

The introduced clam *Ensis americanus* in the Wadden Sea: field experiment on impact of bird predation and tidal level on survival and growth

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Abstract In the Danish Wadden Sea the intertidal distribution of the introduced bivalve *Ensis americanus* (syn. *E. directus*) is restricted to a narrow zone around the mean low water level. To test the possible impact of birds and submersion time on dynamics and distribution of the clams, adult specimens of *E. americanus* collected near the low water line were transplanted to two intertidal sites and established in open and net-covered experimental plots for 9 weeks (autumn 2001). The lowest survival of clams was registered at the low-shore-site (LSS) in plots open to bird predators, suggesting that birds such as Common Eider (*Somateria mollissima*) or Oystercatcher (*Haematopus ostralegus*) may control the abundance of *E. americanus* at the lower tidal levels. For clams showing increment in shell length during the study period, the shell growth rates were highest at the LSS and lowest in the open plots at the high-shore-site (HSS). Differences in immersion time and thus food supply may explain this pattern. Body mass index (BMI) of the clams showed basically the same pattern as the survivorship: lowest BMI in open plots at the LSS and highest in the covered plots at this site. Clams from the HSS were intermediate in their BMI. Disturbance by birds in the open plots at the LSS may explain the low BMI. In

conclusion birds may be an important factor controlling abundance of *E. americanus* in the lower intertidal zone.

Keywords Bird predation · *Ensis* · Field experiment · Intertidal flat · Introduced species · Wadden Sea

Introduction

The American Razor Clam (*Ensis americanus* Binney 1870; syn. *directus* Conrad 1843) was introduced to coastal waters in Europe in the late 1970 s, probably as larvae through ballast water (Von Cosel et al. 1982; Knudsen 1989; Rasmussen 1996). Von Cosel et al. (1982) found *E. americanus* for the first time in European waters in 1979 on a subtidal site near the Elbe river. In the succeeding years the species dispersed widely along the European coastline (Essink 1986; Luczak et al. 1993; Brattegard and Holthe 1997; Knudsen 1997; Armonies 2001), where it now appears to be a persistent member of the macrozoobenthos. *E. americanus* occurs widespread in shallow sublittoral areas (Armonies and Reise 1999) and in the Wadden Sea area its distributional zone span from near the mean low water level (MLWL) and seawards (Mühlenhardt-Siegel et al. 1983; Beukema and Dekker 1995). Though the main population occurs outside the tidal zone, high adult densities have been observed in the lower intertidal zone in some areas in the Danish Wadden sea (TJ, own observations). The size distribution of these clams located in the intertidal zone suggests that they are not just a spin-off from the main population but that they are an integral part of the recruiting stock.

Whereas newly settled and juvenile *E. americanus* specimens in the intertidal zone can be expected to be preyed upon by a range of epibenthic generalist predators and small shorebirds otherwise eating juvenile *Mya arenaria*

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and *Cerastoderma edule* specimens, it is less obvious if predators are able to control stocks of adult *E. americanus*. They reach a refuge given the size-dependent burrow depth and their fast withdrawal response when approached by an enemy. Oystercatcher (*Haematopus ostralegus*) (Swennen et al. 1985), gulls (*Larus* sp.) (Schneider 1982; Dervedde 1994; Knudsen 2001), Common Eider (*Somateria mollissima*) (Freudentahl and Nielsen 2003) and Common Scoter (*Melanitta nigra*) (B. Jacobsen, personal communication) are known as consumers of *E. americanus*, but to what extent their consumption influence the standing stock of clams is unknown.

To test if *E. americanus*-consuming birds could impact clams living on an intertidal flat we have conducted a field experiment in the autumn, where the numbers of potential bird predators (eiders, oystercatchers and gulls) are highest (K. Laursen, personal communication). Experimental plots with and without protective cover and incubated with clams >30 mm were deployed at two sites along an intertidal gradient to test if the impact of birds were dependent on duration of tidal immersion. Lower clam survival and growth rate in open plots compared to covered plots would suggest an impact of waterbirds, whereas differences between sites would indicate the impact of factors related to immersion time. Simultaneously, the experiment allowed us to test if clams can survive and grow higher on the intertidal flat than where they usually are observed.

