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Effects of an increasing filter feeder stock on larval abundance in the Oosterschelde estuary (SW Netherlands)

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ABSTRACT

Predation by adult bivalves on bivalve larvae has been suggested to reduce larval abundance in areas with high bivalve filter-feeder biomass. Although the occurrence of larviphagy is well-studied in the laboratory, its effects in the field have scarcely been studied. We studied larviphagy at different spatial scales in the Oosterschelde estuary. On the scale of individuals, we confirmed that larviphagy occurs in *Crassostrea gigas* and *Mytilus edulis* in the Oosterschelde estuary, by examining stomach contents of adult bivalves. On a local scale, we studied effects of larviphagy by a Pacific oyster (*C. gigas*) bed on presence of larvae in the overlying water column by sampling larvae with fixed plankton nets. Abundance of blue mussel (*M. edulis*) larvae was significantly reduced by the oyster. Abundance of *C. gigas* larvae did not seem to be reduced by the oyster bed, but spawning by the adult oysters during the sampling period may have affected the results. On estuary-scale, the effect of larviphagy on larval abundance of *C. gigas* and *M. edulis* was studied using existing monitoring data over 6 years for *M. edulis* and 13 years for *C. gigas*. Numbers of *M. edulis* larvae showed no significant trend over the 6 years studied. Abundance of *C. gigas* larvae declined with an increasing filter feeder stock (that was mainly caused by an increase in *C. gigas* stock). This decline may be due to direct effects of larviphagy or indirect effects such as lowered food levels, and was not compensated by an increased larval production. All results combined, complemented with a theoretical estimate of the effect of larviphagy on estuary-scale, strongly suggest that larviphagy is major source of mortality for bivalve larvae in the Oosterschelde estuary.

1. Introduction

Predation by adult bivalves on bivalve larvae seems a wide-spread phenomenon. It is suggested to reduce numbers of bivalve larvae in waters with a high adult bivalve filter feeder biomass (Lehane and Davenport, 2004) and it has been demonstrated to reduce settlement success of conspecific larvae in *Cerastoderma edule* (L.) (André and Rosenberg, 1991). Timko (1979) defined the term 'larviphagy' as the feeding by adults on their own larvae. Some species have been shown to predate their own larvae: *Mytilus edulis* L. (Lehane and Davenport, 2004), *C. edule* (Kristensen, 1957; André et al., 1993), *Crassostrea virginica* (Gmelin) (Tamburri and Zimmer-Faust, 1996) and *Dreissena polymorpha* (Pallas) (MacIsaac et al., 1991). Lehane and Davenport (2004) already suggested that bivalves routinely filter larvae from the surrounding water. Because bivalve filter feeders filter all particles above a certain threshold size (Møhlenberg and Riisgård, 1978), they do not seem able to select certain particles above this threshold size. Selection only seems to occur afterwards by the gills, labial palps, stomach and guts (Shumway et al., 1985; Ward et al., 1998; Brillant and MacDonald, 2002). Hence, we broadened the definition of larviphagy following Troost et al. (2008a) to: filtration and ingestion of bivalve larvae by adult bivalves in general. Overall, larviphagy may pose a significant threat to larvae of all bivalve filter feeders as well as other meroplankton with weak swimming and escape abilities (see Singarajah, 1969, 1975; Kiørboe and Visser, 1999; Troost et al., 2008b).

Larviphagy has been demonstrated in laboratory experiments for *M. edulis* (Lehane and Davenport, 2004; Troost et al., 2008a), *C. edule* (Kristensen, 1957; André et al., 1993; Troost et al., 2008a), *C. virginica* (Tamburri and Zimmer-Faust, 1996), *Crassostrea gigas* (Thunberg) (Tamburri et al., 2007; Troost et al., 2008a), and *D. polymorpha* (MacIsaac et al., 1991). Studying larviphagy in the laboratory generally focused on clearance experiments in confined volumes of water (MacIsaac et al., 1991; Troost et al., 2008a), analysis of stomach contents and excreta (MacIsaac et al., 1991; Tamburri et al., 1996, 2007; Lehane and Davenport, 2004; Troost et al., 2008a) and observations on larvae being sucked in by individual bivalves (André et al., 1993; Tamburri et al., 2007). In field experiments larviphagy has been shown to occur in *M. edulis* (Thorson, 1946; Lehane and Davenport, 2002; Lehane and Davenport, 2004; Maar et al., 2007) and *Mytilus galloprovincialis* Lamarck (Jasprica et al., 1997). In these

