cockles (*Cerastoderma edule*) was measured for the first time in this fragile life stage, rather than being calculated from the change in average size. We found that there was much variation between individuals. To find out if the bivalves are preyed upon depending on their size, the staining was combined with a predator exclosure experiment. With small cages, which were covered with a 1 mm mesh screen, a part of the bivalves was protected from shrimp and other predators foraging on the sediment. With the fluorescent mark we could distinguish which bivalves had been present since the onset of the experiment and which had arrived later. We also could check if the protection with a cage possibly changed their growth. The study was conducted in two regions: at Texel in the westernmost part of the Wadden Sea in the Netherlands, and at the island of Sylt, in the North of the German Wadden Sea. In both regions in the first of two rounds of the experiment, fewer bivalves from the lower end of the size range survived in the unprotected sediment.

In **chapter 4** we compared the arrival times of bivalves and crustaceans between the two regions mentioned above. In the year of the field experiment, the bivalves settled at about the same time at Sylt and Texel, while the young shrimp arrived later at Sylt. As the bivalves grew slower at Sylt and at the same time the shrimp had a lower average size than at Texel, the size ratios of predator and prey were very similar at the two islands. In both regions about the same proportion of predator-prey encounters could be fatal for the bivalves. A comparison of Rob Dekkers data from Texel with data that had been collected in coinciding years by Matthias Strasser at Sylt shows, that the bivalves usually settle at the same time in the two distant regions. Only the coldest winter led to a delay at Sylt. At Texel, the arrival of crustaceans differed stronger between years than that of the bivalves. This resulted in very different size relationships. Sometimes the bivalves could outgrow the danger quickly, sometimes they remained in the risky size range. A growth advance for the bivalves did not always lead to advanta-

geous relative sizes. Advantageous size ratios appeared to be a prerequisite, but no guarantee for good recruitment.

In **chapter 5** we investigated feeding rates of Brown shrimp on Baltic tellins in aquarium experiments. We wanted to know what influence the size of the clams has on the time required to find and to handle them. Additional to the shell size, we also varied the densities offered, because at low density searching time has the biggest influence on the feeding rate. At high prey density the handling time limits the number of prey individuals consumed within a certain time. Even at the lowest densities, shrimp were motivated and effective finding their prey. Bigger shells were more difficult to find, because they can burrow deeper. Also handling of the bivalves took longer the larger they were. By these two advantages, the risk to be eaten was about a third lower for the largest than for the smallest shells. That is remarkable, as the "big" bivalves were with 0.85 mm length not even a fourth of a millimeter longer than the smallest animals in this experiment. The consumption by shrimp was disturbingly high. If they could reach this in nature, they could easily erase the whole new year class.

In **chapter 6** we investigated density dependence of the mortality of young bivalves. As described earlier, the number of reproductive adults has little influence on recruitment success. Still, more adults produce more larvae. That means that the relative mortality is higher at high than at low densities of offspring. Through what and when exactly mortality is density-dependent is thus far unknown. Data by Matthias Strasser on Sylt were suitable to analyze them with respect to density dependence. We applied a special statistical analysis that accounts for measurement variation and process variation. We found density-dependent mortality of young Baltic tellins in three of eight cases, but in no case out of six for young cockles. This corresponds to the observation that the cockle population fluctuates stronger from year to year. We had anticipated to detect a pattern when density dependence occurs, and to infer from that on the causes. Yet, the three periods during which the decrease in bivalve numbers was density-dependent had nothing obvious in common. Thus we could not draw conclusions if density dependence is for example related to competition for food among bivalves or to foraging behavior by the predators. Predation rather seemed to add variation. Stochastic variation for example in food availability or environmental factors certainly played an important role, too, in the studied period and region.

