

Distribution of cockles *Cerastoderma edule* in the Eastern Scheldt: habitat mapping with abiotic variables

B. J. Kater^{1,2,*}, A. J. M. Geurts van Kessel², J. J. M. D. Baars¹

¹Netherlands Institute for Fisheries Research-Centre for Shellfish Research, PO Box 77, 4400 AB Yerseke, The Netherlands

²Netherlands Institute for Coastal and Marine Management, PO Box 8039, 4330 EA Middelburg, The Netherlands

ABSTRACT: On the basis of maps of environmental variables and annual surveys, a habitat map was constructed for the cockle *Cerastoderma edule*, a commercially exploited dominant suspension feeder in the Eastern Scheldt (The Netherlands). The results obtained show that the distribution of cockles can be described using emersion time and current velocity. Salinity does not play a significant role, even though low salinities are known to limit the distribution of cockles in other areas. The response to current velocity was as expected, but the response to emersion contradicted results from other studies. These responses cannot be explained as the result of competition for space with the recently expanded Pacific oyster population, because Pacific oysters are most common in habitats that are unsuitable for cockles. Possible explanations for cockles' apparent preference for settling in areas with relatively long emersion times are high predation pressure or instability of the sediment around low water level.

KEY WORDS: *Cerastoderma edule* · Habitat map · Eastern Scheldt

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INTRODUCTION

Alongside the blue mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas*, another dominant suspension feeder in the Eastern Scheldt (The Netherlands) is the cockle *Cerastoderma edule*. Cockles are abundant on most intertidal flats, and densities are generally high, though they vary from year to year depending on the success of spat fall and on mortality (Coosen et al. 1994). Because of their high abundance, cockles are commercially exploited in the Eastern Scheldt (Dijkema 1997). This has led to conflict with conservationists, especially when suction dredges are used in areas of major ecological value, like the Eastern Scheldt. In 1993 the government of The Netherlands implemented a policy to ensure the protection of natural values in such areas, while allowing restricted human activities. Under this policy, cockle fishing is allowed in the Eastern Scheldt, provided that there are

no negative effects on cockle stocks (Kamermans & Smaal 2002). It is known that cockles and cockle stocks are affected by cockle fishing (Piersma et al. 2001, Ens 2003). A major research programme was initiated to evaluate the effect of shellfish fisheries on the natural levels in the Wadden Sea and Eastern Scheldt (Ens et al. 2004). The present study is part of that programme.

Cockle distribution is influenced by abiotic variables including current velocity, emersion time, salinity and sediment composition, by biotic variables including other species and predation, and by human exploitation. Current velocity can have an effect on both settlement of larvae and growth of bivalves. Cockles start their lives as larvae in the water column. After a few weeks they settle to the sediment (spat fall). Current velocity is an important variable in the transition of larvae from the water column to the sediment. Current velocities also have an impact on food availability, which affects cockle growth rates. Reports concerning

*Email: b.j.kater@rikz.rws.minvenw.nl

the effects of increasing flow velocity on bivalve growth rates have been contradictory. Some studies have reported increased growth rates with increased flow velocity. This could be attributed to increased food supplies or feeding efficiency (Wildish & Kristmanson 1985, Eckman 1987). In contrast, other studies have reported that growth rates tend to decrease with increased flow velocity (Wildish et al. 1987, Eckman et al. 1989, Wildish & Saulnier 1992).

In addition to current velocity, emersion time plays an important role in defining cockle habitats. It is commonly accepted that food supply is mainly linked to duration of emersion. Another potential factor limiting habitat is salinity. In the Baltic Sea cockles are found at salinities of 10‰ and higher (Brock 1980). Larvae prefer salinities between 30 and 35‰, but can survive at salinities as low as 5‰ (Kingston 1974). Ysebaert et al. (2002) modelled the Western Scheldt cockle population and predicted cockles would thrive at salinities between 10 and 30‰, with the optimum at 25‰.

