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

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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 *H. sanguineus* were investigated. Whereas *C. maenas* was the most common shore crab in these waters, their 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 exact environments on which juvenile *C. maenas* depends. 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 *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 *Hemigrapsus takanoi* appears to be a fierce interference competitor for small *C. maenas* specimens by expelling them from their shelters. This size-dependent competition has led to increased mortality of juvenile *C. maenas* due to increased predation. 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.

Key words: *Carcinus maenas*; *Hemigrapsus*; crabs; niche segregation; competition

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 when the introduced species do not directly prey on the native ones. 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 (Pillay and Ono 1978; Heck and Thoman 1981; Navarrete and Castilla 1990; Fernandez et al. 1993; Moksnes et al. 1998). When shelter opportunities are not sufficient, the population growth for these decapods can be limited by predation (Wahle and Steneck 1991). 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 (Taylor, 1981; Abele et al. 1986), 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 (Wainwright et al. 1992; Dumbauld et al. 1993). However, the introduction of *H. sanguineus* 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 (Visser 1997).

Introduced ecosystem engineers can provide novel spatial heterogeneity, which may consequently 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 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). *Crassostrea 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 substrate (De Kluijver and Leewis 1994) and also the most abundant crab species on soft substrate (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 *H. takanoi* (originally identified as *H. penicillatus* as it was not classified as a separate species until 2005; Asakura and Watanabe 2005) were introduced into Europe via ballast water or hull fouling. The *Hemigrapsus* species most likely arrived in the Netherlands via oysters transported from France (Nijland, 2000; Nijland and Beekman 2000; Faasse et al. 2002). 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). *Hemigrapsus sanguineus* was also first observed in the Oosterschelde in 1999 (DôUdekem dôAcoz 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 (DôUdekem dôAcoz, 2006; Dauvin, 2009)

The current study investigates the distribution, abundance and population development of *Hemigrapsus takanoi* after 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 ósnapshotô 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.

Methods

The Delta waters

The region of the Dutch delta waters is located where the rivers Scheldt, Rhine and Meuse reach the North Sea (Figure 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 óDelta projectô, which was initiated in the 1950s (Wijnhoven et al. 2008; Troost, 2009). 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 became 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, *Crassostrea 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.

Life histories

Hemigrapsus 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. in press). The duration of brood and larval development are highly dependent on water temperature, but the crabs can go through all larval and juvenile instar stages until they reach maturity after 1-2 years (Fukui 1988). 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).

Hemigrapsus sanguineus

The females of *H. sanguineus* reach maturity at 12-36 mm CW (McDermott 1998) 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 when they are at least a year old (Fukui 1988). *H. sanguineus* inhabits shallow hard-bottom intertidal and sometimes subtidal habitat 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).

Carcinus maenas

Female European green crabs, *Carcinus 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 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 meters of depth. They occupy a variety of habitats from rocky shore, areas with boulders, macro-algae, mussel beds or oyster reefs to sand- or mudflats (Amaral et al. 2009; Almeida et al. 2011).

Soft substrate monitoring

The present study uses the results of a large scale long term monitoring of the macrobenthic communities of the Dutch delta waters executed within the frame of the Dutch Water systems Monitoring Program óMWTLô. Sampling has taken place twice a year, in spring and autumn, according to a standardized methodology from 1990 to 2010 using óReineckô box-corers (from which cores are taken manually) for subtidal areas in the Oosterschelde and the Westerschelde and at depths below -2 meters (relative to the Dutch Ordnance Level; NAP) in Lake Grevelingen and Lake Veerse Meer, óflushing samplersô for the 0-2 meters stratum in the two lakes, and using hand corers in the intertidal areas (Oosterschelde and Westerschelde). The dataset consists of 13600 samples with a sampled surface of 0.020 m^2 for the óflushingô samples and 0.015 m^2 for the box- and hand corer samples, sampled to an approximate depth of 30 cm in the sediment and sieved over a 1 mm mesh to collect the organisms. Some adjustments were made in the number of samples per campaign but samples were always taken equally divided over regions (see distribution of sample sites in Figure 1) and depth strata for each of the water bodies. Lake Grevelingen and Lake Veerse Meer were sampled for the first time in autumn 1990 while the Oosterschelde and the Westerschelde were first sampled in

spring 1990, with data available to autumn 2010. All water bodies were sampled according to a stratified random sampling scheme till 1995 when the random sample sites became fixed sites sampled every year, except for the Westerschelde where samples are still taken randomly every campaign. During the surveys all *Carcinus maenas* and *Hemigrapsus* sp. individuals collected were measured for their carapace width (CW) to the nearest mm. Additionally the sediment type at each sample location was recorded so that it could be determined whether hard elements (i.e. shells, stones) were present. As the monitoring program focuses on soft sediment communities, oyster reefs and commercial mussel plots were not sampled. Due to the relatively small areas sampled, the densities of larger crab specimens might be somewhat underestimated by this methodology.

Observed numbers of crabs were initially calculated into average densities on soft sediment substrates for entire water bodies (i.e. Grevelingen, Oosterschelde, Veerse Meer and Westerschelde). As this study focuses on potential *C. maenas* ï *H. takanoi* interactions, the size frequency distributions of the two species (on basis of total numbers per 5 mm size classes) was compared between water bodies and periods. The entire research period was therefore divided into three, taking the settlement history of *H. takanoi* into account. The years 1990-1998 without *H. takanoi* in the Dutch delta, the years 1999-2004 during which *H. takanoi* was present particularly on hard substrate, but densities were very low or the species was lacking on soft substrate (given that the species was not found during the soft sediment monitoring program), and the years 2005-2010 during which *H. takanoi* was frequently observed on soft sediment, were distinguished. Due to the very low numbers of *C. maenas* (and the absence of *H. takanoi*) during the first two periods in Lake Veerse Meer, which was brackish at that time, the results of those periods were combined. Potential significant differences (at $p<0.05$) in relative abundance of size classes between periods were tested for using t-tests (taking variance into account; i.e. by F-testing). To compare the number and distribution of locations where *C. maenas* was found before and after the arrival of *H. takanoi* in the soft sediment samples, periods of the same length with similar numbers of samples taken were distinguished; i.e. 1997-2003 and 2004-2010.

Hard substrate survey

In May-June 2011 the walls of dykes (foreshore reinforcements) at ten locations in the Oosterschelde were sampled (see Figure 6). While the walls of dykes always contained hard substrata, the substrate types differed between locations, generally with the presence or absence of oyster shells (*Crassostrea gigas*) (Table 1.). At each location two people collected as many crabs of all species as possible by hand over one hour (this generally entailed one person lifting rocks and the other collecting crabs as quickly as possible before they escaped). This provided a ósnapshotô of the crab community at a particular point in time. This method may underestimate small individuals as they were harder to catch, particularly in oyster beds.