Materials and methods

The study was conducted in the Danish Wadden Sea at the intertidal area between the island Mandø and the mainland (55°17'N; 8°38'E) (Fig. 1). In this area the tidal range is approximately 1.8 m and the density of *E. americanus* decreases distinctly in an onshore direction from the MLWL. During low tide the higher tidal areas are influenced by freshwater from a small streamlet.

At two tidal elevations, a High-shore-site (HSS) and a Low-shore-site (LSS), plots were established protected from [+] and exposed [-] to bird predators. Vertically HSS and LSS were placed at tidal elevations of +18 and -47 cm relative to Danish Vertical Datum corresponding to 11 and 19 h duration of tidal immersion each 24 h, respectively. The horizontal distance between the sites was approximately 800 m. The sediment consisted mainly of fine sand (median 125–250 μm , silt <6.4%, organic content 8.1–19.3 mg cm^{-3}), the grain size composition being a little coarser at HSS (Freudentahl and Nielsen 2003).

The densities of macrozoobenthic species were generally higher at the LSS than at the HSS. The polychaetes *Capitella capitata*, *Heteromastus filiformis*, *Phyllodoce maculata*, *Pygospio elegans*, *Scoloplos armiger* and *Tharyx killariensis* were dominant. The pooled density of *Cerastoderma edule* and *Mya arenaria* (potential trophic competitors) was low (150 individuals m^{-2} at the HSS and less at the LSS (Freudentahl and Nielsen 2003).

At each site ten plots of 0.64 m^2 were established with 4 m intervals. Five of the ten plots were covered with chicken wire (net size 3–4 cm), placed 15 cm above the sediment surface (Fig. 2). Sides were left open to avoid accumulation of drifting macroalgae and to minimize potential cage effects (Hamilton 2000). Non-covered squares were marked at each corner by a stick projecting 5 cm above the sediment surface.

Specimens of *E. americanus* used in the experiment were collected close to LSS at low tide. The animals were kept in aquaria in about 24 h (re-established on the experimental plots at the succeeding day time low tide). While kept in the laboratory their shell lengths were measured to nearest 0.1 mm using callipers, and the clams were individually marked with nail polish. The overall size range was 34.2–155.2 mm with a median of 73.3 mm. To each plot were added 20–25 clams showing similar size distribution. Only the inner 0.25 m^2 of each plot was used for the clams. Those that did not burrow within 45 min were discarded,

Fig. 1 Map of the study area near Vester Vedsted in the Danish Wadden Sea. Filled circles indicate the experimental sites (HSS and LSS)

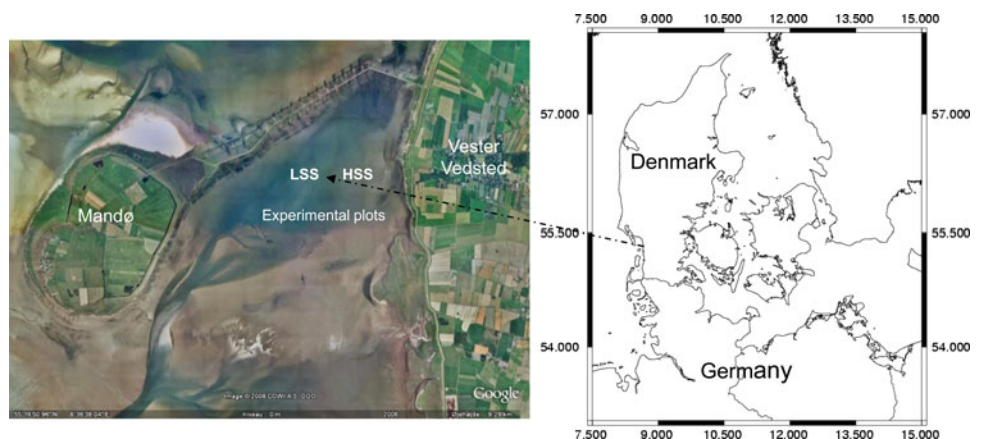




Fig. 2 Photo of the experimental setup at the low-shore-site (LSS) at rising tide. *Inset photo* shows one of the five plots protected [+] from bird predators

and additional clams were collected and established at the succeeding tides. Clams collected at a given low tide period were distributed among the experimental plots and the duration of the experimental period was recorded for each individual.

