

Niche dimension differs among life-history stages of Pacific oysters in intertidal environments

Brenda Walles^{1,2,3,*}, Aad C. Smaal^{1,2}, Peter M. J. Herman³, Tom Ysebaert^{1,3}

¹Wageningen Marine Research, Wageningen University & Research, PO Box 77, 4400 AB Yerseke, The Netherlands

²Aquaculture and Fisheries Group, Wageningen University and Research, PO Box 338, 6700 AH Wageningen, The Netherlands

³NIOZ Yerseke, Royal Netherlands Institute for Sea Research and Utrecht University, PO Box 140, 4400 AC Yerseke, The Netherlands

ABSTRACT: Structure-building, autogenic ecosystem engineers are recognized worldwide as potential tools for coastal protection, which depends on long-term sustainability and persistence of their structures. For reef-building oysters, reefs are maintained through accumulation of shell material, which depends on recruitment and growth and which provides substrate for new generations. Knowledge of the fundamental niche of oysters in relation to biotic and abiotic conditions helps define the area where ecosystem engineers grow and survive well and where their structures are likely to persist and be effective for coastal protection. Response curves of different life-history stages (larvae, juveniles and adults) of the Pacific oyster *Crassostrea gigas* were investigated along a tidal emersion gradient in a manipulative field study. Density of juvenile oysters was maximal around 36 % tidal emersion. Shell growth of juveniles and adults, condition index (CI) of adults and mortality of adults were negatively related to tidal emersion, whereas mortality of juveniles was positively related to tidal emersion. Tidal emersion had a strong effect on oyster survival and growth, with the most favourable being around 20 to 40 % tidal emersion, as indicated by recruit density and the CI of adults. These findings suggest that the area of 20 to 40 % tidal emersion is optimal for reef development, which is in line with other investigations of *C. gigas* and the eastern oyster *C. virginica* across different systems, supporting a broader geographical application of these findings.

KEY WORDS: Oyster reef · Ecosystem engineering · Recruitment · Growth · Niche · Ecosystem-based management · Tidal flats

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Marine habitats such as oyster reefs, mangroves and salt marshes are recognized for their ecological engineering potential for coastal adaptation and hazard mitigation, as they have the natural capacity to reduce flow and dampen wave energy through their physical structures and can keep pace with sea-level rise by natural accretion (Gutiérrez et al. 2011, Cheong et al. 2013, Duarte et al. 2013, Temmerman et al. 2013, Walles et al. 2015a). Structure-forming aggregations of bivalves, such as oyster reefs and mussel beds, deliver many ecosystem services in

marine and estuarine ecosystems (Grabowski & Peterson 2007, Grabowski et al. 2012). In intertidal soft-sediment environments, mussel beds and oyster reefs commonly provide hard bottom substrate (Diederich 2005) essential for many structure-dependent organisms and complex food webs (Tolley & Volety 2005, Scyphers et al. 2011, Spalding et al. 2014) and offer protection against predation, waves, sedimentation and desiccation for many species (Gutiérrez et al. 2003, Commito et al. 2008). These structures alter water flow and reduce wave action (Borsje et al. 2011, Donker et al. 2013), while trapping and stabilizing sediment (van Leeuwen et al. 2010, Walles et

*Corresponding author: brenda.walles@nioz.nl

al. 2015a). Bivalve reefs and beds are therefore increasingly restored for shoreline protection and habitat enhancement (Byers et al. 2006), with restoration success depending on the long term persistence and sustainability of their structures.

Natural intertidal bivalve reefs do not occur randomly over tidal flats nor do they cover the entire area. Local-scale physical processes, food availability, competition and predation limit bivalve occurrence to a fraction of the total intertidal area (Heip et al. 1995). For example, in mussel beds, self-organization generates spatial patterns at different spatial scales, resulting in small-scale net-shaped patterns due to behavioural aggregation of individuals and large-scale banded patterns due to the interplay of intraspecific facilitation and resource depletion (Liu et al. 2014).

Within estuarine environments, biotic and abiotic factors affect species demography and determine the functional and realized niche of species. Predation, diseases, hypoxia, salinity, hydrodynamics, food availability and tidal emersion gradients alter demographic rates, which influence the development and persistence of marine populations. The fundamental niche for a species along one dimension is often conceptualized as a single response curve, with an optimum and thresholds beyond which individuals cannot survive (Jackson et al. 2009). Response curves, however, may differ among life-history stages, with adults often having wider niches than juveniles (Jackson et al. 2009). For sessile organisms, such as oysters, successful establishment and survival of a reef will depend on both the response of larvae and juveniles, which are important for the influx of new individuals into the reef, and the response of adults, which supply offspring and, in the case of oysters, settlement substrate for the next generation (Schulte et al. 2009, Walles et al. 2015b). Understanding the response of different life-history stages of species to environmental factors is critical in predicting how species occurrence might be altered in the future, especially under the influence of climate change.

This study focuses on the reef-forming Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in the Oosterschelde estuary of The Netherlands. In this estuary, tidal flats are eroding and disappearing due to human-induced changes (van Zanten & Adriaanse 2008). These tidal flats not only provide foreshore protection by reducing wave energy to the dikes but also provide foraging grounds for migrating water birds, for which the Oosterschelde is of international importance. *C. gigas* reefs locally protect the tidal flats against erosion in the Oosterschelde estuary

(Walles et al. 2015a). To mitigate erosion, artificial reefs can be constructed where erosion is most severe to provide a stable structure and stimulate reef development (de Vries et al. 2007). Because oysters are sessile organisms, reef development depends on recruitment events followed by growth and survival of juveniles and adults. Response curves of 3 life-history stages (larvae, juveniles and adults) were investigated along a tidal emersion gradient in a manipulative field study on 2 intertidal flats in the Oosterschelde estuary. Recruitment, growth, oyster performance and survival were quantified to determine niches of the life-history stages. We hypothesized that adaptation of oysters to tidal emersion leads to differential responses of growth and survival for the various life stages. Knowledge of Pacific oyster response to tidal emersion at different life stages can help decouple the fundamental and realized niches, identify habitat features where reefs can develop and potentially serve as a valuable predictive tool for management and restoration practices.