One abiotic variable known to influence the distribution of cockles is the composition of the sediment. However, we were unable to investigate this variable due to lack of data.

The Pacific oyster *Crassostrea gigas* was imported to the Eastern Scheldt in 1964 for culturing purposes (Dijkema 1997). In 1976 and 1982 larval outbursts established wild Pacific oysters in the waters of the Eastern Scheldt (Drinkwaard 1999), and since that time oyster beds in intertidal and subtidal areas have expanded. One of the main problems in the Eastern Scheldt associated with the expansion of Pacific oysters is the potential for negative impact on commercially exploited indigenous species. Wild Pacific oysters can compete for food and space with commercial species like cockles and mussels (Smaal et al. 2001).

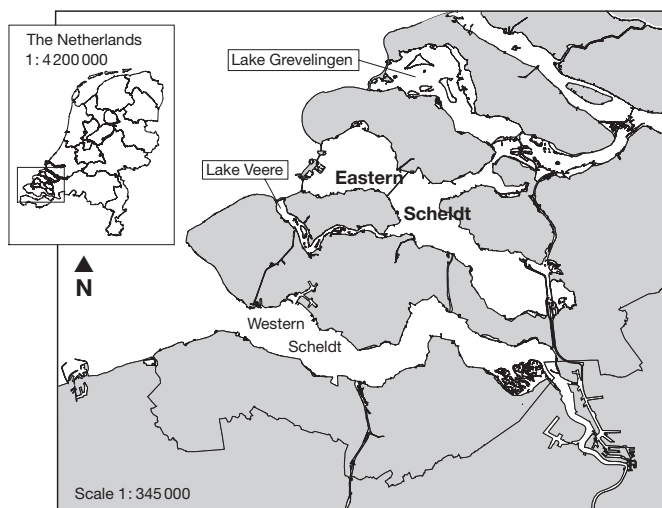


Fig. 1. Map showing location of the Eastern Scheldt estuary

The objectives of this study were to describe the distribution of cockles in the Eastern Scheldt by creating a habitat map using several abiotic variables, and to discuss this distribution, including the potential influence of Pacific oysters.

MATERIALS AND METHODS

Study area and data. This study was performed on intertidal areas in the Eastern Scheldt, The Netherlands (Fig. 1). Cockles have been surveyed annually on the Eastern Scheldt intertidal areas since 1990. Our surveys were performed in spring at approx. 500 sampling stations, lying on north–south vectors. The distance between sampling points was 0.25 geographical minutes (≈ 460 m), while the distance between vectors was 0.5 geographical minutes (≈ 555 m). Samples were taken with a special cockle-sampling device, which has a sample surface of 0.1 m^2 . Samples were collected using a 2 mm mesh sieve, and the cockles in each sample were counted and wet-weighted. The number and wet-weight biomass of cockles m^{-2} were calculated from these data. The biomass measurements for each sampling station from 1990 to 2001 were averaged and used for modelling purposes.

Three datasets of environmental parameters, organised as maps, were used to explain the distribution of cockle biomass in the Eastern Scheldt: emersion time (20×20 m grid), current velocities at ebb during spring tide (50×50 m grid) and salinity (100×100 m grid). Emersion times were based on depths and water levels measured between 1990 and 1994, and varied between 0 and 93%. Current velocities and salinity were calculated using a current velocity model and a salinity model for the Eastern Scheldt. Current velocities varied between 4 and 74 cm s^{-1} and salinity between 28 and 33‰.

All environmental maps dated to 1994, and were encoded into a GIS (ArcView v3.2), together with the cockle sample points. Emersion time, current velocity and salinity were linked to each cockle sample point using Getgridvalue (Davies 2000).