The plots were established ultimo September and maintained until December 2001. As the primary goal was to examine the possible impact of birds on mortality of *E. americanus* this period is considered optimal (many Eiders and Oystercatchers in the Wadden Sea). However, being a period after the main season for phytoplankton production it is less optimal for assessing growth patterns of *E. americanus*. Nonetheless, our interest in this respect is growth differences as a function of experimental treatments and not the absolute growth rates.

After ending the experiment, sediment from each plot to a depth 40 cm was sieved through a 1 mm mesh. The clams were frozen individually until length and weight measurements were undertaken. Length was measured again to nearest 0.1 mm using callipers and to determine ash free dry weight (AFDW), the soft parts were dried at 102°C for 24 h, and ashed at 520°C for 12 h.

Throughout the experimental period the plots were inspected weekly for empty and marked shells. Occasionally, it was necessary to clean the plots for macroalgae. To compare length–weight relationships of the experimental clams with non-manipulated clams, specimens of *E. americanus* were collected in November at the original sampling site.

Statistics

Statistical analyses were carried out using GLM-univariate test from the statistical package SPSS 13.0 for Windows. Data not fulfilling the requirement of variance homogeneity were transformed. For further details of the applied statistical procedures see Sect. "Results." To compensate for the unequal experimental duration among individual clams, post experimental lengths were standardized to 60 days based on the individual average daily growth rate. All clams were inspected visually after the experiment, and individuals with damaged or broken shells were eliminated from analyses of growth and condition.

To examine whether the experimental treatments affected the body condition of the razor clams, a body mass index (BMI, AFDW/shell length³) was calculated. Using *t* tests, BMI of clams with and without positive shell increment during the experimental period was compared for each plot type at both stations.

In analysis of covariance (ANCOVA) and ANOVA tests concerning growth rate and BMI respectively, an identical number of cases were randomly selected from each treatment to ensure balanced data.

The growth rate of experimental clams was compared to non-manipulated clams collected near the LSS.

Results

Mortality

On average 56.8 (± 4.0 SE)% of the razor clams from HSS and from the protected plots at LSS survived the 9 weeks experimental period. In contrast, only 29.5 (± 4.8 SE)% survived in the unprotected plots at LSS (Fig. 3a). The effect of protecting the experimental animals by using chicken wire differed between tidal levels. Statistically this is evident as a significant interaction term [Table 1, $P = 0.05$; considering the low power (0.508) to reject the zero-hypothesis of no interaction, it is not justified to ignore an interaction term based on a marginal non-significant test probability (Zar 1999)]. The results accordingly suggest that selective mortality agents were acting on clams from the unprotected plots at the LSS [–]. This is further confirmed by a *t* test demonstrating a significant difference between the survival rates of clams from the two plot types at LSS (*t* test, $t_8 = 3.316$, $P < 0.05$). Our interpretation is that clam-consuming birds at the LSS caused the observed above-control mortality in the open plots, whereas birds did not manage to locate the food source at HSS.

The clams that died or disappeared during the experiment (in total 168 of the 273 added specimens) had a slightly larger initial length than the surviving clams (*t* test,