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experiments, stomach contents and excreta were analyzed (Jasprica et al., 1997; Lehane and Davenport, 2002, 2004). Although previous laboratory and field studies convincingly demonstrated the occurrence of larviphagy in individual bivalves, effects of larviphagy on a larger scale in the field are still scarcely studied (André and Rosenberg, 1991; Maar et al., 2007).

In the Oosterschelde estuary (SW Netherlands), larval mortality due to larviphagy is expected to have increased over the last three decades due to rapid expansion of the introduced Pacific oyster *C. gigas*. After being first introduced in 1964 (Drinkwaard, 1999) these oysters started to expand rapidly throughout Dutch estuaries in 1975. They developed large and dense oyster reefs in the intertidal and subtidal (Drinkwaard, 1999; Wolff and Reise, 2002; Dankers et al., 2006), and are now potentially in competition with native bivalve filter feeders. In the Oosterschelde estuary the share of the soft-bottom intertidal area (118 km^2) occupied by oyster beds is estimated to have increased from 0.25 km^2 in 1980 to 8.09 km^2 in 2003 and a similar cover and absolute increase was estimated for subtidal soft bottoms (Geurts van Kessel et al., 2003; Kater, 2003; Kater and Baars, 2004; unpublished data Wageningen IMARES). Oyster cover on hard substrates (mainly consisting of 160 km of dikes and sea walls, area estimated at 2–4% of the total Oosterschelde area, Leewis et al., 1994) generally increased from 0–10% in 1985 to 50–60% in 2002, and even to 90% on some locations (AquaSense, 2003). Within this period, stocks of the native blue mussel *M. edulis* and common cockle *C. edule* showed a slight decrease (Geurts van Kessel et al., 2003; Dankers et al., 2006). The total stock of *C. gigas*, *M. edulis* and *C. edule* combined was estimated to have increased from 150 million kg fresh weight (including shells) in the early 1990s to 255 million kg around 2000. As a consequence, the filtration pressure in the Oosterschelde estuary was roughly estimated to have increased from 289 million m^3 water day^{-1} in 1990 to 398 million m^3 day^{-1} in 2000 (Geurts van Kessel et al., 2003; Kater, 2003). This may have resulted in a considerable increase in larviphagy and hence a reduction in larval numbers on estuary scale. Moreover, the increased filtration pressure may not only have affected bivalve larval numbers, it may have affected populations of benthic species with pelagic larval stages in general.

The aim of this study was to find field-evidence for effects of larviphagy on numbers of bivalve larvae. We considered the potential impact of larviphagy on three scales. First, we tested the hypothesis that individual bivalve filter feeders in the Oosterschelde estuary ingest bivalve larvae by analyzing stomach contents of bivalves from the field. Additionally, we sought evidence for larviphagy in *C. gigas*, *M. edulis* and *C. edule* in literature. Second, we studied local effects of a dense bed of filter-feeding bivalves (*C. gigas*) on bivalve larval abundance in the overlying water column. We tested the null-hypothesis that larval abundance was unaffected by the presence of adult filter-feeding bivalves. We expected to find reduced numbers of bivalve larvae above the oyster bed, in comparison to a nearby bare reference site. Third, we related existing time-series of larval abundances of *C. gigas* and *M. edulis* in the Oosterschelde estuary to the increase in total filter feeder stock (≈filtration pressure). Our null-hypothesis was that larval abundance remained the same throughout the years and showed no relationship with an increased filter-feeder stock. Since the increase in total bivalve filter feeder stock was mainly due to an increase in *C. gigas* stock, our expectations are different for larvae of *C. gigas* and *M. edulis.* Numbers of *M. edulis* larvae were expected to decline with an increase in total bivalve filter feeder stock. Production of *C. gigas* larvae and the total volume of water filtered by the oyster population were both expected to increase proportionally to the increase in oyster biomass. Since part of the filtered water will be re-filtered inside oyster beds (see Jonsson et al., 2005), and since filtration is a dilution process (Riisgård, 2001; Riisgård et al., 2004), a potential increase in larval production of *C. gigas* was expected to be higher than, or at least compensate for, a potential decrease in larval numbers due to larviphagy. Our expectations about larval numbers in the estuary are based on the assumption that larvae are distributed homogeneously over the water mass. If, however, in the Oosterschelde estuary early stage larvae occupy higher water layers, as described for *M. edulis* by Bayne (1964), this behaviour may offer the larvae a refuge from predation by benthic filter-feeders. We therefore used existing monitoring data to test the null-hypothesis that young *M. edulis* larvae are distributed homogeneously over the water column. We expected to find a homogeneous distribution since the Oosterschelde estuary is vertically well mixed (see Hendriks et al., 2006).