Habitat modelling and mapping. A stepwise backward generalized linear model was fitted using a Poisson distribution and log link function, using SAS software. The model can be expressed as:

$$B = e^{a + b^x EM + c^x EM^2 + d^x CV + e^x CV^2 + f^x SAL + g^x SAL^2 + h^x EM^x CV + i^x EM^x SAL + j^x CV^x SAL + k^x EM^x CV^x SAL}$$

where B is biomass of cockles, EM is emersion time, CV is current velocity, SAL is salinity, and a to k are parameters to be estimated. Terms were removed when $p > 0.01$.

To create the habitat map, a grid of 100×100 m was made in the GIS using the script Create Map Grid Theme (Banerjee 2000) and overlaid onto the Eastern Scheldt map. The environmental information for each grid cell was derived from the environmental maps, and cockle biomass was estimated for each grid cell using the habitat model. Cockle habitats can be visualised using this grid by giving high biomass and low biomass cells different colours. To achieve this, cockle biomasses were sorted from high to low and divided into 5 cockle 'suitability' groups with an equal number of grid cells, i.e. 20% of the total number of grid cells. The following groups were defined: 'very suitable' areas (highest biomass), 'suitable' areas, 'less suitable' areas, 'marginally suitable' areas, 'least suitable' areas (lowest biomass). The total cockle stock in the Eastern Scheldt was estimated using the estimated biomass and surface area of each grid cell.

Relative distribution of cockles and oysters. The intertidal cockle habitat map can be used to study areas colonised by Pacific oysters, in terms of their suitability to cockles. Comparing intertidal Pacific oyster beds in the Eastern Scheldt and the cockle habitat map determines whether Pacific oysters tend to grow in the 'very suitable' or 'less suitable' cockle habitats. Maps of intertidal Pacific oyster beds in 1990 and 2002 (Kater & Baars 2004) were overlaid onto the cockle habitat map. All grid cells within these polygons were scored, and for each suitability class the number of grids cells within an oyster bed was expressed as a percentage of the total number of grid cells in each class. Differences between years were tested with a χ^2 test for independence.

RESULTS

Habitat modelling

The analysis, utilising generalized linear modelling, showed that the biomass of cockles could be explained using emersion time (first and second order) and current velocities (first and second order). Salinity and all interaction terms were not significant. Table 1 gives an overview of estimates and p-values for significant parameters. This model explained 37.3% of the deviance. There was no correlation between emersion time and current velocities. The relationship between emersion time, current velocity and estimated biomass is shown in Fig. 2. The contour plots show that in the Eastern Scheldt the highest cockle biomasses are estimated at intertidal flats with a current velocity range of 27 to 37 cm s^{-1} , which emerged for 42 to 57% of the time.

The cockle biomass for each grid cell in the Eastern Scheldt was estimated using the parameters in Table 1,

Table 1. Significant parameters in the regression analysis (distribution: Poisson; link: log)

Parameter	Estimate	p-value
Emersion time (first order)	0.11	<0.0001
Emersion time (second order)	-0.0011	<0.0001
Current velocity (first order)	0.15	<0.0001
Current velocity (second order)	-0.0023	<0.0001

and data from the maps on current velocities and emersion times. Grid cells were shaded according to their biomass (Fig. 3). The habitat map shows 'very suitable' cockle areas on large tidal flats (Roggenplaat, Vondelingsplaat and Slikken van den Dortsman). 'Less suitable' areas are mostly found in the northeastern and southeastern part of the Eastern Scheldt. The average cockle stock in the period 1990 to 2001, used for modelling, was 26.5 million kg fresh weight. The total stock estimated by the habitat model was 26.8 million kg fresh weight.