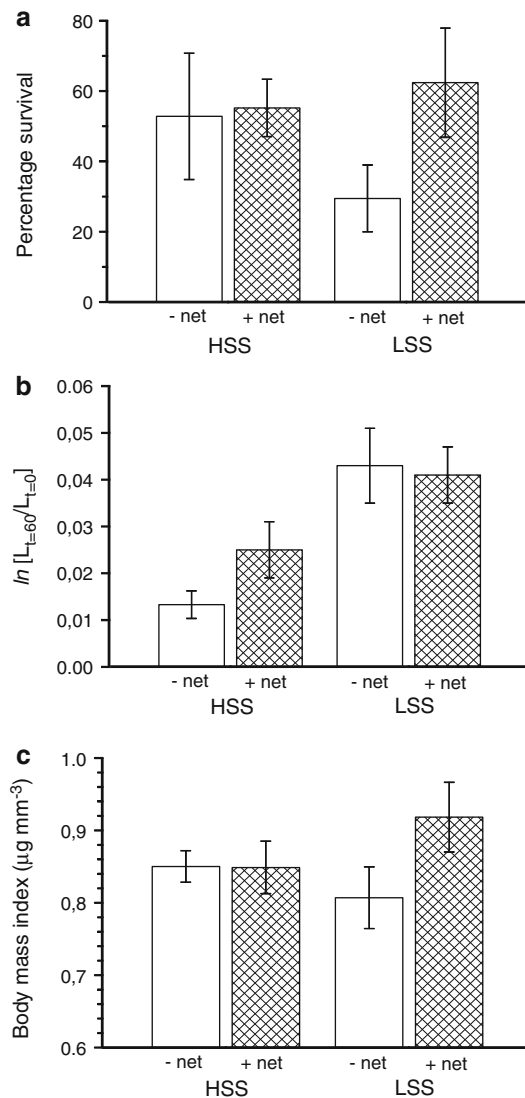


Fig. 3 Survivorship, growth and condition index for *Ensis americanus* from the field experiment on the intertidal flat at Vester Vedsted (Denmark) conducted from late September to early December. **a** Mean percentage survival ($\pm 95\%$ CI) of clams; **b** Mean growth rates [$\ln(\text{length}_{t=60}/\text{length}_{t=0})$] ($\pm 95\%$ CI) of clams showing positive shell increment during the experimental period. For HSS [-] the mean of all sizes is shown as there was no significant regression between growth and initial length [$\ln(\text{length}_{t=0})$]. For the others adjusted mean values are shown based on the ANCOVA indicated in Table. 2. **c** Body mass index ($\text{weight}/\text{length}^3$) of clams showing positive shell increment during the experimental period ($n = 23$ in each group—for details see Table. 3)

$t_{439} = 3.032$, $P < 0.05$): 77.9 ± 2.17 vs. 72.0 ± 2.36 mm (mean $\pm 95\%$ CI).

Growth

Manipulation of the clams (excavation, transport to laboratory, marking, re-establishment) inflicted a disturbance ring on the shells. The shell material added after the disturbance

Table 1 Analysis of variance of survival data of *E. americanus*: Effect of site and experimental plot on percentage survival (arcsine transformed data) of clams

Source of variation	df	MS	F-ratio	P value
Site (HSS vs. LSS)	1	66.84	0.949	0.344
Plot type (+net, -net)	1	452.21	6.421	0.022
Site \times plot type	1	312.48	4.437	0.051
Error	16	70.43		
Total	20			

At both sites (HSS and LSS) five plots with and without net were established. To each plot (0.64 m^2) 20–25 clams were added. The experiment was established in late September and finished in early December
df Degrees of freedom, MS mean square

ring was fragile and easily broken when handling the clams. As a result, it was impossible to demonstrate growth in some of the clams with lost shell material. The fraction of surviving clams that showed positive shell growth varied from 52% at HSS [-] to 71.9% at LSS [-], but the difference between the plots is not significant (Pearson, χ^2 -test, $df = 3$, $P > 0.05$). The shell increment of clams showing growth was generally small during the study period (late September to early December). So, the average shell increment ($\pm 95\%$ CI) of 60–70 mm clams was 2.7 ± 0.5 mm at the LSS and 1.2 ± 0.3 mm at the HSS. In comparison, similar aged non-experimental clams close to LSS grew from 76.4 (mean length) to 82.3 mm (5.9 mm) from August/September to November.

To compare growth rates of clams from the various treatments an ANCOVA can be used assuming a linear relationship between growth rate [$\ln(\text{length}_{t=60}/\text{length}_{t=0})$] and initial shell length [$\ln(\text{length}_{t=0})$] as expected according to the Gompertz growth model (Kaufmann 1981). For all treatments except [HSS-], there is a significant ($P < 0.001$) negative linear relationship (r^2 around 60%) between growth rate [$\ln(\text{length}_{t=60}/\text{length}_{t=0})$] and initial shell length [$\ln(\text{length}_{t=0})$] of the experimental clams. For the growth data from [HSS-] the relationship between growth rate and initial length is not significant (the length spectrum of the survived clams was too narrow in this treatment). An ANCOVA with initial length [$\ln(\text{length}_{t=0})$] as covariate indicates a significant difference between the growth rates of clams from HSS [+], LSS [-] and LSS [+] (Table 2). Adjusted means of growth rates from these treatments are shown on Fig. 3b. For clams from HSS [-] the average growth rate [$\ln(\text{length}_{t=60}/\text{length}_{t=0})$] is depicted. Clams from LSS had on average 73 and 212% higher growth rates than those from HSS [+] and HSS [-], respectively.