Each of the different approaches – pure field observations and their mathematical analysis, field experiments and lab experiments – has its own strengths and weaknesses. Together, they form the picture that size-dependent losses of young bivalves are the rule and that mortality by predation can be substantial. Usually mainly the smallest individuals are affected. It is especially

striking, how small changes already can have a strong effect. The timing of the annual reproduction of Baltic tellins is very similar along the European coast; it is adjusted to the environmental conditions. The bivalves hardly have a chance to adapt to an earlier appearance of the crustaceans, because the growth conditions are insufficient.

In this project I focused on the size dependence of the predator-prey relationship. To further improve our understanding of the influence of crustaceans on young bivalves, the feeding rates that can be realized in nature should be investigated further. Prey choice in the presence of alternative prey species will probably play an important role. Further, there is still need for research on density dependence of mortality in the early life of bivalves. In our analysis of field observations there was no sufficient circumstantial evidence for an underlying cause. Possible processes could be investigated experimentally. High mortality at high densities does not necessarily imply that a population can recover at low densities. The population of Baltic tellins in the western Dutch Wadden Sea has decreased so strongly in recent years that their reproductive success is even in danger.

Samenvatting

Tweekleppige schelpdieren spelen ecologisch een belangrijke rol in getijdegebieden. Zij vormen ongeveer de helft van de biomassa van alle in en op de bodem levende dieren in de Waddenzee en zijn onder andere belangrijk voedsel voor trekvogels. De populatiesterkte van de verschillende schelpdiersoorten schommelt meestal sterk van jaar tot jaar. Analyses van langetermijnobservaties hebben aangetoond, dat het aantal jonge schelpjes dat tot augustus overleefd heeft, ook rekrutering genoemd, beslissend is voor de jaarklassterkte in de toekomst. Daarna heeft verdere sterfte geen belangrijke invloed meer op het totaalplaatje. Bijzonder opmerkelijk is dat het aantal vruchtbare schelpdieren nauwelijks invloed heeft op het aantal overlevende nakomelingen. Ergens na de bevruchting in het voorjaar, tussen de planktonische larvenfase en het einde van de eerste zomer in de wadbodem, moet een hoge en wisselvallige sterfte plaatsvinden. Jaren met extreem goede rekrutering hebben een hint gegeven wat de sterfte zou kunnen bepalen. In zomers na bijzonder koude winters kwamen de predatoren – Noordzeegarnalen (*Crangon crangon*) en strandkrabben (*Carcinus maenas*) die de millimeterkleine schelpjes als prooi eten – later en in geringere aantallen aan op het wad. De jonge schelpdieren hadden een groeivoorsprong en waren snel te groot om door de krabben en garnalen gegeten te worden.

In dit proefschrift "Grootteafhankelijk predatierisico voor jonge schelpdieren" heb ik de rol van lichaamsgrootte in deze predator-prooi relatie verder onderzocht. Kan grootteafhankelijke predatie werkelijk een van de hoofdoorzaken zijn van de sterfte van schelpdieren in de vroege fase van het bodemleven? Welke invloed heeft het verschil in wintertemperatuur tussen gebieden? Hoe snel groeien de schelpen eigenlijk wanneer ze zo klein zijn en hoe groot precies is de invloed van de grootte van de schelpen op de consumptie door de garnalen?

Als eerste beschrijf ik in **hoofdstuk 2** de resultaten van een simulatiestudie. Wadecoloog Rob Dekker heeft meerdere jaren bij het Waddeneiland Texel de grootteontwikkeling van jonge schelpdieren gedurende de zomer gevolgd en tegelijkertijd ook de groottes van de aanwezige kreeftachtigen geobserveerd. Met de data van het nonnetje (*Macoma balthica*) en de Noordzeegarnaal hebben wij geprobeerd de geobserveerde verandering in de grootteverdeling van het ene tijdstip naar het volgende na te bootsen. Dit onder de aanname dat Noordzeegarnalen jonge, groeiende schelpjes grootteafhankelijk eten. Het model werd met verschillende groottepreferenties door de garnalen en verschillende groeisnelheden bij de schelpdieren doorgerekend. In de helft van de 14 onderzochte periodes was het