All crabs were brought to the laboratory where they were determined to species level and their CW was measured. The size and the species proportion of the total number of crabs found was then compared between locations and combined to produce a generalized representation of the crab communities on the hard substrate in the Oosterschelde.

Results

Abundance over time

In Lake Grevelingen densities of *Carcinus maenas* showed a significant decrease throughout the 20 year sampling period (Figure 2; Table 2) although numbers fluctuated. It is only recently (2010) that *H. takanoi* was first observed in Lake Grevelingen, where it was immediately more abundant on soft sediment substrate than *C. maenas*. Whereas *C. maenas* used to be by far the most abundant crab species in the Oosterschelde, from spring 2004 on *H. takanoi* showed up in the samples. From that time on *H. takanoi* was often more abundant than *C. maenas* , although in 2009 it was temporarily the reverse. Taking the whole 20 year period into account, a significant decrease in *C. maenas* densities was found (Table 2). In Lake Veerse Meer, *C. maenas* used to be present in low densities as indicated by the occasional presence in the samples (Figure 2c). After the opening of the connection with the Oosterschelde salinity increased *H. takanoi* appeared. Initially, *H. takanoi* densities remained around 5 $m^{-2,}$ but in 2010 they reached almost 80 m^{-2}. In the Westerschelde *C. maenas* used to be and still is the most abundant crab species on soft sediment (Figure 2d). *H. takanoi* appeared in the samples for the first time in spring 2007, but was only occasionally found.

Distribution patterns

The presence of the species in samples gives a good view of the distribution of the species over Delta waters during a period before *H. takanoi* colonized soft substrates. *Carcinus maenas* appeared to be widely spread over the entire Grevelingen, Oosterschelde and large parts of the western and central part of the Westerschelde (Figure 3a). It is

noteworthy that densities of crabs on soft sediment substrates are quite low, i.e. they are not present in most of the samples. *Carcinus maenas* is for instance found in 2.9% of the samples taken during the period 1997-2003.

Particularly for the Oosterschelde and Grevelingen the chances of observing C. maenas in soft sediment samples are about the same for the entire water bodies. For the next seven years (2004-2010) with about the same sampling intensity, and an even larger area with potentially suitable conditions for *C. maenas* as the Veerse Meer became a salt water lake, *C. maenas* was present in only 1.8% of the samples. In some regions the chances of finding the species are about the same (e.g. most of the Westerschelde area) or larger due to improved conditions (central and eastern part of lake Veerse Meer). It is however clear that *C. maenas* is less widespread in large parts of the Grevelingen and the Oosterschelde. During the period 2004-2010, the chance of finding *H. takanoi* in the samples is about 1.5%. The species was particularly found in the Oosterschelde and recently in lake Veerse Meer. Whereas there is some overlap in the distribution of the two species (*C. maenas* and *H. takanoi*), they were only found together in the same sample twice (once in the Oosterschelde and once in the Westerschelde), which is a factor two lower than can be expected from the encounter rate of the species on soft sediment if the two do not influence each other. For the Oosterschelde alone, observing the two species together only once, is about a factor 3 lower than can be expected from their separate encounter rates. It is striking that the large decrease of the densities of *C. maenas* in a large part of the eastern Oosterschelde (to levels where the species was not found during seven years of monitoring) coincides with the appearance of *H. takanoi* in reasonable numbers.

Although with the MWTL programme the soft sediment substrate communities are monitored, the substrate can also contain hard elements like (pieces of) shells and stones. About 11% of the soft sediment substrates of the Dutch delta waters can be characterized as being a substrate containing hard elements. When hard elements are present in the sediment, the chance of encountering *C. maenas* is more than two times higher than on soft sediment without hard elements (Figure 4). This pattern was observed during the years without *H. takanoi* in the samples (1990-2003). Now that *H. takanoi* can also be found (2004-2010), *C. maenas* can still be substantially more often encountered on soft sediments with hard elements, where the encounter rate on both classes of substrate has decreased to about a factor 2. In the meantime the encounter rate for *H. takanoi* is about 4 times higher on soft sediment with hard elements than on soft sediment without hard elements. This leads to a pattern that currently in the Dutch delta waters the chance of finding *H. takanoi* on soft sediment with hard elements is about the same as for *C. maenas* (slight differences observed are not significant, see Figure 4).

Throughout the recent snapshot survey five species of crabs were collected from the hard substrate at the base of the dykes: *Carcinus maenas*, *Hemigrapsus takanoi*, *H. sanguineus*, *Porcellana platycheles* and a single *Liocarcinus arcuatus* (as these are not relevant to the current study, *P. platycheles* and *L. arcuatus* are not mentioned further). At all locations except around the storm-surge barrier *H. takanoi* was by far the dominant species ranging from 81% of the total number of crabs sampled at Schelphoek to 98% of the total number of crabs sampled at Goese Sas (Figure 5). Outside the barrier *H. sanguineus* was the most dominant crab species, comprising 91.5% of the total number sampled. Just inside the barrier the proportions of *H. takanoi* and *H. sanguineus* found were almost equal with 45% and 43% of the total numbers respectively. *Carcinus maenas* was present at all locations in varying proportions of the total number of crabs collected, but was never close to being in the majority. The proportion of *C. maenas* ranged from 0.7% at the Goese Sas to 17.8% at Viane.

Size structure

Roughly dividing the research period for the Oosterschelde into three, distinguishing a period without *H. takanoi* (1990-1998), a period with known presence of *H. takanoi* at least on hard substrate, but low densities or absence of the species on soft substrate (1999-2004), and a period with *H. takanoi* also abundant on soft sediment (2005-2010), the size distribution graphs for *C. maenas* only show minor changes (Figure 6a,c,e). The relative share of the smaller sized specimens in the total population seems to have decreased (significant for 0-5 mm size class between first and last period) where a tendency in this direction seems to be apparent when *H. takanoi* was not yet present in the samples from soft sediment. It is particularly this size class that makes up the largest part of the *H. takanoi* populations at present. In recent years the share of the 10-15 mm size class for *C. maenas* has increased (significant difference between first and last period. In the Westerschelde, with a similar history concerning the arrival of *H. takanoi*, although densities are much lower so far, a similar pattern seems apparent (Figure 6b,d,f) although only the increase in the 11-15 mm size class from the first to the last period is significant. In Lake Grevelingen, where at least *H. takanoi* seems to be not very abundant or was even lacking till 2010, comparison of the same periods also indicates a significant decrease of the smaller sized *C. maenas* individuals from 1990-1998 to 1999-2004 in favour of the 11-15 mm size class (i.e. a significant increase) (Figure 6g,i,k). During the last six years only a handful of specimens were

observed making the relative comparison of size classes uncertain. But it should be noted that the smaller specimens of *C. maenas* were already less abundant in the *C. maenas* populations in lake Grevelingen than in the Oosterschelde and the Westerschelde during the 90s, and that the species as a whole was only occasionally found in the samples of lake Grevelingen after 2004. Due to the low densities, size distribution patterns for lake Veerse Meer are not very clear for the period 1990-2004 (Fig 3h). After the opening, both *C. maenas* and *H. takanoi* entered the lake, where clearly smaller sized *C. maenas* specimens are relatively less abundant than one would expect under circumstances with local reproduction; moreover the size class 0-5 mm is completely lacking (Figure 6j). This is not the case for *H. takanoi*, for which more than 70% of the population exists of 0-10 mm specimens.