MATERIALS AND METHODS

Study area

The Oosterschelde estuary, located in the southwest of The Netherlands, is a 351 km² semidiurnal tidal basin with tidal flats (118 km²), artificial rocky shore habitats (dikes), deep gullies and shallow water areas. In response to a devastating flood in 1953, a storm surge barrier was constructed at the sea side (finished in 1986), separating the estuary from the North Sea; in the same period, the eastern part of the estuary was closed off by 2 compartmentalization dams. The basin area of the Oosterschelde, the tidal prism, the tidal range and the tidal currents decreased as a consequence of these measures. At present, the estuary has a mean tidal amplitude ranging from 2.47 m near the storm surge barrier to 2.98 m in the northern branch and 3.39 m at the southeast end (Nienhuis & Smaal 1994). The maximum current velocity is ~1.0 m s⁻¹. Salinity throughout the estuary is high, generally >30 psu (Nienhuis & Smaal 1994). Due to the reduction of tidal volume and flow, the Oosterschelde basin is presently not in morphological equilibrium, and the oversized channels are in need of sediment. Sediment erodes from the tidal flats into the channels during storms, whereas tidal forces are too small to redistribute the sediment back to the tidal flats (Mulder & Louters 1994); on average, a net erosion rate of 10 mm yr⁻¹

occurs on the tidal flats (Santinelli & de Ronde 2012). Reduction in tidal flat area and elevation diminishes valuable habitats, impacting bird and seal populations. It also poses a threat to coastal defence as dikes become less protected from waves and currents with the loss of tidal flats and salt marshes. The scale of erosion currently encountered in the Oosterschelde makes this ecosystem a suitable model system to study ecosystem-based coastal defence methods to combat coastal erosion.

Realized niche of Pacific oyster *Crassostrea gigas*

C. gigas was initially introduced in the Oosterschelde estuary in 1964, when the shellfish industry seeded the area with spat originating from British Columbia (Shatkin et al. 1997, Drinkwaard 1998, 1999). More introductions of both spat and adult oysters soon followed (Drinkwaard 1998). The first natural recruitment event after introduction was recorded in 1975 (Drinkwaard 1998). After this, the oysters spread rapidly (Smaal et al. 2009), presently occupying 9 km² of the intertidal (i.e. ~8%) in the Oosterschelde, typically forming dense reefs. The realized niche of oyster reefs in the intertidal zone of the Oost-

erschelde was determined using intertidal Pacific oyster *C. gigas* reef mapping (van den Ende et al. 2014), in combination with bathymetry maps. Oyster maps of 1980, 1990, 2002, 2005 and 2011 were combined with bathymetry maps of 1983, 1990, 2001, 2007 and 2010, respectively.

Site selection

To investigate larval occurrence, recruitment, growth, oyster performance and survival along a tidal emersion gradient, a manipulative field experiment was conducted at 2 tidal flats (Viane and St. Annaland) in the northern branch of the Oosterschelde estuary (Fig. 1). Both tidal flats are connected to dikes and contain natural oyster reefs and areas unoccupied by oysters between the dike and the natural reef and between the low water line and the natural reef. These flats differ in elevation and tidal emersion, with St. Annaland being lower than Viane. Several experimental sites were selected above mean low water, covering a range of 2 to 69% tidal emersion, including 7 at Viane ranging from 36 to 69% tidal emersion and 5 at St. Annaland ranging from 2 to 42% tidal emersion (Fig. 1). Tidal emersion time was calculated by converting height measure-

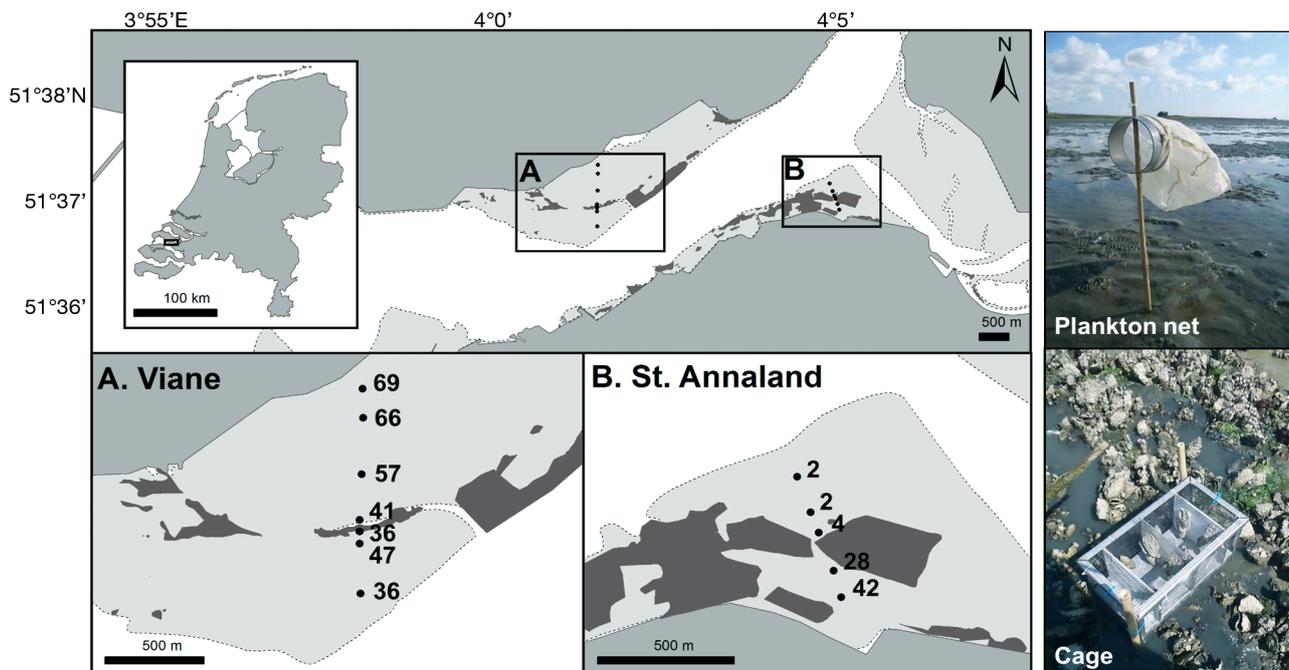


Fig. 1. Location of the 2 tidal flats (Viane and St. Annaland) in the Oosterschelde estuary (The Netherlands). Dotted lines (bordering light grey areas): mean low tide level. Light grey areas: intertidal zone. Dark grey areas: oyster coverage within the intertidal zone. Black dots: experimental sites with plankton nets and cages for the measurement of larvae occurrence, recruitment, growth rate, oyster performance and survival. Numbers: tidal emersion time in percentage

