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Predation by native brown shrimp on invasive Pacific oyster spat

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ABSTRACT

In the last decades, the invasive Pacific oyster (*Crassostrea gigas*) increased dramatically in the Wadden Sea. One of the driving mechanisms for the success of the Pacific oyster could be a relatively low predation pressure by epibenthic predators and shore birds on oyster spat. Nevertheless, observations and experiments on predation rates on early life-stages of the Pacific oyster are rare. Therefore, we examined predation rates of brown shrimps on Pacific oyster spat in a number of laboratory experiments. Our results demonstrate that spat of Pacific oysters are most susceptible to predation by brown shrimps (*Crangon crangon*) in the first days after settlement, when attachment to the substrate (unglazed tiles in our study) is still absent or weak. At this stage the shell length of oyster spat is around ~300 μm, and around 50% of the individuals in the experiment were consumed in the two hour trials. Predation rates decreased rapidly as the spat grew larger and reached zero within 10 days after settlement of the spat (shell length > 700 μm). Additional experiments revealed that the attachment of oysters is probably limiting predation by brown shrimps rather than the size of the spat. This indicates that Pacific oyster spat may limit predation loss faster compared to native bivalves, which commonly depend on size to reduce predation rates. Overall, our results suggest that the invasive success of Pacific oysters may in part be explained by relatively low predation rates throughout their life stages.

1. Introduction

Pacific oysters (*Crassostrea gigas*) were introduced in the Wadden Sea by accident, with the expectation that they would not be able to recruit due to low winter temperatures (Troost, 2010). Contrary to initial expectations, Pacific oysters did expand in both the Dutch and German Wadden Sea (Diederich, 2005; Troost, 2010). Pacific oysters are suspension feeding bivalves that live attached to hard substrates such as mussel and oyster beds, shell fragments or stones (Diederich, 2005; Nehls et al., 2006). According to previous studies the increased abundances of Pacific oysters may be related to, among other factors, a relative large production of larvae and low predation pressure (Diederich, 2005; Troost, 2010).

Experiments and observations with blue mussels showed that predation pressure on blue mussels is size dependent, as larger sized mussels are mainly predated by shore birds while smaller mussels are mostly eaten by epibenthic predators such as brown shrimps, shore crabs and starfish (Andresen and van der Meer, 2010; Reise, 1985). Bivalve spat are heavily predated by brown shrimps (*Crangon crangon*) which might be a major limiting factor for the survival of bivalve spat (Andresen and van der Meer, 2010; Pihl and Rosenberg, 1984; van der Veer et al., 1998). Contrary to predation on native bivalves, predation by waterbirds and shore crabs on adult Pacific oysters is low (Anderson and O'Connell, 1999; Diederich, 2005; Scheiffarth et al., 2007). However, there are no studies on the survival of newly settled Pacific oyster spat in the presence of predators foraging during high tide.

In this study, we examined predation of brown shrimp on different size classes of Pacific oyster spat by following predation rates from the first days until one month after settlement. Pacific oysters release their gametes into the water in July and August after which their larvae have a pelagic phase for about three weeks before they settle on hard substrate (Troost, 2010). After settlement, oysters 'glue' themselves to hard substrates with a calcium-carbonate layer (Arakawa, 1990; Gossling, 2003), which is much stronger than for example the byssal thread attachment of native blue mussels (Wiegemann, 2005). Therefore, we hypothesized that the predation rate of brown shrimp on Pacific oyster spat is high during early settlement stages and decreases rapidly after settlement when the spat attach to the hard substrate and increase in size. To test this hypothesis we set up a laboratory experiment where oyster larvae were allowed to settle on hard substrate (unglazed tiles), after which we measured predation rates over time in two hour trials. Afterwards, we performed two additional experiments to test the influence of attachment of Pacific oysters and trial time on predation rates by shrimps. We hypothesized that attachment to the substrate limits predation rather than the size of the oysters. This hypothesis was studied by analyzing the ingestion rate of dislodged and attached oysters. In addition, we performed additional experiments to check whether the two hour trials were limiting for the ingestion of larger-sized oyster spat.

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2. Materials and methods

2.1. Laboratory conditions and test organisms

Maintenance of organisms and experiments was carried out in artificial seawater (ASW) that was made by mixing demineralized water with synthetic sea salt (Instant Ocean, Spectrum Brands© UK) in climate-controlled rooms (17.5 ± 0.5 °C) with a 14:10-hour day–night light regime. Salinity in the cultures and the experiments was ~29.5 ± 0.5‰, which is within the natural range of Pacific oysters and shrimps in the Wadden Sea.

2.1.1. C. crangon

Brown shrimps were obtained from the tidal flats near the Dutch barrier island Schiermonnikoog (53° 28′ 16.97″ N, 6° 13′ 37.76″ E) in October 2011. They were caught using a push net with an opening of 50 × 45 cm (width × height) and a mesh size of 4 mm. Shrimps were transported to the laboratory in containers with ambient seawater and placed in plastic culturing tanks (80 L) with a flow through system (~2 L/h; replacement rate within the tanks: ~0.5 day^{-1}) within 4 h after collection. The flow through system was connected with a biological filter containing a protein skimmer and nitrifying and denitrifying bacteria to convert potentially harmful ammonia into nitrate and gaseous nitrogen. To maintain water quality, one-third of the water was replaced weekly. Every third day, shrimps were fed with blue mussel flesh (*Mytilus edulis*) that was obtained from the same area as the brown shrimps and frozen upon arrival in the laboratory. We observed no significantly elevated mortality rates in brown shrimps in the first days and overall mortality in the rearing facilities was low (<5% day^{-1}).