In the hard substrate snapshot survey measurements of carapace width (CW) were combined for all locations to produce an overall representation of the size distribution per species on the hard substrate in the Oosterschelde. *Hemigrapsus takanoi* and *H. sanguineus* were abundant in sizes less than 20 mm CW with the greatest number of both species measuring between 10 and 15 mm CW (Figure 7). No *Carcinus maenas* smaller than 10 mm CW were observed and an obvious peak in size for *C. maenas* specimens was lacking. *Carcinus maenas* was found in similar numbers per millimetre class with an average of 6 (±4) crabs at sizes between 15 mm CW and 40 mm CW. Out of a total of 201 *C. maenas* specimens found, 35 (17%) measured more than 40 mm CW. The largest *C. maenas* found was 60.6 mm CW and was found just inside the barrier.

Discussion

Both *Hemigrapsus* species occupy habitats similar to that of *Carcinus maenas*, a native in the Delta waters, but itself a highly successful invader elsewhere (Cohen et al. 1995; Grosholz and Ruiz 1995; Jensen et al. 2002; Thresher et al. 2003). The introduction of the two *Hemigrapsus* species and particularly *H. takanoi* in the Dutch delta waters, therefore presented *C. maenas* with a potential competitor for habitat use.

Compared with other locations in the 2011 snapshot survey of the Oosterschelde, *Hemigrapsus sanguineus* was found in large numbers around the storm-surge barrier and particularly just outside the barrier, while *H. takanoi* was particularly abundant within the barrier. This is likely to be due to the different hydrodynamic properties of the habitats sampled as the storm-surge barrier has reduced the current velocities inside the barrier considerably (Escaravage et al. 2006). In general, the further east in the Oosterschelde, the lower the energy of the habitat, which can explain the reduced numbers of *H. sanguineus* going further east into the tidal bay. This is consistent with the observations by Dauvin et al. (2009) who found *H. takanoi* predominantly in low hydrodynamic muddy habitats, while *H. sanguineus* was found predominantly in high hydrodynamic habitats on the Opal Coast in France. Both species were found to live sympatrically in harbours (Dauvin et al. 2009). This is probably the result of developed habitat segregation in the region of origin (e.g. Japan) (Asakura and Watanabe 2005; Asakura et al. 2008).

The interaction between *Hemigrapsis* and *C. maenas* in the Dutch delta network is complicated by the spread of larvae by water currents. Broadcasting of recruits can prop the population up in a particular water body, but low reproduction in one year could result in the population quickly declining. This means that variation in population changes is expected between each body of water in the delta. *Hemigrapsus takanoi*, which was clearly much more abundant on soft sediment in the Oosterschelde than in the other delta waters, seems to reproduce considerably in this water body. This is also indicated by the size-frequency distribution showing smaller sized individuals being most abundant. In the Westerschelde the densities of *H. takanoi* on soft sediment remain low thus far, indicating rather low reproductive success or populations dependent on recruitment from the Oosterschelde or the North Sea on a yearly basis. The population developments of *H. takanoi* in Lake Grevelingen are highly uncertain. The species has not been recorded for the water body as far as we know, although it might be expected that at least on hard substrate the species might have been present before the first recordings of the present study on soft sediment in 2010. Being all smaller sized individuals, it seems that if populations of *H. takanoi* occurred in Lake Grevelingen, they probably are depending on recruitment from elsewhere, likely the Oosterschelde, and that such an inflow of new recruits occurred in 2010. Also for Lake Veerse Meer this must have been the case until the year 2010. Densities were fluctuating and as for the Oosterschelde, recruitment of the soft sediment environments appeared to be low, for instance in the year 2008. In 2010 the *H. takanoi* populations seem to have exploded in Lake Veerse Meer. Still these specimens might be recruits coming from the Oosterschelde, as also there an increase in the densities was observed. But as the increase in the Oosterschelde is not that spectacular, it might be that 2010 is the first year with successful reproduction of *H. takanoi* in Lake Veerse Meer.

Although soft sediment substrates are not the favoured habitat for *C. maenas*, 20 years of intensive monitoring of these habitats provides a detailed picture of the population developments in the Dutch delta, showing changes in densities and spatial distribution. Over the last 20 years, the *C. maenas* populations show a clear decrease on the soft sediment substrates in the Oosterschelde (Figure 2b). Also, evaluating size frequency distributions in these habitats is of value as changes in the population can be observed.

Our size frequency distributions do not necessarily reflect the total population as the habitats used depend on the life stages, leading to proportional differences in abundances between size classes. Stressors of all kinds such as extreme temperatures, pollution and fluctuations in predator abundances can lead to changes in densities and/or size-frequency distributions as particularly certain life-stages or life-stages in certain habitats are be impacted. Although hard substrates were not monitored, populations on soft sediments will be in linked by recruitment, with other habitats in use by the species.

C. maenas used to be very abundant on hard substrate (e.g. De Kluijver and Leewis 1994), but at present numbers are reduced and they are outnumbered by the *Hemigrapsus* species (Figures 5 and 7). The decrease of *C. maenas* could be the result of interference competition for shelter with the *Hemigrapsus*, indicated by competitive and aggressive behaviour in laboratory studies and as found in other regions (e.g. Jensen et al. 2002; Lohrer and Whitlatch, 2002). At least on soft sediment the decrease in *C. maenas* densities in the Oosterschelde had already started before *Hemigrapsus* appeared in the samples. As the *Hemigrapsus* species are also typical hard substrate species, it is very likely that their appearance on soft sediment in reasonable numbers was delayed compared to hard substrate. We know that this is the case because the species was first observed in the year 2000 in the Oosterschelde (and probably arrived in 1999), and several recordings from hard substrate occurred during the following years (e.g. Breton et al. 2002; Wolff 2005).