ments of each experimental site into average percentage of time the site was exposed between July and November 2010, using water levels measured at the Stavenisse gauge station (51° 35' N, 3° 55' E).

Larval occurrence

Pacific oysters spawn between July and September in the Oosterschelde estuary (Troost et al. 2009). The larvae stay approximately 3 wk in the water column before they are competent to settle on a suitable substrate and metamorphose into the benthic juvenile stage (Troost 2010). Because spawning occurs for several months, larval abundance and shell length were monitored daily from 15 July through 10 August 2010 to observe when oysters became competent to settle. At 5 locations along the platform of Wageningen IMARES (Yerseke, the Netherlands), samples of 20 l surface water were taken with a bucket (in total 100 l) and filtered over a 100 µm mesh. The residue was flushed into a bottle and brought to the lab. Samples were analysed on the same day. Bivalve larvae were counted using a universal camera microscope (Reichert Me-F2, 52.6×). Length of the larvae was measured as longest distance from anterior to posterior. In hatcheries, oyster larvae ready to settle have a length between 320 and 340 µm (Helm & Bourne 2004). When larvae of this size were observed in the samples (beginning of August 2010), plankton nets (Troost et al. 2009) were placed at each experimental site (Fig. 1) to investigate the occurrence of oyster larvae in the intertidal. The net opening (10.0 cm diameter, 60 µm mesh size) was oriented towards the current because the nets could freely rotate around bamboo poles (Armonies 1994). Nets were placed during low tide, with the centre of the opening 30 cm above the sediment. Nets were deployed on 2 different dates at the 2 tidal flats (Viane: 11 August 2010; St. Annaland: 13 August 2010) and collected after 2 tidal cycles. Moist nets were transported in plastic bags to the laboratory, where their contents were flushed into plastic containers and fixed with Lugol's solution, after which bivalve larvae were counted.

Recruitment

Three cages were placed at each experimental site from July 2010 until March 2011. Each cage (40 cm length × 22 cm width × 24 cm height) was constructed of stainless steel covered by 5 mm plastic mesh (Fig. 1). Each cage enclosed 2 vertical settle-

ment plates made from Plexiglas (20 × 18 cm), roughened by sandblasting and covered with a thin layer of chalk. Because settlement plates were in the field from the beginning of July, macroalgae were growing on the plates at the beginning of August, when larval settlement started. To standardize all plates to have an equal starting condition and a defined period during which a new biofilm could develop, we scraped all plates clean in early August. Settlement of juvenile oysters (spat) was monitored monthly until the end of November. All live spat >1 mm in shell length were counted. Pictures were taken of each settlement plate to measure individual shell length (measured as longest distance from anterior to posterior, parallel to the hinge) and individual growth rate. Pictures were georeferenced in ArcGIS, after which the length of individual spat could be measured to the nearest millimetre. To investigate winter mortality, cages were left in the field until March, when cages were brought to the lab where all live spat were counted and measured.

Growth, condition index and mortality of adult oysters

Cages also contained 16 wild-cultured oysters to investigate growth rate and oyster performance of adults. The wild-cultured oysters *C. gigas* (4 yr old, 76 ± 11 mm [mean ± SD] shell length) were collected from bottom culture plots at the Yerseke Bank in the Oosterschelde. Growth was measured as shell length and width increment between the start and end of the experiment, from early July through November 2010. At the end of the experiment, survivors at each tidal emersion level were cleaned free of encrusting organisms and brought to the laboratory to determine their condition index (CI). Initial condition of the wild-cultured oysters was obtained using 100 oysters at the start of the experiment. CI was calculated as:

$$CI \text{ (g ml}^{-1}\text{)} = \text{AFDW} / \text{ICV} \quad (1)$$

in which AFDW is the ash-free dry weight in grams, and ICV is the internal cavity volume in millilitres (Lawrence & Scott 1982). The oysters were dissected, separating the tissue from the shell, after which the flesh was dried at 70°C until weight constancy was achieved (4 d). Subsequently, they were incinerated at 540°C for 4 h to determine their AFDW. Internal cavity volume was determined by submerging the empty oyster shell in water and pushing the 2 valves tightly together, creating a water-retaining oyster shell. The weight of the water in grams corresponds

with the internal cavity volume of the oyster in millilitres. During the monthly visits, the number of dead oysters per cage was recorded, and the dead oysters were removed. Mortality was estimated as follows:

$$M (d^{-1}) = -\ln(N_t/N_0)/t \quad (2)$$

in which N_0 is the number of live oysters at the start of the experiment (t_0), and N_t is the number of live oysters at time t . The total time of the experiment (t) was 146 d.

Statistical analyses

Patterns in larval occurrence, number of recruits, shell length of recruits, shell growth, condition index and survival along the tidal emersion gradient were examined using linear, polynomial and exponential regression. Trends were tested for data from both tidal flats combined, covering a range of 2 to 69% tidal emersion. All analyses were performed using the SPSS statistical software version 21. Statistical significance was set at $\alpha = 0.05$.