inderdaad mogelijk grootteverdelingen te simuleren die niet significant van de op het wad verzamelde schelpen verschilden. In de meeste gevallen waren ook de veronderstelde grootepreferenties en groeisnelheden realistisch. Dat is indruk-wekkend, als je je realiseert dat we er van uitgingen dat de afname in de schelpenaantallen alleen door predatie door garnalen veroorzaakt werd. Als je daarentegen aanneemt dat de verliezen bij de schelpdieren puur toevallig en grootteonafhankelijk zijn, dan komt de alleen met schelpengroei gesimuleerde grootteverdeling nooit met de daadwerkelijke geobserveerde overeen.

In de simulatiestudie werden de groeisnelheden indirect geschat. Het was plausibel, dat de schelpdiersterfte voor een aanzienlijk deel door garnalen veroor-zaakt werd. In **hoofdstuk 3** berichten wij van een uitgebreid veldexperiment, waarbij we individuele groei van schelpen en grootteafhankelijk verlies daadwer-kelijk gemeten hebben. Met de fluorescerende kleurstof calceïne werden de schelpjes in het veld in de wadbodem gekleurd en tien dagen later bemonsterd. Met een speciale microscoop met UV-lamp werd gemeten hoeveel nieuw schelp-materiaal er sinds de opname van de kleurstof bijgekomen was. Op die manier werd voor de eerste keer de individuele groei van nonnetjes en kokkels (*Cerastoderma edule*) in deze fragiele levensfase bepaald. Tot nu toe werd groei berekend uit de verandering in de gemiddelde lengte over de tijd. Nu werd vast-gesteld, dat er een sterke individuele variatie is. Om te onderzoeken of de schelp-dieren afhankelijk van hun grootte gegeten worden, werd het kleuren met de experimentele uitsluiting van predatoren gecombineerd. Een deel van de schelpen werd met kleine kooien, die met een gaas van 1 mm maaswijdte bespannen waren, tegen garnalen en andere op de bodem levende rovers beschermd. Door middel van de kleur konden wij herkennen welke schelpen er al vanaf het begin van het experiment aanwezig waren en welke er pas later bijgekomen waren. Ook konden wij controleren of de bescherming door de kooi mogelijk de groei beïn-vloedde. De studie werd in twee gebieden uitgevoerd: bij Texel in de westelijke Nederlandse Waddenzee en bij het eiland Sylt helemaal in het noorden van de Duitse Waddenzee. In beide gebieden overleefden er in de eerste van twee rondes van het experiment minder schelpdieren uit het onderste einde van het grootte-spectrum in onbeschermde monsterplekken.

In **hoofdstuk 4** hebben wij de aankomsttijden van schelpdieren en kreeft-achtigen en de grootteverhoudingen van predator en prooi in de twee bovenge-noemde onderzoeksgebieden vergeleken. De schelpjes vestigden zich in het jaar van het veldexperiment ongeveer tegelijkertijd bij Sylt en Texel, terwijl de jonge Noordzeegarnalen bij Sylt pas later aankwamen. Doordat de schelpen bij Sylt langzamer groeiden terwijl de garnalen gemiddeld kleiner waren dan bij Texel, leken de grootteverhoudingen van predator en prooi bij de twee eilanden op

elkaar. In beide gebieden kon ongeveer hetzelfde aandeel van alle predator-prooi ontmoetingen fataal voor de schelpdieren zijn. Een vergelijking van Rob Dekker's data van Texel met data die in overeenkomende jaren door Matthias Strasser bij Sylt verzameld werden, laat zien dat de schelpdieren zich meestal op dezelfde tijd in de twee gebieden vestigen. Alleen de koudste winter had een vertraging bij Sylt tot gevolg. Tussen jaren verschilde bij Texel de aankomst van de kreeftachtigen sterker dan die van de schelpdieren. Daaruit resulteerden heel verschillende grootteverhoudingen. Soms konden de schelpen het gevaar snel ontgroeien, soms bleven ze in het riskante gedeelte van de bandbreedte. Een groeivoorsprong van de schelpen leidde niet altijd tot gunstige relatieve groottes. Gunstige grootterelaties bleken een voorwaarde, maar geen garantie voor een goede rekrutering te zijn.

