Journal of Sea Research 73 (2012) 126–136

Contents lists available at SciVerse ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Competition and niche segregation following the arrival of *Hemigrapsus takanoi* in the formerly *Carcinus maenas* dominated Dutch delta

A.M. van den Brink [a,*], S. Wijnhoven [b], C.L. McLay [c]

[a] IMARES Wageningen UR, Wageningen Institute for Marine Resources and Ecosystem Studies, P.O. Box 77, 4400 AB Yerseke, The Netherlands
[b] Monitor Taskforce, Royal Netherlands Institute for Sea Research (NIOZ—Yerseke), Korringaweg 7, P.O. Box 140, 4401 NT, Yerseke, The Netherlands
[c] School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

ARTICLE INFO

Article history:
Received 11 April 2012
Received in revised form 19 June 2012
Accepted 13 July 2012
Available online 25 July 2012

Keywords:
Carcinus maenas
Hemigrapsus
Crabs
Niche Segregation
Competition
Delta

ABSTRACT

In a combined study including a 20 year monitoring programme of the benthic communities of four Dutch delta waters and a snapshot survey conducted in the Oosterschelde tidal bay in 2011, the populations of the native portunid European shore crab *Carcinus maenas* and the introduced varunid crabs *Hemigrapsus takanoi* and *Hemigrapsus sanguineus* were investigated. Whereas *C. maenas* was the most common shore crab in these waters, its numbers have declined on the soft sediment substrates during the last 20 years. As the two exotic crab species were first recorded in the Dutch delta in 1999, they could not have initiated the decline of the native *C. maenas*. However, within a few years *H. takanoi* completely dominated the intertidal hard substrate environments; the same environments on which juvenile *C. maenas* depend. On soft sediment substrate the native and exotic shore crab species are presently more or less equally abundant. *H. takanoi* might initially have taken advantage of the fact that *C. maenas* numbers were declining. Additionally *H. takanoi* are thriving in expanding oyster reefs of *Crassostrea gigas* (Pacific oyster) in the Dutch delta waters, which provide new habitat. Nowadays *H. takanoi* appears to be a fierce interference competitor or predator for small *C. maenas* specimens by expelling them from their shelters. These interactions have led to increased mortality of juvenile *C. maenas*. At present the *C. maenas* populations seem to be maintained by crabs that survive and reproduce on available soft sediment habitats where *H. takanoi* densities are low.

1. Introduction

The introduction of nonindigenous marine organisms can alter an environment and the communities of species therein (Carlton and Geller, 1993; Cohen and Carlton, 1998; Jensen et al., 2002). Introduced species may have an impact on native species through predation, associated parasites or diseases, as fouling organisms or as competitors for food or space (Jensen et al., 2002). While direct predation is likely to have the most obvious impact, increased predation risks due to the presence of nonindigenous species can also be important. Competition for space may result in the displacement of a native species to areas with less shelter and protection from predators, and thus indirectly increase the risk of predation (Jensen et al., 2002).

Several studies have shown that spatial heterogeneity of habitats with rocks, shells and vegetation provide protective refuges from aquatic predators for many species of decapod crustaceans (Fernandez et al., 1993; Heck and Thoman, 1981; Moksnes et al., 1998; Navarrete and Castilla, 1990; Pillay and Ono, 1978). When shelter opportunities are not sufficient, the population growth for these decapods can be limited by predation (Wahle and Steneck, 1991) or regulated by cannibalism (Moksnes, 2004). These spatial refuges are of particular importance in the intertidal zone where shorebirds and other terrestrial predators pose an added predation pressure along with environmental stressors such as extreme temperatures (Abele et al., 1986; Taylor, 1981), desiccation (Grant and McDonald, 1979) and strong water currents or wave action (O'Neill and Cobb, 1979).