RESULTS

Realized niche

Whereas individual oysters can occur over the whole tidal emersion gradient, the occurrence of reefs on tidal flats was limited to areas experiencing <60% tidal emersion in the Oosterschelde estuary (Fig. 2). The upper limits varied little during the 4 time periods from <55 to 60%. The extent of reef coverage increased substantially from 1980 to 2011, with most of the oyster reef area occurring at <25% tidal emersion in the last 2 decades (Fig. 2).

Larval occurrence

Larvae competent to settle (length >320 μm) were observed in the beginning of August. Larvae were present along the full tidal emersion gra-

dient at the 2 study areas, but with high variability (Table 1) and no pattern (linear regression: $F_{1,10} = 6.1$, $R^2 = -0.09$, $p = 0.781$).

Recruitment

Density of juvenile oysters was maximal around 36% tidal emersion, with no juveniles at 69% tidal emersion (Table 1). Recruitment occurred from August through November, but subsequent

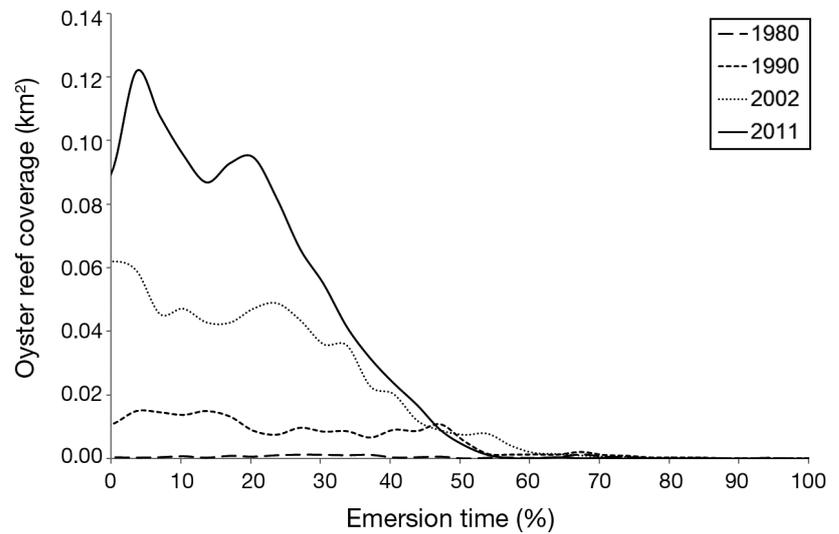


Fig. 2. Oyster reef coverage (km^2) along the tidal emersion gradient in the Oosterschelde estuary (The Netherlands)

Table 1. Number of *Crassostrea gigas* larvae collected per plankton net (Larvae) after 2 tidal cycles and live *C. gigas* recruits m^{-2} (mean \pm SD) per month observed on settlement plates in cages, located at 2 tidal flats (Viane and St. Annaland). Data are ordered by tidal emersion, which differs from the order of the experimental sites from mean low water line toward the dikes; see Fig. 1. nd: cages inaccessible

Tidal emersion (%)	Larvae	No. of <i>C. gigas</i> recruits (m^{-2})			
		Aug	Sep	Oct	Nov
St. Annaland					
2	2415	nd	nd	88 \pm 21	79 \pm 32
2	23251	162 \pm 143	194 \pm 114	181 \pm 137	130 \pm 72
4	2083	245 \pm 255	250 \pm 204	241 \pm 164	269 \pm 197
28	12232	227 \pm 166	181 \pm 155	194 \pm 169	190 \pm 179
42	7153	116 \pm 32	42 \pm 29	65 \pm 67	37 \pm 14
Viane					
36	0	597 \pm 350	532 \pm 326	394 \pm 227	551 \pm 355
36	7235	134 \pm 117	755 \pm 649	301 \pm 158	310 \pm 197
41	6309	56 \pm 63	60 \pm 112	32 \pm 51	51 \pm 90
47	6157	5 \pm 11	65 \pm 123	60 \pm 112	65 \pm 133
57	23553	5 \pm 11	0	14 \pm 15	19 \pm 23
66	14486	0	56 \pm 110	51 \pm 11	56 \pm 123
69	3899	0	0	0	0

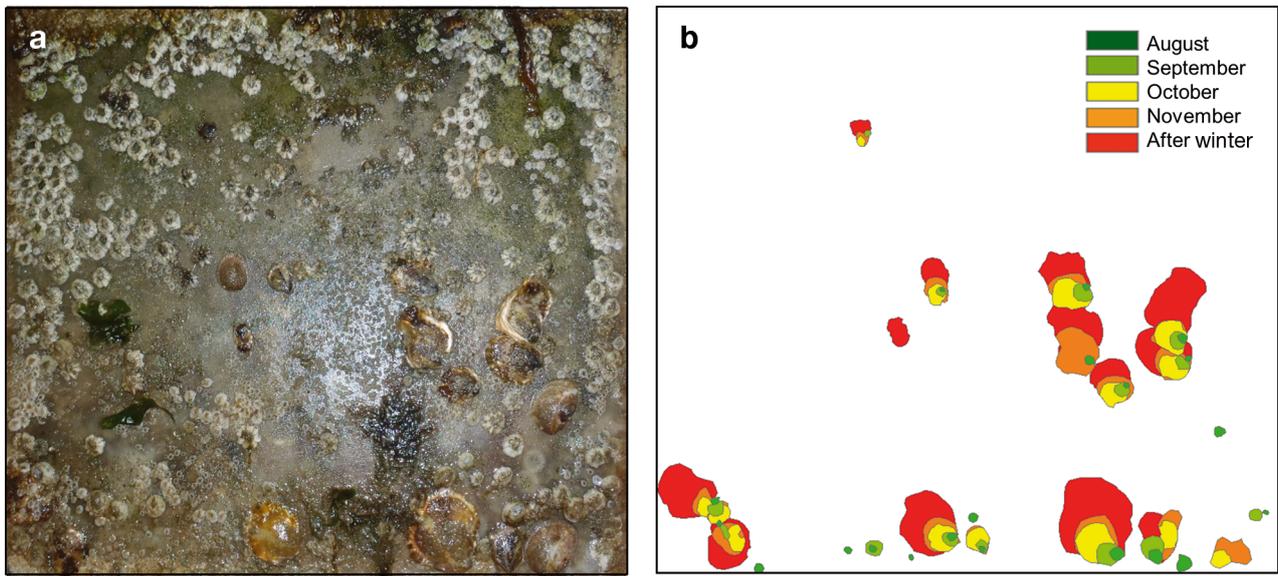


Fig. 3. (a) Settlement plate (located at 36% tidal emersion near the existing reef at Viane) with oyster spat photographed after cages were brought back to the lab in early spring. (b) Individual growth (indicated by the different colours) obtained from the monthly analysis of the photographed settlement plates. As temperatures already rose in March, oyster spat started to grow after winter