In **hoofdstuk 5** hebben wij in aquarium-experimenten de consumptie door Noordzeegarnalen van nonnetjes onderzocht. Wij wilden weten welke invloed de schelpengrootte had op zoektijd en hanteertijd. Behalve de schelpengrootte hebben wij ook de aangeboden dichtheid gevarieerd, want bij een lage dichtheid heeft het zoeken de grootste invloed op de opnamesnelheid. Bij een hoge prooidichtheid werkt dan het proces van het eten zelf limiterend op het aantal binnen een bepaalde tijd geconsumeerde prooidieren. De garnalen waren zelfs bij de laagste dichtheden gemotiveerd en in staat effectief hun prooi te vinden. Grotere schelpen waren moeilijker te vinden, omdat zij zich dieper kunnen ingraven. Ook het eten zelf duurde langer, naarmate de schelpen groter waren. Door deze twee voordelen was het risico om gegeten te worden voor de grootste schelpen ongeveer een derde lager dan voor de kleinste schelpen. Dat is opmerkelijk, want de "grote" schelpdieren waren met 0.85 mm lengte nog geen kwart millimeter langer dan de kleinste dieren in dit experiment. De consumptie door de garnalen was schrikbarend hoog. Als zij die ook in de natuur zouden kunnen bereiken, dan zouden ze zonder moeite de hele nieuwe jaarklasse kunnen uitwissen.

In **hoofdstuk 6** hebben wij dichtheidsafhankelijkheid van de sterfte van jonge schelpdieren onderzocht. Zoals gezegd, heeft het aantal vruchtbare adulte dieren weinig invloed op het rekruteringssucces. Meer adulten produceren echter meer larven. Dat zou betekenen dat de sterfte procentueel bij hoge dichtheden nakomelingen hoger is dan bij lage dichtheden. Waardoor en wanneer precies de sterfte dichtheidsafhankelijk is, is tot nu toe niet bekend. De data van Matthias Strasser op Sylt waren geschikt om ze op dichtheidsafhankelijkheid te onderzoeken. Hiervoor hebben wij een speciale statistische analyse gebruikt die rekening houd met meetvariatie en natuurlijke variatie. Wij hebben in drie van acht gevallen dichtheidsafhankelijke mortaliteit van nonnetjes gevonden, maar in

geen van zes gevallen voor de kokkel. Dat komt overeen met observaties dat de kokkelpopulatie sterker schommelt van jaar tot jaar. Wij hadden verwacht, een patroon te ontdekken wanneer dichtheidsafhankelijkheid optreedt en daaruit conclusies over de oorzaken te kunnen trekken. De drie periodes, waarin de schelpenafname dichtheidsafhankelijk was, hadden echter niets duidelijk gemeenschappelijks. We kunnen dus geen uitspraak doen of dichtheidsafhankelijke sterfte bijvoorbeeld te relateren is aan voedselcompetitie of forageergedrag van de predatoren. Predatie leek eerder nog variatie toe te voegen. Toevalsvariatie bijvoorbeeld in voedselaanbod of omgevingsfactoren speelden in de onderzochte periode en gebied zeker ook een grote rol.