The timespan between the reduction of *C. maenas* numbers during the first years of this century and the arrival of *Hemigrapsus* in the Oosterschelde seems however too short for the exotic populations to expand to such numbers that they have a large impact on the entire *C. maenas* populations. Moreover, the decrease of *C. maenas* does not seem to be a gradual one, but rather one with fluctuations with a period of lower densities during 1992-1995, which cannot be explained by presence of *Hemigrapsus*. Additionally, in the Westerschelde where *Hemigrapsus* was present since the year 2000, such an impact on *C. maenas* cannot be observed. *Hemigrapsus* densities are lower, as indicated by the first occurrences in soft sediment samples not before 2007, but it definitely does not strengthen the hypothesis of *Hemigrapsus* causing the collapse of the *C. maenas* populations in the Dutch delta and the Oosterschelde in particular. In lake Grevelingen a decrease in *C. maenas* populations was also observed although no *H. takanoi* were found (Figure 2, Table 2). It should be noted that general deterioration of the system is taking place here and that several other species show declining trends (Wetsteijn 2011). In lake Veerse Meer the conditions significantly improved for *C. maenas* with the increase in salinity in 2004. For this water body it can be observed that the *C. maenas* populations responded and increased. However after 1 to 2 years, *Hemigrapsus* outnumbered *C. maenas* also in lake Veerse Meer, but it is not evident that *C. maenas* populations suffered from the increase of *Hemigrapsus* because *C. maenas* is still present.

It can however not be neglected that *Hemigrapsus* succeeds in dominating habitats and entire regions where *C. maenas* used to flourish (Figure 4 and 5). It seems that the *Hemigrapsus* species may be profiting from decreasing *C. maenas* populations. Competition between the two species probably also plays a role and leads to the dominance of *Hemigrapsus* particularly on hard substrates, but also a further decrease of the *C. maenas* populations to some extent.

Competition between *Hemigrapsus* and *C. maenas* is especially relevant when *C. maenas* specimens are small. Although *C. maenas* can grow much larger than either *H. sanguineus* or *H. takanoi* (Pillay and Ono 1978; Jensen et al. 2002), there is the possibility of interspecific competition between full grown *Hemigrapsus* individuals and juvenile *C. maenas* of the same size. Once *C. maenas* grows beyond the maximum size of *Hemigrapsus*, they could reach a size refuge where *Hemigrapsus* no longer poses a competitive threat. Furthermore, larger *C. maenas* tend to move to other environments (i.e. deeper waters) (Thiel and Dernedde 1994) and consequently competition is no longer important due to size- and niche-segregation. However reproduction of *C. maenas* and particularly the settlement of the *C. maenas* larvae seem to be largely restricted to intertidal habitats (Thiel and Dernedde 1994; Zeng et al. 1999). This is also indicated by the size-distribution graphs (Figure 6) showing large numbers of smaller sized *C. maenas* specimens in the intertidal Oosterschelde and Westerschelde; as indicated before, particularly before the decrease of the *C. maenas* populations, but the smallest size-classes (0-5 and 5-10 mm CW) largely lacking in the non-tidal lake Grevelingen and lake Veerse Meer. It is likely that almost no reproduction of *C. maenas* takes place in

these non-tidal waters, as in the deeper parts of the tidal waters. This implies that the populations of the species in subtidal waters depend on colonization of sub-adult and adult specimens from intertidal zones, and for the two non-tidal lakes of surrounding tidal waters as the Oosterschelde and the North Sea pre-delta region.

Thiel and Dernedde (1994) found that small *C. maenas* were more likely to be found in high abundances on substrate providing spatial refuges. They found significantly more juveniles on mussel clumps compared to tidal flats. They also showed that to avoid predation juvenile *C. maenas* stayed as long as possible in the intertidal area before emigrating to deeper water for the winter. This is in contrast to larger conspecifics, which are more abundant in deeper waters throughout the year. Although Thiel and Dernedde (1994) did not present data for April-June, it can be assumed that smaller crabs are the first to recolonize the intertidal area at the end of winter as they are still more vulnerable to predation than larger conspecifics. As we found *C. maenas* in the intertidal region at all ten snapshot survey locations and with sizes ranging from 10 mm to 61 mm CW, the recolonisation of the intertidal area by *C. maenas* is likely to have occurred prior to the hard substrate survey which began in May. Berrill (1982) reported that on the central coast of Maine in the United States *C. maenas* recruits measured 16-30 mm in carapace width (CW) after the end of their first winter. The two areas (the coast of Main and the Dutch delta) experience similar water temperatures, suggesting that *C. maenas* would follow a similar growth rate in both locations. This is supported by the results of the present study as no *C. maenas* measuring less than 10 mm were found in May-June.

According to Berrill (1982), small crabs use rocks and shells in the intertidal zone for shelter and protection against predators. The expansion of the Pacific oyster, *Crassostrea gigas*, in the Delta waters has provided plenty new hard substrate with spatial refuges in the last 20 years (Troost, 2010). These new niches are perfect protective nurseries for small *C. maenas*, yet *Hemigrapsus* species still outnumbered them by far even in areas containing oysters. While it cannot be said that the Pacific oyster facilitated the introduction of *Hemigrapsus* because it was present long before the crabs were introduced, the introduced oysters certainly have provided more heterogeneous habitats for the crabs to utilise making it possible to compete successfully and dominate over the native *C. maenas.*

One would expect a peak in the number of smaller *C. maenas* found on the hard substrate at the base of the dykes in May if juvenile *C. maenas* are likely to be found in higher and more heterogeneous substrates (Pillay and Ono 1978) and if the previous yearôs recruits measure between 16-30 mm CW (Berrill 1982). Additionally, in any reproducing population, one would expect more young cohorts than older ones due to mortality of older individuals. However, this was not the case; the numbers of small *C. maenas* found did not exceed that of larger and therefore older *C. maenas* specimens.

Figure 6 indicates that a decline in especially smaller size-classes is particularly evident in the Oosterschelde and was already initiated in the beginning of this century. In the Westerschelde, where *H. takanoi* is less abundant, the pattern is less pronounced and started to develop around 2005 (Figure 6b, d, f). The results for Lake Grevelingen (Figure 6g, i, k) indicate that in the early 1990s the size distribution was already not as one would expect for a water body where reproduction was occurring. As juvenile specimens of *C. maenas* occur mostly in the intertidal zone (Berrill 1982), which is lacking in lake Grevelingen, this is not surprising. The observed collapse of *C. maenas* in Lake Grevelingen is most likely due to deterioration of the lake itself, although a reduced influx from other environments (i.e. the Oosterschelde) might also play a role. The same applies to lake Veerse Meer, currently suitable for *C. maenas*, but without an important habitat for juveniles due to the lacking intertidal zones.

