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

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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.

1. Introduction

Populations of broadcast spawning bivalves in the Wadden Sea fluctuate considerably 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 mortality.

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 particular 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 processes 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 winters, 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.

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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.

2. Materials and methods

2.1. Experimental design

To investigate the functional response of *C. crangon* on juvenile *M. 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 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.

2.2. 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 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	Medium	Large
		616 ± 53 µm long	728 ± 52 µm long	853 ± 67 µm long
		350–430 µm sieve	430–500 µm sieve	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)
1000	31	8 (1, 1, 1, 1, 2, 2)	7 (1, 1, 1, 1, 1, 2)	8 (1, 1, 1, 1, 2, 2)
1778	56	6 (1, 1, 0, 2, 2, 0)	7 (1, 1, 1, 2, 2, 0)	8 (1, 1, 1, 2, 1, 2)
3162	99	4 (1, 1, 0, 1, 1, 0)	4 (1, 0, 1, 1, 1, 0)	5 (1, 0, 1, 0, 1, 2)
5623	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)

2.3. 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 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.

2.4. 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