Elk van de verschillende methodische aanpakken – pure veldobservaties en de mathematische analyse daarvan, veldexperimenten en laboratoriumexperimenten – heeft zijn eigen voor- en nadelen. Echter, alles bij elkaar genomen ontstaat het beeld dat grootteafhankelijk verdwijnen van jonge scheldieren de regel is en dat de sterfte door predatoren een aanzienlijke omvang kan aannemen. Meestal treft het de kleinste individuen. Het is bijzonder indrukwekkend, hoe kleine veranderingen al een groot effect kunnen hebben. Het tijdstip van de voortplanting van nonnetjes is langs de Europese kust bijna hetzelfde, het is precies op de omstandigheden in de omgeving afgestemd. De schelpdieren hebben nauwelijks een kans zich aan een steeds vroeger verschijnen van de kreeftachtigen aan te passen, omdat de groeiomstandigheden daarvoor niet voldoen.

In dit proefschrift heb ik mij op de grootteafhankelijkheid van de predator-prooi relatie geconcentreerd. Om de invloed van kreeftachtigen op jonge schelpdieren nog beter te begrijpen zou de consumptie die in de natuur bereikt wordt nog verder onderzocht moeten worden. Prooikeuze in aanwezigheid van alternatief voedsel zal waarschijnlijk belangrijk zijn. Ook moet de dichtheidsafhankelijkheid van de sterfte in de vroege levensfase verder opgehelderd worden. In onze analyse van de veldobservaties waren niet voldoende aanwijzingen voor de onderliggende oorzaak. Mogelijke processen zouden experimenteel onderzocht kunnen worden. Een hoge sterfte bij hoge dichtheden betekent niet automatisch dat zich een populatie bij lage dichtheden herstellen kan. De nonnetjespopulatie is in de westelijke Nederlandse Waddenzee in de laatste jaren zo sterk afgenomen, dat het voortplantingssucces zelfs in gevaar is.

Zusammenfassung

Muscheln spielen ökologisch eine wichtige Rolle in Gezeitengebieten. Sie machen ungefähr die Hälfte der Gesamtmasse der in und auf dem Boden lebenden Tiere im Wattenmeer aus, und sind unter anderem wichtige Nahrung für Zugvögel. Die Populationsstärke der verschiedenen Muschelarten schwankt meist stark von Jahr zu Jahr. Analysen von Langzeitbeobachtungen haben ergeben, dass die Anzahl junger Muscheln, die bis zum August überlebt haben, auch Rekrutierung genannt, im Wattenmeer entscheidend für die Stärke der Jahrklasse in der Zukunft ist. Danach hat das weitere Absterben der Tiere keinen wesentlichen Einfluss mehr auf das Gesamtbild. Besonders bemerkenswert ist, dass die Anzahl der fortpflanzungsfähigen Muscheln kaum Einfluss auf die Anzahl der überlebenden Nachkommen hat. Irgendwann nach der Befruchtung im Frühjahr, zwischen der planktischen Larvenphase und dem Ende des ersten Sommers im Wattboden, muss eine hohe und wechselhafte Sterblichkeit stattfinden. Jahre mit extrem guter Rekrutierung haben einen Hinweis darauf gegeben, was die Sterblichkeit bestimmen könnte. In Sommern nach besonders kalten Wintern kamen die Fressfeinde der millimeterkleinen Muscheln – Nordseegarnelen (*Crangon crangon*) und Strandkrabben (*Carcinus maenas*) – verspätet und in geringerer Anzahl auf dem Watt an. Die jungen Muscheln hatten einen Wachstumsvorsprung und waren schnell zu groß um von den Krebstieren gefressen zu werden.

In der vorliegenden Arbeit „Größenabhängiges Prädationsrisiko für junge Muscheln" bin ich der Rolle der Körpergröße in dieser Räuber-Beute Beziehung genauer nachgegangen. Kann größenabhängiger Fraßdruck wirklich eine der Hauptursachen für die Sterblichkeit von Muscheln in der frühen Phase des Bodenlebens sein? Welchen Einfluss hat der Unterschied in Wintertemperaturen zwischen Gebieten? Wie schnell wachsen die Muscheln überhaupt, wenn sie so klein sind, und wie groß genau ist der Einfluss der Muschelgröße auf die Fressrate von Nordseegarnelen?