Unfortunately there are no data available for the crab communities at the same hard substrate locations sampled in this study prior to the arrival of *H. takanoi*. However, given the lack of an expected peak in *C. maenas* numbers smaller than 30 mm CW, and that at these smaller sizes *C. maenas* was overwhelmingly outnumbered by *H. takanoi*, it is likely that there is size-dependent inter-specific competition occurring on hard substrate between the two species, and that *H. takanoi* is the more successful species. Jensen et al. (2002) found in the field as well as in the laboratory that in the presence of either *Hemigrapsus sanguineus* or *H. oregonensis* of similar size, *C. maenas* was overwhelmingly out-competed for shelter. They found only about 20% of juvenile *C. maenas* under rocks in the presence of either one of the *Hemigrapsus* species compared with >97% in areas where *Hemigrapsus* did not occur. In southern New England (USA) Lohrer and Whitlatch (2002) observed a 40-90% decline in abundance of *C. maenas* coinciding with a 10-fold increase in *H. sanguineus.* In the laboratory they found a significant predation risk for small, newly recruited *C. maenas* specimens when paired with larger *H. sanguineus* and conspecifics. However, *H. sanguineus* recruits were not affected by larger individuals of either species.

This study shows that while the invading *Hemigrapsus* species were not the initial cause of the reduction of the *C. maenas* populations, they successfully colonised the Dutch delta region due to minimal competition from other crab

species. The ónewô hard substrate environments of the expanding *C. gigas* oyster reefs may well have facilitated this colonization. Once settled and numerous the two *Hemigrapsus* species appeared to be superior competitors for the space occupied by juvenile *C. maenas* shore crabs.

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Figures

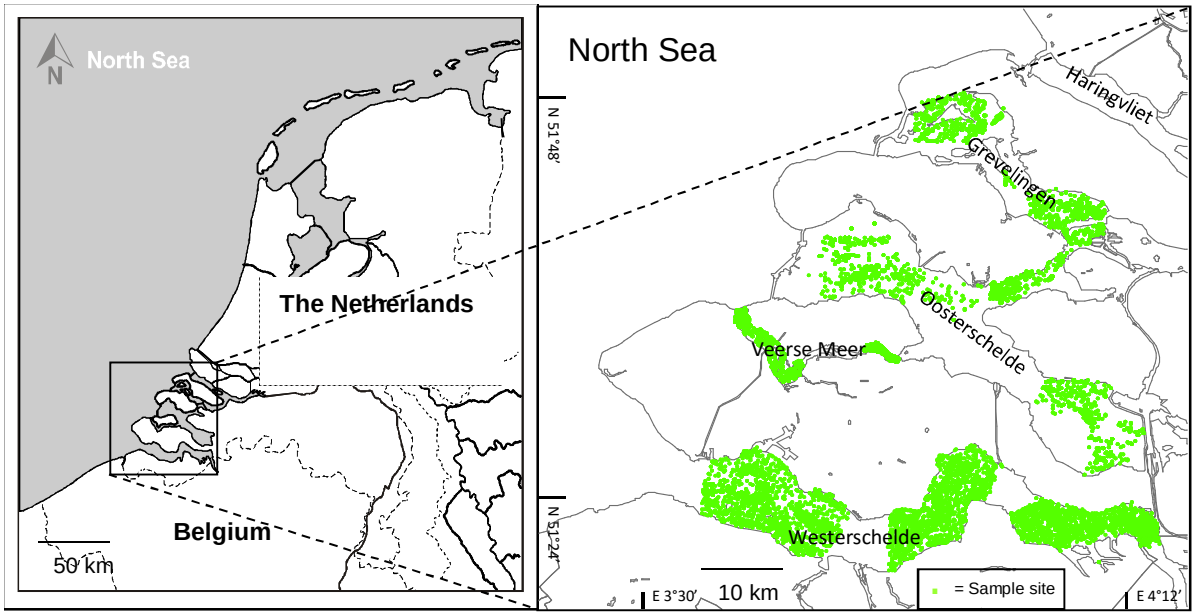
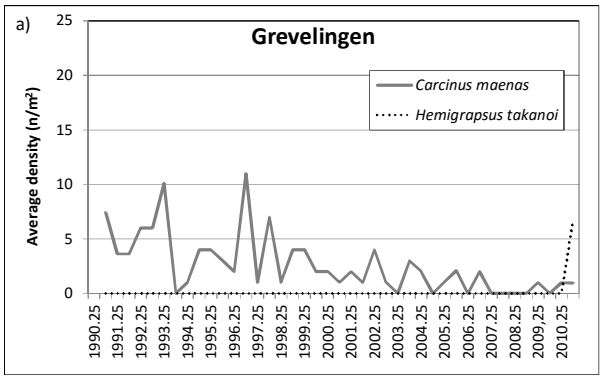
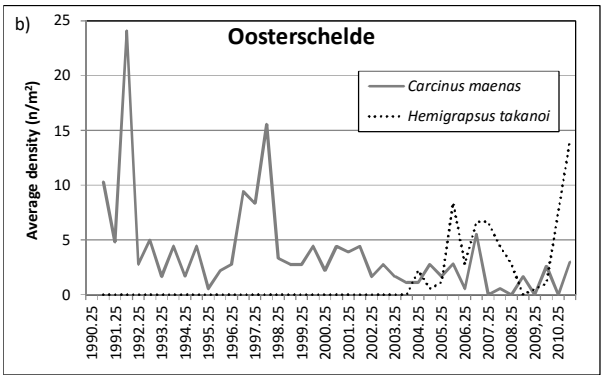


Fig 1 Location of the Dutch delta and the various water bodies in the Netherlands with indication of the sample sites on soft sediment during the 1990-2010 research period





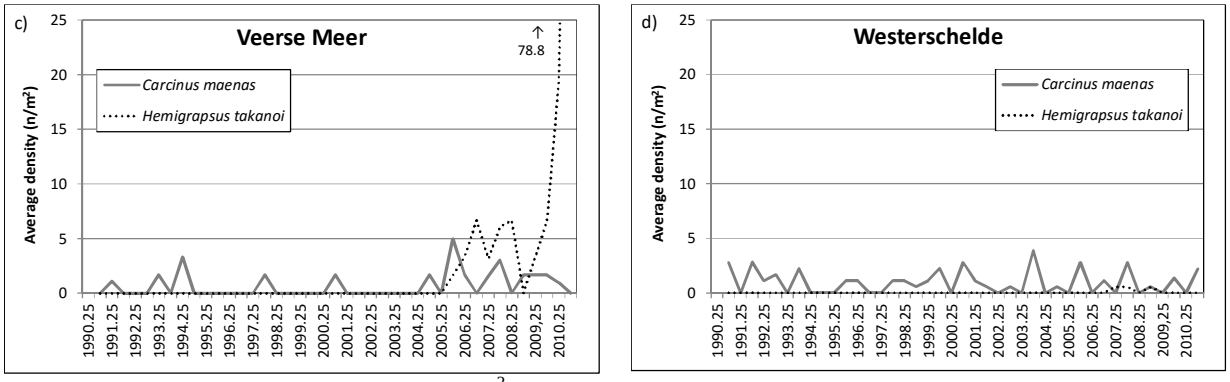


Fig 2 Developments in average densities (n/m^2) of *Carcinus maenas* and *Hemigrapsus takanoi* on soft sediment substrates during the period 1990 ï 2010 in Lake Grevelingen (a), the Oosterschelde (b), Lake Veerse Meer (c) and the Westerschelde (d)