Mean BMI ($\text{weight}/\text{length}^3$) of clams from HSS [-] that showed shell growth ($\text{length}_{t=60} > \text{length}_{t=0}$) is higher than mean BMI of clams where we could not demonstrate growth [$0.83 \pm 0.01 \mu\text{g mm}^{-3}$ ($\pm \text{SE}$; $n = 34$)

Table 2 Analysis of covariance of growth rates of *E. americanus*: Effect of plot-type (HSS [+]/LSS [-]/LSS [+]) on growth rate [$\ln(\text{length}_{t=60}/\text{length}_{t=0})$] of clams with initial shell length [$\ln(\text{length}_{t=0})$] as covariate

Source of variation	df	MS	F-ratio	P value
Treatment: [HSS+/LSS-/LSS+]	2	0.003	11.447	0.000
Covariate:ln (initial length)	1	0.044	153.774	0.000
Error	97	0.000		
Total	101			

Prior to this analysis it was shown that there was no interaction (common slope) between regressions of growth rate on initial length of clams from the different plot-types. Furthermore all regression lines were significant and with r^2 -values around 60%

df Degrees of freedom, MS mean square

vs. $0.78 \pm 0.03 \mu\text{g mm}^{-3}$ ($\pm\text{SE}$; $n = 17$); t test, $t_{49} = -2.01$, $P = 0.05$]. The same tendency is seen among clams from HSS [+] and LSS [+] (we have not weight data of the clams with no shell growth from LSS [-]). A two-way ANOVA on a balanced data matrix of BMI of clams with positive shell growth (specimens were removed at random to equalize the number in each group to 23 specimens) indicates a significant interaction between site [HSS and LSS] and plot type [+ and -] (Table 3; Fig. 3c) due to the difference in BMI of clams from the two plot types at the LSS. Mean BMI of clams from LSS [+] is significantly higher than mean BMI from LSS [-] (t test, $t_{44} = -3.571$, $P = 0.001$).

Discussion

Mortality

The exact reason for the high background mortality remains unresolved, but could be related to stress and physical damage induced during the marking procedure (as discussed under “Growth”). It cannot be excluded that a certain fraction of the clams have escaped from the experimental plots. Disturbance by other organisms could be one reason for

Table 3 Analysis of variance of body mass index [$\text{weight}/(\text{length})^3$] of *E. americanus*: Effect of site and plot-type on BMI

Source of variation	df	MS	F-ratio	P value
Site (HSS vs. LSS)	1	0.004	0.491	0.485
Plot type (+net, -net)	1	0.070	8.521	0.004
Site \times plot type	1	0.073	8.936	0.004
Error	88	0.008		
Total	92			

A balanced data matrix was prepared by removing cases at random to equalize the number in each group to 23 specimens

df Degrees of freedom, MS mean square

such behaviour as reported by Schneider (1982) for a predatory snail disturber. But no such species was observed. The high above background mortality in the LSS [-] plots is most likely caused by clam-eating birds. The experimental density of clams used was much higher than the ambient densities at both sites. Therefore open plots represent small “hot spots” with valuable food resources to such birds.

In the Wadden Sea, oystercatchers have been observed foraging on *E. americanus* at low tide (Swennen et al. 1985; Dervedde 1994). Faecal and stomach studies of Common Eider from Norway and from the Danish and Dutch Wadden Sea have revealed *E. americanus* in its diet (Leopold 2002; Freudendahl and Nielsen 2003; Cadee 2006). We assume, that eider ducks in combination with oystercatchers were the main predators at LSS [-]. Gulls are not considered important in the present experiment as they mostly consume unburied specimens of razor clams, as seen during mass stranding (Knudsen 2001), in connection with escape responses of razor clams from infaunal predators (Schneider 1982) or through kleptoparasitism on oystercatchers (Dervedde 1994). Eiders and oystercatchers are present all year round in the Wadden Sea, but in higher numbers during autumn and winter (Meltofte et al. 1994; Blew and Südbek 2005; K. Laursen, personal communication). Thus the experiment was conducted in a period with high numbers of these birds.