Als erstes berichte ich in **Kapitel 2** von den Ergebnissen einer Simulationsstudie. Wattökologe Rob Dekker hatte mehrere Jahre lang bei der niederländischen Wattenmeerinsel Texel die Größenentwicklung von Jungmuscheln über den Sommer verfolgt und gleichzeitig auch die Größen der anwesenden Krebstiere beobachtet. Mit den Daten für die Baltische Plattmuschel (*Macoma balthica*) und die Nordseegarnele haben wir ausprobiert, ob man die beobachtete Änderung in der Größenverteilung der Muscheln von einem Zeitpunkt zum nächsten nachbilden kann unter der Annahme, dass die Nordseegarnelen größen-

abhängig die jungen, wachsenden Muscheln fressen. Das Modell wurde mit verschiedenen Größenpräferenzen der Garnelen und mit verschiedenen Wachstumsraten der Muscheln durchgerechnet. In der Hälfte der 14 untersuchten Zeiträume war tatsächlich möglich, Größenverteilungen zu simulieren, die sich nicht signifikant von den im Watt gesammelten Muscheln unterschieden. In den meisten Fällen waren auch die angenommenen Größenpräferenzen und Wachstumsraten realistisch. Das ist bemerkenswert, wenn man bedenkt, dass wir die vereinfachende Annahme gemacht haben, die Abnahme in den Muschelanzahlen würde allein durch Garnelenfraß verursacht. Nimmt man dagegen an, dass die Verluste bei den Muscheln rein zufällig und größenunabhängig sind, dann passt die nur mit Muschelwachstum simulierte Größenverteilung nie auf die tatsächlich beobachtete.

In der Simulationsstudie wurden die Wachstumsraten indirekt geschätzt. Es ist plausibel, dass die Muschelsterblichkeit zu einem erheblichen Teil durch Garnelen verursacht wurde. In **Kapitel 3** berichten wir von einem aufwändigen Freilandexperiment, in dem wir individuelles Wachstum von Muscheln und Größenabhängigkeit der Verluste tatsächlich gemessen haben. Mit dem fluoreszierenden Farbstoff Calcein wurden die jungen Muscheln im Freiland im Wattboden gefärbt. Zehn Tage später wurden Proben genommen und unter einem speziellen Mikroskop mit UV-Lampe wurde gemessen, wie viel neues Schalenmaterial seit der Aufnahme des Farbstoffs dazugekommen ist. So wurde zum ersten Mal individuelles Wachstum von Baltischen Plattmuscheln und Herzmuscheln (*Cerastoderma edule*) in dieser fragilen Lebensphase bestimmt, anstatt es aus der Änderung der Durchschnittsgröße über die Zeit zu berechnen. Dabei wurde festgestellt, dass es eine starke Streuung zwischen einzelnen Tieren gibt. Um zu untersuchen, ob die Muscheln abhängig von ihrer Größe gefressen werden, wurde das Färben mit einem Räuberausschlussexperiment kombiniert. Ein Teil der Muscheln wurde mit kleinen Käfigen, die mit einer Gaze von 1 mm Maschenweite bespannt waren, vor Garnelen und anderen bodenlebenden Räubern geschützt. Mit Hilfe der Einfärbung konnten wir erkennen, welche Muscheln schon von Anfang des Experiments an da waren und welche erst später dazugekommen waren. Wir konnten außerdem kontrollieren, ob der Schutz durch den Käfig möglicherweise das Wachstum beeinflusst. Die Studie wurde in zwei Gebieten durchgeführt: bei Texel ganz im Westen im niederländischen Wattenmeer und bei Sylt im nördlichsten deutschen Wattenmeer. In beiden Gebieten überlebten in den Proben vom ungeschützten Wattboden in der ersten von zwei Runden des Experiments weniger Muscheln vom unteren Ende des Größenspektrums.