Competition between cockles and oysters

Using the oyster map of 1990, the highest percentage of Pacific oysters was found in areas classified as 'marginally suitable' for cockles (8.1%). Of the grid cells classified as 'very suitable' or 'suitable' for cockles, fewer than 4% were occupied by Pacific oysters. Using

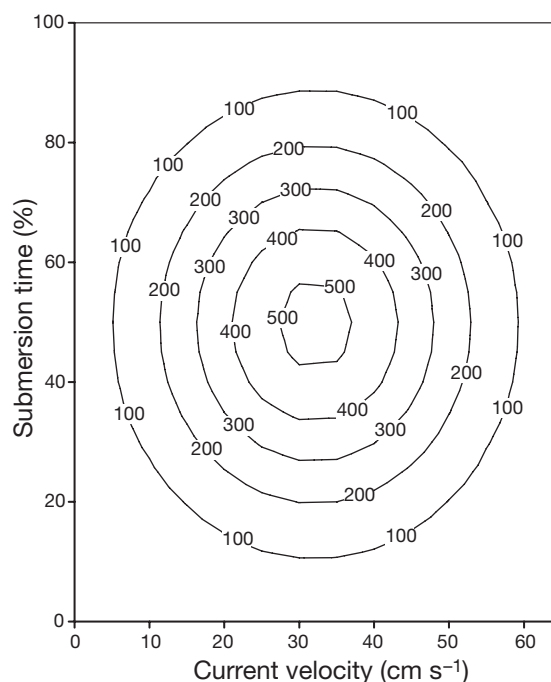


Fig. 2. Contour plot for cockle biomass for given submersion times and current velocities