Shelter is of such importance in the intertidal zone that its increase can greatly influence the resident crustacean communities. An experiment in Japan where the number of rocks was doubled in a given intertidal area resulted in a four-fold increase in the density of the shore crab *Hemigrapsus sanguineus* (Lohrer et al., 2000). The number of juvenile Dungeness crabs, *Cancer magister*, occupying the intertidal area was successfully tripled at some locations due to the addition of extra oyster shells to areas of sand and mud in Grays Harbour, Washington State, the United States (Dumbauld et al., 1993; Wainwright et al., 1992). However, the introduction of *Hemigrapsus oregonensis* to that area and the resulting competition for space caused the displacement of many *C. magister* to more exposed habitats, and consequently their numbers greatly decreased (Jensen et al., 2002).

Introduced ecosystem engineers can provide novel spatial heterogeneity, which may facilitate the establishment and success of other introduced species (Floerl et al., 2004; Wallentinus and Nyberg, 2007). The invasive Pacific oyster, *Crassostrea gigas* has been shown to increase

* Corresponding author. Tel.: +31 317 48 25; fax: +31 317 48 73 59.
E-mail address: anneke.brink@gmail.com (A.M. van den Brink).

1385-1101/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.seares.2012.07.006

spatial heterogeneity and consequently its presence in the form of beds results in higher biodiversity compared to areas where *C. gigas* is absent (Troost, 2010). *C. gigas* is now common throughout NW Europe and has established many oyster beds on the Dutch coast, providing a new habitat for species to occupy (Troost, 2010).

The benthic habitats of Delta waters in the Netherlands are predominantly soft bottom sand/mud flats with sporadic areas of mussel and beds of the introduced oyster *C. gigas*. The waters are also edged by dykes reinforced with rocks and other hard substrata (Bouma et al., 2005). Prior to the 1990s the native European shore crab or green crab, *Carcinus maenas*, was the dominant crab species in the Dutch delta. In the Oosterschelde tidal bay (one of the large Dutch delta waters) it was very abundant on hard substrates (De Kluijver and Leewis, 1994) and also the most abundant crab species on soft substrates (Hostens and Hamerlynck, 1994). In the Westerschelde estuary (also situated in the Dutch delta) only *Liocarcinus holsatus* was more abundant, but no other decapod crabs reached the densities of *C. maenas* (Hostens and Hamerlynck, 1994). In the 1990s two *Hemigrapsus* species; *H. sanguineus* and *Hemigrapsus takanoi* (originally identified as *Hemigrapsus penicillatus* as it was not classified as a separate species until 2005; Asakura and Watanabe, 2005) were introduced into European waters. *H. takanoi* most likely arrived in the Netherlands via oysters transported from France (Faasse et al., 2002; Nijland, 2000; Nijland and Beekman, 2000) while *H. sanguineus* may have arrived as larvae from established French colonies via ballast water resulting in secondary colonization (J.-C. Dauvin, personal communication). The first specimens of *Hemigrapsus* (most likely *H. takanoi*) were observed in the Oosterschelde tidal bay in the year 2000, but probably arrived earlier in 1999. A year later the species was also present in the Westerschelde estuary and within the following few years *H. takanoi* could be found throughout the Dutch delta (Wolff, 2005). *H. sanguineus* was also first observed in the Oosterschelde in 1999 (D'Udekem d'Acoz and Faasse, 2002), but after that this species seems to have spread less abundantly at least in the Dutch delta waters as recordings are restricted to the western shores. On the outer shores; the North Sea coasts, the species is more successful (Dauvin, 2009; D'Udekem d'Acoz, 2006).

The current study investigates the distribution, abundance and population development of *H. takanoi* after its arrival in the Dutch delta waters and the Oosterschelde in particular. By comparing distribution data of surveys conducted on the soft sediment prior to and following the introduction of *H. takanoi*, and using the results of a 'snapshot' survey of the hard substrate, potential impacts on the *C. maenas* populations in the Dutch delta waters are investigated. By way of explanation for the long term changes we focus on competition, replacement and changes in habitat use for the species.