Table 2. Results of linear and polynomial regression analysis of shell length (mm) and growth (mm d⁻¹) of spat along a tidal emersion gradient (x) at monthly intervals

Time	Constant	x	x ²	x ³	R ²	df	F	p
Shell length (mm)								
August	8.231	-0.114			0.55	9	10.8	0.009
September	13.992	0.089	-0.009	7.0 × 10 ⁻⁵	0.86	3, 6	12.1	0.006
October	15.689	0.238	-0.014	0.000	0.80	3, 8	10.7	0.004
November	17.562	0.136	-0.008	4.6 × 10 ⁻⁵	0.85	3, 8	15.1	0.001
Growth (mm d⁻¹)								
August	0.276	-0.004			0.55	8	9.9	0.014
September	0.312	-0.005			0.52	7	7.7	0.027
October	0.149	0.001	-7.8 × 10 ⁻⁵	4.2 × 10 ⁻⁷	0.77	3, 7	7.7	0.013
November					0.15	11	1.9	0.198

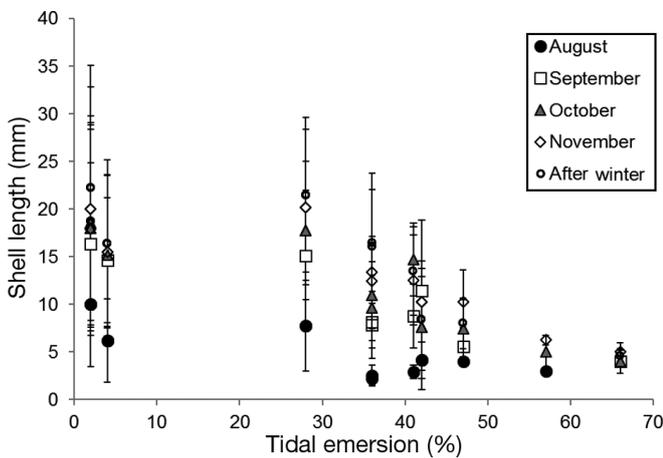


Fig. 4. Shell length (mean ± SD) of *C. gigas* recruits in mm along a tidal emersion gradient at monthly intervals

mortality of settled oysters resulted in varying numbers of live oysters on the settlement plates (Table 1).

Shell length (mm) and growth rates (mm d⁻¹; Fig. 3) were significantly and negatively correlated with tidal emersion (Fig. 4) during all months (Table 2, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m562p113_supp.pdf). Juveniles at 69% tidal emersion did not grow between August and March, whereas juveniles located below 42% emersion time doubled in length during the first month. In November, juveniles reached a maximum size of 56 and 43 mm at St. Annaland and Viane, respectively. Winter mortality was significantly positively related to tidal emersion (exponential regression: $F_{1,10} = 6.1$, $R^2 = 0.38$, $p = 0.034$, mortality = $5.827e^{0.034 \text{tidal emersion}}$, Fig. 5).

Growth, condition index and mortality of adult oysters

Shell length and width increment were negatively related to tidal emersion (Table 3, Fig. S2 in the Supplement). Wild-cultured oysters had an average (± 1 SD) AFDW of 0.72 ± 0.24 g, ICV of 14.8 ± 4.9 ml and CI of 49.9 ± 13.0 g ml⁻¹ in July. In November, CI was negatively correlated with tidal emersion, with an optimum around 20% tidal emersion. CI increased at areas experiencing <50% tidal emersion, whereas CI decreased at areas >50% tidal emersion. AFDW and ICV were also negatively related with tidal emersion (Table 3, Fig. S2). Increases in ICV corresponded with shell length and width increment along the tidal emersion gradient.

Daily instantaneous mortality rate (M ; d⁻¹) was 0.0022 ± 0.0018 d⁻¹ (mean \pm SD) between July and November. Mortality also negatively relates to tidal emersion (Table 3, Fig. S2), with highest mortality (56%) among the oysters located at 2% tidal emersion.

DISCUSSION

Response curves of 3 life-history stages (larvae, juveniles and adults) were investigated along a tidal emersion gradient to identify the fundamental niche of the Pacific oyster *Crassostrea gigas*. Tidal emersion had a strong effect on oyster recruitment, survival and growth, with the most favourable condi-