2.1.2. C. gigas

Pacific oyster larvae were purchased from a commercial hatchery (Seasalter Shellfish Whitstable Ltd., UK). Upon arrival in the laboratory, the larvae were moved into experimental aquaria (60 × 35 × 30 cm) with unglazed tiles (7 × 3 cm) covering the bottom. Two different batches with 3-week old larvae were used in the experiments: the first arrived on October 29, 2011 and the second on November 10, 2011. The larvae were in their late pediveliger stage and sank to the bottom immediately after release into the aquaria.

The rearing tanks with oyster spat were not attached to a flow through system to prevent larvae from being lost in the circulation system. Therefore, 50% of the water in these tanks was replaced on a weekly basis. Ammonia was checked regularly and never exceeded 0.25 μg L^{-1} (JBL© aquarium test kit, Neuhofen, Germany). The oysters were fed every second to third day with a medium consisting of 10 L of ASW and 2 mL of algae mixture (*Isochrysis* spp., *Pavlova* spp., *Tetraselmis* spp. and *Thalassiosira* spp.; shellfish diet from Instant Algae©) that was added to the rearing tank at a rate of 1 mL min^{-1}. This amount of food exceeded the requirements of the oysters at this stage (http://www.reedmariculture.com). We regularly took samples from the oyster spat by scraping them from the tiles and fixing them in Lugol. From these samples, shell length was measured from undamaged individuals using a stereo microscope fitted with an eyepiece graticule.

2.2. Experimental set-up

After receiving the oyster larvae, experiments were carried out over the course of one month, enabling us to test the feeding rate of brown shrimp on different oyster spat size. For each experiment, we used shrimps with a size range of 18 to 42 mm (Table 1). Prior to the experiments, shrimps were measured from the tip of the rostrum to the tip of the telson to the nearest mm. Four days prior to each experiment, individual shrimps were put into a separate aquarium (10 × 40 × 20 cm), one shrimp in each aquarium, and fed with blue mussel flesh. After 6 h, all remaining blue mussel flesh was removed, and the shrimps were starved for four days to standardize starvation levels. At the start of the experiments, oysters were counted and six tiles with a total of 100 oysters were carefully placed in each aquarium with a single brown shrimp. Shrimps were left to feed on the oysters for 2 h, after which they were removed and the remaining oysters on the tiles were counted. We also checked the aquaria for possible dislodged oysters, which was only the case for oysters smaller than 400 μm. All experiments were carried out during night time because shrimps are nocturnal predators (Pihl and Rosenberg, 1984). Procedural controls (n = 3) were conducted for each experiment to test for possible handling effects. After each experiment, all shrimps were fed again with blue mussel flesh and their survival was determined in the following four days. This procedure was repeated 6 times with different size classes of oysters. Shrimps were only used once in an experiment. Shrimps were included in our data analyses if they met the following conditions: they 1) survived the entire experimental procedure, 2) fed prior to and after the experiments and 3) did not molt 4 days prior to the experiment, during the experiment and 4 days after the experiments. This approach resulted in a varying number of replicates of n = 6–14 for each size class of oyster.

To test the importance of attachment strength on ingestion rates, we carried out an additional experiment with larger-sized oysters (1102 ± 78 μm shell length and originated from the batch received on November 10th, 2011). We scraped oysters from the tiles and used undamaged individuals in an experiment with treatments consisting of 30 oysters fixed (n = 3) to a tile and 30 dislodged oysters (n = 3). Each treatment was again conducted in aquaria with only one shrimp predator per unit. After 2 h, we counted the remaining oysters in both treatments.

An additional experiment was carried out to test whether the trial period in our experiments (2 h) was limiting the observed maximum size of oysters that was eaten by the shrimps. To this end, we added 100 oysters of a size that was just beyond the maximum observed edible size in the previous experiments (1102 ± 78 μm shell length from the November-10-batch) to 3 aquaria with a single shrimp. After 2 h, we counted the remaining oysters and placed the tiles back in the same aquaria with the same shrimp. We left the tiles in the aquaria for another 22 h after which we recounted the remaining oysters.

Table 1
Data on the oysters and shrimps used in the experiments. Oyster data shows the average shell length (in μm), age (days after settlement), and batch of oysters (date on which the batch was received in the laboratory). Batch 1 was received on October 29th and batch 2 was received on November 10th, 2011. Data on the shrimps show the mean, minimum and maximum length of the shrimps in the experiments in mm. The replicates varied because the only data we included in our analysis were from experiments in which shrimps fed, survived and did not molt at least four days before and after the experiments. (See text for details).

Oyster data			Shrimp data			Number of replicates in experiment
Length (mean ± SEM in μm)	Age (days after settlement)	Batch	Length (mean ± SEM in mm)	Min (mm)	Max (mm)	–
317 ± 10	3	2	32 ± 0.3	19	42	14
441 ± 26	8	1	31 ± 0.3	18	42	6
676 ± 18	13	2	25 ± 0.1	20.5	32.5	8
728 ± 38	16	1	28 ± 0.2	18	43	8
737 ± 31	19	2	30 ± 0.2	22.5	42	10
1102 ± 78	26	2	30 ± 0.3	23	41	6