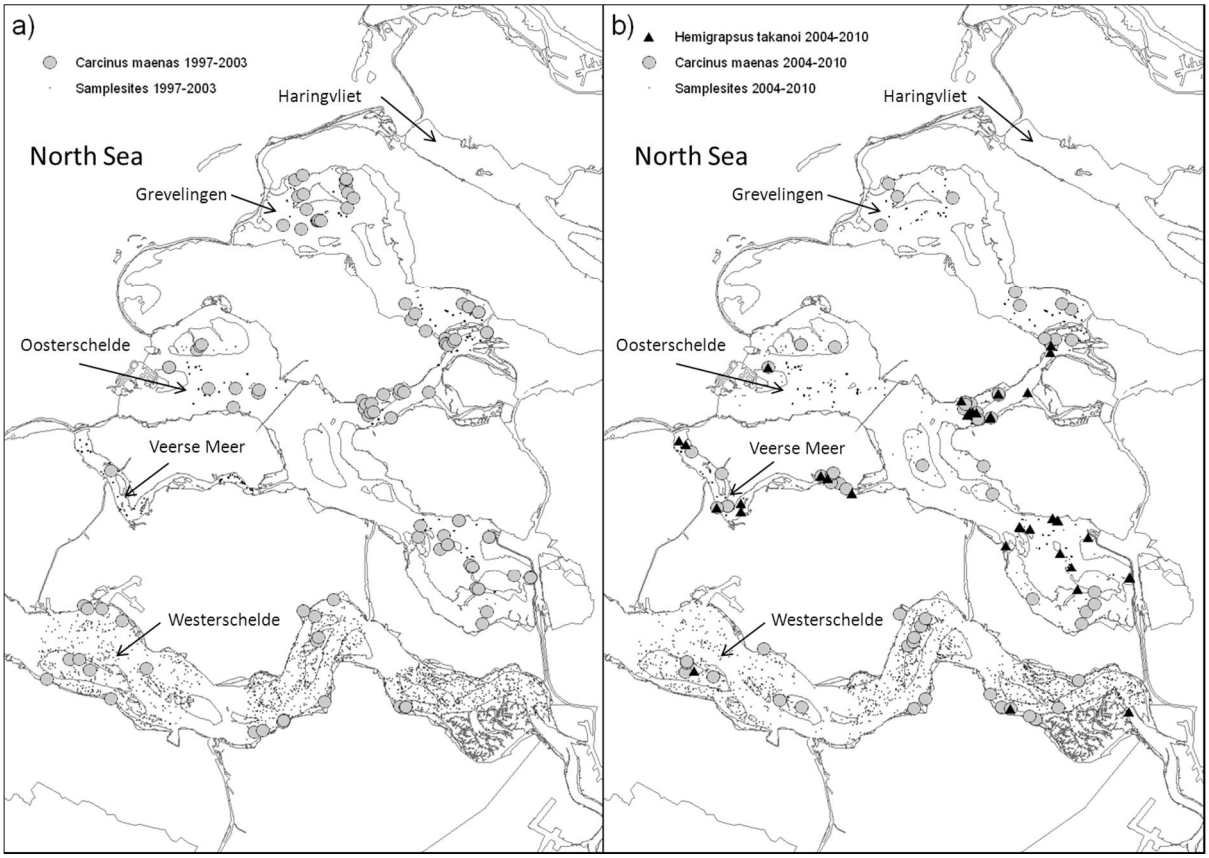


Fig 3 Sites of observation of *Carcinus maenas* and *Hemigrapsus takanoi* for the periods 1997-2003 (a) and 2004-2010 (b) during the monitoring of the soft sediment communities

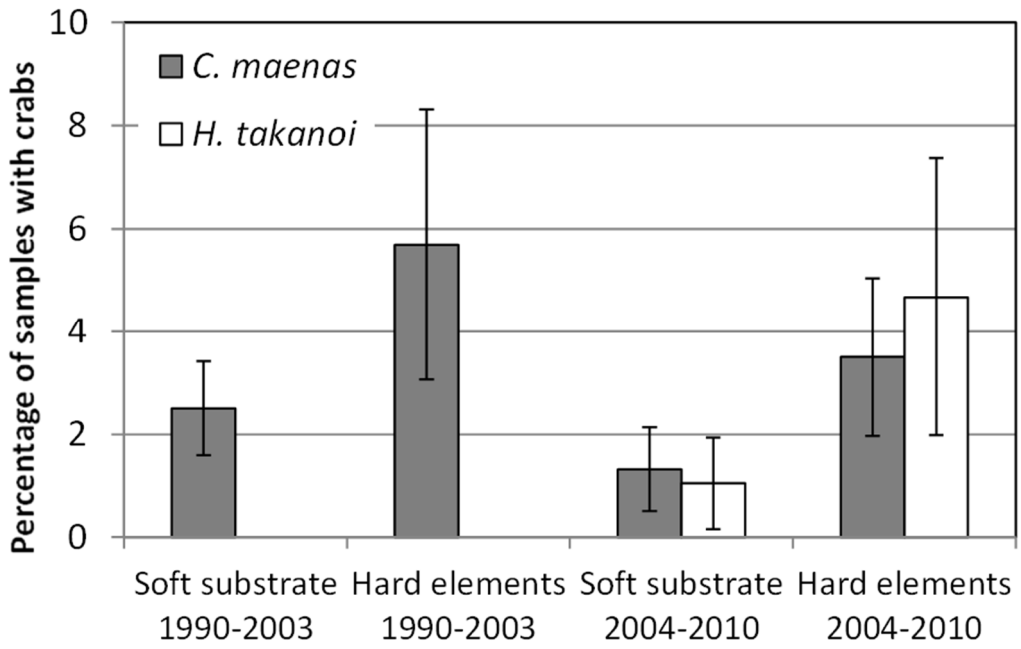


Fig 4 The encounter rate (in %) for *Carcinus maenas* and *Hemigrapsus takanoi* on soft substrate without shells and stones (soft substrate) or on soft substrate with shells or stones (hard elements) during the periods 1990-2003 and 2004-2010 for the entire Dutch delta