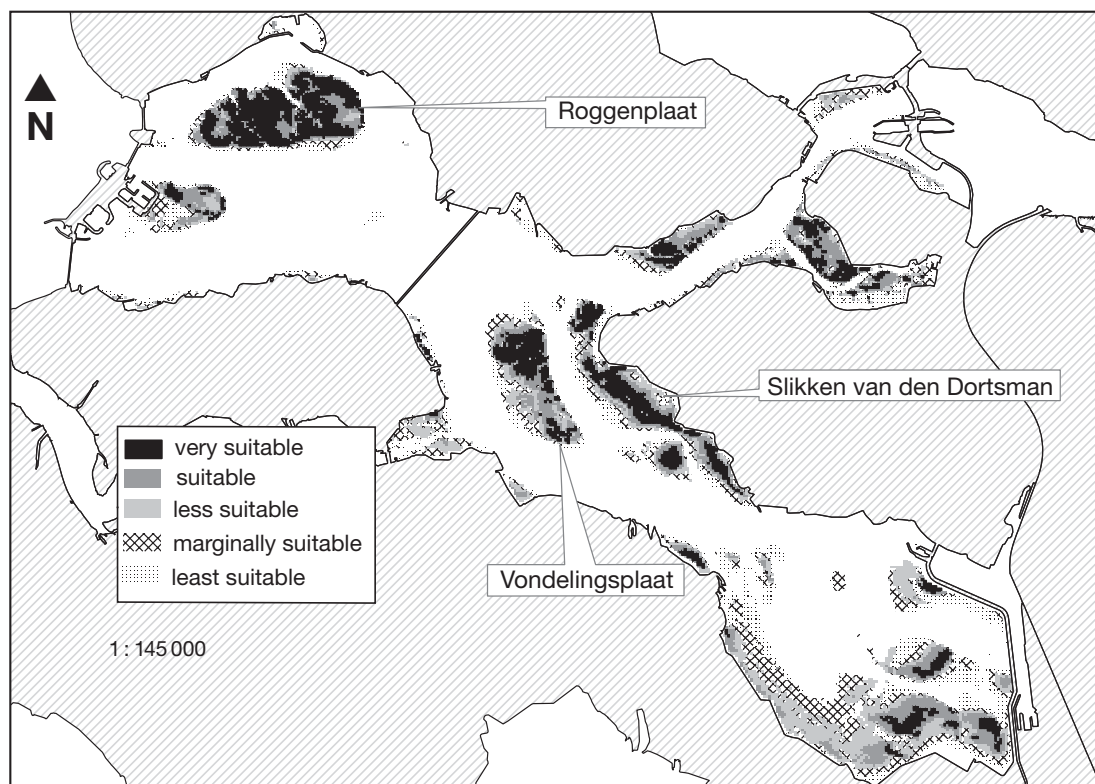


Fig. 3. Cockle habitat suitability map of the Eastern Scheldt

the oyster map of 2002, the highest percentage of grid cells occupied by Pacific oysters was found in areas classified as 'less suitable' for cockles (13%). Oysters occupied fewer than 5% of the grid cells classified as 'very suitable' for cockles. The χ^2 test for independence showed significant differences between the years ($\chi^2 = 17.5$; $p = 0.002$). Generally, Pacific oysters appear in cockle habitat areas classified as 'less suitable', 'marginally suitable' and 'least suitable', as shown in Fig. 4.

DISCUSSION

Habitat model

In this study a habitat model was developed to explain the distribution of cockle biomass in the Eastern Scheldt relative to salinity, current velocity and emersion time. Salinity (first and second order) and all interactions with salinity were non-significant. The fact that salinity does not play an important role is not surprising, given the limited salinity range in the Eastern Scheldt (28 to 33‰) and the relatively broad tolerance range of cockles (10 to 35‰).

Current velocity (first and second order) and emersion time (first and second order) explained 37.3% of

the deviance. García-Charton & Pérez-Ruzafa (2001) used Poisson regression to explain the species richness of reef fish in Spain. They found that 32.2% of species richness could be explained by the number of medium boulders and % *Posidonia* fields, which is about the same as the deviance explained in this study. The estimated cockle stock approximates the measured cockle stock, which shows that the habitat model accurately reflects the actual stock.

Current velocities

In an experimental situation (20°C), using a continuous flow, the Mediterranean mussel *Mytilus galloprovincialis* showed a maximum clearance rate at 25 cm s⁻¹ (Denis et al. 1999). Filtration by blue mussels *Mytilus edulis* is inhibited by increasing the flow velocity from 6 to 25 cm s⁻¹. Flows exceeding 25 cm s⁻¹ cause much reduced consumption of chlorophyll *a* (Wildish & Miyares 1990). Nevertheless, Widdows et al. (2002) found that the clearance rates of mussels from open coast sites were unaffected by current velocities up to 80 cm s⁻¹.

Ysebaert et al. (2002) modelled the cockle population in the Western Scheldt. They predicted a probabi-

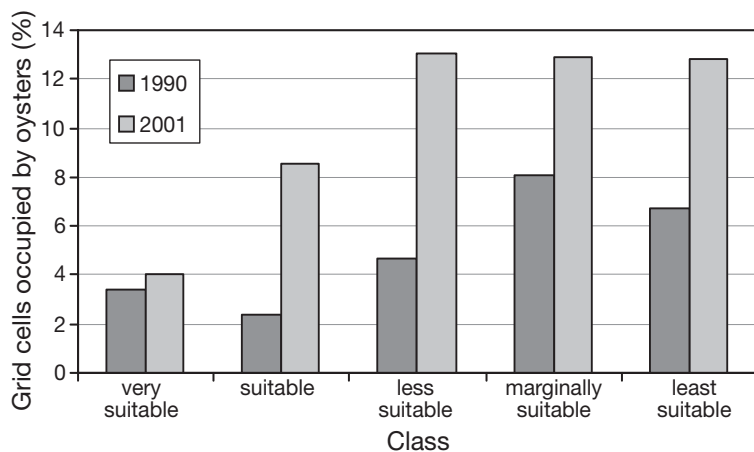


Fig. 4. Percentage of grid cells occupied by Pacific oysters in 1990 and 2001

lity of >10% that cockles would be found at maximum ebb current velocities between 10 and 60 cm s^{-1} . This study shows that maximum biomass occurs at current velocities between 30 and 40 cm s^{-1} , which is more or less in line with other studies. It should be noted that most studies present an average current speed, while this study used the maximum current velocity at ebb during spring tide.