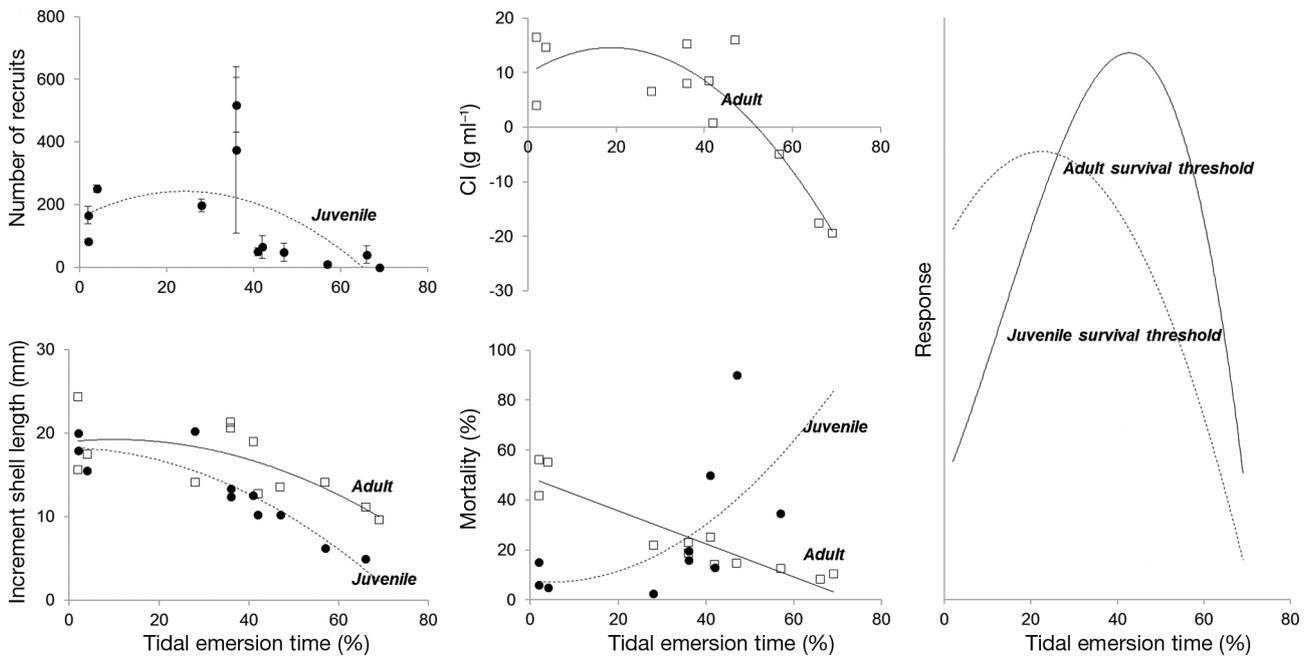


Fig. 5. Summary of the observed response curves of juvenile and adult oysters along a tidal emersion gradient. The number of juvenile oysters showed an optimum around 36% tidal emersion. Shell growth (mm) of both juvenile and adult oysters, changes in condition index (CI) (g ml⁻¹) of adult oysters as well as mortality (%) among adult oysters are negatively related to tidal emersion (%). Mortality (%) among juvenile oysters is positively related to tidal emersion (%). Overall, adult and juvenile oysters differ in their response to the same variable

Table 3. Results of linear and polynomial regression analysis of shell growth, changes in oyster performance and mortality of adult oysters along a tidal emersion gradient (x) for cages located on bare sediment

Dependent	Constant	x	x ²	x ³	R ²	df	F	p
Shell length (mm)	20.499	-0.121			0.41	10	6.9	0.025
Shell width (mm)	14.564	-0.214	0.005	-6.2×10^{-5}	0.75	3, 8	7.9	0.009
Internal cavity volume (ml)	16.148	-0.073	0.000	-8.2×10^{-6}	0.72	3, 8	7.1	0.012
Ash-free dry weight (g)	1.163	-0.008	0.000	-6.2×10^{-6}	0.89	3, 8	21.7	<0.001
Condition index (g ml ⁻¹)	12.871	-0.610	0.028	0.000	0.82	3, 8	11.8	0.003
Mortality (d ⁻¹)	54.517	-1.506	0.020	0.000	0.90	3, 8	32.3	<0.001

tions around 20 to 40% tidal emersion, as indicated by recruit density and CI of adults.

Larval niche

Larval abundance in the water column varied considerably over the tidal emersion gradient without any significant trend. In a well-mixed system with high residence time and small salinity changes, like the Oosterschelde estuary (Nienhuis & Smaal 1994), larvae will be well dispersed throughout the water column (Troost 2010).

Juvenile niche

The juvenile niche was upper limited by tidal emersion time with an optimum around 36% tidal emersion. No juveniles survived at 69% tidal emersion, whereas larvae were present. Absence of juveniles does not imply a lack of recruitment because post-settlement mortality could have been responsible for the lack of juveniles. Oysters settling high in the intertidal zone experience physical stress caused by limited inundation (Rodriguez et al. 2014) or high temperatures, which could have caused the decline of juvenile densities in areas with long emersion times. A decline in juvenile densities in areas with low emersion times could have been due to predation. Fodrie et al. (2014) observed variable recruitment of the eastern oyster *Crassostrea virginica* along an emersion gradient, with highest numbers in the subtidal; however, due to predation pressure in the subtidal region, subsequent survival was highest in the low and mid-intertidal. In the Oosterschelde, adults experience minor predation pressure by birds in the high intertidal, whereas in the subtidal, predation mainly affects juveniles (Troost 2010). The cages did not provide protection against predators smaller than the mesh size (5 mm) of the cages, such as shrimp (Beukema et al. 1998), because shrimps and crabs were observed within the cages. These predators could already have affected spatial variation before the juveniles reached a detectable size >1 mm. This could explain the decline of density in areas with shorter emersion times, as observed for *C. virginica* (Fodrie et al. 2014).

Adult niche

Adult Pacific oysters had an optimum CI around 20% tidal emersion, in line with observations by

Ridge et al. (2015) for *C. virginica*. Above 40 to 50% tidal emersion, CI decreased, which is in line with the lack of growth by *C. gigas* around 36% emersion time in the Menai Straits and 47% in the River Roach in England (Spencer et al. 1978). Although the CI decreased with increasing tidal emersion and declined compared to the initial condition for oysters located above 50% tidal emersion, oysters still grew above 50% tidal emersion. Both shell growth and changes in meat content were negatively correlated with tidal emersion, as also observed by Spencer et al. (1978). The lower shell growth and meat content at long emersion times indicate that oysters had adapted to the physical stress of tidal emersion by reallocating energy away from growth, which widens the realized niche of adult oysters.