Marked shells with clear signs of predation were occasionally found on the flats around the experimental plots, but no birds were observed foraging directly in the plots. Eider ducks had the opportunity to forage at both experimental sites, as HSS and LSS are flooded to a depth of 80 and 150 cm, respectively. The low height (15 cm) of the net-covered cages protected the clams in these cages from birds. Only small birds such as *Calidris* sp. and fish and crabs could move inside the covered cages. However they had all free access to both protected and unprotected plots.

To calculate the daily energy requirement of an eider of 2,500 g we used empirically determined field metabolic rates for birds (Krebs 2001). Given the calorific content of a 60 mm *E. americanus*, we estimate that one eider needs about 250 razor clams pr. 24 h to cover its metabolism. Similar calculations for an oystercatcher indicate 90 clams pr. 24 h. With the dense stock of eider ducks and oystercatchers during autumn in the Danish Wadden Sea, a few foraging birds around the open plots could easily explain the mortality of clams at LSS [-]. Why clams from HSS [-] escaped being eaten by birds is less understandable. However, there is an element of chance and eider ducks are not expected to search for food at this tidal level whereas oystercatchers following the incoming and outgoing tide when foraging will be able to utilize food items at HSS. Retreating to greater depth during low tide exposure and thereby escaping oystercatchers might be an explanation.

A total of only six marked empty shells were found in the sediment at termination of the experiment, two at the LSS and four at HSS. Thus, the majority of dead individuals disappeared from the experimental plots, as would be expected if taken by avian predators such as eider ducks and oystercatchers. Dead or dying individuals could also have been washed away by the tide. The individuals that died during the experiment were, as a whole, significantly larger than the survivors, but both large and small experimental individuals were present in both groups, telling little about the whereabouts of the “missing” individuals.

Growth

A cohort of non-experimental clams collected near the LSS grew from an average shell length of 76.4 (August/September) to 82.3 mm (November). Thus, the experimental clams showed a reduction in shell growth relative to the shell increment of non-manipulated clams. This may partly be explained by their later growth period and partly by growth reduction inflicted through the manipulation of the clams. Though *E. americanus* is well adapted to variation in environmental factors when established in the substratum (Freundendahl and Nielsen 2003), it is much more vulnerable outside. Inability to seal off the soft parts by the shell valves may cause evaporation and loss of substances. Although the specimens were treated carefully before being incubated in the experimental plots, both soft-parts and shells could have been slightly injured during handling (breakage of thin parts of the shells; squeezing of soft-parts).

An additional factor that might contribute to reduced growth of the clams could be intraspecific food competition. In the present experiment, the density was much higher than the ambient density of two adult individuals m^{-2} (MLWL, TJ, own data), but not as extreme as reported from subtidal sites (Armonies and Reise 1999). Both field observations and lab experiments have demonstrated that high densities of suspension feeders on intertidal flats may impact their individual growth rates (Jensen 1992, 1993).

Clams from LSS showed the highest growth rates and those from HSS [–] the lowest, whereas clams from HSS [+] were intermediate in this respect. Apparently the presence of a net above HSS plots caused some interference with the growing conditions. At HSS [+] but not at LSS [+], the net caused some sediment erosion, and a few centimetres of water remained during low tide, probably induced by entanglement of drifting macroalgae in the first weeks of the experimental period. Even if a small pool of water will be depleted for food items by suspension-feeding clams within a short time, the presence of a pool may have caused a less stressful environment for HSS [+] clams. We suspect this “cage-effect” to be responsible for the higher mean growth rate at HSS [+] than at HSS [–].

The difference in length growth between clams from the two tidal sites can be explained by the difference in submersion time varying from approximately 11 at HSS to 19 h at LSS. For suspension feeders, the submersion time during a tidal cycle determines the available time for filtration and thus affects the food intake and amount of energy available for growth (Reise 1985; Jensen 1992; Wanink and Zwarts 1993). Other factors correlated with submersion time could also be important. For instance, the salinity was generally 28–30‰, but occasionally 10‰ in pools during low-water at HSS due to an influence of freshwater from the streamlet at Vester Vedsted (Fig. 1). Though these salinities are within the tolerance spectrum of adult razor clams (Freundendahl and Nielsen 2003) the occurrence of low salinity at the HSS could be a potential stress factor.