In **Kapitel 4** haben wir die Ankunftszeiten von Muscheln und Krebstieren und die Größenverhältnisse von Räubern und Beute zwischen den zwei obengenannten Untersuchungsgebieten verglichen. Die Muscheln siedelten sich in dem Jahr des Freilandexperiments etwa gleichzeitig bei Sylt und Texel an, während die jungen Nordseegarnelen bei Sylt erst später ankamen. Da die Muscheln bei Sylt langsamer wuchsen und gleichzeitig die Garnelen im Durchschnitt kleiner waren als bei Texel, waren die Größenverhältnisse von Räuber und Beute bei den zwei Inseln sehr ähnlich. In beiden Gebieten konnte etwa der gleiche Anteil aller Räuber-Beute Begegnungen für die Muscheln fatal sein. Ein Vergleich von Rob Dekkers Daten von texxel mit Daten, die in übereinstimmenden Jahren von Matthias Strasser bei Sylt erhoben wurden, zeigt, dass die Muscheln sich meist zur gleichen Zeit in den zwei entfernten Gebieten ansiedeln. Nur der kälteste Winter hatte eine Verzögerung bei Sylt zur Folge. Innerhalb der Zeitserie von Texel unterschied sich zwischen Jahren die Ankunft der Krebstiere stärker als die der Muscheln. Daraus resultierten sehr unterschiedliche Größenverhältnisse. Manchmal konnten die Muscheln schnell der Gefahr entwachsen, gefressen zu werden, machmal blieben sie im riskanten Größenbereich. Ein Wachstumsvorsprung der Muscheln führte nicht immer zu günstigen relativen Größen. Günstige Größenverhältnisse schienen eine Voraussetzung, aber keine Garantie für eine gute Rekrutierung zu sein.

In **Kapitel 5** haben wir in Aquarienexperimenten die Fressraten von Nordseegarnelen auf Baltische Plattmuscheln untersucht. Wir wollten wissen, welchen Einfluss die Größe der Muscheln darauf hat, wie lange es dauert, sie zu finden und zu handhaben. Außer der Muschelgröße haben wir auch noch die angebotene Dichte variiert, denn bei niedriger Dichte hat das Suchen den größten Einfluss auf die Fressrate. Bei hoher Beutedichte wirkt dann der Vorgang des Fressens selbst limitierend auf die Anzahl der innerhalb einer bestimmten Zeit konsumierten Beutetiere. Die Garnelen waren selbst bei den niedrigsten Dichten motiviert und effektiv darin, ihre Beute zu finden. Größere Muscheln waren schwieriger zu finden, weil sie sich tiefer eingraben können. Auch das Fressen der Muscheln dauerte länger, je größer sie waren. Durch diese beiden Vorteile war das Risiko, gefressen zu werden für die größten Muscheln etwa in Drittel geringer als für die kleinsten Muscheln. Das ist beachtlich, denn die „großen" Muscheln waren mit 0,85 mm Länge noch nicht einmal einen viertel Millimeter länger als die kleinsten Tiere in diesem Experiment. Der Konsum der Garnelen war insgesamt erschreckend hoch. Wenn sie diesen auch in der Natur hätten, könnten sie mühelos die gesamte neue Jahrklasse auslöschen.

In **Kapitel 6** haben wir Dichteabhängigkeit von Jungmuschelsterblichkeit untersucht. Wie einleitend beschrieben, hat die Anzahl der fortpflan-