Mortality increased at experimental sites with short emersion times, whereas shell growth rates were highest there. In *C. virginica*, subtidally grown oysters dedicate a significantly greater part of their energy to shell growth compared to intertidal oysters (Johnson & Smee 2014). This could be a response to predators because oysters increase shell growth in their presence (Newell et al. 2007). Energy used for shell growth results in lower tissue growth in bivalves, affecting their overall health (CI). In this study, both tissue growth and shell growth were negatively correlated with tidal emersion, which was most likely due to increased feeding time due to longer periods of inundation (Ingle & Dawson 1952, Bishop & Peterson 2006). Increase in both parameters did not occur at the same rate, leading to a parabolic trend for CI, indicating allocation of energy to shell growth. The greater amount of shell growth of the oysters in the low intertidal suggests a greater abundance of predators in this area, which is consistent with our mortality results. Unfortunately, knowledge about predation pressure on oysters is largely missing for our study area.

Implications for reef development

Knowledge of the fundamental niche of the different life-history stages helps to define the realized niche occupied by oysters. Whereas oysters can occur over the whole tidal emersion gradient, reefs are upper limited to 55 to 60% tidal emersion time. Failure in one life-history stage can form a bottleneck for reef development. Larval supply seems not to be limited in well-mixed systems like the Oosterschelde. The juvenile stage (i.e. spat) is limited by tidal emersion, with reduced recruitment success and growth rates with increasing tidal emersion. The adult stage is also lim-

ited by tidal emersion, as shell length increment and CI are negatively related with tidal emersion. Adult oysters are, however, able to adapt to the physical stress of tidal emersion by reallocating energy away from growth, thereby widening their realized niche. Furthermore, mortality of adult oysters is positively correlated with tidal emersion, whereas mortality among the juveniles is negatively correlated. These results complement previous findings for *C. virginica* (Fodrie et al. 2014). Adult oysters have low mortality in the high intertidal zone, but due to the lack of sufficient recruitment, reefs will not develop, however sporadically oysters are observed on debris (authors' pers. obs.). Based on the demographic response (recruitment, growth rate and oyster performance) to tidal emersion, it can be concluded that *C. gigas* reefs mainly develop in the low and mid (20 to 40%) intertidal. As individual oyster growth contributes to overall reef growth (Wallés et al. 2015b), tidal emersion is also expected to effect the growth of the reef (Wallés et al. 2016a). Wallés et al. (2016b) showed that tidal emersion affected reef performance and had a structuring effect on the demographic responses at the reef scale. The fundamental niche helps to predict where ecosystem-engineering oyster reefs can develop and form persistent structures that can form part of in coastal defence schemes. Offering stable substrate in the form of artificial reefs could stimulate reef development at such locations (Wallés et al. 2016b).

In summary, knowledge of the fundamental niche of different life-history stages defined the thresholds for establishment and reef development of the Pacific oyster *C. gigas* and enhanced a mechanistic understanding of the distribution of these ecosystem engineers in space and time. Tidal emersion had a strong effect on oyster survival and growth, with the most favourable conditions being around 20 to 40% tidal emersion. This is in line with Ridge et al. (2015), who observed optimal growth for individual oysters and whole reefs between 20 and 40% tidal emersion time. As studies on both *C. gigas* and *C. virginica* across different systems complement each other, the observed trends in relation to tidal emersion time have a broad geographical application.

Acknowledgements. The work presented in this paper was carried out as part of the innovation programme, Building with Nature, which is funded from several sources, including the Subsidieregeling Innovatieketen Water (Staatscourant no. 953 and 17009), sponsored by the Dutch Ministry of Transport, Public Works, and Water Management, and partner contributions by the participants of the EcoShape Foundation. EcoShape receives co-funding from the European Fund for Regional Development and the municipality

of Dordrecht. Thanks to Aard Cornelissen for providing the wild-cultured oysters. Thanks to Agathe Douabin for assistance in the field and the larval monitoring. We thank anonymous reviewers and the editor for their helpful comments.

LITERATURE CITED

- Armonies W (1994) Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. *Helgol Mar Res* 48:299–320
- ✦ Beukema JJ, Honkoop PJC, Dekker R (1998) Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia* 376:23–34
- ✦ Bishop MJ, Peterson CH (2006) Direct effects of physical stress can be counteracted by indirect benefits: oyster growth on a tidal elevation gradient. *Oecologia* 147: 426–433
- ✦ Borsje BW, van Wesenbeeck BK, Dekker F, Paalvast P, Bouma TJ, van Katwijk MM, de Vries MB (2011) How ecological engineering can serve in coastal protection. *Ecol Eng* 37:113–122
- ✦ Byers JE, Cuddington K, Jones CG, Talley TS and others (2006) Using ecosystem engineers to restore ecological systems. *Trends Ecol Evol* 21:493–500
- ✦ Cheong SM, Silliman B, Wong PP, van Wesenbeeck B, Kim CK, Guannel G (2013) Coastal adaptation with ecological engineering. *Nat Clim Change* 3:787–791
- ✦ Commito JA, Como S, Grupe BM, Dow WE (2008) Species diversity in the soft-bottom intertidal zone: biogenic structure, sediment, and macrofauna across mussel bed spatial scales. *J Exp Mar Biol Ecol* 366:70–81
- de Vries MB, Bouma TJ, van Katwijk MM, Borsje BW, van Wesenbeeck B (2007) *Biobouwers van de kust*. Delft Hydraulics, Delft
- ✦ Diederich S (2005) Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible? *J Sea Res* 53:269–281
- ✦ Donker JJA, van der Vegt M, Hoekstra P (2013) Wave forcing over an intertidal mussel bed. *J Sea Res* 82:54–66
- ✦ Drinkwaard AC (1998) Introductions and developments of oysters in the North Sea area: a review. *Helgol Meeresunters* 52:301–308
- Drinkwaard AC (1999) History of cupped oyster in European coastal waters. *Aquacult Eur* 15:7–14
- ✦ Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marba N (2013) The role of coastal plant communities for climate change mitigation and adaptation. *Nat Clim Change* 3: 961–968
- ✦ Fodrie FJ, Rodriguez AB, Baillie CJ, Brodeur MC and others (2014) Classic paradigms in a novel environment: inserting food web and productivity lessons from rocky shores and saltmarshes into biogenic reef restoration. *J Appl Ecol* 51:1314–1325
- Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) *Ecosystem engineers: plants to protists*. Elsevier, Amsterdam, p 281–299
- ✦ Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG and others (2012) Economic valuation of ecosystem services provided by oyster reefs. *Bioscience* 62:900–909
- ✦ Gutiérrez JL, Clive GJ, David LS, Oscar OI (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79–90