Emergence time

The habitat model predicts maximum biomass at emersions between 40 and 60%. At a study site in France, cockle growth was strongly influenced by habitat. Tidal elevation explained most of the observed differences in growth rate between experimental sites. Growth rates were reduced with emersion times over 50%, and growth was expected to stop at emersion times over 70% (De Montaudouin 1996). De Montaudouin & Bachelet (1996) also found in field experiments that individual growth rate and condition of cockles declined with increasing tidal elevation. These results are not in line with results found by the habitat model, because the model shows a preference for emersions around 50%. This means that cockle biomass in the Eastern Scheldt behaves differently to the French study.

First, we need to establish whether this is a new situation, or if cockles have always had their highest biomass at emersion times around 40 to 60%. Meire et al. (1994a) sampled macrozoobenthos in the Eastern Scheldt in 1985 and 1989, and took depth measurements of the sample points. Filter feeder biomass in this study consisted mainly of cockles. In 1985 the highest biomass was found in depth classes between -0.75 and 0 m below Amsterdam Ordnance Datum (NAP). This means they were found between 30 and

50% emersion time. In 1989 the highest biomass was found between -0.50 and +0.25 m, which is comparable to 35 to 55% emersion time. This means that, since 1985 at least, cockles in the Eastern Scheldt have been achieving their maximum biomass in areas with emersion times around 35 and 50%.

The absence of high biomass at sites with low emersion times may be caused by predation pressure on the population at lower parts of the intertidal area. At high tide organisms like flounder, shrimp and crabs prey upon cockles (Richards et al. 1999), while at low tide birds like oystercatchers prey upon cockles in the same area (Meire et al. 1994b). Models of the Western

Scheldt produced by Ysebaert et al. (2002) showed that the probability of cockle occurrence increased with decreasing depth, which is comparable with an increase in emersion time. Bouma et al. (2001) showed that, on sand flats in the Western Scheldt where the sediment was unstable because of wave action, sediment dynamics and bed-level height were the variables that best explained the early recruitment patterns of cockles. Another possible explanation for the fact that cockles in the Eastern Scheldt are found in places with longer emersion times is that these places are too dynamic to be settled, as in the Western Scheldt.

If Pacific oysters completely took over the part of the habitat with emersion times below 30%, this would lead to an influenced habitat preference of 40 to 60%. However, Meire et al. (1994a) showed that cockle frequencies in the Eastern Scheldt have been high in the intertidal area since 1985. In 1985 the Pacific oyster had not yet established itself widely on intertidal sand flats (Kater & Baars 2004). Therefore, Pacific oysters did not force cockles to move to higher zones in the intertidal area.

These results show that oysters do not occupy places where the map predicts high cockle biomass. This means there is no competition between oysters and cockles at most suitable cockle habitats, though there is competition at less suitable cockle habitats. Further expansion of oyster beds could lead to competition at most suitable cockle habitats in the future.

Cockle fisheries

The intertidal cockle habitat model presented here is composed of data collected over 10 yr. These data were collected in both fished and unfished areas. Due to significant differences between areas open to cockle

fishing and areas where cockle fishing is not permitted, it was not possible to build 2 models and compare both habitats. To see whether cockle fisheries influence the present habitat map, one would need to know where cockles lived before cockle fishing started in the Eastern Scheldt. Unfortunately, no such data are available.

CONCLUSIONS

The distribution of cockles can be described using emersion time and current velocity. Salinity does not play any significant role. Response to current velocity is as expected, but response to emersion times (highest biomass at emersion times around 40 to 50%) contradicts expectations based on other studies. This cannot be explained by competition from Pacific oysters. Possible explanations include high predation pressure around low water level, or instability of the sediment caused by waves preventing cockles from settling in this area. We recommend that the cause-effect relationships be explored further by means of experimental research.

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