2. Methods

2.1. Study area

The Oosterschelde estuary (SW Netherlands; Fig. 1) is a macrotidal system where tidal currents force an extensive vertical mixing. The estuary has a mean tidal volume of 880 million m^3, a total volume at half tide of 2750 million m^3, and a surface area of 351 km^2 of which 118 km^2 tidal flats. Salinity is high, generally >30 psu, throughout the estuary. Freshwater discharge into the estuary is very limited (1 million m^3 per tide) and does not cause salinity stratification. Water residence time is 10–150 days. The mean tidal amplitude ranges from 2.47 m near the mouth to 2.98 m in the most northern part (near Krammer sluices) and 3.39 m at the southeast end. The maximum current velocity is about 1.0 m s^{-1}. The water temperature varies over the season from 0–5 to 18–22 °C (Nienhuis and Smaal, 1994). The average annual chlorophyll-a concentration is about 5 μg l^{-1}, reaching maximum values of about 40–50 μg l^{-1} in May–June (Wetsteyn and Kromkamp, 1994).

The Oosterschelde estuary is extensively used for culture of *C. gigas* and *M. edulis* on subtidal bottom culture plots (Dijkema, 1997; Smaal and Lucas, 2000). The total *M. edulis* stock varies roughly between 20 and 80 million kg fresh weight (Kater and Kesteloo, 2003) and is for >95% controlled through import and removal by mussel farmers. Only 5% of the total stock originates from the Oosterschelde estuary and is mainly found on intertidal hard substrates. The rest is imported, mainly from the Dutch Wadden Sea (Van Stralen and Dijkema, 1994). The majority of the total *C. gigas* stock in the Oosterschelde consists of feral oysters (189 million kg fresh weight in 2002; Kater, 2003). The annual total cultured *C. gigas* stock is about 0.7 million kg fresh tissue weight (7 million kg total fresh weight) (Perdon and Smaal, 2000; Smaal and Lucas, 2000). Spat of *C. gigas* is collected within the Oosterschelde estuary by spreading and retrieving spat collectors (usually broken mussel shells), and seeded on subtidal bottom plots in the eastern compartment where it is left to grow to consumption size (Dijkema, 1997). Another bivalve occurring in relatively high numbers is the edible cockle *C. edule*. This species is fished for consumption but not cultured (Dijkema, 1997). The stock size fluctuates between roughly 2 and 10 million kg fresh tissue weight (about 15–70 million kg fresh weight) (Kesteloo et al., 2007).

2.2. Larviphagy in individual bivalves

Since many authors already described the occurrence of larviphagy in bivalves, and some authors already demonstrated it specifically for the bivalve species that are considered in this paper (discussed in section 4.1.), we conducted only a simple experiment in 2003 to check whether larviphagy also occurs among bivalves in the Oosterschelde estuary. Oysters and mussels, 32 per species, were suspended at Yerseke in the Oosterschelde estuary in cages (mesh size 15 mm) at a tidal height of about 0.5 m above the mean low water level. The average shell length was 110 mm for oysters and 50 mm for mussels. On six dates in May and June, the first date one week after suspending the animals, we took water surface samples of 200 l with a bucket and removed 4–6 individuals per species half an hour before high tide. The stomach contents were immediately removed and analyzed for bivalve larvae as described by Troost et al. (2008a). From the water samples, filtered over a mesh of 60 μm, bivalve larval concentrations