zungsfähigen Adulttiere wenig Einfluss auf den Rekrutierungserfolg. Mehr Adulttiere produzieren jedoch erstmal mehr Larven. Das müsste bedeuten, dass die prozentuale Sterblichkeit bei hohen Dichten an Nachkommen höher ist als bei niedrigen. Zeitpunkt und Ursache der Dichteabhängigkeit sind bisher nicht bekannt. Daten von Matthias Strasser auf Sylt eigneten sich dazu, sie hinsichtlich Dichteabhängigkeit zu untersuchen. Dazu haben wir eine spezielle statistische Analyse angewandt, denn Messvariation und natürliche Variation führen bei dieser Art von Fragestellung sonst typischerweise leicht zu verfälschten Ergebnissen. Wir haben in drei von acht Fällen dichteabhängige Mortalität von jungen Baltischen Plattmuscheln gefunden, aber in keinem von sechs Fällen für Herzmuscheln. Das entspricht der Beobachtung, dass die Herzmuschelpopulation stärker von Jahr zu Jahr schwankt. Wir hatten gehofft, ein Muster zu entdecken, wann Dichteabhängigkeit auftritt und daraus Rückschlüsse auf die Ursachen ziehen zu können. Die drei Perioden, in denen die Muschelabnahme dichteabhängig war, hatten aber nichts Offensichtliches gemeinsam, so dass wir keine Aussage darüber machen können, ob zum Beispiel Nahrungskonkurrenz oder Fressverhalten der Feinde die Ursache waren. Fraßdruck scheint eher noch Variation hinzuzufügen. Zufällige Variationen beispielsweise in Nahrungsverfügbarkeit oder Umwelteinflüssen spielten im untersuchten Zeitraum und Gebiet sicher ebenfalls eine große Rolle.

Jede der verschiedenen gewählten Herangehensweisen – reine Freilandbeobachtungen und ihre mathematische Analyse, Freilandexperimente und Laborexperimente – hat ihre eigenen Stärken und Einschränkungen. Zusammen ergibt sich das Bild, dass größenabhängige Verluste von Jungmuscheln die Regel sind und dass die Sterblichkeit durch Fressfeinde beträchtliche Ausmaße annehmen kann. Meist sind vor allem die kleinsten Individuen betroffen. Besonders beeindruckend ist, wie kleine Änderungen bereits einen starken Effekt haben können. Der Zeitpunkt der jährlichen Fortpflanzung von Baltischen Plattmuscheln ist entlang der europäischen Küste überall sehr ähnlich; er ist genau auf die Umweltbedingungen abgestimmt. Die Muscheln haben kaum eine Chance, sich an ein früheres Auftreten der Krebstiere wegen wärmerer Winter anzupassen, weil dafür die Wachstumsbedingungen nicht ausreichen.

In dieser Arbeit habe ich mich auf die Größenabhängigkeit der Räuber-Beute Beziehung konzentriert. Um unser Verständnis vom Einfluss von Krebstieren auf Jungmuscheln zu erweitern, müssten die Fressraten, die in der Natur realisiert werden, noch weiter erforscht werden. Die Nahrungswahl in Anwesenheit von alternativen Beutearten wird dabei vermutlich eine große Rolle spielen. Außerdem besteht noch Forschungsbedarf in Bezug auf die Dichteabhängigkeit der Sterblichkeit in der frühen Lebensphase der Muscheln. In unserer Analyse

von Freilandbeobachtungen gab es keine ausreichenden Indizien für eine zugrundeliegende Ursache. Mögliche Prozesse könnten aber experimentell untersucht werden. Eine höhere Sterblichkeit bei hohen Dichten bedeutet nicht automatisch, dass sich die Population bei niedrigen Dichten erholen kann. Die Population der Baltischen Plattmuschel ist im westlichen niederländischen Wattenmeer in den letzten Jahren im Gegenteil so stark ausgedünnt, dass ihr Fortpflanzungserfolg sogar in Gefahr ist.

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Henrike

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Author addresses

Rob Dekker, Department of Marine Ecology, Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands

Ine Dorresteijn, Leuphana Universtität Lüneburg, Institut für Ökologie, Scharnhorststr. 1, C11.018, 21335 Lüneburg, Germany

Matthias Strasser, Alfred Wegener Institute, Wadden Sea Station Sylt, Hafenstraße 43, 25992 List/Sylt, Germany

Jaap van der Meer, Department of Marine Ecology, Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands and Faculty of Earth and Life Sciences, Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1085, 1081 HV Amsterdam, The Netherlands