- Gutiérrez JL, Jones CG, Byers JE, Arkema KK and others (2011) Physical ecosystem engineers and the functioning of estuaries and coasts. In: Wolanski E, McLusky D (eds) *Treatise on estuarine and coastal science*, Vol 7. Elsevier, Amsterdam, p 53–81
- Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K (1995) Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr Mar Biol Annu Rev* 33:1–149
- Helm MM, Bourne N (2004) *The hatchery culture of bivalves: a practical manual*. Food and Agriculture Organization of the United Nations, Rome
- Ingle RM, Dawson CE (1952) Growth of the American oyster, *Crassostrea virginica* (Gmelin) in Florida waters. *Bull Mar Sci Gulf Carib* 2:393–404
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proc Natl Acad Sci USA* 106:19685–19692
- Johnson KD, Smee DL (2014) Predators influence the tidal distribution of oysters (*Crassostrea virginica*). *Mar Biol* 161:1557–1564
- Lawrence D, Scott G (1982) The determination and use of condition index of oysters. *Estuaries Coasts* 5:23–27
- Liu QX, Herman PMJ, Mooij WM, Huisman J, Scheffer M, Olf H, van de Koppel J (2014) Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. *Nat Commun* 5:5234
- Mulder JPM, Louters T (1994) Changes in basin geomorphology after implementation of the Oosterschelde estuary project. *Hydrobiologia* 282-283:29–39
- Newell R, Kennedy V, Shaw K (2007) Comparative vulnerability to predators, and induced defense responses, of eastern oysters *Crassostrea virginica* and non-native *Crassostrea ariakensis* oysters in Chesapeake Bay. *Mar Biol* 152:449–460
- Nienhuis PH, Smaal AC (1994) *Oosterschelde Estuary (The Netherlands): a case-study of a changing ecosystem*. Kluwer Academic Publishers, Dordrecht
- Ridge JT, Rodriguez AB, Joel Fodrie F, Lindquist NL and others (2015) Maximizing oyster-reef growth supports green infrastructure with accelerating sea-level rise. *Sci Rep* 5:14785
- Rodriguez AB, Fodrie FJ, Ridge JT, Lindquist NL and others (2014) Oyster reefs can outpace sea-level rise. *Nat Clim Change* 4:493–497
- Santinelli G, de Ronde JG (2012) Volume analysis on RTK profiles of the Eastern Scheldt. *Deltares*, Delft
- Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325:1124–1128
- Scyphers SB, Powers SP, Heck KL, Byron D (2011) Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PLOS ONE* 6:e22396
- Shatkin G, Shumway SE, Hawes R (1997) Considerations regarding the possible introduction of the Pacific oyster (*Crassostrea gigas*) to the Gulf of Maine: a review of global experience. *J Shellfish Res* 16:463–477
- Smaal A, Kater B, Wijsman J (2009) Introduction, establishment and expansion of the Pacific oyster *Crassostrea gigas* in the Oosterschelde (SW Netherlands). *Helgol Mar Res* 63:75–83
- Spalding MD, Ruffo S, Lacambra C, Meliane I, Hale LZ, Shepard CC, Beck MW (2014) The role of ecosystems in coastal protection: adapting to climate change and coastal hazards. *Ocean Coast Manage* 90:50–57
- Spencer BE, Key D, Millican PF, Thomas MJ (1978) The effect of intertidal exposure on the growth and survival of hatchery-reared Pacific oysters (*Crassostrea gigas* Thunberg) kept in trays during their first on-growing season. *Aquaculture* 13:191–203
- Temmerman S, Meire P, Bouma TJ, Herman PMJ, Ysebaert T, De Vriend HJ (2013) Ecosystem-based coastal defence in the face of global change. *Nature* 504:79–83
- Tolley SG, Volety AK (2005) The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. *J Shellfish Res* 24:1007–1012
- Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J Sea Res* 64:145–165
- Troost K, Gelderman E, Kamermans P, Smaal AC, Wolff WJ (2009) Effects of an increasing filter feeder stock on larval abundance in the Oosterschelde estuary (SW Netherlands). *J Sea Res* 61:153–164
- van den Ende D, van Asch M, Brummelhuis EB, Troost K (2014) Japanse oesterbanken op droogvallende platen in de Nederlandse kustwateren in 2014: bestand en arealen. IMARES Wageningen UR, Yerseke
- van Leeuwen B, Augustijn DCM, van Wesenbeeck BK, Hulscher SJMH, de Vries MB (2010) Modeling the influence of a young mussel bed on fine sediment dynamics on an intertidal flat in the Wadden Sea. *Ecol Eng* 36:145–153
- van Zanten E, Adriaanse LA (2008) Verminderd getij. Verkenning naar mogelijke maatregelen om het verlies van platen, slikken en schorren in de Oosterschelde te beperken. Rijkswaterstaat, Middelburg
- Walles B, Salvador de Paiva J, van Prooijen B, Ysebaert T, Smaal A (2015a) The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structures. *Estuaries Coasts* 38:941–950
- Walles B, Mann R, Ysebaert T, Troost K, Herman PMJ, Smaal A (2015b) Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. *Estuar Coast Shelf Sci* 154:224–233
- Walles B, Fodrie FJ, Nieuwhof S, Jewell OJD, Herman PMJ, Ysebaert T (2016a) Guidelines for evaluating performance of oyster habitat restoration should include tidal emersion: reply to Baggett et al. *Restor Ecol* 24:4–7
- Walles B, Troost K, van den Ende D, Nieuwhof S, Smaal AC, Ysebaert T (2016b) From artificial structures to self-sustaining oyster reefs. *J Sea Res* 108:1–9

Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: April 4, 2016; Accepted: October 30, 2016
Proofs received from author(s): December 8, 2016