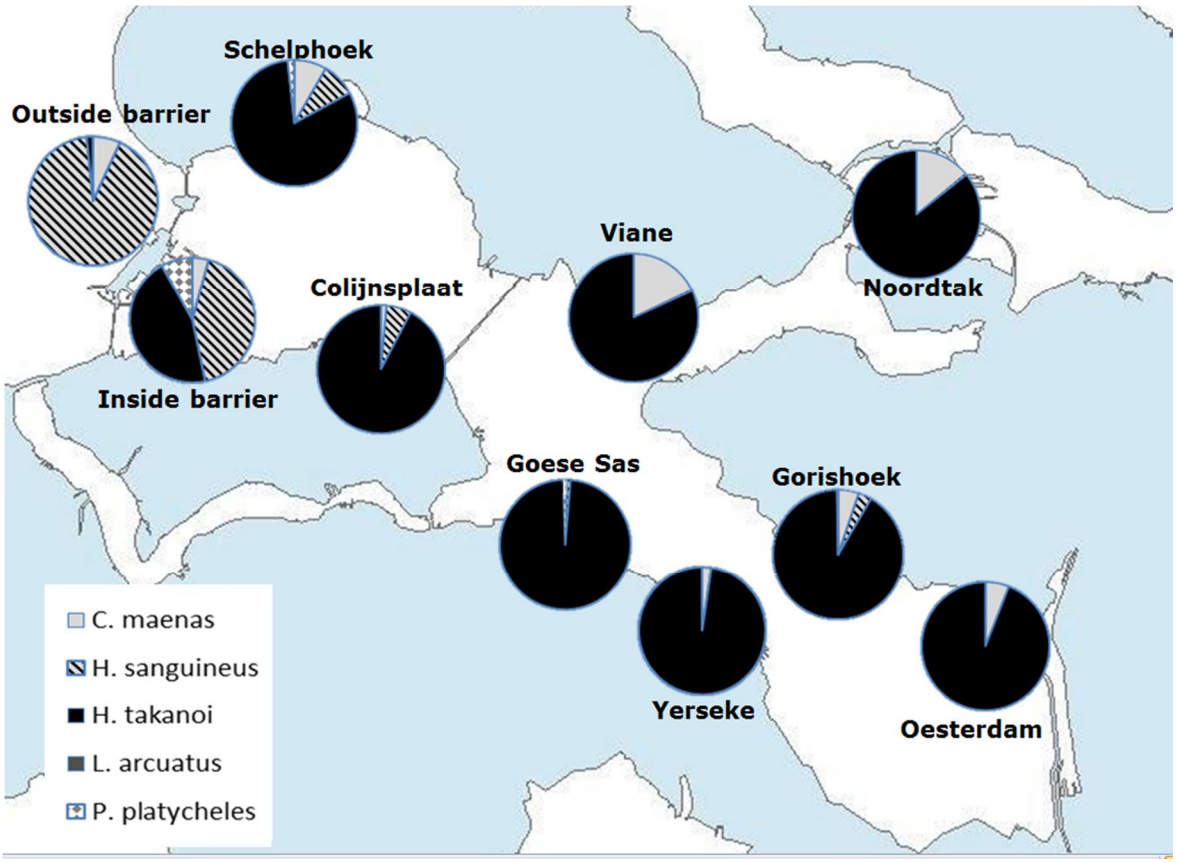
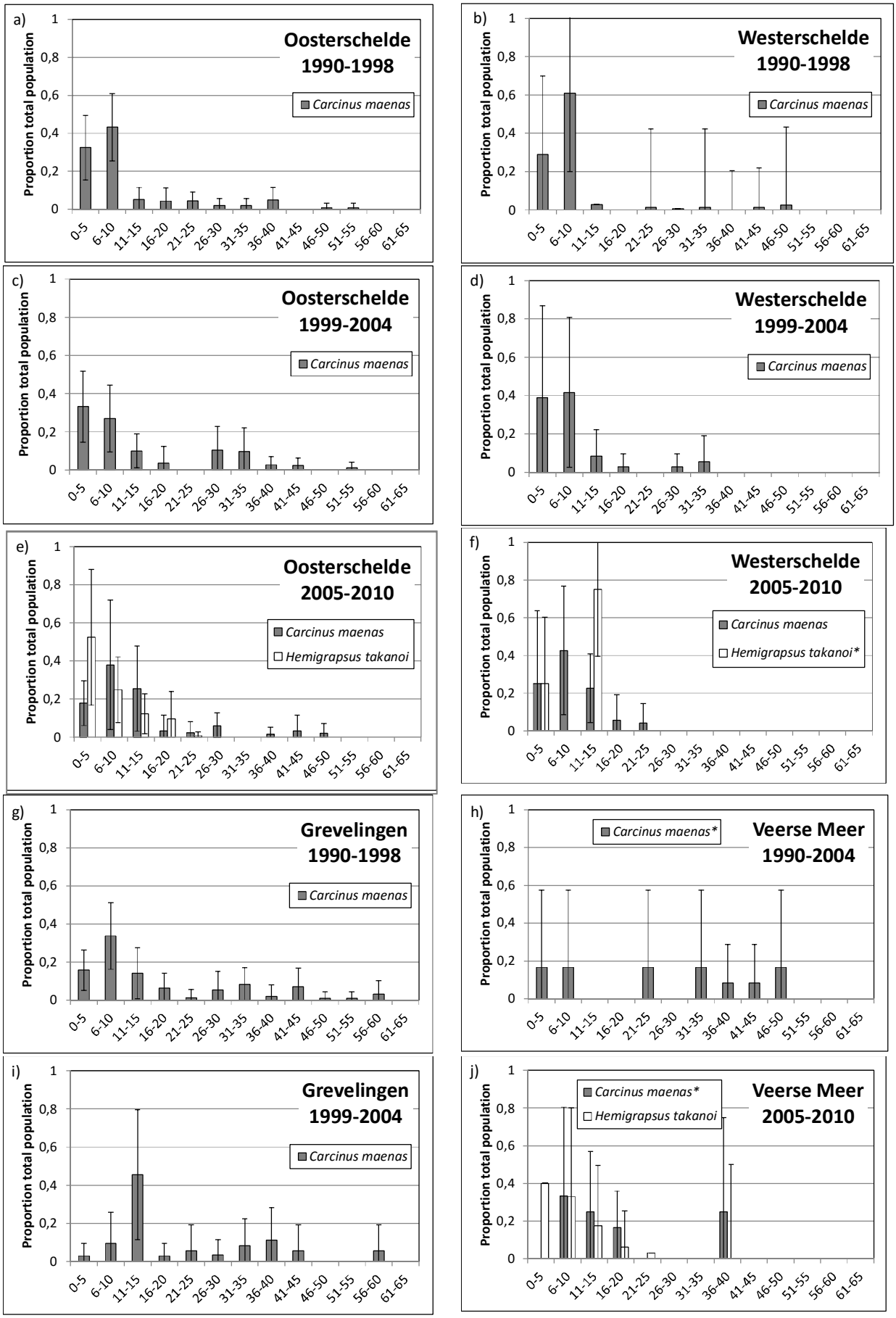