At least 50% of the surviving clams from the HSS were able to grow at a tidal level situated higher up-shore than their normal intertidal habitat close to the MLWL (TJ, own observation). As individuals here in addition had a body condition only slightly lower than non-manipulated clams collected near the MLWL [0.83 ± 0.10 (\pm SD; $n = 96$) at HSS vs. 0.87 ± 0.14 (\pm SD; $n = 238$) of non-manipulated clams], they are considered healthy. But as their mean growth rate was low and because many specimens from the HSS did not grow at all it might indicate that the clams at HSS are close to a critical point between food supply and metabolic demand. As both vary seasonally, the most critical phase could be late summer when the temperature dependent metabolic rate is at a maximum and the phytoplankton biomass can be expected to be low (Cadee and Hegeman 2002).

The low BMI at LSS [–] is surprising because the clams from these plots had a relatively high growth rate. Disturbance from foraging birds might cause clams to use less time for feeding and could explain the low BMI but not the high growth rate. However, shell growth could have been accomplished during the first part of the experimental period (higher temperatures) and the low BMI could be caused by increased frequency of disturbance throughout the season. The latter may have caused a reduction in BMI without changes in shell length.

Factors controlling distribution and abundance

The present study does not corroborate tidal level and bird predation as important to the survival of clams on the HSS. As the clams on this site grew during the study period the absence of clams on this tidal level can not be explained by the physical conditions prevailing during autumn. However, it is still possible that conditions in other seasons or factors impacting settlement and survival of juveniles may determine the limit for their shoreward spread. So, high temperatures during summer combined with limited food

supplies in the upper intertidal zone may control growth and survival up-shore. Likewise cold winters with ice formation may have a more severe impact on high-shore clams than on low-shore clams. Settlement patterns of juveniles and postsettlement processes could also determine the intertidal distribution of *E. americanus*. Newly settled individuals seems only to survive and grow near and below MLWL (Mühlenhardt-Siegel et al. 1983; Beukema and Dekker 1995). The fluctuating environmental conditions at more up-shore sites could be more severe to juvenile clams than to adults and this might control the intertidal distribution of the species.

In contrast to many other exotic species, the success of *E. americanus* in its new ecosystem is not based on escape from predators (i.e. the enemy-release-hypothesis). The present study provides indirect evidence that birds such as eider ducks or oystercatchers may control the abundance of clams on the lower intertidal flat. A recent study of eiders shot in the Danish Wadden Sea indicate the presence of *E. americanus* fragments from clams (length range from 28 to 136 mm) in 41% of the examined ducks ($n = 111$) (Freudentahl and Nielsen 2003). Furthermore, some eider ducks have been observed with several specimens of *E. americanus* in their digestive system (up to 34 specimens in one duck). If given the choice they seem to prefer *E. americanus* for *Mytilus edulis* despite differences in accessibility of the two bivalves to the ducks. Whereas *Mytilus edulis* specimens are established in aggregated beds on the surface, *E. americanus* specimens occur individually in burrows to a depth of 30–40 cm. While feeding and inhaling water they stay in the upper part of their burrows as they only have short siphons, but disturbance elicits immediately their retraction into the deep parts of the burrow (KTJ, own observation). Nonetheless, eider ducks have adapted to this new prey-item in the Wadden Sea region. Other waterbirds such as Common Scoter foraging subtidally in the North Sea area do also include a significant amount of *E. americanus* in their diet (ASLF, own observation). Based on the studies of eiders and scoters it seems that *E. americanus* play an important role in the energy budgets of these ducks. By being a valuable food resource to birds otherwise utilizing native bivalves (*Mytilus edulis* and *Cerastoderma edule*), *E. americanus* may be particularly important in areas where overexploitation of mussels or winter mortality of cockles have reduced these native food resources (Cadee 2006). The presence of *E. americanus* may help stabilizing the resource base to eiders in the Wadden Sea. However, in places with dense stocks competition for phytoplankton may have negative effects on native suspension-feeders (Armonies and Reise 1999) but according to Beukema and Dekker (1995) *E. americanus* mainly inhabits macrozoobenthos poor habitats on very exposed sandy substrata. Although further studies are

required to quantify the overall significance of *E. americanus* in the Wadden Sea ecosystem, available evidence does not support *E. americanus* as a harmful invader.

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