2. Methods

2.1. The delta waters

The region of the Dutch delta waters is located where the rivers Scheldt, Rhine and Meuse reach the North Sea (Fig. 1). The Dutch delta consists of five water bodies, from south to north: the Westerschelde estuary, Lake Veerse Meer, the Oosterschelde tidal bay, Lake Grevelingen and Lake Haringvliet. The Westerschelde estuary is the mouth of the river Scheldt and is still in open connection with the North Sea. The other water bodies used to drain the Rhine, Meuse and also the Scheldt, but have been partially closed off from river inputs and exchange with the North Sea by a coastal engineering project; the 'Delta project', which was initiated in the 1950s (Troost, 2009; Wijnhoven et al., 2008). Since it was dammed off from the Oosterschelde estuary in the east and the North Sea in the west, Lake Veerse Meer used to be a brackish lake with a differing summer and winter water level. Recently (in 2006) the connection with the Oosterschelde has been restored which made the lake saline again (Wijnhoven et al., 2010). The Oosterschelde estuary was largely closed off from river inputs by compartmentalisation dams and locks. A storm surge barrier, which can be closed in times of dangerously high water levels and surges, was built in the mouth of the estuary creating a tidal bay. This has reduced the tidal amplitude and current velocities in the system (Troost, 2009). Lake Grevelingen used to be an estuary, but since it was dammed off from the North Sea and from river inputs, it is now a brackish lake and later gradually a saline lake (Troost, 2009). Although the Haringvliet still discharges water from the rivers Rhine and Meuse, it is now a freshwater lake after it was closed off from the North Sea by a dam and sluices (Wijnhoven et al., 2008), and can therefore be excluded from the current study as the species under investigation are not present there.

All the delta waters have predominantly soft sediment substrate in the form of sand and mud. However, due to the building of dykes, their reinforcement with rocks (Bouma et al., 2005) and the introduction of the pacific oyster, *C. gigas*, in the 1960s (Troost, 2009) rocks, shells and other hard substrata provide substantial areas with shelter refuges in specific areas for otherwise vulnerable species.

2.2. Life histories

2.2.1. H. takanoi

Although there is limited information about the life history of *H. takanoi*, and larval phases have not yet been described (Yamasaki et al., 2011), the similarities between the species and the more commonly documented *H. penicillatus* suggest that their life histories are probably similar. Assuming this; *H. takanoi* females can become ovigerous at about 6–7 mm CW and can lay broods several times per year during the summer months (Pillay and Ono, 1978; Van den Brink et al., 2012). The duration of brood and larval development is highly dependent on water temperature, but the crabs can go through all larval and juvenile instar stages until they reach maturity after several months (J.-C. Dauvin, personal communication). The species predominantly inhabits intertidal areas of mudflats, estuaries and lagoons with sufficient shelter opportunities, typically among rocks and boulders, but can also be found in soft sediment and occasionally in subtidal regions (Asakura and Watanabe, 2005). They have a preference for low hydrodynamic muddy habitats (Dauvin, 2009).

2.2.2. H. sanguineus

The females of *H. sanguineus* can reach maturity at sizes as small as 10.6 mm CW (Dauvin and Dufossé, 2011) and also breed several times a year during the summer months (Epifanio et al., 1998). The larvae hatch and develop in the plankton until they reach the megalopa stage and settle. They then develop through five juvenile instar stages (Epifanio et al., 1998) and reach maturity at about 7.5 months old (Epifanio et al., 1998). *H. sanguineus* inhabits shallow hard-bottom intertidal and sometimes subtidal habitats where they live on artificial structures, on mussel beds and oyster reefs and any habitat with shelter opportunities (McDermott, 1998). They typically can be found in high hydrodynamic habitats with fine and medium coarse sands (Dauvin, 2009).

2.2.3. C. maenas

Female European green crabs, *C. maenas* can reproduce after their pubertal moult at a minimum size of about 34 mm carapace width (CW) (Berrill, 1982). They lay their eggs in spring and after an interval depending on water temperature (Wear, 1974) the larvae hatch into the water column where they develop through four zoeal stages and one megalopa stage before settling as a first instar juvenile crab (Dawirs, 1985). After about seven instars the juveniles mature at about 2–3 years old depending on location and temperature range (Berrill, 1982). The species inhabits coastal waters and intertidal environments, where juveniles can typically be found and adults also inhabit shallow subtidal waters up to 30 m of depth. They occupy a variety of habitats from rocky shore, areas with boulders, macro-algae, mussel