Fig 5 Sampling sites of the hard substrate survey in the Oosterschelde tidal bay in 2011 indicating the species proportions of total number of crabs found.


a)
Oosterschelde
1990-1998
Carcinus maenas
b)
Westerschelde
1990-1998
Carcinus maenas
c)
Oosterschelde
1999-2004
Carcinus maenas
d)
Westerschelde
1999-2004
Carcinus maenas
e)
Oosterschelde
2005-2010
Carcinus maenas
Hemigrapsus takanoi
f)
Westerschelde
2005-2010
Carcinus maenas
Hemigrapsus takanoi*
g)
Grevelingen
1990-1998
Carcinus maenas
h)
Veerse Meer
1990-2004
Carcinus maenas*
i)
Grevelingen
1999-2004
Carcinus maenas
j)
Veerse Meer
2005-2010
Carcinus maenas*
Hemigrapsus takanoi
Proportion total population
0
0,2
0,4
0,6
0,8
1
0-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65

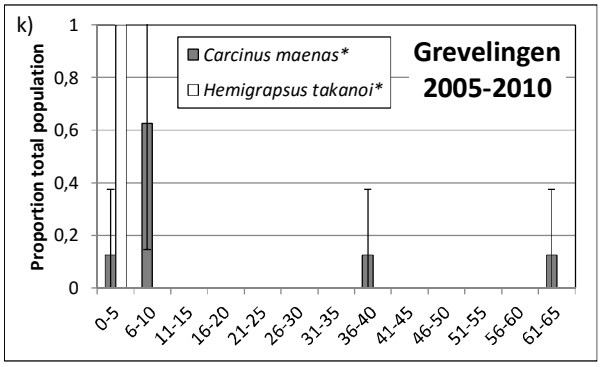


Fig 6 Proportional distribution of the total number of observed specimens per species (*Carcinus maenas*, *Hemigrapsus takanoi*) per period and water body over 5 mm carapace (CW) size classes; a) Oosterschelde from 1990 to 1998; b) Westerschelde from 1990 to 1998; c) Oosterschelde from 1999 to 2004; d) Westerschelde from 1999 to 2004; e) Oosterschelde from 2005 to 2010; f) Westerschelde from 2005 to 2010; g) Grevelingen from 1990 to 1998; h) Veerse Meer from 1990 to 2004; i) Grevelingen from 1999 to 2004; j) Veerse Meer from 2005 to 2010; k) Grevelingen from 2005 to 2010.
*Total number of specimens observed is rather small (<8)

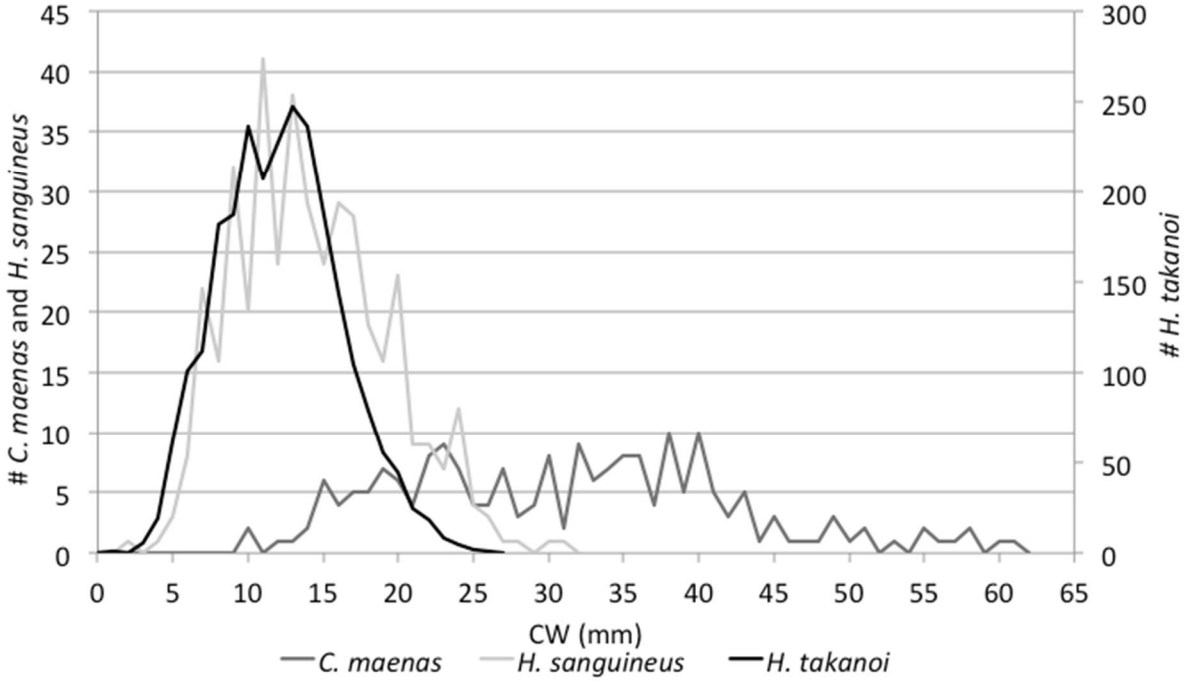


Fig 7
Size distribution of three crab species for the combined hard substrate survey sites in the Oosterschelde for *C. maenas*, *H. sanguineus* and *H. takanoi* in 2011

Tables

Table 1 Substrate types at the ten locations sampled in the Oosterschelde indicated in Figure 6 during the hard substrate survey

Location	**Substrate**
Outside barrier	Rocks, seaweed
Inside barrier	Rocks, oyster shells
Schelphoek	Rocks, oyster shells, debris
Colijnsplaat	Rocks, sand
Viane	Rocks, oyster shells, mud
Goese Sas	Rocks, mud
Gorishoek	Rocks, oyster shells
Yerseke	Rocks, debris, mud
Noordtak	Rocks, sand
Oesterdam	Rocks, sand

Table 2 Trends in *Carcinus maenas* densities during the research period. Indicated are significant regressions according to; Density = a * Year + b, with R^2-value and significance level p; ns = not significant

Water body	A	B	R^2	p
Grevelingen	-0.026	52.3	0.376	0.000
Oosterschelde	-0.055	110.6	0.210	0.003
Veerse Meer				ns
Westerschelde				ns